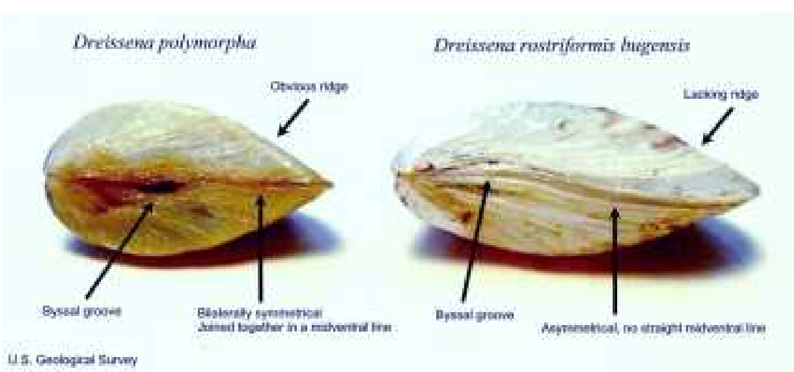
What *Dreissena* species are present in the United States?

Dreissena rostriformis bugensis is one of seven living species of *Dreissena* currently recognized in the world (Rosenberg and Ludyanskiy, 1994). The only two dreissenid mussels known to have been introduced into the US are the notorious zebra mussel (*D. polymorpha*) and the more inconspicuous quagga mussel (*D. r. bugensis*).

What are the morphological (physical) differences between the two species?

The two species can be differentiated by morphological differences of the shell. The zebra mussel has a definite angle, or carina, between the ventral and dorsal surfaces, whereas, the quagga has a rounded carina (May and Marsden, 1992). The ventral side of the shell of zebra mussels is flattened, but the quagga has a convex ventral side. This can sometimes be distinguished by placing shells on their ventral side; a zebra mussel will remain upright whereas a quagga mussel will topple over (Claudi and Mackie, 1994). Overall, quaggas are rounder in shape and zebras are more triangular. The quagga mussel also has a small byssal groove on the ventral side near the hinge and the zebra mussel has a larger groove in the middle of the ventral side. Color patterns vary widely with black, cream, or white bands; a distinct quagga morph has been found that is pale or completely white in Lake Erie (Marsden et al., 1996).

Are the two species easily distinguishable?



Sometimes the species are hard to tell apart due to considerable phenotypic plasticity of all morphological characteristics in dreissenid species that may be a result of environmental factors, meaning the same genotype may express different phenotypes to suit environmental conditions (Claxton et al., 1998). *Dreissena rostriformis bugensis* exhibits many different morphs; yet, there are several diagnostic features that aid in identification. They usually have dark concentric rings on the shell and are paler in color near the hinge. If quaggas are viewed from the front or from the ventral side, the valves are clearly asymmetrical; however, the zebra mussel shells are bilaterally symmetrical and join together in a midventral line (Domm et al., 1993).

How do *Dreissena* spp. reproduce?

Both the quagga mussel and zebra mussel are prolific breeders possibly contributing to their spread and abundance. *Dreissena* are dioecious (either male or female) with external fertilization. A fully mature female mussel is capable of producing up to one million eggs per season. After fertilization, pelagic microscopic larvae, or veligers, develop within a few days and these veligers soon acquire minute bivalve shells. Free-swimming veligers drift with the currents for three to four weeks feeding by their hair-like cilia while trying to locate suitable substrata to settle and secure byssal threads. Mortality in this transitional stage from planktonic veliger to settled juveniles may exceed 99% (Bially and MacIsaac, 2000).

How do they feed?

These mussels are filter feeders; they use their cilia to pull water into their shell cavity where it passes through an incurrent siphon and it is here that desirable particulate matter is removed. Each adult mussel is capable of filtering one or more liters of water each day, where they remove phytoplankton, zooplankton, algae, and even their own veligers (Snyder et al., 1997). Any undesirable particulate matter is bound with mucus, known as pseudofeces, and ejected out the incurrent siphon. The particle-free water is then discharged out the excurrent siphon.

Where is the quagga mussel from?

Dreissena rostriformis bugensis is indigenous to the Dneiper River drainage of Ukraine. It was discovered in the Bug River in 1890 by Andrusov, who named the species in 1897 (Mills et al., 1996). Canals built in Europe have allowed range expansion of this species, and it now occurs in almost all Dneiper reservoirs in the eastern and southern regions of Ukraine and deltas of the Dnieper River tributaries (Mills et al.,1996).

Why should we be concerned about these species?

Dreissena polymorpha, the first Dreissenid mussel introduced in North America, rapidly spread throughout many major river systems and the Great Lakes causing substantial ecological and environmental impacts. When the second dreissenid mussel, *Dreissena rostriformis bugensis*, was discovered in North America, much concern was due to limited knowledge about its possible effects and environmental tolerances. Since the quagga's arrival in North America, scientists have been conducting studies to understand the biology, ecology, and physiology of this mussel. Environmental limitations have been compared for the zebra mussel and quagga mussel, as well as for quagga mussels within and outside their native range. Zebra and quagga mussels appear to have divergent spatial distributions; zebras being primarily warm, eutrophic, shallow water inhabitants, and quaggas being shallow, warm water to deep, oligotrophic, cold-water inhabitants (MacIsaac, 1994).

When was the first quagga mussel found in the United States?

The quagga mussel was first sighted in the Great Lakes in September 1989, when one was found near Port Colborne, Lake Erie, though the recognition of the quagga type as a distinct species was not until 1991 (Mills et al., 1996). In August 1991, a mussel with a different genotype was found in a random zebra mussel sample from the Erie Canal near Palmyra, New York, and after confirmation that this mussel was not a variety of *D. polymorpha*, the new species was named "quagga mussel" after the "quagga", an extinct African relative of the zebra (May and Marsden, 1992).

What is the quagga mussel's current distribution in the United States?

The quagga mussel is currently distributed in all five Great Lakes, throughout the St. Lawrence River north to Quebec City, and in a number of inland water occurrences in New York, Ohio, Michigan, Pennsylvania, and southwestern United States. The first sighting of the quaggas outside the Great Lakes basin was made in the Mississippi River between St. Louis, Missouri and Alton, Illinois in 1995 (S. J. Nichols, pers. comm.). No others have been found in the river since then. The absence of quagga mussels from areas where zebra mussels are present may be related to the timing and location of introduction rather than physiological tolerances (MacIsaac, 1994). The quagga must have arrived more recently than the zebra based on differences in size classes, and therefore it seems plausible that the quagga is still in the process of expanding its nonindigenous range (May and Marsden, 1992; MacIsaac, 1994). In fact in 2005, the first quagga mussel was confirmed from Lake Superior in Duluth Superior Harbor (J. Kelly, pers. comm.). More recently, in January 2007, a population of quagga mussels was discovered in Lake Mead near Boulder City, Nevada (W. Baldwin, pers. comm.). Over the next several months more were discovered in Lake Havasu and Lake Mohave on the California-Arizona border (R. Aikens, pers.comm.). In March, mussels were discovered in the Colorado River Aqueduct which delivers water from the Colorado River to southern California. By the end of 2007, quagga mussels had been detected in 7 southern California reservoirs (D. Norton, pers.comm.). This was an extremely large leap in their range and cause for much concern to limited water supplies in the southwestern US.

How did they get here?

The introduction of both dreissenid species into the Great Lakes appears to be the result of ballast water discharge from transoceanic ships that were carrying veligers, juveniles, or adult mussels. The genus *Dreissena* is highly polymorphic and prolific with high potential for rapid adaptation attributing to its rapid expansion and colonization (Mills et al., 1996). Still, there are other factors that can aid in the spread of these species across North American waters, such as, larval drift in river systems or fishing and boating activities that allow for overland transport or movement between water basins. The success of overland transport of *Dreissena* species depends on their ability to tolerate periods of desiccation, and results suggest that, given temperate summer conditions, adult *Dreissena* may survive 3-5 days of aerial exposure (Ricciardi et al., 1995).

How are they impacting the environment and the economy?

Zebra mussels have caused major ecological and economic problems since their arrival in North America, and quagga mussels pose much of the same threats. Quaggas are prodigious water filterers, removing substantial amounts of phytoplankton and suspended particulate from the water. By removing the phytoplankton, quaggas in turn decrease the food source for zooplankton, therefore altering the food web. Impacts associated with the filtration of water include increases in water transparency, decreases in mean chlorophyll a concentrations, and accumulation of pseudofeces (Claxton et al., 1998). Water clarity increases light penetration causing a proliferation of aquatic plants that can change species dominance and alter the entire ecosystem. The pseudofeces that is produced from filtering the water accumulates and creates a foul environment. As the waste particles decompose, oxygen is used up, and the pH becomes very acidic and toxic byproducts are produced. In addition, quagga and zebra mussels accumulate organic pollutants within their tissues to levels more than 300,000 times greater than concentrations in the environment and these pollutants are found in their pseudofeces, which can be passed up the food chain, therefore increasing wildlife exposure to organic pollutants (Snyder et al., 1997). Another major threat involves the fouling of native freshwater mussels. Zebra mussels are known to heavily colonize any hard substrata, including native mussels and other invertebrates, causing stress and even mortality due to feeding interference, and this fouling has severely reduced populations of native mussels. Quaggas are able to colonize both hard and soft substrata so their negative impacts on native freshwater mussels and invertebrates are unclear. *Dreissena's* ability to rapidly colonize hard surfaces causes serious economic problems. These major biofouling organisms can clog water intake structures, such as pipes and screens, therefore reducing pumping capabilities for power and water treatment plants, costing industries, companies, and communities. Recreation-based industries and activities have also been impacted; docks, breakwalls, buoys, boats, and beaches have all been heavily colonized. Many of the potential impacts of *Dreissena* are unclear due to the limited time scale of North American colonization. Nonetheless, it is clear that the genus *Dreissena* is highly polymorphic and has a high potential for rapid adaptation to extreme environmental conditions by the evolution of allelic frequencies and combinations, possibly leading to significant long-term impacts on North American waters (Mills et al., 1996). Also, the colonization of deeper water by *D. r. bugensis*, exposes the quagga to a new range of environmental conditions and new habitats.

Is hybridization between the two species a concern?

Yes, hybridization between the two species is a concern. Zebra X quagga mussel hybrids were created by pooling gametes collected after exposure to serotonin in the laboratory, indicating that interspecies fertilization may be feasible (Mills et al., 1996).

Although, there is evidence for species-specific sperm attractants suggesting that interspecific fertilization may be rare in nature, and if hybridization does occur, these hybrids will constitute a very small proportion of the dreissenid community (Mills et al., 1996).

How are these mussels being controlled?

After years of infestation in Europe and North America, a chemical toxicant for lake-wide control of *Dreissena* has not been developed mainly because it would be deadly to other aquatic life forms. Prechlorination has been the most common treatment for control, but if this method is used to control both zebras and quaggas the amount of chlorine used may reach hazardous levels (Grime, 1995). Another alternative has been potassium permanganate, especially for drinking water sources, even though chemical controls are not the most environmentally sound solution. Other methods of control include: oxygen deprivation, thermal treatment, exposure and desiccation, radiation, manual scraping, high-pressure jetting, mechanical filtration, removable substrates, molluscicides, ozone, antifouling coatings, electric currents, and sonic vibration. The need to control these mussels has led to multi-million dollar spending. Some industries even built their intake structures and piping at depths too low for zebra mussel colonization; however, when the quagga mussels were discovered at lower water depths these new structures became vulnerable to quagga colonization. Biological control so far has proven to be ineffective in controlling *Dreissena* species. Predation by migrating diving ducks, fish species, and crayfish may reduce mussel abundance, though the effects are short-lived (Bially and MacIsaac, 2000). Other biological controls being researched are selectively toxic microbes and parasites that may play a role in management of *Dreissena* populations (Molloy, 1998). Other prospective approaches to controlling *Dreissena* populations may be to disrupt the reproductive process, by interfering with the synchronization of spawning by males and females in their release of gametes (Snyder et al., 1997). Another approach would be to inhibit the planktonic veliger from settling, since this is the most vulnerable stage in the life cycle (Kennedy, 2002). Researchers are continuously studying these species to learn more about their life cycle, and environmental and physiological tolerances, with hopes of developing environmentally safe controls that can be used to control *Dreissena* populations.

Do quagga mussels colonize deeper waters than zebra mussels?

D. r. bugensis lacks the keeled shape that allows *D. polymorpha* to attach so tenaciously to hard substrata; though, *D. r. bugensis* is able to colonize hard and soft substrata (Mills et al., 1996). The ability to colonize different substratas could suggest that *D. r. bugensis* is not limited to deeper water habitats and that it may inhabit a wider range of water depths. In the Great Lakes, there are reports that the quagga mussel is colonizing at shallower depths, supporting the idea that the quagga can occupy a wider range of depths (Mills et al., 1996). Quagga and zebra mussels have been found to coexist at lower depths in Lake Ontario, but in Lake Erie as the water depth increased *D. r. bugensis* outnumbered *D. polymorpha* 14 to 1, suggesting that this species is a cold-water form of dreissenid (Mills et al., 1996). *Dreissena rostriformis bugensis* has been found at depths up to 130 m in the Great Lakes, but is only known to exist in its native range from depths 0-28 m and the depths at which both species of *Dreissena* are found in Lake Ontario are the deepest ever recorded for this genus (Mills et al., 1996; Claxton and Mackie, 1998). The higher abundance of *D. r. bugensis* in deeper waters in North America is consistent with its native range; however, over time *D. r. bugensis* began to displace *D. polymorpha* at all water depths, eventually almost completely taking over in the Dneiper River systems (Mills et al., 1996). Over the past few years, this similar shift in dreissenid dominance has occurred in the Lower Great Lakes, especially in Lake Erie and Lake Ontario, where one study found that a once dominated *D. polymorpha* shallow area in Lake Erie is now 61% *D. r. bugensis* (Adrian et al., 1994). Patterns of colonization and population dynamics in Ukraine and North America indicate that *D. r. buge*nsis is not limited to deep-water habitats.

Is salinity a limiting factor?

Another possible limiting factor is salinity. Quagga mussels are usually found in fresh water in salinities up to 1ppt; they can reproduce in salinities below 2 ppt, and are killed by salinities exceeding 6 ppt (Setzler-Hamilton et al., 1997). North American comparisons of salinity tolerances for both species of *Dreissena* revealed that neither species could survive salinity levels greater than 5 ppt; however, *Dreissena* in Ukraine, show greater acclimation to salinity extremes than in North America, possibly attributed to experiencing more generations in the native range, compared to the more recent colonization in North America (Mills et al., 1996). Salinity tolerances in zebra and quagga mussels increase with larval age, however, both species are negatively affected as embryos by salinities of 4 ppt and beyond with *D. polymorpha* embryos and larvae demonstrating a higher degree of salinity resistance than *D. r. bugensis* embryos and larvae (Wright et al., 1996).

Do these mussels have different temperature tolerances?

Observations and research suggest that the North American quagga mussel is a cold deep-water form, contrasting with Ukraine populations where *D. r. bugensis* thrives at higher temperatures. In North America, *D. polymorpha* survives indefinitely at 30^oC, but *D. r. bugensis* exhibits high mortality at this same temperature; however, Dneiper River populations indicate that *D. r. bugensis* exhibited lower mortality at elevated temperatures compared to *D. polymorpha* (Mills et al., 1996). Although there are indications that quaggas die at lower temperatures than zebra mussels, there are a few exceptional quaggas that are as tolerant of elevated temperatures as zebra mussels, so the potential thermal range of this species may be higher than recent experiments indicate (Mills et al., 1996). The critical thermal minimum temperature is not known for these species, but there are reports that *D. r. buge*nsis is colonizing waters in North America with a relatively constant low temperature (4-9^oC) (Claxton and Mackie, 1998). Temperature is also a key factor affecting spawning and fertilization in dreissenid mussels. A minimum spawning temperature of 12^oC has been reported for *D. polymorpha* compared to 9^oC spawning temperature for *D. r. bugensis*, which suggests that *D. polymorpha* cannot successfully colonize hypolimnial waters, although they have been reported to survive in the hypolimnion, they cannot reproduce there (Claxton and Mackie, 1998). A female quagga mussel with mature gonads was found in Lake Erie at a temperature of 4.8^{o}C, so areas that were thought to be immune to dreissenid colonization may become infested by *D. r. bugensis* (Claxton and Mackie, 1998).

Are the zebra mussel and quagga mussel to blame for the "dead zones" in Lake Erie?

Scientists have found mysterious dead zones, areas without oxygen, in the central basin of Lake Erie, in which *Dreissena* species may be partly to blame. High phosphorus levels are present once again in Lake Erie, despite controls for chemical pollution. Researchers suspect biological pollution is the reason behind these increases in phosphorus and algae. The dead zones are created when too many nutrients are present, causing algae blooms, followed by die-offs, and as the material decays, oxygen is consumed, producing an oxygen-depleted environment, where no aquatic plants or organisms can survive. *Dreissena* mussels filter organic material from the water and expel the phosphorus in their pseudofeces. The dead zones are located at depths below 40 feet and it is unclear what is causing these dead zones, however, researchers are currently studying these zones to figure out why this is happening.

Are zebra mussels edible?

Most clams and mussels are edible, but that does not mean they taste good! Many species of fish and ducks eat zebra mussels, so they are not harmful in that sense. Zebra mussels are so small and do not have much in the way of "meat" inside them, you would have to be pretty hungry to want to eat them. However, because they are filter feeders, they can accumulate pollutants in their tissues that may not be healthy for people to consume. You should contact local public health officials to learn whether it is safe to eat mussels or fish from a specific waterbody. Therefore to be safe, it is not recommend they be eaten by people.

Source: U.S. Geological Survey, June 2017

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