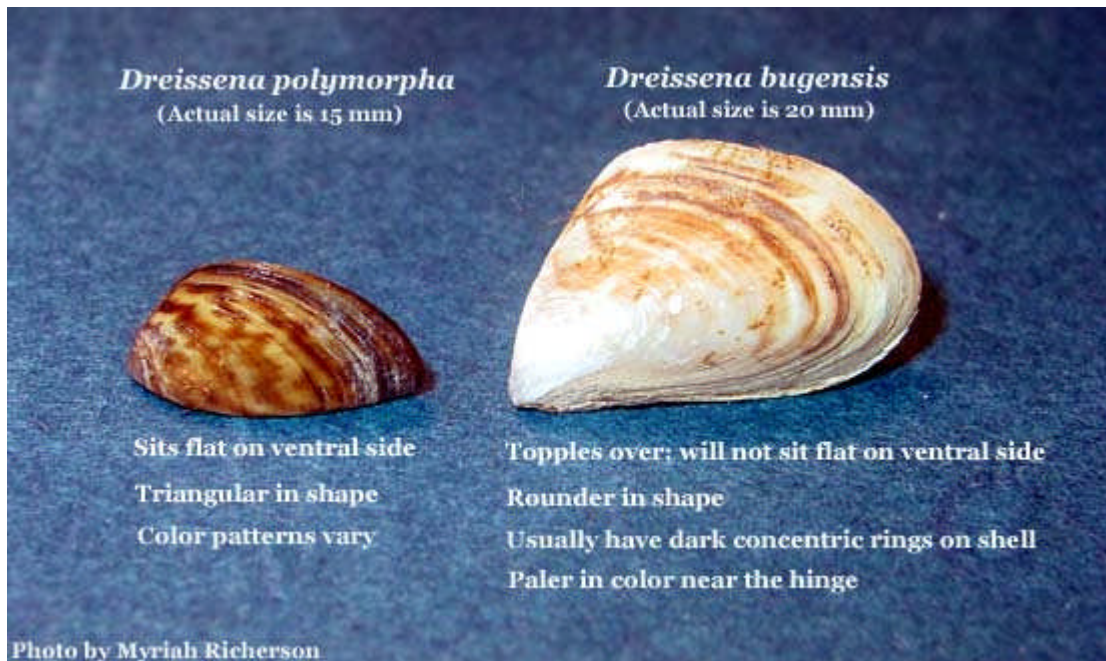


NAS - Nonindigenous Aquatic Species



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***Dreissena polymorpha* Pallas, 1769**

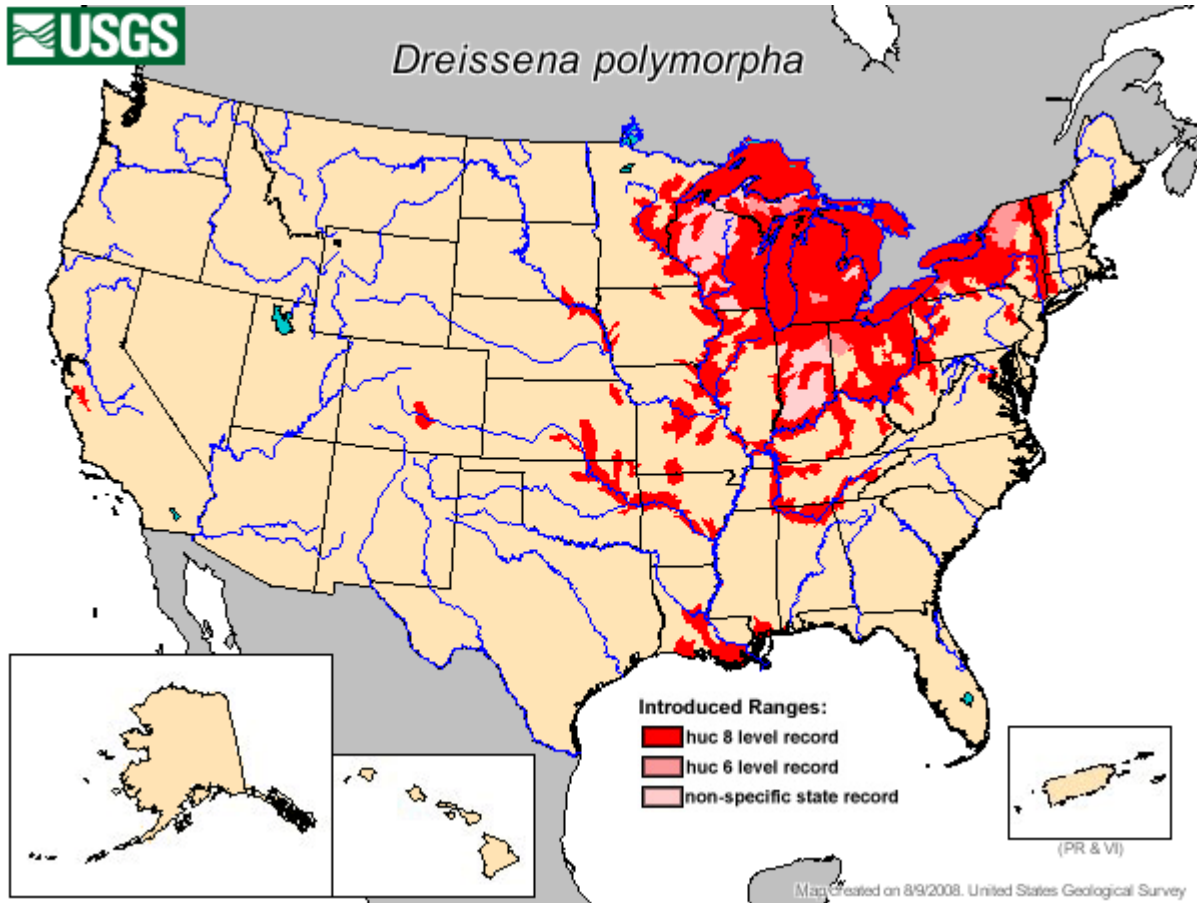
Common Name: zebra mussel

Taxonomy: available through 

Identification: Zebra mussels are small shellfish named for the striped pattern of their shells. Color patterns can vary to the point of having only dark or light colored shells and no stripes. They are typically found attached to objects, surfaces, or each other by threads underneath the shells. Although similar in appearance to the quagga mussel (*Dreissena bugensis*), the two species can be easily distinguished. When placed on a surface zebra mussels are stable on their flattened underside while quagga mussels, lacking a flat underside, will fall over. See Mackie and Schlosser (1996) for a key to adult Dreissenids.

Size: < 50 mm

Native Range: Zebra mussels are native to the Black, Caspian, and Azov Seas. In 1769, Pallas first described populations of this species from the Caspian Sea and Ural River.



Interactive maps: [Continental US](#), [Hawaii](#), [Puerto Rico](#)

Nonindigenous Occurrences:

DETAILED DISTRIBUTION MAP

By the late 18th and early 19th centuries, zebra mussels had spread to most all major drainages of Europe because of widespread construction of canal systems. They first appeared in Great Britain in 1824 where they are now well established. Since then, zebra mussels have expanded their range into Denmark, Sweden, Finland, Ireland, Italy, and the rest of western Europe. Zebra mussels were first discovered in North America in 1988 in the Great Lakes. The first account of an established population came from Canadian waters of Lake St. Clair, a water body connecting Lake Huron and Lake Erie. By 1990, zebra mussels had been found in all the Great Lakes. The following year, zebra mussels escaped the Great Lakes basin and found their way into the Illinois and Hudson rivers. The Illinois River was the key to their introduction into the Mississippi River drainage which covers over 1.2 million square miles. By 1992, the following rivers had established populations of zebra mussels: Arkansas, Cumberland, Hudson, Illinois, Mississippi, Ohio, and Tennessee. By 1994, the following states had reported records of zebra

mussels within their borders or in water bodies adjacent to their borders: **Alabama, Arkansas** (USFWS 2005), **Illinois** (USFWS 2005), **Indiana, Iowa, Kentucky, Louisiana** (USFWS 2005), **Michigan, Minnesota** (USFWS 2005; Karns 2004), **Mississippi, Missouri, New York, Ohio** (USFWS 2005), **Oklahoma** (USFWS 2005), **Pennsylvania, Tennessee** (USFWS 2005), **Vermont, West Virginia** (USFWS 2005), and **Wisconsin** (USFWS 2005; Karns 2004). More recently, **Connecticut** has been added to the list of states where zebra mussels have been found. In 2002, zebra mussels were found in a small isolated quarry in Virginia, a first for this state. During the summer of 2003, zebra mussel larvae known as veligers were collected in the Missouri River, the stretch of the river shared by both **Nebraska** and **South Dakota**. In January 2008, zebra mussels were discovered in San Justo Reservoir in central **California** (D. Norton, pers. comm.) and in Pueblo Reservoir in Pueblo, **Colorado** (V. Milano, pers. comm.).

Means of Introduction: 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, 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.

Status: They are established in all the Great Lakes, most of the large navigable rivers in the eastern United States and in many inland lakes in the Great Lakes region.

Impact of Introduction:

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.* 2001). 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 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 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 ($\mu\text{g F}$ 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 $7.42 \mu\text{m}$ ($\pm 0.13\mu\text{m}$) 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 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.* 1997). 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 be 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).

Remarks:

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 (Raikow, unpubl. data). 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 (Raikow, unpubl. data), 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 1993, Holland 1993, Pace *et al.* 1998, Idrisi *et al.* 2001).

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 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. Optimal temperature for spawning is 14-16°C. 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 downstream with the flow. 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 substratum. They then attach themselves to it by means of a byssus, an "organ" outside the body near the foot consisting of many threads. Although the juveniles prefer a hard or rocky substrate, they have been known to attach to vegetation. As adults, they have a difficult time staying attached when water velocities exceed two meters per second.

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. 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 proteinaceous 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. Once attached, the life span of *D. polymorphais* variable, but can range from 3-9 years. Maximum growth rates can reach 0.5 mm/day and 1.5-2.0 cm/year¹. Adults are sexually mature at 8-9 mm in shell length (i.e. within one year).

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-dreissenid 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. Zebra mussels attach to any stable substrate in the water column or benthos: 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, zebra mussels do not show a preference, indicating that veligers cannot discriminate between substrates (with the exception of substrate rejection due to contaminants). Research on danish lakes shows that factors exist, however, that cause substrate to be unsuitable for both initial and long term colonization: extensive siltation, some sessile benthic macroinvertebrates, macroalgae, and fluctuating water levels exposing mussels to desiccation (Smit *et al.* 1993). 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. 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).

Although discrepancy exists when comparing temperature tolerance limits of North American and European populations, this is probably 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. Eggs are released when the environmental temperature reaches 13°C and release rate is maximized over 17°C. 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. Rapid warming of shallow lakes has been hypothesized to detrimentally affect reproductive rates in Danish populations (Smit *et al.* 1993). 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. Zebra mussels can tolerate only slight salinity.

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 a wide range of salinities, from 0.6 ‰ (Rhine River) to 10.2 ‰ (Caspian Sea). North American populations generally tolerate salinity up to 4 ‰. In European populations, calcium concentrations of 24 mg Ca²⁺/l allow only 10% larval survival due to inhibition of shell development. Optimal calcium concentrations range 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. There are many methods that have been investigated to help control zebra mussels. They are listed below in no particular order. Some methods will work better than others in a particular situation.

- Chemical Molluscicides: Oxidizing (chlorine, chlorine dioxide) and Non-oxidizing
- Manual Removal (pigging, high pressure wash)
- Dewatering/Desiccation (freezing, heated air)
- Thermal (steam injection, hot water 32°C)
- Acoustical Vibration
- Electrical Current
- Filters, Screens
- Coatings: Toxic (copper, zinc) and Non-toxic (silicone-based)
- Toxic Constructed Piping (copper, brass, galvanized metals)
- CO₂ Injection
- Ultraviolet Light
- Anoxia/Hypoxia
- Flushing
- Biological (predators, parasites, diseases)

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