

Zebra Mussels in Western Europe and North America

Cautionary Tale

In a cautionary tale from the nineteenth-century Holland, a poor lockkeeper was faced with additional hardship when masses of mussels suddenly colonized the locks and prevented their operation. Removal of the mussels required hard work and was very time-consuming, and he suffered numerous, easily infected cuts. The poor man had to hire a helper, whom he could barely afford to feed. His luck changed, though, when he discovered that the chickens on his tiny farm, adjoining the locks, eagerly ate the small mollusks and that he, with an unlimited source of free food for them, could thus raise them in large numbers. In the end, he became a wealthy egg producer.

The story is told as one of a blessing in disguise, but there is far from being a consensus that zebra mussels qualify as such.

The Mussel in Its Native Habitat

The **zebra mussel** (*Dreissena polymorpha*) is a small freshwater **mussel** originating in lakes and rivers in Southern Russia. The name zebra mussel derives from the stripes on its triangular shells, although this color pattern is not always prevalent. They are filter feeders and attach themselves to hard substrates with strong byssus threads emanating from their umbo on the hinged side. They often form large colonies with mussels attached to one other, much like *Mytilus* mussels in the marine environment. Densities measured in thousands per m² are common [1], but tens of thousands are not rare, and one study reported as many as 114,000/m². The individual mussels are generally small, 1–2 cm in length, but they can grow up to 5 cm. Their biomass varies as a function of density, size, and condition and is mostly within the range of 0.2–20 kg/m². Their lifetime is relatively short, typically 3–8 years.



Close-up of a typical shell of a zebra mussel (Photo from Wikipedia). http://en.wikipedia.org/wiki/File:Dreissena_polymorpha3.jpg



Live zebra mussels underwater with shells open, animals respiring, and siphons visible (Photo from Wikipedia)

Dependent on the size of the mussel and water temperature, a zebra mussel will filtrate 1–5 L of water a day, consuming what it finds edible and depositing feces and nonfood particles covered in mucus, so-called pseudofeces, on the bottom. Sexual maturation of zebra mussels can occur early, and cases have been reported in which, before they have been settled for 2 months, they already release eggs and sperms [2]. Normally, however, they start doing that in the second year at a size of just under a centimeter.

An adult female can produce million eggs in a year and over five million in her lifetime. Veligers, the tiny, free-swimming larvae of the zebra mussel, will settle onto any hard surface within a week or two of birth. They have some tendency to swim against the current, but are largely carried along with it [3]. Other authors have made much lower estimates of the fecundity of the zebra mussel females, giving 150,000 eggs in a year as a high.

Small zebra mussels have a number of predators in their area of origin. Fish such as sturgeon, catfish, carp, and eel feed on them, as do many species of birds and crayfish.

Copepods such as *Cyclops* also feast on veligers.

The zebra mussel is a freshwater species but tolerates salinities up to 6 PSU (or per mile). Its natural habitat includes brackish water areas of the Caspian and Black Seas.

The Spread to Western Europe

In the eighteenth century, a number of canals were dug to connect Russian rivers going to the Caspian Sea with those emptying into the Black Sea. Later, the canal system was extended further westward and connected to those in Central and Western Europe. The canals and the rivers they connected became the first steps along the route of the zebra mussel's westward spread. They were found in Hungary and Slovakia in 1794 [4], only a quarter of a century after it was first described by Pallas from specimens collected in the Ural, Volga, and Dnieper Rivers. Grossinger, at the time he found the mussel in the Danube basin, did not think of it as an invasive species, but in Rotterdam, the Netherlands, it was very much seen as such when it appeared there in 1827, particularly when it started to interfere with the operation of sluices [5].

The concept of a more western native distribution range of the zebra mussel is, however, not without modern subscribers. The December 2014 issue of the journal *Water Technology* states that "They were originally found in the Balkans, Poland and the former Soviet Union" [6]. Most scholars, however, see the Caspian and Black Sea drainage areas as the native home of the zebra mussel and some only the former.

Already prior to its detection in the Netherlands, the zebra mussel had started its conquest of the British Isles, starting in Cambridgeshire in the early 1820s, reaching London in 1824, Yorkshire in 1831–1833, the Forth and Clyde Canals in 1833, and the Union Canal, near Edinburgh, in 1834 [7, 8].

Obviously, the zebra mussel is much more likely first to have reached England on board a ship rather than attached to the exterior of one, as their saltwater tolerance probably is not high enough for them to have survived the Channel crossing otherwise. Similarly, it is likely that the mussel had reached Lake Mälaren and Sweden with ballast water, or otherwise on board a ship, when it was first spotted there a 100 years later.

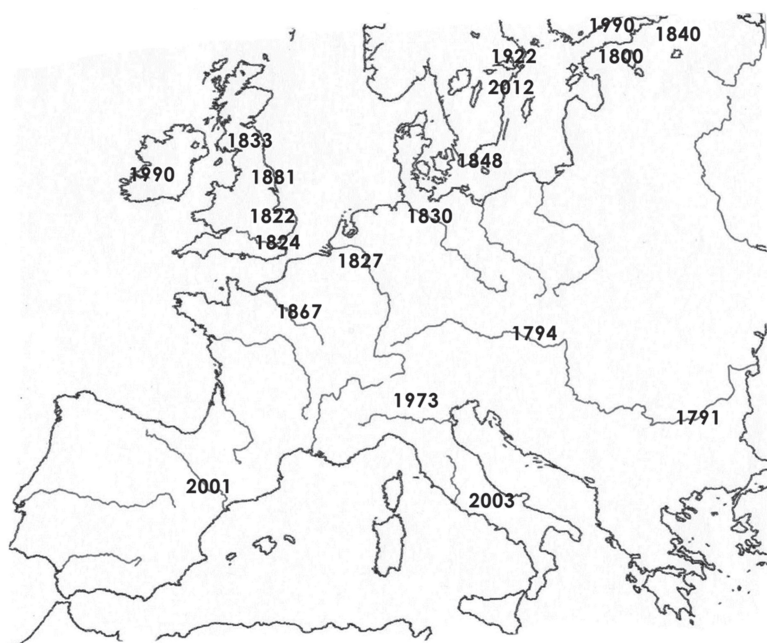
By that time, the zebra mussel had long since taken over the European canal system and was common over most of Germany and France. Hamburg had been reached already in 1830, Copenhagen in 1840 [9] and the river Seine outside of Paris in 1867.

To the Mediterranean parts of Europe, the zebra mussel arrived much later. In Italy, they first appeared in Lake Garda in the north in 1973 [10] and in Tuscany in the central part in 2003 [11, 12]. In Greece, they were first reported in the early 1980s [13].

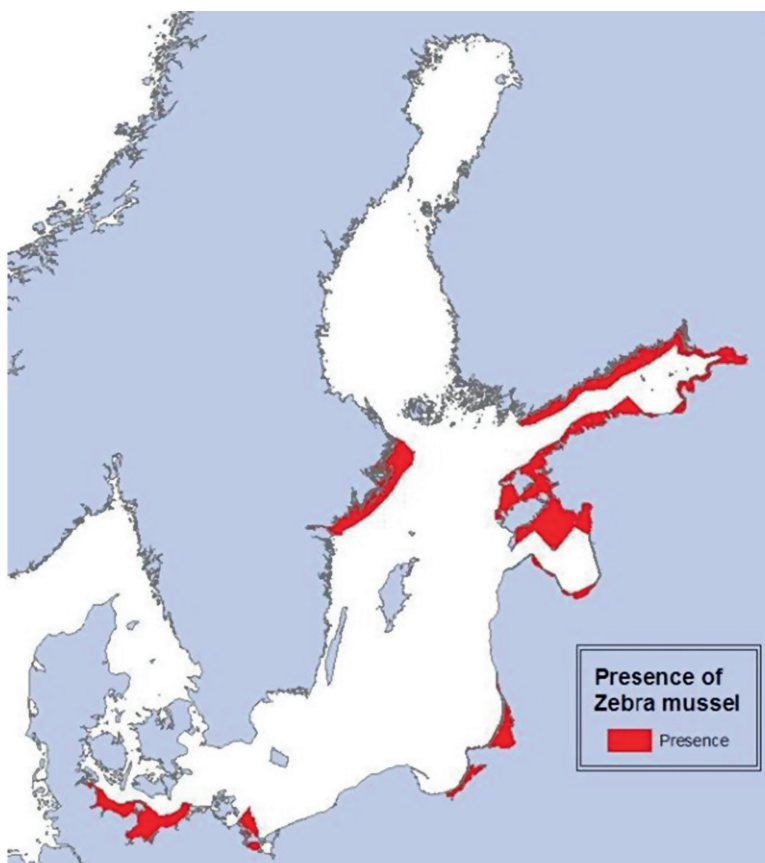
In Spain, the first populations were detected in 2001 in the Flix reservoir, from where they gradually spread until fully colonizing the Ebro basin. Four years later was found in the Sitjar reservoir on the river Mijares [14].

In the more remote areas of Northern Europe, the zebra mussel also arrived later. In the Shannon estuary in Ireland, they appeared in the 1990s, some 170 years after reaching England, and spread throughout the Shannon and Shannon-Erne catchments [15]. To Finnish territorial waters, the zebra mussel came in the 1990s, after having been present in the nearby large Russian Lake Ladoga for 150 years and in Estonia for a similarly long time [16, 17].

The invaded areas of Western Europe also include some other brackish parts of the Baltic, as well as estuaries in the North Sea and Irish Sea. Here, the densities are mostly much lower than in freshwater, and in competition with the *Mytilus* species, *Dreissena*, the zebra mussel loses out as soon as salinity is high enough to support those other marine organisms.



The spread of zebra mussels in Western Europe



The presence of *Dreissena polymorpha* in different coastal areas in the Baltic (source: HELCOM List of non-indigenous species). Note that the distribution in the Gulf of Riga and Swedish Baltic Proper is limited to more freshwater parts

Effects of the Zebra Mussel in Newly Invaded Waters in Western Europe

In West European freshwater systems, the zebra mussel represents a new type of organism due both to the high population densities in which it occurs in suitable habitats and to its filter-feeding mechanism, which relocates nutrients from the water mass to the bottom, thereby depleting the pelagic and enriching the benthic community. Clearer water also allows sunlight to penetrate deeper, thereby extending the reach of attached algae and rooted plants.

Native freshwater mussels in the genera *Anodonta*, *Unio*, and *Margaritifera* have much lower population densities, live much longer, and reproduce more slowly and in a complicated fashion (the larvae during each stage are parasites of different fish species). Several of the species are rare and even threatened by extinction in many or most countries. They also live by filtering water, but have little effect on the nutrient relocation due to their smaller numbers and biomass. The invading zebra mussel affects these native mussel species negatively in two ways: They outcompete them for food, and they overgrow them, thereby hindering their movements, and may even bind them with their byssus threads to the point to which they cannot open or close their shells.

The effects of zebra mussels on phytoplankton communities and on particle deposition rates have been the subject of many studies, for example, on Russian canals and water reservoirs and Polish lakes. Generally, a much increased deposition rate, a substantial reduction of phytoplankton, and a more light penetration have been reported [1, 7].

A meta-study based on 47 underlying reports concluded that the introduction of *Dreissena* generally was associated with increased benthic macroinvertebrate density and taxonomic richness. The effects were positive on the densities of scrapers and predators, particularly leeches (*Hirudinea*), flatworms (*Turbellaria*), and mayflies (*Ephemeroptera*) and also had strong positive effects on gammarid amphipods. Gastropod densities also increased in the presence of *Dreissena*, but large-bodied snail taxa tended to decline, as did sphaeriid clams and other large filter feeders and burrowing amphipods (*Diporeia* spp.) [18].

In a study in the slightly brackish waters (1 PSU) of the western part of the Szczecin Lagoon in Poland, it was found that the fauna of macrozoobenthos, comprised primarily of oligochaetes and chironomids, increased with a factor of 2.4–4.9 near the zebra mussel beds when compared to more remote localities with similar sediment structures. Chironomids, oligochaetes, and *Gammarus* amphipods were particularly favored [19].

With regard to human technical installations in water, the zebra mussel has caused significant damage. In populating supply pipes, they reduce water flows. They damage boats, engines, fishing gear, buoys, locks, and docks and turn bathing beaches into foot- and hand-cutting underwater torture fields.

After Their Introduction, What Happened Next in Western Europe?

The typical picture, repeated many times over in Russia, continental Northern Europe, Britain, Sweden, and, more recently, in Ireland and Spain, is that once established in a water system, the zebra mussel will spread throughout it. This spread will be particularly fast where boat traffic is intensive, as it is in canal systems. In this initial phase, mussel densities will also be extremely high, but after some years, densities decrease and more or less stabilizes at much lower levels [1, 20, 21].

In this context, a special double interaction between zebra mussel and crayfish has been noted. On one hand, crayfish eat (small) mussels and reduce population densities [1, 22, 23].

On the other hand, zebra mussels settle on crayfish and may impair their mobility and feeding possibilities [24].

Studies in Polish lakes have shown that roach, with their strong pharyngeal denticles, adopt to feed almost exclusively (95–100%) on zebra mussels and that their predation impact may become significant [3, 25].



Crayfish covered with zebra mussels.

Photo jpeg mcarp

When zebra mussels are present in a water system, even as natural and human-induced mechanisms for further overland spread to nearby water systems of both veligers and adult mussels can easily be imagined, these mechanisms appear to be relatively ineffective. In Sweden, for instance, the zebra mussel was introduced to Lake Mälaren in the 1920s, but some 80 years passed before they were found to inhabit another freshwater system, the Göta Kanal, despite a low-level presence in the Baltic archipelago to which both systems are connected [26].

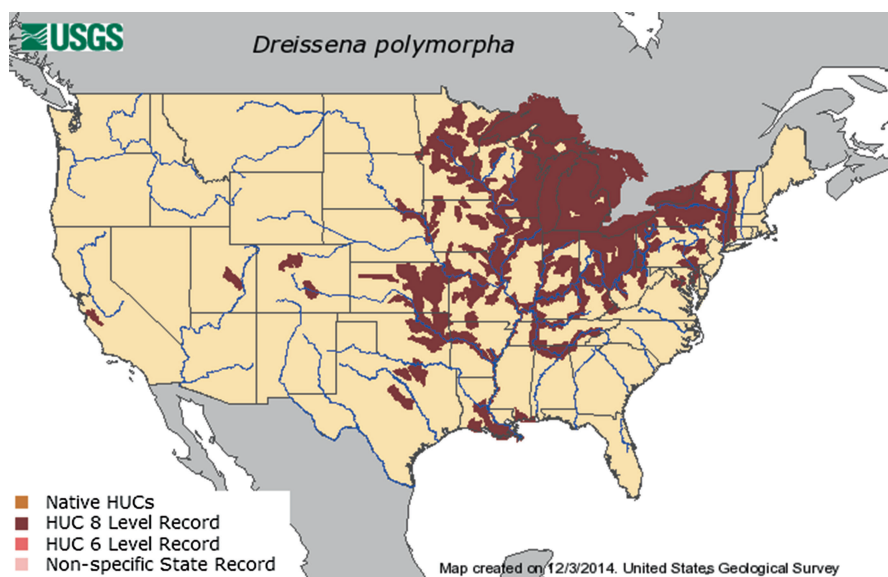
The European attitude to the zebra mussel is not all negative. Most of Europe's inland waters have been affected by eutrophication. Increased nutrient loads, most importantly of phosphorus, have led to increased phytoplankton densities, more turbid waters, anoxic bottoms, diversity losses among aquatic plants, and a shift in fish populations. Environmental measures since the 1970s have reduced but not eliminated these problems. The presence of zebra mussels in many ways counteracts the effects of eutrophication and in some respects restores water bodies to the status they had some 100–150 years ago, which also has a positive effect on shoreline property values. This has in turn led to proposals and experimental attempts to deploy the zebra mussel for restoration of overfertilized bodies of water.

The Spread to North America and Further Invasion There

In North America, the zebra mussel was first found on the Canadian side of Lake Erie in 1988. It is assumed to have arrived with ballast water of an ocean-going vessel that entered the Great Lakes system through the Saint Lawrence Seaway. Given the size of the population and of the individual mussels, it was concluded that the introduction must have taken place some years earlier, probably in 1985 or 1986. By 1990, it had spread to all of the Great Lakes, with especially dense populations in Lake Erie and Lake St. Clair. As some river systems are connected to the Great Lakes and/or one other via canals, the zebra mussel was able quickly to expand its territory, and within less than a decade of its arrival, it was present in the Arkansas, Cumberland, Hudson, Illinois, Mississippi, Ohio, and Tennessee rivers.

Contrary to Western Europe, where zebra mussels did not easily spread from one water system to another, their progress seems to have gone faster in North America—although whether with the help of humans or as hitchhikers on other biota is a matter of sometimes intense debates. Thus, in the following years, the invaders appeared in a number of new places, e.g., in Connecticut in 2001; in a small, isolated quarry in Virginia in 2002; as veligers in the Missouri River in Nebraska and South Dakota in 2003; and so on. More recently, in 2008, they were found in the San Justo Reservoir in Central California and in Colorado, in the Pueblo Reservoir and Pueblo River and in Grand Lake, 50 miles northwest of Denver. Populations in Lake Texoma on the border of Texas and Oklahoma and in western Massachusetts were found in 2009, and zebra mussel veliger was discovered in North Dakota's Red River in 2010 [27].

By March 2014, the zebra mussel had the US distribution shown on the map below and had also entered Canadian freshwater systems in Manitoba (Lake Winnipeg), Quebec (Richelieu River), and Ontario (Lake Muskoka).



Ecological Effects of the Zebra Mussel in North America

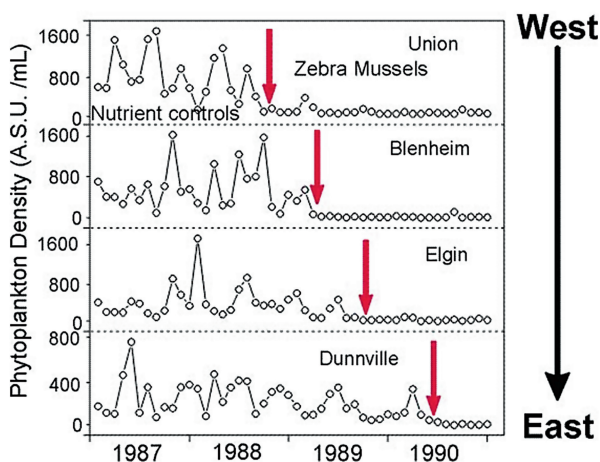
The Great Lakes

Phytoplankton

Initial Effects

A large number of studies were performed to determine the ecological effects of the zebra mussel in the Great Lakes, particularly in Lake Erie in which the species became established in the late 1980s and where it quickly came to dominate that lake's benthic community. The first effects were captured by the many monitoring programs in place since the 1970s, when reducing nutrient loading and algal blooms first became an environmental priority. These found that Secchi disk transparency increased 100% or more and that phytoplankton densities decreased by some 90% [28].

Effects of Zebra Mussels on Phytoplankton in Lake Erie



Also measured as chlorophyll A, the reduction of microscopic algae was dramatic. In the western basin (at the Union water intake), where summer concentrations averaged $6.3 \mu\text{g/L}$ during a 4-year pre-zebra mussel time period and the average value declined to $1 \mu\text{g/L}$ during a 4-year post-zebra mussel time period. Total phosphorus and total nitrogen also went down, phosphorus by the most, however, which resulted in a doubling of summer total N to total P ratios after the arrival of zebra mussels [29]. That report was based on monitoring data from Dr. Ruth Holland Beeton. So another report using data from an area near the Stone Laboratory on Lake Erie said that water transparency was about a meter in the 1970s, before

phosphorus abatement programs began, and improved to 2–3 m in the 1980s after a decade of reduced phosphorus inputs. Water transparency continued to improve, to 3–6 m, after zebra mussels colonized the area [30].

A study quantifying phytoplankton production and zebra mussel algae removal in Lake Erie in 1990 found that the zebra mussel population consumed 5.0 million tons of phytoplankton, while a further 1.4 million tons of phytoplankton were captured and deposited as pseudofeces. Thus, a total of 6.4 million tons of phytoplankton were removed from the water column by zebra mussel in western Lake Erie during that year. As primary production was estimated to be 24.8 million tons, zebra mussel removed the equivalent of 26% of the primary production for western Lake Erie [31].

The exact figures differed between studies and between the lakes and lake basins in the Great Lakes region, but overall, the pattern was the same—a dramatic decrease in planktonic algae and increased water clarity following the introduction of the zebra mussel.

Subsequent Development

From the mid-1990s, the trend of low algal standing stocks during summer was reversed with the appearance of toxic *Microcystis* blooms. A large study, supported in part by the Lake Erie Protection Fund, was undertaken to explore hypothesized mechanisms of *Microcystis* bloom creation by zebra mussels using statistical and dynamic modeling. The ensuing results supported the idea that zebra mussels, through selective feeding and nutrient excretion and by avoiding the toxic *Microcystis*, promoted blooms in both Saginaw Bay, Lake Huron, and Lake Erie [32].

I have some reservations, based on my own experience with zebra mussels, about these conclusions. In connection with a project to test whether the zebra mussel could be used to treat water from fish farms before its release, we also tested how the mussel handled blue-green algae. So did Vanderploeg et al. [33] and we found, like they did, that (most of) the cyanophytes were not consumed but excreted with the pseudofeces. However, in our tests, the algae were not unharmed, but covered with mucus, and stuck together in sediment-bound lumps, effectively preventing them from returning to the water mass. Further, they and we found that nutrient recycling from zebra mussels increased the N/P ratio (in line with the Lake Erie results in [29] above). As blue-green algae with nitrogen fixation abilities are especially competitive when phosphorus levels are high and nitrogen levels are low, this result shows, in my understanding, it to be less, rather than more, likely that a *Microcystis* bloom is induced when zebra mussels are present in high numbers.

Zooplankton

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. 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 and Lake Huron [34].

Benthic Fauna

Initial Effect

The bottom fauna represented the mirror image of the planktonic community. In a comparison between two studies undertaken with the same methodology, in the same area of western Lake Ontario, one pre- and one post-*Dreissena* found that in 1991–1992, the zebra mussel accounted for 93% of the macroinvertebrates (insects, crustaceans, worms, and mollusks) collected, replacing the sideswimmer (*Gammarus fasciatus*) as the numerically dominant taxon, a place the amphipod held in 1983. Although the number of sideswimmers was also significantly higher, the sheer number of non-*Dreissena* macroinvertebrates was many times greater in 1991–1992 than in 1983, skyrocketing from 127–1159/m² to 1316–5267/m². Other taxa with great increases in numbers were annelid worms (*Manayunkia speciosa*, *Spirosperma ferox*) and unidentified tubificids, gastropod snails (*Helisoma anceps*, *Physa heterostropha*, *Stagnicola catascopium*, *Valvata tricarinata*, *Goniobasis livescens*, *Ammicola limosa*), insects of the order Trichoptera (*Polycentropus* sp.), and the decapod crayfish (*Orconectes propinquus*). No taxon was less abundant in 1991–1992 than in 1983 [35, 36].

The study concluded that:

“by occurring in large clumps and filter-feeding intensively, *Dreissena* may benefit other macroinvertebrate taxa in Lake Ontario by increasing the complexity of benthic substrate and by increasing the flow of energy to benthic environments. While some factors (e.g., increased water clarity due to *Dreissena* biofiltration and phosphorus abatement programs) may be acting synergistically to favorably impact benthic organisms, biodeposition by *Dreissena* may keep benthic food resources at high levels despite overall declines in fertility of the Lake Ontario ecosystem.” [37]

Similar population changes were reported by scholars who studied the impacts of the zebra mussel on benthic macroinvertebrates in Lake Erie and Lake St. Clair at about the same time.

A group of benthic organisms that suffered heavily from the zebra mussel invasion, however, was the native unionid mussel. Zebra mussels readily colonize clam shells, disrupting feeding, movement, and reproduction. The otherwise long-lived clams generally die within 1–2 years after infestation. This die-off has been well

documented in the Great Lakes [38, 39], with near total mortality reported throughout most of western Lake Erie.



Many zebra mussels attached to a native mussel (Photo from Minnesota Department of Natural Resources)

Subsequent Development

However, in 1996, a large population of native clams was discovered in a western Lake Erie wetland, Metzger Marsh [37], and subsequently more populations were detected, mostly in shallow waters in which the zebra mussel does not thrive. In an interview, one of the active scientists, Dr. Dave Zanatta, gave an account of the development timeline:

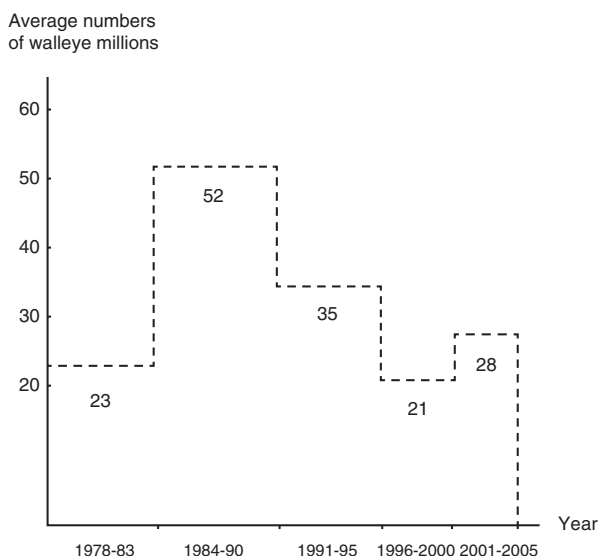
“Native mussels were already threatened by pollution. Once zebra mussels arrived, they were nearly extirpated. Come the late 1980s and early 1990s, all the native mussel populations crashed in Lake St. Clair, Lake Erie and the Great Lakes in general. Average density of native mussels before the arrival of zebra mussels was two per square meter in Lake St. Clair. By 1990, zebra mussel density was at 1,600 per square meter.

By 1992, native mussel populations are almost gone from the southeastern portion of the lake and declining rapidly in the northwestern portion of the lake. By 1994, there were almost no native mussels left in the lake, with zebra mussels now at 3,000+ per square meter. But there was reason for hope. Remnant populations of native mussels were beginning to be found in coastal wetlands in western Lake Erie in the late 1990s. In addition, zebra mussel populations started showing dramatic declines between 1994 and 2001 in Lake St. Clair, even though their sheer numbers remained staggering.”

“In expanded research funded through the Great Lakes Restoration Initiative, we found that the St. Clair Delta and western Lake Erie were the most healthy areas of the lakes in terms of native mussel abundances. Most of the 124 sites he investigated contained more than five unique species of native mussel. The native mussels appear to prefer very shallow water, less than two meters deep, with soft sediments, fluctuating water levels, good wave action and the fast water flow in the Delta, all of which curb the spread of zebra mussels and help make them available to predators.” [40, 41]

Fishes

There are a large number of articles postulating that fish that largely feed in the pelagic zone, such as the walleye, will suffer, both as the organisms on which they feed are depleted and as their spawning grounds are taken over by zebra mussels. There is, however, hardly any factual data that show such a decrease. In fact, the spawning ground argument has been contradicted by observations in the Great Lakes of walleye successfully spawning over zebra mussel beds [42] and evidence that the peak of the walleye population in the period 1979–2005 partly overlapped with the peak density of zebra mussels.



Walleye population (2+) in Lake Erie from 1978 to 2005. Based on data from the Detroit River-Western Lake Erie Basin Indicator Project [43]

Other fish species, such as smallmouth bass and yellow perch that rely more on benthic organisms for food, have in line with forecasts benefitted from the bottom fauna enrichment provided by the zebra mussel and have also gradually increased consumption of the mussel itself as part of their diets. In Lake St. Clair, the yellow perch population rose in the late 1980s and 1990s, as did the smallmouth bass population of Lake Erie [44].

In the Huron River, the increase in the smallmouth bass has been attributed to the increase in benthic macrophytes, following increased water transparency, providing suitable places for spawning and for fry growth and development [45].

Lake sturgeon, freshwater drum, catfish, and all sunfish species also feed heavily on zebra mussels. Some migratory ducks have even changed their migration stopover habits so they can feast for some days on the zebra mussel beds [46].

The Quagga Mussel, Dreissena rostriformis bugensis

The quagga mussel is a close relative of the zebra mussel. Quagga was the name of a subspecies of African plains zebra, extinct since the nineteenth century, with pale brown and white stripes mainly on the front of the body and solid brown on the rump. The quagga mussel was named precisely for this pattern of colorization (although those in Lake Erie are pale or white and have no stripes) and its close relation to the zebra mussel. The quagga mussel came from the Dnieper River drainage area in Ukraine, an area neighboring that of the zebra mussel, and in most respects, the two species are quite similar.

The quagga mussel came to the Great Lakes through the same route as the zebra mussel, namely, in ballast water. In Lake Erie, it was first collected in 1989, near Port Colborne, Ontario, but was not identified as a different species from the zebra mussel until 2 years later.

Like the zebra mussel, the quagga mussel spread throughout the Great Lakes system and beyond, but the spread was slower, and it has not yet reached the same distribution.

On the other hand, in the part of the Great Lakes, notably Lake Erie and Lake St. Clair, to which the two *Dreissena* species first came, the quagga mussel has now taken over and totally dominates: a study in Lake Erie from 2004 revealed a drop in total *Dreissena* density with 50% compared to 4 years earlier, to some 4000 individuals/m², but noted that about 97% were quagga mussels [47].

The ecological and economic effects of the two species are very similar.

Also in Western Europe, the quagga mussel has followed in the footsteps of its zebra mussel cousin, but it started a century later. Only in the 1940s did it start the spread from its Dnieper River native area, and up to the 1980s, the westward advance was slow. Since then, the speed has been higher and is now present in a large part of the waters of Continental Europe. Once in a water system, the zebra mussel quickly colonizes it and reaches the peak density within 1–4 years. For the quagga mussel, it takes 6–19 years [48].

In the Dnieper River basin, where the species coexist, the dominance shifts between areas and years. In water bodies invaded by both species, *D. polymorpha* generally has the upper hand in those with no or only a small profundal zone, especially in the shallow areas, while *D. rostriformis bugensis*, after a decade or more, dominates where the profundal zone is large.

Hudson River

The zebra mussel was first found in the Hudson River estuary in May 1991. The population grew extremely rapidly and had reached an average density over the freshwater tidal river of 4000/m² within 18 months. With an estuarine surface area of 135 km², this means a staggering 550 billion individuals. They constituted more than 70% of the zoobenthic biomass and almost exclusively lived on sub-tidal rocks.

After the rapid population growth in 1991–1992, their reproductive success fell four orders of magnitude in 1993–1994, and the young of the year were small, only 20–30% of the size of those in 1991 [49]. In all likelihood, the adult zebra mussels outcompeted the larvae for food or just cannibalized a major part of the veligers.

Phytoplankton biomass declined 85% following mussel invasion in the Hudson River [50]. The total biomass of zooplankton declined 70%, due both to a reduction in body size of large zooplankton and a reduction in abundance of microzooplankton, the first as a result of less phytoplankton to feed on and the latter from direct predation by the zebra mussels [51].

A decade later, the situation was very different. The number of mussels was still very large, but their dry biomass (without shells) had gone from 3000 tons to a small fraction thereof, as there were few individuals over a year old. Since the filtering capacity of adolescents, both with regard to volume and to particle size, is much smaller than of adults, this allowed zooplankton such as *rotifers* to return to almost pre-zebra mussel invasion densities of about 1000 individuals per liter in the summer. The main reason for this dramatic change in the zebra mussel population was that blue crabs (*Callinectes sapidus*) that migrate into the estuary in the late summer consumed the adult zebra mussels and over the time period of a decade did so to such an extent that only a small proportion of the mussels survived. Only the high fecundity of the zebra mussel kept their numbers up. As the blue crabs themselves had not increased notably in numbers during this time, the most likely explanation is that zebra mussels had become a gradually larger part of their diet, although it could not be ruled out that other, larger predators also contributed to the zebra mussel consumption. The process can be seen as one in which a native predator with time “tames” an invasive species [52].

Economic Effects of the Zebra Mussel in North America

Solid structures, in particular those of steel or concrete standing in running water with relatively low and even flow rates, are ideal places for the zebra mussel to settle. Consequently, many man-made structures attract large conglomerations of *Dreissena* mussels. There, the mussels quickly multiply, enough significantly to reduce flow rates. The zebra mussel thus colonizes water supply pipes of hydroelectric and nuclear power plants, public water supply plants, and industrial facilities. It populates the pipes’ interiors, constricting water flow and reducing the intake in heat exchangers, condensers, firefighting equipment, and air-conditioning and cooling systems. Zebra mussels can also damage boats, engines, navigational buoys, fishing gear, and dock pilings, as well as diminish steel and concrete structural integrity. In the USA, congressional researchers estimated the mussel costs the power industry alone \$3.1 billion in the 1993–1999 period, with its combined impact on industries, businesses, and communities climbing to over \$5 billion [53]. Since then, the zebra mussel population has almost collapsed in the areas into which it was first introduced, but has spread to new ones. The annual control costs are

likely to be smaller, although some sources project an estimated cost of \$5 billion for the coming decade [54].

The intensity of the problem has decreased in the area around the Great Lakes, where it first emerged, but it has spread geographically. Technical adjustments, such as using Teflon-like material on which the mussel does not so easily settle, have also reduced the costs for regular mussel removal, but at the price of higher investment costs.

There are no methods available to kill or remove zebra mussels on a large scale in the environment. In technical installations, mechanical removal and killing the adolescent mussels with hot water, chlorine gas, salt, or detergents are methods in use. To overcome the rejection and valve-closing response generally seen when zebra mussels are exposed to toxic substances, more advanced methods of delivery are sometimes practiced. Foremost among these is microencapsulation of toxins in particles that are edible for the mussels. The active ingredient used is potassium chloride, which is not lethal at low doses to most organisms, including fish, but which is particularly toxic to freshwater bivalves. Another emerging control for *D. polymorpha* is the use of endocannabinoids, anandamide, and other compounds that have been tested to inhibit zebra mussel byssal attachment. These naturally occurring and synthetic cannabinoids can serve as efficacious, nontoxic zebra mussel anti-foulants [55].

Some attempts have also been made with biological control agents such as the common soil bacterium, *Pseudomonas fluorescens*, which is toxic to the zebra mussel but harmless to man. No such methods have yet reached commercial applications.

In some situations, in which *Dreissena* mussels destroy bathing beaches or hinder operations of recreational boats, their presence has reduced property values. The bigger picture, however, is that clearer and more transparent water increases beach-front property values [56]. No large-scale, nationwide assessment of this economic effect seems to have been done yet, though.

The Likely Future

Based on experience in Western Europe, it seems likely that the spread of the zebra mussel to new water systems in the suitable temperature ranges of North America will continue and that following their introduction, rapid colonization, and mass development, the associated ecological effects and economic problems will occur there, too.

In areas in which the mussel is already present in the initial mass occurrence, the densities are likely to go down and the ecological effects to become milder. However, the need to prevent them from settling or to remove mussels from technical installations will probably remain high. The fecundity of the zebra mussel means that even with fewer adults around, there will still be plenty of veligers eager to settle. In addition, many man-made surfaces, for example, water intake pipes, provide not

only a suitable hard substrate and a water stream with food and oxygen but also protection from predators.

In Europe, the slow advance in the Mediterranean area is likely to continue, and with a warming climate, the zebra mussel may go on to conquer more northern territory as well.

As the slower spread of the quagga mussel also continues, the two *Dreissena* species are likely to share territory and split dominance dependent on factors such as temperature, depth, sediment structure, and salinity. In areas where the zebra mussel is the first and only invader now, this means that it is likely that it will eventually have to cede some territory to its cousin.

Summary

Since the first part of the nineteenth century, the zebra mussel has invaded most freshwaters of Western Europe, as well as, since the 1980s, important parts of the waterways of the Northeastern USA and southern Canada. It is an extremely efficient invader and often, within a few years after having entered a water system, totally dominates the non-photosynthesizing biomass. They will then filter and clear large volumes of water, not seldom a whole lake within days or a week, consuming the phyto- and micro-zooplankton and extracting calcium to build their shells. As a result, the pelagic part of the food web becomes impoverished, accompanied by a corresponding flourishing of the littoral part. However, other mussel species there may suffer severely from the competition. In many ways, the impacts of the zebra mussel on the aquatic ecosystem are the opposite of those of eutrophication. Mostly, the period of extreme zebra mussel population density is short, typically a decade or so, after which time the native predators have learned to consume the newcomers and their densities decrease with a factor of 10 or more.

A number of man's installations in water, including water intake pipes, offer attractive settling places for the zebra mussel and necessitate costly removal operations.

Generally speaking, it seems that both the ecological and economic effects of zebra mussel invasions have been more pronounced in North America than in Europe. It could, however, be that more attention is now paid to ecological effects than was the case 150 years ago and also that water-based technical systems are much more prolific and sensitive now than they were then.

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