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Past, current, and future of the central European corridor for aquatic invasions in Belarus

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Abstract We analyzed the role of the waterways of Belarus in the spread of aquatic exotic invertebrates through the central European invasion corridor. Present day Belarus became critically important when in the end of the 18th—beginning of the 19th century three interbasin canals connecting rivers from the Black and Baltic seas basins were constructed for international trade. These canals became important pathways facilitating the spread of aquatic alien species. For more than a hundred years, only Ponto-Caspian species colonized Belarus using ships and especially timber in rafts exported by Russia into Western Europe. In the second half of the 20th century, new vectors of spread appeared in Belarus, such as stocking of economically important invertebrates and accidental introductions. This paper is the first comprehensive review of aquatic exotic invertebrates in Belarus. Currently, 19 exotic aquatic invertebrates are known in Belarus, including 14 species of Ponto-Caspian origin. The rate of spread of aquatic invasive species in the second half of the 20th century increased 7-fold compared to the 19th—beginning of the 20th century. We found a significant positive correlation between the time since initial invasion and number of waterbodies colonized. We predict a further increase in the rate of colonization of Belarus by exotic invertebrates as well as an increase in the diversity of vectors of spread and donor areas of alien species, especially when the ongoing reconstruction of the interbasin canals will be completed and the hydrological connection between Black Sea and Baltic Sea basins will be reestablished after an interruption that has lasted for almost a century.

Keywords Aquatic exotic species · Dispersal · Geographic spread · Vectors of spread · Central invasion corridor · Invertebrates · Belarus

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Introduction

The spread of exotic species can be considered at both spatial and time scales, with regions of high and low concentration of alien species as well as periods with high and low intensity of invasion. The introduction of exotic species has not been a continuous process, but rather punctuated by periods of rapid spread. Each such 'jump' has been associated with changes in the tempo of some human activity, including: construction of shipping canals for trade, building of reservoirs, human migration, changes in political boundaries, or political systems, changes in the mode and volume of international trade, or industrial practices and environmental laws (Karatayev et al. 2007a). However, various factors dominated in different periods of human history and not all of them may be equally important in each part of the World. The reconstruction of the history of spread may not only help in the understanding of patterns of former invasions but may also be used to predict future invasions.

The current study is based on the analysis of the history of spread and modern distribution of aquatic exotic invertebrates in the Republic of Belarus. Belarus is a relatively small country of very recent political origin located in the geographical center of Europe. This region became critically important when in the end of the 18th—beginning of the 19th century three interbasin canals connecting the River Dnieper with several rivers from the Baltic Sea basin were constructed for international trade (Table 1, Fig. 1). These canals established corridors for shipping and trade among Black Sea and Baltic Sea basins that previously had no hydrological links, and also provided important passages for the introduction of numerous Ponto-Caspian species to the Baltic Sea basin (Mordukhai-Boltovskoi 1964; Bij de Vaate et al. 2002; Jazdzewski and Konopacka 2002; Olenin 2002; Karatayev et al. 2007a, b). According to Bij de Vaate et al. (2002), the invasion of Ponto-Caspian macroinvertebrates into Europe have been facilitated by three inland migration corridors, including: northern corridor (River Volga → Lake Beloye → Lake Onega → Lake Ladoga → River Neva → Baltic Sea), central corridor (River Dnieper → River Vistula → River Oder → River Elbe → River Rhine), and southern corridor (Danube and Rhine Rivers). The central corridor at the territory of Belarus actually embraced three different shipping canals connecting the River Dnieper with rivers Zapadnyi Bug, Neman and Zapadnaya Dvina (Fig. 1). The first canal is still in operation; the two others were abandoned at the first half of the 20th century, however they played a critical role in the spread of the zebra mussel, *Dreissena polymorpha* (and possibly some other species) in the 19th century. For example, the Dnieper-Zapadnaya Dvina canal has clearly been the most influential in the spread of zebra mussels within Belarus (Karatayev et al. 2003a), while

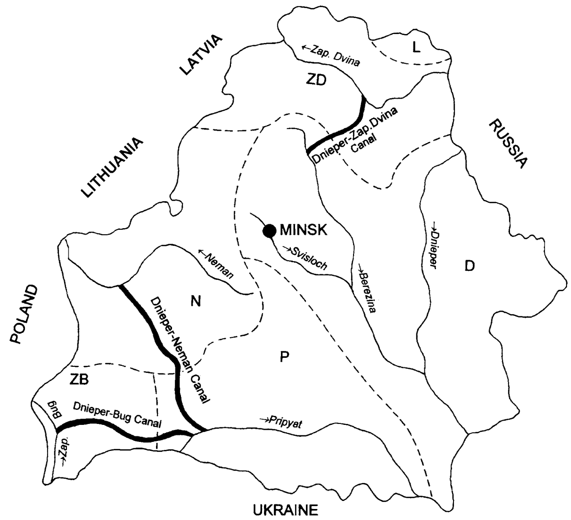

Fig. 1 Map of the Republic of Belarus. Dashed lines indicate the drainage basins of the Zapadnaya Dvina (ZD), Dnieper (D), Neman (N), Pripyat (P), Zapadnyi Bug (ZB), and Lovat (L) rivers

Table 1 Shipping canals in Belarus

Canal	Construction	Ship traffic existed	Future
Dnieper-Bug Canal	1775–1848	Early 1800s-1919 1940–1941 1946-present day*	To be re-established after scheduled reconstruction
Dnieper-Neman Canal	1770–1784	1784–1915 **	In future canal may be reopened
Dnieper-Zapadnaya Dvina Canal	1797-1805	1805–1917 **	In future canal may be reopened
Neman-Vistula Canal	1824–1839	1839–1864	Reopened in 2006

* Hydrological connection between Mukhavets and Zapadnyi Bug rivers is terminated

** In the 20th century, canal was used mostly locally for moving rafts and occasionally for shipping two other canals, the Dnieper-Bug and the Dnieper-Neman, were considered the primary routes for the spread of zebra mussels to the rest of Europe (Kinzelbach 1992; Starobogatov and Andreeva 1994).

Although more than a hundred papers have been published on the distribution, biology and ecological effects of zebra mussels in Belarusian waterbodies (reviewed in Karatayev et al. 2007b), other alien aquatic invertebrates were mentioned only sporadically in several papers (e.g., Rozen 1907; Polischuk 1983; Alekhnovich 1999; Tischikov and Tischikov 1999, 2005) and a comprehensive review of aquatic exotic invertebrates in Belarus has never been conducted.

The goal of this paper is to show the role of the waterways of Belarus in the spread of aquatic exotic invertebrates through the central European invasion corridor. We have analyzed vectors of spread, historic and current distribution of exotic species and predicted patterns for their future invasions. This paper also provides the first known checklist of exotic aquatic invertebrates in Belarus (for additional information see Mastitsky et al. 2007 http://www.aliensinbelarus.com). To accomplish this goal, we analyzed a database on Belarusian macroinvertebrates that contains over 15,060 entries and is based on information from 205 literature sources published in the last 110 years, as well as the authors' unpublished data on over 500 various waterbodies. In addition, whenever possible, we provided detailed information on shipping canals that were built in what is now Belarus, including the time of their construction and operation, because these data are critically important to understand the spread of aquatic exotics both into and through Belarus, while existing literature is controversial.

Study area

Although the current boundaries of the Republic of Belarus include a little over 200,000 km^2, its geographic location is very important for the spread of exotic species, as it includes the continental divide between the Black Sea and Baltic Sea basins. Abundant lakes and rivers also assist the spread of exotic species across the area. However, the most important factor that facilitated the colonization of Belarus by alien species, as well as their further spread into Eastern and Western Europe, was the construction of several shipping canals.

Lakes

There are 1072 glacial lakes in Belarus with the surface area > 0.1 km^2 (Kurlovich and Serafimovich 1981). The majority of these lakes (72.7%) are situated in the Northern part of Belarus, in the drainage basin of the River Zapadnaya Dvina (Fig. 1). In addition to glacial lakes, there are over 1000 floodplain lakes in Belarus. These lakes are usually very small and especially abundant in the Dnieper, Pripyat, and Sozh rivers basins. Most lakes in Belarus are isolated, while large lake systems connected by navigable waterways are rare.

Rivers

From over 20,800 streams and rivers found in Belarus, only 6 (Dnieper, Berezina, Pripyat, Sozh, Neman, Zapadnaya Dvina) are longer than 500 km, 42 are longer than 100 km, and 19,300 are less than 10 km (Blue Book of Belarus 1994). The Dnieper and Pripyat rivers drain 56% of Belarusian territory into the Black Sea, and other 46% of the territory drains into the Baltic Sea through the Neman, Zapadnaya Dvina, Narev, Zapadny Bug, and Lovat rivers. About 56% of the Belarusian riverine flow discharges into Ukraine, 25% into Latvia, 17% into Lithuania, and 2% into Russia and Poland. Belarus receives its river water from Russia (70%) and Ukraine (30%). The total length of navigable rivers in Belarus is about 3,900 km, with the most intense navigation on the Dnieper, Pripyat, Berezina and Sozh rivers (Blue Book of Belarus 1994).

Dnieper-Bug Canal (Korolevskiy Canal)

This canal was built between the rivers Dnieper and Vistula (Black Sea → River Dnieper → River Pripyat → River Pina → canal → River Mukhavets → River Zapadnyi Bug → River Vistula → Baltic Sea) to establish ship traffic between Kherson on the Black Sea and Gdansk (Danzig) on the Baltic Sea. The whole canal is 196 km long and includes a canalized part of the River Pina (74 km), a canal through the continental divide (Korolevskiy Canal, 58 km) and a canalized part of the River Mukhavets (64 km). Construction of this canal began in 1775, but work on it soon halted, and it was finally finished in 1848 (Tyulpanov et al. 1948). However, some traffic existed before the construction was completely finished. In 1817, for example, 382 ships and 221 timber rafts had been transported through the canal (Lopukh 1989).

Shipping was possible only in years with high water and mainly during the spring (Blue Book of Belarus 1994). This canal was built primarily to float timber in rafts, and therefore the traffic was mostly one-way, with the vast majority of ships and rafts moving towards Vistula. For example, in 1897, 241 ships and 14,290 rafts went from the River Mukhavets to the River Vistula passing Brest-Litovsk (now Brest) and only 14 ships with no rafts came from the opposite direction (Dnieper-Bug System 1903). Between 1919 and 1939, much of the main construction fell apart. In 1940 the canal was rebuilt, and enlarged for shipping (Tyulpanov et al. 1948). During World War II, main constructions were destroyed again and rebuilt later in 1945–1946. However, a dam was built on the River Mukhavets in Brest during the latter reconstruction in order to keep high water level in the canal, so the hydrological connection between the rivers Mukhavets and Zapadnyi Bug was halted (Tyulpanov et al. 1948; Lopukh 1989; Blue Book of Belarus 1994). Several Belarusian ships sold thereafter were transported to Poland by making temporary connections between these rivers. Special reservoirs were dug, in which ships were moved from the River Mukhavets; then a dam was built behind the ship, closing this connections and another dam was removed in front of the ship allowing it to move into the River Zapadnyi Bug. Therefore, hydrological connection was temporarily reestablished for each ship sold, and this may have allowed some aquatic organisms to migrate from Mukhavets to the River Zapadnyi Bug. Currently, locks on this canal are under reconstruction to fit European standards. After reconstruction, ship traffic between the rivers Dnieper and Vistula is to be reestablished, which will also reestablish a hydrological connection and a migration corridor for aquatic organisms between Black Sea and Baltic Sea basins.

Dnieper-Neman Canal (Oginsky Canal)

This canal connected rivers Dnieper and Neman (River Dnieper → River Pripyat → River Yaselda → canal → Lake Vygonovskoe → River Shchara → River Neman/Nemunas → Curonian Lagoon → Baltic Sea). The whole canal is 54 km long. Its construction was initiated and originally funded by Polish hetman, composer and poet Michael Kasimir Oginsky. The canal lasted from 1770 to 1784, and then several repeated reconstructions were performed during 1866–1868 (Tyulpanov et al. 1948; Table 1). The canal was mostly used to export Russian timber by rafts. However, it was also used to transport grain, fur, linen, honey etc. by ships and steamships to the ports in the south-eastern Baltic Memel (now Klaipėda) and Königsberg (now Kaliningrad). The peak of cargo transportation was reached in 1847–1848 (Lopukh 1989). Heavily damaged during World War I, the canal was almost completely restored in 1924–1939. However, the importance of the Dnieper-Neman Canal ceased by the end of the 19th century because of development of the railroads. In the first part of the 20th century, it was used for local timber rafting operations and, occasionally, for shipping. In 1942, during a battle between Soviet partisans and German troops, the navigational system of the canal was destroyed and has never been rebuilt. In 1980, the canal was blocked with a land dam at the outlet from Lake Vygonovskoe (Geography of Belarus 1992). Currently, the Belarusian government is planning to reconstruct the canal and to establish commercial shipping in the near future, which also will reestablish a hydrological connections and a migration corridor for aquatic organisms between the Dnieper and Neman rivers.

Dnieper-Zapadnaya Dvina Canal (Berezinskaya Vodnaya Sistema)

This was a very complex system of rivers, lakes and canals to connect the River Berezina (River Dnieper tributary) with River Zapadnaya Dvina (River Dnieper → River Berezina → Serguchskiy Canal → River Serguch → lakes Manets and Plavno → Berezinskiy Canal → Lake Berescha → River Berescha → Verbskiy Canal → River Essa → Lake Prosho → First Lepelskiy Canal → Lake Lepelskoye → Second Lepelskiy Canal → River Ulla → Chashnitskiy Canal → again River Ulla → River Zapadnaya Dvina/Daugava → Gulf of Riga, Baltic Sea). The whole canal was 162 km long and had 14 locks. It was constructed between 1797 and 1805 (Berezinskaya Sistema 1904; Tyulpanov et al. 1948; Blue Book of Belarus 1994). Initially, the canal was unidirectional and allowed to transport the timber and agricultural products only from the River Berezina to the River Zapadnaya Dvina (to the Port of Riga). In 1823–1836, the system was reconstructed for transportation in both ways (Tyulpanov et al. 1948). However, at the beginning of the 20th century, shipping was almost completely terminated because of excessive forest cuttings, lowering of the rivers and intensive development of railroads (Tyulpanov et al. 1948). Only a few parts of the canal were still in operation for occasional timber transportation in rafts until 1941. The government of Belarus is planning to reconstruct the canal in order to establish commercial shipping in the near future; this will also reestablish a hydrological connection and a migration corridor for aquatic organisms between Dnieper and Zapadnaya Dvina rivers.

Neman-Vistula Canal (Avgustovskiy Canal)

This canal connects rivers Neman and Vistula (River Neman → canal → River Chernaya Gancha → Lake Mikashevo → canal → Lake Krivoe → lakes Panevo and Orlovo → canal → Lake Studenichnoe → lakes Beloe and Netta → River Netta → River Vistula → Baltic Sea). The whole canal was 102 km in length, including 22 km within Belarus and 80 km in Poland, and had 18 locks. The canal was built between 1824 and 1839 for timber in rafts and commercial ships up to 130 tons (Tyulpanov et al. 1948; Blue Book of Belarus 1994). By the end of the 19th century (after the rebellion by Kastuś Kalinoūsky in 1863), ship traffic trough this canal was terminated and only its Polish part has been used for timber transportation, with peak traffic recorded in 1928 (Tourism and recuperation in Grodno oblast 2007). Most of the canal was destroyed during the war of 1941–1945. Reconstruction of the Belarusian part of this canal was completed in 2006 and it has been opened for transboundary cruise boats. Although this is not an interbasin canal (as it only connects the Neman and Vistula rivers that both belong to the Baltic Sea basin), it essentially facilitates the spread of exotic invertebrates (e.g., invasion of *Orconectes limosus* into Belarus from Poland, see below).

Exotic invertebrates and their invasion histories

Caspiobdella fadejewi

It was first reported in Belarus from the River Ptich by Polischuk et al. (1976) and later from the River Berezina (Tischikov and Tischikov 1999), and River Zapadnyi Bug with its tributaries (Tischikov and Tischikov 2005) (Table 2). In Eastern and Western Europe, *C. fadejewi* was reported from two River Vistula tributaries in Poland in 1989, from the lower River Rhine in 1998, and from Austrian and German parts of the River Danube (reviewed in Bij de Vaate et al. 2002). Around 2002, this species was found in France (reviewed in Devin et al. 2005). Bij de Vaate et al. (2002) suggested that River Rhine was colonized through the southern invasion corridor; however, we suggest that Belarus (and possibly some other European countries, especially Poland) was colonized through the central corridor (River Dnieper → Dnieper-Bug Canal → River Zapadnyi Bug → River Vistula).

Hypania invalida

This is a very recent invader in Belarus, which is known from middle courses of the rivers Berezina, Zapadnyi Bug and Mukhavets (Tischikov and Tischikov 2005). In Western Europe, *H. invalida* was first observed in 1967 in the River Danube in Germany and in the River Rhine in 1995 (reviewed in Bij de Vaate et al. 2002). In 1998, this polychaete was found in France (reviewed in Devin et al. 2005). We suggest that introduction of *H. invalida* into Belarusian waterbodies was independent from Western Europe colonization event and almost certainly happened through the River Dnieper. A similar process of gradual upstream spread of this polychaete in the River Volga was described by Slynko et al (2002).

Tubifex newaensis

This oligochaete was reported for the first time in Belarus in 1949 from Lake Chervonoye (Winberg 1956) and later was found in many waterbodies, including rivers (Sokolskaya 1956; Vladimirova et al. 1965; Polischuk 1983), floodplain lakes (Sokolskaya 1956; Vladimirova et al. 1965) and fish ponds

Table 2 List of exotic aquatic invertebrates in Belarus

##	Taxon	Native area	Date of first observation or report	Estimated time of colonization	Waterbody type, References
HIRUDINEA:					
1	*Caspiobdella fadejewi*	Ponto-Caspian	1976	Early 1970-s	Rivers (Polischuk et al. 1976; Tischikov and Tischikov 1999)
POLYCHAETA:					
2	*Hypania invalida*	Ponto-Caspian	2005	Around 2000	Rivers (Tischikov and Tischikov 2005)
OLIGOCHAETA:					
3	*Tubifex newaensis*	Ponto-Caspian	1949	19th century	Lakes (Winberg 1956)
					Rivers (Sokolskaya 1956; Vladimirova et al. 1965; Polischuk 1983)
					Floodplain lakes (Sokolskaya 1956; Vladimirova et al. 1965)
					Ponds (Lyakhnovich 1964)
4	*Potamothrix moldaviensis*	Ponto-Caspian	1949	19th century	Rivers (Sokolskaya 1956)
					Lakes (Karatayev 1988)
5	*Potamothrix bavaricus*	Ponto-Caspian	1986	19th century?	Lakes (Grigelis 1985)
6	*Potamothrix bedoti*	Ponto-Caspian	1988	19th century?	Lakes (Karatayev 1988)
CRUSTACEA:					
7	*Eurytemora velox*	Ponto-Caspian	1956	1940s	Rivers, floodplain lakes, canals (reviewed in Vezhnovets 2005)
8	*Chaetogammarus ischnus*	Ponto-Caspian	2006	1900	Rivers (Mastitsky and Makarevich 2007)
9	*Chelicorophium curvispinum*	Ponto-Caspian	1914	1900	Rivers (Wolski 1930, Lyakhnovich 1956; Vladimirova et al. 1965; Polischuk et al. 1976; Tischikov and Tischikov 1999)
10	*Dikerogammarus haemobaphes*	Ponto-Caspian	2006	1980s	Rivers (Mastitsky and Makarevich 2007)
11	*Dikerogammarus villosus*	Ponto-Caspian	2006	1990s	Rivers (Mastitsky and Makarevich 2007)
12	*Pontogammarus robustoides*	Ponto-Caspian	2006	1990s	Rivers (Mastitsky and Makarevich 2007)
13	*Macrobrachium nipponense*	Southern Asia	1982	1982	Lake Beloye (Khmeleva et al. 1982)
14	*Orconectes limosus*	North America	1997	Around 1995	Rivers (Alekhnovich 1999)
MOLLUSCA:					
15	*Dreissena polymorpha*	Ponto-Caspian	1927	Early 1800s	Lakes, rivers, reservoirs, floodplain lakes, canals (reviewed in Karatayev et al. 2003a, 2007b)

Table 2 continued

##	Taxon	Native area	Date of first observation or report	Estimated time of colonization	Waterbody type, References
16	*Lithoglyphus naticoides*	Ponto-Caspian	1905	Around 1850	Rivers (Rozen 1907; Ovchinniukov 1927; Adamowicz 1939; Drako 1956; Vladimirova et al. 1965)
					Lakes (Guseva 1936; Adamowicz 1939; Winberg 1957; Nekhaeva and Shevtsova, 1982; Mitrakhovich et al. 1987; Karatayev et al. 1999b; Mastitsky and Samoilenko 2006)
					Floodplain lakes (Ovchinnikov 1927; Drako 1956)
					Canals (Arabina and Loseva 1982; Arabina et al. 1988)
17	*Physella acuta*	North America	1983	Around 1960	Rivers (Naumova et al. 1983)
					Marshes (Naumova et al. 1983)
18	*Physella integra*	New-Zealand	1985	1982	Lake Beloye (Karatayev 1988)
19	*Potamopyrgus antipodarum*	New-Zealand	1976	Around 1960	Rivers (Polischuk et al. 1976)

(Lyakhnovich 1964) (Table 2). According to Milbrink and Timm (2001), this Ponto-Caspian species colonized European waterbodies at least 100 years ago (or possibly much earlier) through canals constructed in Russia in the 18th century. However, in spite of being widely distributed in Europe, *T. newaensis* is not currently included in the lists of exotic species of most European countries, including Germany, The Netherlands, France, Poland, and Lithuania (e.g., Nehring 2002; Van der Velde et al. 2002; Devin et al. 2005; Alien species in Poland Database 2007; Baltic Sea Alien Species Database 2007). Therefore, further evidence is necessary to confirm that the spread of *T. newaensis* from the Ponto-Caspian basin was not a result of natural spread in early postglacial time but was associated with human activities.

Potamothrix moldaviensis

This oligochaete was found for the first time in Belarus in 1953 in the River Pina (part of the Dnieper-Bug Canal) by Sokolskaya (1956). Later, it was reported also from Lake Lukomskoe (Karatayev 1988). *Potamothrix moldaviensis* spread across Europe from the Ponto-Caspian basin through the interbasin canals built in the 18–19th centuries. According to Milbrink and Timm (2001), this species colonized Europe from the River Volga to the River Neva, then probably from the Rybinskoe Reservoir to lakes Beloe and Ladoga, and finally reached the Severnaya Dvina River System. These authors hypothesized that afterward *P. moldaviensis* has been carried by ships from the River Neva into several river-mouths in the Baltic Sea, including Daugava (Zapadnaya Dvina) and Nemunas (Neman) rivers. Milbrink and Timm (2001) admitted that there was another canal connecting rivers Dnieper and Neman, but there are no records of *P. moldaviensis* from this area, and that there is no hydrological connection between rivers Dnieper and Zapadnaya Dvina. However, as we mentioned above, *P. moldaviensis* was found in the Dnieper-Bug Canal as early as 1949. Moreover, a canal connecting Dnieper and Zapadnaya Dvina rivers did exist in the 19th century (Berezinskaya Vodnaya Sistema). We suggest that Belarus, Poland and possibly several other Baltic states were colonized by *P. moldaviensis* through the central invasion corridor and, therefore, the initial colonization of Belarus by this species might have occurred in the 19th century.

Potamothrix bavaricus

There is only one record of *P. bavaricus* from Belarus, namely from Lake Drisvyaty on the Northern border of Belarus with Lithuania (Grigelis 1985). *Potamothrix bavaricus* is a widespread exotic oligochaete in Europe (Grigelis 1985; Timm 1987).

Potamothrix bedoti

This Ponto-Caspian oligochaete is probably very common in Europe; however, since *P. bedoti* usually does not reproduce sexually, it is extremely difficult to distinguish sexually immature *P. bedoti* from *P. hammoniensis*. Therefore, the records of *P. bedoti* from Europe are very sporadic (Grigelis 1985; Timm 1987). In Belarus, *P. bedoti* was found only in Lake Lukomskoe (Karatayev 1988).

Eurytemora velox

The euryhaline Ponto-Caspian copepod *E. velox* was found for the first time in Belarus in July of 1956 in the River Pripyat and its tributary, and later in rivers Pina, Skolodinka, Sozh, and in one floodplain lake (reviewed in Vezhnovets 2005). *Eurytemora velox* became invasive species in the River Dnieper and its basin in the first half of the 20th century and is still spreading there (reviewed in Samchishina 2000). There is no doubt that this species colonized Belarus from the River Dnieper and the estimated time of colonization is around 1940–1950. In Western Europe, *E. velox* is known to be an invasive species since early 20th century (reviewed in Gaviria and Forró 2000). This is the only one planktonic exotic invertebrate found in Belarus to date.

Chaetogammarus ischnus

The amphipod *C. ischnus* is one of the most common species in its native Ponto-Caspian basin and is also widespread in Europe. It was first recorded in Poland in 1928, and later was found in many other European countries in the Baltic Sea basin (reviewed in Jazdzewski and Konopacka 2002). In 1960, *C. ischnus* was found in the mouth of the River Neman (Nemunas) in Lithuania (Gasiūnas 1963). By that time, it might already be present in Belarusian part of this river. Nevertheless, in Belarus this species was found only recently in the River Dnieper near the border with Ukraine (Mastitsky and Makarevich 2007).

Chelicorophium curvispinum

This is the oldest known Ponto-Caspian exotic species among crustaceans in Belarus. *Chelicorophium curvispinum* was found for the first time in 1914 by Wolski (1930) in the River Pripyat near Mozyr. In 1912, it was reported from the Spree-Havel system near Berlin in Germany and in 1920s this species was found in Poland, where, probably, it had established well before (reviewed in Jazdzewski and Konopacka 2002). There is no doubt that *C. curvispinum* colonized Europe through the Dnieper-Bug Canal (reviewed in Bij de Vaate et al. 2002; Jazdzewski and Konopacka 2002). In the Lithuanian part of the River Neman, *C. curvispinum* was found in 1921 (Szidat 1926) but, again, it might have colonized this river long before, sometime in the 19th century. Moreover, by that time it might be already present in Belarusian part of this river. Therefore, Dnieper-Neman Canal that was in operation from 1784 to 1915 could also play an important role in the spread of *C. curvispinum* into Europe. Although *C. curvispinum* is widely spread across Europe, in Belarus it was found so far in Dnieper, Pripyat and Berezina rivers only (Table 2).

Dikerogammarus haemobaphes

This is a relatively recent invader in Eastern and Western Europe. It was found in Germany in 1976, in Poland in 1997, and recently in Moscow (reviewed in Bij de Vaate et al. 2002; Jazdzewski and Konopacka 2002). In Poland, *D. haemobaphes* became a dominant gammarid in middle and lower courses of the River Vistula (Jazdzewski and Konopacka 2002). *Dikerogammarus haemobaphes* colonized Europe both through the southern and central invasion corridors, where it was found in several rivers including the River Zapadnyi Bug (reviewed in Bij de Vaate et al. 2002). Although *D. haemobaphes* was found for the first time in Belarus only in 2006 (Mastitsky and Makarevich 2007), its initial colonization has likely occurred well before that.

Dikerogammarus villosus

This gammarid species is also a very recent invader of Belarus. It was found in 2006 and so far is known from the River Dnieper only (Mastitsky and Makarevich 2007). *Dikerogammarus villosus* is also a recent invader in Western Europe. In 1992, it was found in the upper reaches of the Danube River, and two years later has been discovered in lower reaches of the River Rhine (reviewed in Bij de Vaate et al. 2002). Until now, *D. villosus* has been colonizing Europe through the southern invasion corridor (Bij de Vaate et al. 2002); however, the presence of this species in the River Dnieper in Belarus and in the Zapadnyi Bug in Poland (Konopacka 2004) indicates that it has also begun to spread through the central corridor.

Pontogammarus robustoides

This species was recently found in Poland in the River Vistula, in the mouth of the River Oder, and in Germany (reviewed in Bij de Vaate et al. 2002). The mechanism of spread of *P. robustoides* across Europe is not clear. Since its native range includes the lower courses of the River Dnieper, where it is quite common, and because it was recently found in Belarus in 2006 (Mastitsky and Makarevich 2007), *P. robustoides* might have colonized at least part of the Europe through the Dnieper-Bug Canal. On the other hand, *P. robustoides* was repeatedly intentionally introduced into many reservoirs and glacial lakes in Ukraine, Lithuania, and Estonia, including Curonian Lagoon (Gasiūnas 1963; Grigelis 1985; Jazdzewski and Konopacka 2002; Arbačiauskas 2005). At least in several of these waterbodies *P. robustoides* has established stable populations that could be the secondary sources for further invasion across Europe.

Macrobrachium nipponense

Subtropical freshwater prawn *M. nipponense* was introduced into Lake Beloye (the water cooling reservoir for Berezovskaya Power Plant) in 1982 (Khmeleva et al. 1982). It dominates the zoobenthos of the discharge canal of the power plant, where native fauna is inhibited by high temperature reaching up to 38°C in summer (Karatayev 1988). The spread of *M. nipponense* into other Belarusian waterbodies is impossible as this prawn can not tolerate low winter temperatures.

Orconectes limosus

The first introduction of this North American crayfish in Europe was into a fish pond in Germany in 1890 and later in early 1900s it was repeatedly introduced into natural waterbodies of France and Poland (reviewed in Westman 2002). Currently, *O. limosus* dominates the crayfish fauna in fresh waters of France, Germany, Poland, and is still spreading across Eastern and Western Europe. In 1995, *O. limosus* was found for the first time in a lake in Lithuania (Burba et al. 1996) and in 1997 in Belarus in the north-western part of the country. This species invaded Belarus from Poland using Avgustovskiy Canal and colonized several rivers connected to it (Alekhnovich 1999). So far, *O. limosus* is known from the rivers Neman, Viliya, Shlyamitsa, Marykha, and Chernaya Gancha.

Dreissena polymorpha

Dreissena invasion history is obviously the best documented among all other exotic species in Belarus (reviewed in Karatayev et al. 2003a; Karatayev et al. 2007b). There is no doubt that *D. polymorpha* colonized Eastern and Western Europe through Belarus (Zhadin 1946; Kinzelbach 1992; Starobogatov and Andreeva 1994). Although *Dreissena* was mentioned for the first time in Belarus in 1929 (Ovchinnikov 1933), it was estimated to colonize the part of Russian Empire that is now Belarus between 1800 and 1825 (Karatayev et al. 2007b). Southern Belarus, Poland and, probably, most of other European countries were colonized by the zebra mussel through the Dnieper-Bug Canal, while Northern Belarus was almost certainly colonized through the Dnieper-Zapadnaya Dvina Canal (Karatayev et al. 2003a). *Dreissena* reached the Curonian Lagoon of the Baltic Sea through the Dnieper-Neman Canal (Olenin 2002 and references therein).

Lithoglyphus naticoides

During the first malacological study of the southern Belarus in 1905, *L. naticoides* was recorded already in several rivers connected to the Dnieper-Bug Canal (Rozen 1907). Later this species was repeatedly recorded from rivers, canals, glacial and floodplain lakes (Table 2). In Belarus, *L. naticoides* prefers lotic waters; however, it also colonizes lakes, especially those connected to rivers. In Western Europe, *L. naticoides* was first reported from the Netherlands in the second half of the 19th century (reviewed in Bij de Vaate et al. 2002) and from France in 1909 (reviewed in Devin et al. 2005). Later *L. naticoides* was reported from Lithuania (Gasiūnas 1959) and Poland (reviewed in Grigelis 1985). Early records of *L. naticoides* from the part of the former Russian Empire what is now Belarus support the hypothesis that Europe was colonized by this Ponto-Caspian gastropod through the Dnieper-Bug and, possibly, Dnieper-Neman canals.

Physella acuta

The gastropod *P. acuta*, native to North America, was found in Belarus in rivers and marshes in the River Pripyat drainage basin (Naumova et al. 1983). In Western Europe, *P. acuta* was reported from France as early as 1862 (reviewed in Devin et al. 2005). Because this gastropod is present in Poland (Alien Species in Poland Database 2007) and not found in Lithuania (Lithuanian National Invasive Species Database 2007), it is likely that *P. acuta* colonized Belarus through Poland.

Physella integra

This gastropod, native to New Zealand, was probably introduced into Lake Beloye (a cooling water reservoir for Berezovskaya Power Plant) in 1982 accidentally along with the intentional introduction of a subtropical freshwater prawn *M. nipponense* (see above). *Physella integra* is very common in periphyton community of the discharge canal from Berezovskaya Power Plant (Karatayev 1988). The spread of *P. integra* into other Belarusian waterbodies with natural temperature regime is unlikely as this gastropod can not tolerate low winter temperatures.

Potamopyrgus antipodarum

There is only one record on this native to New Zealand snail in Belarus. It was found by Polischuk et al. in 1976 in the wetlands (sometimes in high densities) of lower courses of the Pripyat River. In Europe, *P. antipodarum* was first identified as *Hydrobia jenkinsi* by Smith in 1889 (reviewed at Joint Nature Conservation Committee 2007). By the beginning of the 20th century this species was established in mainland Europe and now spreads widely (reviewed by Devin et al. 2005; Wallace 1985).

Invasion patterns

The analysis of invasion histories of 19 known alien invertebrates revealed two distinct invasion phases in Belarus: an early stage related to construction of navigation waterways (opening of invasion corridors), and a recent one characterized by involvement of vectors of spread other than artificial canals.

Early invasions

First aquatic exotic invertebrates appeared in the part of Russian Empire what is now Belarus in the 19th century after the construction of interbasin canals. We estimated that four species of oligochaetes, the amphipod *C. curvispinum* and two species of molluscs colonized Belarus in the 19th—beginning of the 20th century (Table 2). All these species are of the Ponto-Caspian origin. Two reasons may be suggested why Baltic Sea basin did not play an important role as a donor area in colonization of Belarus: (1) unidirectional pattern of ship traffic through the interbasin canals, and (2) lower species diversity in the Baltic Sea area than in the Ponto-Caspian region.

The major reason for the construction of interbasin canals at the end of the 18th—beginning of the 19th centuries was the export of Russian timber to Western Europe. This firewood was transported often as rafts and these rafts were excellent substrate for the attachment of many invertebrates. It should be mentioned that during more than a hundred years this invasion corridor worked in one direction only. Although ship traffic in the 19th—beginning of the 20th centuries existed in both ways, none of exotic species colonized Belarus from Western Europe.

Several recent studies showed that the invasion vector is usually directed from a more species rich region to a poorer one: from the Red Sea to Mediterranean via Suez Canal, from the North Sea to the Baltic via Kiel Canal, from the Caspian Sea to the Baltic via Volga-Baltic waterway (Slynko et al. 2002; Gollasch et al. 2006). The Baltic Sea region is geologically younger than the Ponto-Caspian region, and therefore has lower species diversity (Morduk-hai-Boltovskoi 1964).

Recent invasions

In the second half of the 20th century, a freshwater subtropical shrimp *M. nipponense* was introduced into a cooling reservoir of the power plant along with an accidental introduction of a subtropical gastropod *P. integra* (Table 2). In addition, two new species of gastropods were reported from Belarus: North American *P. acuta* in 1983 (Naumova et al. 1983) and a New Zealand *P. antipodarum* in 1976 (Polischuk et al. 1976). In 1997, a second alien species of North American origin, crayfish *O. limosus*, was found in Western Belarus (Alekhnovich 1999). Nevertheless, Ponto-Caspian macroinvertebrates still dominate among recent invaders, forming more than 73% (14 out of 19) of all exotic macroinvertebrates found so far in Belarus. In contrast, in the Netherlands only 27% (12 out of 40), in France 31% (14 out of 44) and in Germany 43% (15 out of 35) of freshwater alien macroinvertebrate species are of Ponto-Caspian origin (Nehring 2002; Van der Velde et al. 2002; Devin et al. 2005). Therefore, although the total number of Ponto-Caspian species in each of these countries is very similar to Belarus, the relative proportion of Ponto-Caspian species is much higher in Belarus than in other European countries. The reason for this is that the central invasion corridor, which is used for spread mainly by Ponto-Caspian invertebrates, is the main source of alien species in Belarus.

The cumulative curve of the introduction of exotic invertebrates in Belarus shows a tremendous increase at the last quarter of the 20th century (Fig. 2). This is a typical trend across the World (Mills et al. 1993; Leppäkoski and Olenin 2000; Devin et al. 2005) associated with the rapid globalization of economy and trade. In addition, recent rapid spread of exotics in Belarus was facilitated by changes in the political and socio-economic regime (Karatayev et al. 2007a). The estimated rate of spread of aquatic alien species (excluding oligochaetes for which we do not have reliable time of colonization) for the first 150 years (from 1800 to 1950) was 0.33 species per 10 years, and for the last 50 years (1950–2000)—2.2 species per 10 year, i.e. almost 7-fold increase. We predict a further increase in the rate of colonization of Belarus

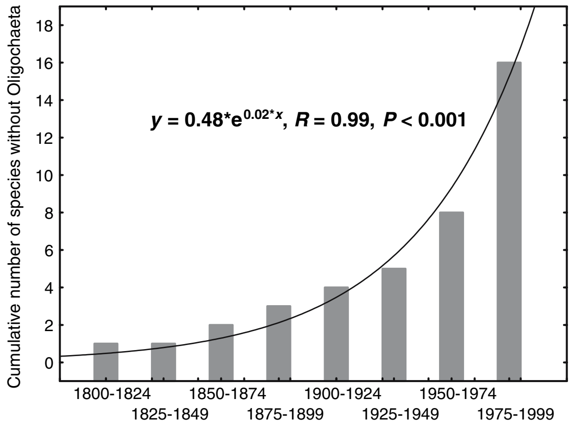

Fig. 2 The relationship between the cumulative number of exotic aquatic invertebrate species in Belarus (excluding oligochaetes with unknown time of colonization) and time since the first record of invasion (1800)

by exotic invertebrates as well as an increase in the diversity of donor areas and the origin of alien species. We also predict that this process will be even faster when ongoing or planning reconstructions of interbasin canals will be completed (Table 1), and a hydrological connection between the Black Sea and Baltic Sea basins will be reestablished after a break that lasted for almost a century.

Current distribution

Among 19 exotic invertebrates in Belarus only few are known to be widely distributed. *Dreissena polymorpha* has spread across the entire territory of Belarus and colonized all five major river basins. By 2000, zebra mussels were known to have invaded at least 121 lakes, 7 reservoirs, all 6 large Belarusian rivers (Dnieper, Zapadnaya Dvina, Pripyat, Berezina, Neman, and Sozh), and 11 small rivers (reviewed in Karatayev et al. 2003a, 2007b). *Dreissena* is common in glacial and floodplain lakes, rivers, and canals. However, the rate of invasion is very slow. In spite of almost 200 years of continuous invasion, only about 20% of all lakes are colonized (reviewed in Karatayev et al. 2007b). *Lithoglyphus naticoides* is another widespread species of gastropods already known from 17 rivers, 9 glacial and 15 floodplain lakes and two canals. It is still spreading in Belarusian waterbodies and recently was found in Lake Lukomskoe (Mastitsky and Samoilenko 2006). *Lithoglyphus* is clearly more reophilic than *Dreissena* and is more common in rivers and floodplain lakes than in glacial lakes.

Among exotic oligochaetes, only *T. newaensis* was reported from several waterbodies, including rivers, ponds, glacial and floodplain lakes (Table 2). Data on the distribution of other oligochaetes are very sporadic because this group has never been studied extensively in Belarus, i.e. during most hydrobiological surveys oligochaetes were not taxonomically identified. Nevertheless, existing records of Ponto-Caspian species from those few waterbodies where oligochaetes were studied in detail may suggest that these species are widely distributed in Belarus (e.g. present in lakes that are not directly connected to canals or large rivers). Exotic crustaceans are found so far in Belarus exclusively in rivers, mostly connected to interbasin canals.

There is a significant correlation between the time since initial invasion and number of waterbodies colonized (Fig. 3). The relationship could be expressed as an exponential regression, indicating that the process is not linear. This suggests that the speed of exotic species spread might not be constant, and might change dramatically when species is present for over 100 years.

Vectors of spread

During the 19th century, the invasion corridors in Belarus worked in one direction only and the ship

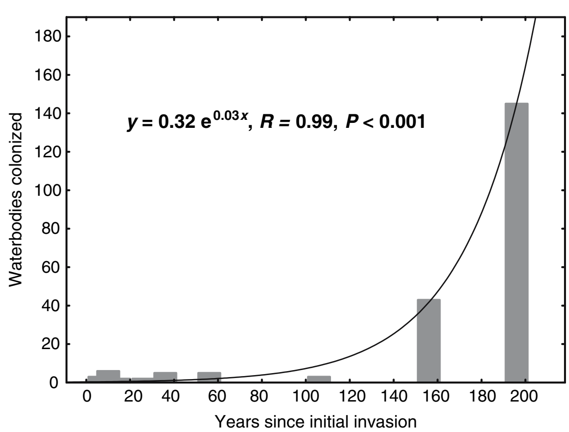

Fig. 3 The relationship between the numbers of waterbodies colonized by exotic aquatic invertebrates (excluding oligochaetes with unknown distribution, and *Macrobrachium nipponense* and *Physella integra* restricted to cooling reservoirs) and time since initial colonization of Belarus

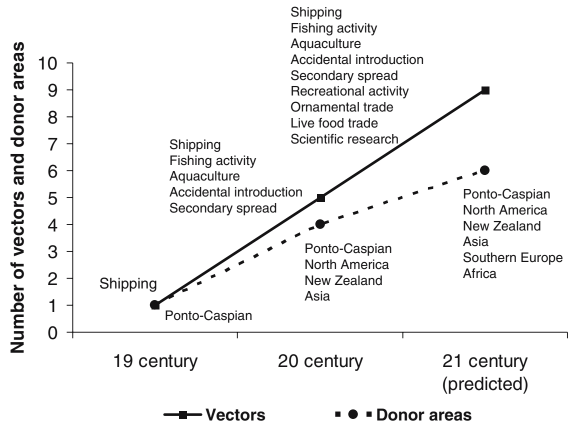

Fig. 4 Vectors of spread and donor areas of exotic aquatic invertebrates in Belarus

and raft traffic was the single vector of introduction of exotic invertebrates (Fig. 4). All species introduced in the 19th—first half of the 20th century were of Ponto-Caspian origin (Table 2). However, the importance of this vector had been reduced in the beginning of the 20th century when the intensity of ship and raft traffic decreased and later was terminated (Table 1). The establishment of a socialist political system in Eastern Europe, including Belarus, had strong impacts on the economy and restricted trade with Western Europe. As a result, different vectors became responsible for the spread of exotic species in these two parts of Europe (Karatayev et al. 2007a). In contrast to Western Europe, where leisure boat traffic was the major vector of spread of exotic species, especially to isolated waterbodies (Kinzelbach 1992), in the Soviet Belarus commercial fishing subsidized by the government was the major vector that spread *D. polymorpha* and other invertebrates to isolated lakes (Deksbakh 1935; Karatayev et al. 2003a). Other vectors of spread that became important in Soviet Belarus include deliberate introduction of commercially important species or aquaculture (e.g., prawn *M. nipponense*), accidental introductions associated with deliberate ones (e.g., gastropod *P. integra*), and natural (i.e. secondary) spread of exotics previously introduced to Europe (e.g., *O. limosus*). As a result, in the 20th century (especially in its second half) both donor regions and vectors of spread of exotic species became more diverse, along with the decline in the importance of shipping activity (Fig. 4).

After the Soviet Union has dissolved, governmental subsidies for commercial fisheries stopped, causing a rapid decline in commercial fishing activity (Karatayev et al. 1999a). As a result, commercial fishery became much less important as a vector of spread of exotic species. At the same time, the recent shift in socio-economy of Belarus toward capitalism may be associated with the appearance of new vectors of spread of exotic species. We predict that in the 21st century both donor areas and vectors of spread will be more diverse and may include recreational activities (e.g., leisure boats), ornamental trade (aquaria, ornamental ponds, etc.), live food trade, scientific research and other activities common for countries with a market economy (Fig. 4).

Among most probable future introductions, we predict colonization of Belarus by at least two species of oligochaetes, seven species of crustaceans and a mollusc *D. rostriformis bugensis* (Table 3). Some of these species might be already present in Belarus, while other may appear in the near future as they all are present in adjacent countries in waterbodies with very similar environmental conditions.

Effect on biodiversity

Among 19 exotic aquatic invertebrates found in Belarus, 18 species are benthic and only one, *E. velox*, is planktonic. Although the number of alien species among benthic macroinvertebrates in Belarus so far is less than 2% from the total revealed biodiversity, their proportion is very high in selected taxonomic groups (e.g. in crustaceans, Table 4). At the same time, we did not find any exotic species among insects that are by far the most diverse group of aquatic invertebrates. Thus, the introduction of invasive species may shift strongly the taxonomical structure of benthic communities. In Germany, 35 alien freshwater species represent 9% of the total biodiversity of benthic macroinvertebrates (Nehring 2002), and in France 43 alien species form 1.2% of all macroinvertebrates (Devin et al. 2005).

The direct negative effect of invasive species on biodiversity includes dramatic reduction of densities and sometimes almost complete local extirpation of native species. Catastrophic mortality of unionids after the introduction of zebra mussels is well documented both in Europe and in North America (reviewed in Karatayev et al. 1997; Burlakova et al. 2000). *Chelicorophium curvispinum* is known to be able to outcompete native isopods *Asellus aquaticus* and several chironomids, and *D. villosus* outcompetes both native (*Gammarus duebeni*) and invasive (*D. haemobaphes* and *Gammarus tigrinus*) amphipods (reviewed in Bij de Vaate, et al. 2002). North American crayfish *O. limosus* that now is spreading in Belarus, has aggressive behavior, much faster growth rate, higher reproduction potential and is more tolerant to low oxygen, pollution and eutrophication than native crayfish species (reviewed in Westman 2002). Therefore, *O. limosus* occupies a wider range

Table 3 Exotic aquatic invertebrates which may be found in Belarus in the near future

Taxon	Native range	Most probable donor country	Reference for presence in donor country
OLIGOCHAETA:			
Branchiura sowerbyi	Indo-Pacific	Poland	Gruszka (1999)
Paranais frici	Ponto-Caspian	Poland	Alien Species in Poland Database (2007)
CRUSTACEA:			
Cercopagis pengoi	Ponto-Caspian	Ukraine	Jazdzewski and Konopacka (2002)
Chaetogammarus warpachowskyi	Ponto-Caspian	Lithuania	Arbačiauskas 2005
Gammarus tigrinus	North America	Poland	Jazdzewski et al. (2002)
Hemimysis anomala	Ponto-Caspian	Lithuania	Arbačiauskas (2005)
Limnomysis benedeni	Ponto-Caspian	Lithuania	Arbačiauskas (2005)
Obesogammarus crassus	Ponto-Caspian	Lithuania	Arbačiauskas (2005)
Paramysis lacustris	Ponto-Caspian	Lithuania	Arbačiauskas (2005)
MOLLUSCA:			
Dreissena rostriformis bugensis	Ponto-Caspian	Ukraine	Orlova et al. (2005)

Table 4 Species richness of bottom macroinvertebrates from Belarusian waterbodies (modified from Karatayev 1999)

Taxon	All species	Exotic species	Percent of the total number of species
Hirudinea	11	1	9.1
Polychaeta	1	1	100.0
Oligochaeta	75	4	5.3
Amphipoda	8	5	62.5
Decapoda	4	2	50.0
Bivalvia	31	1	3.2
Gastropoda	45	4	8.9
Insecta	675	0	0
Others	120	0	0
Total	970	18	1.9

of waterbodies and may outcompete native species (*Astacus leptodactylus* and *A. astacus*). In addition, *O. limosus* is resistant to crayfish plague (caused by fungus *Aphanomyces astaci*) to which European species are highly susceptible, but may serve as a vector of this disease (Alekhnovich 1999; Westman 2002). Devastating effect of crayfish plague caused local extirpations and fragmentation of previously uniform European crayfish populations, as well as more then 10-fold drop in the commercial catches (reviewed in Westman 2002).

Introduction of endosymbionts

While spreading into new areas, exotic species themselves could serve as vectors of spread of their symbionts (Karatayev et al. 2000; Mastitsky 2004). At least 4 species of ciliates specific to *D. polymorpha* were co-introduced into Belarusian waterbodies with their host: *Conchophthirus acuminatus*, *Ophryoglena* sp. (Burlakova et al. 1998; Karatayev et al. 2000, 2003b; Mastitsky 2004), *Sphenophrya dreissenae* and *Hypocomagalma dreissenae* (Daniel P. Molloy, New York State Museum, personal communication). Among several parasites known to be specific to *L. naticoides* (Zhokhov and Pugacheva 2001; Biserova 2005), two species were also found in Belarus, i.e. *Apophallus muehlingi* and *Rossicotrema donicum* (Sergey E. Mastitsky, unpublished data). The ecological role of endosymbionts of exotic species is usually overlooked but potentially may have a devastating effect on invaded ecosystems (e.g., the introduction of the crayfish plague mentioned above). Obligate symbionts that spend their whole life within their host will probably just contribute to the diversity of the invaded ecosystem without serious ecological effect. However, parasites that use exotic species as their intermediate host may have strong negative effect on their final hosts. In the worse case scenario, this may cause epizootics among native species. For example, invasion of *L. naticoides* into the River Volga Delta was accompanied with co-introduction of the trematode *Apophallus muehlingi*, which is highly pathogenic to its second intermediate hosts, i.e. cyprinid fishes. Extremely high density reached by *Lithoglyphus* in the River Volga (up to 8800 ind/m^2) resulted in serious epizootics, especially among susceptible young fishes, whose death rate was up to 80% (Biserova 1990). *A. muehlingi* is also pathogenic to the final hosts, i.e. birds and mammals (including humans) (Biserova 2005).

Conclusions

- First aquatic exotic invertebrates appeared in Belarus in the 19th century after the construction of the interbasin canals, when ‘central invasion corridor’ for the spread of the Ponto-Caspian species was established. During more than a hundred years, this corridor worked in one direction only and was the major source of the invasion of aquatic invertebrates. Therefore, Ponto-Caspian species dominate the alien macroinvertebrates, forming more than 73% of all exotic species found in Belarus.
- The rate of spread of aquatic alien species in the second half of the 20th century increased almost 7-fold as compared to the first 150 years of invasion. We predict a further increase in the rate of colonization as well as an increase in the diversity of donor areas and the origin of alien species.
- The number of vectors and pathways of introduction dramatically increased from one (shipping) in the 19th century to five (shipping, fishing activity, aquaculture, accidental introduction, secondary spread) in the 20th century. We predict a further diversification of the vectors of spread in the 21st century including recreational activity, ornamental, and live food trade, etc.

- An exponential relationship between the time since initial invasion and number of colonized waterbodies suggests that the speed of colonization might not be constant, and might increase dramatically when alien species is present for over certain period of time.
- Although the number of invasive species is less than 2% from the total revealed biodiversity of aquatic invertebrates in Belarus, their proportion is very high in selected taxonomic groups, especially in crustaceans. In contrast, we did not find any exotic species among insects that are by far the most diverse group of aquatic invertebrates. Therefore, the introduction of invasive species may shift strongly the taxonomical structure of benthic communities.
- The direct negative effect of invasive species on biodiversity may include dramatic reduction and, occasionally, almost complete local extirpation of native species. In addition, exotic species themselves could serve as vectors of spread of their symbionts, including highly pathogenic parasites and diseases. The ecological role of these species is usually overlooked but potentially may have a devastating effect on ecosystems they invade.

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