Chapter 9

# *DREISSENA POLYMORPHA* IN BELARUS: HISTORY OF SPREAD, POPULATION BIOLOGY AND ECOSYSTEM IMPACTS

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# TABLE OF CONTENTS

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# 9. *Dreissena polymorpha* in Belarus: history of spread, population biology and ecosystem impacts

**Alexander Y. Karatayev, Lyubov E. Burlakova and Dianna K. Padilla**

**Abstract**

An overview is presented of long-term studies on the patterns of continued spread of zebra mussels *(Dreissena polymorpha)* across Belarus, aspects of their population biology, life history, endosymbionts and ecosystem impacts. Although 80% of Belarussian lakes are suitable for *Dreissena*, in spite of 200 years of continuous invasion, zebra mussels are currently found in only 21% of the 553 lakes studied. In Belarus *Dreissena* reproduces from the beginning of June to the end of August with one or several peaks in abundance of their larvae in the plankton. Zebra mussels growth rate depends on temperature, season of the year, trophic conditions of a waterbody, and water current. *Dreissena* population density and biomass differs among and within waterbodies, and depends upon the waterbody type, available substrates, time since initial colonization, and local pollution. Sixteen species and higher taxa of endosymbionts have been found within the mantle cavity and/or associated with zebra mussel tissue, including ciliates, trematodes, nematodes, chironomids, oligochaetes, mites, and leeches. The introducton of *Dreissena* may have both local and system wide effects, including changes in species composition, density, and biomass of native bottom invertebrates, as well an increase in water transparency, macrophyte growth, abundance of benthivorous fish, and decreases in the densities of phytoplankton and zooplankton, concentrations of chlorophyll, total phosphorus, and suspended matter.

## Introduction

Belarus is a relatively small country and of very recent political origin. The current boundaries of Belarus encompass 207,600 km$^2$ and include over 1,000 glacial lakes in five major river basins. The freshwaters of Belarus are the most important for the invasion of zebra mussels, and there has been a long, rich tradition in scientific investigations of the biology, ecology and impacts of this important invader.

Present day Belarus is land locked, and is located to the east of Poland, west of Russia, north of the Ukraine and south of the Baltic states. Historically it was considered strategically valuable, for both the east and the west, providing the border between Russia and Poland, which moved regularly depending on political will and power. It was an independent country for some time just after World War I, until 1922 when it became a part of the Soviet Union. It reformed as an independent country after the fall of the Soviet Union in 1991.

Its geographic location is very important as it includes the continental divide separating the Black Sea and Baltic Sea basins. Thus, this region was critically important for international trade early in the 19th century when three interbasin canals connecting the Dnieper and Zapadnyi Bug rivers, the Dnieper and Neman rivers and Dnieper and Zapadnaya Dvina rivers, were constructed (Fig. 1).

These canals established connections among these river basins that previously had no hydrological links, and provided not only corridors for shipping and trade, but corridors for the introduction of numerous Ponto-Caspian species from the Black Sea basin into the Baltic Sea basin, including *Chelicorophium curvispinum* and *Dreissena polymorpha*, among many others. However, unlike North America, *D. bugensis* has not invaded Belarus.

The region was glaciated during the Pleistocene and the retreat of the glaciers left a region rich in lakes. There is a long, rich history of hydrobiological studies in what is now Belarus from the late 19th century to the present (reviewed

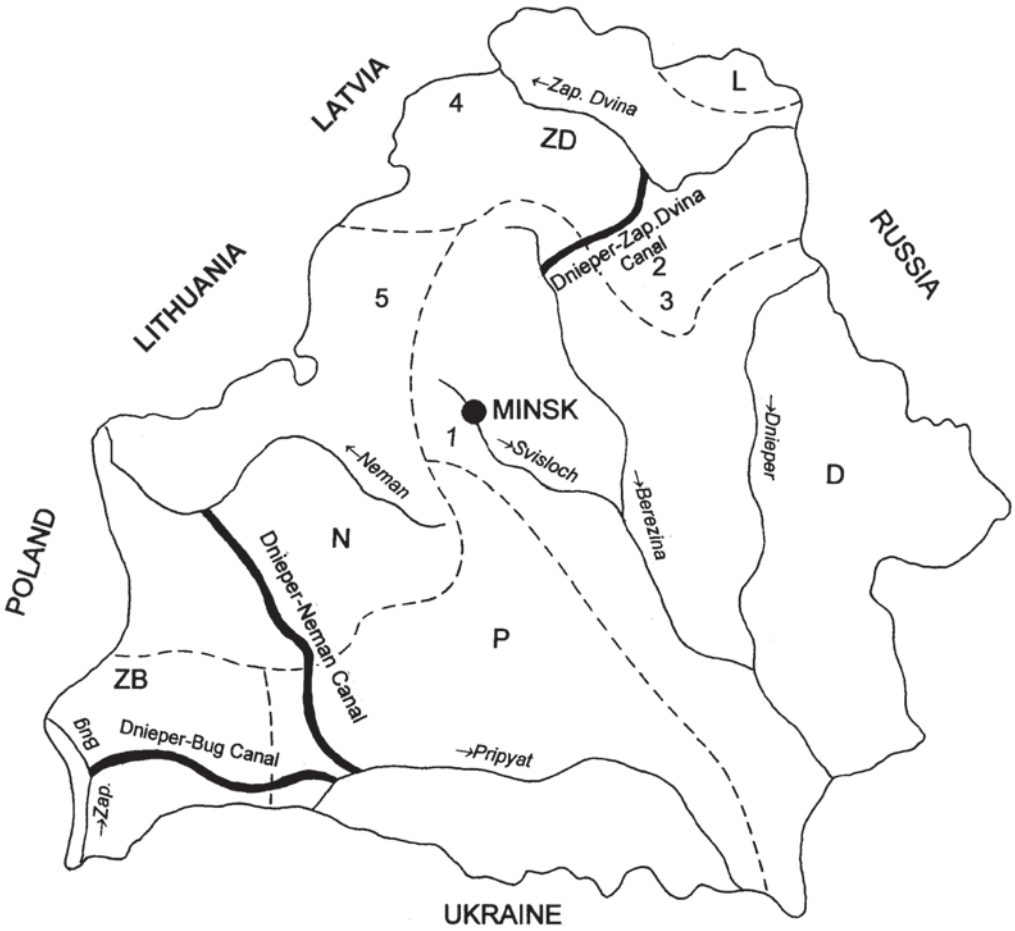


***Figure 1.*** Map of the Republic of Belarus. Interbasin canals (bold lines) include: Dnieper-Zapadnyi Bug (opened in 1775), Dnieper-Neman (1804), and Dnieper-Zapadnaya Dvina (1805). Studied waterbodies: 1 - Svisloch River, 2 - Lake Lepelskoe, 3 - Lake Lukomskoe, 4 - Braslavskie lakes, 5 - Narochanskie lakes. Borders of the major Belarusian drainage river basins (dashed lines): Zapadnaya Dvina River drainage basin (ZD), Dnieper River basin (D), Neman River basin (N), Pripyat River basin (P), Zapadnyi Bug River basin (ZB), and Lovat River basin (L).

in Karatayev, 1999). Much of this work was initiated by the eminent scientist George Winberg, who was the Chair of the Invertebrate Zoology Department of Belarusian State University from 1947 to 1967. Together with his colleagues, he studied various aspects of the structure and functioning of aquatic systems in Belarus and became a leader of hydrobiological research in the former Soviet Union.

Wide-scale surveys of Belarusian lakes started in late 1940s - early 1950s and have continued since that time. As a result more than 550 lakes (from total 1,040 glacial lakes in Belarus) have been comprehensively studied, including lake morphometry, hydrology, chemistry, and the species composition, density and biomass of phytoplankton, zooplankton, and zoobenthos. Investigation of different aspects of the ecology and biology of zebra mussels has also been an important component of this research. Extensive research has focused on zebra mussels in Belarus since the 1970s, when *D. polymorpha*, among a few other species, was selected as a model organism for a project entitled "Species and its productivity in the distribution range" within a UNESCO Program "Man and Biosphere" (Karatayev, 1994b; Starobogatov, 1994). More than a hundred papers have been published on the distribution of zebra mussels (Ovchinnikov, 1933; Drako, 1953; Drako and Gavrilov, 1972; Gavrilov et al., 1976; Lyakhnovich, 1956; Lyakhnovich et al., 1984; Tischikov, 1984; Karatayev, 1995; Karatayev and Burlakova, 1995a; Kraft et al., 2002; Karatayev et al., 1998b, 2003a; Burlakova, 1999; Burlakova and Karatayev, 1999; Burlakova et al., 2006a), their population dynamics (Karatayev, 1983; Karatayev and Burlakova, 1995a, 1995b; Burlakova, 1998; Burlakova et al., 2006a), reproduction (Karatayev, 1981; L'vova et al., 1994a; Mitrakhovich and Karatayev, 1986; Burlakova, 1998), and growth (Karatayev and Tischikov, 1979; Karatayev 1983, 1984a, 1985, 1988; L'vova et al., 1994b; Burlakova, 1998), as well as their impacts on the ecosystem (Karatayev and Tischikov, 1979; Lyakhnovich et al., 1982; 1983a, 1988; Karatayev, 1983, 1984b, 1988, 1994a; Karatayev et al., 1983, 1997, 2002a, 2005; Karatayev and Lyakhnovich 1990; Karatayev and Burlakova, 1992, 1993, 1995a, 1995b; Burlakova, 1995, 1998; Burlakova et al., 2000, 2005; Ostapenya et al.,

1993, 1994a, 1994b; Kryuchkova and Derengovskaya, 1999, 2000; Zhukova, 2000, 2001) and their endosymbionts (Karatayev, 1983; 1988; Lyakhnovich et al., 1983b; Zdun et al., 1994; Burlakova, 1998; Burlakova et al., 1998; Karatayev et al., 1998b, 1999b, 2000a, 2000b, 2002b, 2003b, 2003c; Mastitsky, 2004; Mastitsky and Samoilenko, 2005). Unfortunately, due to language and political barriers this extensive body of work has not been readily available to most of the Europeans and other western scientists. The goal of this chapter is to summarize and to review research conducted on zebra mussels in Belarus over the past seven decades, focusing on the patterns and continued spread of zebra mussels across Belarus, aspects of their population biology, life history and impacts, as well as on endosymbionts.

### History of spread and current distribution

Before the end of the 18th century the distribution of *D. polymorpha* was limited to the Black and the Caspian Sea basins. However, with increasing commerce and industrialization, markets developed in Western Europe for Russian firewood, as well as other goods. Thus shipping routes were needed to connect the Black Sea and Baltic Sea basins. A series of canals were built to facilitate shipping trade, and very soon after the canals were open, zebra mussels began to spread across Europe (Zhadin, 1946; Kerney and Morton, 1970; Kinzelbach, 1992; Starobogatov and Andreeva, 1994; Karatayev et al., 2003a).

In spite of this very rapid spread through waterways, the spread of zebra mussels from these major rivers and canals to the lakes of Belarus was very slow. In 1929 Ovchinnikov (1933) found *D. polymorpha* only in 3 glacial lakes, three large rivers (Dnieper, Pripyat and Berezina) and several small rivers. At that time, present day Belarus was divided almost in half between the Soviet Union and Poland, and Ovchinnikov (1933) surveyed only the Soviet (eastern) part. In the 1940s and 1950s *D. polymorpha* was found in only 6 lakes (Drako, 1953; Drako and Gavrilov, 1972), but by the early 1980s Lyakhnovich et al. (1984) reported that zebra mussels had already been found in 4 additional rivers, one reservoir and 73 lakes. These initial survey efforts, from 1800s to the mid-1950s were sporadic and not conducted in a systematic way, limiting our ability to determine the full extent of invasion by *Dreissena*. Subsequent surveys revealed the presence of *D. polymorpha* in several additional lakes, and by 1996 zebra mussels were known to have invaded at least 93 lakes, 7 reservoirs, all 6 large Belarusian rivers (Zapadnaya Dvina, Dnieper, Pripyat, Berezina, Neman, and Sozh), and 11 small rivers (Burlakova, 1998; Karatayev et al., 2003a). From 1996 to 2000, an additional 28 lakes in Belarus were found to be recently invaded by zebra mussels.

Of the 1,040 glacial lakes in Belarus, 553 have been examined for the presence of zebra mussels. In spite of almost 200 years of continuous invasion, by 2000 zebra mussels were found in only 21.2% of these lakes (Burlakova, 1998; Karatayev et al., 2003a). Although some of the lakes that have not been invaded may be unsuitable for zebra mussels due to low pH or low calcium concentration (Ramcharan et al., 1992b; Burlakova, 1998), 80% of these lakes have high enough calcium (Ca $\geq$ 25 mg $l^{-1}$) and suitable pH ( $\geq$ 7.5) for *D. polymorpha* survival and growth (Burlakova, 1998, 1999).

Thus, the historic rate of spread of *D. polymorpha* from the major rivers and canals to the Belarusian glacial lakes was slow, and dispersal likely limited. During the late 18th and early 19th centuries, *D. polymorpha* was limited to those few lakes directly connected to shipping routes (e.g., Lake Lepelskoe). Most lakes in Belarus are isolated, and large lake systems connected by navigable waterways are rare. Therefore, the spread of zebra mussels to most Belarusian lakes depends on overland dispersal (Karatayev et al., 2003a). Leisure boat traffic was the major vector of spread of zebra mussels to isolated lakes in Western Europe (Kinzelbach, 1992), however, in the Soviet Belarus commercial fishing was the major vector that spread *D. polymorpha* to isolated lakes (Deksbakh, 1935; Karatayev et al., 2003a). During Soviet times, freshwater fisheries were subsidized by the government, and therefore were much more active than in the west, which had no subsidies. After the Soviet Union dissolved, commercial fisheries subsidies stopped, causing a rapid decline in commercial fishing activity (Karatayev et al., 1999a). In contrast, recreational activities have become much more common and are now responsible for the spread of zebra mussels in Belarus, resulting in the colonization of many isolated lakes and lake systems that are used only for recreation (Karatayev and Burlakova, personal observations). The rate of spread of zebra mussels from the early 1800s to the mid-1950s was very low, approximately 4 lakes every 50 years. However, the rate of spread of zebra mussels since the 1960s has dramatically increased to an average of 23 lakes every 10 years (Fig. 2). This rapid increase in the rate of spread was mostly due to commercial fishing as well as the secondary invasion of lakes connected by rivers and streams by recreation vessels.

In general, the slow rate of spread of zebra mussels to isolated lakes in Belarus corresponds well with data from North America (Buchan and Padilla, 1999; Kraft and Johnson, 2000). Buchan and Padilla (1999) found that only 6 of 15,000 inland Wisconsin lakes were colonized by zebra mussels in 1998, over 10 years since their initial introduction. By 2005 less than 1% of Wisconsin lakes had been colonized (Padilla, 2005). Kraft and Johnson (2000) estimated that between 3 to 8% of the inland lakes surrounding the Laurentian

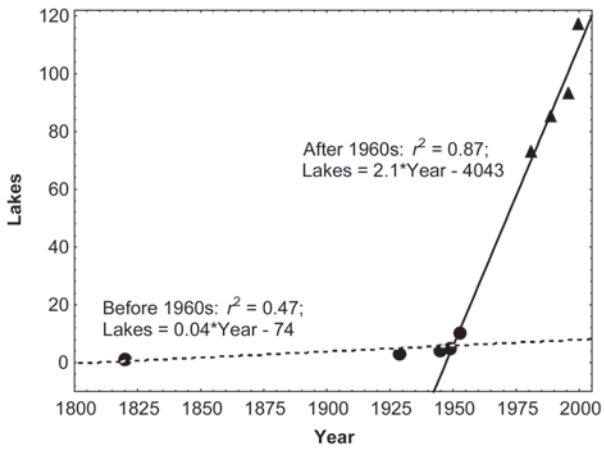


***Figure 2.*** Total number of Belarusian lakes (of 553 studied) colonized by *Dreissena polymorpha* since 1820. The colonization rate was very slow from 1820 to 1960s (0.04 lakes per year, $r^2$ = 0.47) but dramatically increased from 1960s to 2000 (2.1 lakes per year, $r^2$ = 0.87).

Great Lakes are being invaded each year. Belarusian data provides a similar picture, but over a much longer time scale, i.e., centuries rather than decades (Kraft et al., 2002).

Once *Dreissena* colonized a lake, they generally do not go locally extinct, except in areas with excessive pollution or extreme eutrophication (Karatayev et al., 2003a). Stanczykowska and Lewandowski (1993b) found that anthropogenic eutrophication caused the extinction of *D. polymorpha* in 6 Masurian lakes (Poland) between 1959 and 1988. In Belarus the local extinction of *Dreissena* has been documented for at least 3 lakes in the Braslav Lake System (Burlakova, 1999). All the 3 lakes were colonized in the 1970s and early 1980s, but due to extensive pollution by metropolitan waste in late 1980s these lakes were transformed into hyper-eutrophic waterbodies with low oxygen content (Karatayev et al., 1995c). In the 1990s zebra mussels were no longer found in these lakes.

## Life history and population biology larval stage

Zebra mussel reproduction and larval dynamics have been studied in both the lakes and rivers of Belarus (Karatayev, 1981, 1983; Burlakova, 1998). Based on analyses of size-frequency distributions of zebra mussel larvae in the plankton, it was surmised that in Belarusian waters *Dreissena* are usually reproduce over three summer months, from early June to late August, when water temperature is $\geq 15^0$C (Karatayev, 1981, 1983; Burlakova, 1998). Temperature is the key factor that triggers spawning (Kirpichenko, 1964, 1971a, 1971b; Stanczykowska, 1977; Smit et al., 1993; Neumann et al., 1993; L'vova et al., 1994a; Burlakova 1998) and many studies have found that zebra mussel larvae first appear in the plankton when water temperatures reach $15^0$C (e.g. Kirpichenko, 1964; Hillbricht-Illkowska and Stanczykowska, 1969; L'vova, 1977; L'vova et al., 1994a).

Veliger densities are characterized by one or more peaks in abundance, usually in mid-summer. In years with cold springs and early summers, *Dreissena* larvae appear in the plankton later and have a single, pronounced and short peak of abundance (Burlakova, 1998), indicating synchronized spawning of different age or size classes of mussels. L'vova (1977) found that in the Uchinskoe Reservoir (Russia), typically the first peak in zebra mussel larval abundance is observed in June, 2 - 3 weeks after the first appearance of larvae in the plankton. This first peak results from the mass spawning of older mussels that were all sexually mature before the beginning of the current growing season. A subsequent peak in larval abundance results from the spawning of *Dreissena* that settled in the previous year, and then became reproductive for the first time. However, unusually cold springs may greatly delay the reproduction of all age classes of zebra mussels, resulting in a single spawning event when temperatures finally rise, producing a single, pronounced, short peak in larval densities. In a more typical year, with a warm spring, zebra mussel larvae may show several small peaks in abundance or one extended peak (Karatayev, 1981, 1983; L'vova et al., 1994a; Mitrakhovich and Karatayev, 1986; Burlakova, 1998).

By September, all D-stage veligers are gone from the plankton in Belarusian waters, however late stage larvae may stay in the plankton until November. According to Kirpichenko (1964, 1971a), in Volga River reservoirs late stage veligers may stay in the plankton and overwinter, however, they are not found in the winter in the majority of the waterbodies that have been studied (reviewed in L'vova et al., 1994a).

*Dreissena* larvae dominate the zooplankton during the summer, comprising 18 to 43% of the total zooplankton density, and from 6 to 25 % of the total zooplankton biomass and production within lakes (Karatayev, 1983; Mitrakhovich and Karatayev, 1986), providing a new food resource to at least eight species of native fish (Molloy et al., 1997). For five Belarusian lakes and reservoirs, Burlakova (1998) found a significant, strong correlation (r = 0.91, P = 0.03) between the average biomass of *Dreissena* across the total bottom area of a lake (g $m^{-2}$) and the average larval density (in terms of individuals per $m^{-2}$ of the bottom) during the three months of summer.

## Growth rate

In Belarusian waterbodies, growth rates of *Dreissena polymorpha* have been estimated using a variety of techniques, each with certain biases and often resulting in different estimates, including: counting annual rings on shells (Karatayev and Tishchikov, 1979), analysis of size frequen-

cy distributions (Burlakova, 1998), monitoring the growth of tagged mussels in experimental cages (Karatayev, 1983; Burlakova, 1998), and monitoring the growth of uncaged, tagged mussels on their natural substrates (Burlakova, 1998). Following tagged mussels under natural conditions provides the most realistic estimates of growth (reviewed in Karatayev et al., 2006).

*Dreissena* growth rates depend on temperature (Karatayev and Tishchikov, 1979; Karatayev, 1983, 1984a; Smit et al., 1992; L'vova et al., 1994b), season of the year (Karatayev, 1983; Sprung, 1995a; Burlakova, 1998), trophic conditions of a waterbody (Smit et al., 1992; Dorgelo, 1993; Sprung, 1992, 1995a; Burlakova, 1998), and water current (Bij de Vaate, 1991; Smit et al., 1992; Burlakova, 1998). Burlakova (1998) found that zebra mussel growth was higher in the Svisloch River than in three other lakes with similar water temperatures, and hypothesized this difference was most likely due to the constant unidirectional water currents delivering food and oxygen to the mussels. Other authors have also found that *Dreissena* growth rates are higher in flowing than in still water (Kachanova, 1963; Smit et al., 1992).

The growth rates of zebra mussels are also positively affected by the trophic status of the waterbody. For example, *Dreissena* grew faster in eutrophic Lake Myastro than in mesotrophic Lake Naroch (Burlakova, 1998). Similar results have been found in other European studies of zebra mussel growth (Mothes, 1985; Dorgelo, 1993). Growth rate is significantly correlated with the average mass of individual mussels in a population; larger mussels are found in areas with higher growth, thus size and age are decoupled (Burlakova, 1998).

The range of the zebra mussel growth rate in Belarusian lakes is very similar to the growth rates in other lakes, including Lake Wawasee, US (Garton and Johnson, 2000) and Mikolajskie Lake, Poland (Stanczykowska and Lewandowski, 1995). Although there is no information available on the effect of lake mixing processes on growth rate, there appear to be substantial differences in growth between mussels in reservoirs and lakes – mussels of equal size grow much faster in reservoirs than lakes (reviewed in Karatayev et al., 2006). It could be possible that reservoirs provide a better overall growth environment in terms of temperature, nutrition, and more intense water mixing than do natural lakes.

### Population density

The densities of zebra mussel populations have been studied in numerous lakes, reservoirs and rivers in Belarus (Karatayev, 1983; Karatayev and Burlakova, 1995a, 1995b; Burlakova, 1998; Burlakova et al., 2006a). In general, the density and biomass of *Dreissena* differs among regions within waterbodies as well as among waterbodies, and depends upon the time since initial colonization, type of waterbody, available substrates, and the degree of local pollution.

From a number of studies in Belarus and Europe in general, we know that there is a lag time between the time of initial invasion by zebra mussels and the time when their populations rapidly increase in size (reviewed in Karatayev et al., 1997). For example in Lake Lukomskoe *Dreissena* were not found during a benthic survey in 1969, but by 1972 they were dense enough to produce a benthic biomass of 39.5 g $m^{-2}$, and the population reached a maximum in 1975 (487 g $m^{-2}$) (Karatayev, 1983). Similarly, *D. polymorpha* invaded Lake Naroch around 1986 and by 1990, the density of zebra mussels averaged only 7 $m^{-2}$. However during the next 3 years the population density increased over 100 fold, and then did not change significantly during following 9 years (Burlakova et al., 2006a).

In rivers, zebra mussels can be negatively affected by unstable bottom sediments and high concentrations of suspended matter, especially during periodic flooding events. Constant unidirectional water flow can make it difficult for local populations of zebra mussels in rivers to increase in density, as larvae are swept downstream (refer to Karatayev et al., 1998a for review). However, *D. polymorpha* can form high densities in rivers flowing from lakes or reservoirs populated by zebra mussels (Lyakhnovich et al., 1984) where the downstream population is constantly supplied with larvae and when the river flow is regulated to avoid flooding (Burlakova, 1998). Within the city of Minsk, the Svisloch River flows through a cascade of dams and reservoirs and stretches of the river have been transformed into canals. Zebra mussels in the Svisloch River are at higher average densities and have a higher average biomass per unit area than any other Belarusian lakes that have been studied (Table 1). High densities of zebra mussels are typical in canals where, in contrast to lakes, there is a constant, unidirectional water current, which delivers food and oxygen, and in contrast to unregulated rivers, bottom sediments are much more stable and the concentration of suspended matter is much lower, particularly during episodic floods (reviewed in Karatayev et al., 1998a). In Lake Lukomskoe the average density of zebra mussels in 1978 was 758 $m^{-2}$, and average biomass 124 g $m^{-2}$, while in the canal flowing from this lake the average density of *Dreissena* was 44,000 $m^{-2}$, and biomass was 6,873 g $m^{-2}$ (Karatayev, 1983).

One of the main factors that affects the distribution and abundance of *Dreissena* within a water body is the availability of suitable substrate for attachment (reviewed in Karatayev et al., 1998a). Among most suitable substrates for zebra mussel attachment are rocks, sand, silty sand, and submerged portions of macrophytes. As *Dreissena* populations develop through time, they generate a new substrate - dead zebra mussel shells, which are subsequently colonized (Bur-

***Table 1.*** Average density, biomass and occurrence (percentage of all samples in each lake that contained zebra mussels) of *Dreissena polymorpha* in Belarusian waterbodies in June and July 1995 (Burlakova, 1998) (Mean ± SE).

| Waterbody | Density (ind $m^{-2}$) | Biomass (g $m^{-2}$ | Sample size | Occurrence (%) |
|---|---|---|---|---|
| Lake Naroch | 1,521±451 | 107±44 | 116 | 50 |
| Lake Myastro | 645±147 | 288±117 | 45 | 75 |
| Lake Batorino | 262±88 | 100±36 | 37 | 47 |
| Drozdy Reservoir | 838±411 | 348±192 | 29 | 71 |
| Chizhovskoe Reservoir | 81±68 | 32±23 | 35 | 39 |
| Svisloch River (within the city of Minsk) | 2,500±1,585 | 1,183±883 | 28 | 54 |

lakova et al., 2006a). High densities of zebra mussels have been found attached to shells in many lakes in Belarus and elsewhere in Europe and North America (reviewed in Lyakhnovich et al., 1994; Karatayev et al., 1998a). Among substrates, the highest absolute (44,800 $m^{-2}$) and average (7,050 $m^{-2}$) density of zebra mussels have been found on submerged macrophytes in Lake Naroch in 1995, and the highest biomass of zebra mussels (7,500 g $m^{-2}$) was found on rocky substrates in the Svisloch River (Burlakova, 1998).

Silt appears to be the poorest substrate for zebra mussels (reviewed in Lyakhnovich et al., 1994; Karatayev et al., 1998a). However, *D. polymorpha* can colonize silty sediments with plant fragments, wood, shells, and stones, as they use these small hard fragments for initial attachment and subsequently attach to each other forming druses (reviewed in Karatayev et al., 1998a). In North America *Dreissena* has been reported to colonize silty sediments in the Laurentian Great Lakes (Hunter and Bailey, 1992; Dermott and Munawar, 1993). The mechanism of colonization was exactly the same as in Belarus. Zebra mussels colonized silt substrates in Lake St. Clair by lateral extension of druses which originated from attachment to small pieces of hard substrate, including unionids, their empty shells, or clusters of zebra mussels (Hunter and Bailey, 1992).

The effect of pollution on zebra mussels was studied in two reservoirs within the city of Minsk (Burlakova, 1998). The upper most reservoir, Drozdy, is located upstream the city, and has low levels of industrial and metropolitan pollution, is well oxygenated, and has an abundance of sand and rubble substrates. Silts are rare. In 1995 the average density of zebra mussels across the total bottom area of the river was 840 $m^{-2}$ and the average biomass was 349 g $m^{-2}$. Zebra mussels were most abundant in shallow areas, 0.5 m deep, on sandy-rocky substrates. In contrast, Chizhovskoe Reservoir is located downstream of the main industrial regions of the city, is heavily polluted, and is very silty. In 1993 the concentrations of heavy metals and oil products in the bottom sediments of this reservoir were 5 - 188 times higher than the maximum acceptable limits for Belarusian waterbodies (Dr. V. Vinokurov, personal communication). In 1995 the average density and biomass of *Dreissena* were ten times lower (81 ind. $m^{-2}$, 33 g $m^{-2}$) in the polluted Chizhovskoe Reservoir than in the cleaner upper Drozdy Reservoir. In addition, within the Chizhovskoe Reservoir zebra mussels were not found below 1.5 m depth, even when there were suitable substrates such as unionids, stones and wood at deeper depths (Burlakova, 1998).

## Endosymbionts

Belarus has also been the focus of studies of endosymbionts in *Dreissena,* and patterns of appearance, spread and prevalence of endosymbionts can be used to infer important processes in invasion and population biology of this invader. At least 25 various waterbodies in Belarus have been studied (some multiple times) for the presence of *Dreissena* endosymbionts. Sixteen species and higher taxa of commensals and parasites have been found within the mantle cavity and/or associated with zebra mussel tissue, including ciliates, trematodes, nematodes, chironomids, oligochaetes, mites, and leeches (Table 2). Of those, 14 taxa were found through dissection and 2 (*Sphenophrya dreissenae* and *Hypocomagalma dreissenae*) by studying histological samples.

### *Conchophthirus acuminatus*

*Conchophthirus acuminatus* is the most common endosymbiont of *D. polymorpha* in Europe, and has the highest prevalence and intensity of infection (Molloy et al., 1997; Burlakova, 1998; Burlakova et al., 1998; Karatayev et al., 2000a). Its relationship with zebra mussels, although obligate, is far more likely to be commensal than parasitic (Molloy et al., 1997). *C. acuminatus* is known to be extremely host specific, and has only ever been found in *D. polymorpha* and *D. bugensis* (Molloy et al., 1997; Karatayev et al., 2000b). There have been many studies of *C. acuminatus* in Belarus, including estimates of intensity of infection, transinfection experiments (Burlakova et al., 1998), monitoring of the emergence of *C. acuminatus* from healthy and dying hosts (Burlakova et al., 1998; Karatayev et al., 2003b) and studies of the seasonal dynamics of the prevalence and

intensity of infection of *D. polymorpha* and *D. bugensis* by *C. acuminatus* (Karatayev et al., 2000b; 2003c).

In Belarusian waterbodies, the prevalence (percent of infected mussels in a population) of *C. acuminatus* infection ranges from 35% to 100% (Burlakova et al., 1998; Karatayev et al., 2000a, 2003c). The highest infection intensity (number of ciliates per infected mussel) ever reported for *C. acuminatus* was 14,035 ciliates mussel$^{-1}$ and was observed in a 26.4 mm mussel, and the smallest mussel ever found to be infected was 1.1 mm long, and had one *C. acuminatus* (Karatayev et al., 2000a). Intensity and/or prevalence can be affected by host-dependent factors, such as mussel size and the presence of highly infected mussels in a microhabitat (Burlakova et al., 1998). Infection intensity is correlated with mussel size ($r^2$ = 0.83-0.92), and the presence of mussels with high infection intensities will increase the levels of infection in other nearby individuals. In laboratory experiments it was found that *C. acuminatus* rapidly leave a dying host *Dreissena*, suggesting that this process is a likely mechanism for the spread of *C. acuminatus* infection (Burlakova et al., 1998). In addition, *C. acuminatus* commonly leave their live hosts, and the rate of emergence is temperature dependent and episodic with periods of no emergence followed by periods of high emergence (up to 720 ciliates per mussel per day) (Karatayev et al., 2003b). In a 24 day experiment Karatayev et al. (2003b) found that the average number of *C. acuminatus* that emerged from each mussel at 21°C (207 ciliates mussel$^{-1}$) was significantly higher than the number that emerged at 14°C (29 ciliates mussel$^{-1}$), and that *C. acuminatus* can survive only brief periods in open water (< 6 days) when they transfer to new hosts (Karatayev et al., 2003b). In the field *C. acuminatus* infection intensity usually has a pronounced maximum in the summer and is positively correlated with water temperature (Karatayev et al., 2003c). In addition, the mean size of *C. acuminatus* is negatively correlated with temperature, and temperature is positively correlated with asexual reproduction, with a peak in cell division in April as water temperature increases (Karatayev et al., 2003c).

*Conchophthirus acuminatus* infects only juvenile and adult zebra mussels, thus not their larvae. If a waterbody was colonized by larvae, the water current that brought veligers would also have to be the source of free-swimming *C. acuminatus* (Karatayev et al., 2000a). Because this ciliate is found in all European populations of zebra mussel, including those in Ireland, which was only recently invaded (Burlako-

***Table 2.*** Prevalence (percent of mussels with symbionts) and average intensity (number of symbionts per mussel) in a population of *Dreissena polymorpha* endosymbionts in Belarusian waterbodies. Standard error in parentheses. C - Commensal, P - Parasite, n. r. - not recorded.

| Endosymbiont | Type of symbiont | Prevalence range,% | Intensity range | Reference |
|---|---|---|---|---|
| CILIOPHORA | | | | |
| *Conchophthirus acuminatus* | C | 86 – 100 | 67 (7) – 3224 (556) | Burlakova et al., 1998; Karatayev et al., 2000a, 2003c |
| *Ancistrumina limnica* | C | 0.3 – 94 | 3.7 (0.5) – 95.6 (12.2) | Karatayev et al., 2000a, 2003c; Mastitsky, 2004 |
| *Ophryoglena* sp. | P | 0 – 100 | 8.4 (1.1) – 65.8 (5.8) | Karatayev et al., 2000a, 2003c |
| *Sphenophrya dreissenae* | P | 0 – 10 | 4.2 – 43.5 | Molloy, pers. com. |
| *Hypocomagalma dreissenae* | P | 0 – 5 | 3.8 – 22.7 | Molloy, pers. com. |
| TREMATODA | | | | |
| Echinostomatidae | P | 0 – 70.3 | 1 – 8.3 (2.4) | Karatayev et al., 2000a; Mastitsky, 2004 |
| *Phyllodistomum* sp. | P | 0 – 13.0 | n.r. | Karatayev, 1983; Karatayev et al., 2000a |
| *Bucephalus polymorphus* | P | 0 – 10.2 | n.r. | Karatayev et al., 2000a; Mastitsky, 2004 |
| *Aspidogaster* sp. | P | 0 – 0.2 | n.r. | Karatayev et al., 2000a |
| NEMATODA | C | 2 – 77 | 1 – 3.7 (0.8) | Karatayev et al., 2000a, 2003c |
| HIRUDINEA | | | | |
| *Helobdella stagnalis* | C | 0 – 0.5 | 1 | Karatayev et al., 2000a |
| *Erpobdella octoculata* | C | 0 – 0.05 | 1 | Karatayev et al., 2000a |
| OLIGOCHAETA | | | | |
| Unidentified oligochaete | C | 0 – 0.6 | 1 | Karatayev et al., 2000a |
| *Chaetogaster limnaei* | C | 0 – 9.2 | 1 – 1.5 (0.4) | Karatayev et al., 2000a |
| HYDRACARINA | C | 0 – 8.5 | 1 – 1.8 (0.5) | Karatayev et al., 2000a; Mastitsky, 2004 |
| CHIRONOMIDAE | C | 0 – 18.2 | 1-3 | Karatayev et al., 2000a; Mastitsky and Samoilenko, 2005 |

va et al., 2006b), and has not been found in North America, Karatayev et al. (2000a) hypothesized that: (1) larval rather than adult *Dreissena* invaded North America, and (2) that all European waterbodies invaded by *Dreissena* where *C. acuminatus*-infestations are found, were more likely colonized by adult mussels than by veligers.

### *Ophryoglena*

A species specific ciliate in the family Ophryoglenidae (suborder Ophryoglenina), has been found inside the digestive gland of *D. polymorpha* (Zdun et al., 1994; Molloy et al., 1997). Although widespread in European *D. polymorpha* populations (Molloy et al., 1997; Karatayev et al., 2000a), *Ophryoglena* is much less common than *C. acuminatus*. During a large-scale parasitological study of *D. polymorpha* in Belarus in 1996–1997 this ciliate was found only in the Dnieper-Bug Canal (Karatayev et al., 2000a), which was the route of zebra mussel invasion in Europe, and thus has one of the oldest *D. polymorpha* populations in Belarus. *Ophryoglena* sp. was found in the Svisloch River for the first time in 2000, and now is widely distributed throughout this river system (Karatayev et al., 2003c). Since zebra mussels colonized the Svisloch River in the mid-1980s, we estimated that *Ophryoglena* sp. infected this population ~15 years after the initial colonization by *D. polymorpha*. These data support the hypothesis that the spread of endosymbionts may depend on the duration of time since initial colonization by zebra mussels, and therefore, the maximum numbers of alien species associated with *D. polymorpha* are probably found in the oldest zebra mussel populations (Karatayev et al., 2000a). The infection prevalence for *Ophryoglena* sp. in *Dreissena* in Belarus is moderate to high (40 to 100%). In the Svisloch River the mean infection intensity is low to moderate, ranging from 1.4 ± 0.1 to 65.8 ± 5.8 ciliates mussel$^{-1}$ (Karatayev et al., 2000a, 2003c). The maximum intensity seen in Belarus is 429 ciliates mussel$^{-1}$ in the Svisloch River (Mastitsky, 2004). There is a significant positive correlation between *Ophryoglena* sp. prevalence and infection intensity and a slight negative but significant correlation between *Ophryoglena* sp. prevalence and temperature (Karatayev et al., 2003c).

### Trematodes

Several species of trematodes have been reported as zebra mussel parasites in Belarus, including *Bucephalus polymorphus*, *Phyllodistomum* sp., *Echinoparyphium recurvatum*, and *Aspidogaster* sp. (Lyakhnovich et al., 1983b; Karatayev et al., 2000a). *D. polymorpha* can be the first intermediate host (*B. polymorphus* and *Phyllodistomum* sp.), the second (*E. recurvatum*), or the only host (*Aspidogaster* spp.) (Molloy et al., 1997). In Belarus *B. polymorphus* and *Phyllodistomum* sp. are found in three waterbodies, where the prevalence of infection varies from 0.4% to 3.3% for *Bucephalus* and from 0.3% to 2.0% for *Phyllodistomum* (Karatayev et al., 2000a). In contrast, *E. recurvatum* is very common and has been found in 10 waterbodies, with an infection prevalence ranging from 0.3% to 28.5%, the highest prevalence ever reported for *Dreissena*. *Aspidogaster* is rare in Belarus, and was found only once (Karatayev et al., 2000a).

### Other endosymbionts

Among other zebra mussel symbionts, nematodes are the most frequently observed, and live within the mantle cavity of *D. polymorpha* (Table 2). They are likely free-living species without any obligate association with zebra mussels (Molloy et al., 1997). Karatayev et al. (2000a) found nematodes in all 25 Belarusian zebra mussel populations they studied, and the prevalence of infestation varied from 2% to 52%. The maximum intensity of 41 nematodes mussel$^{-1}$ was found in the Svisloch River. In addition, several other endosymbionts including an oligochaete, *Chaetogaster limnaei*, a common commensal on snails (Timm, 1987; Monakov, 1998), two species of leeches, chironomid larvae and mites have been found in the mantle cavities of *D. polymorpha* from Belarusian waterbodies (Table 2).

At least five species of ciliates, among all known zebra mussel endosymbionts, are known to be species specific. In addition there is evidence that some trematodes are specific to *D. polymorpha* (Molloy et al., 1997). Therefore, when *D. polymorpha* invades new habitats several additional alien species may be introduced (Karatayev et al., 2000a). In Belarus the maximum number of alien symbionts associated with *D. polymorpha* were found in the oldest zebra mussel populations; in contrast, in the most recently colonized lakes only one alien symbiont was found. Through time zebra mussel populations will continue to accumulate symbionts (Karatayev et al., 2000a). Although trematode species that use zebra mussels as an intermediate host usually use either waterfowl or fish for final hosts and are occasionally fatal to those final hosts (Molloy et al., 1997), there is no evidence thus far that the zebra mussel parasites cause any significant fish pathology in Belarusian lakes (Karatayev et al., 1998b). In addition, at present there is no evidence that parasites or any of these endosymbionts can cause any effect on zebra mussel population dynamics in Belarus or elsewhere (Molloy et al., 1997).

### Ecological impact

Belarus has been a center for studies on the ecological impacts of *Dreissena*, including some pioneering studies on their local effects on native benthic communities (Lykhnov-

ich et al., 1982; Karatayev et al., 1983; Karatayev and Tishchikov, 1983; Karatayev and Lyakhnovich, 1990; Karatayev and Burlakova, 1992) as well as their effects on the entire ecosystem (Karatayev, 1983; Lyakhnovich et al., 1983a, 1988; Karatayev and Burlakova, 1995a).

To assess the effect of *Dreissena* on the benthic invertebrates, Karatayev and his associates conducted a study on sandy littoral of the Lake Lukomskoe, where zebra mussels formed isolated druses on various substrates (mostly unionids, or their dead shells) (Karatayev, 1983; Karatayev et al., 1983). Although 48 species of native benthic organisms were identified from both sand sediments and *Dreissena* druses, only 26 were found in both communities. In the sandy community small macroinvertebrates, mostly chironomids and oligochaetes that live within the sediment were the most common. The space between mussels in druses is much larger than between sand grains and thus is more suitable for colonization by larger organisms (snails, amphipods, isopods, Trichoptera, and leeches). The total density of native benthic maroinvertebrates in the sandy community was 1.5 times higher than in druses (40,995 ± 3,263 $m^{-2}$ versus 27,536 ± 4,085 $m^{-2}$, excluding *Dreissena*). In contrast, total wet biomass in sand (15.1 ± 1.0 g $m^{-2}$) was 8 times lower than in druses (114.8 ± 20.0 g $m^{-2}$). Therefore, the presence of *Dreissena* formed a new community, not generally found in sandy sediments, and invertebrates typical in sandy sediment communities disappeared, creating a mosaic pattern in the benthos (Karatayev et al., 1983, 1994).

An extensive survey (including > 100 samples collected with SCUBA) across Lake Lukomskoe showed that the spread of two crustaceans, *Asellus aquaticus* and *Gammarus lacustris*, was determined by the presence of *D. polymorpha* (Karatayev and Lyakhnovich, 1990). Both species were abundant in shallow areas (depth < 1 m) regardless of zebra mussels, however in water deeper than 2 m, *A. aquaticus* and *G. lacustris* were only found with *Dreissena,* and the density of *A. aquaticus* was positively correlated with the zebra mussel density.

The relationship between *D. polymorpha* and infaunal taxa may not be simple. Some species, such as *A. aquaticus* and *G. lacustris*, may be positively affected by *D. polymorpha*, while others are negatively affected and therefore the net effect of *Dreissena* on the local biodiversity may not be negative. *Dreissena* have been shown to have positive effects on isopods, larval chironomids, leeches, snails, amphipods, and oligochaetes (reviewed in Karatayev et al., 1997, 2002a). Negative effects of *Dreissena* have been found for native suspension feeders including unionids, sphaeriids and some chironomid larvae (reviewed in Karatayev et al., 1997, 2002a; Burlakova et al., 2000).

The long-term study of Lake Lukomskoe was the first comprehensive investigation of the impact of *Dreissena* on an entire lake ecosystem (Lyakhnovich et al., 1983a, 1988; Karatayev, 1983, 1992; Karatayev and Burlakova, 1995a). In the late 1960s this glacial lake was colonized by zebra mussels, and in 1969 it was transformed into a cooling reservoir for the largest power plant in the North West of the former Soviet Union. The introduction of zebra mussels coincided with an increase in the summer water transparency from 2 m in 1965 to 4 m in 1980. In addition, the biomass of zooplankton sharply declined and the wet biomass of native benthic macroinvertebrates increased almost 10 times. The trophic status of the lake shifted from a typical eutrophic lake towards mesotrophy (Lyakhnovich et al., 1983a; Karatayev, 1983). Because the transformation of a lake into a cooling reservoir is usually associated with an increase in eutrophication (Mordukhai-Boltovskoi, 1975), zebra mussels were suggested to be the main reason for these changes (Karatayev, 1983; Lyakhnovich et al., 1983a, 1988; Karatayev and Burlakova, 1995a). By mid 1970s the zebra mussel population reached a maximum biomass (~ 400 g $m^{-2}$ across the whole lake) in Lake Lukomskoe, and they were able to filter a volume equivalent to that of the lake in 17 days. Dramatic changes associated with the introduction of zebra mussels were also observed for the phytoplankton, macrophyte and fish communities (Lyakhnovich et al., 1988; Karatayev and Burlakova, 1995a). Increased water transparency resulted in an expansion of macrophyte cover from 6 to 30% of the total lake area, mainly due to an increase in the depth at which macrophytes can grow, from 2.5 to 5 m. After the invasion of zebra mussels, the biomass of phytoplankton declined. Fish productivity almost doubled, mainly due to an increase in the relative abundance and change in the composition of the commercial catch of benthophagous fishes (roach, rudd, white bream and bream) which feed mainly on zebra mussels (Karatayev, 1983, 1988, 1992; Lyakhnovich et al., 1983a, 1988; Karatayev and Burlakova, 1995a). Moreover, the conversion of primary production to higher trophic levels increased from 3.7% (before the introduction of *Dreissena*) to 5.5% (after introduction) for the second trophic level, and for predatory fish from 0.15% to 1% (Lyakhnovich et al., 1988; Karatayev and Burlakova, 1995a; Karatayev et al., 1997, 2002a).

By the mid-1980s, the zebra mussel population density in Lake Lukomskoe declined compared to that found during the initial invasion (late 1960s), resulting in decreased summer transparency to 3 m. Phytoplankton and zooplankton biomass increased, but were still lower compared to their pre-invasion abundance. The extent of macrophytes decreased from 30% to 20% of the lake surface area, but did not return to pre-invasion levels (6%) (reviewed in Karatayev et al., 2002a). This system was last studied in 1992, and was very similar to what it was in the mid-1980s.

In the mid-1980s zebra mussels colonized the Narochanskie lakes (mesotrophic Lake Naroch, eutrophic Lake

Myastro and highly eutrophic Lake Batorino). Extensive data are available on these lakes from the pre-zebra mussel invasion period, including montly samples of phytoplankton, zooplankton, bacterioplankton, and water chemistry (among other data) since the end of 1940s, allowing an assessment of the effects of *D. polymorpha* invasion (Ostapenya et al., 1993, 1994a, 1994b). Although these lakes differ in their morphometry and trophic type, the invasion by *Dreissena* resulted in similar changes in all three lakes (Ostapenya et al., 1993, 1994a, 1994b; Kryuchkova and Derengovskaya, 1999, 2000; Zhukova, 2000, 2001), and these changes were very similar to those seen in Lake Lukomskoe. Thus, after the invasion of zebra mussels, by mid-1990s water transparency in the Narochanskie lakes increased 1.3-2.4 times, the concentration of total phosphorus in the water column decreased, seston was reduced 2.3-6.9 times, and the chlorophyll concentration in the plankton decreased 2.7-6.9 times. Phytoplankton and zooplankton biomass, primary production, BOD5, and organic carbon content in the water also decreased. All these changes were associated with the reduction of the trophic status of all three lakes from eutrophic to mesotrophic (Naroch and Myastro) and from strongly eutrophic to eutrophic (Batorino). Thus, 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, 1988, 1992). Other European scientists have proposed to use zebra mussels as a biofilter to decrease the effects of anthropogenic eutrophication in lakes (Reeders et al., 1989, 1993; Reeders and Bij de Vaate, 1990; Noordhuis et al., 1992a).

Similar changes associated with the colonization of *Dreissena* have been reported for North American waterbodies, including an increase in water transparency, benthic algal abundance, and macrophyte coverage (reviewed in Karatayev et al., 1997, 2002a). Turbidity and phytoplankton abundance, chlorophyll content and production have decreased (Caraco et al., 1997; Idrisi et al., 2001). In addition, the effect of zebra mussels on native macroinvertebrates is similar to those found in Belarus, e.g., an increase in biomass associated with changes in benthic community structure (Botts et al., 1996; Stewart et al., 1998). Thus, the overall effect of *Dreissena* on aquatic ecosystems is very similar in Europe and in North America (reviewed in Karatayev et al., 1997, 2002a).

## Conclusions

1. In spite of 200 years of continuous invasion, by 2000 zebra mussels were found in only 21% of the 553 Belarusian lakes that have been studied. Although some of the lakes that have not been invaded may be unsuitable for zebra mussels due to low pH or low calcium concentrations, 80% of these lakes are suitable for *D. polymorpha* survival and growth.
2. In Belarusian waters, zebra mussels are usually reproductive from the beginning of June to the end of August. The seasonal dynamics of *Dreissena* veligers in the plankton is characterized by one or several peaks in abundance, depending on spring and summer temperature dynamics.
3. Growth rates of *D. polymorpha* have been studied in Belarus using several methods: counting annual rings on shells, analysing size frequency distributions, monitoring the growth of tagged mussels in experimental cages, and monitoring the growth of uncaged, tagged mussels on their natural substrates. This last method provides the most realistic estimates of zebra mussel growth. *Dreissena* growth rate depends on temperature, season of the year, trophic conditions of a waterbody, and water current.
4. Population density and biomass of *Dreissena* differs among regions within waterbodies as well as among waterbodies, and depends upon the type of waterbody, available substrates, the amount of local pollution and time since initial colonization.
5. Sixteen species and higher taxa of commensals and parasites have been found within the mantle cavity and/or associated with zebra mussel tissue, including ciliates, trematodes, nematodes, chironomids, oligochaetes, mites, and leeches. *Conchophthirus acuminatus* is the most common endosymbiont of *D. polymorpha* in Belarus and in Europe in general, and has the highest prevalence and intensity of infection. Intensity and/or prevalence of symbionts can be affected by host-dependent factors, such as mussel size and the presence of highly infected mussels in a microhabitat, or by host-independent factors such as temperature or season of the year.
6. The introducton of zebra mussels may have both local and system wide effects. Local effects include changes in species composition, density, and biomass of native bottom invertebrates and is more pronounced in areas populated with high densities of *D. polymorpha.* System wide effects alter all aspects of aquatic communities and abiotic parameters and include, but are not limited to, an increase in water transparency, macrophyte growth, abundance of benthivorous fish, and decreases in the densities of phytoplankton and zooplankton, as well as decreases in the concentrations of chlorophyll, total phosphorus, and suspended matter.

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