Aquatic Invasions (2007) Volume 2, Issue 3: 174-184
doi: http://dx.doi.org/10.3391/ai.2007.2.3.4
© 2007 The Author(s) . Journal compilation © 2007 REABIC
Open Access

Research Article

Native range of the zebra mussel and quagga mussel and new data on their invasions within the Ponto-Caspian Region

Mikhail O. Son

Odessa Branch Institute of Biology of the Southern Seas, National Academy of Sciences of Ukraine, Odessa, Ukraine

E-mail: michail.son@gmail.com

Received: 19 July 2007 / Aaccepted: 15 August 2007

Abstract

This is a special review on the native ranges of the zebra mussel (*Dreissena polymorpha polymorpha*) and quagga mussel (*Dreissena bugensis*). Revision of museum collections showed that the Dniepr Delta is a native locality of the quagga mussel, for example in the Lower Southern Bug and that *Dreissena presbensis* occurs in the Aegean Sea Basin in Greece. The native range of the zebra mussel includes Danube, Dniestr, Berezan, Southern Bug, Dniepr, Molochnaya, Don, Kuban, Kamchia, and Veleca river basins; isolated and semi-isolated relic estuarian reservoirs along the Bulgarian, Romanian, Ukrainian, and Russian Black and Azov seas coasts; and in zones of these seas influenced by freshwater. Invasive dreissenids in Turkish rivers are local species and subspecies. More recent locations of the dreissenid expansion within the Ponto-Caspian region (Lake Sasyk, Baraboj River, and Sukhoj Liman Basin for the zebra mussel; Dniestr River Basin for the quagga mussel) are described. One empty valve of *Dreissena polymorpha andrusovi* was found in the Taganrog Bay.

Key words: alien species, *Dreissena bugensis, Dreissena polymorpha, Dreissena presbensis*, molluscs, native range, Ponto-Caspian relics

Introduction

Freshwater dreissenids have attracted attention for a long time. Two species of freshwater *Dreissena*: *Dreissena polymorpha* (Pallas, 1771) and *Dreissena bugensis* (Andrusov, 1897) have been indicated as invaders in different continents (Kharchenko 1995, Bobat 2004, Orlova 2004, Therriault et al. 2005, Gelembiuk et al. 2006, May et al. 2006, Molloy et al. 2007). Interest in both species is enormous: and the bibliography on their ecology and impact according to Schloesser et al. (1994) numbers thousands of papers.

While the overwhelming majority of publications on *Dreissena* concerns invasive range, information on distribution within their native range is limited. Even in a special review on the distribution of dreissenids in Ukraine (Kharchenko 1995) there is almost no data present on their native range. Knowledge about borders of dreissenid native range and nearby expansion is very important for both studies and prediction of their widespread expansion.

For many years, all recent freshwater dreissenids, except *D. bugensis* (quagga mussel), were recorded as *D. polymorpha polymorpha* (zebra mussel). According to this conception the native range of *D. polymorpha polymorpha* includes the Ponto-Caspian Basin and the ancient lakes of the Balkan Penninsula and Asia Minor. A taxonomic revision of *Dreissena* by Lvova and Starobogatov (1982) showed that *Dreissena* from Lake Ohrid (Republic of Macedonia) is a separate species, *Dreissena stankovici* Lvova et Starobogatov 1982. Later this species was identified from nearby Lake Prespa (Gelembiuk et al. 2006). Recent investigations showed what *D. stankovici* is actually a synonym of *Dreissena presbensis* (Kobelt, 1915), which occurs in Balkan lakes as another Balkan endemic dreissenid – *Dreissena blanci* (Westerlund, 1890) (Albrecht et al. 2007). According this work dreissenids from the Balkan lakes – Ohrid, Prespa, Mikri Prespa, Skutari, Dojran, Trichonis Vegoritis, Amvrakia, Pamvotis – are the above-mentioned Balkan endemics.

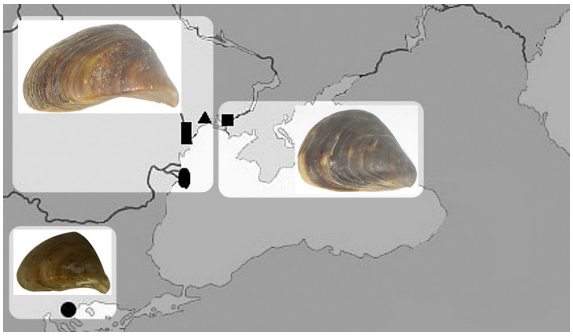

Figure 1. Some important records of dreissenids in their native range: the most eastern record of *Dreissena presbensis* (Kobelt, 1915) (round); *Dreissena polymorpha polymorpha* (Pallas, 1771) in a zone of the Black Sea freshened by the Danube (ellipse); *D. polymorpha polymorpha* in streams entering the Dniestr Liman (rectangular); *D. polymorpha polymorpha* from a steep small stream, the Berezan River (triangle); native locality of *Dreissena bugensis* (Andrusov, 1897) in the Dniepr Delta (square).

Figure 2. Valve of *Dreissena polymorpha andrusovi* (Brusina in Andrusov, 1897) from the Taganrog Bay, scale = 1 cm (Photo: M. O. Son).

Molecular revision of dreissenids shows that those from some other regions form separate taxa (Gelembiuk et al. 2006, May et al. 2006): *Dreissena polymorpha anatolica* (Bourguignat, 1884) (Anatolian tectonic lakes), *Dreissena polymorpha gallandri* (Locard, 1893) (lakes of Marmara Sea Basin), and *Dreissena caputlacus* (Schütt, 1993) (Golbasi tectonic basin).

These studies did not include some regions with autochthonous populations of freshwater dreissenids: rivers and relic lakes along the Bulgarian Black Sea Coast (Hubenov 2005), Lake Volvi and the Aliakmon River from the environs of Thessaloniki in the Aegean Sea Basin (Greece) (Zarfdjian 2000).

Our study on dreissenids from Lake Volvi (collection of Zoological Institute of Russian Academy of Sciences, St.-Petersburg; coll. A. Yu. Karatayev, N 40°37´50" - 40°41´50", E 23°21´10" - 23°36´40"; 27 October 1995) showed these to be *D. presbensis* (Figure 1). According to labels, the late Starobogatov intended further revisions in the identification of these specimens. Data on *D. polymorpha* from Bulgarian Black Sea Coast was not used in taxonomic revisions, and will be considered as *D. polymorpha polymorpha* unless disproved. So, the native range of *D. polymorpha polymorpha* is limited by the Northern Black Sea Region and the Caspian Basin.

With rare exceptions, only dreissenids from the Northern Black Sea Region are known as invasive species. Expansion of other dreissenids is localized in nature and mainly of concern to Turkey. Local dreissenids invaded many reservoirs in the Turkish Euphrates River Basin, Aegean, Mediterranean, and Black Sea coasts (Bobat 2004), but data on the expansion of separate species and subspecies are absent. As is generally known, the dreissenids which invaded the Seyhan Dam Reservoir were *D. caputlacus* and *D. polymorpha anatolica* (Gelembiuk et al. 2006). According to Bobat (2004) at least some cases of dreissenid expansion in the Turkish Black Sea Basin (Lakes Acarlar in the Sakarya Basin and dams on the Kizilirmak Basin) concerned *D. polymorpha gallandri* (native to the surroundings of Istanbul and Lake Uluabat in the Marmara Sea Basin).

A dreissenid invasion of unknown origin (true zebra mussel or autochthonous Balkan dreissenids) was reported from Greek reservoirs (especially Tavropos, Kremasta, and Kastraki), where invaders were noted as *D. polymorpha* (Economou et al. 1991, Petridis and Sims 1993, Conides et al. 1995).

Among Caspian dreissenids, we found one empty valve of *Dreissena polymorpha andrusovi* (Brusina in Andrusov, 1897) in the western part of Taganrog Bay (Figure 2). The subspecies is wide-spread in the Northern Caspian Sea. This shell might have been being dropped as empty valve with building sand or by a ship.

Material and Methods

This paper is based on material collected by the author as well as on literature data. Original material is deposited in the mollusk collection of the Odessa Branch Institute of Biology of the Southern Seas (OB IBSS). All collected material

Figure 3. Conchological diversity of the zebra mussel from different river basins, scale = 1 cm; A: Dniepr River; B: Danubian lakes; C: Berezan River (Photo: M.O. Son).

Figure 4. Giant zebra mussel from the Middle Dniestr, scale = 1 cm (Photo: M. O. Son).

was fixed in 70% ethanol. Danube, Dniepr, Dniestr, Don, and Volga river basins, small rivers and reservoirs of the Azov and Black sea coasts were investigated annually from 1999 to 2007. Field research was undertaken according to standard methods (Zhadin 1965).

Results and Discussion

Borders between native and invasive ranges of the zebra mussel

The modern native range of *D. polymorpha polymorpha* includes different habitats in the Ponto-Caspian Region.

In the rivers of the Caspian Sea Basin (Volga and Ural deltas) *D. polymorpha polymorpha* occurs in biotopes of river channel and wetlands (Pirogov 1974, Pirogov et al. 1994).

In the Azov-Black Sea Basin (where estuarian biotopes are characterized by higher diversity, than in the Caspian Sea Basin) the native range of the zebra mussel has a complicated disjunctive structure. This kind of native range causes high geographical variability in *D. polymorpha polymorpha* (Figure 3).

The zebra mussel was noted from Bulgarian relic lakes: Varnensko, Beloslavsko, Mandrensko, Bourgasko, and also in the Rivers Kamchia and Veleca (Hubenov 2005).

In eastern Bulgarian lakes the zebra mussel was situated within the Sinoie-Razim lagoonal complex (Romania) connected with Danube Delta.

In the Danube Basin it occupied riverine lentic habitats and associated estuarine reservoirs – Kagul, Kugurluj, Yalpug, Katlabug, and Kitaj (Grossu and Paladian 1956, Milashevich 1908, new data). Along the Danube channel it was located as a native species up to the Middle Danube (Mordukhay-Boltovskoy 1960). We found it also in a zone of the Black Sea, freshened by the Danube (shallows Kurilskije).

The zebra mussel occurred in branches of the Dniestr Delta and in the main channel of the Lower and Middle Dniestr, and in estuarine reservoirs – Dniestr Liman and Kuchurgan Liman. In the Middle Dniestr we observed the largest specimens of the zebra mussel (length of the shell = 49 mm) found in all native habitats (Figure 4).

Along the coasts of the Dniestr Liman, *D. polymorpha polymorpha* was found in streams (the first records of Ponto-Caspian bivalves in this type of habitat). It now seems to have disappeared from the floodplain lakes of the Dniestr, where it was recorded in last century (Grinbart 1967). This is probably connected with disimproved oxygen levels in these reservoirs. In the Dniestr Liman the zebra mussel was recorded in the northern (freshwater) and central (brackishwater) parts and in springs in its basin.

In the Tiligul Liman, where *D. polymorpha polymorpha* was identified in the early twentieth century (Grinbart 1967) it disappeared after a rise in salinity when the liman was connected by channel with the Black Sea.

In the Berezan Liman, the zebra mussel occurs in brackish water in central and northern parts of the liman (Grinbart 1955). We found it also in the Lower Berezan River.

In the Southern Bug River and Dniepr River the zebra mussel was located in the lower and middle stretches including a zone upstream of rapids (up to Vinnitsa City and Kiev accordingly) (Polishchuk 1978, Krasheninnikov 1929). This species also occurred in their large tributaries: Ingul River, Ingulets River, and Saxagan River (tributary of the Ingulets River) (Polishchuk 1978). All these streams were situated on locations of former large brackishwater resevoirs

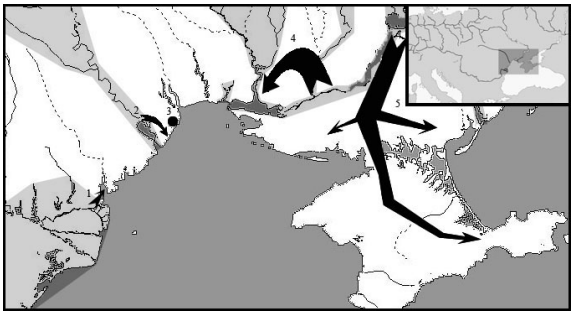

Figure 5. Directions of nearby expansion of the zebra mussel within North Black Sea Region: 1) Lake Sasyk; 2) Baraboj River; 3) Sukhoy Liman Basin; 4) Ingulets Channel; 5) Kahovka and North Crimean Channel.

or coastal bays that are established on paleontological data (Polishchuk 1978). The zebra mussel is a dominant species in estuaries of these rivers, which form an estuarine complex – the Dniepr-Bug Liman.

On the Northern Azov Sea Coast it was noted in the Molochnaya River (Lubyanov 1954) and in the mouth of the Kalmius River (Mordukhay-Boltovskoy 1960). At present, this mollusc is absent in the last river; this absence is probably connected with the construction of a giant industrial complex in this place.

The zebra mussel was widespread in the estuarine system of the Don River, including the brackishwater Taganrog Bay of the Azov Sea, Mius Liman, Yejsk Liman, and the Don Delta; along the Don River its native range spread upstream to Voronezh City (Mordukhay-Boltovskoy 1960). It also was recorded from the Manych River (tributary of the Don River) and in large reservoirs of the Don and the Manych (Ust-Manych, Proletarskoye reservoir, and Tsimlyansk reservoirs) (Zhulidov et al. 2004).

In the nineteenth century the zebra mussel was recorded in the Severskij Donets River (tributary of the Don River) (Krynicki 1837). Later this species was not recorded in this river until construction of the Dniepr-Donbass Channel. Probably it was occasionally acclimatization.

In the Eastern Don River, the zebra mussel lives in the Kuban River from its mouth to Krasnodar City (Rosen 1911) and in the estuarine reservoirs: Ahtanizovskij Liman (Puzanov 1929) and Dolgij Liman (Povazhnyj and Semin 2005).

These basins in the Black Sea Region are the most eastern native locations of dreissenids' population. According to Mordukhay-Boltovskoy (1960) dreissenids have not been found in the relic lakes of the Caucasian Region (Abrau and Paleostomi) where other Ponto-Caspian species are known. Now the zebra mussel is a major species in Lake Abrau (M. V. Nabozhenko, personal communication).

In the time of acclimatization of aquatic invertebrates into Georgian reservoirs (Hramskoje and Tkibulskoje) the zebra mussel was introduced there (Sergeyeva 1968) but has not since been recorded.

During the twentieth century, range expansion for the zebra mussel was described in a number of channels and reservoirs, associated with the Lower Dniepr Basin (Kahovka Meliorative System, Ingulets Channel, North Crimean Channel, etc). This spread took place only within artificial systems and has not impacted on natural ecosystems. Penetration of this species to new Ponto-Caspian Rivers began at the end of the twentieth century (Figure 5).

Expansion in the Danube-Dniestr Meliorative system

In the 1960s the creation of a common meliorative system was planned between the Danube and Dniepr. The building of the Danube-Dniestr Meliorative system was planned as the first stage of its creation. The marine gulf – Sasyk Lake (in this project – a reservoir in the Danube-Dniestr Meliorative system) was desalinated by separating it from the Black Sea and by building the Danube-Sasyk Channel, which connected Lake Sasyk and the Danube River. This remedial plan included a large lagoonal complex Tuzly Limans between the Danube and Dniestr basins.

In 1981 the project began, but irrigation by mineralized water made a catastrophic impact on local soils and the project was disrupted.

As result of the desalination of Lake Sasyk and its connection with the Danube many freshwater species invaded this reservoir. *D. polymorpha polymorpha* is widespread in this reservoir and found along all its length (more than 30 km).

Both the zebra mussel and other Ponto-Caspian bivalves have a very specific impact on the ecosystem of Lake Sasyk: their empty shells make enormous deposites which have caused shallowing and transformation of a southwestern part of this reservoir into a swamp.

The next penetration of Danubian species was through Lake Sasyk into the higher part of the

Danube-Dniestr Meliorative system (channels and transformed Rivers Kogilnik and Sarata) is this is complex, because introduced species in Lake Sasyk include mainly species with high sensivity to hypoxia. This interferes with their penetration to the above-mentioned streams which have a variation in oxygen concentration.

Expansion in the Lower Dniestr Meliorative System

The Baraboj River was connected by channels with the Dniestr River to the Lower Dniestr Meliorative System in the second half of the twentieth century. During this time the upper part of the Baraboj River was turned into the Baraboj Reservoir. This reservoir has two applications: as part of a meliorative system and as a cooler of a planned power plant. Before this building, the Baraboj River was temporarily dry and many species, occurring in large rivers, would not live in this river.

The population of zebra mussels there was formed as a result of water transferring from the Odessa Channel (water-mine with pumping station on the Dniestr River near Belyajevka City) to the Baraboj Reservoir and Baraboj River. Now this species is found in the Baraboj Reservoir and in a little pond in the river mouth.

Invasion to the Sukhoy Liman Basin

A population of *D. polymorpha polymorpha* was recorded in the Sukhoy Liman Basin in July 2006 in a small rapid stream. This stream is the remains of the Gross-Libental River (the middle section) which flowed into the Sukhoy Liman. The connection between the Gross-Libental River and Sukhoy Liman was disrupted by the building of a road. Now the lower part of the river is a small floodplain. The total sampled population consisted of juvenile specimens only (some at pediveliger stage). Adult shells were not found. Molluscs occurred on the stones and on other hard substrates.

In the Black Sea Region, this record is a unique case of dreissenid invasion to a small stream. Upstream of the sampling site, a limnic reservoir feeds water to the stream via pipework and hence the stream flow is artificially sped up. Range expansion in the human-made rheophilic biotopes of small stream was also noted for other species.

In this biotope we also found the exotic mudsnail *Potamopyrgus antipodarum* (Gray, 1843) and an aquarium snail *Physella heterostropha* (Say, 1817). Both these species were also found in all small rivers of the Sukhoy Liman Basin (Son, 2007a). In similar biotopes in the Baraboj River we found the rheophilic *Viviparus vivparus* (Linnaeus, 1758) and the Ponto-Caspian species *Euxinipirgula lincta* (Milashevitch, 1908), both of which are non-indigenous for this river (Son, 2007a).

To summarise these facts we conclude that this type of biotope is characterized by high invasibility. Similar biotopes probably play an important role in the expansion of rheophilic species into steep droughted rivers.

The native range of the quagga mussel

The question on chronology of the quagga mussel invasion history is extremely confusing. The data published till now on its distribution testifies, that its native range is in a lower stretch of the Southern Bug, whence it has been described, and its expansion in the Dniepr and moving on the cascade of reservoirs date from the 1930-1940s (Tseeb et al. 1966, Zhuravel 1967).

The designation of its native range as “a lower stretches of the Southern Bug and Dniepr rivers” in some English-written literature was based on a vagueness of the term “Dniepr-Bug Liman”. This name is modular for estuaries of the Dniepr and Southern Bug rivers. *D. bugensis* has been described from the Lower Southern Bug, and the introduction of the concept “Dnepr-Bug Liman” in the twentieth century has resulted in the beginning of a designation of this species locus typicus as Dniepr-Bug Liman and the subsequent transferral to the English-written literature as “lower stretches of the Dniepr River”. This is absolutely inadmissible, because the locus typicus of *D. bugensis* is the estuarine Southern Bug – Bug Liman (expanded river mouth), whereas the estuarine system of the Dniepr River includes two parts – Dniepr Delta – the expanded river mouth and Dniepr Liman (part of Dniepr-Bug Liman) – the freshened sea gulf between the Bug Liman and Dniepr Delta.

For this reason, the occurrence of *D. bugensis* in the Dniepr Delta may be considered as the beginning of the quagga mussel’s expansion into the Dniepr Basin.

However malacological investigations of the Dniepr and Southern Bug basins at the time of the quagga mussel’s description were fragmen-

tary and the two similar species concerned could not simply be differentiated.

In Lindgolm's article (1908), the first complex malacological investigation in the given region, *D. bugensis* was not sampled at all in the south of the Russian Empire.

While this author was processing collection of Zoological Institute of Russian Academy of Sciences, *D. bugensis* was found among them; this was collected by Brauner in the Dniepr Delta (Lake Beloje, surrounding Kherson City). The sample year was absent from the label but Lindgolm (1908) indicated it as 1899 in a publication. Thus, *D. bugensis* was already present in the Lower Dniepr practically at the same time, when it had been described from the Southern Bug. This raises doubts as to whether this species is alien to the Dniepr Basin.

References on recent native localities of the quagga mussel in the Ingulets River are consistent with ambiguity in reporting by Polishchuk for the Soviet malacological meeting. This was reprinted by Malacological Review (Polishchuk 1978). In the original text it states clearly that *D. bugensis* was recorded in geological sediments of the Ingulets River.

The quagga mussel invasion within the Ponto-Caspian region

The quagga mussel has grasped, within Ponto-Caspian region, some large river basins and has expanded its distribution to the Dnepr Basin.

In the Dniepr Basin, the quagga mussel is widespread in the Dniepr Cascade of Reservoirs which occupy almost all the Ukrainian part of the Dniepr River and the associated artificial systems of hydrotechnical buildings (Kahovka Meliorative System, Ingulets Channel, North Crymean Channel, etc).

In the Don River Basin (first record in the 1980) it occurs in the Lower and Middle Don River, Manych River and large reservoirs of the Don and Manych (Ust-Manych, Proletarskoye reservoir, and Tsimlyansk reservoirs) (Zhulidov et al. 2004, 2005).

In the Volga River Basin (first record – 1981) it occurs in the Volga River (including Volga Delta) and Volga Cascade of Reservoirs (Orlova et al. 2004, Zhulidov et al. 2005).

The quagga mussel also penetrates to freshened zones of the Azov and Caspian seas. In the Northern Caspian Sea it was recorded as recently as 1994-1997 (Orlova et al. 2004). In the Azov Sea it lives in the Taganrog Bay – a brackishwater part of sea which is an estuary of the Don River (see Annex).

More recently, the quagga mussel invasion has expanded in the western Ponto-Caspian rivers: Dniestr and Danube.

Invasion in the Danube River was recorded during recent years and is known from some local findings in the Lower (except delta) and Middle Danube (Micu and Telembici 2004, Popa and Popa 2006).

A very intensive expansion of the quagga mussel has taken place in the Dniestr Basin. The first record of *D. bugensis* in the Dniestr Basin was the invasion of the Dniestr Reservoir (Middle Dniestr) in 1992-1993 (Kharchenko, 1995). Now it occupies a number of habitats in the Dniestr River and Dniestr estuarine system. The quagga mussel has been recorded in the main channel of the Middle and Lower Dniestr River, branches of the Dniestr Delta, the northern part of the Dniestr Liman and streams entering to the Dniestr Liman (see Annex). Unique specimens of quagga mussel were recorded in the estuarine reservoir – Kuchurgan Liman (Filipenko and Lejderman 2006).

Biotopical distribution of dreissenids in the Azov-Black Sea Region, ecological barriers and vectors of invasions

Both species of dreissenids occur in the Black Sea region in various habitats, where hypoxia is absent (see Table 1). We also noted an interesting way of supporting dreissenids' populations in the shallows along coasts of the Dniestr Liman, where hypoxia, periodically takes place. Number of dreissenids accumulate in the streams, which enter the estuary, and in the shallows near the streams' mouths (Figure 6). Until 2007 we found only zebra mussel in these habitats, but in 2007 massive populations of the quagga mussel were located in the four streams along the southern coast of the Dniestr Liman.

Table 1 shows the significant extension of the quagga mussel's biotopical distribution in the range of invasion. Characteristically, the biotopical distribution of both dreissenids in the range of invasion is very similar, whereas in the native range *D. polymorpha polymorpha* occurred in more kinds of habitats than *D. bugensis*.

The widespread invasion of the dreissenids is caused by a diversity of successful vectors.

Dreissenids can use different modes of spread in different stages of their life cycle as they have

Table 1. Biotopical distribution of the zebra mussel and quagga mussel in their native and invasive range within Ponto-Caspian Region.

Habitats	*D. polymorpha polymorpha*		*D. bugensis*	
	Native range	Range of invasion	Native range	Range of invasion
River channel and branches of deltas	+	+	+	+
Rapids	+	-	-	-
Tributaries	+	-	-	-
Streams	+	+	-	+
Freshened zones of seas	+	-	-	+
Freshwater parts of estuaries	+	+	-	+
Brackishwater parts of estuaries	+	+	+	+
Small rivers	+	+	-	-
Artificial reservoirs	+	+	-	+
Lakes	+	+	+	+

Figure 6. Dreissenid, field in the stream mouth (Photo: M. O. Son).

a planktonic larval stage (trochophora, veliger), settling benthic stages (pediveger, juvenile mollusc), and stationary attached stage (adult mollusc attached by byssus).

During these different stages dreissenids use different modes of invasion. Downstream drift is possible for planktonic larvae by current and for other life stages on aquatic plants drifting downstream (Sullivan et al. 2003, Son 2007a). Drift is a very rapid way of spread and it helps dreissenids penetrate through stretches which have unfavorable conditions. This vector of spread is not available to another highly invasive exotic bivalve genus, *Corbicula*. *Corbicula fluminea* (Müller, 1774) and *Corbicula fluminalis* (Müller, 1774), which at the end of the twentieth century had invaded the Lower Danube and were widespread through most of the Danube Delta branches, but similar to dreissenids (both genera have marine origin) had avoided colonizing stretches with variations in oxygen regime. Both species of *Corbicula* recorded in Europe lack a free–living larval stage and have not penetrated into Lake Sasyk, which is connected with various branches of the Danube Delta (Voloshkevitch and Son 2002, Son 2007b). Contrary to this, it appears that the zebra mussel has successfully overcome this barrier by larval drift.

Spread by shipping is typical for planktonic larvae via ballast water and also by biofouling by the adult stage on the hull. Water movement (flow and wave action) and animal vectors are also important for spread of pediveger and juvenile molluscs. Use of animal vectors is also notable in adult dreissenids; including birds, aquatic insects, amphipods, crayfish, and, probably some other animals (Mordukhay-Boltovskoy 1960, Dedyu 1963, McCauley and Wehrly 2007).

What kinds of ecological barriers have limited dreissenids' spread within native range?

It is obvious, that the native range of the zebra mussel and quagga is less than the basic ecological limiting factors would allow.

The most important factors for dreissenids are salinity, mineralization, and speed of current isolation between river basins, oxygen concentration, and drying (Mordukhay-Boltovskoy 1960, Spidle et al. 1995, Orlova et al. 2005).

The last two factors prevent occurrence in some habitats, but do not limit distribution of dreissenids along river networks of the Ponto-Caspian Region (excluding drying rivers and salt lakes). However in the Ponto-Caspian Region salinity and high velocity in streams do not usually limit dreissenids' spread in situ.

The distribution of dreissenids within their native range is limited by the presence of all habitat requirements, necessary to form stable populations.

Such as many marine species with planktonic larvae, dreissenids can form a compound structure of metapopulations. The concept of metapopulation (where integral genetic system without free interbreeding but is not mixed on

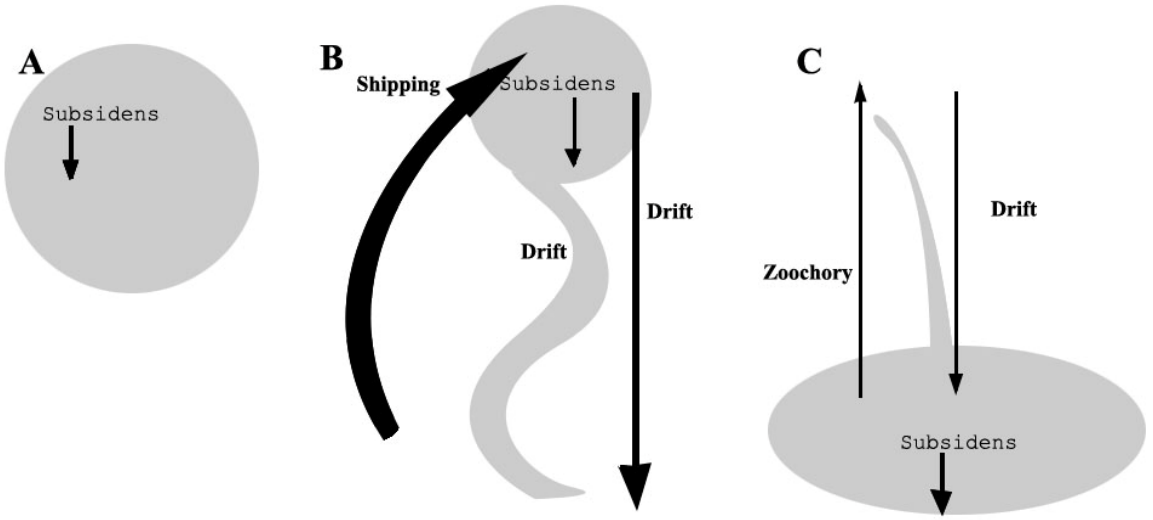

Figure 7. Different variants of spatial structure of the dreissenids' occurring: A – isolated lentic reservoirs, estuaries, freshened parts of seas; B – reservoirs and channel downstream; C – reservoirs and small streams upstream.

isolated populations) are discussed in detail in the issues of the "Helgoland marine research" (volume 56, number 4), which defined the metapopulation concept. In the Ponto-Caspian Region we observe some variants of spatial structure of the dreissenids' occurrence.

Three main genetic variants are showed in Figure 7. First variant (A) is known in the Ponto-Caspian Region from the Caspian Sea, Taganrog Bay, and from a lot of estuaries in the native and invasive ranges of the zebra mussel and quagga mussel. In these cases we observe the "classic population".

Even in the desalinated parts of the sea (such as the shallows of Kurilskije in the Black Sea) dreissenids don't form a metapopulation, because transfer by sea currents along coast, not only brings larvae to other freshened localites in the sea, but also passes through marine habitats which are characterized by high salinity.

A good example of the variant B occurs in the Volga and Dniepr cascades of reservoirs by both dreissenids (invasive ranges) or in the Lower Danube by *D. polymorpha polymorpha* (native range). In the cascades of reservoirs the dreissenids form an integral genetic system (metapopulation) with asymmetric genetic drift caused by drift of larval drift downstream. A similar situation was observed in the Ukrainian stretch of the Danube, where the river is connected by small channels with a series of separate estuarine lakes, which are a "donor fund" of the dreissenids for the main river channel.

Variant C was found in the first investigation of the Dniestr Liman. In some streams entering into this estuary the zebra mussel was record above sea level. In this case we suggest transfer by amphipods. A similar stream habitat for the zebra mussel was observed on the Uglich Reservoir (Volga River). Meanwhile we have not recorded this type of habitat for the quagga mussel.

Acknowledgements

We are grateful to Alexey V. Korniushin for his help in questions of dreissenid taxonomy, and to Frances Lucy (Institute of Technology Sligo, Ireland) for valuable comments and English editing. This work was partly supported by the European Commission 6th Framework Program Integrated Project ALARM (contract GOCE-CT-2003-506675).

References

Albrecht C, Schultheiß R, Kevrekidis T, Streit B, Wilke T (2007) Invaders or endemics? Molecular phylogenetics, biogeography and systematics of *Dreissena* in the Balkans. *Freshwater Biology* 52: 1525–1536, http://dx.doi.org/10.1111/j.1365-2427.2007.01784.x

Bobat A (2004) Zebra Mussel, Fouling Problems in the Euphrates Basin. *Turkish Journal of Zoology* 28: 161–177

Conides A, Koussorius T and Gritzalis K (1995) Zebra mussel, *Dreissena polymorpha*: population dynamics and notes on control strategies in a reservoir in Western Greece. *Lake and Reservoir Management* 11: 329–336, http://dx.doi.org/10.1080/07438149509354214

Dedyu II (1963) On the role of amphipods in geographical distribution of *Dreissena*. *Izvestiya AN Moldavskoj SSR. Ser. Zool.* 5: 64–65

Economou AN, Daoulas Ch, Economidis P (1991) Observations on the biology of *Leuciscus* 'svallize' in the Kremasta reservoir (Greece). *Hydrobiologia* 213: 99–111, http://dx.doi.org/10.1007/BF00014996

Filipenko SI, Lejderman AI (2006). Dynamics of development of the dreissenid's population in the Kuchurgan Reservoir – water-cooler of the Moldova GRES. In: Academician Leo Berg – 130. Eco-Tiras, Bender, pp 116–118

Gelembiuk GW, May GE, Lee CE (2006) Phylogeography and systematics of zebra mussels and related species. *Molecular Ecology* 15: 1033–1050, http://dx.doi.org/10.1111/j.1365-294X.2006.02816.x

Grinbart SB (1955) Materials for studying the zoobenthos of the Berezan Liman. *Trudy Odesskogo Gosudarstvennogo Universiteta im. I. I. Mechnikova. Ser. Biol.* 145(7): 3–180

Grinbart SB (1967) Zoobenthos of limans of the North-Western Black Sea Region and nearby zones of the sea. Dissertation. Odessa State University

Grossu AV, Paladian G (1956) Contributini la studiul molustelor din delta si Bazinul Dunarii inferioare. *Analele Institutului de Cercetari Piscicole* 1: 401–10

Hubenov Z (2005) *Dreissena* (Bivalvia: Dreissenidae) - systematics, autochthonous and anthropogenic areas. *Acta zoologica bulgarica* 57(3): 259–268

Kharchenko TA (1995) *Dreissena*: range, ecology, biological handicaps. *Hydrobiologicheskij Zhurnal* 31(3): 3–21

Krasheninnikov S (1929) The studying of freshwater malacofauna around Kiev. *Trudy Fiziko-matematicheskogo Viddilennya Vseukrainskoj Akademii Nauk* 11(3): 421–429

Krynicki J (1837) Conchylia tam terrestrial, quam fluviatilia et e maribus ajacentribus Imperii Rossici indigena, quae pro mutual offeruntur historiae naturalis cultoribus commutatione. *Bulletin de la Societe Imperiale des Naturalistes de Moscou* 10(2): 50–64

Lindholm WA (1908) Materialien zur Molluskenfauena von Südwestrussland, Polen und der Krim. *Zapiski Novo-rossijskogo obschestva jestestvoispytatelej* 31: 199–232

Lubyanov IP (1954) Bottom fauna of the Molochnaja River. *Zoologicheskij Zhurnal* 33(3): 537–544

Lvova AA, Starobogatov YaI (1982) New species of Dreissena (Bivalvia: Dreissenidae) from Lake Ohrid. *Zoologicheskij Zhurnal* 61(11): 1749-1752

May GE, Gelembiuk GW, Panov VE, Orlova MI, Lee CE (2006) Molecular ecology of zebra mussel invasions. *Molecular Ecology* 15: 1021–1031, http://dx.doi.org/10.1111/j.1365-294X.2006.02814.x

McCauley SJ, Wehrly KE (2007) Zebra mussel, *Dreissena polymorpha* (Pallas), attachment to Odonata larvae. *Odonatologica* 36(1): 63–69

Michaloudi E (2005) Dry weights of the zooplankton of Lake Mikri Prespa (Macedonia, Greece). *Belgian Journal of Zoology* 135(2): 223–227

Micu D, Telembici A (2004) First record of *Dreissena bugensis* (Andrusov 1897) from the Romanian stretch of River Danube. In: Abstracts of the International Symposium of Malacology, August 19–22, 2004, Sibiu, Romania

Milashevich KO (1908) Molluscs collected during excursion of S. A.Zernov on torpedo boat N 264 on Danube River from June, 28 till July, 3, 1907. *Izvestija Imperatorskoj Akademii Nauk* 6(2): 991–996

Molloy DP, Vaate A bij de, Wilke Th, Giamberini L (2007) Discovery of *Dreissena rostriformis bugensis* (Andrusov 1897) in Western Europe. *Biological Invasions* 9: 871–874, http://dx.doi.org/10.1007/s10530-006-9078-5

Mordukhay-Boltovskoy PhD (1960) Caspian fauna in the Azov-Black seas basin. The Academy of Sciences of the USSR Press, Moscow-Leningrad

Orlova MI, Muirhead JR, Antonov PI, Shcherbina GKh, Starobogatov YaI, Biochino GI, Therriault ThW, MacIsaac HJ (2004) Range expansion of quagga mussels *Dreissena rostriformis bugensis* in the Volga River and Caspian Sea basin. *Aquatic Ecology* 38: 561–573, http://dx.doi.org/10.1007/s10452-004-0311-y

Orlova MI, Therriault ThW, Antonov PI, Shcherbina GKh (2005) Invasion ecology of quagga mussels (*Dreissena rostriformis bugensis*): a review of evolutionary and phylogenetic impacts. *Aquatic Ecology* 39: 401–418, http://dx.doi.org/10.1007/s10452-005-9010-6

Petridis D, Sims A (1993) Benthic macrofauna of Tavropos reservoir (central Greece). *Hydrobiologia* (262): 1–12, http://dx.doi.org/10.1007/BF00010985

Pirogov VV (1974) Malacofauna of the Volga Delta. Dissertation. Leningrad

Pirogov VV, Tarasov AG, Kazantseva SZ (1994) Malacofauna of typical waterbodies of the middle and lower Ural River. *Ruthenica* 4(1): 61–65

Polishchuk VV (1978) Brackish and freshwater molluscs from anthropogenic deposits in the valleys of the Ingul, Ingulets and South Bug Rivers, and their relationship with recent malacofaunas. *Malacological Review* 11(1-2):146–147

Popa OP, Popa LO (2006) The most westward European occurrence point for *Dreissena bugensis* (Andrusov, 1897). *Malacologica Bohemoslovaka* 5: 3–5

Povazhnyj VV, Semin VL, (2005) Fauna of zooplankton and zoobentos of the East Azov Sea Region and Taman Penninsula. In: Ecosystem investigations of environment and biota of the Azov Basin and the Kerch strait, vol. 7.Print. Kola Science Centre RAS, Apatity, pp185–209

Puzanov I (1929) Zoologische ergebnisse einer Reise nach der Halbinsel Taman und Cis-Kaukasien. Ezhegodnik Zoologicheskogo Muzeya Akademii Nauk SSSR, pp 43–52

Rosen O (1911) Die Mollusken Ciskaukasiens und speciell des Kubangebietes. *Annualre du Musee Zoologique de l' Academie Imperiale des Sciences de St.-Petersbourg* 16: 86–142

Schloesser DW, Bij De Vaate A, Zimmerman A (1994) A bibliography of "*Dreissena polymorpha* in European and Russian waters: 1964-1993". *Journal of Shellfish Research* 13(1): 243–261

Sergeyeva ZhN (1968) Results of acclimatizations of the forage invertebrates into inland waters of Georgia. In: Karpevitch AF (ed), Acclimatization of fishes and invertebrates into the reservoirs of the USSR. Nauka, Moscow

Son MO (2007a) Invasive molluscs in fresh and brackish waters of the Northern Black Sea Region. Druk Press, Odessa

Son MO (2007b) Invasive Mollusks (Mollusca, Bivalvia, Gastropoda) in the Danube Delta. *Vestnik zoologii* 41(3): 213–218

Spidle AP, Mills EL, May B (1995) Limits to tolerance of temperature and salinity in the quagga mussel (*Dreissena bugensis*) and the zebra mussel (*Dreissena polymorpha*).

Canadian Journal of Fishery and Aquatic Sciences 52: 2108–2119, http://dx.doi.org/10.1139/f95-804

Sullivan M, Lucy F, Minchin D (2003) The association between zebra mussels and aquatic plants in the Shannon River system, Ireland. *Aquatic Invaders* 13: 6–9

Therriault TW, Docker MF, Orlova MI, Heath DD, MacIsaac HJ (2004) Molecular resolution of the family Dreissenidae (Mollusca: Bivalvia) with emphasis on Ponto-Caspian species, including first report of *Mytilopsis leucophaeata* in the Black Sea basin. *Molecular Phylogenetics and Evolution* 30:479–489, http://dx.doi.org/10.1016/S1055-7903(03)00240-9

Therriault TW, Orlova MI, Docker MF, MacIsaac HJ, Heath DD (2005) Invasion genetics of a freshwater mussel (*Dreissena rostriformis bugensis*) in eastern Europe: High gene flow and multiple introductions. *Heredity* 95: 16–23, http://dx.doi.org/10.1038/sj.hdy.6800691

Tseeb YaYa, Almazov AM, Vladimirov VI (1966) Laws of change of hydrological, hydrochemical and hydrobiological modes in connection with menegement a drain of Dniepr and their impact on a biological and sanitary condition of water basins. *Hydrobiologicheskij Zhurnal* 2(3): 3–18

Voloshkevitch EV and Son MO (2002) *Corbicula fluminalis* – a new species of bivalve mollusk for Ukrainian fauna. *Vestnik zoologii* 36(6): 94

Zarfdjian M-H, Michaloudi E, Bobori DC, Mourelatos S (2000) Zooplankton abundance in the Aliakmon River, Greece. *Belgian Journal of Zoology* 130 (Supplement 1): 29–33

Zhadin VI (1965) Mollusks of fresh and brackish waters of the USSR. Israel Program for Scientific Translation, Jerusalem, 368 pp

Zhulidov AV, Pavlov DF, Nalepa TF, Scherbina GH, Zhulidov DA, Gurtovaya TYu (2004) Relative distributions of *Dreissena bugensis* and *Dreissena polymorpha* in the Lower Don River System, Russia. *International Revue of Hydrobiology* 89 (3): 326–333, http://dx.doi.org/10.1002/iroh.200310727

Zhulidov AV, Zhulidov DA, Pavlov DF, Nalepa TF, Gurtovaya TY (2005) Expansion of the invasive bivalve mollusk *Dreissena bugensis* (quagga mussel) in the Don and Volga River Basins: revisions based on archived specimens. *Ecohydrology and Hydrobiology* 5(2): 127–133

Zhuravel PA (1967) About the spread of the quagga mussel in artificial reservoirs. *Hydrobiologicheskij Zhurnal* 3(2): 87–90

Supplementary material

The following supplementary material is available for this article:

Annex. Records of dreissenids in their range of invasion.

Annex. Records of dreissenids in their range of invasion.

Species	Location	Record coordinates		Date of record	Collector
		Latitude,°N	Longitude,°E		
Dreissena bugensis	A mouth of the anonymous river entering to the Dniestr Liman	46°20'02"	30°06'06"	03.05.2007	M. O. Son
	Alexandrovskij Erik	46°40'50"	30°25'18"	04.05.2006	M. O. Son
	Dniestr River, Republica Moldova, Site 1	47°05'43"	29°04'40"	13.10.2006	M. O. Son
	Dniestr River, Republica Moldova, Site 2	47°41'43"	28°58'35"	02.08.2005	M. O. Son
	Dniestr River, Ukraine, Site 1	46°27'48"	30°15'39"	July 2006	M. O. Son
	Dniestr River, Ukraine, Site 1	46º27'40"	30º14'58"	May 2007	M. O. Son
	Dniestr River, Ukraine, Site 2	46°44'34"	30°19'17"	22.08.2006	M. O. Son
	Dniestr River, Ukraine, Site 3	46°25'48"	30°10'16"	08.07.2001	M. O. Son
	Dniestr River, Ukraine, Site 4	46°22'28"	30°16'19"	28.04.2007	M. O. Son
	Dniestr River, Ukraine, Site 5	46°42'16"	30°17'49"	05.05.2007	M. O. Son
	Dniestr River, Ukraine, Site 6	46°41'15"	30°26'21"	22.08.2006	M. O. Son
	Lake Mertvyj Turunchuk	46°25'00"	30°14'20"	04.05.2007	M. O. Son
	Spring entering to the Dniestr Liman	46°17'49"	30°07'58"	02.05.2007	M. O. Son
	Taganrog Bay of the Azov Sea, Taganrog City, Russia	47°12'49"	38°56'31"	08.06.2007	M. O. Son
	Turunchuk River (branch of Dniestr Delta), Site 1	46°27'21"	30°11'36"	29.05.2002	M. O. Son
Dreissena polymorpha andrusovi	Taganrog Bay of the Azov Sea, Ukraine	47°06'40"	38°03'52"	09.08.2004	M. O. Son
Dreissena polymorpha polymorpha	Pond in the mouth of the Baraboj River	46°12'24"	30°33'42"	05.09.2003	M. O. Son
	Baraboj Reservoir, Site 1	46°28'51"	30°20'29"	02.07.2006	M. O. Son
	Baraboj Reservoir, Site 2	46°28'54"	30°20'53"	02.07.2006	M. O. Son
	Small river entering to the Sukhoj Liman	46°20'52"	30°35'43"	18.07.2006	M. O. Son
	Lake Sasyk, Site 1	45°32'23"	29°38'51"	19.07.2002	M. O. Son
	Lake Sasyk, Site 2	45°34'28"	29°41'44"	05.07.2002	M. O. Son
	Danube-Sasyk Channel	45°33'13"	29°36'08"	29.04.2003	M. O. Son