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Review of Zebra Mussel Biology, Spread and Impacts and the Potential Detriment to South Dakota Waters

South Dakota
Department of
Game, Fish and Parks
Wildlife Division
Joe Foss Building
Pierre, South Dakota 57501-3182

Completion Report
No. 2021-17

Review of Zebra Mussel Biology, Spread and Impacts, and the Potential Detriment to South Dakota Waters

by

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Date .... October 2021

Preface

Information in this report was collected between October 2019 and September 2021. Copies of this report and reference to the information are not for publication and can only be made with written permission from the author(s), Director of the Division of Wildlife, or the Secretary of the South Dakota Department of Game, Fish and Parks, Pierre, South Dakota 57501-3182.

EXECUTIVE SUMMARY

Information presented in this report was gathered by doing an extensive literature review of published research and other materials. Zebra mussel *Dreissena polymorpha* information was compiled into four informational sections (biology, spread, impacts, and control) and then was used to assess potential detriments to South Dakota waters.

The zebra mussel is a bivalve native to eastern Europe. It is known to inhabit large freshwater lakes and rivers, but has been found in a variety of other habitats. Their high fecundity and ability to attach to a variety of surfaces has allowed them to spread quickly to new regions. The first report of zebra mussels in North America was from Lake St. Clair, Michigan in 1988, and within a month they were detected in the western basin of Lake Erie. Zebra mussels have spread across much of North America since first being detected just over 30 years ago.

The first indication of zebra mussel establishment in South Dakota waters occurred in 2015 in Lewis and Clark Lake, a Missouri River reservoir, and McCook Lake, a small oxbow lake that is maintained by pumping water up from the mainstem Missouri River. In 2017, zebra mussels were detected in Lake Yankton, and then in Lake Francis Case and Lake Sharpe in 2019. In 2020, zebra mussel adults were found in four eastern South Dakota lakes (Pickerel, Kampeska, Cochrane and Wall).

Zebra mussels can influence various abiotic (e.g. clarity, habitat) and biotic (e.g. plankton, invertebrates, fish and macrophytes) factors. The impacts can either be a direct result of the physical presence of zebra mussels or indirectly through change brought about by mussel filtering (clearance). Predicting the impact that zebra mussels will have on an aquatic ecosystems is often difficult. Many studies have demonstrated the ability of zebra mussels to increase water clarity, however, some have found little to no change in water clarity after introduction. Clearing by zebra mussels has the potential to reduce the abundance of phytoplankton, however, not all zebra mussel introductions have had this effect, but rather some have created a shift in the phytoplankton community. Unfortunately, selective feeding by zebra mussels can favor blue green algae (blue-green algae), and an increased density of blue green algae after zebra mussel introduction is not uncommon.

Most mussel families native to North America have been impacted by the introduction of zebra mussels. Zebra mussels can settle upon native mussels which negatively impacts condition or results in death by increasing costs of movement, restricting or preventing the opening or closing of the shell, or creating toxic conditions with their waste. However, competition for food between native mussels and the attached zebra mussel is probably the primary mechanism behind the decline of native mussels. Although attributed to the decline of native mussels, the introduction of zebra mussels has often coincided with an increased abundance of other invertebrates (e.g. amphipods, chironimids, oligochaetes, hydrozoans, smaller molluska spp.). Benthic invertebrates may benefit from the presence of zebra mussels through several pathways including increased abundance of food with greater water clarity, an increase in hard surface area, and enrichment through the excretion of zebra mussel feces. However, most studies attribute the increase in hard structure with zebra mussels as the primary reason behind higher invertebrate abundance because the presence of druses increases bottom complexity providing

protection to benthic invertebrates from predators, and their presence provides a hard surface required by many benthic invertebrates to live, thus increasing the amount of suitable habitat.

The fish community is affected by many of the same factors impacting invertebrates, both direct and indirect. Foremost, increased water clarity alters fish habitat having a varied impact on different species. For example, Walleye *Sander vitreus* habitat may be decreased as the lake bottom is exposed to more light, thus reducing the amount of ideal "optical habitat" for Walleye. However, other species not restricted by optical habitat may benefit from increased water clarity as it often coincides with an increased abundance of macrophytes. Increased water clarity and more aquatic macrophytes improve foraging conditions, forage abundance, and habitat for fish species that include Bluegill *Lepomis macrochirus*, Largemouth Bass *Micropterus salmoides*, Yellow Perch *Perca flavescens* and Northern Pike *Esox lucius*, and Muskellunge *Esox masquinongy*.

One of the most detrimental impacts of zebra mussel infestation has been the damage to submerged infrastructure especially water intakes. Zebra mussels attach to various man-made structures including buoys, docks, and dams. The damage to power generating facilities is of greatest concern as structures that prevent foreign objects from entering dams or intake pipes can become infested restricting water flow to the facility and reducing generator output efficiency. Additionally, pipes or valves used for fire protection systems, cooling systems, maintenance and general use or domestic purposes can become blocked with zebra mussels inhibiting function or causing overheating of components. The impact of zebra mussels can extend past the boundaries of a waterbody through their impact on facilities that utilize water and the increased costs to the consumers of the products produced by these facilities.

Once zebra mussels are established in a waterbody, there is some potential to control or possibly eradicate them on smaller bodies of water using chemicals, but this method can be costly, limiting its use. Unfortunately, methods to eradicate zebra mussels on larger waterbodies have had little to no success. Thus, slowing the spread of zebra mussel is imperative and will be in part related to our ability to educate the public about the mechanisms behind the spread, detrimental effects, and high costs associated with zebra mussel infestation. Public knowledge and awareness of zebra mussels and their impacts will improve public participation in efforts to prevent the rapid spread across South Dakota. Ways to increase awareness include signs at water access areas, use of social media, public meetings, and booths at sport shows as well as a variety of other outlets often used to spread awareness of aquatic invasive species (AIS) and help educate the public. An informed public can become a powerful tool to prevent the spread of AIS as informed individuals can help with detection of AIS, generation of funds and outreach to other members of the community.

Table of Contents

List of Figures

Section 1: Zebra Mussel Biology

The zebra mussel *Dreissena polymorpha* is a bivalve native to eastern Europe (Mackie et al. 1989; Morton 1993). This small freshwater mussel has a brown and cream-colored zebra-stripe pattern that varies among individuals (Morton 1993). It is known to inhabit large freshwater lakes and rivers (Strayer 1999) but has been found in a variety of other habitats such as flooded quarries, cooling ponds and golf course ponds (Mackie and Schloesser 1996). Their high fecundity (Mackie et al. 1989; Borcherding 1992; Marsden 1992) and ability to attach to a variety of surfaces (Marsden and Lansky 2000; Ackerman et al. 1993; Sprung 1993; Kobak 2014) has allowed them to spread quickly to new regions.

There are only three families of freshwater mussels native to North America, Sphaeriidae, Margaritiferidae and Unionidae, with Unionidae being the most common (Haag 2012). The introduction of zebra mussels added a new family of freshwater mussels, Dreissenidae (Haag 2012), that possess biological characteristics not found in native mussels. Zebra mussels were the first species of the Dreissenidae family to be introduced into North America, with quagga mussels *Dreissena bugensis* identified a short time later (Haag 2012; Benson 2014). There are several distinct characteristics of zebra mussels, not exhibited by native mussels, that allow them to spread rapidly, inhabit a wide range of habitats, and outcompete native mussel species. First, zebra mussels have planktonic larvae that do not require a host to develop or disperse whereas native mussels must rely on host species to complete development. Second, native mussels are infaunal often burying themselves in the sediments (Haag 2012), while zebra mussels are epifaunal and use byssal threads to attach to hard surfaces and substrates not available to native mussels (Haag 2012). Byssal threads have also allowed zebra mussels to attach to native mussels often resulting in the death of the "host" mussel (see Haag 2012 for review). These unique characteristics of Dreissenidae have allowed them to quickly spread throughout North America and outcompete native mussels.

Infestation of zebra mussels into new waterbodies is generally believed to occur during early life stages (Sprung 1989; Pollux et al. 2010). This belief is founded through the biology of this species with its external fertilization of eggs in the water column (Walz 1973; Ackerman et al. 1994) and free-swimming larvae (Sprung 1989; Nichols 1996), both capable of movement by either natural or anthropogenic means (Griffiths et al. 1991; Carlton 1993; Benson 2014). Spawning of sexually mature zebra mussels generally starts when water temperatures reach 12°C (Sprung 1989; Borcherding 1992; Marsden 1992; McMahon 1996) with optimal temperatures at around 18°C (McMahon 1996). Once spawning starts, it can continue into early fall in some regions (Bartell and Orr 2007) if temperatures are adequate. A single female zebra mussel can release between 30,000–40,000 eggs per spawning event (Mackie et al. 1989; Borcherding 1992; Marsden 1992), and within a year, can produce and release over a million eggs (Mackie et al. 1989; Borcherding 1992). Several days after fertilization, free swimming larvae emerge and disperse throughout a waterbody (Nichols 1996).

Larval zebra mussels undergo various phases of development and shifts in behavior. Shortly after hatching, larvae (hereafter referred to as veligers) develop velum, an organ used for feeding and movement (Ackerman et al. 1994). The veliger life stage involves various substages of development. Within the first seven days post-hatching, veligers develop an unornate D-shaped shell followed by development of a more ornate shell a few days later (Ackerman et al. 1994). After shell formation, veligers develop various organs including a foot and gill filaments in the mantle cavity (Ackerman et al. 1994). While gill filaments will not become fully developed until later life stages, the foot is fully developed at the veliger stage and can be used either for swimming near or crawling along the bottom (Ackerman et al. 1994). At 16–88 days post-hatch and with the proper cues, veliger behavior will change, and they will begin to "settle" (Ackerman et al. 1994) which requires them to swim or crawl along the bottom in order to find suitable surfaces to settle upon.

Veligers can settle upon a variety of surfaces, but the selection of a suitable surface will increase the likelihood of survival. Suitable surfaces are generally hard structures (Ackerman et al. 1993; Sprung 1993; Marsden and Lansky 2000; Kobak 2014) both natural (i.e., hard surfaces and rocks [Ackerman et al. 1993; Sprung 1993; Marsden and Lansky 2000]) and artificial (i.e., cement, steel, rope, etc. [Kilgour and Mackie 1992; Ackerman et al. 1993; Marsden and Lansky 2000]). However, veligers will also settle upon macrophytes (Sprung 1993; Stanczykowska and Lewandoski 1993; Ackerman et al. 1994; Porter and Marsden 2008), as well as on other invertebrates (Mackie 1993; Sprung 1993). Mortality during the settling stage can be as high as 99% as veligers often have difficulty locating suitable substrate for settling (Sprung 1993). After initial settlement, zebra mussels can relocate to more suitable locations if needed (Kobak 2014).

Once initial settlement has occurred, veligers then secrete byssal threads to attach to the selected substrate (Lewandowski 1982) and undergo further development and maturity. After settlement, the velum is replaced by fully functioning gill filaments and a mouth, and the foot moves to a new position and increases in size (Ackerman et al. 1994). These developments facilitate the excretion and formation of the adult shell (Ackerman et al. 1994). Even after the development of the adult shell, zebra mussel juveniles are not classified as adults until they become sexually mature (Kirpichenko 1964; Ackerman et al. 1994). In North America, sexually maturity is reached at about 8 mm in length and often just after their first year of growth (Bartell and Orr 2007; Marsden 1992; Mackie 1993). Mature mussels commonly congregate into colonies or "druses" often in shaded areas (Toomey et al. 2002). Lifespan is typically between 2-9 years (Bartell and Orr 2007; Marsden 1992; Mackie 1993; Chase and Bailey 1999).

A variety of environmental factors influence growth of zebra mussels. Growth generally occurs between 6°–32°C (summarized in Cohen 2005), with 10°–15°C being optimal (Walz 1978). Though temperatures above 30°C are generally considered lethal to zebra mussels, they can continue to live and grow at these high temperatures, at least over a short period of time (Spidle et al. 1995; McMahon 1996; Elderkin and Klerks 2005). Zebra mussels located in deep water tend to grow slower most likely due to lower water temperature and reduced food availability (Garton and Johnson 2000). Growth is also affected by calcium concentration with a minimum concentration of 12─15 mg/L of calcium required for proper shell development and growth (Hinks and Mackie 1997; Neary and Leach 1991; Baker et al. 1993; McMahon 1996; Cohen 2007). The uptake of calcium by zebra mussels is influenced by pH (Hinks and Mackie 1997) with zebra mussels tolerating a pH range of 6.5–9.5 (summarized in Cohen 2005). The various environmental factors that influence zebra mussel growth can impact it individually or in concert with one another (Hinks and Mackie 1997).

Factors that influence zebra mussel growth can also affect survival. Zebra mussels can survive at water temperatures ranging from 1°–30°C (McMahon 1996; Cohen 2007; Pollux et al. 2010), and in North America, have been found to survive at somewhat higher temperatures (Spidle et al. 1995). Although zebra mussels can survive for short periods at temperatures ≥ 30°C (Spidle et al. 1995), they cannot survive at temperatures ≤ 0°C (Spidle et al. 1995; McMahon 1996; Elderkin and Klerks 2005; Cohen 2007; Pollux et al. 2010). Calcium, a factor influencing growth, is also a factor limiting survival with a similar tolerance range (~12─15 mg/L [Neary and Leach 1991; Baker et al. 1993; McMahon 1996; Cohen 2007]). Low calcium levels can hinder egg development and basic physiological functions of zebra mussels (e.g., muscular contractions, cellular cohesion, nervous functions and pH balance [Chetail and Krampitz 1982; Hinks and Mackie 1997; Pollux et al. 2010]). Zebra mussels are considered intolerant of low dissolved oxygen (Garton et al. 2014), with a minimum required oxygen content of around 4–6 mg/L (summarized in Cohen 2005). Areas of low dissolved oxygen such as the hypolimnion of lakes, impoundments (Garton and Johnson 2000) or river floodplains (Mihuc et al. 1999) may not be suitable for zebra mussels. Zebra mussels can tolerate salinity ranging from 0.6–12 mg/L (Strayer and Smith 1993; Mills et al. 1996; Cohen 2007) with laboratory experiments demonstrating that temperature can influence lethal limits (Mills et al. 1996; Cohen 2005). A high concentration of suspended solids can hinder the acquisition of energy from food sources by negatively affecting ingestion and clearance rates (Madon et al. 1998). Similar to growth, the environmental factors that impact mortality can act independently or in concert (Hinks and Mackie 1997; Mihuc et al. 1999; Garton and Johnson 2000; Cohen 2005).

Zebra mussels obtain energy by filter feeding (hereafter referred to as clearing) and feed primarily on algae, but also consume micro-invertebrates, bacteria, detritus and other organic matter (Sprung 1989). Zebra mussels clear by taking particles into their mantle and can clear particles ranging in size from 0.5–1200 µm (Lei et al. 1995; Horgan and Mills 1997) with preferred food sizes ranging from 15–40 µm (Ten Winkel and Davids 1982). Clearance rate of zebra mussels is affected by temperature, with optimal temperatures ranging from 14°–26°C (Lei et al. 1995). Suspended solids can impact clearance rates most notably when the concentration of suspended solids is above 1 mg/L (Madon et al. 1998). Growth rates have been found to decrease with increased turbidity (Madon et al. 1998). When zebra mussels ingest non-food or less desirable prey items, they catch items in a mucus and expel them as pseudofeces (Morton 1969; Madon et al. 1998). Increased turbidity can increase the amount of pseudofeces produced, resulting in increased respiration and energy costs (Madon et al. 1998). Temperature and suspended solid concentrations impact clearance rates of zebra mussels, and accordingly, play a determining role in the impact zebra mussels will have on a waterbody.

Generally considered nonmobile and fixed to a permanent location, individual zebra mussels can detach and relocate when conditions become unfavorable. Zebra mussels voluntarily detach proteinaceous byssal threads from a structure and then seek out more suitable habitat generally using their foot (Eckroat et al. 1993). Juvenile zebra mussels have the potential to resuspend into the water column with special floating byssal threads and drift to new locations (Martel 1993). Toomey et al. (2002) found that smaller mussels (e.g., 5– 10 mm) tend to move a greater distance (e.g., 284 mm) than larger mussels (e.g., size 10–20 mm and >20 mm; distance 115 mm and 47 mm, respectively) over a 2-h period. Zebra mussels will often move to higher quality, particularly rough-textured structures, when available (Kobak 2014). Due to their negative phototaxis nature, zebra mussels of all sizes prefer and seek out darker locations (Toomey et al. 2002; Kobak 2014) such as crevices and corners and edges (Zhang et al. 1998; Kobak 2005). While hypoxic conditions will stimulate movement (see Kobak 2014 for review), calcium levels and water temperature, two factors impacting zebra mussel biology, do not appear to stimulate movement (Toomey et al. 2002).

Zebra mussels move less in the presence of other mussels (Kobak 2004) as they prefer to aggregate into druses (Kobak 2014). The grouping of mussels into druses is influenced by their preference for certain types of substrates, the lack of suitable substrate, or as a measure to avoid predation (Kobak 2014). Druses are formed in the presence of predators to reduce the chances of predation by increasing handling difficulties with multiple mussels instead of an individual mussel (Kobak 2014). Additionally, druses can cause confusion by creating a dilution effect that also reduces the chances of predation (Kobak 2014). However, druses have the potential to reduce growth and condition of zebra mussels because of the buildup of wastes and local depletion of dissolved oxygen and food items (Burks et al. 2002; Tuchman et al. 2004). Smaller individuals can move upward out of the druse to avoid deteriorating conditions around the druse, while larger individuals cannot move often resulting in death (Stanczykowska 1964; Burks et al. 2002; Tuchman et al. 2004).

Section 2: The Spread of Zebra Mussels

Zebra mussels are native to eastern Europe originally occupying areas around the Volga River and the Aral, Black and Caspian Seas (see Morton 1993 for review). During the 1800s, zebra mussels started spreading throughout western Europe primarily due to the development of canals across the continent (Mackie et al. 1989; Morton 1993; Benson 2014). The first report of zebra mussels in North America was from Lake St. Clair, Michigan in 1988 (Hebert et al. 1989), and within a month they were detected in the western basin of Lake Erie (Leach 1993). Zebra mussels have spread across much of North America since first being detected just over 30 years ago.

Their initial introduction into North America was believed to be caused by the release of zebra mussel infested ballast water into the Great Lakes (Hebert et al. 1989; Griffiths et al. 1991; Garton and Haag 1993). Although not confirmed as the source of introduction, it is quite likely that ballast water was responsible as large numbers of organisms, often bivalves, are commonly found within ballast water (Carlton et al. 1990), and the release of ballast water into the Great Lakes from ships originating from Europe was a common practice until May 1989 (Carlton 1993). In addition to zebra mussels, spiny water flea *Bythotrephes cedertroemi*, ruffe *Gymnocephalus cernuus* and various other species have been introduced into the Great Lakes via transport in ballast water (Carlton 1993).

A total of 31 states now report having zebra mussels in some of their waters (Benson et al. 2019). The spread of zebra mussels across North America was enabled by movement along connected river systems and overland transport. In 1991, zebra mussels were detected at several locations along the Mississippi River (Cope et al. 1997; Benson 2014) and later were found in the river all the way from Minnesota to Louisiana (Benson 2014). The spread throughout the Mississippi River facilitated the introduction of zebra mussels into connected river systems and major tributaries (Benson 2014). Transportation of zebra mussels upriver by anthropogenic means allowed for colonization and rapid spread back downstream into uninfested stretches of river (Johnson and Padilla 1996). The interconnection of waterbodies via canals has and will continue to expedite the spread of zebra mussels (Johnson and Padilla 1996; Johnson et al. 2001). Interconnected waterbodies are more susceptible to infestation than isolated waterbodies.

The introduction of zebra mussels into the Missouri River is of specific interest to resource managers and user groups within South Dakota. Zebra mussels were first detected in the Missouri River just south of Sioux City, Iowa, in 1999 (Benson 2014; Benson et al. 2019). The delayed introduction into the Missouri River, when compared to other rivers, is believed to be due to the high-water velocity and turbid conditions inhibiting establishment (Benson 2014). The first indication of zebra mussel establishment in South Dakota waters occurred in 2015 in

Lewis and Clark Lake (Benson et al. 2019). Not surprisingly, in that same year, adult zebra mussels were also found in McCook Lake, a small oxbow lake near North Sioux City, South Dakota, that is maintained by pumping water from the mainstem Missouri River into the lake (Benson et al. 2019). In 2017, zebra mussels were detected in Lake Yankton, South Dakota, a manmade lake located just below Gavins Point Dam (Wollman 2019). Further zebra mussel infestations were not detected again in South Dakota waters until 2019 with adults found in Lake Francis Case and Lake Sharpe, two large Missouri River reservoirs upriver from Lewis and Clark Lake (Benson et al. 2019; SDGFP, *personal communication*). Zebra mussels were then found in four eastern South Dakota lakes (Pickerel, Kampeska, Cochrane and Wall) in 2020 and Lake Mitchell in 2021.

Although barge traffic is believed to have facilitated the transportation of zebra mussels upriver in many river systems (Carlton 1993; Benson 2014), it may not be directly responsible for introductions into South Dakota waters. This is most likely the case because only the lower 734 river miles (Sioux City to the confluence with the Mississippi River), is maintained for navigation (U.S. Army Corps of Engineers, Omaha District). Additionally, Missouri River dams upstream from Sioux City do not have locks to permit passage of watercraft across dams. However, barges may have played a role in the introduction to South Dakota waters by transporting zebra mussels upriver to Sioux City where that population may have served as a source population for introduction by overland transport to locations upriver.

However, it is more likely that vessels used for industrial work (e.g. construction, bridge maintenance, etc.), research or recreation were unknowingly responsible for the overland transport and subsequent introduction of zebra mussels into South Dakota waters (Carlton 1993; Johnson and Padilla 1996; Johnson et al. 2001). Both zebra mussel adults and veligers have the potential to be transported overland under the right conditions (Griffiths et al. 1991; Claudi and Mackie 1993; Ricciardi et al. 1994; Tucker et al. 1997). Adult zebra mussels can attach to various parts of a vessel such as the hull, motor, or anchor (Carlton 1993; Johnson and Padilla 1996; Johnson et al. 2001), and macrophytes attached to trailers or boats can contain zebra mussels and facilitate transportation (Johnson et al. 2001). Under cool, moist conditions, attached adult mussels can survive out of water for about 4 days (Griffiths et al. 1991; Claudi and Mackie 1993; Ricciardi et al. 1994; Tucker et al. 1997). Standing water located in bilges, motors, live wells and other systems capable of holding water can serve as a vector for the transport of zebra mussel veligers (Carlton 1993; Johnson and Padilla 1996; Johnson et al. 2001). Though there were numerous potential avenues for the initial introduction of zebra mussel into Lewis and Clark Lake, and more recently Lake Francis Case, Lake Sharpe and several eastern South Dakota lakes, the most plausible explanation was through inadvertent, overland transport by fishing and recreational boats (Carlton 1993; Johnson et al. 2001).

Zebra mussels entering waterbodies through various modes of overland transportation do not always result in an introduction and established population. Standing water may become contaminated or fouled killing the veligers during transport (Sprung 1989) or the vessels can be out of water long enough to desiccate and kill the zebra mussels. Even though zebra mussels can survive transportation, a single introduction may not be adequate to establish a population (Johnson and Carlton 1992) because various environmental and biological constraints can influence survival and reproduction (Spidle et al. 1995; McMahon 1996; Mills et al. 1996; Cohen 2005 & 2007; Pollux et al. 2010). Even if environmental conditions favor introduction, it may require multiple introductions to establish a viable population (Johnson and Carlton 1992; Johnson and Padilla 1996). Thus, waterbodies most frequented by recreational users and those closest to other contaminated waters are most susceptible to invasion (Padilla et al. 1996). Frequently used, contaminated waterbodies can act as a "gateway" (Johnson and Padilla 1996) for the spread of zebra mussels to surrounding waterbodies.

Wildlife such as ducks, turtles, fish, and other organisms have the potential to transport zebra mussels within a waterbody and between waterbodies (Carlton 1993; Johnson and Carlton 1996). Though other organisms have the potential to spread zebra mussels between waterbodies, it is likely that ducks and other water birds would be the primary vector of spread (Carlton 1993; Johnson and Carlton 1996). Transportation between waterbodies would likely occur due to veligers and juvenile zebra mussels becoming trapped within feathers or debris caught on waterbirds' feathers or feet (Carlton 1993; Johnson and Carlton 1996; Banha et al. 2016). Little research has examined the spread of zebra mussels by waterbirds. Rather, the focus has been on anthropogenic transportation because it is more likely to transport a large enough number of viable veligers (Johnson and Carlton 1996) to enable successful reproduction and establishment (Johnson and Carlton 1992; Johnson and Carlton 1996).

It is anticipated that in time other waterbodies across South Dakota will become infested with zebra mussels. The probable vector of spread will be recreational vessels moving from popular contaminated waters to other waterbodies. Within South Dakota, Missouri River reservoirs infested with zebra mussels may act a source population and facilitate the spread of zebra mussels. Temperatures generally reach the minimum threshold for zebra mussel spawning in the three reservoirs in late spring and early summer and are adequate for spawning until late fall (Figure 1, 2 and 3). Lake Francis Case may be of concern since angling within this reservoir is highest from May through July when temperatures are rising and become suitable for zebra mussel spawning (Figure 2). Boat fishing pressure during these months is at least twice that of the other two reservoirs. Residents from around the state travel to Lake Francis Case and the other reservoirs primarily to fish Walleye. If proper cleaning methods are not employed and conditions are suitable for zebra mussel introduction, anglers may spread the mussels to new locations across the state. Popular local waterbodies frequented by anglers who periodically travel to the Missouri River Reservoirs to fish Walleye may become infested and then act as source population to further the local spread zebra mussels. However, spread of zebra mussels is not limited to fishing boats, but any boat used for recreation or industrial work. The infestation of zebra mussels into all but one of the Missouri River Reservoirs is troublesome in that it will more than likely soon lead to other infestations across the state unless preventative measures such as widespread boat checks and decontamination opportunities are implemented immediately.

Section 3: Impacts of Zebra Mussels

The impact of zebra mussels on aquatic ecosystems in North America has varied from a dramatic change to the trophic state and/or micro- and macro-invertebrate communities (Haag et al. 1993; MacIsaac 1996; Pace et al. 1998; Jack and Thorp 2000; Zhu et al. 2006; Ward and Ricciardi 2007; Higgins et al. 2008) to virtually no effect at all (MacIsaac 1996; Vanderploeg et al. 2002; Barbiero and Tuchman 2004; De Stasio et al. 2008). Much of the research on the impacts of zebra mussels has been conducted on the Great Lakes and Hudson River. Zebra mussels can influence various abiotic (e.g., clarity, habitat) and biotic (e.g. plankton, invertebrates, fish and macrophytes) factors and damage infrastructure associated with water use (e.g. power plants, water treatment plants, etc.). The impacts can either be a direct result of the physical presence of zebra mussels or indirectly through change brought about by mussel clearance. Predicting the impact that zebra mussels will have on an aquatic ecosystem is often difficult.

Many studies have demonstrated the ability of zebra mussels to increase water clarity (Griffiths 1993; Leach 1993; MacIsaac 1996; Yu and Culver 2000; Zhu et al. 2006), however, some have found little to no change in water clarity after introduction (Barbiero and Tuchman 2004). Two studies (Oneida Lake, New York and Hargus Lake, Ohio) recorded a 1 m increase in water clarity (Yu and Culver 2000; Zhu et al. 2006) after the introduction of zebra mussels while an even greater increase in water clarity (1.7–6.0 m) was documented during spring in the eastern basin of Lake Erie (Barbiero and Tuchman 2004). However, water clarity in the western and central basins of Lake Erie did not experience such a large increase in spring or summer (Barbiero and Tuchman 2004). Turbidity in the Detroit River decreased by about 33% after zebra mussel introductions (MacIsaac 1996), while water clarity in the Hudson River only increased by 7% (Pace and Caraco cited by MacIsaac 1996). MacIsaac (1996) suggested that holomictic lakes and slow-flowing rivers with little mixing will experience a larger increase in water clarity with the introduction of zebra mussels than meromictic lakes and fast-flowing, highly mixed rivers.

Clearing by zebra mussels has the potential to reduce the abundance of phytoplankton or primary productivity, often measured as chlorophyll *a* (MacIsaac 1996). Zebra mussels have significantly reduced chlorophyll *a* in waterbodies of varying sizes (Lavrentyev et al. 1995; Idrisi et al. 2001; Raikow et al. 2004; Barbiero et al. 2006; Depew et al. 2006; Higgins et al. 2008), with one of the most drastic reductions (41%) recorded in a small lake in Ireland (Higgins et al. 2008). However, not all zebra mussel introductions have resulted in a lower abundance of phytoplankton, but rather have created a shift in the phytoplankton community (Wilson 2003;

Naddafi et al. 2007; De Stasio et al. 2008). De Stasio et al. (2008) found that after the establishment of zebra mussels in Green Bay, Lake Michigan, the phytoplankton community, previously dominated by chlorophytes, was replaced by blue green algae and diatoms. Increased density of blue green algae after zebra mussel introduction is not uncommon (MacIsaac 1996; Vanderploeg et al. 2001; Raikow et al. 2004; Sarnelle et al. 2005; Bykova et al. 2006; Knoll et al. 2008). Zebra mussel introduction in Saginaw Bay, Lake Huron and Lake Erie coincided with large blooms of *Microcystis aeruginosa* (Vanderploeg et al. 2001). Sarnelle et al. (2005) found that selective feeding by zebra mussels favored the blue green algae, *M. aeruginosa*, in several of their experiments, but also found that zebra mussels will consume *M. aeruginosa*. Although zebra mussels have been shown to consume *Microcystis*, they tend to favor other types of phytoplankton as the hepatotoxins or microcystins in some blue green algae can reduce assimilation rate and survival (Carmichael 1996, Vanderploeg et al. 2001, Naddafi et al. 2007), generally rendering them unpalatable. Although zebra mussels can alter the phytoplankton community, the overall biomass may not change, which would explain the lack of improvement in water clarity on some waterbodies (De Stasio et al. 2008).

The impact of zebra mussels on zooplankton has varied among waterbodies. Zebra mussels can reduce zooplankton abundance directly through consumption and indirectly through competition for food (Jack and Thorp 2000). Selective consumption of zooplankton by zebra mussels seems to be the primary mechanism behind change in species composition (Pace et al. 1998; Jack and Thorp 2000; Thorp and Casper 2002) as well as the decline in abundance (MacIsaac et al. 1991; Richardson and Bartsch 1997; David et al. 2009). Pace et al. (1998) found that after the zebra mussel introduction, zooplankton biomass in the Hudson River was reduced by more than 70%. In Lake St. Clair, cladoceran and copepod abundance was reduced by 50% after zebra mussel introduction while rotifers declined by over 80% (David et al. 2009). While predation by zebra mussels can impact all sizes of zooplankton, it appears that smaller zooplankton are more susceptible to consumption (MacIsaac et al. 1991; Jack and Thorp 2000; Idrisi et al. 2001). The enhanced swimming strength of larger zooplankton most likely makes them less susceptible to predation (MacIsaac et al. 1991). Additionally, smaller zooplankton may be even more susceptible to consumption in holomictic lakes that often support larger populations of zebra mussels (MacIsaac et al. 1991).

Lake size alone may not explain the varying impact of zebra mussels on zooplankton communities. For example, in Oneida Lake, New York, zebra mussels reduced the amount of food available to zooplankton, however, there was no corresponding decrease in Daphnia spp. biomass, but only a shift to larger bodied species (Idrisi et al. 2001). There is also a potential that with larger waterbodies, impacts of zebra mussels on zooplankton can be patchy, isolated to areas suitable for zebra mussel habitation (Wu and Culver 1991; Idrisi et al. 2001).

Most mussel families native to North America have been impacted by the introduction of zebra mussels (Haag et al. 1993; Strayer 1999). Zebra mussels can settle upon native mussels which negatively impacts condition or results in death by increasing costs of movement, restricting or preventing the opening or closing of the shell, or creating toxic conditions with their waste (Strayer 1999). However, competition for food between native mussels and the attached zebra mussel is probably the primary mechanism behind the decline of native mussels (Haag et al. 1993; Strayer 1999). The decline in native mussel populations with the expansion of zebra mussels across North America is a major concern to natural resource managers (Haag et al. 1993; Strayer 1999; Haag 2012).

Although native mussels may be negatively impacted by the presence of zebra mussels, this is often not the case for other types of invertebrates. The presence of zebra mussel druses often coincides with an increase in the abundance of invertebrates (e.g. amphipods, chironimids, oligochaetes, hydrozoans, smaller molluska spp., etc. [Botts et al. 1996; Ricciardi et al. 1997; Steward et al. 1998; González and Downing 1999; Steward et al. 1999; Mayer et al. 2002; Beekey et al. 2004; Ward and Ricciardi 2007]), with exceptions for some larger invertebrates (e.g. large molluska, large net-spinning caddisfly [Ricciardi et al. 1997]) or for those that utilize soft substrates (Beekey et al. 2004). Invertebrates may benefit from the presence of zebra mussels through several pathways. First, food available to macro-invertebrates can increase with greater water clarity (Griffiths 1993; Leach 1993; MacIsaac 1996; Yu and Culver 2000; Zhu et al. 2006) and an increase in hard surface area. Both of these factors are favorable for benthic algae and can result in increased algal biomass and organic matter (Mayer et al. 2002). However, filter feeding (e.g. depositing feces, trapped organisms in pseudofeces and stimulating algal growth through N and P excretion [Izvekova and Lova-Katchanova 1972; Klerks et al. 1996; Roditi et al. 1997]) by zebra mussels may even be a larger contributor to increased organic matter, and subsequently, an increased abundance of macroinvertebrates.

Most studies attribute the increase in hard structure with zebra mussels as the primary reason behind the increase in invertebrate abundance (Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998; Horvath et al. 1999; Mayer et al. 2002; Reed et al. 2004; Ward and Ricciardi 2007). This is because the presence of druses (i.e., living and dead mussel shells, byssal threads) increases bottom complexity providing protection to invertebrates from predators (Mayer et al. 2002; Beekey et al. 2004). Also, the presence of a druse on soft sediment provides the hard surface required by many invertebrates to live, thus increasing the amount of suitable habitat

(Stewart et al. 1998; Bailly and MacIsaac 2000). The consensus is that while zebra mussels can alter community composition, they tend to have a positive effect on invertebrate abundance.

The fish community is affected by many of the same factors impacting invertebrates, both direct and indirect. Foremost, increased water clarity alters fish habitat (Griffiths 1993; Leach 1993; MacIsaac 1996; Yu and Culver 2000; Zhu et al. 2006) having a varied impact on different species. For example, Walleye *Sander vitreus* habitat may be decreased as the lake bottom is exposed to more light, thus reducing the amount of ideal "optical habitat" for Walleye (Lester et al. 2004). Walleyes are best suited to feed under low light conditions (e.g. dim-light, nighttime and turbid conditions [Ali et al. 1977]), and the increased water clarity and penetration of sunlight further into the water column reduce "optical habitat", potentially reducing foraging success (Lester et al. 2004). This effect was evident in Lake St. Clair where after the introduction of zebra mussels, Walleye moved into deep shipping channels (MacIsaac 1996) and their abundance decreased between 50% - 70% (Vanderploeg et al. 2002). However, other species, not restricted by optical habitat, may benefit from increased water clarity. Increased water clarity often coincides with an increase in abundance of macrophytes (Skubinna 1994; Zhu et al. 2006) benefitting sight-feeding fish, such as Centrarchids, through improved habitat, invertebrate and fish forage, and foraging conditions. After infestation by zebra mussels, the vegetated zone in Oneida Lake increased from 3.0 m to 5.1 m deep, species richness of macrophytes increased, and macrophyte composition changed from low-light species to a wide range of light tolerant species (Zhu et al. 2006). Increased macrophyte abundance can benefit fish species like Muskellunge *Esox masquinongy*, Smallmouth Bass *Micropterus dolomieu* and Yellow Perch *Perca flavescens* by increasing the amount of available spawning and feeding habitat and has the potential to triple abundance of these species (Vanderploeg et al. 2002). Thus, the introduction of zebra mussels can shift a fish community to one dominated by species best adapted to clear water and abundant macrophytes like Centrarchids.

Druses of zebra mussels can influence the foraging capacity of fish. Both Bluegill *Lepomis macrochirus* and Yellow Perch were found to have a lower success rate with capturing invertebrates when druses were present (Gonzalez and Downing 1999; Mayer et al. 2001). Though Yellow Perch experienced a decrease in foraging success, their stomachs generally contained 50% more content and growth was better compared to when mussels were absent (Thayer et al. 1997). Apparently, the large increase in abundance of invertebrates in the presence of zebra mussel druses more than compensates for the lower foraging efficiency of fish due to the increased complexity of habitat. This would explain why many of the fish species present in western Lake Erie (i.e., White Bass *Morone chrysops*, Yellow Perch, Freshwater Drum *Aplodinotus grunniens*, Walleye, Emerald Shiner *Notropis hudsonius*, and Trout-Perch *Percopsis omiscomaycus* [Gopalan et al. 1998; Trometer and Busch 1999]) were unaffected by the introduction of zebra mussels. However, Gizzard Shad *Dorosoma cepedianum* abundance appears to have been affected in western Lake Erie likely due to higher levels of competition for food resources (Gopalan et al. 1998).

Though information is limited, existing research has shown changes in habitat due to zebra mussels can impact spawning success of some species. Zebra mussels negatively impacted Lake Trout *Salvelinus namaycush* spawning success in Lake Michigan by reducing the quality of reef spawning habitat. Reef spawning habitat was less suitable in the presence of zebra mussels due to a reduction in local water quality and interstitial spaces as well as increased potential for egg predation (Marsden and Chotkowski 2001). To the contrary, Walleye spawning success in spawning shoals in Lake Erie was not significantly impacted by zebra mussels (Leach 1993; Fitzsimons et al. 1995).

Zebra mussels can serve as an additional food source for some species. Various organisms have been found to consume zebra mussels, but consumption has most often been observed in laboratory settings, and in the wild, consumption appears to be limited (Molloy et al. 1997; Perry et al. 1997; Naddifi and Rudstam 2014). Molloy et al. (1997) assembled an extensive list of organisms that have been found to consume zebra mussels at either the juvenile or adult life stage. In southern Lake Ontario, Alewife and Rainbow Smelt were found to consume zebra mussel veligers (Mills et al. 1995). Several other species have also been found to consume veligers (Blueback Herring *Alosa aestivalis*, Gizzard Shad *Dorosoma cepedianum* and White Perch *Morone Americana* [see Molloy et al. 1997]) elsewhere. Adult zebra mussels are commonly consumed by Freshwater Drum *Aplodinotus grunniens* (Morrison et al. 1997; Magoulick and Lewis 2002), Blue Catfish *Ictalurus furcatus* (Magoulick and Lewis 2002; Eggleton et al. 2004; Gatlin et al. 2013), and Redear Sunfish *Lepomis microlophus* (Magoulick and Lewis 2002), but various other fish species have also been observed to consume zebra mussels (Marsden 1997; Molloy et al. 1997; Morrison et al. 1997; Naddafi and Rudstam 2014). Additionally, some species of ducks and other birds have been observed to consume adult zebra mussels (Hamilton et al. 1994; Molloy et al. 1997; Petrie and Schummer 2002). Diving ducks, such as Lesser Scaup *Aythya affinis*, Greater Scaup *Aythya marila* and Buffleheads *Bucephala albeola*, can consume large amounts of zebra mussels (Hamilton et al. 1994; Petrie and Schummer 2002). Petrie and Schummer (2002) found that diving duck populations increased by nine-fold, while Canada Goose *Branta canadensis* and dabbling duck populations increased by about two-fold between 1980 and 2000 along the Canadian shoreline of Lake Ontario. Other organisms such as crayfish (Molloy et al. 1997; Perry et al. 1997), turtles (Molloy et al. 1997; Serrouya et al. 1995) and Muskrats *Ondatra zibethicus* (Molloy et al. 1997; Sietman et al. 2003) all have been found to consume zebra mussels. Though organisms have been found to consume zebra mussels, that does not mean that they are a beneficial prey resource. Abundant zebra mussels may serve as easily accessible prey (Petrie and Schummer 2002), but not the most energetically profitable prey (Magoulick and Lewis 2002).

One of the most detrimental impacts of zebra mussel infestation has been the damage to submerged infrastructure, especially water intakes. Zebra mussels attach to various man-made structures including buoys, docks, and dams. Although zebra mussels can impact all these structures, the damage to power generating facilities is of greatest concern (MacIsaac 1996). Prescott et al. (2014) thoroughly described how zebra mussels can impact various parts of hydroelectric dams. Structures that prevent foreign objects from entering dams (e.g. floating barriers, trash-racks, grates, or other types of barriers) or intake pipes can become infested restricting water flow to the facility and reducing generator output efficiency. Additionally, pipes or valves used for fire protection systems, cooling systems, maintenance and general use or domestic purposes can become blocked with zebra mussels inhibiting function or causing overheating of components. Other water-using facilities including sewage treatment plants, nuclear power plants, industrial facilities and fish hatcheries can be similarly impacted. Removing zebra mussels to restore proper function of these facilities is costly and must be done periodically (O’Neill 1997). The impact of zebra mussels can extend past the boundaries of a waterbody through their impact on facilities that utilize water and the increased costs to the consumers of the products produced by these facilities.

Zebra mussels have been called an environmental engineer (Stewart et al. 1998; Vanderploeg et al. 2002; Zaiko et al. 2009) due to the various impacts they exert on aquatic environments. These mussels can influence the abiotic (e.g., water clarity and habitat) and biotic (e.g., zooplankton, phytoplankton, macrophytes, fish and other species) characteristics of a waterbody in complex ways. Although some limited benefits with zebra mussels have been identified, their introduction into North America has generally had negative consequences and due to the complex nature of their impacts on native species and their environments, their total impact may yet be known.

Section 4: Control

Various methods of prevention, detection and removal are employed worldwide to control the spread and consequential effects of zebra mussel introductions. However, zebra mussel biological characteristics such as high fecundity (Mackie et al. 1989; Borcherding 1992; Marsden 1992), free swimming larvae (Sprung 1989; Nichols 1996) and ability to attach to a variety of surfaces (Marsden and Lansky 2000; Ackerman et al. 1993; Sprung 1993; Kobak 2014) makes preventing the spread to new waterbodies difficult. Though preventing further spread of zebra mussels would be optimal, it is likely zebra mussels will continue to spread and efforts to reduce or slow that spread should be undertaken.

Success with slowing the spread of zebra mussels will be in part related to our ability to educate the public about the mechanisms behind the spread, detrimental effects and high costs associated with zebra mussel infestation. Public knowledge and awareness of zebra mussels and their impacts will improve public participation in efforts to prevent the rapid spread across South Dakota (Eiswerth et al. 2011). Ways to increase awareness include signs at water access areas, use of social media, public meetings, and booths at sport shows as well as a variety of other outlets often used to spread awareness of aquatic invasive species (AIS) and help educate the public. Lee et al. (2015) found that the number of boaters that "never" participated in any kind of aquatic invasive species prevention decreased over a 10-year period. The study attributed this decline to multiple exposures to information over that period and stated that a single exposure to information is not enough to influence boater behavior. Additionally, an informed public can become a powerful tool to prevent the spread of AIS. Informed individuals can help with detection of AIS, generation of funds, and outreach to other members of the community (Witmer et al. 2009). A well-informed public in South Dakota will help prevent the spread of zebra mussels and potentially can help identify any new introductions across the state.

Once zebra mussels are established in a waterbody, there is some potential to control or possibly eradicate them on smaller bodies of water using chemicals (Galil 2009) but this method can be costly, limiting its use (Helfrich and Hipkins 2009; Fernald and Watson 2014). A wide range of chemicals such as oxidizing agents, nonoxidizing biocides, heavy metals and organic acids (Nalepa and Schloesser 1993; Galil 2009) and chlorine have been used in attempts to eradicate zebra mussels Chlorine has been a popular chemical used by industrial and water treatment facilities (Claudi and Mackie 1993). Zebra mussels were discovered in Millbrook Quarry, Virginia, a 12-acre enclosed system separated from Broad Run River by a berm (Fernald and Watson 2014). A potassium solution was used to successfully eradicate zebra mussels without impacting other organisms in the quarry (Fernald and Watson 2014). Another eradication was attempted in Offutt Air Force Base Lake, Nebraska, with copper sulfate in 2008, but in early 2010 adult zebra mussels were again found in the lake (Tony Barada Nebraska Game and Parks, *personal communication*). Chemicals have only been used in closed systems (Galil

2009) and may have limited use in South Dakota. However, with limited success of eradication of zebra mussels, further eradications of zebra mussels may not be feasible.

There are often issues associated with using chemicals to eliminate target organisms. One issue with chemical use is the lack of targeted eradication. Chemicals such as copper sulfate, chlorine and other molluscicides have the potential to impact native mussel species in addition to zebra mussels (Mackie and Claudi 2010; Fernald and Watson 2014) as well as zooplankton, macroinvertebrates, and fish species (Bettoli and Maceina 1996; Fernald and Watson 2014). Additionally, high numbers of decomposing zebra mussels may negatively impact water quality by creating an odor that affects palatability (Cohen et al. 1960 and 1961). Even if there are no negative impacts with chemical treatment, the public will often disapprove or be skeptical of their use (Witmer et al. 2009).

Physical removal can also be used to remove zebra mussels from infrastructure (Culver et al. 2013). Mechanical removal is often used when chemical eradication is not possible and may be used in conjunction with other methods to control zebra mussels (Culver et al. 2013). One method of mechanical removal employs divers to clean structures. Repeated removals by divers in Lake George, New York, a 28,170-acre glacial lake (Sutherland et al. 1983), were able to reduce zebra mussel populations to the point that reproduction and recruitment were encumbered, and further recruitment prevented (Wimbush et al. 2009). However, water conditions in Lake George, primarily calcium levels (Frischer et al. 2005) were unfavorable for zebra mussel development, and that might have allowed for scuba removals to be successful (Wimbush et al. 2009). Infrastructure within power plants and water treatment facilities can be drained and cleaned with high-pressure power washers or by hand (Prescott et al. 2014). Facilities that utilize water can use ultraviolet radiation and antifouling paint to kill or prevent the establishment of zebra mussels (Mackie and Claudi 2010). The placement of tarps over zebra mussels to deprive mussels of oxygen, paired with applications of chemicals, has been used in California to expedite the eradication process (Culver et al. 2013).

Drawdowns are another mechanical control method used in some waterbodies. A drawdown simply involves lowering the water level to expose zebra mussels to air or cold causing desiccation or freezing. In Nebraska, Zorinsky and Cunningham Reservoirs were drawn down to expose zebra mussels (Tony Barada Nebraska Game and Parks, *personal communication*). Zorinsky Reservoir, a 170-acre waterbody, was drawn down in the winter of 2010–2011, and this measure was combined with a chemical treatment the following spring. No zebra mussels were detected until 2016; however, no further detections were made, and the reservoir is no longer “suspected” of being infested according to Western Regional Panel guidelines (Tony Barada Nebraska Game and Parks, *personal communication*). Cunningham Reservoir, a 390-acre waterbody, was drawn down in the winter of 2018─2019 after adult zebra mussels were found in 2018. Due to infrastructure enhancements being completed during the drawdown, the reservoir has not been refilled, but sampling for zebra mussels has occurred at the lowered water levels with no positive detections and will continue after refilling in the summer of 2020. Drawdowns could help control zebra mussels in South Dakota in the Missouri River reservoirs, but due to water-use needs for powerplants, water supply, irrigation, and navigation will likely not be implemented at a scale large enough to eradicate mussel populations.

Recently, a relatively new chemical designed for zebra mussel control called Zequanox® has shown the potential to specifically target and kill zebra mussels (Culver et al. 2013). The biopesticide uses a killed strain of *Pseudomonas flourescens* (*Pf*-CL145A), that when ingested damages the digestive tract of mussels causing death (Molloy et al. 2013a). This biopesticide has been found to have no impact on fish, native mollusks, birds, plants, algae, and various invertebrate species (Culver et al. 2013; Molloy et al. 2013b; Pletta 2013). Christmas Lake, a 247-acre waterbody just west of Minneapolis, Minnesota, was partially treated with Zequanox® and zebra mussels were completely removed within the treatment area (Lund et al. 2018). However, the use of Zequanox® can be costly ranging from 2,000 – 11,000 USD per acre (Adams and Lee 2012) and may not be feasible in most waterbodies.

There are now a variety of effective methods that can be used to control or possibly eliminate zebra mussels in small or closed systems. It is nearly impossible to completely eradicate zebra mussels in larger waterbodies, but annual drawdowns in reservoirs such as the Missouri River Reservoirs may help limit abundance. Eradication of zebra mussels in smaller waterbodies may be feasible when using both mechanical (i.e., drawdowns) and chemical (i.e. Zequanox®) methods. However, preventing the introduction of zebra mussels into new waters still stands as the best method of control in South Dakota and elsewhere.

Section 5: Zebra Mussels in South Dakota Waters: Potential Detriments

The recent discovery of zebra mussels in 2019 in Lake Francis Case and Lake Sharpe and in six eastern South Dakota lakes in 2020 and 2021 have elevated concerns about the negative impacts of invasions to the state's reservoirs and lakes as well as the spread of zebra mussels to other South Dakota waters. In 2020, zebra mussels were documented outside of the Missouri River reservoirs (and reservoir-fed lakes McCook and Yankton) for the first time. Although it is difficult to know exactly what impact zebra mussels will have on the aquatic landscape in South Dakota, we can speculate based on changes observed in similar aquatic systems elsewhere.

Since detection in 2015, zebra mussels have rapidly expanded throughout Lewis and Clark Lake, and we would expect a similar type of expansion in Lake Francis Case and Lake Sharpe. Water temperatures and calcium levels, suspended solids, pH and dissolved oxygen are favorable for expansion of zebra mussels in these newly infested reservoirs, and if zebra mussels were introduced into Lake Oahe, conditions would be favorable for infestation there, too. Water temperature in these reservoirs never exceeds the upper threshold of zebra mussel tolerance (30° C), and the period where water temperatures are favorable for reproduction (≥ 12° C) often lasts from early-spring into fall (Figures 1 – 4). Calcium, pH, and dissolved oxygen levels are also within the suitable range for zebra mussels (Figure 5; USACE 2018a, 2018b, 2018c, 2018d). Although suspended solids may exceed optimal levels for zebra mussels in all reservoirs except Lake Oahe, the highest levels were recorded in Lewis and Clark Lake (Figure 5) and these levels have not prevented establishment and rapid expansion of zebra mussels in that reservoir. Therefore, suspended solids would not be expected to inhibit zebra mussels in the other reservoirs.

The distribution of zebra mussels in the Missouri River reservoirs in South Dakota will most likely be influenced by depth as well as several other factors. Highest concentrations of zebra mussels will most likely be in shallow, littoral areas which tend to be warmer and contain more food items (i.e., phytoplankton and zooplankton). Tributary confluences often have poor water clarity and high levels of suspended solids that may hinder zebra mussel filtering and negatively influence establishment or abundance in these areas. Additionally, mixing due to wind and wave action within each reservoir may limit habitable areas or influence establishment in some areas due to high levels of suspended solids. Annual winter drawdown in Lake Francis

Case will expose shallow-water druses killing the mussels, however, reproduction during summer months will likely repopulate druses.

Zebra mussels have the potential to significantly change the aquatic ecosystem in the Missouri River Reservoirs of South Dakota although our ability to accurately predict their total impact is limited. Increased clarity, often associated with zebra mussel introductions, may impact the "optical" habitat of Walleye forcing them to select deeper water locations in both the riverine and lake sections of these waterbodies. Increased water clarity may also favor increased abundance of aquatic macrophytes potentially favoring centrarchids or esocids (Vanderploeg et al. 2002). However, the largest impact by zebra mussels on reservoir Walleye may be their potential to negatively impact Gizzard Shad abundance through competition for phytoplankton and zooplankton. Gizzard Shad are a major prey species of Walleye and other game fish within these reservoirs (Wuellner et al. 2010) and are responsible for fast growth and good condition. The potential negative impact to Walleye populations is of great concern. Reservoir fisheries are almost entirely dependent on fast growing, abundant Walleye, and a decline in the fishery would greatly impact local and regional economies that rely heavily on revenues generated from Walleye fishing. Each reservoir generates roughly $7 million dollars or more annually from anglers primarily targeting Walleye (SDGFP 2019e).

In addition to creating problems with the Walleye fisheries, zebra mussel in these reservoirs will negatively impact power plants located at dam sites by fouling equipment and causing malfunctions requiring costly cleaning methods. Within Gavins Point Dam, located at the bottom reach of Lewis and Clark Lake in South Dakota, lake water is filtered through 1/8" diameter strainers to catch and remove adult zebra mussels. After water is strained it passes through UV lights that destroy protein chains within veligers causes unrepairable damage to cells, resulting in mortality (U.S. Army Corps of Engineers, Omaha District, *personal communication*). Other facilities upstream of Gavins Point Dam are currently considering the use of a copper ionization system and evaluating various antifouling paints (U.S. Army Corps of Engineers, Omaha District, *personal communication*). The potential impacts zebra mussels may have on powerplants and water related infrastructure may not only affect the local economies of river towns but areas outside the Missouri River corridor through increased cost for electrical power.

Lakes Cochrane, Kampeska, Pickerel and Wall, in eastern South Dakota were found to contain zebra mussels in 2020 and Lake Mitchell in 2021. The introduction of zebra mussels into these waterbodies and other waterbodies in South Dakota likely did not solely originate from mussels transported from Missouri River reservoir source populations, but from anglers and recreational boaters transporting mussels or veligers from infested waters in surrounding states. Surrounding states, excluding Wyoming and Montana, have reported cases of zebra mussel infestation with Minnesota having the most reported cases at over 300 documented occurrences (some lotic systems may have multiple cases of documentation at various points within the system; MNDNR 2020). Iowa, Nebraska, and North Dakota also have documented cases of zebra mussels, and of these three states, Iowa has the most with 20 reported cases (Kim Bogenschutz Iowa Department of Natural Resources, *personal communication*). Nonresident anglers from these states utilize popular waterbodies in South Dakota and will undoubtedly play a role in the establishment of secondary source population within South Dakota. Additionally, some waterbodies near state lines may be a part of a multi-state lake “rich” area. Once one of these border waters becomes infested, secondary expansion into nearby waters may be rapid.

There is little information about how zebra mussels impact small waterbodies as most research is focused on the Great Lakes and other larger waterbodies. Heavy eutrophication in many smaller prairie lakes creates favorable trophic conditions for zebra mussels (Egertson et al. 2004). An abundant phytoplankton food source in eutrophic lakes may facilitate rapid expansion of zebra mussels. However, in contrast, their ability to expand may be confined by limited hard substrate (Colvin et al. 2015) as lake bottoms are often comprised primarily of soft substrates (e.g., silt, muck). Although zebra mussels can expand into these habitats by attaching to the shells of both living and dead conspecifics (Haag 2012), expansion can be slow relative to the colonization of hard substrates (Colvin et al. 2015).

Zebra mussel clearing of phytoplankton may increase water clarity and quality. As is possible in the Missouri River reservoirs, increased water clarity in natural lakes may impact the “optical” habitat of Walleye forcing them to inhabitant deeper water or further confine their feeding to low light periods (nighttime). Increased water clarity may also favor increased abundance of aquatic macrophytes potentially favoring Northern Pike, Yellow Perch, Bluegill and Largemouth Bass over Walleye (Vanderploeg et al. 2002). Zebra mussels also divert energy from the pelagic to benthic portion of the food web (Mayer et al. 2014; Colvin et al. 2015) and this could negatively impact food availability for Walleyes dependent on pelagic forage like Gizzard Shad or shiners (i.e., Emerald Shiner, Spottail Shiner). Increased macrophytes also have the potential to hinder shore angling opportunities. It is difficult to predict the extent to which new zebra mussels will impact fish communities in South Dakota waters as the impacts of zebra mussels in lakes elsewhere has varied greatly by waterbody.

Zebra mussels are selective filter feeders, preferring green algae and diatoms over blue-green algae, which has been shown to result in more frequent and intense blue-green algal blooms (MacIsaac 1996; Vanderploeg et al. 2001; Raikow et al. 2004; Sarnelle et al. 2005; Bykova et al. 2006; Knoll et al. 2008). Shifts in the zooplankton community caused by zebra mussels may be further influenced by blooms of blue green algae which also tend to favor smaller zooplankton species (Hanazato 1991; Ferrão-Filho et al. 2002). Not only can blue green algae impact zooplankton, but when blooms of blue green algae die and decompose, they can reduce available oxygen causing a fish kill (Boyd et al. 1975). Additionally, blue green algae can affect drinking water, fish taste, and the health of humans, pets, and livestock (Falconer and Humpage 2005). Blue green algae have been known to give water an earthy or dirty taste making it unpalatable for human consumption (Izaguirre et al. 1982) and have even been known to affect the taste of fish (Schrader and Rimando 2003).

Some management or control of zebra mussels in South Dakota may be possible, but waterbody size as well as other factors will limit effectiveness. It is unlikely that zebra mussels will be exterminated from infested reservoirs, due to their size and potential for reestablishment from upstream sources. Control or eradication of zebra mussels in smaller waterbodies is possible, but even if eradicated, there is a possibility for reintroduction from nearby infested waterbodies. Chemicals will likely be the most effective method of zebra mussel management and Zequanox® or other biological and environmentally friendly treatments that specifically target zebra mussels and may be more favored by the public, could be used to eliminate zebra mussels from smaller waterbodies. Preventing further spread of zebra mussels within South Dakota is the most effective form of management and can avert a need for costly eradication measures. Zebra mussels are now a permanent fixture within the South Dakota aquatic landscape and time will define how they will change newly infested waterbodies.

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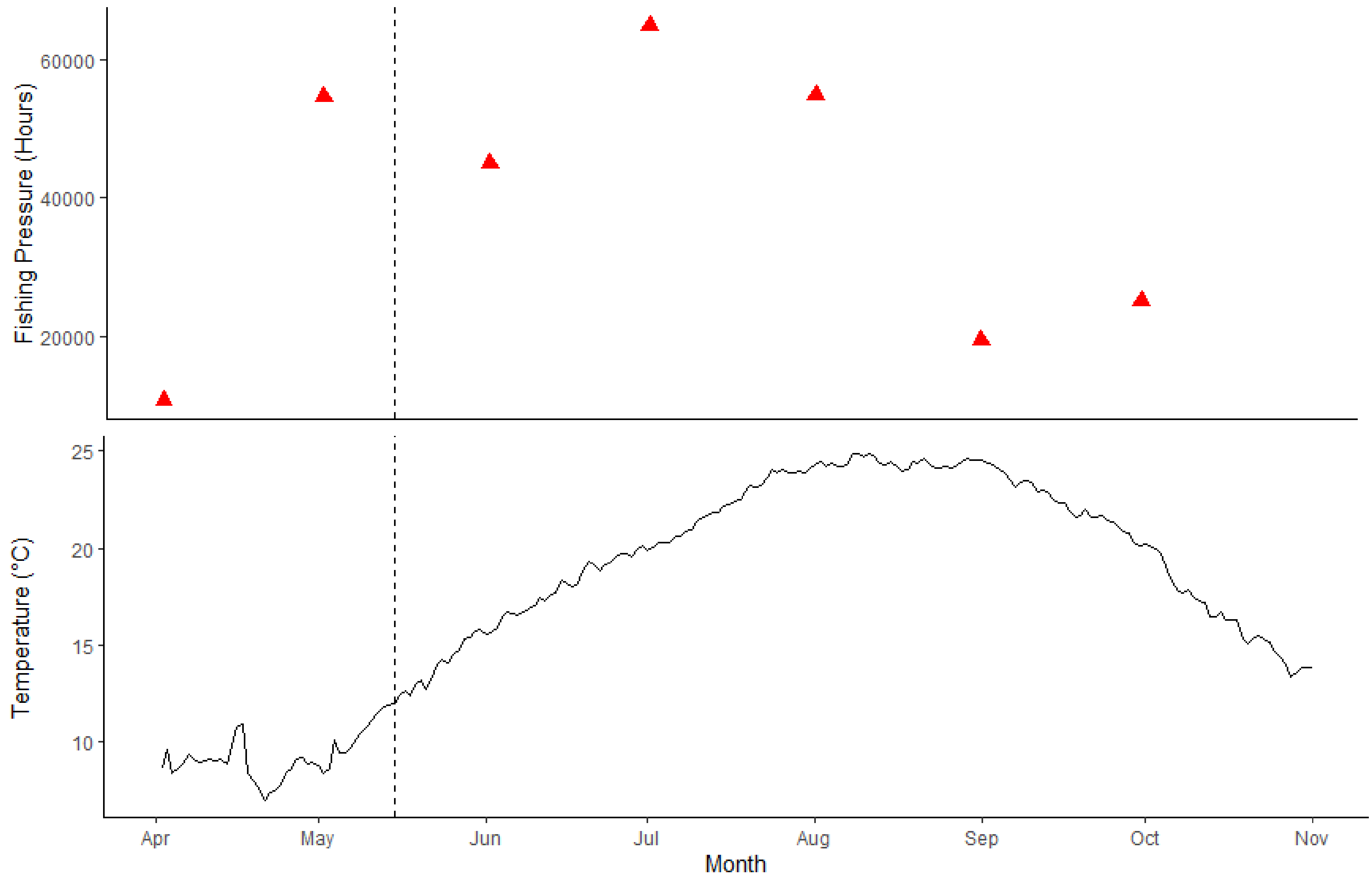

Fishing Pressure (Hours)
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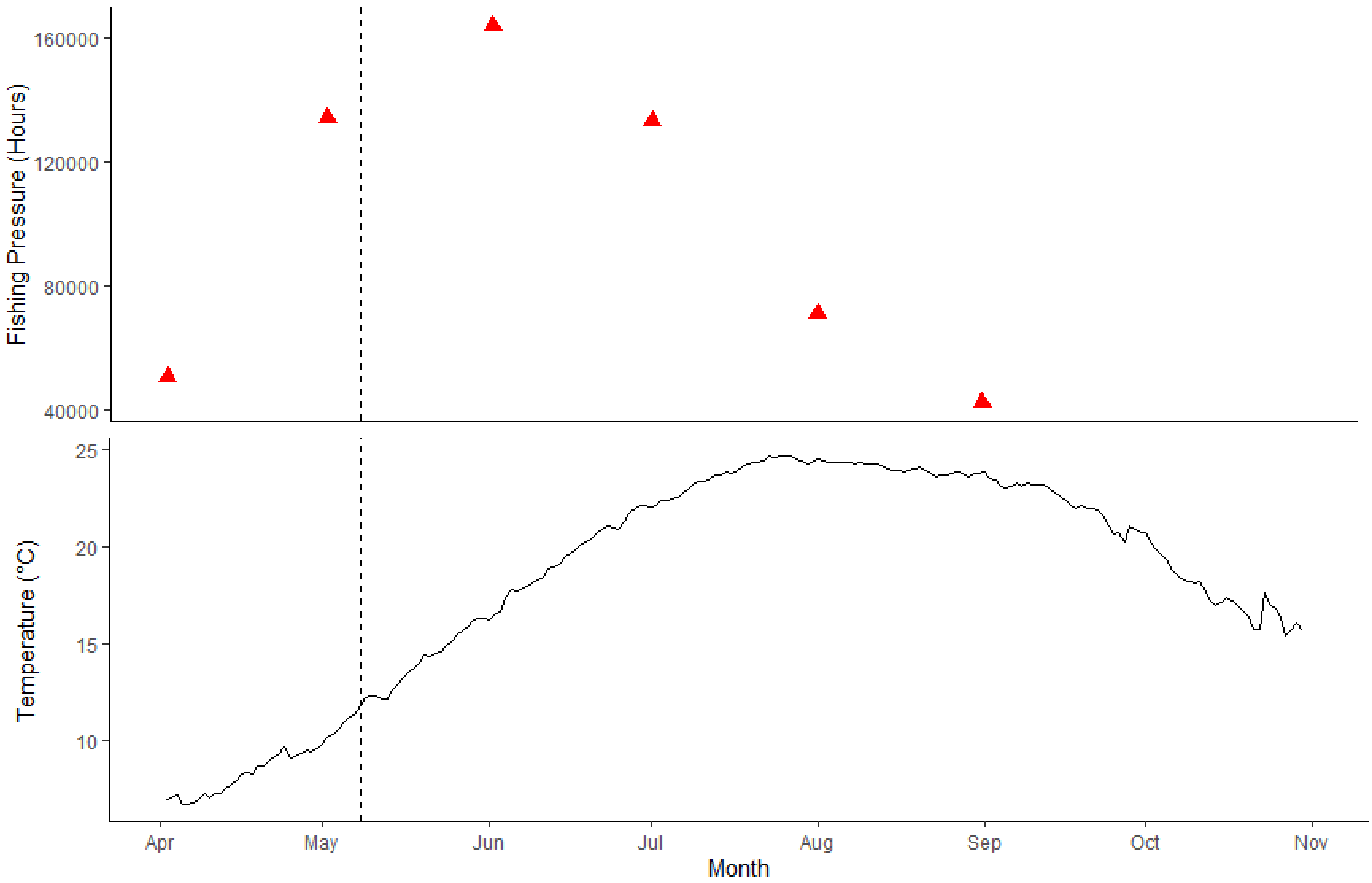
Month



Fishing Pressure (Hours)
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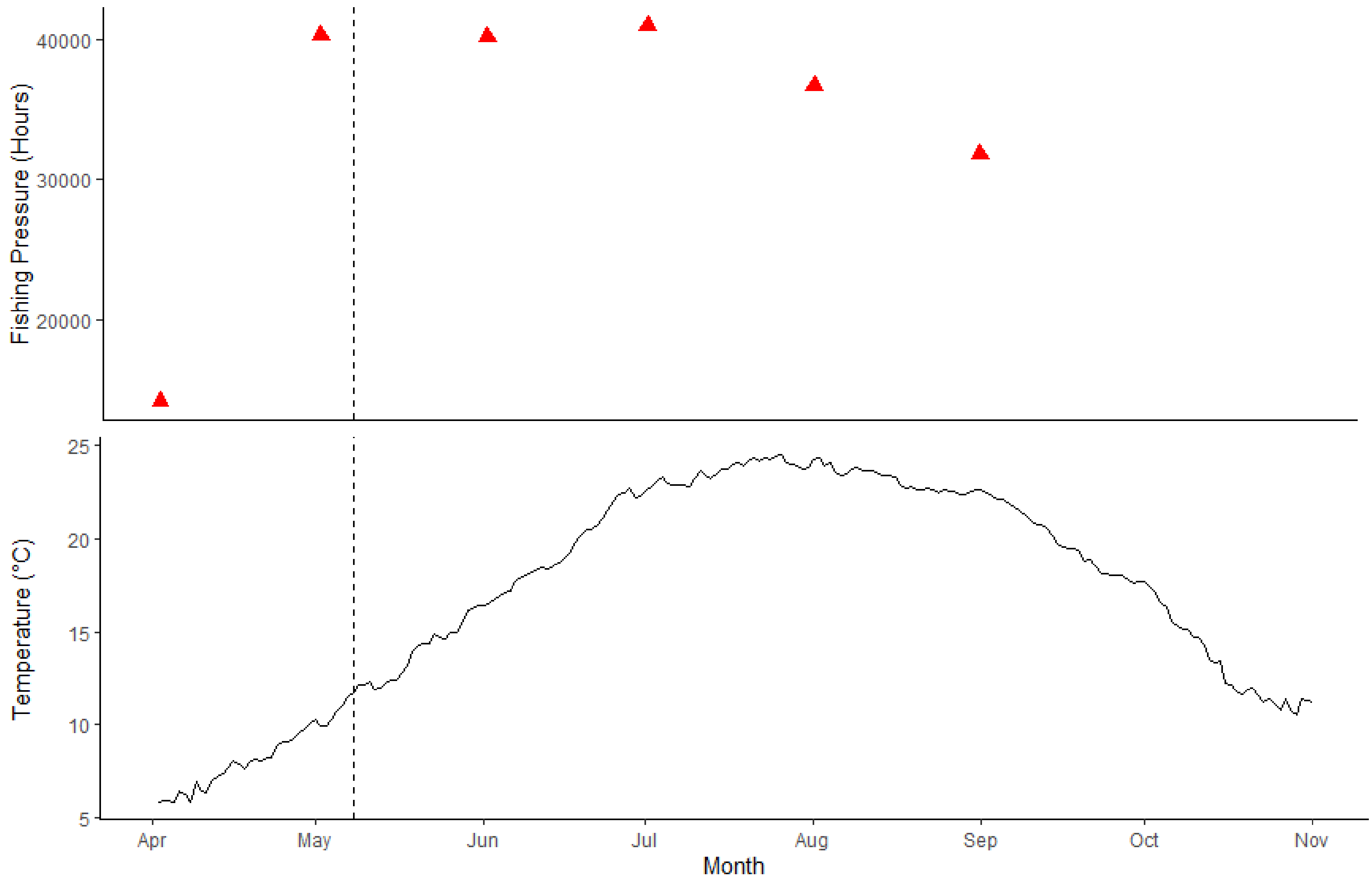

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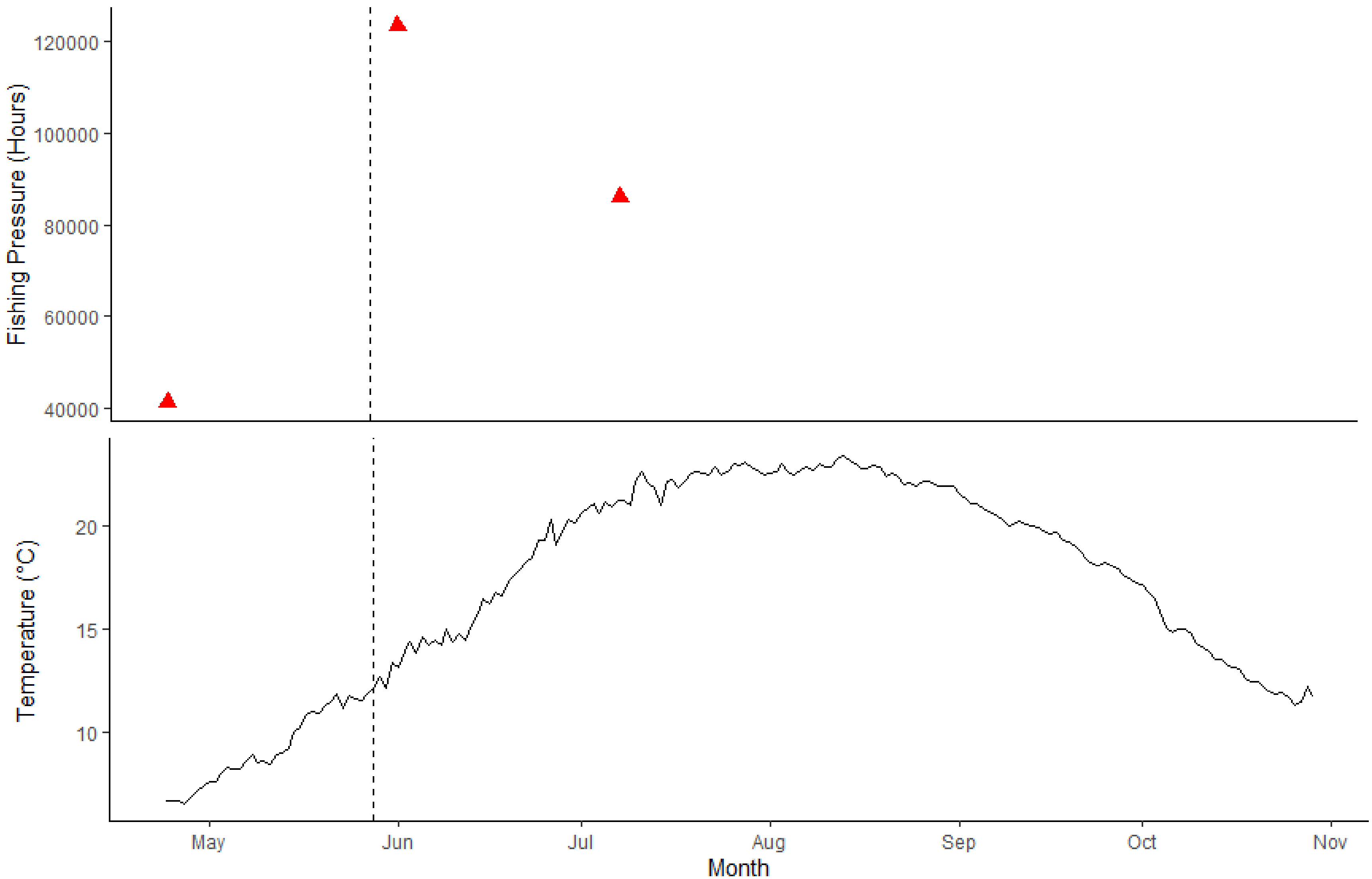

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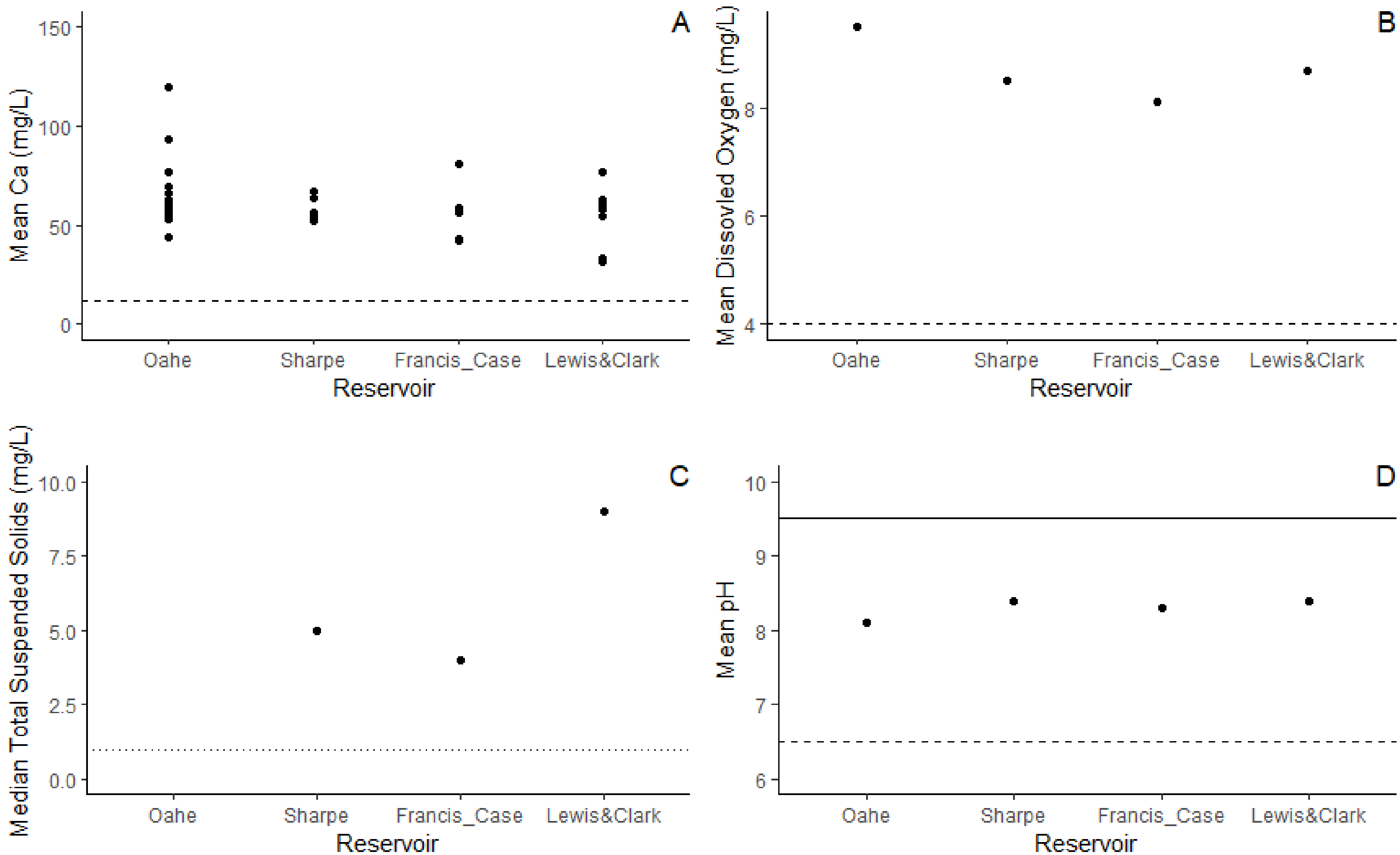
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Francis_Case
Lewis&Clark
Reservoir
B
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8
6
4
Oahe
Sharpe
Francis_Case
Lewis&Clark
Reservoir
C
Median Total Suspended Solids (mg/L)
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7.5
5.0
2.5
0.0
Oahe
Sharpe
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Lewis&Clark
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