

THE EFFECTS OF *DREISSENA POLYMORPHA* (PALLAS) INVASION ON AQUATIC COMMUNITIES IN EASTERN EUROPE

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ABSTRACT *Dreissena polymorpha* has been invading fresh waterbodies of eastern and western Europe since the beginning of the 19th century and is still invading. A long history of monitoring and experimental studies conducted in the Former Soviet Union (FSU) has provided us with an understanding of the effects of zebra mussels on waterbodies they invade. However, this work has not been generally available. We review work conducted in the FSU and eastern Europe over the past 60 y on the community effects of this invading species. In freshwater areas, where *Dreissena* are the only bivalves that attach to hard substrates and have a planktonic larval stage, they can become enormously abundant and, within a short period of time, can obtain a biomass 10 times greater than that of all other native benthic invertebrates. When zebra mussels invade, benthic invertebrate communities change dramatically in terms of total biomass, species composition, and relative abundance of functional groups. Native filter feeders are outcompeted by *D. polymorpha* and decrease in abundance, while animals feeding on the sediments increase in abundance. Although *D. polymorpha* can cause a dramatic decline in the abundance of unionids, after initial peaks in zebra mussel abundance, *D. polymorpha* coexist with unionids. *Dreissena* are very effective filter feeders and shift materials from the pelagic to the benthos through their filter feeding and deposition of pseudofeces. When zebra mussels invade phytoplankton and zooplankton abundance decreases, the biomass of benthophage fish increases, and a greater percentage of the primary productivity is consumed by higher trophic levels than in systems without zebra mussels.

KEY WORDS: Zebra mussels, freshwater ecosystems, benthic-pelagic coupling, benthic communities, unionids

INTRODUCTION

The zebra mussel, *Dreissena polymorpha* Pallas (1771), was found across Europe before the last glaciation (Starobogatov and Andreeva 1994). The Caspian Sea, the Black Sea Basin, the Azov Sea, and lower parts of rivers feeding them formed the postglacial distribution of the zebra mussel until early in the 19th century, when shipping canals for transportation and commerce were developed from the Black Sea basin to the Baltic Sea basin (Köppen 1883, Andrusov 1897, Arwidsson 1926, Ovchinnikov 1933, Deksbakh 1935, Zhadin 1946, Mordukhai-Boltovskoi 1960). The zebra mussel invaded through new waterways, primarily through the Dnieprovsko-Nemansky route, which connected the Dnieper (Black Sea basin) and the Neman rivers (Baltic Sea basin) (Starobogatov and Andreeva 1994), and the canal that connected the Dnieper and Zapadniy Bug rivers (Kinzelbach 1992). The first ships traveled the Dnieper-Neman Canal in 1804 and Dnieper-Zapadniy Bug Canal in 1775. By 1824, zebra mussels were found in England, and by 1825, they were found in eastern Prussia (Starobogatov and Andreeva 1994). Zebra mussels continued to spread rapidly through the freshwaters of Eurasia. Today, new lakes and rivers in eastern and western Europe are still being invaded (Géroutet 1966, Lyakhnovich et al. 1984, Karatayev 1989, Kinzelbach 1992, and others). Although *Dreissena bugensis* (quagga mussel) has invaded the Ukraine and spread in the South Bug and Dnieper River basins (Starobogatov and Andreeva 1994), only *D. polymor-*

pha has invaded northwestern former Soviet Union (FSU), including Belarus, and has been the major target of study by FSU scientists.

There is a long, rich history of research on *Dreissena* in the FSU and eastern Europe, focusing on taxonomy, biology, food web ecology, productivity, and ecosystem function. Problems associated with electric power plants, industry, and municipal water supplies due to invasions of *Dreissena* after World War II stimulated research on the biology and control of this invading species. In addition, in the 1970s, zebra mussels and several other freshwater taxa were targeted for study under a project that was part of an international research program coordinated by UNESCO, the Man and Biosphere Program (Starobogatov 1994). This project stimulated further studies of the ecological roles and effects of *D. polymorpha*. Given this extensive history of research, we have long-term data on both pre- and post-zebra mussel invasion communities for a variety of waterbodies. In addition, many studies have been conducted on specific lakes at different stages of invasion, early when zebra mussel populations and biomass are highest, and later when they decline. This has allowed us to determine the role and function of *Dreissena* during all phases of invasion and in different types of waterbodies.

Unfortunately, because of language and political barriers, this extensive body of work has not been readily available to North America and English-speaking scientists. Our goal is to provide access to this information. We summarize 60 y of research conducted to elucidate the role and function of *D. polymorpha* in freshwater systems studied in the FSU and eastern Europe. We

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consider how zebra mussels alter benthic communities both by their feeding activities and by creating a new habitat type for benthic species, and how their filtering affects planktonic species and food web interactions. We address the ecological role of zebra mussels as filter feeders. In many cases, differences in methodologies have made direct comparisons of studies difficult. We address this issue by converting existing data to similar units (where possible) for direct comparison and make recommendations for preferred methods and units for future research.

EFFECT ON BENTHIC COMMUNITIES

In benthic communities within their native distribution, such as the brackish waters of the Caspian Sea, Aral Sea, and Azov Sea, *Dreissena* generally are not the dominant species. For example, in Taganrog Bay of the Azov Sea, the bivalve *Monodacna colorata* is the dominant species and is only occasionally codominant with *D. polymorpha* (Vorobiev 1949, Nekrasova 1971). In the northern part of the Caspian Sea, *D. polymorpha* and *Dreissena rostriformis* comprise only 25% of the bivalve biomass; *Didacna* and *Monodacna* are typically more abundant (Shorygin and Karpevich 1948). In freshwaters, where they are the only bivalves that attach to hard substrates and have a planktonic larval stage, dreissenids, especially *D. polymorpha*, can become enormously abundant and, within a short period of time, can obtain a biomass 10 times greater than that of all other native benthic invertebrates (Sokolova et al. 1980a, Shevtsova and Kharchenko 1981, Karatayev 1983, Kharchenko 1983, Karatayev 1988, Karatayev and Lyakhnovich 1988, Lyakhnovich et al. 1988, Kharchenko 1990, Protasov and Afanasiev 1990, Karatayev 1992, Karatayev et al. 1994a, Sinityna and Protasov 1994, Karatayev and Burlakova 1995a). When outside its original distribution, the zebra mussel is frequently competitively dominant over native freshwater fauna and has large effects on all parts of the ecosystem, especially benthic animals (Dusoge 1966, Wiktor 1969, Wolnomiejski 1970, Sokolova et al. 1980b, Kharchenko and Protasov 1981, Karatayev 1983, Karatayev et al. 1983, Afanasiev 1987, Karatayev and Lyakhnovich 1988, Karatayev 1992, Karatayev et al. 1994a, Karatayev and Burlakova 1995a).

Changes in Benthic Community With Zebra Mussels

By aggregating in large densities, *D. polymorpha* create new two- and three-dimensional habitats for different organisms, and pseudofeces and feces provide an abundant food supply for detritivores (Izvekova and Lvova-Kachanova 1972, Lvova-Kachanova and Izvekova 1973, Spiridonov 1976, Lvova et al. 1980, Sokolova et al. 1980b, Karatayev 1983, Karatayev et al. 1983, Kharchenko 1983, Karatayev 1988, Karatayev and Lyakhnovich 1988, Kharchenko 1990, Karatayev et al. 1994a, Slepnev et al. 1994). In addition, water flow induced by zebra mussel filtering improves oxygen conditions in the benthos. As a consequence, a different community forms in mussel aggregations.

The complex of *Dreissena* and its associated species forms a coherent, biologically generated interactive community, which has been called a consortium (Kharchenko and Protasov 1981, Kharchenko 1990, Karatayev et al. 1994a). Although a variety of animals can have a similar function in marine systems (e.g., marine mussel beds, coral reefs), only *Dreissena* has this role in freshwater. According to Kharchenko and Protasov (1981), there are several direct functional relationships between *Dreissena* and associated species: (1) formation of habitat (*Dreissena* create a habitat for

benthic species); (2) trophic relationships (*Dreissena* and their associates can have mutually beneficial feeding associations); (3) material relationships (*Dreissena* provide the materials, such as shell fragments, byssus, and small mussels, used by associated species for the construction of houses); (4) dispersal relationships (*Dreissena* can be transported by associated taxa).

The relationship between *D. polymorpha* and infaunal taxa may not be simple. Some species may be positively affected by *D. polymorpha*, while others are negatively affected (Sebestyen 1937, Dusoge 1966, Wolnomiejski 1970, Sokolova et al. 1980b, Karatayev 1983, Karatayev et al. 1983, Afanasiev 1987, Karatayev and Lyakhnovich 1990, Karatayev and Burlakova 1992, Karatayev et al. 1994a, Slepnev et al. 1994). We use studies done in Lukomskoe lake (Belarus), where isolated aggregations of zebra mussels, or druses, form in the sandy littoral zone, to demonstrate the effects of *D. polymorpha* on benthic communities (Karatayev 1983, Karatayev et al. 1983, Karatayev 1988, Karatayev et al. 1994a). Similar patterns have been observed in most other waterbodies studied (Dusoge 1966, Wiktor 1969, Wolnomiejski 1970, Kharchenko and Protasov 1981, Afanasiev 1987, Karatayev et al. 1994a, Slepnev et al. 1994, and others).

To assess the effect of druses on the benthic community, Karatayev and his associates sampled both sand and druse communities. The presence of individual *D. polymorpha* on the bottom did not change the qualitative and quantitative composition of the benthic community (Karatayev 1983, Karatayev et al. 1983, Karatayev 1988, Karatayev et al. 1994a). However, in the presence of druses, the community changed radically. Species density and community composition depended on the size of druses. With increasing druse size, species richness increased and then stabilized in druses of more than 80 individual mussels. Forty-eight species and higher taxa of benthic animals were identified in the absence and presence of druses, but only 26 appeared to be members of both communities. In the sandy community, chironomids and oligochaetes were the most common taxa, as in preinvasion communities. The majority were small animals that live within the sediment. In the zebra mussel aggregations, the benthic community was composed of larger animals such as snails, amphipods, isopods, trichoptera, and leeches. For each species in each habitat type, they calculated a dominance index, $P \cdot \sqrt{B}$ (Mordukhai-Boltovskoi 1940) where P is the percentage of samples with a given species, and B is the average biomass of that species across all samples. The dominant species in the sand habitat was the chironomid *Stictochironomus psammophilus*, whereas in the druses, only a single individual of this species was found. The snail *Limnaea lagotis* and the amphipod *Gammarus lacustris* were dominant in zebra mussel druses, whereas in the sand community, only a single *L. lagotis* and no *G. lacustris* were found. Subdominant taxa were also dissimilar between these two habitat types (Karatayev 1983, Karatayev et al. 1983, Karatayev 1988, Karatayev et al. 1994a).

Total benthic density in sandy sediments was $40,995 \pm 3,263 \text{ m}^{-2}$, and total wet biomass was $15.1 \pm 1.0 \text{ g m}^{-2}$. In *D. polymorpha* druses (without including mussels), the density of benthic animals was $27,536 \pm 4,085 \text{ m}^{-2}$, and the biomass was $114.8 \pm 20.0 \text{ g m}^{-2}$. Invertebrate biomass was 8 times greater in druses, even though densities were 1.5 times lower than in sandy sediments because the community consisted of larger species. Therefore, a new community, not generally found in sandy sediments, forms in *D. polymorpha* druses, and the typical sandy sediment

community disappears, creating a mosaic pattern in the benthos (Karatajev 1983, Karatajev et al. 1983, Karatajev 1988, Karatajev et al. 1994a).

Slepnev et al. (1994) compared invertebrate colonization of zebra mussel druses and rubber models of druses in a cooling pond for the Krivoy Rog Power Plant (Ukraine). They found that after 14 days of exposure, the total density of invertebrates in the containers with *D. polymorpha* was significantly higher ($346,687 \pm 56,276 \text{ m}^{-2}$) than that in containers containing rubber models ($116,000 \pm 20,335 \text{ m}^{-2}$). The largest differences were found for Cyclopidae (19.7 times greater), *D. polymorpha* veligers (9.9 times greater), and Chydoridae (5 times greater) (Slepnev et al. 1994).

Kharchenko and Protasov (1981), using the Shannon index, found that the diversity of benthic communities increased more than two times in the presence of *Dreissena* (*D. polymorpha* + *D. bugensis*) in the North-Crimean Canal (Ukraine). They also found substantial increases in species richness, density, and biomass of benthic fauna. Shevtsova and Grigorovich (1989) found the same result in the Dnieper-Donbass Canal (Ukraine).

Karatajev and Lyakhnovich (1990) found that without *D. polymorpha*, the crustaceans *Asellus aquaticus* and *G. lacustris* populated the shallow littoral zone of Lukomskoe lake. At depths over 2 m, these two species were only found with *D. polymorpha*, and the density of *A. aquaticus* was positively correlated with the density of *D. polymorpha* ($r = 0.7$) (Karatajev and Lyakhnovich 1990).

Similar patterns have been found in other European studies. Dusoge (1966) found that the abundance of benthic invertebrates in Mikolajskie Lake (Poland) was positively correlated with zebra mussel abundance. Afanasiev (1987) found positive correlations between zebra mussel biomass and the density of some oligochaetes in the cooling reservoir of a power plant (Ukraine) (e.g., *Aulodrilus limnobius*, $r = 0.98$; *Psammoryctides albicola*, $r = 0.99$; *Limnodrilus hoffmeisteri*, $r = 0.98$), but for others, he found no correlation or negative correlation (e.g., *Nais bretscheri*; $r = -0.76$). Wolnomiejski (1970) reported that *D. polymorpha* provide substrate or shelter for many benthic taxa, including the isopod, *A. aquaticus*, larval chironomids *Microtendipes* gr. *chloris* and *Limnochironomus* gr. *nervosus*, and the leech *Helobdella stagnalis*. Also, Wiktor (1969) found that the benthic biomass near colonies of *D. polymorpha* was twice that found elsewhere. Spatially complex groups of *D. polymorpha* create favorable microhabitats for small organisms as well. The abundance of oligochaetes in the Chernobyl Nuclear Power Station cooling pond (Ukraine) increased from 17,000 to 39,000 m^{-2} with the addition of *D. polymorpha*, and densities were significantly correlated with *D. polymorpha* biomass (A. A. Protasov and O. O. Sinitsyna, personal communication, Institute of Hydrobiology Ukrainian Academy of Sciences, Kiev, Ukraine).

In North America, zebra mussels seem to have similar effects on benthic communities (Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts et al. 1996). Wisenden and Bailey (1995) found that the density of macroinvertebrates in Lake Erie associated with higher densities of *D. polymorpha* (720.8 m^{-2}) was $3,452.2 \pm 1,192.3 \text{ m}^{-2}$, and the taxonomic richness was 6.0 ± 0.6 ; the density of invertebrates associated with low densities of *D. polymorpha* (152.2 m^{-2}) was $411.6 \pm 58.7 \text{ m}^{-2}$, and the taxonomic richness was 3.1 ± 0.5 . Botts et al. (1996) compared the density of benthic invertebrates in bare sand and in sand associated with zebra mussel druses in Lake Erie. In a survey, they found that the densities of amphipods, chironomids, oligochaetes, turbellarians, hydrozoans,

and the total invertebrate density were significantly higher in sand with druses than in bare sand. In an experiment with mesh bags containing either living druses, artificial druses made from cleaned zebra mussel shells, or no zebra mussels, they found that chironomids were significantly more abundant in living druses than in nonliving druses. There were no significant differences in oligochaetes among all three treatments. Therefore, it seems that North American and FSU benthic invertebrate communities respond similarly to the addition of zebra mussels.

Trophic Shifts

When zebra mussels invade, the development of a large population of effective filter feeders causes a radical shift in the benthic trophic structure (Lvova-Kachanova and Izvekova 1978, Sokolova et al. 1980a, Sokolova et al. 1980b, Karatajev 1992, Karatajev and Burlakova 1992, Karatajev et al. 1994a). Native filter feeders are outcompeted by *D. polymorpha* and decrease in abundance, whereas animals feeding on the sediments increase in abundance (Karatajev and Burlakova 1992, Karatajev et al. 1994a). Studies of Lukomskoe lake provide the most complete information on the affect of *D. polymorpha* on the trophic structure of invertebrate communities (Karatajev and Burlakova 1992). The feeding mode of 117 of the 245 species living in Lukomskoe lake were determined from the literature (Burlakova, unpublished data). These 117 species constitute more than 99% of the total biomass of benthic invertebrates in this lake. Karatajev and Burlakova (1992), using data from Lyakhnovich et al. (1982), collected in 1968 and 1969 for information on the community before the zebra mussel invasion, and Karatajev (1983) data from 1978 (8 y after *D. polymorpha* invaded), determined the trophic structure of the zoobenthos before and after zebra mussel invasion. Using a classification scheme based on feeding characteristics developed by Izvekova (1975), the community of benthic invertebrates was divided into the following trophic groups: I, detritus filterers; II, detritus filterers + gatherers; III, detritus gatherers; IV, deposit feeders; V, omnivorous gatherers + grabbers; VI, predators-active grabbers. This scheme is similar to that developed by Cummins (1978), but differs in some important ways. The first four groups in Izvekova's scheme (detritus filterers, detritus filterers + gatherers, detritus gatherers, and deposit feeders) are equal to Collectors in Cummins' scheme. The fifth group in Izvekova's classification (omnivorous gatherers + grabbers) includes Shredders and Scrapers in Cummins' classification. The sixth group (predators-active grabbers) is equal to Piercers and Engulfers (predators) in Cummins' classification.

Before the appearance of *D. polymorpha*, the littoral zone was dominated by detritus gatherers (III) and detritus filterers (I), mainly snails and bivalves (Table 1). Other trophic groups were not a significant part of the community. The trophic structure of the profundal zone was more complex and included predators-active grabbers (VI, larval chironomids, *Procladius choreus*, and *Chaoborus*), deposit feeders (IV), and detritus filterers + gatherers (II, mainly *Chironomus plumosus*). For the whole lake, the most important groups were the detritus gatherers (III) and detritus filterers (I) (Karatajev and Burlakova 1992).

After the invasion of *D. polymorpha*, without including *D. polymorpha*, the role of detritus gatherers (III) in the littoral zone increased because of the expansion of their food supply, organic matter deposited by *D. polymorpha*. The number of predators-active grabbers (VI) and omnivorous gatherers + grabbers (V) also increased. The proportion of native detritus filterers (I) decreased

TABLE 1.
Trophic structure of the zoobenthos of Lukomskoe lake before and after the appearance of zebra mussels.

Trophic Group	Littoral Zone			Profundal Zone			Whole Lake		
	Preinvasion	Postinvasion		Preinvasion	Postinvasion		Preinvasion	Postinvasion	
		Without Zebra Mussels	With Zebra Mussels		Without Zebra Mussels	With Zebra Mussels		Without Zebra Mussels	With Zebra Mussels
I Detritus filterers	43.7	5.1	95.9	8.1	5.5	7.5	40.9	5.3	94.8
II Detritus filterers + gatherers	0.3	1.4	0.1	21.7	7.5	7.4	2.0	3.0	0.2
III Detritus gatherers	48.2	71.3	3.1	8.3	59.6	58.3	45.2	69.7	3.8
VI Deposit feeders	6.8	8.3	0.3	21.8	18.4	18.0	7.9	10.9	0.6
V Omnivorous gatherers + grabbers	0.5	3.6	0.2	0.3	2.8	2.7	0.4	3.2	0.2
VI Predators-active grabbers	0.5	10.3	0.4	39.8	6.2	6.1	3.6	7.9	0.4

Cell values are the percentage of the total benthic biomass (g) found in each trophic group (from Karatayev and Burlakova 1992).

eightfold. In the profundal zone, the dominant group of benthic animals was detritus gatherers (III) and then deposit feeders (IV). The biomass of detritus filterers + gatherers (II), detritus filterers (I), and predators-active grabbers (VI) decreased relative to preinvasion communities. Except for *D. polymorpha*, the community was dominated by animals using food from sediments (Karatayev and Burlakova 1992, Karatayev et al. 1994a).

If *D. polymorpha* is considered with the rest of the benthic community, the trophic structure of the benthic community is characterized by an extremely high dominance of one trophic group—detritus filterers (I)—which accounts for 95% of the total biomass of benthic invertebrates (Karatayev and Burlakova 1992). As a result, the trophic structure of the littoral zone is reduced, and the remaining trophic groups contribute relatively small amounts of biomass to the total. The filter feeding species, which were dominant before the zebra mussel invasion, disappeared or became rare and gave way to detritus gatherers (III), predators-active grabbers (VI), and deposit feeders (IV) (Karatayev and Burlakova 1992, Karatayev et al. 1994a).

Similar patterns have been observed in four other waterbodies across the FSU (Karatayev et al. 1994a) (Table 2). Similar changes in trophic structure were found in Uchinskoe reservoir, where the invasion of *D. polymorpha* resulted in drastic changes in the benthos (Lvova-Kachanova and Izvekova 1978, Sokolova et al. 1980a, Sokolova et al. 1980b). *D. polymorpha* replaced the dominant species (the chironomid *Glyptotendipes paripes*) and changed the relative abundance of different species and trophic groups, especially chironomids that collect loose detrital particles (gatherers), who became most abundant in zebra mussel commu-

nities. Sokolova et al. (1980b) hypothesized that, as a result of the constant water exchange created by *D. polymorpha*, a habitat similar to nearshore benthos is created in druses. This would allow littoral zone species, such as the chironomid *Microtendipes pedilus*, which move from nearshore when water levels fluctuate to inhabit zebra mussel-dominated areas. Thus, the shift in benthic trophic structure induced by *D. polymorpha* in Lukomskoe lake is typical of that in waterbodies with established zebra mussel populations across the FSU (Karatayev et al. 1994a).

Geographic Clines in Benthic Communities With Zebra Mussels

Because zebra mussels occur over such vast geographic areas, the species they are associated with change with geographic region. To determine if the role of *D. polymorpha* is the same in spite of large faunal differences associated with different geographic areas, Karatayev et al. (1994a) analyzed data collected for six waterbodies located in different climatic zones of FSU: Lukomskoe lake (55°N), Volgogradskoe (49°N) and Tsimlyanskoe (48°N) reservoirs, Dniester (46°N) and Dnieper Bug (47°N) Limans (coastal brackish lakes), and Taganrog Bay (47°N) of the Sea of Azov (Karatayev et al. 1994a). Over 100 species and higher taxa of macroinvertebrates are found in all of these zebra mussel communities, and 46 occur more than once; thus, when *D. polymorpha* spread north, beyond the limits of their original distribution, they also spread beyond the distribution of their natural complex of associated species (i.e., inhabitants of Ponto-Caspian basin).

The most diverse benthic taxa found in zebra mussel commu-

TABLE 2.
Trophic structure of zoobenthos of zebra mussel communities from different waterbodies across the FSU.

Trophic Group	Lukomskoe Lake	Tsimlyanskoe Reservoir	Dniester Liman	Dnieper-Bug Liman	Taganrog Bay
I Detritus filterers	94.8	93.1	93.3	97.1	93.7
II Detritus filterers + gatherers	0.2	3.7	3.6	1.6	4.0
III Detritus gatherers	3.8	0.1	0.1	0.3	0.0
IV Deposit feeders	0.6	1.1	2.8	0.6	0.3
V Omnivorous gatherers + grabbers	0.2	1.9	0.1	0.3	0.3
VI Predators-active grabbers	0.4	0.1	0.1	0.2	0.1

Cell values are the percentage of the total benthic biomass (g) found in each trophic group (from Karatayev et al. 1994a).

nities were: Crustacea (22 species), Chironomidae (8 species), Gastropoda (4 species), and Oligochaeta (4 species) (Karatayev et al. 1994a). Crustaceans play particularly important roles in zebra mussel communities across Europe. Cumaceans (*Pterocuma pectinata*, *Schizorhynchus endorelloides*) dominate in waterbodies close to the original geographic distribution of zebra mussels. Further north, amphipods, especially gammarids, are dominant (Karatayev et al. 1994a). High densities of gammarids have also been found associated with *D. polymorpha* in other European waterbodies (Kharchenko 1983, Shevtsova and Grigorovich 1989, Protasov and Afanasiev 1990) and in North America (Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts et al. 1996).

Although the total species composition varied, *D. polymorpha* had an extremely high dominance index ($P \cdot \sqrt{B}$) in all communities studied. As a rule, when *D. polymorpha* are in freshwater, they are the single, dominant benthic species in terms of biomass, with a biomass 10–50 times greater than the total mass of all other benthic invertebrates in these communities (Sokolova et al. 1980a, Shevtsova and Kharchenko 1981, Karatayev 1983, Kharchenko 1983, Karatayev 1988, Karatayev and Lyakhovich 1988, Lyakhovich et al. 1988, Kharchenko 1990, Protasov and Afanasiev 1990, Karatayev 1992, Karatayev et al. 1994a, Sinitsyna and Protasov 1994, Karatayev and Burlakova 1995a).

Affects on Unionids

Before the invasion of *D. polymorpha*, the only large bivalves in freshwater benthic communities were unionids (superfamily Unionacea). Unionids have a very different lifestyle and life history than *D. polymorpha*. They live in soft sediment, crawl through sediment with a large foot, live solitary or in groups (but not in as extreme densities as *D. polymorpha*), have slow growth, have low fecundity, are long lived, and have parasitic glochidia larvae (McMahon 1991). Unionids can provide the most abundant source of hard substratum for the colonization of *D. polymorpha* in many lakes, reservoirs, and rivers (Sebestyen 1937, Zhadin and Gerd 1961, Wiktor 1963, Biryukov et al. 1964, Kuchina 1964, Wolff 1969, Lewandowski 1976, Karatayev 1983, Karatayev and Tishchikov 1983, Arter 1989, Karatayev and Burlakova 1995b). By attaching to their valves, *D. polymorpha* can make it more difficult for unionids to burrow and move through sediment, and the added mass of *D. polymorpha* can weigh down unionids, resulting in burial in very soft or unconsolidated sediments (Karatayev 1983, Karatayev and Tishchikov 1983). Mussel attachment to unionid valves can increase drag and the likelihood of dislodgment by water motion for species living nearshore (Karatayev 1983, Karatayev and Tishchikov 1983). In addition, zebra mussel attachment can occlude the openings in unionid valves, either preventing opening, for filtration and feeding, or closing the valves. *D. polymorpha* directly compete with unionids for food and occupy otherwise available space.

Many European scientists have found that *D. polymorpha* attached to living unionids more frequently than to other substrates (Sebestyen 1937, Biryukov et al. 1964, Wolff 1969, Lewandowski 1976, Karatayev 1983, Karatayev and Tishchikov 1983, Karatayev and Burlakova 1995b). Similar patterns have been found in North America in Lake St. Clair (Hebert et al. 1989).

The density of *D. polymorpha* in druses attached to living unionids is much higher than in those found on any other substrates within the same region of the littoral zone, including stones and empty valves (Karatayev 1983, Karatayev and Tishchikov

1983). This may indicate that live unionids provide better living conditions for *D. polymorpha*. Lewandowski (1976) found a strong correlation between the degree of overgrowth of unionids by zebra mussels and the average density of zebra mussels in lakes in Poland. In addition, he found that the mass of shells of *Anodonta piscinalis* heavily overgrown by *D. polymorpha* was significantly higher than the mass of shells of similar-sized unionids without *D. polymorpha*.

Unionids can actively move to areas with good food and oxygen conditions and, by mixing the water while filtering, can improve the local food and oxygen conditions for attached *D. polymorpha* (Karatayev 1983, Karatayev and Tishchikov 1983). However, overgrowth by zebra mussels adversely affects the host unionid. The extent of this effect depends on a number of factors, including: (1) time since invasion of *D. polymorpha* (Sebestyen 1937, Dussart 1966, Karatayev and Burlakova 1995b); (2) type of bottom sediment (Arter 1989, Karatayev and Burlakova, unpublished data); (3) unionid species (Lewandowski 1976, Arter 1989, Haag et al. 1993, Strayer and Smith 1996); and (4) unionid sex (Haag et al. 1993).

Extensive overgrowth by *D. polymorpha* of unionids, resulting in mass mortality, is characteristic of periods of rapid population growth of zebra mussels when they invade a new waterbody (Sebestyen 1937, Dussart 1966, Karatayev and Burlakova 1995b). Subsequent to this period, *D. polymorpha* coexist with native bivalves in FSU freshwaters. Although overgrowth can cause some host mortality, populations of unionids are not only preserved, but also can maintain high densities (Karatayev 1983, Karatayev and Tishchikov 1983, Miroshnichenko et al. 1984, Miroshnichenko 1987).

In the profundal zone of Lukomskoe lake, dominated by silt, *D. polymorpha* were found only on unionids. On average, about 20% of the total density and biomass of *D. polymorpha* in this lake were attached to living unionids (Karatayev 1983). Lewandowski (1976) found similar patterns in Mikolajskie Lake (Poland): *D. polymorpha* inhabited 85% of the unionids, and the total mass of attached *D. polymorpha* exceeded the mass of host unionids 35% of the time. Although there was a drop in the number of unionid species in Mikolajskie Lake from 1972 to 1987 from 5 (*Unio tumidus*, *Unio pictorum*, *Anodonta piscinalis*, *Anodonta cygnea*, and *Anodonta complanata*) to 3 (*U. tumidus*, *U. pictorum*, and *A. piscinalis*), this drop was not a direct result of zebra mussel effect (Lewandowski 1991). During this same time, the average density of zebra mussels declined from more than 2,000 m⁻² to less than 100 m⁻² (Stanczykowska and Lewandowski 1993). The decline in unionid diversity and zebra mussel density was attributed to increasing lake eutrophication and pollution (Lewandowski 1991).

In the Tsimlyanskoe reservoir (Russia), unionids (mainly *U. pictorum* and *A. cygnea*) successfully coexist with *D. polymorpha* (Miroshnichenko et al. 1984, Miroshnichenko 1987). Since 1960, the average annual biomass over the entire reservoir was 571 g m⁻² for *D. polymorpha*, 88 g m⁻² for *U. pictorum*, and 46 g m⁻² for *A. cygnea* (Miroshnichenko et al. 1984). According to Ponyi (1992), in Lake Balaton, the average density of unionids before the zebra mussel invasion (1932) was 3 m⁻²; between 1966 and 1968, it was 2 m⁻². The decline in the abundance of unionids (*U. tumidus*, *U. pictorum*, *A. cygnea*) in Lake Hallwil (Switzerland) from the 1910s to the 1980s was explained by a decrease in the number of host fish for unionid larvae, an increase in eutrophication, and the influence of *D. polymorpha*, which colonized the lake in the 1970s (Arter 1989).

The effect of *D. polymorpha* on unionids may depend on the

type of bottom sediment. In the Svisloch river (Belarus), sandy and rubble sediments alternate with silt. In sandy and rubble areas, unionids have up to 100 attached *D. polymorpha* per individual, whereas in silt, unionids bury in sediments and are completely free of zebra mussels, even though the density of unionids was up to 100 m⁻² (Karatayev and Burlakova, unpublished data). Arter (1989) found that in Lake Hallwil, *U. tumidus* is usually buried in the sediments and is rarely overgrown by zebra mussels. However, *A. cygnea* is often only partly buried and is colonized more often by zebra mussels.

Although the appearance of *Dreissena* in the North American waterbodies has been correlated with negative effects on aboriginal unionids (Haag et al. 1993, Gillis and Mackie 1994, Nalepa 1994, Schloesser and Nalepa 1994), a large decline in the diversity and abundance of unionids was detected long before the appearance of *Dreissena* (Nalepa et al. 1991, Schloesser and Nalepa 1994). Will *Dreissena* have greater effects on unionids in North America than in Europe? In preglaciation Europe, *Dreissena* and

unionids coexisted. Because North American aboriginal species have no evolutionary history of coexistence with *Dreissena*, *Dreissena* may have a larger effect on North American than European species. The species composition of unionids in North America is much different than that in Europe, and there may be species-specific differences in response to fouling. The bivalve fauna of North American freshwaters is the most diverse in the world, consisting of 250 native and 6 introduced species, 227 of which belong to the superfamily Unionacea (families Margaritiferidae and Unionidae) (McMahon 1991). The bivalve fauna in Europe consists of 62 species and only 14 species in the superfamily Unionacea (Jaekel 1967).

North American scientists have reported extremely high densities of *D. polymorpha*, more than several thousand per unionid (Hebert et al. 1991, Schloesser and Kovalak 1991, Gillis and Mackie 1994, Schloesser and Nalepa 1994). These densities are much higher than those reported by European scientists (Table 3). Do these differences constitute a significant difference in the

TABLE 3.
Effect of zebra mussels on unionids.

Location	% of Unionids Colonized	Number of Zebra Mussels per Host Unionid	Biomass of Zebra Mussels per Host Unionid (g)	Ratio of Mass of Zebra Mussels and Host Unionid	References
Europe: rapid growth of zebra mussel population					
Naroch lake, 1990	60	9.5	1.8	0.3	Karatayev and Burlakova 1995b
		(1-90)	(0.3-12.4)	(0.04-1.7)	
Naroch lake, 1993	100	135	34.0	2.8	Karatayev and Burlakova, unpublished data
		(41-200)	(9.5-46.1)	(0.3-6.6)	
Drozdy reservoir, 1995	100	38.1	12.6	1.8	Karatayev and Burlakova, unpublished data
		(7-280)	(3.9-57.4)	(0.5-11.0)	
Europe: established zebra mussel population					
Lukomskoe lake, 1978	75	40	7.6	1.2	Karatayev and Tishchikov 1983
		(2-216)	(0.2-49.8)	(0.04-9.10)	
Myastro lake, 1993	94	10	5.9	0.6	Karatayev and Burlakova, unpublished data
		(1-23)	(1.3-11.8)	(0.2-1.2)	
Mikolajskie Lake, 1972	85	20			Lewandowski 1976
		(<99)			
Mikolajskie Lake, 1974	92	52			Lewandowski 1976
		(<132)			
North America					
Lake St. Clair, 1989 (1 site only)		5,496		2-3	Hebert et al. 1991
		(<10,520)			
Lake St. Clair, 1990 (avg. of 15 sites)	97			1.2	Nalepa 1994
		(0-1,360)		(0-8.5)	
Western Lake Erie, September 1989	100	6,805	36	2/6	Schloesser and Nalepa 1994
		(<11,550)			
Western Lake Erie, May 1990	100	346	9	0.5	Schloesser and Nalepa 1994
Lake Erie, Power Plant Canal, August 1989	100	6,777	44.8	0.74	Schloesser and Kovalak 1991
		(2,491-10,732)	(30.0-54.9)	(0.46-3.79)	
Lake Clark, Michigan May 1996	100	219	5.8	0.40	Karatayev and Burlakova, unpublished data
		(60-473)	(1.9-13.6)	(0.08-0.97)	
Lake Vineyard, Michigan May 1996	100	118	16.1	0.22	Karatayev and Burlakova, unpublished data
		(34-179)	(3.8-34.9)	(0.07-0.41)	

Cell values are means. Ranges are in parentheses.

effect of zebra mussels on native unionids? From the perspective of the unionid, the mass of attached *D. polymorpha*, or the ratio of the mass of attached zebra mussels to the mass of the host unionid, is probably more important than density. Unfortunately, North American scientists rarely report their data in terms of mass. Of the studies that we could compare with European data, the mean ratio between the biomass of attached *D. polymorpha* and the host unionid was very similar to that found in Europe (Table 3).

Differences between the density of attached mussels reported by North American and European scientists could result if the size-frequency composition of zebra mussel populations is much smaller in North America, or if North American scientists include smaller mussels in their estimates of density than European scientists. In general, European scientists do not include mussels smaller than 1 or 2 mm in density estimates (Lvova 1977, Lvova 1980, Karatayev 1983, Lyashenko and Kharchenko 1988, Lvova et al. 1994, and others); however, sometimes they do not include mussels smaller than 5 (Bij de Vaate 1991) or 8 mm (Hamburger et al. 1990). The overwinter mortality of young-of-the-year and 1-y-old mussels is very high, and by the spring, the number of live mussels is greatly reduced. For example, in western Lake Erie in February 1989, the density of *D. polymorpha* was 24 ± 3.9 per unionid, and in August, after larval settlement, the density of mussels averaged $6,777 \pm 811$ per unionid (Schloesser and Kovalak 1991). In September 1989, the mass of mussels attached to unionids was three times greater than the unionid mass. By May and June 1990, the mass of attached mussels dropped to one-third of host unionid mass (Schloesser and Nalepa 1994).

Currently, North America is in the early phase of zebra mussel invasion, and populations are growing rapidly. At this stage of invasion, *D. polymorpha* caused a dramatic decline in the abundance of unionids in Europe (Sebestyen 1937, Dussart 1966, Karatayev and Burlakova 1995b). However, to our knowledge, the zebra mussel invasion did not result in the complete disappearance of unionids in any European lakes. After initial peaks in zebra mussel abundance, *D. polymorpha* coexist with unionids in all lakes, reservoirs, and rivers studied. Will this pattern hold true for

North America? With time, perhaps the effect of *D. polymorpha* on unionids will decrease.

EFFECT ON PELAGIC COMMUNITIES

Filtering Rate

Dreissena are filter feeders, capable of filtering large quantities of water in a relatively short period of time. Many of the effects of zebra mussels on freshwater ecosystems are linked to their filtering. They circulate water for respiration and feeding and remove particles from the water, which are either consumed or bound as pseudofeces and expelled to the benthos. Although many researchers have investigated the filtering of *D. polymorpha* (Voskresenski 1957, Kondratiev 1962, Mikheev 1966, Mikheev 1967a, Mikheev 1967b, Stanczykowska 1968, Kondratiev 1969, Kondratiev 1970; Morton 1971, Lvova 1977, Reeders and Bij de Vaate 1990, Karatayev and Burlakova 1993, Karatayev and Burlakova 1994), standardized methodology has not been used, and often, experimental setups are not adequately described to permit direct comparisons of results.

Filtering rates of *Dreissena* can be difficult to measure in the laboratory, and therefore, experimental design can affect results. If filtration cannot be measured in a flow-through system where concentrations of particles are held constant, it is recommended that experiments be in relatively large volumes of water and be of short duration such that the concentration of particles is not depressed more than 20–30% during the entire experiment (Zihon-Lukanina et al. 1990). In addition, experimenters must consider the differential filtration of particles of different sizes and qualities. Filtration estimates for natural seston may be much different than for single-species cultures or inert particles (Table 4).

FSU scientists generally calculate the filtering rate of *D. polymorpha* based on shell length or wet total mass (WTM, shell plus soft tissue) (Kondratiev 1962, Mikheev 1966, Mikheev 1967a, Mikheev and Sorokin 1966, Kondratiev 1969, Lvova 1977, Karatayev and Burlakova 1993, Karatayev and Burlakova 1994, Karatayev and Burlakova 1995b), as do many other Europeans

TABLE 4.
Filtering rate of zebra mussels from various studies.

Reference	Food	Temperature (°C)	Filtering Rate (mL g WTM ⁻¹ h ⁻¹)	Author's Units
Europe				
Kondratiev 1962	Natural seston	16–17	43	mL g WTM ⁻¹ h ⁻¹
Mikheev and Sorokin 1966	<i>Chlorella</i>	n.r.	69	mL ind. ⁻¹ h ⁻¹
Stanczykowska 1968	Natural seston	17–20	35	mL g WTM ⁻¹ h ⁻¹
Lvova 1977	Natural seston	17–20	40	mL g WTM ⁻¹ h ⁻¹
Dorgelo and Smeenk 1988	<i>Chlamydomonas eugametos</i>	15	35	mL ind. ⁻¹ h ⁻¹
Reeders and Bij de Vaate 1990	Natural seston	10–21	83	mL ind. ⁻¹ h ⁻¹
Wisniewski 1990	Natural seston	n.r.	110	mL ind. ⁻¹ h ⁻¹
Karatayev and Burlakova 1993	Natural seston	20	66	mL g WTM ⁻¹ h ⁻¹
Karatayev and Burlakova 1995a	Natural seston	20	38	mL g WTM ⁻¹ h ⁻¹
North America				
Bunt et al. 1993	<i>Cryptomonas</i> sp.	20	49	mL ind. ⁻¹ h ⁻¹
Aldridge et al. 1995	<i>Chlorella</i>	20	79	mg mg DBM ⁻¹ h ⁻¹
Heath et al. 1995	Natural seston	24	100	mL mg AFDM ⁻¹ h ⁻¹
Lei et al. 1996	Clay with adsorbed bacteria	15	83	mL mg AFDM ⁻¹ h ⁻¹

Filtering rates calculated by different authors were converted to volume of water filtered (mL) per hour per gram of WTM of zebra mussel. n.r., not reported. ind.⁻¹, per individual.

(Stanczykowska 1968, Morton 1971, Reeders and Bij de Vaate 1990, Wisniewski 1990), although some Europeans calculate filtering rate per dry body mass (soft tissue only, DBM) (Kryger and Riisgård 1988). The majority of North American scientists also calculate the filtering rate of zebra mussels per DBM (Aldridge et al. 1995) or per ash-free dry mass (soft tissue only, AFDM) (Fanslow et al. 1995, Heath et al. 1995, Lei et al. 1996).

To compare estimates of filtration calculated by different authors, we converted all available literature data to volume of water filtered (in milliliters) per gram of WTM per hour (Table 4). We used the relationship between shell length and WTM determined by Karatayev (1983) to convert reported zebra mussel shell lengths to WTM. For example, Mikheev and Sorokin (1966) measured the size-specific filtering rate of 9- to 29-mm mussels in short-duration experiments with C_{14} -labeled algae and bacteria. We calculated that the filtering rate in their study ranged from 38 to 160 mL g^{-1} per hour and averaged 69 mL g^{-1} per hour.

Comparing all of these various studies (Table 4), we found a relatively narrow range of measured filtering rates for *D. polymorpha* (from 35 to 110 mL g of WTM^{-1} per hour; average = 58 mL g of WTM^{-1} per hour), in spite of the fact that these studies were made by different researchers, for different waterbodies, and by different methods. Filtering rates depend on food concentrations (Walz 1978a, Sprung and Rose 1988, Karatayev and Burlakova 1994). According to Sprung and Rose (1988), filtering rates of individual *D. polymorpha* decreased from 290 to 50 mL h^{-1} when food concentrations (*Chlamydomonas reinhardtii*) increased from 0.1 to 85 cells μL^{-1} . The extremely high filtering rates (273 mL g of WTM^{-1} per hour) found by Kryger and Riisgård (1988) may be the result of very low concentrations of algae. Most North American scientists have calculated filtering rates of *D. polymorpha* ranging from 49 to 100 mL g of WTM^{-1} per hour, averaging 78 mL g of WTM^{-1} per hour, similar to European results (Table 4).

Common units are essential for cross-study comparisons of filtering rates of *D. polymorpha*. We suggest that the most appropriate units to use are milliliters of filtered water per gram of WTM per hour. WTM varies much less during one growing season than either AFDM or DBM (Karatayev 1983), and WTM can be measured easily and directly, even in the field. We also recommend that field estimates of zebra mussel-filtering rates be calculated as a function of WTM, not density of *D. polymorpha*. Different-sized mussels will filter at different rates; therefore, similar densities of mussels with different size-frequency distributions will have dramatically different filtering rates (Young et al. 1996).

Zebra Mussel as a Biofilter

Because zebra mussels occur in high densities over large areas in lakes, they can filter large volumes of water in relatively short periods of time and deposit vast quantities of pseudofeces on the bottom. In Uchinskoe reservoir (Russia), the population of *D. polymorpha* during the summer could filter the volume of water equivalent to that of the entire waterbody in 45 days (Lvova et al. 1980), Pyalovskoe reservoir (Russia) could be filtered in 20 days (Mikheev 1967a), and the cooling reservoir of the Chernobyl Nuclear Power Station (Ukraine) could be filtered in 5–6 days (Protasov et al. 1983). The time required to filter the entire volume of a variety of lakes in Poland ranged from several days to the entire growing season (Stanczykowska 1977). In two Dutch lakes, the zebra mussel population could filter the volume of water equivalent to that of the entire lake once or twice a month (Reeders et al. 1989).

Water that has been filtered by *D. polymorpha* is almost free of suspended matter (Lvova 1977). Filtered particles that are not ingested are deposited on the bottom as pseudofeces, and post-digested material are deposited as feces. In areas populated with *D. polymorpha* in Uchinskoe reservoir, mussels deposit 1,071 g^{-2} of seston annually (Lvova 1977, Lvova 1979). Before the invasion of *D. polymorpha*, the annual deposition of sediment at these sites was only 470 g^{-2} . The total population of zebra mussels in Pyalovskoe reservoir deposits more than 36,000 tons of suspended matter per year (Mikheev 1967a). In the North-Crimean Canal, *Dreissena* mineralize 786.9 tons of organic matter and deposit 8,872.9 tons in the form of agglutinates per year (Shevtsova and Kharchenko 1981). *D. polymorpha* in the Szczecin Gulf (Poland) filter 53 tons of seston per hour (Wiktor 1969).

D. polymorpha also transform ingested organic matter through digestion. For example, in Volgograd reservoir (Russia), zebra mussels mineralize about 700,000 tons of organic matter in one growing season (Spiridonov 1973). According to Hamburger et al. (1990), 9–18% of the net phytoplankton production is ingested and assimilated by *D. polymorpha* in Lake Esrom (Denmark).

The deposition of large amounts of seston significantly improves the food base for many benthic animals. According to Alimov (1981), in Mikolajskie Lake, the annual dietary requirement for all of the noncarnivorous animals is met by 16% of the seston deposited each year by bivalves. *D. polymorpha* produce 160 of the 164.5 tons of dry seston deposited by all bivalves in this lake.

Before the appearance of *D. polymorpha* in Lukomskoe Lake, benthic filter feeders were capable of filtering the volume equivalent of that of the lake in 15 y, and planktonic filterers could filter that same volume in 5 days, using Kryuchkova's (1989) estimate that zooplankton can filter 120 mL g^{-1} per day in a eutrophic lake. After *D. polymorpha* invaded Lukomskoe Lake, zooplankton abundance declined, and the time required for the zooplankton to filter the equivalent of the volume of the lake increased to 17 days (Karatayev and Burlakova 1992, Karatayev and Burlakova 1995a). By 1975, because of the presence of *D. polymorpha*, the filtering capacity of benthic invertebrates had increased 320 times, and the equivalent of the volume of the lake could be filtered in 17 days. At present, the benthos can filter this volume in 45 days.

BENTHIC PELAGIC COUPLING

Dreissena shift materials from the pelagic to the benthos by transporting suspended matter from the water column to the benthic community (Lvova-Kachanova 1971, Stanczykowska et al. 1976, Lvova 1977, Lvova 1980, Alimov 1981, Karatayev 1983, Lyakhnovich et al. 1983, Kharchenko and Lyashenko 1985, Karatayev 1988, Karatayev and Lyakhnovich 1988, Lyakhnovich et al. 1988, Shevtsova 1989, Karatayev 1992, Karatayev and Burlakova 1992, Reeders et al. 1993, Karatayev and Burlakova 1995a). A portion of filtered material is metabolized and used for the growth of soft body and shell, and the rest is available to other benthic organisms. Shell materials are permanently removed from the pelagic system and are buried after the death of the zebra mussel.

The movement of seston from the plankton to the benthos induced large changes in all aspects of lake ecosystems after the invasion of *D. polymorpha* (Karatayev 1983, Lyakhnovich et al. 1983, Mitrakhovich et al. 1983, Mitrakhovich 1984, Karatayev 1988, Lyakhnovich et al. 1988, Reeders and Bijde Vaate 1990,

Karatayev 1992, Karatayev and Burlakova 1992, Reeders et al. 1993, Karatayev and Burlakova 1995a). In Lukomskoe lake, early in the invasion of *D. polymorpha* during the growing season, water transparency increased from 1.8 to 4 m, and seston concentrations decreased threefold (Fig. 1). (Lyakhnovich et al. 1983, Lyakhnovich et al. 1988, Karatayev 1992, Karatayev and Burlakova 1995a). Dissolved organic matter in the water column also decreased. Increased water clarity resulted in an expansion of macrophyte cover (from 6 to 30% of total lake area) due to an increase in the depth at which macrophytes can grow (from 2.5 to 5 m). Subsequent to the invasion of *D. polymorpha*, the biomass of phytoplankton and zooplankton declined more than 10 times, whereas the abundance of zoobenthic organisms increased more than 10 times. The productivity of the fishery doubled, and the composition of the commercial catch is now characterized by an increase in benthophagus fishes that feed on *D. polymorpha* including roach, rudd, white bream, and bream (Karatayev 1983, Lyakhnovich et al. 1983, Mitrakhovich et al. 1983, Mitrakhovich 1994, Karatayev 1984, Lyakhnovich et al. 1988, Karatayev 1988, Karatayev 1992, Karatayev et al. 1994b, Karatayev and Burlakova 1995a).

After *D. polymorpha* declined in abundance after its initial invasion in Lukomskoe lake, summer transparency decreased to 3 m, but remained above preinvasion levels (1.8–2.0 m) (Karatayev 1992, Karatayev and Burlakova 1995a). Similar patterns were found for phytoplankton and zooplankton; abundance decreased when *D. polymorpha* initially reached very high abundance, but increased after *D. polymorpha* densities declined (Fig. 1). Again, they did not return to their original abundance. The overgrowth of

the lake by macrophytes has also decreased from 30 to 20% of the surface area, but remains higher than that before the zebra mussel invasion (6%) (Karatayev 1992, Karatayev and Burlakova 1995a).

D. polymorpha invaded the Narochansk lake system (mesotrophic Naroch lake, eutrophic Myastro lake, and highly eutrophic Batorino lake) in the mid-1980s, after regular studies of these lakes had been conducted for approximately 40 y (Karatayev and Burlakova 1995b). Although morphometry, trophic status, species composition, and density of macrophytes, planktonic, and benthic organisms were different in these lakes (Babitsky 1985, Gavrilov 1985, Kryuchkova 1985, Mikheeva 1985, Ostapenya 1985, Winberg 1985), *D. polymorpha* was associated with similar changes in all three ecosystems (Ostapenya et al. 1993, Ostapenya et al. 1994a, Ostapenya et al. 1994b). After *D. polymorpha* invaded, water transparency increased 1.3–2.4 times, the concentration of seston was reduced 2.3–6.9 times, and the chlorophyll content decreased 2.7–6.9 times. Organic carbon content, BOD_5 , primary production, respiration, and biomass of phytoplankton decreased (Ostapenya et al. 1993, Ostapenya et al. 1994a, Ostapenya et al. 1994b). *D. polymorpha* reduce the effects of eutrophication in these lakes. Thus, highly eutrophic Batorino became eutrophic (Ostapenya et al. 1994b), and eutrophic Myastro became slightly eutrophic (Ostapenya et al. 1994a). It appears that *D. polymorpha* can be used to control the negative effects of anthropogenic eutrophication, including increased phytoplankton abundance and decreased water clarity (Karatayev 1983, Karatayev 1984, Karatayev 1988, Karatayev 1992). Some western European scientists have proposed using *D. polymorpha* for biofilters to decrease

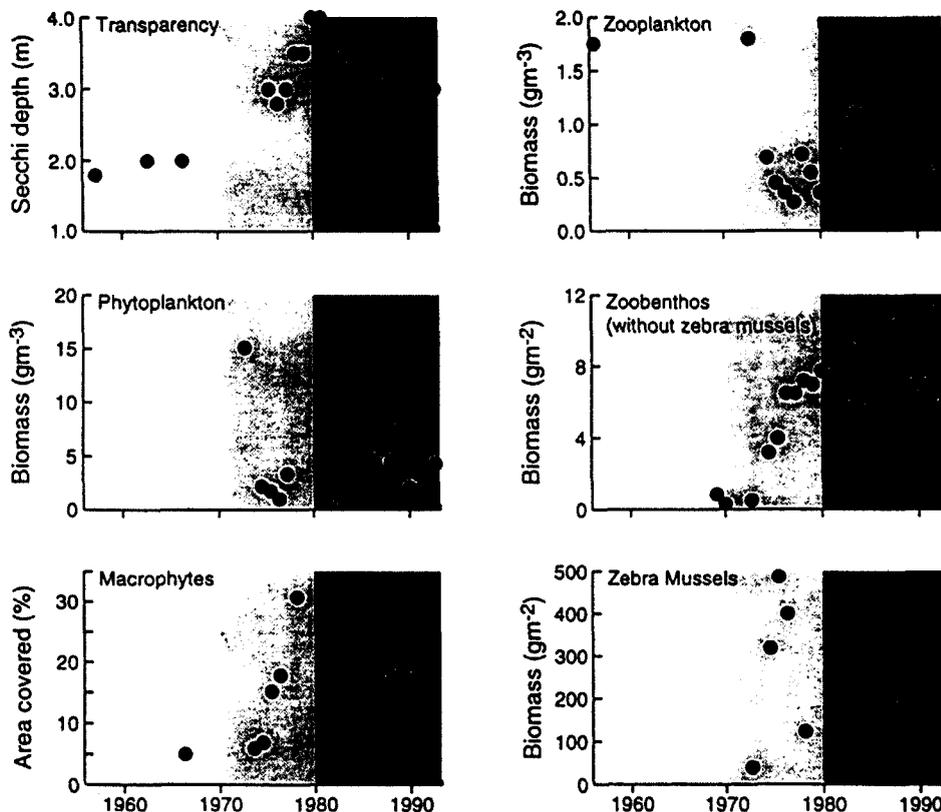


Figure 1. Long-term changes in Lukomskoe lake from before the zebra mussel invasion (before 1970), during the initial invasion (1970–1980), and after there was an established population of zebra mussels (after 1980). Transparency was measured as Secchi depth; phytoplankton and zooplankton are in g of wet biomass m^{-3} , macrophytes are in % from the total area of the lake; zoobenthos (without zebra mussels) are in g of wet biomass m^{-2} ; zebra mussels are in total wet biomass $g m^{-2}$.

the effects of anthropogenic eutrophication in lakes (Reeders et al. 1989, Reeders and Bij de Vaate 1990, Noordhuis et al. 1992, Reeders et al. 1993).

North American scientists have reported similar changes in lake ecosystems after the recent appearance of *Dreissena* in the Great Lakes. *Dreissena* have been associated with increases in water transparency (Hebert et al. 1991, Holland 1993, Leach 1993, Fahnenstiel et al. 1995b); increases in benthic algal abundance (Lowe and Pillsbury 1995); expansion of macrophyte beds (Skubinna et al. 1995); decreases in turbidity (Skubinna et al. 1995); decreases in chlorophyll, phytoplankton abundance, and production (Leach 1993, Nichols and Hopkins 1993, Fahnenstiel et al. 1995a, Fahnenstiel et al. 1995b); increases in the density of benthic animals; and changes in benthic community structure (Dermott and Munawar 1993, Griffiths 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts et al. 1996). In all cases, patterns of zebra mussel effects are similar to those found in FSU and European freshwaters.

INFLUENCE ON FOOD WEBS

The only studies on the effect of zebra mussel on food webs and the energetic balance of the ecosystem in the FSU have been conducted in Lukomskoe lake. Before the invasion of *D. polymorpha*, the total primary production (phytoplankton, 98%; macrophytes, 2%) in this lake was 2,596 kcal m⁻² (Table 5) (Karatayev 1992, Karatayev and Burlakova 1995a). The production of non-predator zooplankton (97%) and zoobenthos (3%) together were 3.7% of total primary production. Fish production was 0.15% of the total primary production (Karatayev 1992, Karatayev and Burlakova 1995a). Lukomskoe lake was similar to many lakes studied

by Bullion and Winberg (1981), and in general, fish production averaged 0.1–0.3% of primary production.

In 1978, after the appearance of *D. polymorpha* in Lukomskoe lake, macrophyte production increased 3.3 times, and phytoplankton production decreased more than 4 times (Karatayev 1992, Karatayev and Burlakova 1995a). Total primary production decreased more than three times. Total production of planktonic and benthic nonpredatory invertebrates declined from 95 to 44 kcal m⁻², and benthic invertebrates increased from 3 to 77% of the total. The production of nonpredatory invertebrates increased to 5.5% of primary production, compared with 3.7% before the invasion of *D. polymorpha*. Fish production increased from 0.15 to 1% of primary production (Karatayev 1992, Karatayev and Burlakova 1995a). This high rate of fish production is typical of commercial fish ponds but is much higher than that of most natural lake communities (Bullion and Winberg 1981). Therefore, subsequent to the appearance of *D. polymorpha*, the conversion of primary production to higher trophic levels increased (Karatayev 1992, Karatayev and Burlakova 1995a).

By 1989, the zebra mussel population in Lukomskoe lake had declined and, in terms of biomass, was relatively stable, and a reanalysis of the biotic balance was compared with that found in 1978 (Karatayev 1992, Karatayev and Burlakova 1995a). Total primary production had increased 13%, and the contribution of macrophytes to the total decreased from 20% in 1978 to 11% in 1989 (Table 5). The total production of nonpredatory zooplankton and benthos was nearly twice that in 1978 as a result of the increased proportion of zooplankton from 23% in 1978 to 45% in 1989. The production of benthic invertebrates increased two times. Fish production remained approximately 1% of primary production, as in 1978 (Karatayev 1992, Karatayev and Burlakova 1995a).

TABLE 5.
Biomass and production of Lukomskoe Lake before and after the appearance of zebra mussels.

Trophic Level	Preinvasion		Postinvasion				P/B
	B	P	1978		1989		
			B	P	B	P	
Primary production							
Phytoplankton	50.9	2,544.5	12.5	624.5	16.1	805.0	50.0
Macrophytes	40.9	51.1	132.8	166.0	81.3	101.6	1.25
Total	91.8	2,595.6	145.3	790.5	97.5	906.6	
Zooplankton filterers							
Crustacea	6.37	92.4	0.70	10.2	3.55	51.5	14.5
Rotifers	0.03	1.4	0.10	4.6	0.36	16.6	46.0
Total	6.40	93.8	0.80	14.8	3.91	68.1	
Nonpredatory zoobenthos	0.38	1.4	3.22	12.2	6.44	24.5	3.8
Zebra mussels	0.00	0.0	27.80	16.7	40.00	24.0	0.6
Zooplankton filterers + nonpredatory zoobenthos	6.78	95.2	31.82	43.7	50.35	116.6	
Predatory zooplankton							
Crustacea	1.22	11.7	0.18	1.7	0.87	8.4	9.6
Rotifers	0.02	1.5	0.05	3.7	0.12	8.8	73.3
Total	1.24	13.2	0.23	5.4	0.99	17.2	
Predatory zoobenthos	0.02	0.1	0.28	1.0	0.56	2.0	3.5
Predatory zooplankton + predatory zoobenthos	1.26	13.3	0.51	6.4	1.55	19.2	
Fish							
Nonpredators	8.75	3.5	17.00	6.8	21.25	8.5	0.4
Predators	1.25	0.5	3.00	1.2	1.25	0.5	0.4

Biomass (B) and production (P) are given in kcal m⁻² (from Karatayev and Burlakova 1995a).

CHANGES IN FISHES

Twenty-seven fish species in Europe and 14 species in North America are known to consume *Dreissena* (Molloy et al. 1997 and references therein). Common carp (*Cyprinus carpio*), pumpkinseed (*Lepomis gibbosus*), and round goby (*Neogobius melanostomus*) have been field documented as predators on both continents. Another 13 North American species have been mentioned in the literature as potential predators (Molloy et al. 1997).

Dreissena are readily eaten by fish in the North Caspian Sea, where approximately 90% of the annual production of mussels (130,000 tonnes) are eaten by fish (Yablonskaya 1985). The roach is the most prominent consumer of *Dreissena* in European freshwaters (Pliszka 1953, Grigorash 1963, Mikheev 1963, Filuk and Zmudzinski 1965, Prejs 1976, Lvova 1977, Stanczykowska 1987, Karatayev et al. 1994b, and others). *D. polymorpha* comprise from 95 to 100% of the diet of roach larger than 18 cm in a number of Polish lakes (Pliczka 1953, Prejs 1976, Stanczykowska 1987). Since the *D. polymorpha* invasion in the reservoirs of the Volga cascade (Russia), a new population of mussel-eating roach has developed, characterized by very high individual growth rates and large body size (Poddubnyi 1966). In Uchinskoe reservoir, benthophages fish (mainly roach) eat approximately 80% of the yearly production of *D. polymorpha* under 15 mm (Lvova 1977) and were the most abundant fish in this reservoir (Spanowskaya 1963). Before the zebra mussel invasion, the growth rate of young-of-year roach was almost the same as that in other reservoirs. However, when the roach were able to eat *D. polymorpha*, their growth rate and lipid content significantly increased and exceeded those of roach in reservoirs without *D. polymorpha* (Lyagina and Spanowskaya 1963).

Freshwater drum (*Aplodinotus grunniens*) are active consumers of *Dreissena* in North America (French 1993, French and Bur 1993). Another recent invader to the Great Lakes, the round goby, also feeds on *Dreissena* (Jude et al. 1995). Therefore, the presence of *Dreissena* may enhance the spread of this second invader.

The effect of zebra mussels on fish may be direct or indirect. The direction and intensity of these effects are dependent on the feeding method of the majority of the fish in a waterbody. In general, we may expect an enhancement of all benthic feeding fishes, even those that do not feed on *Dreissena*, because *Dreissena* increase the biomass of other benthic invertebrates (Kharchenko and Protasov 1981, Karatayev 1983, Lyakhovich et al. 1983, Lyakhovich et al. 1988, Karatayev 1992, Karatayev and Burlakova 1992, Dermott and Munawar 1993, Griffiths 1993, Stewart and Haynes 1994, Karatayev and Burlakova 1995a, and others). We found no documented effects of zebra mussel presence on planktivorous fish.

GENERAL FINDINGS

The measured effects of *D. polymorpha* on a community will depend on the amount of time since the appearance of zebra mussels, the density of zebra mussels, and the potential species pool of the community. Usually, there is a lag time between when zebra mussels first invade a new waterbody and when they are abundant enough to detect and have ecologically relevant effects. Five to 10 y after initial invasion, *Dreissena* generally rapidly increase in population size (Sebestyen 1937, Berg 1938, Zhadin 1946, Zhuravel 1951, Ovchinnikov 1954, Kondratiev 1958, Lyakhov 1961, Lyakhov 1962, Lvova 1977, Lvova 1980, Karatayev 1983, Karatayev et al. 1994a, Karatayev and Burlakova 1995b). For

example, zebra mussels invaded Narocho in the mid-1980s and were at relatively low densities for several years. In 1990, the entire lake average densities were 7.2 m⁻², but rapidly increased to 798 m⁻² in 1993 (Karatayev and Burlakova 1995b). The first zebra mussel was found in Uchinskoe reservoir in 1945, but biomass did not reach a maximum until 1957. Although mussel densities remained similar for several years, the size structure of the population changed, such that total biomass declined and was then relatively stable for 10 y. In 1972, the water flow through the Uchinskoe reservoir was increased three times, increasing local food availability, and the average biomass of zebra mussels increased.

Although *Dreissena* take several years to colonize all regions of lakes they invade, they spread very rapidly through canals of moving water. The North-Crimean Canal (Ukraine) was built in 1966 (Kharchenko and Protasov 1979), and by 1967–1969, the number of *Dreissena* in some areas was 1,782 m⁻² and the biomass was 96.4 g m⁻² (Kaftannikova 1975). By 1984, *Dreissena* had colonized the entire Dnieper-Donbass Canal, which was opened in 1983 (Lyashenko and Kharchenko 1988).

The general pattern that has emerged from long-term studies in Europe, including the FSU, is that initial populations of zebra mussels grow to very high densities, but because of density-dependent processes, total sustainable biomass declines as the system changes and densities well below the maximum achieved persist (Sebestyen 1937, Zhadin 1946, Zhuravel 1951, Lyakhov 1962, Lvova 1977, Walz 1978b, Lvova, 1980, Karatayev 1983, Karatayev and Burlakova 1995a). However, all populations of zebra mussels do not stabilize and can change widely (Ramcharan et al. 1992). On the basis of observations from 1959 to 1988 on 12 Mazurian lakes (Poland) with established zebra mussel populations, Stanczykowska and Lewandowski (1993) found 4 lakes with stable zebra mussel populations, 4 lakes with unstable populations, and 4 lakes with populations that had declined. The most dramatic changes were found in Lake Mikolajskie. From 1959 to 1960, the average density of zebra mussels in this lake decreased from 2,200 to less than 50 m⁻². In 1976, the population increased to more than 2,000 m⁻² and then again dramatically declined (Stanczykowska and Lewandowski 1993).

We hypothesize that early in an invasion, when population levels are climbing and are high, *D. polymorpha* will have their largest effects on communities, and most of the effects will be direct. The effects of *D. polymorpha* on communities after the initial stages of invasion are much less predictable, and much more likely to be caused by indirect effects through changes in the ecosystem. The filtering activity of zebra mussels increases water transparency and organic matter mineralization (Table 6). *D. polymorpha* reduce the concentration of seston in the water column and reduce densities and the production of phytoplankton. Improved water transparency increases macrophyte biomass and coverage as macrophytes grow deeper in the lake. Increased macrophyte abundance may act as a barrier hindering the influx of allochthonic nutrients used by phytoplankton. Increased light penetration is also likely to stimulate an increase in periphyton. Only scattered data are available on bacterioplankton and suggest an increase in abundance with zebra mussels.

In the presence of *Dreissena*, the abundance of zooplankton is reduced and is accompanied by structural changes in the plankton community. The numbers, biomass, and production of benthic invertebrates are increased, and the taxonomic and trophic structure of benthic animals changes.

TABLE 6.
The influence of zebra mussels on freshwater
ecosystem characteristics.

Parameter	Change With Zebra Mussels	References
Transparency	Increase 1.5, 2, and >2x	Stanczykowska 1968, Lvova-Kachanova 1971, Stanczykowska 1977, Lvova 1979, Karatayev 1983, Karatayev 1984, Karatayev 1992, Griffiths 1993, Holland 1993, Reeders et al. 1993, Fahnenstiel et al. 1995b
Seston	Decrease 1.5–10x	Lvova et al. 1980, Kharchenko and Lyashenko 1985, Leach 1993, Reeders et al. 1993, Ostapenya et al. 1994a, Ostapenya et al. 1994b, Karatayev and Burlakova 1995a
Organic matter	Decrease. Increase of organic matter mineralization	Kharchenko and Lyashenko 1985, Shevtsova 1989, Ostapenya et al. 1994a, Ostapenya et al. 1994b, Karatayev and Burlakova 1995a
BOD ₅	Decrease 1.5x	Kharchenko and Lyashenko 1985, Ostapenya et al. 1994a, Ostapenya et al. 1994b
Phytoplankton	Decrease 1.5–4x quantity, chlorophyll	Lyakhnovich et al. 1988, Karatayev 1992, Noordhuis et al. 1992, Holland 1993, Leach 1993, Nichols and Hopkins, 1993, Reeders et al. 1993, Ostapenya et al. 1994a, Ostapenya et al. 1994b, Karatayev and Burlakova 1995a
Primary production of phytoplankton	Decrease 2–4x	Ostapenya et al. 1994a, Ostapenya et al. 1994b, Fahnenstiel et al. 1995a, Fahnenstiel et al. 1995b
Bacterioplankton	Slightly increase numbers	Ostapenya et al. 1994a, Ostapenya et al. 1994b
Macrophytes	Increase biomass and overgrowth rate	Lyakhnovich et al. 1988, Reeders and Bij de Vaate 1990, Griffiths 1993, Skubinna et al. 1995
Phytoperiphyton and phytobenthos	Increase quantity, chlorophyll and primary production	Lowe and Pillsbury 1995
Zooplankton	Decrease quantity, structural changes in community	Lyakhnovich et al. 1983, Mitrakovich et al. 1983, Mitrakhovich 1984, Shevtsova et al. 1986, Karatayev et al. 1994a
Zoobenthos	Increase quantity, changes in taxonomic and trophic structures	Dusoge 1966, Wiktor 1969, Kharchenko and Protasov 1981, Karatayev 1983, Karatayev et al. 1983, Kharchenko 1989, Karatayev 1992, Karatayev and Burlakova 1992, Griffiths 1993, Dermott and Munawar 1993, Stewart and Haynes 1994, Winseden and Bailey 1994, Karatayev and Burlakova 1995a, Botts et al. 1996
Fishes	Increase quantity of benthophages	Karatayev 1983, Lyakhnovich et al. 1988, Karatayev 1992, Karatayev and Burlakova 1995a

By comparing the effect impact of *D. polymorpha* across different waterbodies located in a variety of geographical areas in the Old World, we found similar changes in native ecosystems. Would we expect the same to be true in North America? North American freshwaters may be influenced more by *D. polymorpha* than the waterbodies of Eurasia if the lack of evolutionary history with dreissenids is important, or if dreissenids have different effects on very large lakes such as the Laurentian Great Lakes. In order to determine if North America and Europe are different, we must have comparable, similarly collected data. Differences in methodology and what data are collected have hindered our ability to compare current North American information with that from Europe. The types of information that would be most useful are: (1)

Estimates of whole-lake densities of *Dreissena* with either size-frequency distributions or WTM. Information should be collected using randomized survey techniques to ensure that all habitat types are included, not just those with high densities of *Dreissena*. (2) Before and after invasion measures of the biomass of phytoplankton, zooplankton, fish, macrophytes, periphyton, and benthic invertebrates, especially bivalves. In addition, the abundance of ecologically important groups (predators, gatherers, filterers, etc.) before and after invasion should be determined. With these data, we will not only be able to establish the general effects of *Dreissena* on freshwater ecosystems, but we will be able to test whether *Dreissena* have different effects on large versus small lakes and on different continents.

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