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Patterns of spread of the zebra mussel (*Dreissena polymorpha* (Pallas)): the continuing invasion of Belarussian Lakes

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Abstract

The invasion of the freshwaters of Belarus by the zebra mussel, *Dreissena polymorpha* (Pallas), began at least 200 years ago by the opening of shipping canals linking the Black Sea and Baltic Sea drainage basins. However, zebra mussels have invaded only 93 (16.8%) of 553 studied lakes; at least 20 of these lakes were invaded within in the past 30 years. Zebra mussels were found disproportionately in lakes that were mesotrophic, larger, and had some commercial fishing. Although larger lakes have more intensive fisheries with larger catches, the intensity of the fishery and average catch did not affect the probability of zebra mussel invasion. Zebra mussels were not found in dystrophic lakes (10% of the lakes studied), probably due to their low pH and calcium content. Zebra mussels became locally extinct in one lake due to anthropogenic eutrophication and pollution. Many ecologically suitable lakes have yet to be invaded, which suggests that natural vectors of overland dispersal, e.g., waterfowl, have been ineffective in Belarus. Thus, future spread of this species will continue to depend on human activities such as commercial fishing.

Introduction

The invasion of North America by the zebra mussel (*Dreissena polymorpha*) has focused attention on economic and environmental problems associated with exotic species. As with many exotic species, the spread of zebra mussels has been tightly linked to human activities. Carlton (1993) identified over 20 potential ways in which zebra mussels can be dispersed and made important contrasts between (1) the dispersal of larvae and adults, (2) natural and human-mediated dispersal, and (3) dispersal overland between bodies of water and dispersal within a body of water. A planktonic larval stage (veliger) makes zebra mussels well suited to spread naturally within lakes and reservoirs or downstream within a watershed. However, this life history appears to prevent the establishment of populations in streams or rivers that do not have a source population in a headwater lake (Horvath et al. 1996). The ability of the adult stage to attach to submerged objects (e.g., wood, macrophytes) can also aid in downstream dispersal (Horvath and Lamberti 1997). Obviously, any human activity that moves either water (e.g., fish stocking) or objects (e.g., boats) within or between waterbodies has the potential to disperse this species. Unfortunately, we are only beginning to understand the relative importance of different potential vectors of spread (Johnson and Carlton 1996; Johnson et al. 2001).

Studies in eastern and western Europe have provided useful information on a variety of aspects of zebra mussel biology (Morton 1969; Stanczykowska 1977; Lvova 1980; Karatayev 1988), ecology

(Stanczykowska 1977; Stanczykowska and Lewandowski 1993; Karatayev et al. 1994, 1997, 1998), and distribution (Kinzelbach 1992; Starobogatov and Andreeva 1994). The spatial and temporal dynamics of the invasion of this and other exotic species has been difficult to address, especially at the regional level (Johnson and Padilla 1996; Buchan and Padilla 1999). However, studies of the geographic pattern and rate of spread of zebra mussels are extremely helpful if we are to predict, slow or stop the spread of zebra mussels and other exotics to new freshwater bodies, as well as identify important vectors for spread (Buchan and Padilla 1999; Bossenbroek et al. 2001; Kraft et al. 2002).

Because the initial invasion of zebra mussels across eastern and western Europe occurred largely during the 1800s (Andrusov 1897; Skorikov 1903; Deksbakh 1935; Kinzelbach 1992; Ludyanskiy et al. 1993), detailed quantitative information on the spread of zebra mussels in Europe is generally lacking. Zebra mussels were originally found in the fresh and brackish waters of the Caspian and Black Sea drainage basins including large tributary rivers (Andrusov 1897; Mordukhai-Boltovskoi 1960; Starobogatov and Andreeva 1994). Because shipping was restricted to the largest rivers, canal systems were built in the late 1700s–early 1800s, through what is now Belarus, to connect these large rivers and the Black, Caspian and Baltic Seas for commerce (Andrusov 1897; Zhadin 1946; Kinzelbach 1992; Starobogatov and Andreeva 1994). After these canals were built and commercial ships traveled regularly through them, zebra mussels appeared throughout eastern and western Europe (Zhadin 1946; Kinzelbach 1992; Starobogatov and Andreeva 1994). They appeared in England in 1824, the Netherlands in 1826, Germany in 1830, Denmark in 1840, and in France shortly thereafter (Kerney and Morton 1970; Kinzelbach 1992; Starobogatov and Andreeva 1994). Zebra mussels continue to spread to new lakes and areas across Europe, and have recently invaded Ireland (Minchin 1998). Although there is some information about the spread of zebra mussels through major rivers and canal systems, there is very little information available on the spread of zebra mussels from these river and canal systems to other waterbodies, especially those not directly connected to rivers.

Systematic searching of waterbodies across a region is required to adequately study the pattern and timing of spread of any invading species, and it is equally important to know where they are and are not found (Johnson and Padilla 1996; Kraft and Johnson 2000). Although such information is rare, it has been collected in the Republic of Belarus over the past 200 years. To assess the historic and present spread of zebra mussels across Belarus, we reviewed the literature on the history of the spread of zebra mussels across Belarus. We also used a unique data set for 553 lakes of a wide range of sizes and trophic types assembled during the past 25 years as part of a comprehensive limnological study, to address questions about the spread and invasion of zebra mussels. We tested whether zebra mussels were more likely to be found in lakes with different trophic status, different sizes, with or without fishing, with different degrees of fishery activity, and in different drainage basins.

Materials and methods

There are 1072 lakes with surface area greater than 0.1 km^2 in Belarus (Kurlovich and Serafimovich 1981). Most of these lakes were formed during the last glaciation and are found in northern Belarus (Belarussian Lakeland), especially the Zapadnaya Dvina River drainage basin (Figure 1; Table 1). Due to intensive agriculture, all Belarussian lakes suffer from anthropogenic eutrophication. Therefore, no lakes are oligotrophic, few are meso-oligotrophic or mesotrophic and most are eutrophic. Some Belarussian lakes are dystrophic. Although there are many flood-plain lakes in Belarus, they are usually very small, and were not considered in our study.

To determine the current distribution and recent spread of zebra mussels in Belarus, we examined data collected from 553 glacial lakes between 1971 and 1996. As part of a larger survey of Belarussian lakes, a variety of chemical, geological, physical, biological, and socioeconomic data were systematically collected for each of these lakes [Lakes Research Laboratory of the Belarussian State University (LRL)].

The data we used for this paper were: lake surface area, trophic status, presence of commercial fishing during a 15 year period, the average fishery catch over that same 15 years, and presence or absence of zebra mussels. Although the availability of substrate for the attachment of zebra mussels can limit their distribution in some lakes, all of the lakes in our data set had at least some substrate adequate for zebra mussel attachment, therefore, this factor was not considered in our

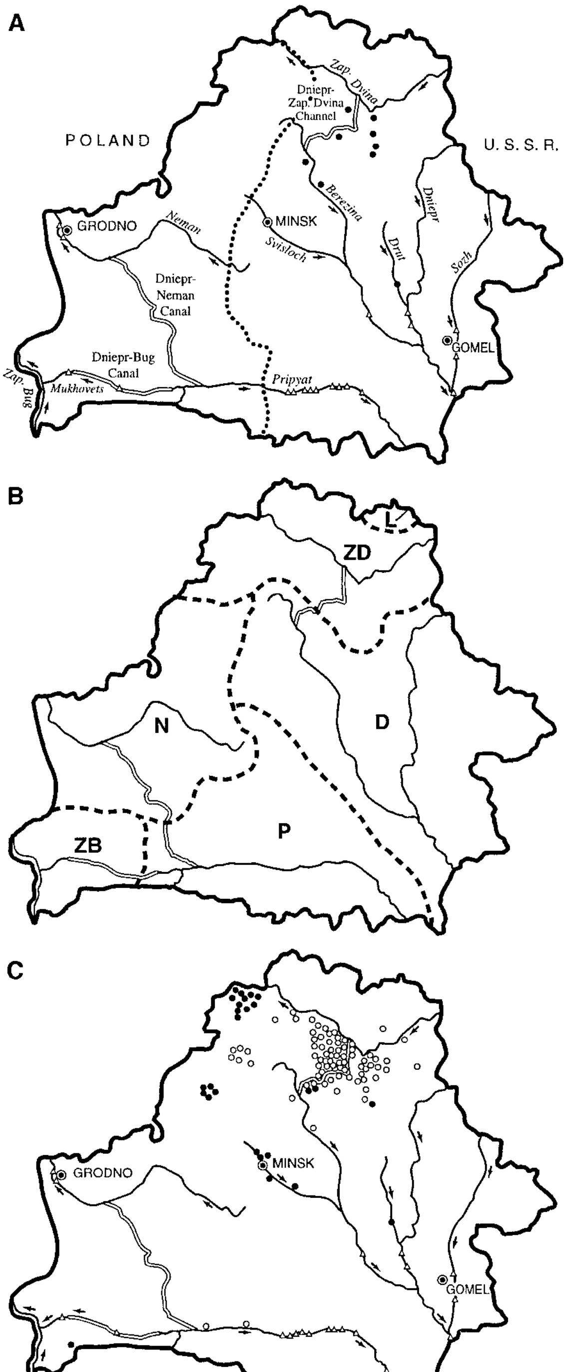

Figure 1. Map of the Republic of Belarus. (A) The first studies of the invasion of zebra mussels were conducted when Belarus was split between Poland and the USSR (dashed line indicates border), and only the USSR portion was surveyed. The filled circles (lakes) and open triangles (rivers) indicate the known populations of zebra mussels before our study. (B) The drainage basins of the Zapadnaya Dvina (ZD), Dnieper (D), Neman (N), Pripyat (P), Zapadnyi Bug (ZB), and Lovat (L) rivers. (C) Circles (lakes) and open triangles (rivers) indicate all known populations of zebra mussels in Belarus. Filled circles indicate lakes and reservoirs where we know the approximate date of zebra mussel invasion.

Table 1. The presence of zebra mussels in Belarussian lakes with surface area $>0.1\ km^2$. The locations of river basins can be found in Figure 1. The total number of lakes in each river basin is from Kurlovich and Serafimovich (1981).

River basin	Total number of lakes	Number of lakes studied (%)	Number of studied lakes with zebra mussels (%)
Zapadnaya Dvina (ZD)	757	474 (62.6)	86 (18.1)
Dnieper (D)	117	11 (9.4)	3 (27.3)
Neman (N)	91	33 (36.3)	3 (9.1)
Pripyat (P)	86	20 (23.3)	0
Zapadnyi Bug (ZB)	13	9 (69.2)	1 (11.1)
Lovat (L)	8	6 (75.0)	0
Total	1072	553 (51.6)	93 (16.8)

analyses. Lake surface areas were estimated from maps (1 : 25,000 scale). Trophic status (oligotrophic, meso-oligotrophic, mesotrophic, eutrophic, dystrophic) was assigned by the LRL staff, and was determined using chemical (total ion content, organic content, phosphorous content), physical (transparency, color), and biological (phytoplankton density, biomass, species composition) data (Winberg 1960; Yakushko 1971; Rossolimo 1977). Karatayev and Burlakova (1995) examined a similar data set; however, the data set we used in this study was revised and updated in 1995 and 1996. The re-evaluation of trophic status of these lakes included more emphasis on the biological data, and included the summer biomass of phytoplankton, zooplankton and benthos, and the taxonomic structure of planktonic and benthic communities. In many cases, a re-examination of the data by both hydrochemists and biologists resulted in reassignment of lake trophic status from the data set used by Karatayev and Burlakova (1995).

The intensity of the commercial fishery was estimated from 1961 to 1976 with records from the Fish Conservation Committee of the State Committee of Ecology and Conservation of Natural Resources, Republic of Belarus. We chose this 15 year period for several reasons. To test if fisheries have been important vectors for the spread of zebra mussels, we needed to use fisheries data that were collected prior to the sampling dates for the majority of the lakes in our dataset. For this 15 year period we have good annual data on fisheries. The commercial fisheries in Belarus were relatively stable from the early 1960s through the early 1990s, but then collapsed when the Soviet Union was dissolved. We used the number of years during that 15 year period as an estimate of fishery intensity, and the average annual catch as an estimate of the size of the fishery.

The presence or absence of zebra mussels was determined from 6 to 25 benthic samples (depending on the size of the lake such that sampling effort was as similar as possible across lakes) collected from sites systematically distributed across the lake (Mitropolsky and Mordukhai-Boltovskoi 1975). Benthic samples were collected with an Ekman or Petersen grab (sampling area = 0.025 m^2) and washed through a 550 μm mesh. After sampling, all macroinvertebrates were transferred to containers with 10% neutral buffered formalin and labeled. All macroinvertebrates were identified to the genus or species level, counted and weighed to the nearest 0.0001 g after being blotted dry on absorbent paper. Because this technique is not appropriate for an accurate estimate of zebra mussels density (Karatayev et al. 1990), here we considered only presence/absence of *Dreissena* in studied lakes. The sampling regime was designed to maximize the coverage of the lake bottom and to include all major microhabitats. In addition, benthic species composition along a 100–150 m stretch of the littoral zone (down to 1.5 m depth) and 6–25 plankton samples (for veligers) were examined. The densities of zebra mussel populations in European lakes have been recorded to fluctuate greatly (reviewed in Ramcharan et al. 1992b). Although this sampling regime might not detect a zebra mussel population that was either very localized or very small, it did standardize the search effort among lakes. Because of the scale of this project, different lakes were examined in different years, and most lakes were only examined once. However, over 100 lakes of various sizes were sampled more than once, and more than 50 lakes were studied >2 times.

Differences in frequencies in the presence and absence of zebra mussels in different categories of lakes where tested using multi-way G-tests. These tests are a log-linear estimator of goodness of fit and are recommended when expected values within cells are low (below 30) and when some cell values are zero (Fienberg 1970).

Results

Zebra mussels were found in 93 (16.8%) of the 553 lakes examined (Table 1). At least 20 of the lakes were invaded between 1971 and 1996 (as determined by repeated sampling of the same lake during that time period). Using a 3-way G-test, we found that zebra mussels were found more often in larger lakes ($0.01 > P > 0.005$; Table 2) and lakes with lower trophic status ($P \ll 0.001$; Table 3) than would be expected by random chance. Zebra mussels were found disproportionately more often in mesotrophic lakes (39.2%), and they were completely absent from dystrophic lakes (Table 3). With respect to lake size, zebra mussels were found over four times more often in the largest lakes (>15 km^2) than in the smallest lakes (0.1–0.25 km^2; Table 2). Overall, larger lakes tended to have a higher trophic status than would be expected by random ($0.05 > P > 0.025$, 3-way G-test). All of these results were the same when dystrophic lakes were eliminated from the analysis.

Using a 3-way G-test including lake size and fishery intensity, we found that zebra mussels were more common in large lakes than small lakes

Table 2. Occurrence of zebra mussels in lakes of different size. The total number of lakes in Belarus is from Kurlovich and Serafimovich (1981).

Lake area (km^2)	Total number of lakes	Number of lakes studied (%)	Number of studied lakes with zebra mussels (%)
0.11–0.25	545	122 (22.4)	11 (9.0)
0.26–0.50	330	135 (40.9)	15 (11.1)
0.51–1.00	197	114 (57.9)	19 (16.7)
1.01–5.00	217	143 (65.9)	33 (23.1)
5.01–15.0	44	27 (61.4)	10 (37.0)
15.1–79.6	18	12 (66.7)	5 (41.7)
Total	1072		

Table 3. Occurrence of zebra mussels in lakes of different trophic type.

Trophic type	Total number of lakes studied	With zebra mussels	
		Number of lakes	Percent of lakes
Meso-oligotrophic	26	5	19.2
Mesotrophic	51	20	39.2
Eutrophic	421	68	16.2
Dystrophic	55	0	0
Total	553	93	16.8

($0.025 > P > 0.0001$), and more common in lakes with fisheries than those without ($P < 0.001$). Larger lakes were much more likely to have an intensive fishery than small lakes ($P \ll 0.0001$). When we considered the size of the lake fisheries (average annual catch), we again found that large lakes were more likely to have large fishery catches ($P \ll 0.0001$). Greater fish catches were not associated with zebra mussel invasion, when lake size was taken into account ($P < 0.15$), however, small samples size and low power could account for this lack of statistical significance. When we eliminated lakes without a fishery from the analysis, we found that large lakes were more likely to have intensive and large catch fisheries ($P \ll 0.0001$), and large lakes were more likely to have zebra mussels ($0.01 > P > 0.005$). However, lakes with more years of fishing or higher fish catches were not more likely to have zebra mussels ($0.50 > P > 0.25$).

Lake colonization by zebra mussels was not equally likely among drainage basins ($0.025 > P > 0.01$, G-test; Table 1). Lakes in the Zapadnaya Dvina River basin were more likely to have zebra mussels (86 lakes), and in the Dnieper River basin, zebra mussels were present in a disproportionate number of lakes, occurring in 3 of 11 lakes. No zebra mussels were found in glacial lakes in the Pripyat or Lovat drainage basins. In addition, zebra mussels were found in 85 of 356 lakes studied on the southern bank of the Zapadnaya Dvina River but only 1 of 118 lakes studied on the northern bank was found to contain zebra mussels.

Discussion

Zebra mussels have been invading the freshwaters of eastern Europe for over 200 years, but not all lakes in Belarus have been invaded. Although the spread of zebra mussels along shipping canals and the rivers they connect may have occurred quickly, the subsequent spread to unconnected waters has occurred much more slowly. Another dreissenid mussel, *D. bugensis*, is abundant in the Ukraine, however, only the zebra mussel, *D. polymorpha,* has invaded Belarus. *D. polymorpha* has been the most important invader across Europe, and, at present, it is not known why these two species seem to differ in their ability to invade new lakes and rivers.

Historic spread of zebra mussels

The spread of zebra mussels to lakes and rivers in Belarus (former USSR) began over 200 years ago and was probably associated with shipping activities, especially through canals (Ovchinnikov 1933; Lyakhnovich et al. 1984; Starobogatov and Andreeva 1994). Three canals connecting the Dnieper and Zapadnyi Bug Rivers (1775), the Dnieper and Neman Rivers (1804) and Dnieper and Zapadnaya Dvina Rivers (1805), were constructed in Russia (what is now Belarus) to connect shipping routes between the Black Sea and Baltic Sea basins (Figure 1). Not only did these canals increase traffic along these rivers, they also established connections to river basins that previously had no navigable or hydrological links to the Black Sea basin, in particular, the lake-rich basin of the Zapadnaya Dvina River.

The first study of the distribution of zebra mussels in what is now Belarus was by Ovchinnikov in 1929. At that time, present day Belarus was divided between the USSR and Poland, and he was only able to study the eastern (Soviet) part. Although his expedition surveyed many lakes, he only reported those where he found zebra mussels. He found zebra mussels in three glacial lakes, three large rivers (Dnieper, Pripyat, and Berezina), and several small rivers (Ovchinnikov 1933). From 1948 to 1953 zebra mussels were reported from five additional lakes in the Zapadnaya Dvina River basin and in Palik Lake which is connected to the Berezina River (Drako 1953; Drako and Gavrilov 1972). Lyakhnovich et al. (1984) reported that zebra mussels had invaded the Drut River (Chigirinskoe Reservoir), the Sozh River (near Gomel), the Neman River (near Grodno), and the Mukhovets River. Thus, before 1970, zebra mussels were known to have invaded at least nine glacial and two flood-plain lakes, six large and four small rivers and one reservoir in Belarus (Figure 1).

Present distribution

Zebra mussels were found in only 93 (16.8%) of 553 lakes studied. Because of repeated sampling for some of the lakes, we know that at least 20 (21.5%) of those lakes have been invaded during the past 30 years. Although some of the lakes that have not been invaded are unsuitable for zebra mussels due to low pH or low calcium, most are suitable for zebra mussels based on the properties of invaded lakes and predictions from other European lakes (Ramcharan et al. 1992a).

Lakes do not appear to have been invaded in a random geographic pattern. At a large spatial scale, the percentage of lakes invaded by zebra mussels is greatest in the Dnieper (27%) and Zapadnaya Dvina (18%) drainage basins which were connected by the Dnieper–Zapadnaya Dvina canal in 1805. This canal and the rivers it connects run through the Belarussian Lakeland in northeastern Belarus which contains more than 62% of the lakes in Belarus (Figure 1, Table 1). Although this canal system has clearly been most influential in the spread of zebra mussels within Belarus, two other canals, the Dnieprovsko-Bugskyi and the Dnieprovsko-Nemanskyi, were considered the primary routes for the spread of zebra mussels to the rest of Europe (Kinzelbach 1992; Starobogatov and Andreeva 1994).

Different attributes of lakes also affected their probability of being invaded by zebra mussels. Larger lakes, lakes with commercial fisheries, and lakes with lower trophic status were more likely to be invaded than expected by random chance alone. The presence of zebra mussels enhances the production of bottom feeding fish, such as roach, white bream, and bream (Karatayev 1983; Lyankhnovich et al. 1988) and in some cases, doubled the size of a lake's fishery (Karatayev 1992; Karatayev and Burlakova 1995). Therefore, it is unclear whether the association between zebra mussel invasion and fisheries is because zebra mussels enhance fish production, stimulating commercial fishing, or because fishing activities directly affect zebra mussel invasion, or both. Similarly, we do not know if zebra mussels invade more often or survive better in lakes with lower trophic status, or if they are found in lakes with lower trophic status because they reduce the trophic status of lakes they invade, or both. The presence of zebra mussels can shift the trophic status of a lake to a lower level by reducing phytoplankton abundance (Karatayev and Burlakova 1995; Karatayev et al. 1997).

Zebra mussels were more common in large lakes, and large lakes were much more likely to have more intensive fisheries with higher fish catches. Although lakes with fisheries were more likely to have zebra mussels, zebra mussels were not more common as a function of fishing intensity or the size of fishery catch. Again, it is difficult to separate the relative importance of lake size and the presence of a fishery on the likelihood of zebra mussel invasion because these two factors are completely confounded.

The slow spread of zebra mussels from the major rivers and canals to the lakes of Belarus appears to be due to dispersal limitations. Early during the initial invasion, zebra mussels were able to invade those few lakes directly connected to rivers and their interbasin canals (Ovchinnikov 1933). However, most lakes in Belarus are not connected by navigable waterways, and thus the subsequent spread of zebra mussels has had to depend on overland dispersal. In North America, recreational boating and fishing are thought to be the primary overland vectors for the dispersal of zebra mussels (Johnson and Carlton 1996; Padilla et al. 1996; Schneider et al. 1998; Buchan and Padilla 1999; Johnson et al. 2001), but in Belarus, recreational motor boats are quite rare, and boats of any kind are seldom transported between bodies of water. Although many other potential dispersal mechanisms exist (Carlton 1993), commercial fishing is most likely responsible for transporting mussels between the lakes in Belarus. Not only are zebra mussels associated with the presence of fisheries, direct observations of fishing activity indicate that they are capable of transporting zebra mussels among lakes. Sweep-nets, used by fishermen, can harbor hundreds of zebra mussel druses in an individual net (Karatayev 1983). Such fishing equipment is often used in multiple lakes, and because zebra mussels can survive up to several weeks in wet nets (Deksbakh 1935), zebra mussels can be easily spread to other lakes in this manner. The government commercial fishery from the 1960s to 1990s was very intensive. Several fishery groups harvested fish from more than 400 lakes. Although some lakes were harvested only annually, some were fished almost daily (Karatayev et al. 1999).

Waterfowl have been suggested to be a possible vector for transporting zebra mussels as adults or as larvae among unconnected waterbodies (Charlemagne 1914; Reichholf and Windsperger 1972). Johnson and Carlton (1996) have experimentally shown that this mechanism is unlikely to spread zebra mussels, and our study supports their conclusion. Waterfowl are abundant and diverse in all of the lakes in Belarus, however, only a small fraction of these lakes have been invaded by zebra mussels during the past 200 years. Therefore, we do not expect waterfowl to be important vectors for the transport of zebra mussels to uninfected lakes.

Although the majority of the spread of zebra mussels depends on overland dispersal vectors, not all invasions are independent events. While transport to an individual isolated lake may be a stochastic and rare event (Buchan 1997; Buchan and Padilla 1999), once a lake is invaded, zebra mussels can easily spread to downstream lakes through the dispersal of their larvae which spend up to several weeks drifting in the plankton. For example, a group of 11 hydrologically connected lakes in the Zapadnaya Dvina River basin (northwestern Belarus) were colonized between the mid-1960s and the early 1980s. The invasion began in 1964–1966 when zebra mussels appeared in Drivyaty Lake, the largest lake in this group, and then spread downstream to the other 10 lakes (Lyakhnovich et al. 1984). This could explain why zebra mussels were found disproportionately on the southern bank compared to the northern bank of the Zapadnaya Dvina River. In Belarus, zebra mussels spread from south to north – downstream in the Zapadnaya Dvina River basin. They were less likely to spread upstream and colonize lakes on the right bank of the river. Similarly, in the Narochanskie Lake system in the Neman River basin, zebra mussels were first detected in Myastro Lake in 1984 (Ostapenya et al. 1994) and then spread downstream (<1 km) into Naroch Lake where they were found in 1989 (Ostapenya et al. 1993). However, we also found zebra mussels in lakes Myadel and Volchin which, although near the other lakes (2 and 12 km, respectively), are a part of another drainage basin. The mechanisms of these latter invasions are not obvious.

As we have no historic information on the presence or absence of zebra mussels for the majority of lakes studied, it is difficult to estimate when zebra mussels colonized each waterbody. However, data from multiple surveys of individual lakes can give insights into the timing of an invasion. For example, zebra mussels were not found in 1968–1969 in Lukomskoe Lake but were detected in a subsequent survey in 1972 (Lyakhnovich et al. 1982; Karatayev 1983). Based on similar data, the colonization of 20 lakes, 7 reservoirs, and 3 rivers in Belarus has been documented since the end of the 1960s.

Once zebra mussels invade a waterbody, they generally do not go extinct, except in areas suffering from pollution or high levels of anthropogenic eutrophication. According to Kinzelbach (1992), zebra mussels were commonly found in the Middle Elbe River after 1827, but then disappeared due to water pollution. Anthropogenic eutrophication also appears to have caused the extinction of zebra mussels in six Masurian lakes (Poland) between 1959 and 1988 (Stanczykowska and Lewandowski 1993). We found only one case where zebra mussels went extinct for any period of time. Between 1972 and 1986, zebra mussels colonized Boloiso Lake in the Zapadnaya Dvina River drainage basin. At that time, it was a well-oxygenated, mesotrophic lake with good water quality and summer transparency >3 m. Since the mid-1980s Boloiso has been heavily polluted by metropolitan waste from the city of Braslav (Karatayev et al. 1995) and has been transformed into a hyper-eutrophic lake. Phosphate concentrations have increased from $0.05\,\mathrm{mg\,l^{-1}}$ in 1972 to $0.25\,\mathrm{mg\,l^{-1}}$ in 1986 and to $0.50\,\mathrm{mg\,l^{-1}}$ in 1996; summer transparency has now decreased to 0.6 m. In the early 1990s zebra mussels were no longer found in this lake. No other populations of zebra mussels in over 50 other lakes that have been sampled after zebra mussels were first detected are known to have disappeared.

Zebra mussels have proven to be very effective invaders worldwide when transported by human activities. Without the construction of canals and human shipping activity, the spread of zebra mussels beyond their native waters would have been much slower and more restricted. Much like an earlier invasion by *Corbicula fluminea*, another freshwater bivalve (McMahon 1982), the rapid spread of the zebra mussel in North America over the past decade appears largely due to downstream dispersal of larvae and the movement of commercial ships and barges within the hydrologically connected lakes, rivers, and canals of the drainage basins of the Mississippi and St. Lawrence Rivers and the Laurentian Great Lakes (Johnson and Carlton 1996). The overland spread of zebra mussels is much slower (Johnson and Carlton 1996; Padilla et al. 1996; Buchan and Padilla 1999). Kraft and Johnson estimated that between 3% and 8% of the inland lakes surrounding the Laurentian Great Lakes are being invaded each year although this rate is highly variable (0–20%) among different regions (Kraft and Johnson 2000). Our study of Belarussian lakes and rivers provides much the same picture but over a much longer time scale, i.e., centuries rather than decades. Obviously, there are many differences between these two systems, especially in terms of the relative importance of different human-mediated dispersal mechanisms. However, this study offers rare information of the dispersal patterns of an invading aquatic species at a spatial scale for which we know very little (Johnson and Padilla 1996). The rapid increase of the range of geographic extent of zebra mussels across Europe during the past two centuries and across eastern North America during the past decade has lead to its reputation of being a highly invasive species (Ludyanskiy et al. 1993). However, our data from Belarus, one of the countries closest to the native range of the zebra mussel, indicates that the invasion of European waters within that total range is slow, and far from over. More extensive examination of the geographic spread of zebra mussels across the rest of Europe will greatly enhance our understanding of how this and other aquatic exotic species spread.

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