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Impact of the Zebra Mussel, a Bivalve Invader

Dreissena polymorpha *is rapidly colonizing hard surfaces throughout waterways of the United States and Canada*

Michael L. Ludyanskiy, Derek McDonald, and David MacNeill

Just when the threat of a Russian invasion of North America seemed to have disappeared with the end of the Cold War, an invasion has been found to be not only under way but proving to be successful. Rather than missiles, a naval force of hordes of zebra mussels has secured beachheads in many US and Canadian lakes and rivers. One could call it biological warfare, but not directed by any human admiral.

The freshwater bivalve mollusk *Dreissena polymorpha* (Pallas 1773), better known as the zebra mussel, is a native of southern Russia; since its introduction into the Great Lakes, apparently in 1985 or 1986, this mollusk has been quickly spreading throughout the waterways of both the United States and Canada. The zebra mussel was introduced to North America via water ballast from a foreign ship (Roberts 1990). Since then, however, the mussel has spread dramatically, and many utilities, industrial and municipal water consumers, and fisheries have felt its impact.

The zebra mussel is both an efficient filter feeder and a notorious biofouler

As with previous accidental introductions of nonnative species, a lack of natural ecological constraints, such as predators, parasites, and diseases, has fostered the rapid expansion of the zebra mussel's North American range. It seems that most hard substrates (now most of which within the current distribution range of the zebra mussels have been successfully colonized) are an open niche in North American freshwater ecosystems. In addition, the broad physiological adaptive capabilities and genetic plasticity of this species, coupled with inadvertant dispersal via human transport, predispose it to eventually becoming widely distributed in North America, with potentially serious economic and environmental consequences.

Two features of *D. polymorpha* make it of special concern to people who depend on the aquatic environment. First, it is an efficient suspension feeder. Although its filtering can have a positive effect on polluted (or eutrophic) aquatic ecosystems by improving water clarity, its efficient removal of phytoplankton and detritus from the water column can also cause a multitude of ecological problems. Second, *D. polymorpha* is one of the most notorious biofoulers in the world.

The economics of the problem are only now beginning to be understood as the extent of the zebra mussel's invasion becomes clear, and its impact on utilities and other water users begins to be felt. The US Fish and Wildlife Service has estimated that the cost of industrial, utility, and municipal-water-use reductions due to biofouling, plus the impact of the zebra mussel on navigation, boating, and sport fishing, could reach $5 billion by the year 2000 in the Great Lakes alone.[1]

Recognition of potential ecological and economic impact has generated considerable research by North American scientists. Millions of dollars have been allocated for ongoing studies of zebra mussel biology and its impact on the ecology and for development of environmentally benign control strategies. In 1990, the US Congress earmarked $150 million for research and control through 1995 (Sheffer 1990). Unfortunately, only a small proportion of this amount has been actually set aside for basic biological research.

In this article, we provide the cur-

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[1] Donald W. Schloesser, US Fisheries and Wildlife Service, Ann Arbor, MI, 1989, unpublished data.

Table 1. Chronology of living *Dreissena* discoveries in Russia and Europe.

	Location	
Year	Russia	Europe
1769	Ural River	
1771	Volga River	
1771	Caspian Sea	
1794		Hungary
1800	Dnieper River	
1824		England
1826		The Netherlands
1830		Germany
1840		Denmark
1840s		France
1845	Dvina River	
1845	Daugava River	
1847	Moscow River	
1855	Don River	
1875	Kama River	
1940s		Scandinavia
1960s		Switzerland
1970s		Yugoslavia, Italy, and Spain

rent understanding of the zebra mussel's origins, biology, environmental requirements, and potential impact. We examine its distribution, estimate its future spread, and look briefly at measures being taken to lessen its impact.

Origin, history, and world distribution

Biologists believe that the Dreissenoidea evolved from a corbiculoidean ancestor in the early Eocene (Babak 1983, Morton 1970). During the early Quaternary period, the zebra mussel spread widely over the Volga River and its tributaries, occupied northern areas of eastern Europe, penetrated western Europe, and also settled in the Aral Sea (Andrusov 1897). During the last glacial epoch, the geographic range of *Dreissena* declined dramatically and was reduced to small areas, including brackish waters of the Caspian and Aral Seas, low-salinity portions of the Azov and Black Seas, and some bodies of water of the Balkan Peninsula (Babak 1983, Mordukhai-Boltovskoi 1960, Zhadin 1946).

The first report of zebra mussels was in the Ural River in 1769 by the Russian naturalist Peter Pallas (Pallas 1773). Both Andrusov (1897) and Skorikov (1903) have shown that the mussel is a native species of the Pontocaspian region and that it had rapidly spread all over Europe by the middle of the nineteenth century, mostly, it is supposed, via river canals (Zhadin 1946).

At first, the Mariinsk canal system was probably the sole migration route to western Europe, but several other routes and means opened up quickly. The construction of the Oginski Canal, connecting the Dnieper and the Neman river basins, provided a second alternative waterway. Martens (1865) suggested that the zebra mussel may also have spread to Europe on timber imported from Russian rivers. In addition, Binder (1965) has even suggested that the zebra mussel rode along with Napoleon's army as it retreated back to Europe.

Stanczykowska (1977) said the spread throughout Europe was still occurring in the 1970s. She noted that the mussel first appeared in Scandinavia as late as the 1940s, in Swiss lakes during the late 1960s and early 1970s, and even later in Italy. But as of the mid-1970s, it had not yet reached Spain, Norway, Finland, or Ireland.

Walz (1991) describes a slightly different scenario. He believes the zebra mussel spread through central Europe in two stages: the first at the beginning of the nineteenth century and the second, only after 1960, when it moved into many alpine and prealpine lakes of Austria, Germany, Switzerland, and France. This spreading continued into the 1970s with the infestation of the prealpine lakes of southern Europe, including Yugoslavia, Italy, and Spain. Table 1 summarizes the chronology of living zebra mussel findings in Russia and Europe.

In either scenario, it took approximately 200 years for the zebra mussel to spread from its origins to the rest of western Russia and all of Europe. One can only speculate how much time the mussel will need to occupy North America, but the evidence suggests this invasion is happening much more quickly than the mussel's spread across Europe.

Distribution in North America

The first living North American specimen of the zebra mussel was collected on 1 June 1988 near the Belle River in Lake St. Clair (Hebert et al. 1989). Most scientists agree that the mussel was probably introduced in 1985 or 1986 in ballast water discharged from foreign shipping. Carlton (1993) states that he has proven the source of the Laurentian Great Lakes infestation to be mussels transported in the ballast water of transoceanic vessels from Europe. Ludyanskiy (1993), based on a comparison of shell morphology, has suggested an alternative hypothesis: that the zebra mussel was brought to the Great Lakes from the Black Sea/Caspian Sea region.

Table 2. Chronology of first sightings of *Dreissena* in North America.

Year	Location
1988	Southern Lake St. Clair
	Western Lake Erie
Spring 1989	Central Lake St. Clair
	Northern and Southern Lake Erie
	Western Lake Michigan (Green Bay)
	St. Clair River
Fall 1989	Niagara River
	Western Lake Ontario
	Detroit River
Spring 1990	Eastern Lake Ontario
	St. Lawrence River
	Lake Superior (western tip)
	Western Lake Huron
Fall 1990	Southern and Southeastern Lake Michigan
	New York State Barge Canal
	Mohawk River
	Hudson River
	Fingerlakes (New York)
	St. Lawrence Seaway
1991	Eastern Lake Huron
	Northeastern Lake Michigan
	Illinois River
	Susquehanna River
	Mississippi River
	Ohio River
	Kentucky Lake
	Indian Lake (Ohio)

No matter how the zebra mussel arrived, in the six years since its discovery in North America, it has quickly spread to all of the Great Lakes and entered eight river systems (the St. Lawrence, Hudson, Mississippi, Ohio, Illinois, Tennessee, Susquehanna, and Arkansas rivers). Table 2 shows a chronology of the first sightings in these river systems.

In late 1990, the "*Dreissena polymorpha* Information Review," published by the New York Sea Grant, began to compile a map of the current distribution of the zebra mussel in the Great Lakes Basin (DPIR 1990). Figure 1 shows that distribution as of 21 November 1990. Two years later, on

Figure 1. North American range of the zebra mussel as of 21 November 1990 (DPIR 1990).

Figure 2. North American range of the zebra mussel as of 15 October 1992 (DPIR 1992).

15 October 1992, the zebra mussel had spread to the range shown in Figure 2 (DPIR 1992). A comparison of these two maps allows an estimate of the rate of zebra mussel spread in North American fresh waters: by the year 2000, the zebra mussel can be expected to have colonized all North American rivers, lakes, and reservoirs that fit its broad ecological requirements.

Unfortunately, it is not only the main waterways used by major shipping that are susceptible to infestation by the zebra mussel. Griffiths et al. (1991) have suggested that virtually any body of water that can be reached by boaters and fishermen within a few days' travel of the Great Lakes, particularly Lake Erie, seems to be at risk. It is only a matter of time, then, before the zebra mussel reaches even small lakes, ponds, and streams.

The biology of the zebra mussel

Life history. The lifespan of the zebra mussel is typically 3–5 years, but there are data in the Russian literature that it can live 6–9 years (Mikheev 1964) and even up to 15 years (Karpevich 1964). Such a difference can probably be explained by differences in water temperature among habitats, because lifespan of mussels both in fresh water and seawater depends on water temperature. The shells of adult mussels average 25–35 mm in length, with some mussels having shells as long as 50 mm (Kirpichenko 1971).

Typically, zebra mussels in Europe mature sexually in their second year, usually at more than 10 mm (Edel 1981), although in Lake Erie and Lake St. Clair they generally have been maturing in their first year of life. Sexual maturity has been achieved in mussels as small as three millimeters in length, according to recent North American studies (Nichols 1993, Nichols and Kollar 1991). These scientists also emphasized that the reproductive cycle of the mussel is readily affected by local environmental conditions.

The mussel sexes are separate, and gametes are released either synchronously or asynchronously into the water column for external fertilization. Occasional hermaphroditism has been reported. For fertilization, the temperature must be higher than 12°C (Neumann et al. 1993, Sprung 1993). An individual female 25–30 mm long releases more than one million eggs during one spawning event (Sprung 1990, 1993, Walz 1978), and eggs can be released in batches two to five times a year (Walz 1973). Half or more of all eggs in one spawning season are released during the first spawn (Sprung 1990). Within a temperature range of 12–24°C, the eggs can be fertilized 2.50–4.75 hours after release, whereas the sperm can remain motile much longer, up to 22 hours (Sprung 1992).

The free-swimming larvae, called veligers, appear in the plankton for anywhere from five days to five weeks, as long as the water temperature is between 10 and 24°C (Katchanova 1961, Shevtsova 1968, Walz 1975). The veligers are dispersed at this stage mainly by water currents. Initially approximately 70 microns in diameter, they have the appearance of ciliated protozoa and grow rapidly to 150–300 microns in diameter (Kirpichenko 1971, Walz 1973). During this period of growth, shell material is secreted by the mantle edges, which not only increases the size of the larva but also changes its shape. A ciliated crown (the velum) of the young veliger assists in filter feeding and locomotion.

Additional developmental changes during growth include the secretion of a second larval shell and finally a functional foot. This pediveliger swims and crawls on surfaces searching for a suitable substrate, where it begins a relatively sedentary life as a postveliger (Ackerman and Claudi 1991; Figure 3). Mortality is 97% during the settling stage. Postveliger sizes range from 250 to 700 microns. Growth and development of postveligers are manifested externally by changes in the shell shape and size, with the settling veliger having a symmetric round shell that begins to elongate and grow asymmetrically, eventually acquiring a triangular shape. At this point, the incurrent and excurrent siphons develop, and, on settlement, the mussel secretes threads of schleroproteins from the byssal gland in the foot, which solidify in water to form the so-called byssus and firmly attach the mussel to the substratum.

Taxonomy. Because of high variability in shell morphology, the zebra mussel's taxonomy is complicated. Research with the *Dreissena* species in the Caspian and the Aral Seas by Russian biologists distinguished there different species: *D. polymorpha*, *Dreissena rostriformis*, and *Dreissena stancovici*, as well as some subspecies including (*Dreissena polymorpha* var. *andrusovi*, *Dreissena rostriformis bugensis*; Karpevich 1955, Logvinenko and Starobogatov 1968, Zhadin 1952). By contrast, Western European taxonomists have recognized only two extant species, *D. polymorpha* and *D. rostriformis*, and consider other varieties to be ecomorphs (Marelli 1991).[2]

In North America, two species of *Dreissena* have been found: *D. polymorpha* (zebra mussel) and what biologists are calling the quagga mussel and have not yet assigned a species name (May and Marsden 1992). The two species can generally be distinguished by morphological characteristics of the shell (Figure 4). *D. polymorpha* has a distinctive carina (the angular configuration between lateral and ventral portions of shell), whereas the quagga mussel is acarinate: it has a rounded configuration at the lateral-ventral part of the shell. Based on the apparent absence of the quagga mussel from many sites around the Great Lakes, May and Marsden have suggested that the two species were introduced into the Great Lakes at different places and times. They hypothesize that the quagga mussel was the later entry, having been present only since 1989. But some evidence suggests that the quagga has been resident in Lake Erie since at least 1987.[3]

The place of the quagga mussel in the Dreissenidae has not yet been defined, but it would seem that the quagga mussel should be identical to one of the other Russian species or subspecies, probably either *D. polymorpha andrusovi* or *Dreissena rostriformis bugensis* (Ludyanskiy 1993), if the North American *Dreissena* was brought from the Caspian Sea/Black Sea Region.

Nichols and Black (1993) reported on the laboratory creation of hybrid larvae, which were intermediate in appearance between pure quagga and zebra mussels, with some overlap of shell characteristics. However, none of the hybrids have been reared through settlement. The potential for hybrid formation under field conditions remains unknown. At this time, no hybrid adults have been collected from field locations. This research makes the question of specific differentiation between mussels even more complex. Future research should compare genetic and morphological characteristics of North American, European, and Russian specimens to produce an exact definition for the quagga mussel.

Dispersion. The dispersal abilities of the zebra mussel are tremendous. Carlton (1993), in his comprehensive review of its dispersal mechanisms, lists 3 natural mechanisms (currents, birds, and other animals) and 20 human-related mechanisms (such as trailered boats). All these methods of dispersal can transport the zebra mussel overland, upstream, and downstream.

Morton (1993) emphasized that *D. polymorpha* "is ideally suited for the successful exploitation of freshwater systems." He noted that the retention of a free-swimming veliger larva, which also may be carried over great distances by the current, and of an active byssus apparatus in adult life, which helps the mollusk to attach itself to ships, rafts, water fowl, fishing gear, and other aquatic organisms, enables zebra mussels to colonize locations normally not occupied by other bivalves.

Dispersion can take place in every stage of the mollusk's development—as veligers, juveniles, and adult mollusks—and the dispersal mechanisms are different for each stage. The rapid expansion of the mussel within the Great Lakes probably took place via boats and ships carrying adult mollusks on their bottoms and hulls, followed by selection of the most favorable substrates in the infested water bodies by newly spawning veligers and translocating juveniles. Most of the initial spread of the zebra mussel out of the Great Lakes region into other water bodies has been via canals and by transport of trailered boats to distant overland sites (Carlton 1993). The probability of the mussel spreading all over North America in the future is complicated by, among other things, uncertainties in the ecological requirements of the quagga mussel (as

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[2] B. S. Morton, 1992, personal communication. University of Hong Kong, Hong Kong.

[3] J. D. Ackerman, 1991, unpublished data. University of Toronto, Toronto, Ontario, Canada.

opposed to the zebra mussel). It is possible that this species may extend into areas not colonized by the zebra mussel.

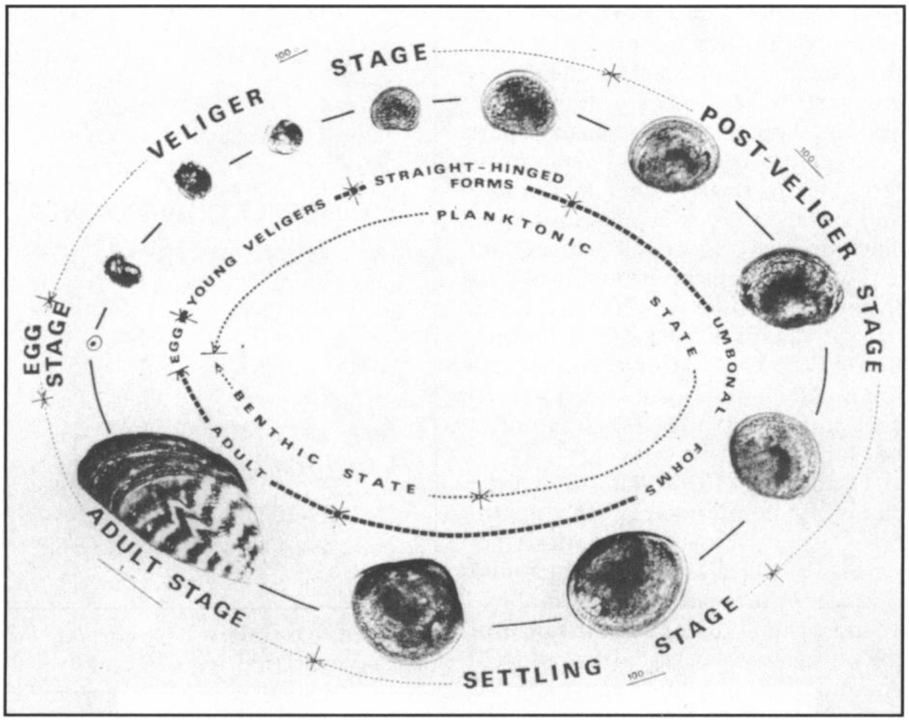

Figure 3. The developmental stages of *Dreissena polymorpha* (Mackie 1991).

Environmental requirements of the zebra mussel

Predicting where and in what densities the zebra mussel will colonize North American waters is made easier if the mussel's tolerance to environmental conditions is known. Knowledge of the tolerance levels may also be helpful in developing measures to lessen the negative impact of the mussel.

Historic data on zebra mussel infestation of Russian and European waters have demonstrated that not all bodies of water have been successfully colonized and that population sizes among the mussel's habitats vary by several orders of magnitude due to the differences in physical and chemical conditions in the environment (Stanczykowska 1977, Walz 1978, Zhadin 1946). For example, Lyakhnovich et al. (1984) investigated the zebra mussel populations in the Zapadnaya Dvina River basin, where the majority of Byelorussian lakes is located. They found that of the 475 lakes studied, the mussel was found in only 73. Antonov and Shkorbatov (1983) investigated the variability of populations taken from six locations along the Volga River flow over a distance of nearly 2500 kilometers from north to south (Rybinsk, Kostroma, Kuibyshev, Samara, Chapayev, and Astrakhan). Among other parameters, the scientists investigated the mussel's thermal resistance and salinity tolerance. Their results suggested that the most southern group (that at Astrakhan and closest to the Caspian Sea) was most tolerant to higher salinity and temperature levels, whereas the least resistant mussels were in the Rybinsk group, most distant from the Caspian Sea.

Recent work by some North American scientists has been directed toward predicting the potential distribution and abundance of the zebra mussel on the basis of European experience and knowledge of water chemistry and temperature (McMahon 1990, Neary and Leach 1992, Ramcharan et al. 1992, Strayer 1991, Trulear et al. 1990). Researchers agree that the most critical parameters for future zebra mussel spreading in North America are likely to be water salinity, temperature, pH level, and calcium concentration.

Primary environmental requirements of the zebra mussel are those that are essential for its vital functions; where favorable, they are good indicators of future infestation. These primary requirements include temperature and water quality (salinity, pH level, calcium concentration, dissolved oxygen, and turbidity). Secondary environmental requirements are those that may have an impact on the abundance of the mussels in specific locations and may show the vectors of probable colonies in already infested waters. These secondary requirements are water velocity, substrate types and availability, local peculiarities in hydrology, and the geometry of dams, intakes, and other structures.

A review of Russian, European, and recent North American literature (Dyga and Lubyanov 1975, Edel 1981, Mackie et al. 1989, Zhadin 1946) reveals the optimal environmental requirements of the zebra mussel. Its primary requirements are salinity of 0–4 ppt, average summer water temperature of 17–23°C, pH level of 7.4–9.0, calcium concentration of 20–125 ppm, turbidity of 40–200 cm (measured by Secchi disc), and dissolved oxygen content of 8–10 ppm. Its secondary requirements are water velocity of 0.2–1.2 m/sec and the presence of solid substrates (rocks, wood, or gravel).

Environments with parameters close to these will probably be colonized first, but in Russia and Europe zebra mussels do inhabit bodies of water with less than optimal ecological parameters. Because of their strong genetic plasticity, zebra mussels can tolerate changes over time in their environment to levels outside these ranges (Zhadin 1946).

Salinity. Perhaps the most important primary environmental requirement is salinity (or rather the lack thereof). Although primarily a freshwater animal, the zebra mussel has a considerable tolerance of salinity and is likely to invade estuaries and brackish waters as well as fresh bodies of water (Strayer and Smith 1993). The zebra mussel originates from the brackish waters of the Caspian and the Aral Seas (Babak 1983, Zhadin 1952) and is also found in estuaries and brackish waters throughout its European range, including the Caspian Sea, the brackish parts of the Black Sea, and the estuaries of the Baltic Sea and eastern

Atlantic. The Caspian Sea is a brackish reservoir with salinities that vary from fresh (0.1–0.5 ppt) in the northern part to 12–14 ppt in the middle and to 20 ppt in the southeastern part (Zenkevitch 1965). The Caspian waters, however, are richer in calcium and sulfate and lower in sodium and chloride than are oceanic waters, and this ion composition probably allows the mussel to tolerate higher salinities in the Caspian Sea (Mordukhai-Boltovskoi 1960). Currently, the zebra mussel inhabits only the northern part of the Caspian Sea with salinities not higher than 10 ppt.

Osadchikh (1988) has studied the changes in the abundance of the northern Caspian mussel populations between 1935 and 1985, and she found that when the mean salinity was above 10 ppt, the abundance and range of the zebra mussel was sharply reduced. A similar decline has been recorded during the recent dramatic increase in salinity in the Aral Sea (Andreeva and Andreev 1990) and in the Black Sea estuaries due to human diversion of waters from tributaries (Mordukhai-Boltovskoi 1960).

Zhadin (1946) believes it is possible that such changes in salinity in native habitats have made zebra mussels more genetically tolerant to salinity and other changes in their environment. On the other hand, Strayer and Smith (1993) believe there is no genetic adaptation to salinity, so that North American zebra mussels should behave like a composite of the European populations.

The upper limit of salinity is thus important, and some scientists think that limit is 0.5–12 ppt for zebra mussel survival, depending on the ionic composition of the water (e.g., Kilgour and Kepple 1993, Strayer and Smith 1993, Zenkevitch 1965, Zhadin 1952).

Based on these numbers, Barber (1991) hypothesized future infestation even in the Chesapeake Bay. Strayer and Smith (1993), reviewing the distribution of the zebra mussel in European estuaries and brackish waters, made these predictions for North America:

- In estuaries with considerable short-term variation in salinity due to tides and fluctuation of freshwater input, the seaward limit of zebra mussels will probably be at only 0.4–2.0 ppt.
- In nontidal lagoons and stable estuaries, the zebra mussel may survive in waters with salinities as high as 6 ppt.
- In brackish lakes and other sulfate-rich waters, the mussel will probably tolerate salinities as high as 10–14 ppt.

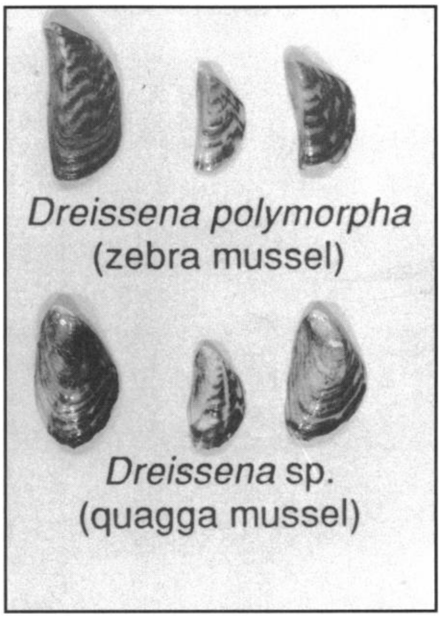

Figure 4. *Dreissena polymorpha* and quagga mussel (courtesy of J. E. Marsden).

Based on preliminary studies, these scientists made rough projections of the distribution and abundance of the zebra mussel in the Hudson River estuary in New York. Their expectation that the mussel would appear from the head of the estuary at Troy/West Point and further downriver was partially fulfilled by actual colonization in 1991–1992. The southernmost limit of the mussel was West Haverstraw, where the salinity range was 2–3 ppt.

Temperature. The second primary environmental requirement for zebra mussel survival is temperature. As noted earlier, the optimal average summer temperature range is 17–23°C, but there is considerable disagreement as to the upper limit of temperature that the mussel can tolerate.

Three years ago, McMahon et al. (1990) made a preliminary assessment of the possible range of the zebra mussel in North America based on its thermal biology. They concluded that the mussel is unlikely to move into the drainages of the southern and southwestern United States where water temperatures commonly approach 28–32°C during the summer. Strayer (1991) projected the same upper limit a year later.

Most recent studies, however, have shown that zebra mussels acclimated to 25°C appear to survive at temperatures slightly higher than 30°C (Iwanyzki and McCauley 1993) and even at 34–36°C (McMahon et al. 1993b). In addition, Russian geneticists, studying the impact of increased temperature on the genetic structure of the zebra mussel, have found genetic selection at higher temperatures (Fetisov et al. 1990). If these studies prove correct, the zebra mussel may well survive in higher water temperatures and spread into the southern and southwestern regions of the United States.

Water chemistry. Of the water quality factors other than salinity, the most important are pH level and calcium concentration. Although the pH range of *D. polymorpha* in nature is normally between 7.0 and 9.0 (Edel 1981), laboratory experiments show that even a pH level as low as 7.4 will sterilize a mussel population and prevent recruitment (Sprung 1987). This threshold was used by Neary and Leach (1992) in their prediction models. Vinogradov et al. (1993) showed that in water with low pH levels, the zebra mussel displayed a high sensitivity and low efficiency of mineral metabolism, and this factor may limit its distribution.

As for calcium concentration, the zebra mussel apparently prefers hard water (Feigina 1959, Kirpichenko 1971, Zhadin 1946). For instance, Alimov (1981) has shown that, to a great extent, water hardness defines the external morphology of the mollusk shell and the most rapid growth of zebra mussels occurs in waters with calcium concentration of approximately 70 ppm. Some of the most widely accepted data on calcium constraints is from the article by Sprung (1987), which was devoted to the ecological requirements of developing eggs. Sprung showed that of all ions, the calcium ion is of overriding importance and that the threshold concentration of calcium for rearing success is 12 mg/l. Similar threshold data were determined by Vinogradov et al. (1993), who investigated the mussel's calcium metabolism, and by Hincks and Mackie (1992), who checked zebra mussel tolerance to water samples from 16 Ontario Lakes having a wide range of pH, calcium, and phosphorus levels.

Substrate preferences. The zebra mussel usually prefers solid substrates for settlement, such as rocks, wood, and gravel, and it avoids silted sand, mud, silt, and clay. In these latter materials, one may find zebra mussels attached to plants or to other mollusks. Almost all available solid surfaces, provided the water quality is right, are usually completely covered by zebra mussels. Many field experiments have been performed recently on the habitat selectivity of the zebra mussel, including artificial and construction materials (Ackerman et al. 1993, Kilgour and Mackie 1993, Marsden 1993, Protasov 1979, Yankovich and Haffner 1993). Most of these scientists agree that the zebra mussel is selective in choosing where to settle and suggest that the abundance of the mussel on structures can be reduced by selection of antifouling construction materials.

Positive environmental impact

Despite the large negative impact it can have on the economy and environment, the zebra mussel does have its good points and a place in the ecological scheme. Like all bivalves, zebra mussels are significant natural biofilters, playing an important role in biological self-purification and improving water quality in aquatic systems. Consider, for instance, that these mussels can filter a wide range of suspended particles (10–450 microns) from the water column. Cilia in the mantle cavity and stomach select food particles of suitable size (10–40 microns), which are ingested (Morton 1969, Ten Winkel and Davids 1982). Rejected particles are captured in mucus and are discharged as pseudofeces via the inhalant siphon, whereas real feces leave the body at the exhalant siphon. (In the River Meuse, Reeders and bij de Vaate [1992] observed that more than 90% of all feces particles produced by zebra mussels consisted of pseudofeces).

The filtering capacities of the zebra mussel have been investigated in many laboratory and field studies (Mikheev 1967, Reeders et al. 1989, Stanchykowska et al. 1975). Calculations on European and Russian water bodies show that zebra mussel populations can filter large volumes of water, often equivalent to several times that of a lake or reservoir during a 12-month period (Lvova 1980, Reeders et al. 1989). Fisher et al. (1993), for example, predicted that it would take 24 and 52 days, respectively, for zebra mussels to completely filter all of Lake St. Clair and the western basin of Lake Erie, assuming the mussels are present at densities of only 10,000/m^2 and that they cover 1% of the lake bottom. If a more realistic mussel density of 50,000/m^2 is assumed, filtering time is reduced to a mere 10 days.

Zebra mussels can also affect nutrient and mineralization pathways by removing dissolved nutrients, phosphorus, calcium carbonate, and other minerals. They can also accelerate the conversion of toxic nitrogenous metabolic wastes (e.g., ammonia and nitrite) to consumable nutrients for other benthos and phytoplankton (Mackie 1989). In Russian canals, for instance, the mussel is an important component of what is called a "biological plateau" (an artificial structure for natural water purification; Kharchenko and Lyashenko 1985). As Kaftannikova et al. (1987) has reported, the zebra mussel population can exceed one to two million mussels per square meter. Such high densities of zebra mussels combined with their high filtration capacity, make them an important component of an aquatic environment, influencing water chemistry and ecology.

Biomanipulation. Several biologists speculate that zebra mussels can contribute to the restoration of lakes and other bodies of water by removing excessive amounts of algae. For example, Reeders et al. (1989) have reported that the current zebra mussel populations in two Dutch lakes are sufficient to filter both lakes at least once or twice a month, and they have suggested the use of the mussel in biomanipulation programs.

Other applied research activities in the Netherlands in the last decade have also increasingly focused on the positive applications of the zebra mussel for water quality management (Smit et al. 1993), and studies are currently being conducted to examine the possibility of construction of a biological filter consisting of hanging cultures of zebra mussels at the freshwater inlet of Lake Volkerak-Zoommeer (Reeders and bij de Vaate 1992). The purpose of the filter is to process suspended materials in the water through the zebra mussel colonies, which would then deposit those materials as sedimentary pseudofeces. Preliminary studies for this experiment indicate that the mussels can be used effectively to control eutrophication in the lake.

Biomonitoring. Because the zebra mussel is very sensitive to water contamination and cannot live in bodies of water polluted with waste or industrial effluents (Zhadin 1946), it becomes an effective monitor of such contamination, much like the canaries taken into coal mines to warn of dangerous gases. The mussel thrives only in clean, oxygen-saturated, nonturbid water.

In Europe, the zebra mussel is currently a popular testing organism in ecotoxicological studies, monitoring systems, and specimen banking (Alekseyev and Antipin 1976, Jenner and Janssen-Mommen 1993). In these studies, three zebra mussel vital functions are used as monitors: valve movement behavior is used as an early warning system; pumping behavior response to pollutants is used as a method for toxicity screening; and pollution effect monitoring is used at the histological level. Zebra mussels also are used as a bioindicators for trace metals, organochlorines, and radionuclides, as well as a specimen in Germany's environmental specimen banking program (Neumann and Jenner 1992).

Negative environmental and industrial impacts

Parallel to the ecological benefits of the zebra mussel is the negative impact it is having on native biota, phytoplankton, and fisheries. In addition to the natural consequences is the equally devastating effect the mussel is wreaking on utilities, industries, and municipalities that use fresh water.

In the natural realm, the growth of zebra mussel populations can cause ecological consequences throughout a community, especially because they remove large percentages of primary productivity, which may reduce the energy available to pelagic food webs (Ramcharan et al. 1992, Schneider 1992, Stanczykowska 1977). Fish recruitment and growth may also be affected by such growth in zebra mussel colonies.

One consequence is the removal of large amounts of seston from water, thus promoting a shift in habitat structure from a relatively homogeneous environment of turbid water and silty sand substrata to an environment of clearer water with patches of macrophytes and mussel colonies (Griffiths et al. 1991, Hebert et al. 1991, Neary and Leach 1992). For example, in western Lake Erie, mean Secchi disc transparencies for the May-October period almost doubled and mean chlorophyll *a* declined 54% between 1988 and 1989 (Leach 1993). Leach also found that concentrations of chlorophyll are now in the range classing that part of Lake Erie at the oligotrophic end of the trophic scale (Leach 1993), and Griffiths (1993) predicts that the oligotrophication of Lake St. Clair will continue until the mussel population stabilizes or declines.

Mackie (1991) has gone further and hypothesized the following scenario in Lake St. Clair because of clarification of the water by the zebra mussel. He predicts biodeposition of most of the nutrients in the water on the lake floor, a decline in primary production, increased development of the benthic community, and reduction in biomass and production of zooplankton and other components including fish. Eventually, according to Mackie, this single exotic bivalve species will alter the entire pelagic-benthic energy balance of Lake St. Clair. Needless to say, this change may have severe socioeconomic impact, especially for the commercial and sports fisheries.

Another important negative impact of the zebra mussel is its ability to remove contaminants from the water and concentrate them on the lake floors and shorelines. For example, De Kock and Bowmer (1993) examined the transfer of cadmium and organochlorine contaminants, from zebra mussels to the tufted duck, and showed a subsequent transfer to the duck eggs with resulting teratogenic effects. The two scientists emphasized that "given the capacity of *D. polymorpha* to accumulate contaminants and its ideal position as a prey item along the banks of water bodies, it would be wise to carefully examine the pathways and flux of organic contaminants in this new part of the ecosystem."

Negative impacts of the zebra mussel on native unionids have been observed in Lake St. Clair and Lake Erie (Mackie 1991, 1993, Schloesser and Kovalak 1991). Zebra mussels are not selective and are colonizing all species of unionids in Lake St. Clair and Lake Erie. Unionids with 15,000 zebra mussels on their shells were found, probably equal to five times the weight of the unionid itself. Often unionids were not able to open their valves fully or could not close their valves. Thus, as a direct consequence of the zebra mussel invasion, the rich diversity of the unionid community in these lakes may be reduced because of the extinction of some species.

The zebra mussel as a biofouler

The most expensive problem caused by the mussel, in the short term at least, is its potential to foul raw water intakes such as those at reservoir pumping stations, electric generating plants, and industrial facilities. Zebra mussel communities are abundant on human-built structures such as dams, pipes, and water intakes, which provide more solid substrate than do natural surfaces within lakes and rivers (Protasov and Afanas'yev 1984, Zhadin 1946). Lyakhnovich et al. (1987) found that in Lukomskoye Lake, which is used as a cooling pond for a fossil-fuel power plant, mean quantities of mussels at the intake structures of the plant were 11 times greater than in the most abundant biotope of the lake. In terms of its biomass, it was seven times greater.

Reservoirs and cooling ponds have especially good conditions for zebra mussels. Favorable hydrochemistry and water temperature, plentiful food, and the presence of excellent settlement sites on the solid surfaces of underwater structures encourage mass development of mussel colonies at these sites. For example, in the former Soviet Union, huge densities of zebra mussel veligers have been found in the Saratov Reservoir, where they have reached a density of 550,000 per cubic meter (Dzyuban and Kirpichenko 1971). In other reservoirs, even larger densities have been found: Lebedeva (1978) has reported consistent densities of 300,00–400,000, but a density of two million veligers per cubic meter is not uncommon. The largest quantities per square meter have been reported by Kaftannikova (1987): in 1981 in the intake canal of the cooling pond at the Chernobyl nuclear power plant, the abundance of animals was one to two million animals per square meter and fouling build-up in the cooling pond was 1.69 million kg. The largest biomass in this pond was 19 kg/m^2.

In North America, the problem has only just began, but already the Detroit Edison power plant has reported mussel densities as high as 750,000 animals per square meter in its intake canal (O'Neill and MacNeill 1991). There is a little doubt that other power plants will be severely affected as the zebra mussel takes hold in lakes and rivers.

In industrial raw-water facilities, the infestation is also severe. The zebra mussel fouls trashracks, bar racks, culverts, waterways, raw wells, screenhouse walls, traveling and stationary screens, inlet pumping tubes, strainers, inlet condenser waterboxes, and settling tanks. The greatest impact is from clusters of shells that clog the equipment, thus causing severe reduction in water flow and sometimes resulting in plant shutdowns. (The diameter of tubing is sometimes reduced to 20–30% of the original opening.) Several such outages during one summer at some power plants in the former USSR have been reported by Edel (1981), and McMahon et al. (1990) have already noted similar problems in North America, including reduction of water flow in fouled piping, blockage of small-diameter tubes and piping by single shells and shell clusters, aggravation of sedimentation and metal corrosion, and fouling of stationary components. There have already been some outages at

North American facilities on the Great Lakes, including several in the fall and early winter of 1989 and the spring of 1990 at the Monroe waterworks, which withdraws water from the western basin of Lake Erie (LePage 1993).

Finally, the zebra mussels are negatively affecting both commercial navigation and recreational boating, infesting barges, ships, boats, docks, and piers. Even recreational beaches at the northern shoreline of Lake Erie are being affected: some swimming areas are littered with sharp shells and the air is polluted with the smell of decaying mussels. Thus, the tourism economy is beginning to feel the zebra mussel's impact as well.

The impact of the zebra mussel in North America will only worsen until natural equilibrium is achieved, unless steps are taken to control its spread and lessen its effect. In the long run, we predict that zebra mussels will become an important, but not dominant, part of their environment.

Control strategies

In general, most of current zebra-mussel control activities now being tried in North America were attempted in Russia and Europe in previous decades. These measures include mechanical, chemical, thermal, electrical, and acoustic methods (Clarke 1952, Dzyuban and Kirpichenko 1971). For years, the most effective control methods have been chlorine, thermal treatment, and protective coatings, and these measures have been summarized in reviews by Edel (1981), Jenner and Janssen-Mommen (1993), Ludyanskiy (1992), and Mackie et al. (1989). An extensive review of monitoring and control measures was prepared by the Electric Power Research Institute (Zebra Mussel Monitoring and Control Guide 1993). Among many other methods, the most widely used current North American activities in mitigation and control of zebra mussels include chemical measures (Claudi and Evans 1993, Klerks et al. 1993, Klerks and Fraleigh 1991, Van Benschotten et al. 1993), protective coatings (Leitch and Puzzuoli 1992), thermal treatment (Iwanizki and McCauley 1993, McMahon et al. 1993a, Neuhauser 1993), and acoustics (Kowalewski et al. 1993).

In fact, it is difficult to find a technique that has not been tried. Mattice et al. (1990) have listed the top 45 research and development projects on zebra mussel control. Topping the list as most effective control measures are chemical treatment, nontoxic antifouling coatings, and thermal backflush.

Unfortunately, most control methods are harmful to the surrounding environment. For instance, current molluscicides are not selective and thus have a negative impact on other organisms. For that reason, the Environmental Protection Agency and other agencies are restricting the use of both oxidizing and nonoxidizing biocides, as well as many antifouling coatings. As a result, scientists are now looking into natural chemical control measures (chemicals derived directly from a plant; Lee et al. 1993) and biological measures (Edel 1981).

Given this situation, we recommend future research and development of environmentally safe methods of zebra mussel control and mitigation. Such methods should include further development of nontoxic coatings, use of natural predators (e.g., diving ducks and crayfish), spawning control measures, control of natural environmental parameters (e.g., salinity, temperature, and dissolved oxygen), identifying specific life stages and seasonal peaks when treatment would be most effective, and disposable substrates.

Conclusions

Originating in Russia, the zebra mussel population remained relatively stable and localized until human beings and industrialization entered the picture. Human activities appear to have carried the zebra mussel into Europe, slowly at first and then with increasing speed as industrialization took place. Now the mussel can be found infesting most European waters.

Because industrialization and waterborne traffic were already well established when the zebra mussel was introduced to North America, and because there were few natural predators, the mussel has been spreading rapidly throughout most US lakes and rivers. Within the next few years, and certainly by the turn of the century, the zebra mussel will be found in almost all parts of the United States and southern Canada and will have a serious effect on the ecosystems it infests and on a portion of the economies of both countries.

Although much more is known about the zebra mussel's etiology and biology than a few years ago, further basic research is required for a full understanding of the mussel's biology, potential range of habitats, and its susceptibility to control measures. Then further experimentation and trials of new types of control activities will be feasible. In addition, the zebra mussel's potential as a positive influence on the environment should be investigated.

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References cited

Ackerman, J. D., and R. Claudi. 1991. The early life history of zebra mussels: overwintering juveniles and post-settlement movements. *J. Shellfish Res.* 11: 217.

Ackerman, J. D., C. R. Ethier, D. G. Aleen, and J. K. Spelt. 1993. Patterns of recruitment and persistence of zebra mussels on a variety of materials. Paper presented at the Third International Zebra Mussel Conference, Toronto, Ontario, 25 February 1993.

Alekseyev, V. A., and B. N. Antipin. 1976. Toxicological characteristics and symptoms of acute phenol poisoning in some freshwater crustaceans and mollusks. *Gidrobiol. Zh.* 12: 27–33. (In Russian)

Alimov, A. F. 1981. *Funktsionalnaya Ekologiya Presnovodnykh Dvustvorchatykh Mollyuskov (Functional Ecology of Freshwater Bivalves).* Nauka Press, Leningrad. (In Russian)

Andreeva, S. I., and N. I. Andreev. 1990. Effect of changes in the regime of the Aral Sea (USSR) on the trophic structure of benthic communities. *Ekologiya* 2: 61–67. (In Russian)

Andrusov, N. I. 1897. *Fossil and living Dreissensidae of Eurasia.* Trudy Sankt-Peterburgskogo obshchestva Estestvoispytatelei vol. 25. Saint Petersburg, Russia.

Antonov, P. I., and G. L. Shkorbatov. 1983. Ecophysiological and ecomorphological variability of the Volga River communities of *Dreissena polymorpha polymorpha* (Pall.). Pages 116–128 in *Vid i Yego Produktivnost v Areale (Species and its Productivity in the Distribution Range).* Nauka Press, Moscow. (In Russian)

Babak, E. V. 1983. Pliocene and Quaternary Dreissenids (Dreissenidae, Bivalvia) of the Euxinic Basin. *Tr. Paleontol. Inst. Acad.*

Nauk SSSR vol. 204.

Barber, B. J. 1991. Preliminary investigation of the salinity tolerance of zebra mussels, *Dreissena polymorpha*: implications for Chesapeake Bay. Paper presented at the Second International Zebra Mussel Conference, Rochester, NY, 20 November 1991.

Binder, E. 1965. Un mollusque enhavissant, la *Dreissena polymorpha. Musee de Geneve* 54: 2–4.

Carlton, J. T. 1993. Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*). Pages 677–697 in T. F. Nalepa and D. W Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Clarke, K. B. 1952. The infestation of waterworks by *Dreissena polymorpha*, a freshwater mussel. *Journal of the Instute of Water Engineers* 6: 370–379.

Claudi, R., and D. W. Ewans. 1993. Chemical addition strategies for zebra mussel (*Dreissena polymorpha*) control on once-through service water systems. Pages 563–573 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

De Kock, W. C, and C. T. Bowmer. 1993. Bioaccumulation, biological effects and food chain transfer of contaminants in the zebra mussel (*Dreissena polymorpha*). Pages 503–535 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Dreissena Polymorpha Information Review (DPIR). 1990. Zebra Mussel Information Clearinghouse. New York Sea Grant, Brockport, NY.

______. 1992. Zebra Mussel Information Clearinghouse, Brockport, NY.

Dyga, A. K., and I. P. Lubyanov. 1975. Biological peculiarities of *Dresissena* in the Zaporozhye Reservoir. Pages 40–52 in I. P. Lubyanov, ed. *Tekhnicheskaya Gidrobiologiya: Sbornik Stratyey* (*Technical Hydrobiology* Papers). DGU Press, Dnepropetrovsk. (In Russian)

Dzyuban, N. A., and M. Y. Kirpichenko. 1971. Biofouling and control of *Dreissena* at the hydrotechnical constructions. Pages 76–87 in N. S. Stroganov, ed. *Biopovrezhdeniya Materialov i Izdeliy v Presnykh i Morskikh Vodakh (Biodamage to Materials in Fresh and Sea Waters).* Nauka Press, Moscow. (In Russian)

Edel, Y. U., ed. 1981. *Zashchita Gidrosooruzheniy ot Korrozii i Obrastaniya (Protection of Hydraulic Constructions from Corrosion and Fouling).* Energoizdat Press, Moscow. (In Russian)

Feigina, Z. S. 1959. Thermal treatment of *Dresissena* fouling at the power plants. *Elektricheskiye Stantsii* 10: 38–40. (In Russian)

Fetisov, A. N., A. V. Rubanovich, T. S. Slypchenko, and V. A. Shevchenko. 1990. The influence of temperature factor on the genetic structure of *Dreissena polymorpha* populations. *Genetika* 26: 1770–1775. (In Russian)

Fisher, S. W., D. C. Gossiaux, K. A. Bruner, and P. L. Landrum. 1993. Investigation of the toxicokinetics of hydrophobic contaminants in the zebra mussel (*Dreissena polymorpha*). Pages 465–489 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Griffiths, R. W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on benthic fauna of Lake St. Clair. Pages 415–437 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Griffiths, R. W., D. W. Schloesser, J. H. Leach, and W. P. Kowalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48: 1381–1388.

Hebert, P. D. N., B. W. Muncaster, and G. L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 46: 1587–1591.

Hebert, P. D. N., C. C. Wilson, M. H. Murdoch, and R. Lazar. 1991. Demography and ecological impacts of the invading mollusc, *Dreissena polymorpha. Can. J. Zool.* 69: 405–409.

Hincks, S. S., and G. L. Mackie. 1992. Environmental parameters limiting the success of the exotic zebra mussel (*Dreissena polymorpha*) in sixteen Ontario Lakes. Paper presented at the Second International Zebra Mussel Conference, Toronto, Ontario, 23 February 1992.

Iwanyzki, S, and R. W. McCauley. 1993. Upper lethal temperatures of adult zebra mussels (*Dreissena polymorpha*). Pages 667–675 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Jenner, H. A., and J. P. M. Janssen-Mommen. 1993. Monitoring and control of *Dreissena polymorpha* and other macrofouling bivalves in the Netherlands. Pages 537–553 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Kaftannikova, O. G., A. A. Protasov, R. A. Kalinichenko, and S. Afans'yev. 1987. Biofouling in the reservoirs and water supply systems of fossil and nuclear power stations. Pages 56–61 in O. A. Skarlato, ed. *Izucheniye Morskogo Obrastaniya i Pazrabotka Metodov Borby s Nim* (Marine Biofouling Study and Development of New Control Methods). ZIN Press, Leningrad, Russia.

Karpevitch, A. F. 1955. Some data on the formation of species in Bivalvia. *Zool. Zh.* 34: 40–67. (In Russian)

______. 1964. The characteristic of reproduction and growth of bivalves in brackish seas of USSR. Pages 3–60 in L. A. Zenkevich, ed. *Ekologiya Bespozvonochnykh Yuzhnykh Moryey SSSR (The Ecology of Invertebrates in Southern Seas of USSR).* Nauka Press, Moscow. (In Russian)

Katchanova, A. A. 1961. Some data on *Dreissena polymorpha* Pallas reproduction in the Uchinsk Reservoir (USSR). *Tr. Vses Gidrobiol. Ova.* 11: 117–121. (In Russian)

Kharchenko, T. A., and A. V. Lyashenko. 1985. Destruction of allochthonous organic matter in canals in the presence of *Dreissena. Gidrobiol. Zh.* 21: 93–98. (In Russian)

Kilgour, B., and R. Kepple. 1993. Effects of salinity on the survival of zebra mussel veliger larvae. Paper presented at the Third International Zebra Mussel Conference, Toronto, Ontario, 25 February 1993.

Kilgour, B.W., and G.L. Mackie. 1993. Colonization of different construction materials by the zebra mussel (*Dreissena polymorpha*). Pages 167–173 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Kirpichenko, M. Y. 1971. Freshwater *Dreissena* on the northern-eastern vicinity of the areal. *Proceedings of the Institute of the Biology of Inland Waters of the Academy of Sciences of the USSR* 21(24): 130–141. (In Russian)

Klerks, P. L., and P. C. Fraleigh. 1991. Controlling adult zebra mussels with oxidants. *J. Am. Water Works Assoc.* 89 (12): 92–100.

Klerks, P. L., P. C. Fraleigh, and R. C. Stevenson. 1993. Controlling zebra mussel (*Dreissena polymorpha*) veligers with three oxidizing chemicals: chlorine, permanganate, and peroxide + iron. Pages 621–641 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Leach, J. H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western lake Erie. Pages 381–397 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Lebedeva, G. D. 1978. The main foulers in the fresh waters of European Russia. Pages 12–23 in N. S. Stroganov, ed. *Biopovrezhdeniya Materialov i Zashchita ot Nikh (Biodamage to Materials and its Control).* Nauka Press, Moscow. (In Russian)

Lee, H. H. 1993. Field testing of Endod, a botanical molluscicide, in the mitigation of zebra mussel. Paper presented at the Third International Zebra Mussel Conference, Toronto, Ontario, 25 February 1993.

Leitch, E. G., and F. V. Puzzuoli. 1992. Evaluation of coatings to control zebra mussel colonization: preliminary results 1990–1991. *Journal of Protective Coatings and Linings* 9(7): 27–41.

LePage, W. L. 1993. The impact of *Dreissena polymorpha* on waterworks operations at Monroe, Michigan: a case history. Pages 333–357 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Logvinenko, B. M., and Y. I. Starobogatov. 1968. Type Mollusca. Pages 368–385, 407–410 in Y. A. Birshtein and L. G. Vinogradov, eds. *Atlas Bespozvonochnykh Kaspiyskogo Morya (Atlas of Invertebrates of the Caspian Sea).* Pishchevaya Promyshlennost Press, Moscow. (In Russian)

Ludyanskiy, M. L. 1992. Potential for fouling by zebra mussels at Public Service Electric and Gas Utilities. Report to PSEG, Sandwich, MA.

______. 1993. Recent introductions of *Dreissena* and other forms into North America: the Caspian Sea/Black Sea connection. Pages 699–704 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Lvova, A. A. 1980. Ecology of *Dreissena* (*Dreissena polymorpha* Pall.). Pages 101–119 in G. G. Vinberg, ed. *Bentos Uchinskogo Vodokhranilishcha (Benthos of the Uchinsk Reservoir)*. Nauka Press, Moscow. (In Russian)

Lyakhnovich, V. P., A. Y. Karatayev, P. A. Mitrakhovich, L. V. Guryanova, and G. G. Vezhnovets. 1987. Productivity of and prospects for using the ecosystem of Lake Lukomskoye, the cooling reservoir of a thermoelectric power plant. *Ekologiya* 5: 43–48. (In Russian)

Lyakhnovich, V. P., A. Y. Karatayev, and G. M. Tishchikov. 1984. Historic and contemporary situation of settlement by *Dreissena polymorpha* Pallas in waters of Byelorussia. Pages 62–63 in V. N. Olshvang, ed. *Vid i Yego Produktivnost' v Areale (The Species and its Productivity within its Distribution Range). Part 4. Invertebrates.* Nauka Press, Sverdlovsk. (In Russian)

Mackie, G. L. 1991. Biology of exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia* 219: 251–268.

______. 1993. Biology of the zebra mussel (*Dreissena polymorpha*) and observations of mussel colonization on unionid bivalves in Lake St. Clair of the Great Lakes. Pages 153–165 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Mackie, G. L., W. N. Gibbons, B. W. Muncaster, and I. M. Gray. 1989. The zebra mussel, *Dreissena polymorpha*: a synthesis of European experiences and a preview for North America. Water Resources Branch, Great Lakes Section, Queen's Printer, Toronto, Ontario.

Marelli, D. 1991. Zhadin's systematic account of *Dreissena*: are the species valid? *Dreissena polymorpha Information Review* 2(4): 3.

Marsden, J. E. 1993. Substrate preferences of newly settled zebra mussels. Paper presented at the Third International Zebra Mussel Conference, Toronto, Ontario, 26 February 1993.

Martens, E. 1865. Eine eingewanderte Muschel. *Zool. Gart.* 6: 50–59, 89–97.

Mattice, J. S., B. Fellers, T. Armor, J. Tsou, M. Miller, and B. Nott. 1990. Zebra mussels: the EPRI response. Electric Power Research Institute, Palo Alto, CA.

May, B., and J. E. Marsden. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 49: 1501–1506.

McMahon, R. F. 1990. The zebra mussel: US utility implications. Electric Power Research Institute GS-6995, Project 1689-24, Palo Alto, California.

McMahon, R. F., B. N. Shipman, and D. P. Long. 1993. Laboratory efficacies of nonoxidizing molluscicides on the zebra mussel (*Dreissena polymorpha*) and the Asian clam (*Corbicula fluminea*). Pages 575–597 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

McMahon, R. F., T. A. Ussery, A. C. Miller, and B. S. Payne. 1993. Thermal tolerance in zebra mussels (*Dreissena polymorpha*) relative to rate of temperature increase and acclimation temperature. Paper presented at the Third International Zebra Mussel Research Conference, Toronto, Ontario, 24 February 1993.

Mikheev, V. P. 1964. Linear growth of *Dreissena polymorpha* in some reservoirs of the European USSR. Pages 55–65 in B. K. Shtegman, ed. *Biology and Control of Dreissena.* Trudy Instituta Biologii Vnutrennikh Vod, Soviet Academy of Sciences Press, Moscow-Leningrad. (Translated into English)

______. 1967. Filtrational nutrition of *Dreissena. Proceedings of the Institute of Pond Fisheries* 15: 117–129. (In Russian).

Mordukhai-Boltovskoi, F. D. 1960. *The Caspian Fauna in the Azov-Black Sea Basin.* Soviet Academy of Sciences Press, Moscow-Leningrad. (In Russian)

Morton, B. S. 1969. Studies on the biology of *Dreissena polymorpha* Pall. 4. Habits, habitats, distribution and control. *Water Treat. Exam.* 18(3): 233–240.

______. 1970. The evolution of the heteromyarian condition in the Dreissenacea (Bivalvia). *Paleontology* 13: 563–572.

______. 1993. The anatomy of *Dreissena polymorpha* and the evolution and success of the heteromyarian form in the Dreissenoidea. Pages 185–215 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Neary, B. P., and J. H. Leach. 1992. Mapping the potential spread of the zebra mussel (*Dreissena polymorpha*) in Ontario. *Can. J. Fish. Aquat. Sci.* 49: 406–415.

Neuhauser, E. F. 1993. Thermal treatment to control zebra mussels in circulating water systems. Paper presented at the Third International Zebra Mussel Conference, Toronto, Ontario, 25 February 1993.

Neumann, D., and H. A. Jenner, eds. 1992. *The Zebra Mussel* Dreissena polymorpha: *Ecology, Biological Monitoring and First Applications in Water Quality Management.* Gustav Fisher Verlag, New York.

Neumann, D., J. Borcherding, and B. Jantz 1993. Growth and seasonal reproduction of *Dreissena polymorpha* in the Rhine River and adjacent waters. Pages 95–109 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Nichols, S. J. 1993. Spawning of zebra mussels (*Dreissena polymorpha*) and rearing of veligers under laboratory conditions. Pages 315–329 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Nichols, S. J., and M. G. Black. 1993. Veligers: zebra mussel, quagga, and hybrids. Paper presented at the Third International Zebra Mussel Conference, Toronto, Ontario, 25 February 1993.

Nichols, S. J., and B. Kollar. 1991. Reproductive cycle of zebra mussels (*Dreissena polymorpha*) in Western Lake Erie at Monroe, Michigan. Paper presented at the Second International Zebra Mussel Conference, Rochester, NY, 19 November 1991.

O'Neill, C. R. Jr., and D. B. MacNeill. 1991. The zebra mussel (*Dreissena polymorpha*): an unwelcome North American Invader. Sea Grant Coastal Resources Fact Sheet.

Osadchikh, V. F. 1988. Long-term abundance of *Dreissena polymorpha* in the Northern Caspian Sea. Pages 22–42 in *Kolichestvennoye i Kachestvennoye Raspredeleniye Bentosa: Kormovaya Basa Bentosoyadnykh Ryb (Quantitative and Specific Distribution of Benthos: Food Supply of Benthophage Fishes).* VNIRO Press, Moscow. (In Russian)

Pallas, P. S. 1773. *A Voyage to Various Places in the Russian State.* Part 1. M. G. Karpinskiy, ed. Saint Petersburg, Russia. (In Russian)

Protasov, A. A. 1979. Dynamics of specific abundance of zooperiphyton on the artificial substrates under influence of heated discharge of power plant. *Gidrobiol. Zh.* 15(4): 48–50. (In Russian)

Protasov, A. A., and S. A. Afanas'yev. 1984. Lateral types of *Dreissena* populations in the cooling pond of the Chernobyl nuclear power plant. *Zh. Obsh. Biol.* 45: 272–277. (In Russian)

Ramcharan, C. W., D. K. Padilla, and S. I. Dodson. 1992. A multivariate model for predicting population fluctuations of *Dreissena polymorpha* in North American Lakes. *Can. J. Fish. Aquat. Sci.* 49: 150–158.

Reeders, H. H, and A. bij de Vaate. 1992. Bioprocessing of polluted suspended matter from the water column by the zebra mussel (*Dreissena polymorpha* Pallas). *Hydrobiologia* 239: 53–63.

Reeders, H. H, A. bij de Vaate, and F. J. Slim. 1989. The infiltration rate of *Dreissena polymorpha* (Bivalvia) in three Dutch lakes with reference to biological water quality management. *Freshwater Biol.* 22: 133–141.

Roberts, R. 1990. Zebra mussel invasion threatens US waters. *Science* 249: 1370–1372.

Schloesser, D. W., and W. P. Kovalak. 1991. Infestation of native unionids by *Dreissena polymorpha* in a power plant intake canal in lake Erie. *J. Shellfish Res.* 10: 355–359.

Schneider, D. 1992. A bioenergetics model of zebra mussel growth in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 49: 1406–1416.

Sheffer, B. 1990. Zebra mussels: the Great Lakes' latest menace. New York State Senate Majority Task Force on Zebra Mussels, Albany.

Shevtsova, L. V. 1968. Spawning and development of *Dreissena* in the canal Dnieper-Krivoi Rog. *Gidrobiol. Zh.* 4: 70–72. (In Russian)

Skorikov, A. S. 1903. Recent distribution of *Dreissena polymorpha* Pallas in Russia. *Ezhegodnik Volzhskoi Biologicheskoi Stantsii* 4: 205–250. (In Russian)

Smit, H., A. bij de Vaate, H. H. Reeders, E. H. van Nes, and R. Noordhuis. 1993. Colonization, ecology, and positive aspects of *Dreissena polymorpha* in the Netherlands. Pages 55–77 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Sprung, M. 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. *Arch. Hydrobiol. Suppl.* 79: 69–86.

______. 1990. Costs of reproduction: a study on metabolic requirements of the gonads and fecundity of the bivalve *Dreissena* *polymorpha. Malacologia* 32: 267–274.

______. 1993. The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha.* Pages 39–53 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. *Pol. Arch. Hydrobiol.* 24: 461–530.

Stanczykowska, A., W. Lawacz, and J. Mattice. 1975. Use of field measurements of consumption and assimilation in evaluating the role of *Dreissena polymorpha* Pall. in a lake ecosystem. *Pol. Arch. Hydrobiol.* 22: 509–520.

Strayer, D. L. 1991. The projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Can. J. Fish. Aquat. Sci.* 48: 1389–1395.

Strayer, D. L., and L. C. Smith. 1993. Distribution of the zebra mussel (*Dreissena polymorpha*) in estuaries and brackish waters. Pages 715–727 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis, Chelsea, MI.

Ten Winkel, E. H., and C. Davids. 1982. Food selection by *Dreissena polymorpha* Pallas (Mollusca: Bivalvia). *Freshwater Biol.* 12: 553–558.

Trulear, M. G., E. W. Ekis, and G. Elliot. 1990. Macrofouling control. Paper presented at the 51st Annual Meeting of the International Water Conference, Pittsburgh, PA, 22 October 1990.

Van Benschotten, J. E., J. N. Jensen, D. Lewis, and T. J. Brady. 1993. Chemical oxidants for controlling zebra mussels (*Dreissena polymorpha*): a synthesis of recent laboratory and field studies. Pages 599–619 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Vinogradov, G. A., N. F. Smirnova, V. A. Sokolov, and A. A. Bruznitsky. 1993. Influence of chemical composition the water on the mollusc *Dreissena polymorpha.* Pages 283–293 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.

Walz, N. 1973. Studies on the biology of *Dreissena polymorpha* in Lake Constance. *Arch. Hydrobiol. Suppl.* 42: 452–482.

______. 1975. Die Besiedlung von kuntlichen Substraten durch Larven von *Dreissena polymorpha. Arch. Hydrobiol. Suppl.* 47: 423–431.

______. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* in laboratory experiments and in Lake Constance. 2. Reproduction. *Arch. Hydrobiol. Suppl.* 55: 106–119.

______. 1991. New invasions, increase, and ecological equilibrium of *Dreissena polymorpha* populations in central and southern European lakes and rivers. Paper presented at the Second International Zebra Mussel Conference, Rochester, NY, 19 November 1991.

Zenkevich, L. A. 1965. *The Biology of the Seas of the USSR.* Interscience Publ., New York.

Zhadin, V. I. 1946. Travelling mussel *Dreissena. Priroda* 5: 29–37. (In Russian)

______. 1952. *Mollusks of Fresh and Brackish Waters of the USSR: Keys to the Fauna of the USSR.* Soviet Academy of Sciences Press, Moscow-Leningrad. (Translated into English)

Zebra Mussel Monitoring and Control Guide. 1993. Electric Power Research Institute TR-101782s, Palo Alto, CA.

Yankovich, T. L., and G. D. Haffner. 1993. Habitat selectivity by the zebra mussel (*Dreissena polymorpha*) on artificial substrates in the Detroit River. Pages 175–183 in T. F. Nalepa and D. W. Schloesser, eds. *Zebra Mussels: Biology, Impacts, and Control.* Lewis Publ., Chelsea, MI.
