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A Review of Zebra Mussel Biology, Distribution, Aquatic Ecosystem Impacts, and Control with Specific Emphasis on South Dakota, USA

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Abstract

Zebra mussels *Dreissena polymorpha* are a native bivalve from eastern Europe. They were first detected in North America in Lake St. Clair in 1988 and were presumably introduced via infested ballast water. Zebra mussels have spread rapidly across the United States, with 31 states reporting infestations as of 2019. Zebra mussels were first detected in South Dakota, USA, in 2015 in Lewis and Clark Lake and McCook Lake, with subsequent infestations occurring in Lake Yankton in 2017, Lakes Francis Case and Sharpe in 2019, and Pickerel Lake, Kampeska Lake, and Lake Cochrane in 2020. This review paper presents information on zebra mussel biology and control, with specific information on the waters of South Dakota, USA.

Keywords

Zebra Mussel, *Dreissena polymorpha*, South Dakota, North America

1. Introduction

The zebra mussel *Dreissena polymorpha* is a bivalve native to eastern Europe [1] [2]. It is a small, brown, freshwater mussel with a cream-colored zebra stripe pattern that varies among individuals [2]. It inhabits large freshwater lakes and rivers [3] but has also been found in a wide variety of aquatic habitats, including flooded quarries, cooling ponds, and golf course ponds [4]. Zebra mussels exhibit high fecundity [1] [5] [6] and an ability to attach to a variety of surfaces [7] [8] [9] [10] that has allowed them to spread quickly and colonize new locations.

Sphaeriidae, Margaritiferidae and Unionidae are the only families of freshwater mussels native to North America, with Unionidae being the most common [11]. Zebra mussels belong to the Dreissenidae [11], a mussel family possessing characteristics not found in native mussels. Dreissenid mussels have planktonic larvae that do not require a host to develop. In contrast, native mussels must rely on host species to complete development. In addition, zebra mussels are epifaunal, using byssal threads to attach to hard surfaces and substrates not available to native mussels, which are infaunal and typically bury themselves in sediments [11]. Zebra mussels can attach directly to native North American mussels, which frequently leads to native mussel mortality [11].

Infestation of zebra mussels into new waterbodies is generally believed to occur during early life stages [12] [13] because of external fertilization of eggs in the water column [14] [15] and free-swimming larvae [12] [16]. Both eggs and larvae are capable of movement by either natural or anthropogenic means [17] [18] [19].

Spawning of sexually mature zebra mussels begins when water temperatures reach 12˚C [5] [6] [12] [20] with optimal spawning temperatures near 18˚C [20]. Spawning continues as long as temperatures are adequate, even into early fall [21]. A single female zebra mussel releases 30,000 to 40,000 eggs per spawning event [1] [5] [6]. Within a year, one female can produce and release over a million eggs [1] [5]. Several days after fertilization, free swimming larvae emerge and disperse throughout a waterbody [16].

Larval zebra mussels undergo multiple stages of development, with corresponding shifts in behavior. Shortly after hatching, larvae, called veligers, develop velum, an organ used for feeding and movement [15]. Within the first seven days post-hatching, veligers also develop an unornate D-shaped shell followed by a more ornate shell a few days later [15]. After shell formation, organs, including a foot and gill filaments, develop in the mantle cavity [15]. 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 [15]. At 16 to 88 days post-hatch, veligers begin to swim or crawl along the bottom in order to find suitable surfaces upon which to settle [15].

Although veligers can settle upon a variety of surfaces, survival is influenced by surface selection. Suitable surfaces are generally hard structures [7] [8] [9] [10], including both natural surfaces such as rocks [7] [8] [9] and artificial surfaces such as cement, steel, or rope [7] [9] [22]. Veligers will also settle upon macrophytes [8] [15] [23] [24], as well as on other invertebrates [8] [25]. Veligers often have difficulty locating suitable substrate for settling, with mortality rates as high as 98% [26]. After initial settlement, zebra mussels can relocate to more suitable locations [10].

Once initial settlement has occurred, veligers secrete byssal threads to attach to the selected substrate [27] and undergo further development. The velum is replaced by fully functioning gill filaments and a mouth, and the foot moves to a new position and increases in size [15]. These developments facilitate the excretion and formation of the adult shell [15]. However, even after the development of the adult shell, zebra mussel juveniles are not classified as adults until sexually maturity [15] [28]. In North America, sexually maturity typically occurs at a length of approximately 8 mm, which frequently happens after just one year of growth [6] [21] [25]. Mature mussels commonly congregate into colonies called druses, which are often located in shaded areas [29]. All sizes of zebra mussels exhibit negative phototaxis and prefer darker locations [10] [29] such as crevices, corners and edges [30] [31]. The zebra mussel lifespan is typically between two and nine years [6] [21] [25] [32].

Although generally considered nonmobile, if conditions become unfavorable, zebra mussels can detach their byssal threads and use their feet to seek more suitable habitat [33], particularly rough-textured structures [10]. Juvenile zebra mussels also have special floating byssal threads allowing them to resuspend into the water column and drift to new locations [34]. Toomey *et al.* [29] found that smaller mussels (5 - 10 mm) tend to move a greater distance (e.g. 284 mm) than larger mussels. Specifically, over a two-hour period, mussels at a length of 5 to 10 mm mussels move 284 mm, compared to mussels at a length of 10 to 20 mm that moved 115 mm, and those longer than 20 mm that moved 47 mm [29]. While hypoxic conditions will stimulate movement [10], unfavorable calcium levels and water temperature will not [29].

The presence of conspecifics reduces zebra mussel movement [35], leading to their aggregation druses [10]. The formation of druses likely is influenced by the availability of preferred substrates and a predator-avoidance mechanism [10]. However, druses have the potential to reduce mussel growth and condition due to the accumulation of wastes and the depletion of dissolved oxygen and food supplies [36] [37]. If deteriorating conditions in the druse do occur, smaller mussels exit the druse upward, while larger mussels frequently remain stationary and die [36] [37] [38].

Zebra mussel survival and growth is greatly influenced by water temperature. McMahon [20], Cohen [39], and Pollux *et al.* [13] indicate zebra mussel survival in temperatures ranging from 1˚C to 30˚C, while Spidle *et al.* [40] determined that they could survive at somewhat higher temperatures in North America. Although zebra mussels can survive, and grow, for short periods at temperatures greater than 30˚C [20] [40] [41], they cannot survive at temperatures less than 0˚C [13] [20] [39] [40] [41]. Growth generally occurs between 6˚C and 30˚C [42], with optimal temperatures for growth ranging from 10˚C to 15˚C [43]. Zebra mussels located in relatively deep water tend to grow slower, most likely due to lower water temperature and reduced food availability [44].

In addition to temperature requirements, adequate calcium levels are also critical for zebra mussel survival and growth. Minimum calcium concentrations in the range of 12 to 15 mg/L are required for proper shell development and growth [20] [39] [45] [46] [47]. Low calcium levels can hinder egg development, as well as interfere with muscular contraction, nerve function, cellular cohesion, pH balance, and other aspects of mussel physiology [13] [47] [48]. Mussel calcium uptake is influenced by pH [47] with a desirable range from 6.5 to 9.5 [42].

Zebra mussels are considered intolerant of low dissolved oxygen [49], requiring minimum values of 4 to 6 mg/L depending on other environmental conditions [42]. As such, the hypolimnion of lakes, impoundments, river floodplains, or other areas with water containing low dissolved oxygen may not be suitable habitat for zebra mussels [44] [50]. Other environmental factors that impact zebra mussel growth and mortality include suspended solids, turbidity, and salinity. High suspended solid concentrations and turbidity can hinder zebra mussel growth by negatively affecting ingestion and clearance rates [51]. Zebra mussels can tolerate salinity ranging from 0.6 to 12 mg/L [37] [52] [53] with upper lethal limits dependent on temperature [42] [53]. Environmental factors can affect zebra mussel growth and mortality both by acting independently and in combination with each other [44] [46] [47] [50].

Zebra mussels feed primarily on algae, but also consume micro-invertebrates, bacteria, detritus and other organic matter [12]. Food items are obtained by clearing (filter feeding) particles ranging in size from 0.5 to 1200 μm into the mantle of the mussel [54] [55]. The preferred size for food items ranges from 15 - 40 μm [56]. Clearance rates are affected by mussel size [57] and temperature, with the most advantageous rates occurring at temperatures between 14˚C and 26˚C [54]. Clearance rates and food ingestion are also negatively affected by high levels of suspended solids and turbidity, with clearance rates most notably affected when concentrations of suspended solids are greater than 1 mg/L [51]. In addition to the effects on clearance rates, increased suspended solids can also increase the production of pseudofeces, which are mucous-coated particles expelled from the siphon or mantle [51] [57] [58]. Pseudofeces production does result in increased respiration and energy costs however [51].

2. Distribution and Spread

Zebra mussels are native to eastern Europe, originally occupying areas around the Volga River and the Aral, Black, and Caspian Seas [2]. Canal construction during the 1800s facilitated their spread throughout western Europe [1] [2] [19]. Zebra mussels were first reported in North America in 1988 from Lake St. Clair, Michigan [59], likely having been introduced via ballast water [17] [59] [60]. Within a month they were detected in the western basin of Lake Erie [61] and have subsequently spread across much of North America. In 1991, zebra mussels were detected at several locations along the Mississippi River [19] [62] and later were found in the river all the way from Minnesota to Louisiana [19]. Zebra mussels are now found in 31 states [63].

The Missouri River, the longest tributary of the Mississippi, bisects the state of South Dakota and also forms part of the border between South Dakota and Nebraska. Zebra mussels were first detected in the Missouri River near Sioux City, Iowa in 1999 [19] [63]. Zebra mussels were first observed in South Dakota waters in 2015 in Lewis and Clark Lake, which is the furthest downstream Missouri River mainstem reservoir [63]. In the same year, adult zebra mussels were also found in McCook Lake, a small lake near North Sioux City, South Dakota maintained by pumping water from the Missouri River [63]. In 2017, zebra mussels were detected in Lake Yankton, South Dakota, a manmade lake located adjacent to the Missouri River, just below Lewis and Clark Lake [64]. Further zebra mussel infestations were not detected again in South Dakota waters until 2019 when adult mussels were found in Lake Francis Case and Lake Sharpe, two Missouri River reservoirs immediately upriver from Lewis and Clark Lake [63]. In 2020, zebra mussel infestations were observed in Pickerel Lake, Lake Kampeska, and Cochrane Lake, all of which are located in Eastern South Dakota at distances in excess of 250 km from the Missouri River and its reservoirs. Most of the waters in South Dakota have the water chemistry and other environmental characteristics suitable for zebra mussels.

Although barge traffic is believed to have facilitated the transportation of zebra mussels upriver in many river systems [18] [19], it is likely not responsible for mussel introductions into South Dakota waters. Only the lower 1,181 km of river (Sioux City to the confluence with the Mississippi River), is maintained for navigation and the Missouri River dams upstream from Sioux City lack locks for watercraft passage. However, barges may have indirectly facilitated zebra mussel introduction into South Dakota by transporting them upriver to Sioux City, Iowa, where that population may have served as a source population for introduction by overland transport to Lewis and Clark Lake or Lake Yankton. However, it is more likely that water vessels used for recreation, research, or industrial work such as construction or bridge maintenance, were responsible for introduction [18] [65] [66]. Both zebra mussel adults and veligers have the potential to be transported overland under the right conditions [17] [67] [68] [69]. Adult mussels can attach to boat hulls, motors, and anchors [18] [65] [66], as well as macrophytes attached to trailers or boats [66]. Under cool, moist conditions, attached adult mussels can survive out of water for four days [17] [67] [68] [69]. Veligers can be transported via standing water in boat bilges, motors, and live wells [18] [65] [66]. The most plausible explanation for the spread of zebra mussels in South Dakota is via overland transport by fishing and recreational boats [18] [66].

While wild animals such as ducks, turtles, fish, and other organisms have the potential to transport zebra mussels, [18] [70], waterfowl are the most likely animals to contribute to mussel spread [18] [70]. Although little research has been conducted, it has been hypothesized that veligers and juvenile mussels could become trapped within feathers or debris carried on the feathers or feet of birds [18] [70] [71].

Even though zebra mussels can survive transportation, a single introduction may not be adequate to establish a population [72]. Even in favorable environmental conditions, multiple introductions may be needed to establish a self-sustaining population [13] [20] [39] [40] [42] [53] [65] [72] [73]. Thus, waterbodies that are the closest to existing mussel populations and those most frequented by recreational users are most susceptible to zebra mussel colonization [74]. In addition, frequently used waterbodies containing zebra mussels can act as reservoirs facilitating zebra mussel spread [65].

3. Impacts on Aquatic Ecosystems

The impact of zebra mussels on aquatic ecosystems in North America has varied from a dramatic change in trophic state [75]-[81] to virtually no effect at all [76] [82] [83] [84]. The ability of zebra mussels to increase water clarity is well-documented [61] [76] [79] [85] [86], however some studies have found little to no change in water clarity after introduction [83]. In two Ohio lakes, water clarity increased by 2 m after zebra mussel introduction [79] [86], while an even greater water clarity increase was observed in the eastern basin of Lake Erie [83]. However, the western and central basins of Lake Erie did not experience a similar water clarity increase [83]. Turbidity in the Detroit River decreased by about 33% after zebra mussel introductions [76], while water clarity in the Hudson River only increased by 7% [76]. In general, holomictic lakes and slow-flowing rivers with little water mixing may likely experience a larger increase in water clarity after the introduction of zebra mussels than meromictic lakes or fast-flowing, highly mixed rivers [76].

Zebra mussel impacts on phytoplankton have also varied. The mussels have reduced chlorophyll *a* in a wide variety of water bodies [81] [87] [88] [89] [90] [91], with a 41% reduction observed in a small lake in Ireland [81]. However, not all zebra mussel introductions have reduced phytoplankton abundance [84] [92] [93]. Phytoplankton communities may change because of zebra mussels. De Stasio *et al.* [84] reported a change in the phytoplankton community in Green Bay, Lake Michigan, from chlorophytes to cyanobacteria and diatoms. Increased cyanobacteria densities after zebra mussel introduction are not uncommon [76] [89] [94] [95] [96] [97]. The presence of zebra mussels may be favorable for blooms of the cyanobacteria *Microcystis aeruginosa* [94] [95], which they find unpalatable due to the presence of hepatotoxins or microcystins [93] [98]. Although zebra mussels can alter the phytoplankton community, overall biomass may stay the same [84].

Zebra mussels may affect zooplankton, both directly through consumption and indirectly through competition for food [78]. Selective consumption appears to be the primary mechanism contributing to changes in zooplankton species composition [77] [78] [99] and abundance [100] [101] [102]. Pace *et al.* [77] reported that after zebra mussel introduction, zooplankton biomass in the Hudson River decreased over 70%. After mussel introduction into Lake St. Clair, cladoceran and copepod abundance decreased by 50%, while rotifers declined by over 80% [102]. However, in Oneida Lake, New York, there was no decrease in Daphnia spp. biomass, but only a shift to larger bodied species [88]. The relatively weaker swimming strength of smaller zooplankton may make them more susceptible to zebra mussel predation [78] [88] [100]. It is also possible that any impacts of zebra mussels on zooplankton may be isolated to only those areas of a lake suitable for zebra mussels. There is also a potential that with larger waterbodies, impacts of zebra mussels on zooplankton can be patchy, isolated to areas of a lake with suitable zebra mussel habitat [88] [103].

Most mussel families native to North America have been negatively affected by the introduction of zebra mussels [3] [75]. These impacts can occur by zebra mussels settling on native mussels or by the creation of toxic conditions because of zebra mussel waste, but food competition is likely the primary mechanism behind the decline of native mussels after zebra mussel introductions [3] [75]. The decline in native mussel populations with the expansion of zebra mussels across North America is a major concern to natural resource managers [3] [11] [75].

Zebra mussel introductions have a positive effect on many aquatic invertebrate populations. The appearance of zebra mussel druses often coincides with an increase in the abundance of most invertebrates, such as amphipods, chironomids, oligochaetes, hydrozoans, and smaller mollusks [80] [104]-[110]. Large mollusks, large net-spinning caddisfly, and those invertebrates that use soft substrates may be negatively impacted by zebra mussels [105] [110]. Macro-invertebrates likely benefit from zebra mussels by increasing the availability of food and hard structure. Improved water clarity makes food more accessible [61] [76] [79] [85] [86], and macro-invertebrate food may increase due to increased organic matter resulting from zebra mussel filter feeding [111] [112] [113]. However, most studies attribute increased hard structure due to zebra mussels as the primary reason for increased macro-invertebrate numbers [80] [104] [106] [109] [113] [114] [115]. Druses, with living mussels, dead shells, and bysaal threads, increase bottom complexity, providing protection to invertebrates from predators [109] [110]. In addition, a druse on soft sediment provides the hard surface required by many invertebrates [106] [116].

Evidence of zebra mussel impacts on fish populations is limited. In Lake Erie, walleye *Sander vitreus*, white bass *Morone chrysops*, yellow perch *Perca flavescens*, freshwater drum *Aplodinotus grunniens*, emerald shiner *Notropis hudsonius*, and trout-perch *Percopsis omiscomaycus* populations did not change after zebra mussel introduction [117] [118]. However, gizzard shad *Dorosoma cepedianum* abundance may have been affected [117]. A decrease in walleye of 50% to 70% in Lake St. Clair was observed after the introduction of zebra mussels [82], although this may or may not be a cause-and-effect relationship. The decrease may have been due to mussel-induced water quality decreasing the lower light and higher turbidity conditions more conducive to walleye foraging success [119] [120]. However, increased water clarity and the subsequent increase in aquatic macrophytes [79] [121] benefits other fish species such as muskellunge *Esox masquinongy*, yellow perch, smallmouth bass *Micropterus dolomieu*, and other centrarchids [82].

Zebra mussel veligers and adults are consumed by a number of fish species [122] [123]. Predation on veligers has been reported for alewife *Alosa pseudo-*

harengus, rainbow smelt *Osmerus mordax*, gizzard shad, blueback herring *Alosa aestivalis*, and white perch *Morone americana* [122] [124]. Adult mussels are commonly consumed by freshwater drum, blue catfish *Ictalurus furcatus*, redear sunfish *Lepomis microlophus*, pumpkinseed *Lepomis gibbosus*, round goby *Neogobius melanostomus*, and several other fish species [122] [123] [125] [126] [127] [128] [129].

Indirectly, zebra mussels appear to increase yellow perch growth by increasing invertebrate abundance [130]. Although yellow perch and bluegill *Lepomis macrochirus* foraging success may decrease with the presence of druses [108] [131], any such decrease is more than compensated by the large increase in invertebrate numbers.

Walleye spawning success in Lake Erie was not impacted by zebra mussels [61] [132]. However, Marsden and Chotkowski [133] suggested that zebra mussels decreased lake trout *Salvelinus namaycush* natural reproduction in Lake Michigan by altering reef spawning habitat and increasing the potential for egg predation.

No impacts on fish populations due to zebra mussels have been identified in South Dakota. However, zebra mussels do not have a long history in the state and specific studies focused on potential zebra mussel impacts have not been undertaken.

4. Control

Characteristics such as high fecundity [1] [5] [6], free swimming larvae [12] [16], and the ability to attach to a variety of surfaces [7] [8] [9] [10] make zebra mussel control extremely difficult. Once a zebra mussel population is established, chemical control is possible on smaller water bodies in closed systems [134]. However, chemical control is very expensive, limiting its use [135] [136]. A potassium solution was used to successfully eradicate zebra mussels from a 12-acre enclosed lake in Virginia [136]. Copper sulfate was used for zebra mussel control at Offutt Air Force Base Lake, Nebraska in 2008, but two years later, adult zebra mussels were again found in the lake (Tony Barada Nebraska Game and Parks, *personal communication*). Copper sulfate and other chemical molluscicides have the potential to negatively impact native mussel species [136] [137], as well as zooplankton, macroinvertebrates and fish species [136] [138].

Physical removal has also been used for zebra mussel control [139]. Repeated zebra mussel removals by divers in Lake George, New York [140], reduced zebra mussel populations to where reproduction and recruitment were encumbered, and further recruitment prevented [141]. However, water chemistry in Lake George was unfavorable for zebra mussel development which may have allowed for scuba removals to be successful [141]. The placement of tarps over zebra mussels to deprive them of oxygen, paired with chemical applications, has been used for mussel control in California [139].

Drawdowns are another mechanical control method. A drawdown simply involves lowering the water level to expose zebra mussels to adverse environmental conditions leading to desiccation or freezing. In Nebraska, zebra mussels were eradicated from Zorinsky and Cunningham Reservoirs using drawdowns (Tony Barada Nebraska Game and Parks, *personal communication*). In Zorinsky Reservoir the drawdown was followed by a chemical fish treatment.

Biological control has also been used against zebra mussel populations. A biopesticide (Zequanox, Marrone Bio Innovations, Davis, California, USA) contains a killed strain of *Pseudomonas flourescens* (*Pf*-CL145A), that when ingested damages the digestive tract of mussels causing death, with no impacts on fish, native mollusks, birds, plants, algae, and numerous invertebrates [139] [142] [143]. When used at Christmas Lake in Minnesota, zebra mussels were completely removed within the treatment area [144]. However, such treatments can be costly, at up to 11,000 USD per acre [145].

Because of the difficulty and expense of control after zebra mussel introductions, preventing the anthropogenic spread of zebra mussels has become a focus of natural resource managers in North America [146]. Considerable attention has focused on recreational watercraft inspections and disinfections [147] [148]. In addition, protocols to allow for the safe movement of fish and fish eggs between water bodies have also been developed [149] [150] [151] [152]. All of these preventative measures have been used in South Dakota.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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