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Alien Macroinvertebrates and Fish in the Dnieper River Basin

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Abstract—The results of the study on spread, pathways, vectors, and ecological impact on the native fauna of alien invertebrate and fish species in the Dnieper River basin are presented. The relationship between invasive processes and basin hydrology is analyzed. It is shown that the main factor in spreading of alien species in the central part of the basin was related to the damming of the river, turning it into a cascade of reservoirs, and introduction of Ponto-Caspian species into the reservoirs. The differences in pathways and vectors for upstream, middle, and downstream parts of the river were revealed. In the midstream reservoirs, the main pathway was intentional introduction aimed at the improvement of valuable fish food resources, whereas that for the upstream part of the Dnieper and Pripyat rivers was shipping and natural spread. The "Black List" of invertebrates and fish for the studied basin is proposed.

Keywords: alien invertebrate and fish species, spreading, pathways and vectors, ecological impact, Dnieper River basin

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INTRODUCTION

The Dnieper River is one of the largest rivers in Europe. The Dnieper totals 2201 km in length: 981 km within the territory of Ukraine; 595 km in Belarus. These two parts of the river differ considerably in terms of both hydrology and intensity of anthropogenic impact. The hydrological regime within the Belarusian part is natural, while within the Ukrainian part the river flow is regulated by a cascade of reservoirs.

The pollution from the large cities of Mozyr', Zhlobin, and Rechitsa poses the main impact on the Dnieper River. Within the Ukrainian part, in addition to pollution by industrial cities, a considerable impact comes from the extraction of water for irrigation through a system of canals. As a result, the annual river discharge for last 50 years was reduced by a factor of 1.5, leading to the rise of salinity from 2 to 4‰ in the Dnieper-Bug estuary water (Denisova et al., 1989; Romanenko, 2004).

The Dnieper River is an important part of the Central European invasion corridor of the spread of Ponto-Caspian species toward Central and Western Europe (Bij de Vaate et al., 2002; Galil et al., 2007; Panov et al., 2009). This spread runs through the canals connecting the Dnieper to the Baltic Sea basin (Olenin, 2002; Karataev et al., 2007).

The Dnieper basin is connected to the Baltic region by a system of canals. At the end of the 18th century to the beginning of the 19th century, two main canals connecting the Pripyat River to the rivers of the Baltic basin were built on the territory of Belarus: the Dnieper–Bug and Dnieper–Neman canals. The former has played and still plays an important role in the introduction of the Ponto-Caspian fauna from the Dnieper to the Baltic Sea basin (Karataev et al., 2007; Semenchenko et al., 2011). The role of the latter canal as a possible pathway for invasions of the Ponto-Caspian species is much less important: first, the shipping along this canal was less intense; second, the canal was fully destroyed during the Second World War (Karataev et al., 2007). However, two Baltic fish species penetrated into the Pripyat River presumably through this canal, since these species mainly occur in the river close to the canal inlet. One more canal (Dnieper–Zapadnaya Dvina) may also play certain role in the spread of dreissena within the northern part of Belarus (Karataev et al., 2007).

It is likely that the alternative pathway for spread of alien species between the upper Pripyat and Zapadnyi Bug lies in the region of the Shatskiye Lakes intercon-

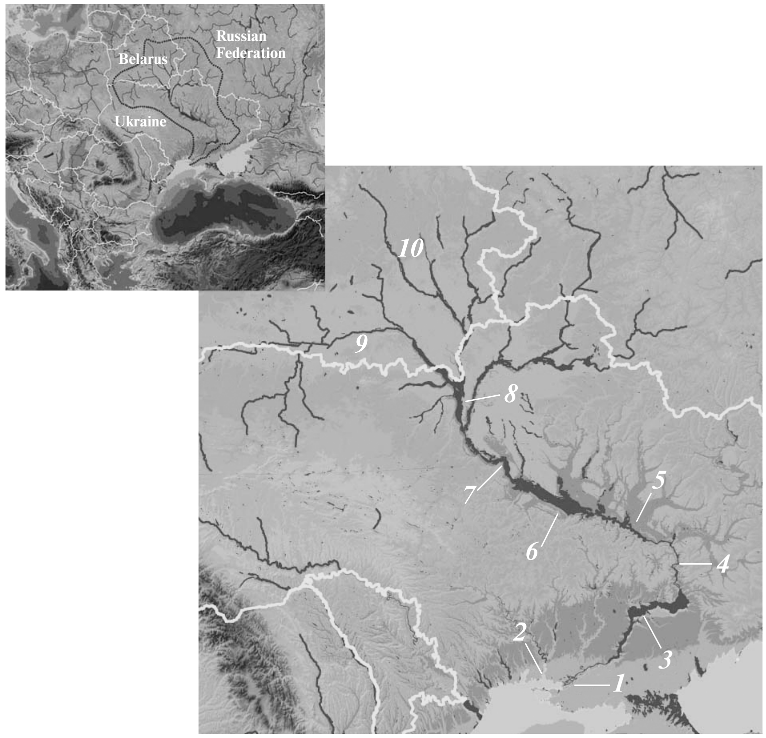

Fig. 1. Studied parts of the Dnieper River basin. (*1*) Dnieper delta; (*2*) Dnieper-Bug estuary; (*3*) Kakhovskoye reservoir; (*4*) Zaporozhskoye reservoir; (*5*) Dneprodzerzhinskoye reservoir; (*6*) Kremenchugskoye reservoir; (*7*) Kanevskoye reservoir; (*8*) Kievskoye reservoir; (*9*) Pripyat River (Belarus); (*10*) Dnieper River (Belarus).

nected to both basins by irrigation canals. The expansion of the range of zebra mussel presumably introduced from the Pripyat upstream was observed in the Shatskiye Lakes region (Son, 2010). In addition, an increase in the ranges of Amur sleeper and common bullhead from the Kopayuvskaya irrigation system at the Western Bug to the upper Shatskiye Lakes was observed in 2009.

The systems of canals built within the Ukrainian part for irrigation and modification of the river discharge make the Dnieper a donor for invasion of alien species to the basin of the Sea of Azov and further to the Volga River.

There are several papers concerning the fauna of alien invertebrate and fish species both in the Dnieper River basin and in certain parts of it (Grigorovich et al., 2002; Alexandrov et al., 2007; Karataev et al., 2007; Semenchenko et al., 2009, 2011; Slynko et al., 2010). However, a number of problems related to the vectors and pathways of spread of these species are either poorly studied or described not in full detail.

The goals of the present work are to determine the current state of alien fauna (macroinvertebrates and fish) in the Dnieper River basin; to analyze the invasion spread rates, pathways, and origins of species; and to assess the consequences of their establishment and prospects of new invasions both in the basin itself and in the Baltic Sea region.

MATERIALS AND METHODS

The results of the original studies carried out in the last years along with the published data on the study region served as a basis for the analysis.

We analyzed ten parts of the Dnieper River basin (Fig. 1).

All species were divided into several groups considering their taxonomic position, origin, and pathways and vectors of introduction and spread within the basin.

To assess the potential impact on the aboriginal fauna, we composed a species “Black List” using the earlier developed algorithm (Panov et al., 2009). In the process, the following principle was considered: inclusion of a species in the “Black List” is based on the information concerning its ecological and social impacts not only within the studied basin but also in other regions of Europe.

Since the terminology in the field of invasions of alien species is not yet fully accepted, we used the terms that were published in *Invasive Species Compendium* (2014).

RESULTS

Changes in the Hydrologic Network and History of Biological Invasions in the Dnieper River

The history of biological invasions in the Dnieper basin is closely related to the modification of the hydrologic network. The vast zone of rapids (totaling about 75 km in length) with pronounced drops of water levels served as a natural barrier preventing the spread of alien species in the Dnieper River. A variety of relict species (*Dreissena polymorpha* (Pallas, 1771), *Astacus leptodactylus* (Eschscholtz, 1823), *Lithoglyphus naticoides* (C. Pfeiffer, 1828), *Chelicorophium curvispinum* (G.O. Sars, 1895), various gobies, etc.) inhabited the zone of rapids and upstream of it (to the upper reaches of the Dnieper) before the rapids were flooded. Presumably, this also concerns the rheophilic amphipods found later in the reservoirs: these species spread far upstream and are quite common particularly in the piedmont rapid regions (Dedu, 1967). It is quite possible that initially these species inhabited the rapids within the zone of the future Dnieper reservoir or even far upstream.

The early invasion of *D. polymorpha* that, as was indicated, spread to the upper reaches of the Dnieper from the Dnieper-Zapadnaya Dvina canal in the 19th century (i.e., from north to south) is best known (Karataev et al., 2007). However, the spread of the species to these reaches (as to the Pripyat River) may have originated from the midstream part of the Dnieper basin, in which the species has lived since the last glaciations.

The dam erected in 1932 and impounding the reservoir (1933) provided straight-through shipping of the "river–sea" type until the destruction of the dam during Second World War. These changes had no considerable impact on the patterns of spread of Ponto-Caspian species: the only documented exception concerns the spread along the Dnieper of *Dreissena bugensis* Andrusov, 1897.

In 1948, the dam was rebuilt and the zone of the modern Zaporozhskoye reservoir was flooded for the second time. This was followed by active impoundment of new reservoirs: Kakhovskoye (1955–1958), Kremenchugskoye (1959–1961), Dneprodzerzhinskoye (1963–1965), Kievskoye (1964–1966), and Kanevskoye (1972–1973). As a result of creation in the Dnieper River basin of the cascade of reservoirs totaling 6974 km^2 in water surface area, the river hydrological regime has changed considerably (Romanenko, 2004).

Flooding of the zone of rapids by the Kakhovskoye Reservoir followed by impoundment of new reservoirs formed conditions for the spread of Ponto-Caspian fauna towards midstream and upstream reaches of the river. At the time of creation of new reservoirs, the programs (developed in the 1940s) of intentional introduction of Ponto-Caspian fauna into various water bodies aimed at improvement of fish food resources were started. Introductions of mysids, mollusks, polychaetes, and "just forage" invertebrates were especially intense in 1949–1951, 1955, and 1957. These programs were implemented both in the restored Dneprovskoye (Zaporozhskoye) Reservoir and in the areas sited for creation of future reservoirs (Markovskii, 1954; Zhuravel', 1965, 1974; Pligin and Emelyanova, 1989). It is worth noting that practically all data concerning Ponto-Caspian invertebrates in the 1950s are retrospective. These data concern the times of the first attempts at introduction (many of which failed) and may differ from the real time of establishment of the populations.

Most probably, the spreading of the Ponto-Caspian fauna outside the areas of intentional introduction started only after filling of the Kakhovskoye reservoir, resulting in the formation of a continuous chain of water bodies stretching from the downstream to midstream reaches of the Dnieper River. In 1948–1957, the list of species that were not the subjects of intentional introduction included only gammarides: as was noted above, these invertebrates either may have inhabited the zone of rapids or were unintentionally introduced at nonspecialized introduction of Ponto-Caspian benthos.

In addition to reservoirs, numerous systems of irrigation and river discharge diversion became vast artificial biotopes. Numerous irrigation systems of arid steppes were created in the Dnieper basin: Kakhovskii channel, Krasnoznamenskaya and Inguletskaya irrigation system, the systems of discharge diversion to the industrial regions in basins of the Yuzhnyi Bug (the Dnieper–Krivoy Rog canal created in 1958–1961) and the Don (Dnieper–Donbass canal, 1969–1982), the system of the North Crimean canal (1961–1971) providing water supply to the Crimean Peninsula, and a range of other similar hydraulic engineering systems (Romanenko, 2004). Like the reservoirs, these artificial ecosystems were invaded to a significant degree by Ponto-Caspian species.

In contrast to the species that expanded their range in the basin, the chronology of invasion of exotic species exhibits no clear relations to large-scale changes in the basin hydrology. Aquarium species were introduced into the basin when they first appeared at the local market. The earliest example concerns finding of *Physa acuta* Draparnaud, 1805 in the vicinities of Kyiv in 1919 (Son, 2007). Such exotic species as *Ferrissia fragilis* (Tryon, 1863) and *Eriocheir sinensis* H. Milne Edwards, 1853 invaded the basin relatively recently (Novitskii, 2003; Son, 2007). Some species long known to inhabit the estuarine part of the basin (*Rhithropanopeus harrisii* Maitland, 1874, *Lepomis gibbosus* (Linnaeus, 1758)) recently exhibited a sharp expansion of their ranges (Bulakhov et al., 2008; Son et al., 2013).

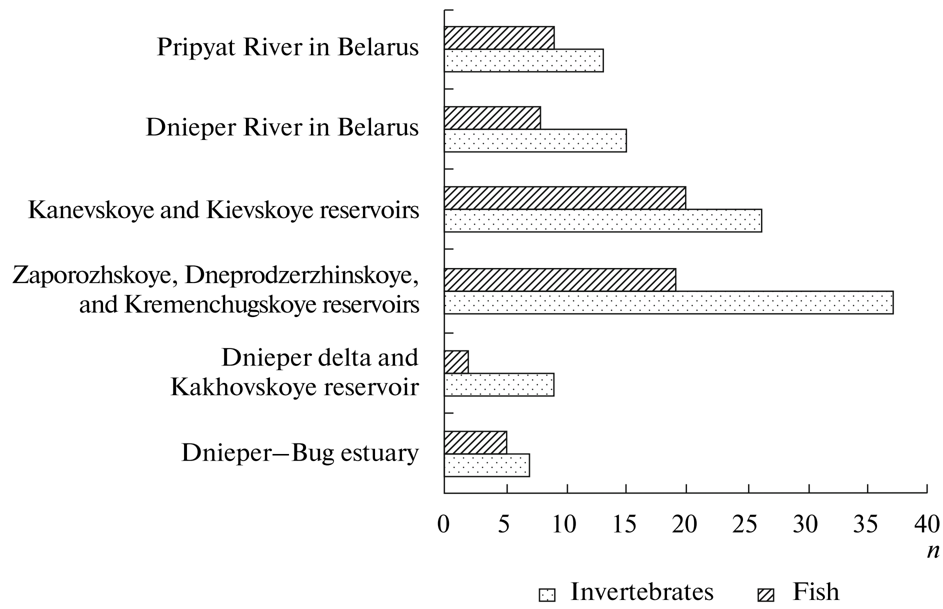

Fig. 2. Number of alien macroinvertebrate and fish species at various parts of the Dnieper River basin.

TAXONOMIC COMPOSITION AND ORIGIN OF SPECIES

To date, 56 alien macrozoobenthos and 32 fish species live in the Dnieper River basin. From the taxonomic list of macrozoobenthos, the most numerous are Amphipoda (35%), Mysida (12%), and Veneroida (10%); of fish, Perciformes (42%) and Cypriniformes (16%) (Fig. 2). A range of alien species were recorded at all noted parts of the Dnieper. Often the abundance of these species is high, which makes it possible to list them as the earliest and most successful invaders that mastered the river basin to the highest extent. First of all, this concerns Ponto-Caspian gammarides and gobies. Other species occur only at some parts of the Dnieper.

The analysis of the species composition indicates that the number of both macrozoobenthos and fish species decreases in the upstream direction (Fig. 2). For instance, Ponto-Caspian species of the orders Cumacea and Isopoda along with fish of orders Atheriniformes and Mugiliformes are not found in the upstream part of the basin.

On one hand, such a pattern is related to the slower spread rates of macrozoobenthos in the upstream direction; on the other hand, it is related to the sequence of creation of the system of reservoirs on the Dnieper River starting from the downstream reaches of the river.

Not surprisingly, more than 50% of alien macrozoobenthos and fish species in the Dnieper basin are of Ponto-Caspian origin (Fig. 3). In contrast to invertebrates, the share of species of Asian and North European origins is quite high in fish. This is related predominantly to the intentional introduction of these fish into the reservoirs.

SPREAD VECTORS AND INVASIONS

It is believed that the sharp increase in the number of alien species observed during the last decades in European water bodies is determined by the following factors: global climate change (Walther et al., 2009; Slynko et al., 2010), intentional introduction of species (Grigorovich et al., 2002), creation of various canals and manmade lakes (Galil et al., 2007; Panov et al., 2008; Leuven et al., 2009), increase in the intensity of shipping (Alexandrov et al., 2007; Galil et al., 2007; Minchin, 2007; Semenchenko et al., 2011), etc.

The spread of Ponto-Caspian invertebrates in the Dnieper basin was determined by two key factors: modification of the river to a cascade of reservoirs and large-scale programs of intentional introduction of Ponto-Caspian fauna. Thus, the conversion of the river to a cascade of reservoirs made it possible for Ponto-Caspian bivalve mollusks, dreissenids and cardiids having planktic larvae, to establish mass populations.

It is worth noting that, after creation of the Kievskoye reservoir and introduction of macrozoobenthos, this reservoir became a donor water body of Ponto-Caspian fauna for the Belarusian part of the Dnieper and Pripyat rivers. This is why we performed the analysis of the data on the spread pathways of alien macroinvertebrates and fish in the Dnieper basin separately for three parts of the basin: upstream of the cascade of reservoirs (the Belarusian part of the basin, Dnieper and Pripyat rivers); the cascade of reservoirs; and the estuarine part of the river (Fig. 4).

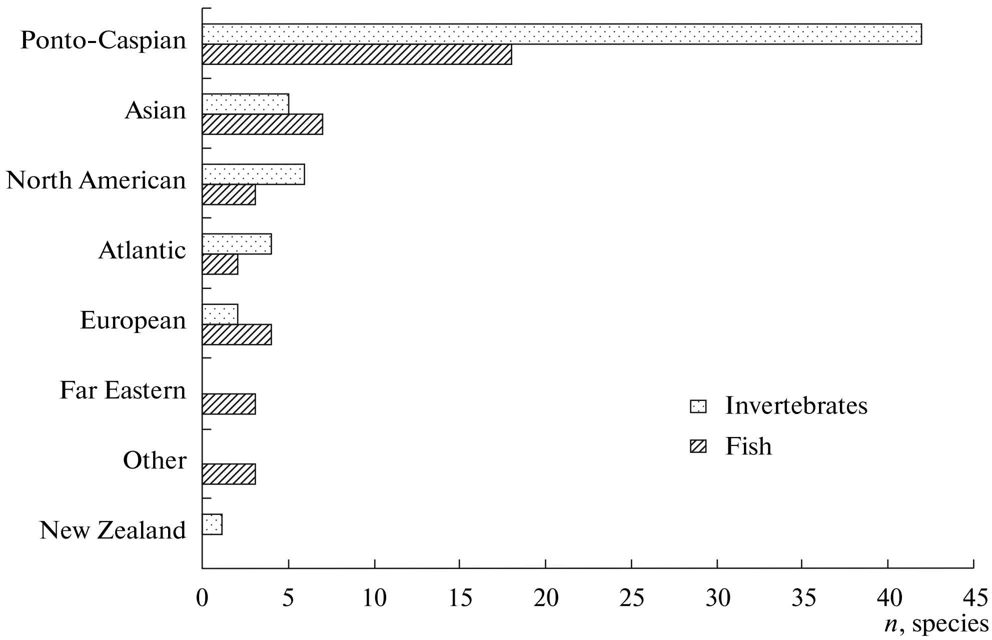

Fig. 3. Number of macroinvertebrate and fish species of various origins in the Dnieper River basin.

Shipping is the main spread vector of macrozoobenthos in the estuarine zone and within the Belarusian part of the basin. For instance, the maximum number of alien macroinvertebrates in the Belarusian sector was recorded in the river ports of the Pripyat River (Semenchenko et al., 2009). At the same time, the role of shipping in the spread of fish typically migrating upstream is inconsiderable.

For the macrozoobenthos in the Dnieper basin, the main vector of spread is the process of natural upstream expansion (Fig. 5). However, in the central reservoirs (Dneprovskoye, Dneprodzerzhinskoye, and Kremenchugskoye), a large number (if not a majority) of such cases may be related to "hidden" introductions but not to natural spread. For example, the intentional introduction of valuable forage invertebrates was accompanied by introduction of large numbers of other species of macrozoobenthos.

In fish, the situation is similar. However, in this case, intentional introduction of some species also plays an important role (Fig. 5).

The data given above show that the main vectors facilitating the spread of alien species differ considerably in the different parts of the Dnieper River basin: in the midstream Dnieper reservoirs, the main vector was mass intentional introduction aimed at the improvement of fish food resources; in the upstream reaches of the Dnieper and Pripyat rivers, shipping and natural expansion served as the main vectors.

Ponto-Caspian fauna is aboriginal for the downstream part of the Dnieper. The invasions of alien species in this zone were mainly related to shipping, the discharge of ballast waters, in particular.

According to Grigorovich et al. (2002), introduction and shipping (29 and 22%, respectively) are the main vectors facilitating the spread of alien species in the Ponto-Caspian basin, while hydraulic engineering accounts only for 14% of the total sum of factors. We believe that, in the Dnieper basin, the creation of the cascade of reservoirs and the system of canals played one of the most important roles both for successful spread of nonindigenous fauna in the basin and for its further expansion to other basins.

Additional factors of fast colonization of new habitats by Ponto-Caspian species are increasing ecosystem disturbances and pollution (Leuven et al., 2009). For instance, there is a reverse correlation between the biocontamination and ecological quality of water as assessed by the BMWP biotic index (Arbačiauskas et al., 2008). To a certain extent, this corresponds to the hypothesis of "vacant niches" that become devoid of native species owing to deterioration of ecological conditions (Simberloff, 1981).

The upstream reaches of the Dnieper and the Pripyat River are especially interesting for the assessment of the species spread rates: the analysis of the data on these areas allows for an approximate evaluation of the spread rates of some species within the basin. The calculated rates of the spread from the Pripyat River to the Vistula River basin for Black Sea gobiids were as follows: tubenose goby *Proterorhinus marmoratus* (Pallas, 1814), about 600 km/year; monkey goby *Neogobius fluviatilis* (Pallas, 1814), 120 km/year; racer goby *Neogobius gymnotrachelus* (Kessler, 1857), 68 km/year; round goby *Neogobius melanostomus* (Pallas, 1814), 10 km/year (Semenchenko et al.,

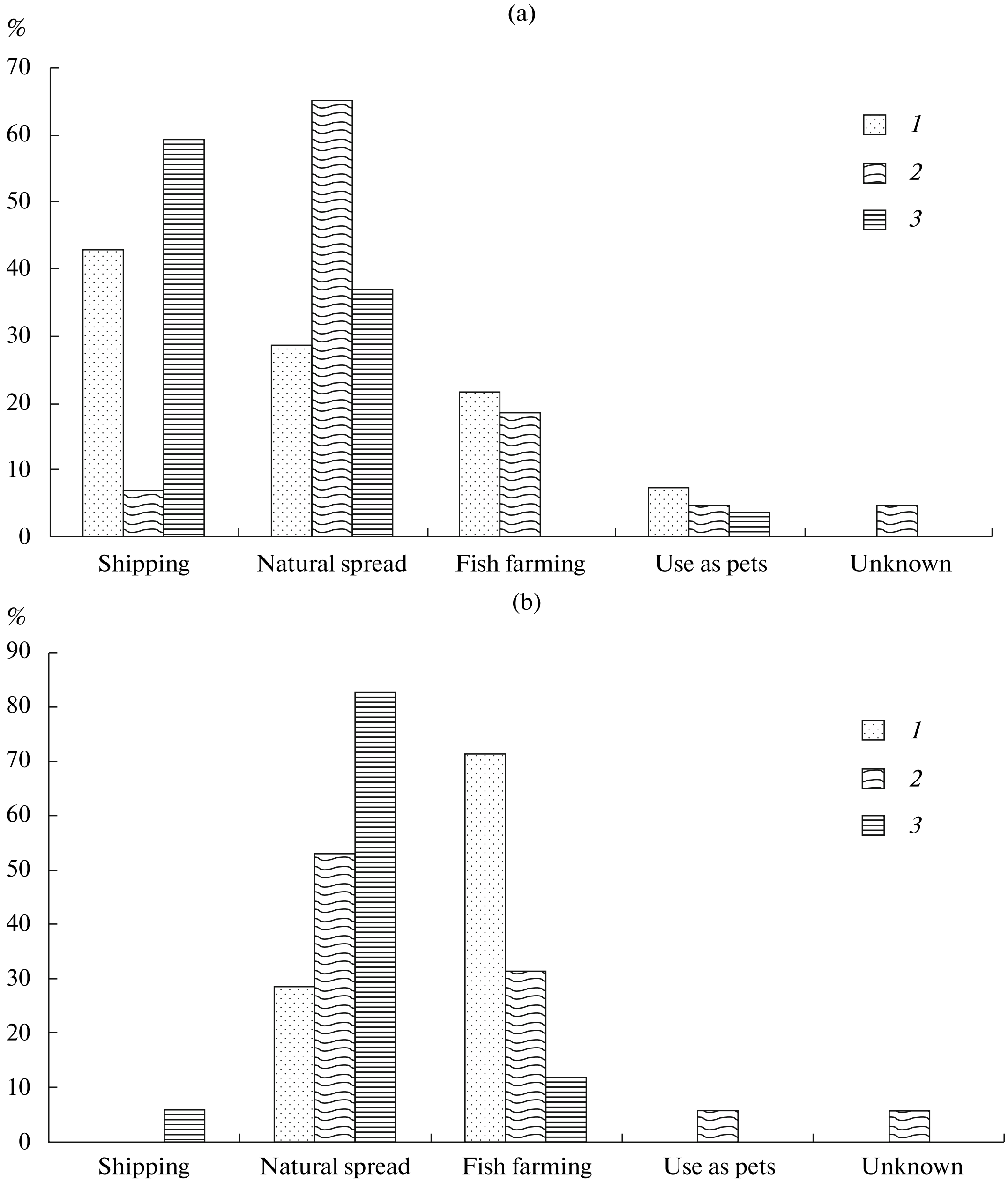

Fig. 4. Main pathways of the spread of macroinvertebrates (a) and fish (b) at various parts of the Dnieper River basin; (*1*) Dnieper–Bug estuary, Dnieper delta, and Kakhovskoye reservoir; (*2*) Zaporozhskoye, Dneprodzerzhinskoye, Kremenchugskoye, Kanevskoye, and Kievskoye reservoirs; (*3*) Dnieper and Pripyat rivers (Belarus).

2011). According to the data obtained, the rate of spread of round goby from the downstream Dnieper (Zaporozhskoye reservoir) to the Kievskoye reservoir is 10 km/year, i.e., similar to that for the Pripyat River, while the spread rate of Black Sea sprat *Clupeonella cultriventris* (Nordmann, 1840) is about 20 km/year.

The assessment of the spread rates in invertebrates is a much more complicated task since the construction of the Dnieper reservoirs was accompanied by mass introduction of these species. In contrast to fish, in the Belarusian part of the Dnieper basin, shipping is one of the main vectors of spread for the species of macrozoobenthos (see below). This is why to assess the spread rates of these species we used the data only on the upstream part of the Dnieper River and the Pripyat River.

The most complete data on the spread rates concern Ponto-Caspian amphipods for which the Kievskoye reservoir served as a donor water body. Amphipods were intentionally introduced to the water

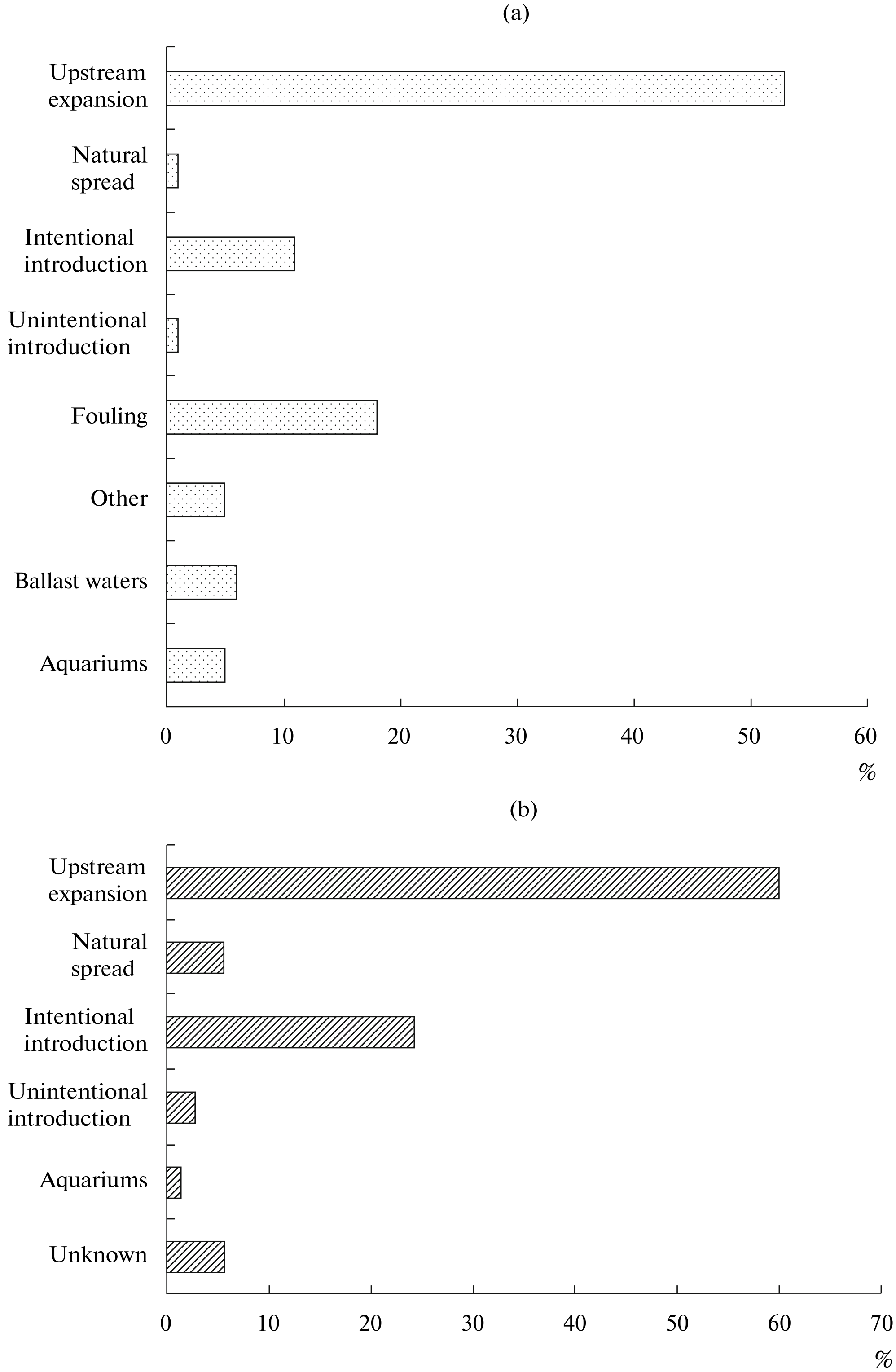

Fig. 5. Main vectors of invasions of macroinvertebrates (a) and fish (b) in the Dnieper River basin.

body in 1950–1955 (Karpevich, 1975). According to Jazdzewski et al. (2002), first findings of the gammarides that penetrated into the Vistula River through the Pripyat and Dnieper–Bug canal were recorded in 1997 (*Dikerogammarus haemobaphes* (Eichwald, 1841)) and in 2001 (*Dikerogammarus vilosus* (Sowinsky, 1894)). Thus, these species covered the distance of about 600 km (the Pripyat River and Dnieper–Bug

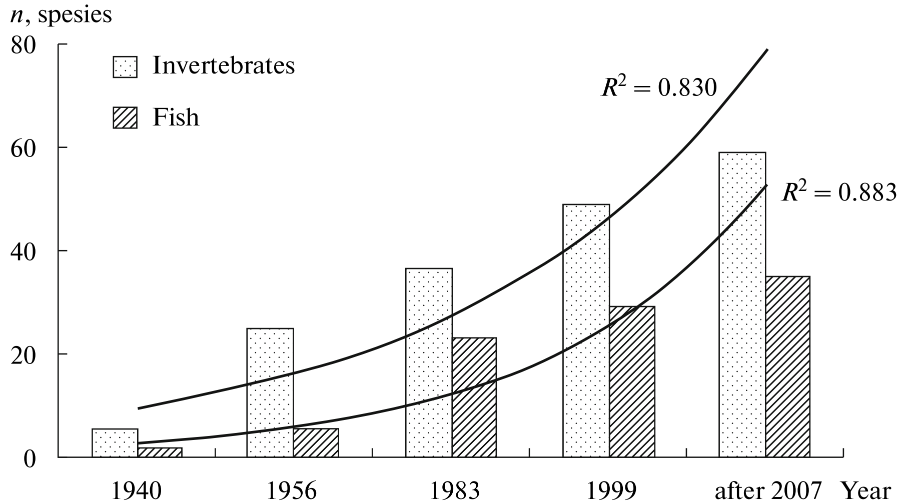

Fig. 6. Dynamics of cumulative number of alien macroinvertebrate and fish species in the Dnieper River basin.

canal) at an average rate of about 10 km/year. The high spread rate of these species may be related to shipping, which peaked in the Pripyat River in the period from 1990 to 1995 (Semenchenko et al., 2011).

In general, in the temporal aspect, the cumulative increase in the numbers of both invertebrates and fish is observed in the Dnieper basin (Fig. 6). A similar situation was revealed for nonindigenous fauna in the water bodies of Belarus (Karataev et al., 2007) and for a number of aquatic plant and animal species in Ukraine (Alexandrov et al., 2007).

ECOLOGICAL IMPACT OF ALIEN SPECIES AND THE "BLACK LIST"

Although freshwater ecosystems are more vulnerable than marine ones, it is often difficult to evaluate the damage associated with invasions of alien species in the former (Moyle, 1996; Vilà et al., 2010). Such damage is mainly known for alien species of fish, decapods (*Orconectes limosus* (Rafinesque, 1817), *Procambarus clarki* (Girard 1852)), and mollusks (*D. polymorpha*, etc.) (Vilà et al., 2010). At the same time, the data on the damage caused by the invasions of the majority of macroinvertebrates are based mainly on the data on their competition with native fauna. For instance, almost complete extinction of *Gammarus lacustris* G.O. Sars, 1864 in the upper part of the Dnieper basin (Semenchenko et al., 2013) and a sharp decrease in the abundance of aboriginal gammarides *G. lacustris* and *Gammarus pulex* (Linnaeus, 1758) in the Dnieper reservoirs (Zimbalevskaya et al., 1989) are related to the steadily increasing abundance of Ponto-Caspian gammarides, in particular, *D. vilosus*. A similar situation is observed in the Rhine River in the territory of the Netherlands, where *G. pulex* was fully forced out by Ponto-Caspian amphipods (Leuven et al., 2009).

Similarly, in the upper part of the Dnieper, *Carassius gibelio* (Bloch, 1782) rapidly displaces *Carassius carassius* (Linnaeus, 1758). According to Lukina (2011), in the Belarusian part of the Dnieper basin, *Perccottus glenii* Dybowski, 1877 competes with aboriginal fish species for trophic resources. The most abundant gobiib in the Pripyat and Dnieper rivers, *N. fluviatilis*, has a similar effect (Zhukov, 1965).

In the Dnieper basin, *D. polymorpha*, forcing out native species of unionids (Karataev et al., 2007) and *L. naticoides*, as an intermediate host of fish parasites (Mastitsky and Samoilenko, 2006), considerably affect the ecosystems.

The assessment of the impact of alien species in reservoirs is a more complicated task since native fauna was in fact eradicated upon construction of the reservoirs. The alien species (Ponto-Caspian species, first of all) were not the reason for the environmental changes, but they formed a fundamentally new ecosystem. At the same time, the creation of the reservoirs provided some advantages for Ponto-Caspian invaders over the native species in colonization of water bodies. That is, the invaders were sort of "backseat drivers" (Bauer, 2012). However, in this case, Ponto-Caspian species did not change the native ecosystems and communities but competed with native species in the process of colonization of new water bodies and formation of new communities in the artificial ecosystems.

Thus, the negative aspect of colonization by alien species of the cascade of reservoirs is related not to the local ecological impacts but mostly to the risk of their further spread to new regions likewise Ponto-Caspian invaders colonize artificial ecosystems of channels and rivers.

The effect of alien species of Atlantic origin (*Mya arenaria* Linnaeus, 1758, *R. harrisi*, *Balanus improvisus* Darwin, 1854) on the ecosystem of the Dnieper–Bug estuary is clearer. These species are the typical representatives of the fauna of tidal estuaries of the western Atlantic and are well adapted to sharp changes in water salinity. To date, these species are mass species in the "marine" part of the Dnieper–Bug estuary and together with most euryhaline native species formed new communities.

At the same time, anthropogenic modifications of the hydrological regime served as a prerequisite for the above-mentioned phenomena. On one hand, the sharp decrease in the river discharge volume fundamentally changed the pattern of spread of Ponto-Caspian species in the areas of the sea subject to the impact of the Dnieper flow (Son et al., 2010). On the other hand, the decreased discharge formed in the Dnieper–Bug estuary, the zone unfavorable for oligohaline Ponto-Caspian species but favorable for the estuarine Atlantic animals.

According to Ricciardi and Cohen (2007), the mechanisms of invasions (spread rate and success of colonization) and impact of alien species are not necessarily interconnected. However, the compilation of a list of species that either already cause certain damage (both direct and indirect) or may cause damage under certain conditions is an important task (table).

As was noted above, at the inclusion of a species in the "Black List," we considered its observed impacts on European territory. There is a range of data indicating that some species, in particular, of Ponto-Caspian origin, exhibit negative effects in North America, but such effects are not observed in Europe.

For instance, *Chaetogammarus ischnus* (Stebbing, 1899) co-inhabits the Pripyat River with native *Gammarus varsoviensis* Jazdzewski, 1975, but forces out aboriginal *Gammarus fasciatus* Say, 1818 in the St. Lawrence River (United States) (Palmer and Ricciardi, 2005). A similar phenomenon is observed in the Great Lakes of North America (Dermott et al., 1998; Ricciardi and MacIsaac, 2000). In the Dnieper basin, monkey goby (*N. fluviatilis*) is mainly a competitor for food with native species, but it does not force out the latter. At the same time, in Lake Michigan, it suppressed in fact the population of native sculpin *Cottus bairdi* Girard, 1850 (Vanderploeg et al., 2002).

The reverse effects are also possible: invasion of North American species may cause observed or potential negative effects in Europe. For instance, introduction of pumpkinseed *L. gibbosus* in European water bodies already caused a range of negative effects (Bulakhov et al., 2008).

The analysis of the "Black List" shows that, in the majority of cases, the negative ecological impacts of alien species are observed outside the region we describe in the present study. As for exotic species, this is due to either their relatively recent introduction (*E. sinensis*, *P. glenii*) or limited spread in the basin (*M. arenaria*, *R. harrisii*, *B. improvisus*).

It is clear that, in the areas where the Ponto-Caspian fauna were present in historic times, its impact on the native species is much less pronounced compared to the areas outside the Ponto-Caspian basin. Widespread European freshwater species historically constantly contacted and co-evolved with the freshwater rheophilic fraction of the Ponto-Caspian fauna and the Ponto-Caspian basin served as a refugium during the periods of glaciations (Devin et al., 2005). In turn, the spread of some Ponto-Caspian species in the Quaternary period along the Dnieper basin reached at least the lower part of Belarus close to the Pripyat River (Yakushko, 1971). The lack of Ponto-Caspian species in the communities of main river channels is a historically recent and episodic phenomenon. In general, considerable overlapping of ecological niches of Ponto-Caspian and widespread European invertebrates that may force out the native species primordially is not a large scale process in the Dnieper basin.

It is worth noting that, for the highly mobile amphipods (and perhaps for some other groups), the separation of the ecological niches between the Ponto-Caspian and other rheophilic invertebrates may take place not only at the level of biotopes but also at the level of water body types. For example, the studies on the amphipod faunas in some river basins (Dniester, Prut, and Don) revealed a similarity in the patterns of species distribution. Ponto-Caspian species of amphipods and species of Mediterranean marine origin occupy the estuaries and main river channels, while other groups of amphipods (*Gammarus*, *Niphargus*, *Sinurella*) occupy tributaries, springs, and mountain parts of the rivers (Dedu, 1967; Lyubina and Sayapin, 2008). Presumably, recent forcing out of native amphipods in the upstream areas of the Dnieper basin is an intermediate stage of return to such a distribution of ecological niches which is historically a characteristic of the Ponto-Caspian region.

In other European regions, i.e., the centers of aggregation of Mediterranean marine, Boreal, or Balkan species, these organisms never came into contact with Ponto-Caspian fauna. The Ponto-Caspian species included in the "Black List" pose a serious threat to the aboriginal fauna outside the Dnieper basin. The Vistula and Rheine basins provide an example of how Ponto-Caspian amphipods force out the aboriginal species (van der Velde et al., 2000; Jazdzewski et al., 2004).

CONCLUSIONS

The analysis of the data on fauna, distribution, and ecological impacts of alien species in the Dnieper River basin reveals that this process will be intensified and the alien species must be treated as unavoidable harm related to human activity (Moyle, 1996).

According to some researchers, recently the central invasion corridor lost its main importance as a pathway for new invasions to Eastern Europe and further to the Baltic Sea, while the southern corridor via the Danube River is the most important (Karataev et al., "Black List" of alien macroinvertebrate and fish species in the Dnieper River basin

	Species	Observed impact	Potential impact	Reference
		Macrozoobenthos		
1	*Cordylophora caspia* (Pallas, 1771)	–	Fouling of ships and hydroengineering structures	Folino-Rorem and Indelicato, 2005
2	*Urnatella gracilis* Leidy, 1851	–	Fouling of ships and hydraulic engineering structures	Protasov, 1997
3	*Lithoglyphus naticoides* (C. Pfeiffer, 1828)	Transfer of parasites	Transfer of parasites	Mastitsky and Samoilenko, 2006; Tyutin and Slynko, 2008
4	*Potamopyrgus antipodarum* (J.E. Gray, 1853)	–	Decline of primary production and areas of substratum for other macroinvertebrates	Strzelec, 2005; Alonso and Castro-Diez, 2008
5	*Dreissena polymorpha* (Pallas, 1771)	Decline of primary production and areas of substratum for other macroinvertebrates; fouling of ships and hydraulic engineering structures	Decline of primary production and areas of substratum for other macroinvertebrates; fouling of ships and hydraulic engineering structures	Kharchenko, 1995; Karataev et al., 1997
6	*Dreissena bugensis* Andrusov, 1897	Competition with native spcies of bivalve mollusks; fouling of ships and hydraulic engineering structures	Competition with native spcies of bivalve mollusks; fouling of ships and hydraulic engineering structures	Kharchenko, 1995
7	*Mya arenaria* Linnaeus, 1758	–	Competitions with small species of bivalve mollusks	Zaitsev and Ozturk, 2001
8	*Balanus improvisus* Darwin, 1854	–	Combined impact on communities owing to changes in substratum, fouling of ships and hydraulic engineering structures	Zaitsev and Ozturk, 2001
9	*Chelicorophium curvispinum* (G.O. Sars, 1895)	–	Modification of substratum; competition with native species	van den Brink et al., 1993; Bij de Vaate et al., 2002; Noordhuis et al., 2009
10	*Chaetogammarus ischnus* (Stebbing, 1899)	–	Predation	Bij de Vaate et al., 2002
11	*Pontogammarus robustoides* (Sars, 1894)	–	Predation	Arbačiauskas et al., 2011; Bacela-Spychalska and van der Velde, 2013
12	*Dikerogammarus villosus* (Sowinsky, 1894)	Elimination of native amphipod species	Elimination of native amphipod species	Bacela-Spychalska and van der Velde 2013
13	*Dikerogammarus haemobaphes* (Eichwald, 1841)	–	Elimination of native amphipod species	Bacela-Spychalska and van der Velde 2013
14	*Hemimysis anomala* Sars, 1907	–	Decrease in fish food resources; aggressive behavior	Ketelaars et al., 1999; Bij de Vaate et al., 2002
15	*Rhithropanopeus harrisii* Maitland, 1874	–	Competition with species of crabs and benthivores; predation	Roche and Torchin, 2007
16	*Eriocheir sinensis* H. Milne Edwards, 1853	–	Eating of fish eggs and macrozoobenthos	Gollasch, 2011

Table. (Contd.)

	Species	Observed impact	Potential impact	Reference
		Fishes		
17	*Pseudorasbora parva* (Temminck et Schlegel, 1846)	–	Eating of eggs of native species; transfer of infections	Karabanov et al., 2010
18	*Lepomis gibbosus* (Linnaeus, 1758)	–	Predation; decrease in food resources of native fish species	Boltachev et al., 2003; van Kleef et al., 2008
19	*Perccottus glenii* Dybowski, 1877	Competition, eating of eggs of native fish species	Competition, eating of eggs of native fish species; creating problems for aquaculture	Reshetnikov, 2001; original data
20	*Neogobius fluviatilis* (Pallas, 1814)	Competition for trophic resources	Competition for trophic resources; aggressive behavior; transfer of parasitic infections	Zhukov, 1965; Smirnov, 2001
21	*Carassius gibelio* Bloch, 1782	Displacement of *Carassius carassius*; hybridization	–	Original data

2007; Leuven et al., 2009). At the same time, findings of new Ponto-Caspian species of macroinvertebrates and fish in the Vistula River basin indicate that the central corridor is still an important pathway for new invasions to the Baltic Sea region (Grabowski et al., 2007; Semenchenko et al., 2011).

Assessing from the above point of view the risk of new invasions, one has to consider the two most vulnerable areas: the upstream part of the Dnieper River and further via the Dnieper–Bug canal to the region of the Baltic Sea and Dnieper–Bug estuary. As for the first part, the Kievskoye Reservoir plays an important role as a donor water body of alien species. Many Ponto-Caspian species such as *D. bugensis*, amphipods *Chelicorophium robustum* (G.O. Sars, 1895), *Ch. warpachowskyi* (G.O. Sars, 1897), and *Pontogammarus aralensis* (Uljanin, 1875), and also fish *Benthophilus nudus* (Berg, 1898), *Syngnathus abaster* Risso, 1827, and *Neogobius kesslery* (Günther, 1861) dwelling in the Kievskoye Reservoir are potential invaders in the Dnieper and Pripyat rivers. Recent findings of some Ponto-Caspian species (*Chelicorophium mucronatum* (G.O. Sars, 1895), *Paramysis lacustris* (Czerniavsky, 1882)) in the Dnieper River upstream of the Kievskoye Reservoir confirm this suggestion (Semenchenko et al., 2009).

As for the Dnieper–Bug estuary, it is expected that the number of alien species will rise mainly owing to species of Atlantic origin through increasing discharges of ballast waters (Alexandrov et al., 2007).

The invasions of alien species into freshwater ecosystems represent an irreversible process and will strengthen as a result of intensification of human activity, in particular, shipping, and transformation of aquatic ecosystems. There is only one way to minimize the negative impact of alien species on the native communities: to prevent new invasions even if it is difficult to achieve (Moyle, 1996). However, the knowledge on the main pathways facilitating the invasive processes already allows us if not to minimize then at least to assess the possible consequences of new invasions.

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