U.S. Fish & Wildlife Service

Zebra Mussel (*Dreissena polymorpha*)
Ecological Risk Screening Summary

U.S. Fish & Wildlife Service, March 2020
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Organism Type: Mussel
Overall Risk Assessment Category: High

Photo: Bj.schoenmakers. Licensed under Creative Commons CC0 1.0 Universal Public Domain Dedication. Available: https://commons.wikimedia.org/wiki/File:Dreissena_polymorpha_(Zebra_mussel),_Arnhem,_the_Netherlands.jpg. (March 2020).

1 Native Range and Status in the United States

Native Range

From Benson et al. (2020):

"The zebra mussel is native to the Black, Caspian, and Azov Seas. In 1769, Pallas first described populations of this species from the Caspian Sea and Ural River."

According to CABI (2019) *Dreissena polymorpha* is native to Romania, the Mediterranenan Sea, the Black Sea, and the Ukraine.

Status in the United States

According to Benson et al. (2020) *Dreissena polymorpha* has been introduced to Alabama, Arkansas, California, Colorado, Connecticut, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New York, North Dakota, Ohio, Oklahoma, Pennsylvania, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, West Virginia, and Wisconsin.

From Benson et al. (2020):

"Established in all the Great Lakes, all of the large navigable rivers in the eastern United States, and in many small lakes in the Great Lakes region."

"The initial invasive range of zebra mussels in the Great Lakes has decreased due to displacement by the congeneric quagga mussel."

Dreissena polymorpha was officially listed as an injurious wildlife species in 1991 under the Lacey Act (18.U.S.C.42(a)(1)) by the U.S. Fish and Wildlife Service (USFWS 1991). The importation of zebra mussels into the United States, any territory of the United States, the District of Columbia, the Commonwealth of Puerto Rico, or any possession of the United States, or any shipment between the continental United States, the District of Columbia, Hawaii, the Commonwealth of Puerto Rico, or any possession of the United States is prohibited.

From Arizona Office of the Secretary of State (2013):

"K. Mollusks listed below are considered restricted live wildlife: […]
2. All species of the family *Dreissenidae*. Common names include: zebra and quagga mussel."

From California Department of Fish and Wildlife (2019):

"It shall be unlawful to import, transport, or possess live animals restricted in subsection (c) below except under permit issued by the department. […]
(10) Class Bivalvia-Bivalves: All members of the genus *Dreissena* (zebra and quagga mussels)-(D)."

Dreissena polymorpha is prohibited to import or possess in Colorado (Colorado Secretary of State 2019).

The Florida Fish and Wildlife Conservation Commission has listed the mussel, *Dreissena polymorpha* as a prohibited species. Prohibited nonnative species (FFWCC 2020), "are considered to be dangerous to the ecology and/or the health and welfare of the people of Florida. These species are not allowed to be personally possessed or used for commercial activities."

Dreissena polymorpha is listed as invasive species in Idaho (Idaho Office of the Administrative Rules Coordinator 2019). “No person may possess, cultivate, import, ship, or transport any invasive species, into or through the state of Idaho following the effective date of this rule, unless the person possessing, importing, shipping or transporting has obtained a permit under Section 103 or unless otherwise exempt by this rule, as set forth in Section 104.”

From Kentucky General Assembly (2019):

“The live aquatic organisms established in subsections (1) through (7) of this sec-tion shall not be imported, bought, sold, or possessed in aquaria: […]
(6) *Dreissena polymorpha* – zebra mussel;”

From Mississippi Secretary of State (2019):

“All species of the following animals and plants have been determined to be detrimental to the State's native resources and further sales or distribution are prohibited in Mississippi. No person shall import, sell, possess, transport, release or cause to be released into the waters of the state any of the following aquatic species or hybrids thereof. […]
Zebra Mussel *Dreissena polymorpha*”

Dreissena polymorpha falls within Group IV of New Mexico’s Department of Game and Fish Director’s Species Importation List (New Mexico Department of Game and Fish 2010). Group IV species “are prohibited for the general public but may be allowed for, scientific study, department approved restoration and recovery plans, zoological display, temporary events/entertainment, use as service animal or by a qualified expert.”

From State of Nevada (2018):

“Except as otherwise provided in this section and NAC 504.486, the importation, transportation or possession of the following species of live wildlife or hybrids thereof, including viable embryos or gametes, is prohibited: […]
Zebra and quagga mussels………………..All species in the genus *Dreissena*”

Dreissena polymorpha is listed as a prohibited species in New York (New York State Senate 2019). “Prohibited invasive species cannot be knowingly possessed with the intent to sell, import, purchase, transport or introduce. In addition, no person shall sell, import, purchase, transport, introduce or propagate prohibited invasive species.”

From Ohio DNR (2020):

"Under Ohio Administrative Code 1501:31-19-01, it shall be unlawful for any person to possess, import or sell live individuals of the species listed below. […] Zebra Mussel *Dreissena polymorpha*"

From Texas Parks and Wildlife (2020):

"The organisms listed here are legally classified as exotic, harmful, or potentially harmful. No person may possess or place them into water of this state except as authorized by the department. Permits are required for any individual to possess, sell, import, export, transport or propagate listed species for zoological or research purposes; for aquaculture(allowed only for Blue, Nile, or Mozambique tilapia, Triploid Grass Carp, or Pacific White Shrimp); or for aquatic weed control (for example, Triploid Grass Carp in private ponds).
[…]
Zebra and Quagga Mussels, family Dreissenidae
All species of genus *Dreissena*, including but not limited to *Dreissena polymorpha* (Zebra mussel)"

From Utah Office of Administrative Rules (2019):

"Zebra mussel, (*Dreissena polymorpha*) family Dreissenidae is prohibited for collection, importation and possession."

From Virginia DWR (2020):

"A special permit is required, and may be is- sued by the Department, if consistent with the Department's fish and wildlife management program, to import, possess, or sell the following non-native (exotic) amphibians, fish, mollusks, aquatic invertebrates, and reptiles: […] zebra mussel,"

From Washington State Senate (2019):

"The following species are classified as prohibited level 1 species:
(1) Molluscs: Family Dreissenidae: Zebra and quagga mussels: *Dreissena polymorpha* and *Dreissena rostriformis bugensis*."

Means of Introductions in the United States

From Benson et al. (2020):

"A release of larval mussels during the ballast exchange of a single commercial cargo ship traveling from the north shore of the Black Sea to the Great Lakes has been deduced as the likely vector of introduction to North America (McMahon 1996). Its rapid dispersal throughout the Great Lakes and major river systems was due to the passive drifting of the larval stage (the free-floating or "pelagic" veliger), and its ability to attach to boats navigating these lakes and rivers (see Remarks section below). Its rapid range expansion into connected waterways was probably due to barge traffic where it is theorized that attached mussels were scraped or fell off during routine navigation. Overland dispersal is also a possibility for aiding zebra mussel range expansion. Many small inland lakes near the Great Lakes unconnected by waterways but accessed by individuals trailering their boats from infested waters have populations of zebra mussels living in them. At least nineteen trailered boats crossing into California had zebra mussels attached to their hulls or in motor compartments; all were found during inspections at agricultural inspection stations. Under cool, humid conditions, zebra mussels can stay alive for several days out of water."

"The rapid invasion of North American waterways has been facilitated by the zebra mussel's ability to disperse during all life stages. Passive drift of large numbers of pelagic larval veligers allows invasion downstream. Yearlings are able to detach and drift for short distances. Adults routinely attach to boat hulls and floating objects and are thus anthropogenically transported to new locations. Transporting recreational boats disperses zebra mussels between inland lakes. In addition, speculation exists that waterfowl can disperse zebra mussels, but this has yet to be conclusively demonstrated. While byssal threads develop in the larvae of some non-dresissenid endemic bivalves and are used to attach to fish gills, there are no endemic freshwater bivalves with byssal adult stages. This adaptation has been important to the zebra mussel's success in invading North America."

In March 2021, the U.S. Geological Survey was alerted to the presence of zebra mussels in moss balls (*Aegagrophila linnaei*) in a shipment at an aquarium shop. After further investigation infested moss balls were reported from more than 25 States (USFWS 2021).

Remarks

From Benson et al. (2020):

"Zebra mussels represent one of the most important biological invasions into North America, having profoundly affected the science of Invasion Biology, public perception, and policy. In the 1980's Invasion Biology began to emerge as a true sub-discipline of ecology as evidenced by an exponential increase in scientific output on the subject. Most work on the subject was terrestrial. Invasions were not a large component of the popular environmental movement, and no serious legislation existed concerning invasions beyond agricultural pests. After the discovery of zebra mussels in 1988 the exponential rate of scientific output on invasions itself increased, the Nonindigenous Aquatic Nuisance Prevention and Control Act was written and passed, and invasions became a topic discussed in the media. Today biological invasions are described as the second leading cause of extinction behind habitat destruction. Aquatic invasions are a topic of much research. For these reasons the zebra mussel is often described as the "poster child" of biological invasions."

"A long tradition of zebra mussel study exists in Europe and the former Soviet Union, where the zebra mussel has been present for 150 years (see Mackie et al. 1989 for an annotated bibliography of European references). Work includes spatial distribution patterns, demography, tolerance limits for physical and chemical parameters, and physiology. Extensive ecological work in the United States began soon as the zebra mussel was discovered and peaked in the early 1990's. The literature on ecosystem and community-level effects of zebra mussels has been dominated by work investigating Lake Erie, Saginaw Bay, the Hudson River, and Oneida Lake (e.g. Fahnenstiel [et al.] 1993, Holland 1993, Pace et al. 1998, Idrisi et al. 2001)."

This ERSS was previously published in July 2015. Revisions were completed to incorporate new information and to bring the document in line with current standards.

2 Biology and Ecology

Taxonomic Hierarchy and Taxonomic Standing

From ITIS (2020):

"Taxonomic Status:
Current Standing: valid"

Kingdom Animalia
Subkingdom Bilateria
Infrakingdom Protostomia
Superphylum Lophozoa
Phylum Mollusca
Class Bivalvia
Subclass Heterodonta
Order Veneroida
Superfamily Dreissenoidea
Family Dreissenidae
Genus *Dreissena*
Species *Dreissena polymorpha* (Pallas, 1771)

Size, Weight, and Age Range

From Benson et al. (2020):

"The life span of *D. polymorpha* ranges between 3–9 years. Maximum growth rates can reach 0.5 mm/day and 1.5–2.0 cm/year. Adults are sexually mature at 8–9 mm in shell length (i.e. within one year in favorable growing conditions)."

"**Size:** < 50 mm"

Environment

From Benson et al. (2020):

"The optimal temperature range for adults extends to 20–25°C, but *D. polymorpha* can persist in temperatures up to 30°C. Short term tolerance of temperatures up to 35°C is possible if the mussels were previously acclimated to high temperatures."

"Oxygen demands are similar to those of other freshwater bivalves including unionids. Tolerance of "anaerobic" conditions has been reported for short time periods under certain temperatures and sizes, but zebra mussels cannot persist in hypoxic conditions. The lower limit of pO2 tolerance is 32–40 Torr at 25°C. Zebra mussels have been found in the hypolimnetic zone of lakes with oxygen levels of 0.1-11.2 mg/l, and in the epilimnetic zone with oxygen levels of 4.2–13.3 mg/l. Zebra mussels are described as poor O2 regulators, possibly explaining their low success rate in colonizing eutrophic lakes and the hypolimnion. Indeed, the distribution of Dreissenid mussels is severely limited in the central basin of Lake Erie, which routinely experiences bottom hypoxia (Karatayev et al. 2017).

The salinity tolerance of zebra mussels is low. Although some populations of European zebra mussels can be found in estuaries, their persistence has been speculatively attributed to reduced tidal fluctuation. Upper limits of freshwater bivalve salinity tolerance reach 8–10 ‰, and populations of European zebra mussels have been found to tolerate and [sic] range of salinities, from 0.6 ‰ (Rhine River) to 10.2 ‰ (Caspian Sea). North American populations generally tolerate salinity up to 4 ‰. Calcium and pH levels also influence survival and growth. In European populations, calcium concentrations of 24 mg Ca2+/l allow only 10% larval survival due to inhibition of shell development. Optimal calcium concentrations ranges from 40–55 mg Ca2+/l, but North American populations have been found in lakes with lower concentrations. North American populations require 10 mg Ca2+/l to initiate shell growth and 25 mg Ca2+/l to maintain shell growth. Larval development is inhibited at pH of 7.4. Higher rates of adult survival occur at a pH of 7.0–7.5, but populations have been found in the hypolimnetic zone of lakes with a pH of 6.6–8.0, and in the epilimnetic zone with a pH of 7.7–8.5. Optimal larval survival occurs at a pH of 8.4, and optimal adult growth occurs at pH 7.4–8.0."

From GISD (2020):

"Zebra mussels […] occur from the lower shore to depths of 12 m in brackish parts of seas and to 60 m in lakes (DAISIE 2006)."

Climate

From GISD (2020):

"Zebra mussels prefer moderately productive (mesotrophic) temperate water bodies […]."

Distribution Outside the United States

Native

From Benson et al. (2020):

"The zebra mussel is native to the Black, Caspian, and Azov Seas. In 1769, Pallas first described populations of this species from the Caspian Sea and Ural River."

According to CABI (2019) *Dreissena polymorpha* is native to Romania, the Mediterranenan Sea, the Black Sea, and the Ukraine.

Introduced

From Van Damme (2014):

"It is a highly invasive mussel, and has spread throughout Europe, to southern Scandinavia and Britain, east into Eurasia and south to Turkey via shipping canals."

According to CABI (2019) *Dreissena polymorpha* has been in introduced to Turkey, Belarus, Belgium, Bulgaria, Czechia, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Poland, Russia, Slovenia, Spain, Sweden, Switzerland, the United Kingdom, Canada, and Mexico.

Means of Introduction Outside the United States

From CABI (2019):

"The spread of *D. polymorpha* from the Black Sea and Aralo-Caspian Sea basins has largely taken place in the past 200 years. How the initial expansion took place is unclear. *D. polymorpha* may have penetrated via the Oginskij Canal (completed in 1804) from Dnieper to the River Neman and further to the Curonian Lagoon in the southeast Baltic (Olenin, 2005), in which case the Black Sea is the probable origin. However it may have come via canals using the Volga and its tributaries and lakes Onega and Ladoga at the beginning of the eighteenth century and so originate from the Caspian region. Outside the Baltic Sea region it was found in England, in the London docks, in the 1820s (ISSG, 2008). By 1827 it was found in the mouth of the Rhine, and 1838 in the Elbe River. During the nineteenth century *D. polymorpha* occupied most of the inland water systems of western and central Europe: in the 1920s it appeared in Sweden (Jansson, 1994), in the 1960s it was found in alpine lakes around the Alps, and it had reached Ireland by 1993 (McCarthy et al., 1997). In 1990 it was reported from brackish water in the eastern partof the Gulf of Finland after being present for 150 years in the nearby freshwater Lake Ladoga (NOBANIS, 2008)."

"There are many ways that *D. polymorpha* are able to spread from place to place. There are naturally occurring vectors of dispersal and there are human-mediated means. Human-mediated means of dispersal tend to occur on a larger scale and over a longer period of time. There is very little chance that enough *D. polymorpha* could be moved by a naturally occurring vector to establish a substantial population.

Natural Dispersal (Non-Biotic)

Larval *D. polymorpha* are free-swimming, microscopic, and planktonic. These factors contribute to their rapid spread from one body of water to another. Any body of water downstream of an infected area has a high probability of being infected if there is continuous water flow from the upstream area.

Vector Transmission (Biotic)

Substrates with high densities of *D. polymorpha* in shallow areas are the preferred foraging areas, and these mussel colonies can be located rather quickly by migrating waterfowl. Migrating waterfowl may carry larval or juvenile mussels in their feathers or on their feet, but it is highly unlikely that they disperse mussels from one waterbody to another.

Crayfish can be the site of *D. polymorpha* settlement. If they are moved from an infected area to an uninfected area after settlement, but prior to their molting event, it is possible that they could transport mussels.

Adult *D. polymorpha* will settle on and colonize submerged aquatic plants. If plants are transported from an infected lake to an uninfected body of water, it is likely that adult *D. polymorpha* may well be transported, too. Some possible means of unintentional transport include plants attached to boat trailers and plants in or on bait buckets or other fishing gear.

Accidental Introduction

Human-mediated dispersal mechanisms (e.g., artificial waterways, ships, fishing activities, amphibious planes and recreational equipment) are the most probable means for rapid spread of the species."

Short Description

From GISD (2020):

"The shell of *D. polymorpha* is triangular (height makes 40-60 % of length) or triagonal with a sharply pointed shell hinge end (umbo). The maximum size of *D. polymorpha* can be 5 centimetres, though individuals rarely exceed 4 cm (Mackie et al. 1989). The prominent dark and light banding pattern on the shell is the most obvious characteristic of *D. polymorpha*. The outer covering of the shell (the periostracum) is generally well polished, a light tan in colour with a distinct series of broad, dark, transverse colour bands which may be either smooth or zigzag in shape."

From CABI (2019):

"The shape of *D. polymorpha* shells is generally triagonal or triangular with sharply pointed umbos (the hinge end). Underlying the umbos, the hinge plate or myophore plate is broad and well developed with no pseudocardinal or lateral teeth. The valves are joined by a proteinaceous ligament located posterior to the umbos. The valves are quite inflated posteriorly tapering to a more flattened profile along the ventral and anterior margins; an acute ridge runs from the umbos to the posterior point of the ventral margin forming a distinctive "shoulder". The mussel attaches itself to hard surfaces by byssal threads which are secreted from a byssal gland just posterior to the foot. The byssal threads emerge from the between the valves through a byssal notch along the posterior margin."

Biology

From Benson et al. (2020):

"The life history of zebra mussels differs greatly from most endemic Great Lakes-region bivalves (Pennak 1989, Mackie and Schlosser 1996). Exotic dreissenids are dioecious, with fertilization occurring in the water column. Endemic bivalves are monoecious, dioecious or hermaphroditic, and some are internally fertilized by filtering sperm from the water column. Under natural thermal regimes, zebra mussel oogenesis occurs in autumn, with eggs developing until release and fertilization in spring. In thermally polluted areas, reproduction can occur continually through the year. Females generally reproduce in their second year. Eggs are expelled by the females and fertilized outside the body by the males; this process usually occurs in the spring or summer, depending on water temperature. Spawning may start when the water temperature reaches 12°C and release rate is maximized above 17-18°C (McMahon 1996). Over 40,000 eggs can be laid in a reproductive cycle and up to one million in a spawning season. Spawning may last longer in waters that are warm throughout the year.

After the eggs are fertilized, the larvae (veligers) emerge within 3 to 5 days and are free-swimming for up to a month. Optimal temperature for larval development is 20–22°C. Dispersal of larvae is normally passive by being carried with water currents. The dispersion of zebra mussels within a lake is controlled by physical conditions including wind strength, lake/shore morphometry, and current patterns (Stanczykowska and Lewandowski 1993). These conditions affect both spatial patterns of pelagic veliger density and benthic adult dispersion. Once the veliger undergoes morphological changes including development of the siphon, foot, organ systems and blood, it is known as a postveliger. Further subdivision of the larval stage has been delineated: (veliger) preshell, straight-hinged, umbonal, (postveliger) pediveliger, plantigrade, and (juvenile) settling stage (ZMIS 1996). The settling stage attaches to a substrate via protienaceous threads secreted from the byssal gland. The vast majority of veliger mortality (99%) occurs at this stage due to settlement onto unsuitable substrates. Sensitivity to changes in temperature and oxygen are also greatest at this stage. The larvae begin their juvenile stage by settling to the bottom where they crawl about on the bottom by means of a foot, searching for suitable substrate. They then attach themselves to it by means of byssal threads. Although the juveniles prefer a hard or rocky substrate, they have been known to attach to vegetation. As adults, mussels have a difficult time staying attached when water velocities exceed two meters per second.

Zebra mussels attach to any stable substrate in the water column or benthos, including rock, macrophytes, artificial surfaces (cement, steel, rope, etc.), crayfish, unionid clams, and each other, forming dense colonies called druses. Long-term stability of substrate affects population density and age distributions on those substrates. Within Polish lakes, perennial plants maintained larger populations than did annuals (Stanczykowska and Lewandowski 1993). Populations on plants also were dominated by mussels less than a year old, as compared with benthic populations. These populations of small individuals allow higher densities on plants. In areas where hard substrates are lacking, such as a mud or sand, zebra mussels cluster on any hard surface available. Given a choice of hard substrates, mussels prefer dark, rough substrates that are above the bottom of the lake bed (Kobak 2013). They also respond to the presence of predators by using byssal threads to attach more strongly to the substrate, forming aggregations, and reducing their upward movement (Kobak 2013). Research on Danish lakes shows factors that cause substrate to be unsuitable for both initial and long term colonization, including extensive siltation, some sessile benthic macroinvertebrates, macroalgae, and fluctuating water levels exposing mussels to desiccation (Smit et al. 1993). Population density of benthic adults has been observed to vary as widely as two orders of magnitude (e.g., <100 to >1500 individuals/m2) within individual Polish lakes due to these physical conditions. Tolerance limits of physical and chemical parameters are well known (Sprung 1993, Vinogradov et al. 1993, McMahon 1996).

Discrepancy exists when comparing temperature tolerance limits of North American and European populations, potentially due to the American population being founded by mussels from the southern limit of the European population's range. Most work in Europe has been done in the northern range. North American populations are generally adapted to warmer temperature regimes than their European counterparts. Although shell growth has been reported to occur at temperatures as low as 3°C, Lake St. Clair populations and some European populations display shell growth at 6–8°C."

"Zebra mussels are filter feeders having both inhalant and exhalant siphons. They are capable of filtering about one liter of water per day while feeding primarily on algae. Zebra mussels are able to filter particles smaller than 1 µm in diameter, although they preferentially select larger particles (Sprung and Rose 1988). At a 90% efficiency rate, zebra mussels are much more efficient at filtering such small particles than are unionids and Asiatic clams (Noordhuis et al. 1992). Bacteria, which *D. polymorpha* also tends to filter more effectively than native unionids, may represent another important food source (Cotner et al. 1995, Silverman et al. 1996, Silverman et al. 1997). Microzooplankton (e.g., rotifers and veligers) are ingested by zebra mussels, but larger zooplankton are not eaten (MacIsaac et al. 1991, MacIsaac et al. 1995). Veligers also filter material, but their impact is far less than that of sessile adults. Settled mussels exerted 103 times the grazing rate of veligers in western Lake Erie, for example (MacIsaac et al. 1992).

Filtration rate is highly variable, depending on temperature, concentration of suspended matter, phytoplankton abundance, and mussel size (reviewed by Noordhuis et al. 1992). Zebra mussels can adjust their filtration rates (more frequent interruption of filtering or slower pumping rates) and/or produce pseudofeces [materials that collect on the zebra mussel's gills and are rejected before entering the gut, definition from Ciborowski (2007)] above an incipient limiting concentration (ILC) of algae to maintain a constant consumption rate (Fanslow et al. 1995, MacMahon 1996, Sprung and Rose 1988). Feeding activity can be described by the clearance rate (percentage of algal biomass removed from the water column over time), biomass of cleared algae (BCA), feces production and pseudofeces production (µg F or P/BCA). For example, Berg et al. (1996) examined the effects of zebra mussel size and algae species and concentration on zebra mussel feeding activity. Clearance rates were constant over varying concentrations of pure cultures of *Chlamydomonas reinhardtii*, a spherical unicellular species 7.42 µm (± 0.13 µm) in diameter. This indicates that the concentrations used in experiments were below the ILC. However, clearance rates decreased, with increasing concentrations of *Pandorina morum*, a species made up of colonies with varying numbers of cells that are individually as large as *C. reinhardtii*. This indicates that the concentrations used in experiments were above the ILC. Large zebra mussels (20-25 mm in length) displayed a higher clearance rate across all concentrations of *C. reinhardtii* than did small mussels (10-15 mm). Incipient limiting concentration differed in this study from previous studies conducted with European populations. Vanderploeg et al. (2017) found that seston quality and availability affects zebra mussel feeding rate and excretion levels. In Saginaw Bay, filtration rate increased with higher seston concentrations and water temperatures, but was not found to be related to seston composition (POC:TSS, chl:TSS) (Fanslow et al. 1995). No diel patterns of filtration rate have been found. During spring, filtration rates rise dramatically as waters warm from 5–10°C, then level off with respect to temperature, and may be inhibited at temperatures over 20°C. Increased suspended matter can reduce filtration activity to a minimum required to maintain oxygen demand. A sigmoidal relationship exists with filtration rate and size, but this may be an effect of aging. Thus, zebra mussel size, phytoplankton species, and regional population differences will affect clearance rates, ILC, and feces/pseudofeces production.

Material filtered by zebra mussels is either ingested or expelled as feces or mucus-covered pseudofeces. True fecal pellets are chemically altered, larger, and denser. Zebra mussels produce pseudofeces to avoid ingesting non-food material. Pseudofeces production may also be a mechanism to deal with overabundance of food (e.g., algal concentrations above the ILC, incipient limiting concentration), and possibly as a way to reject unpalatable algae. Pseudofeces production increases with increasing suspended solid concentration, as well as increasing temperature, albeit to a much lesser extent (MacIsaac and Rocha 1995, Noordhuis et al. 1992)."

Human Uses

From GISD (2020):

"Bioindicator: Due to its sensitivity to anthropogenic influences *Dreissena* is important as a bioindicator and biomonitoring organism (Franz 1992, in Birnbaum 2006), and quantitative assessments have been conducted regularly since the 1960s in the context of water quality surveys (e.g. in the Rhine) (Schiller 1990, in Birnbaum 2006).

Products: Crushed shells of the zebra mussel can be used as fertiliser [*sic*] and poultry feed (Birnbaum 2006). Zebra mussels have been used as fishing bait and for fish meal production (DAISIE 2006)."

Diseases

NO OIE-reportable diseases (OIE 2020) have been documented for this species.

According to Poelen et al. (2014) *Dreissena polymorpha* is the host of *Haplosporidium raabei*, *Hymenostomatia*, *Aspidogaster limacoides*, *Bucephalus polymorphus*, *Phyllodistomum, Phyllodistomum folium*, and *Chaetogaster limnaei*.

Threat to Humans

From CABI (2019):

"The occurrence of *D. polymorpha* in shallow areas where bathing occurs has resulted in an increase in foot lacerations with possible consequences of infection from a number of freshwater organisms that may include *Leptospira interogans* that causes Weil's disease (Minchin et al., 2002)."

"The sharp shell of the *D. polymorpha* is razor-like and is a hazard to barefoot swimmers and beachcombers."

3 Impacts of Introductions

From Benson et al. (2020):

"Zebra mussels are notorious for their biofouling capabilities by colonizing water supply pipes of hydroelectric and nuclear power plants, public water supply plants, and industrial facilities. They colonize pipes constricting flow, therefore reducing the intake in heat exchangers, condensers, fire fighting equipment, and air conditioning and cooling systems. Zebra mussel densities were as high as 700,000/m2 at one power plant in Michigan and the diameters of pipes have been reduced by two-thirds at water treatment facilities. Although there is little information on zebra mussels affecting irrigation, farms and golf courses could be likely candidates for infestations. Navigational and recreational boating can be affected by increased drag due to attached mussels. Small mussels can get into engine cooling systems causing overheating and damage. Navigational buoys have been sunk under the weight of attached zebra mussels. Fishing gear can be fouled if left in the water for long periods. Deterioration of dock pilings has increased when they are encrusted with zebra mussels. Continued attachment of zebra mussel can cause corrosion of steel and concrete affecting its structural integrity.

Zebra mussels can have profound effects on the ecosystems they invade. They primarily consume phytoplankton, but other suspended material is filtered from the water column including bacteria, protozoans, zebra mussel veligers, other microzooplankton and silt. Large populations of zebra mussels in the Great Lakes and Hudson River reduced the biomass of phytoplankton significantly following invasion. Diatom abundance declined 82–91% and transparency as measured by Secchi depth increased by 100% during the first years of the invasion in Lake Erie (Holland 1993). As the invasion spread eastward during 1988 to 1990, successive sampling stations recorded declines in total algae abundance from 90% at the most western station to 62% at the most eastern (Nichols and Hopkins 1993). In Saginaw Bay, sampling stations with high zebra mussel populations experienced a 60–70% drop in chlorophyll-a and doubling of Secchi depth (Fahnenstiel et al. 1993). Phytoplankton biomass declined 85% following mussel invasion in the Hudson River (Caraco et al. 1997). The extent of change that zebra mussels can exert on species composition of the phytoplankton community is unresolved. Increased water clarity allows light to penetrate further, potentially promoting macrophyte populations (Skubinna et al. 1995). As macrophytes can be colonized by veligers, the macrophyte community may be altered if such colonization proves detrimental. Increased light penetration may also cause water temperatures to rise and thermoclines to become deeper, but these effects have not yet been documented. As phytoplankton are consumed, the dissolved organic carbon (DOC) concentration may drop. Indeed, inland lakes with zebra mussels have been found to have lower concentrations of DOC (Raikow 2002). Macrophytes could eventually compensate for this since they are also a source of DOC, but there may be a lag period between the time when phytoplankton biomass is down and macrophytes proliferate. This could produce a period of time when UV-B light penetrates deeper into the water column, because DOC absorbs UV-B radiation. Zebra mussels have also recently been shown to be able to directly assimilate DOC (Roditi et al. 2000). Zebra mussels are able to filter particles smaller than 1µm in diameter, although they preferentially select larger particles (Sprung and Rose 1988). Thus bacteria may represent an important food source (Cotner et al. 1995, Silverman et al. 1996). At a 90% efficiency rate, zebra mussels are much more efficient at filtration of such small particles than are unionids and Asiatic clams. Filtering rate is highly variable, depending on temperature, concentration of suspended matter, phytoplankton abundance, and mussel size (reviewed by Noordhuis et al. 1992). Although European zebra mussels are less active in winter, this seasonal pattern is temperature driven. No diel patterns of filtration rate have been found. During spring, filtration rates rise dramatically between 5 and 10oC [sic], then level off with respect to temperature, and may be inhibited at temperatures over 20oC [sic]. Increased suspended matter can reduce filtration activity to a minimum required to maintain oxygen demand. A sigmoidal relationship exists with filtration rate and size, but this may be an affect of aging. Material filtered by zebra mussels is either ingested or expelled as feces or mucus covered pseudofeces. True fecal pellets are chemically altered, larger and more dense. Pseudofeces production increases with increasing suspended solid concentration, as well as increasing temperature, albeit to a much lesser extent (Noordhuis et al. 1992, MacIsaac and Rocha 1995). The rate of biosedimentation through pseudofeces production was very high (28mg/cm2 day at a density of 1180 individuals/m2) under turbid conditions in Lake Erie, lending support to the hypothesis that zebra mussels are responsible for increased water clarity observed since mussel introduction (Klerks et al. 1996). Filtration rate was not related to seston composition (POC:TSS, chl:TSS) in Saginaw Bay (Fanslow et al. 1995). Veligers also filter material, but their impact is far less than that of sessile adults. Settled mussels exerted 103 times the grazing rate of veligers in western Lake Erie, for example (MacIsaac et al. 1992). Microzooplankton, e.g. rotifers and veligers, are ingested by zebra mussels, but larger zooplankton are not eaten (MacIsaac et al. 1991, MacIsaac et al. 1995). It has been speculated that benthic deposition of feces and pseudofeces may aid bacterial productivity, thus producing a source culture that zebra mussels can feed upon (Silverman et al. 1996). It has also been speculated that biodeposition of feces and pseudofeces might cause observed increases in benthic macroinvertebrate populations (Stewart and Haynes 1994).

Biomagnification of Polychlorinated Biphenyls (PCBs) was observed in *Gammarus* associated with zebra mussels, indicating concentration of pollutants in zebra mussel feces or pseudofeces can transfer to other trophic levels (Bruner et al. 1994). In an experimental study, however, Botts et al. (1996) found greater abundances of macroinvertebrates associated with both living and non-living (i.e. empty shell) zebra mussel druses compared with their no-druse treatment. Thus the increased physical habitat complexity of a mussel colony may benefit macroinvertebrates rather than deposition of feces and pseudofeces. Zebra mussels can reduce filtration rates (more frequent interruption of filtering or slower pumping rates) and/or produce pseudofeces above an incipient limiting concentration (ILC) of algae to maintain a constant consumption rate (Sprung and Rose 1988, Fanslow et al. 1995, MacMahon 1996). Feeding activity can be described by the clearance rate (percentage of algal biomass removed from the water column over time), biomass of cleared algae (BCA), feces production and pseudofeces production (µg F or P/BCA). For example, Berg et al. (1996) examined the effects of zebra mussel size and algae species and concentration on zebra mussel feeding activity. Clearance rates were constant over varying concentrations of pure cultures of *Chlamydomonas reinhardtii*, a spherical unicellular species of 7.42 µm (± 0.13µm) in diameter. This indicates that the concentrations used in experiments were below the ILC. However, clearance rates decreased, with increasing concentrations of P*andorina morum*, a species made up of colonies with varying numbers of cells that are individually as large as *C. reinhardtii*. This indicates that the concentrations used in experiments were above the ILC. Large zebra mussels (20-25 mm in length) displayed a higher clearance rate across all concentrations of *C. reinhardtii* than did small mussels (10-15 mm). Incipient limiting concentration differed in this study from previous studies done with European populations. Thus zebra mussel size, phytoplankton species, and regional population differences affect clearance rates, ILC and feces/pseudofeces production. Zebra mussels produce pseudofeces to avoid ingesting non-food material (e.g. clay), as a mechanism to deal with overabundance of food (e.g. algal concentrations above the ILC), and possibly as a way to reject unpalatable algae. Zebra mussels readily reject blue-green algae, such as Microcystis, as pseudofeces (Vanderploeg et al. 2001). The presence of this cyanobacterium does not inhibit filtering, except in mass abundances such as a bloom (Noordhuis et al. 1992, Lavrentyev et al. 1995). Zebra mussels can select material for rejection through pseudofeces production internally, perhaps identifying cyanobacteria by chemical cues (ten Winkel and Davids 1982). Inland lakes with lower nutrient levels have been observed to be more frequently dominated by Microcystis when invaded by zebra mussels (Raikow et al. 2004). Understanding of the fate of pseudofeces once it expelled is poor. Zebra mussels removed metals from the water column of Lake Erie and deposited it to the bottom at high rates (Klerks et al. 1996). Roditi et al. (1997) found that the biodeposits of zebra mussel were organically enriched, including 3.9% live algae by weight. Resuspension of this material occurred in their system, a tidal estuary, reducing the potential impact of biodeposition to the benthos. Less well known is the fate of live algae bound into pseudofeces. Bastviken et al. (1998) speculate that phytoplankton which survives the pseudofeces process must be resuspended in order for long term survival, a process less likely to occur in inland lakes than in tidal estuaries. If survivorship following filtration is equal between phytoplankton species, then community species composition can remain unchanged. Other factors may affect the phytoplankton community, however, including increased light.

The zooplankton community has also been affected by the invasion of zebra mussels. Zooplankton abundance dropped 55-71% following mussel invasion in Lake Erie, with microzooplankton more heavily impacted (MacIsaac et al. 1995). Mean summer biomass of zooplankton decreased from 130 to 78 mg dry wt. m-3 between 1991 and 1992 in the inner portion of Saginaw Bay. The total biomass of zooplankton in the Hudson River declined 70% following mussel invasion, due both to a reduction in large zooplankton body size and reduction in microzooplankton abundance. These effects can be attributed to reduction of available food (phytoplankton) and direct predation on microzooplankton. Increased competition in the zooplankton community for newly limited food should result from zebra mussel infestation. The size of individual zooplankters might decrease. Hypotheses can be formulated specifying which species will prevail based on knowledge of competitive ability.

Effects may continue through the food web to fish. Reductions in zooplankton biomass may cause increased competition, decreased survival and decreased biomass of planktivorous fish. Alternatively, because microzooplankton are more heavily impacted by zebra mussels the larval fish population may be more greatly affected than later life stages. This may be especially important to inland lakes with populations of pelagic larval fish such as bluegills. Benthic feeding fish may benefit as opposed to planktivorous fish, or behavioral shifts from pelagic to benthic-feeding may occur. In addition, proliferation of macrophytes may alter fish habitat. Experimental evidence exists that zebra mussels can reduce the growth rate of larval fish through food web interactions (Raikow 2004). Conclusive negative impacts on natural populations of fish, however, have yet to observed (see Raikow 2004). Other effects include the extirpation of native unionid clams through epizootic colonization (Schloesser et al. 1996, Baker and Hornbach 1997). Zebra mussels restrict valve operation, cause shell deformity, smother siphons, compete for food, impair movement and deposit metabolic waste onto unionid clams. Survival rates of native unionid mussels in the Mississippi River, Minnesota have been shown to decline significantly with the increase in zebra mussel colonization (Hart et al. 2001).To date, unionids have been extirpated from Lake St. Clair and nearly so in western Lake Erie. Many species of birds known to be predators of zebra mussels occur in the Great Lakes region. While a new food source may benefit such predators, biomagnification of toxins into both fish and birds is possible. Some effects have been hypothesized as worst-case scenarios. For example, zebra mussels may cause a shift from pelagically to benthically-based food webs in inland lakes. Zebra mussels may also shift lakes from a turbid and phytoplankton-dominated state to clear and macrophyte-dominated state, i.e. between alternative stable equilibria (Scheffer et al. 1993)."

From Ricciardi et al. (1998):

"A comparison of species loss at various sites before and after invasion indicates that *D. polymorpha* has accelerated regional extinction rates of North American freshwater mussels by 10-fold. If this trend persists, the regional extinction rate for Mississippi basin species will be 12% per decade. Over 60 endemic mussels in the Mississippi River basin are threatened with global extinction by the combined impacts of the *D. polymorpha* invasion and environmental degradation."

From Ciborowski (2007):

"Before the arrival of zebra mussels, there were approximately 40 species of native mussels in the Detroit River and approximately 20 in Lake St. Clair. Nalepa et al. (1996) collected Unionidae from 29 sites in Lake St. Clair in 1986 (before the first zebra mussels were found), in the years 1990, 1992, and 1994. They collected 281 (18 species), 248 (17 species), 99 (12 species), and 6 (5 species) native mussels in the four years, respectively, which shows the devastating impact to native mussels. Zebra mussels attach themselves to unionids by byssal threads. The zebra mussels interfere with the unionid mussels' ability to open and close their shells […]. This prohibits the unionids' ability to burrow. The zebra mussels also consume the algae and suspended sediment that the unionids would otherwise filter from the water."

"The solid waste particles (feces and pseudofeces) from zebra mussels are much larger than the food particles eaten, and build up on the lake bottom, thereby transferring energy from the pelagic (open water) to the benthic (bottom) zone. Pseudofeces are materials that collect on the zebra mussel's gills and are rejected before entering the gut. Through filtration, zebra mussels clarify the water and decrease local algal densities (Mellina et al. 1995)."

4 History of Invasiveness

The zebra mussel, *Dreissena polymorpha*, has been recorded as introduced and established in several countries in Europe and throughout the United States. Not only is it introduced into those areas but it has also been recorded as having negative impacts, with some sources going as far as saying that there have been no positive impacts in the areas it has been introduced. Negative impacts reported include extirpation of multiple populations of native unionid mussels, significant reductions in phyto- and zooplankton, changes in macrophytes, altered fish habitat, changes in water quality, and damage to infrastructure. It is because of this that the history of invasiveness is High.

5 Global Distribution

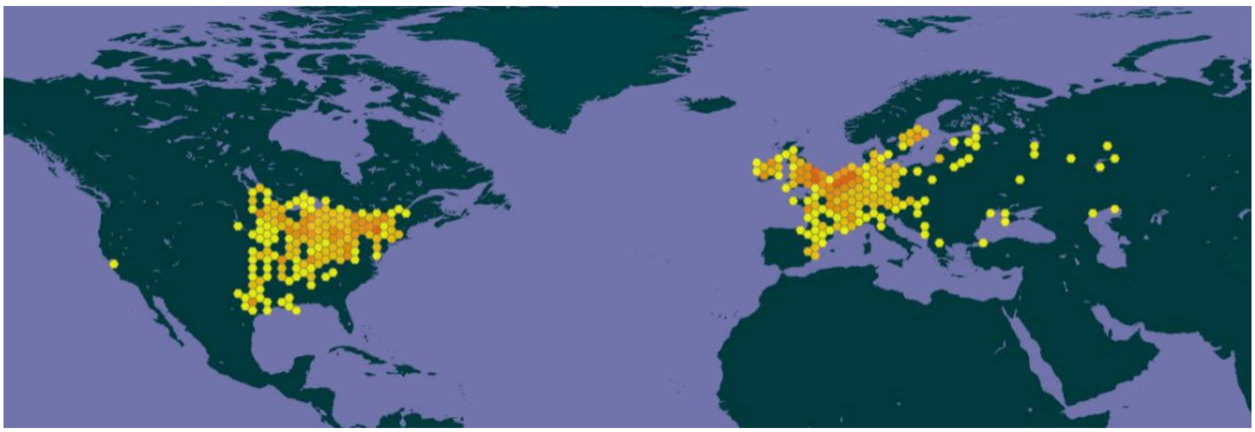

Figure 1. Known global distribution of *Dreissena polymorpha*. Observations are reported from Austria, Belgium, Bulgaria, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Lithuania, Luxembourg, Montenegro, Macedonia, Netherlands, Poland, Russia, Slovenia, Spain, Sweden, Switzerland, Turkey, the United Kingdom, the United States and Canada. Map from GBIF Secretariat (2020).

6 Distribution Within the United States

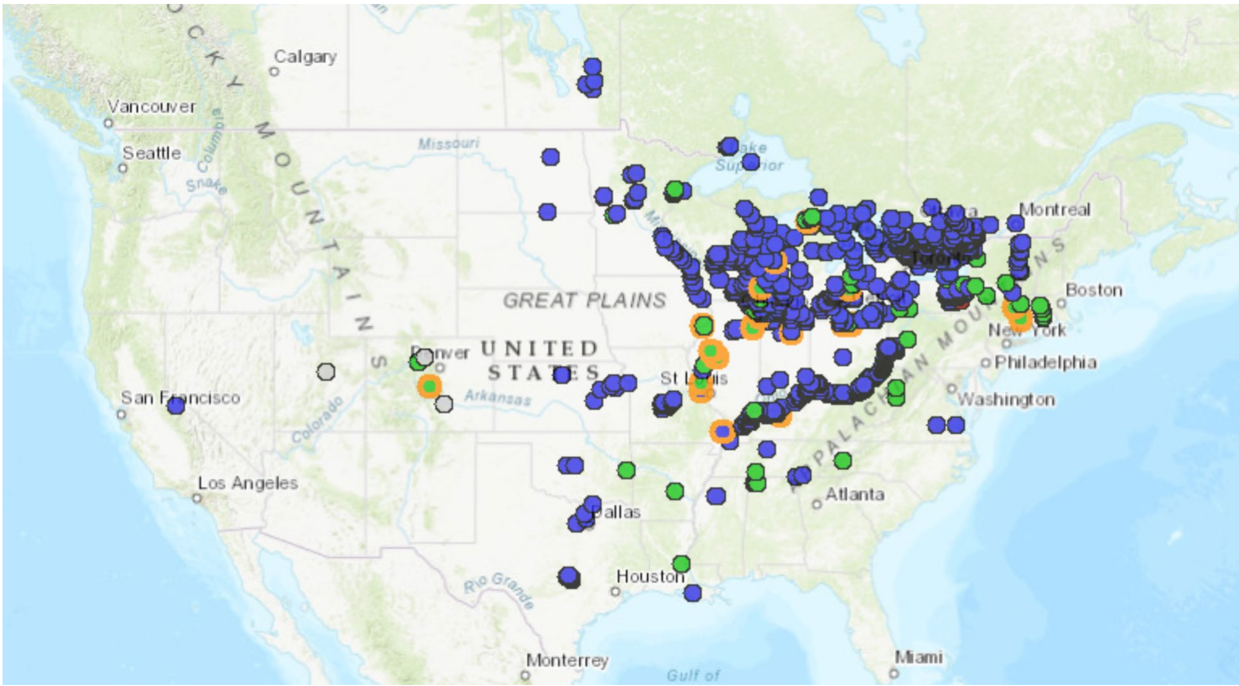

Figure 2. Known distribution of *Dreissena polymorpha* in the United States and southern Canada. Map from BISON (2020).

7 Climate Matching

Summary of Climate Matching Analysis

The majority of the contiguous United States had a high climate match with only a very small area of low climate match in the Northwest and some areas of medium match in peninsular Florida and along the western States. The overall Climate 6 score (Sanders et al. 2018; 16 climate variables; Euclidean distance) for the contiguous United States was 0.84, a categorically high climate score (scores greater than 0.103, inclusive, are classified as high). All States had high individual Climate 6 score.

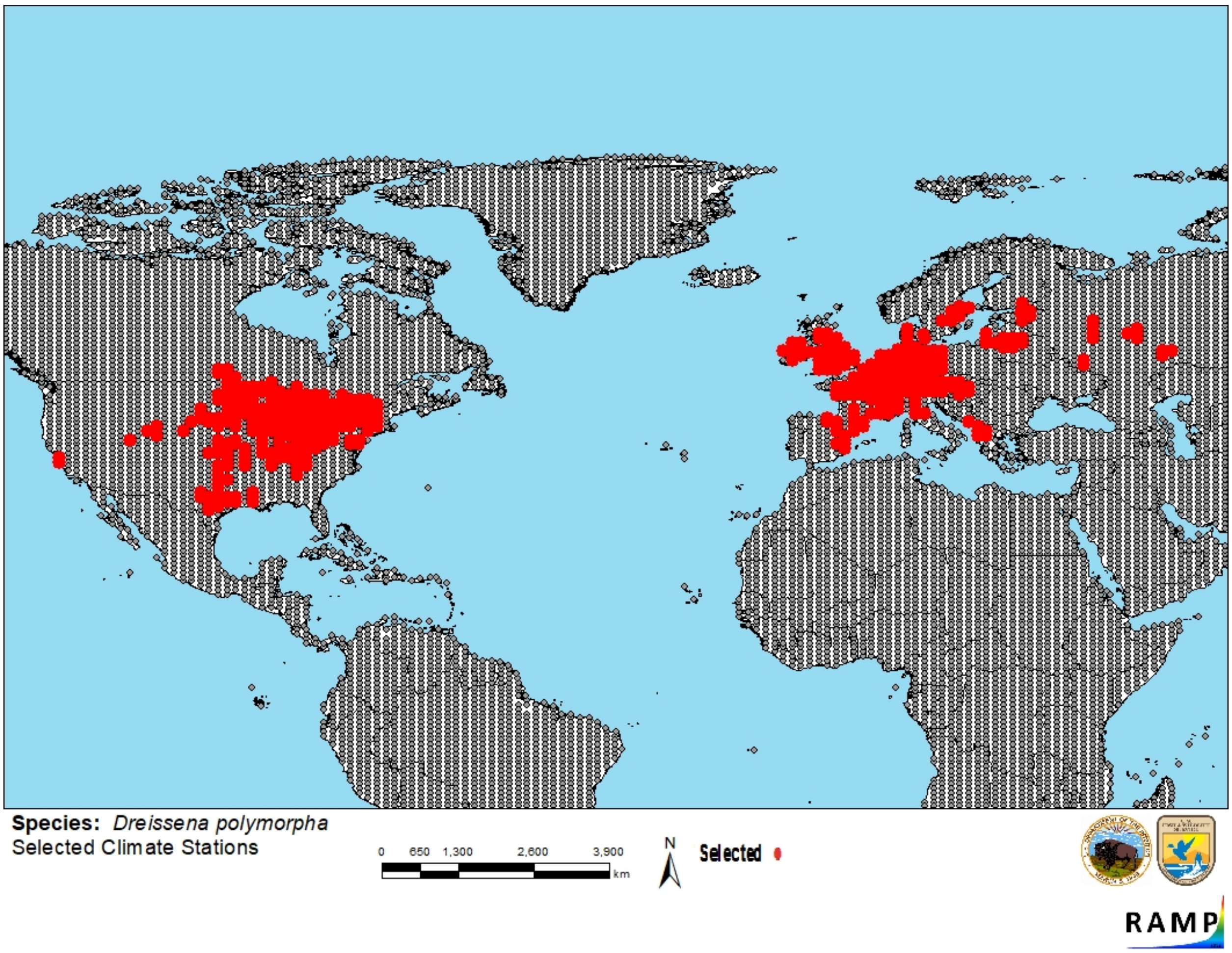

Figure 3. RAMP (Sanders et al. 2018) source map showing weather stations in North America, Europe and Russia selected as source locations (red) and non-source locations (gray) for *Dreissena polymorpha* climate matching. Source locations from GBIF Secretariat (2020). Selected source locations are within 100 km of one or more species occurrences, and do not necessarily represent the locations of occurrences themselves.

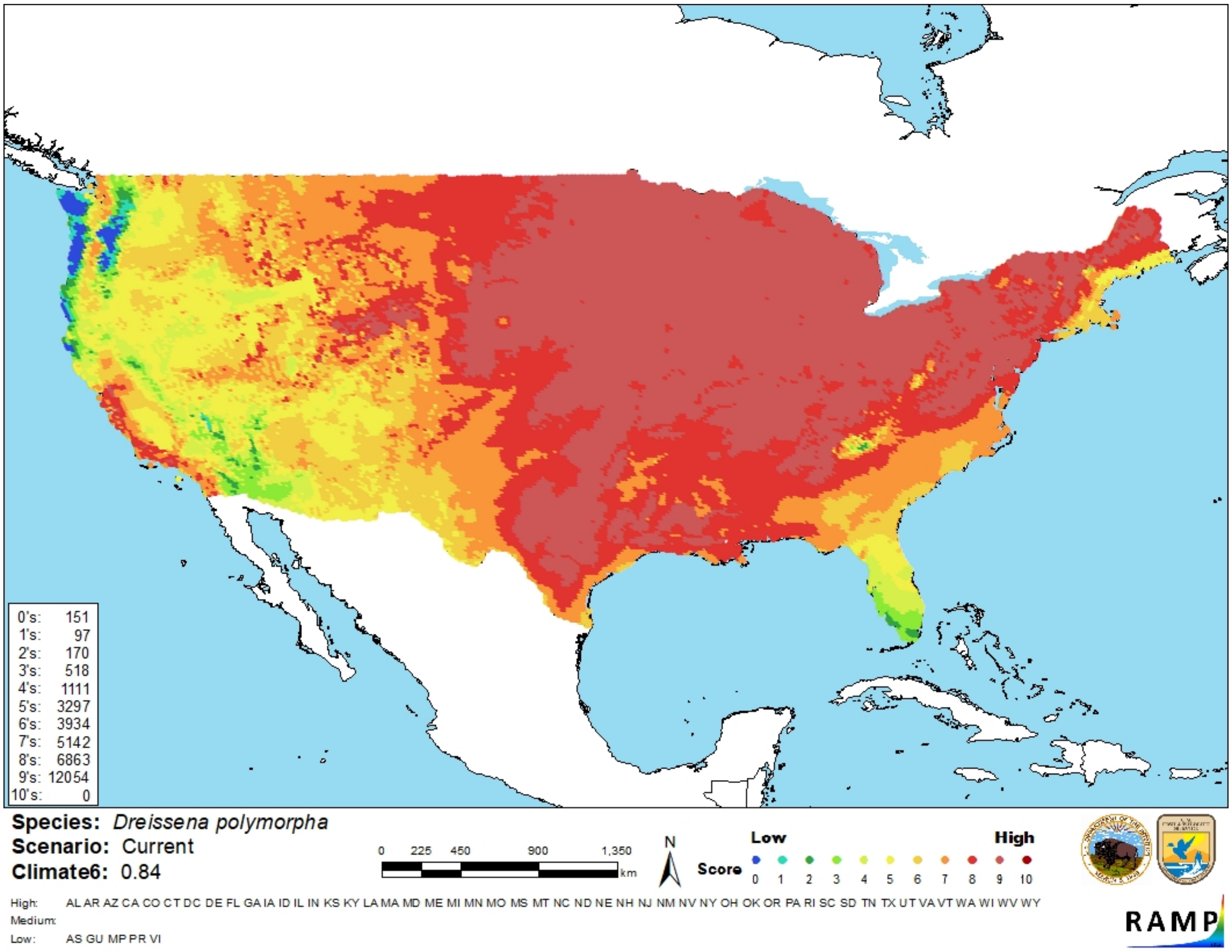

Figure 4. Map of RAMP (Sanders et al. 2018) climate matches for *Dreissena polymorpha* in the contiguous United States based on source locations reported by GBIF Secretariat (2020). Counts of climate match scores are tabulated on the left. 0/Blue = Lowest match, 10/Red = Highest match.

The High, Medium, and Low Climate match Categories are based on the following table:

Climate 6: (Count of target points with climate scores 6-10)/ (Count of all target points)	Overall Climate Match Category
0.000≤X≤0.005	Low
0.005<X<0.103	Medium
≥0.103	High

8 Certainty of Assessment

The biology and ecology of *Dreissena polymorpha* are well-known. Negative impacts from introductions and spread of this species are adequately documented in the scientific literature. No further information is needed to evaluate the negative impacts the species is causing where introduced. Certainty of this assessment is High.

9 Risk Assessment

Summary of Risk to the Contiguous United States

Dreissena polymorpha, the Zebra Mussel, is native to the Black, Caspian, and Azov Seas. This species has been introduced throughout much of Europe and North America. The introduction of this species is a serious threat to our native ecosystems, especially native mussels. It covers native shells and smothers the organism while competing for food. It alters habitats by invading and competing for space and food. Zebra mussels eat large numbers of phytoplankton which affects larval fish and their growth. The mussels can clog up pipes and attach to ship hulls. When they die, their decay can speed up corrosion. Shells are sharp and can cause injury to recreational bathers and shore users. All of these negative impacts mixed with the abundant information available on this species makes it history of invasiveness High. The overall climate match for *Dreissena polymorpha* in the contiguous United States is High with all States having a high individual Climate 6 score. This species has many currently established populations in the United States. The concern now is the rapid spread of the species. Climate match data indicates that suitable climate for *Dreissena polymorpha* exists in almost all areas of the United States. All of the information provided and the negative impacts this species has had in its introduced areas makes the certainty of assessment High and the overall risk assessment category High.

Assessment Elements

- **History of Invasiveness (Sec. 4): High**
- **Overall Climate Match Category (Sec. 7): High**
- **Certainty of Assessment (Sec. 8): High**
- **Remarks, Important additional information: No additional remarks**
- **Overall Risk Assessment Category: High**
-

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