

DREISSENA (D.) POLYMORPHA: EVOLUTIONARY ORIGIN AND BIOLOGICAL PECULIARITIES AS PREREQUISITES OF INVASION SUCCESS

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Abstract

The evolution of *Dreissena polymorpha* took place in changeable conditions in the successive series of Paratethys Great Lakes and Seas and their estuaries. Complicated intraspecific structure of species and sufficient divergence in environmental requirements among its subspecies allows *Dreissena polymorpha* to inhabit a variety of environmental conditions in its native area, the Ponto-Aralo-Caspian region. The only subspecies, *Dreissena p. polymorpha*, is known as an amphiatlantic invader in fresh and oligohaline waters of Europe and North America. Wide and fast dispersal and the successful establishment of this subspecies are facilitated both by biological peculiarities of the zebra mussel (e.g. unusual for freshwater bivalve mode of life, wide limits of environmental requirements, genetic polymorphism) and availability of man-mediated vectors.

1 Introduction

Dreissena polymorpha (Pallas, 1771): Type: Mollusca; Class: Bivalvia; Order: Cardiida Ferussac, 1822; Family: Dreissenidae (Andrusov, 1897); Genus: *Dreissena* Van Beneden; Subgenus: *Dreissena s. str.* (Synonyms: *Mytilus polymorpha* Pallas, 1771; *Dreissensia polymorpha* (Pall.) Andrusov, 1897)

Available natural and man-mediated vectors of invasion and similarity in environmental conditions of donor and recipient water bodies have promoted rapid dispersal of the zebra mussel. The species is a classic example of "neozoans" (Kinzelbach 1992). It has a remote marine ancestor and hence the success of its invasion to freshwater has been greatly facilitated by unusual biological peculiarities remaining from the species' "marine past". Long-term adaptation to oligohaline and freshwater conditions through the course of evolution in ancient series of the Paratethys Great Lakes and Seas (Zenkevich 1963; Dumont 1998), and their estuaries now succeeded by basins of the Ponto-Caspian region, is also a prerequisite of the success of invasion and establishment in target regions.

2 Origin of two invasive freshwater dreissenids

Dreissena polymorpha is a representative of the Caspian autochthonous faunal group (Mordukhai-Boltovskoi 1960, 1978; Zenkevich 1963). Palaeontological evidence leads to the conclusion that genus *Dreissena* has a polyphyletic origin. Modern representatives of the genus *Dreissena* originated from at least two branches of the genus *Congerina* (Baback 1983). Nevesskaya (1976) studied evolution of different species in genera *Dreissena* and *Congerina* and concluded that *Dreissena* originated from *Congerina* by "fetalization", i.e., by retaining of juvenile features (intact septum and absence of apophysis) of ancestral forms in adults of descendant species. First transitional forms

between *Congerina* and *Dreissena* were found in Late Miocene - Early Pliocene deposits in the Pannonian basin, in Later Maeotice deposits in the Dacian basin and Euxinian basins (Baback 1983), as well as in estuaries of the eastern Mediterranean part of Paratethys (Starobogatov 1994). The appearance of *D. polymorpha* is referred to Late Miocene (approx. 14 mya) or the transition from Miocene to Pliocene. It is suggested to occur along the northern margin of the range of the genus *Dreissena*, in estuarine portions of rivers draining into Paratethys Lakes-Seas. Geological evolution of the region was characterised by a series of transgressive and regressive stages and changes of salinity from fresh water up to 20-25 PSU (Starobogatov 1994; Dumont 1998). The species invaded successively all accessible areas of the lacustrine parts of the Paratethys, where it diverged into a range of endemic species and subspecies, and colonised various habitats along main environmental gradients (e.g. salinity, depth, type of substrate; Starobogatov 1994). Regressive and transgressive phases in the geological history of Paratethys created conditions of temporary isolation and connection between the basins, which facilitated the adaptive radiation of *Dreissena* within basins, and exchange of species and subspecies between basins during latter phases. One more invasive species *Dreissena* (*Pontodreissena*) *bugensis* (Andr.) is thought to have evolved in the Euxinian part of the eastern Paratethys. It has evolved rather recently (less than 1 mya in the freshened Chauda lake; salinity < 4 PSU) and later in estuaries of the succeeded Neo-Euxinian Basin (Starobogatov 1994). Until the 1960s, *D. bugensis* distribution was restricted to a few rivers and estuaries of the Black Sea basin (Zhuravel 1967). Since the 1990s *D. bugensis* is known from the Volga River and the northern part of the Caspian Sea (Antonov 1996; Orlova et al. 1998). It was reported from the North American Great Lakes some years earlier, in 1989 (Domm et al. 1993).

3 Native range and intraspecific structure

The range of *D. polymorpha* was in early Holocene limited to the Black, Azov, Caspian and Aral Seas, estuaries and lower and middle reaches of the Ponto-Aralo-Caspian rivers. In that time the northern margin of its range was restricted by a line from Mogilev, Kursk, Voronezh and Nizhniy Novgorod to Izhevsk (Fig. 1) (Starobogatov & Andreeva 1994). Meanwhile, during the Mindel-Riss interglaciation, this margin was situated far northward. *D. polymorpha* is considered to be a species that is extremely variable both in morphology and habitat requirements (Karpevich 1955). Currently, the species comprises three living subspecies (the fourth one, *D. p. obtusicarinata* became extinct due to the salinity increase in the Aral Sea in the 1980s) and several varieties, all of them characterised by slightly different environmental requirements. Therefore, the species' range covers both fresh, oligohaline and particularly mesohaline conditions along the native area. For example, in the Caspian Sea basin *D. p. polymorpha*, the most widespread subspecies, occurs in the Volga River and its delta. In the Northern Caspian Sea it inhabits a freshwater zone mainly in the north-western part of the sea. The subspecies is also known from the oligohaline zone of the central and western parts of the Northern Caspian Sea.

Within this subspecies, four main varieties can be distinguished: *D. polymorpha* var. *typica* Karpevitch, inhabiting now fresh waters lakes, rivers and reservoirs of Europe and North America; *D. p. var. fluviatilis* (Locard), occurring in branches of the upper

part of the Volga delta, in conditions of fast stream and high turbidity of water; *D. p.* var. *tschapurica* Karpevitch occurs in freshwater or slightly oligohaline conditions of the northern Caspian Sea in the transition area, where water masses of Volga River are mixed with water masses of the Caspian Sea. Individuals from brackish water conditions (*D. p.* var. *marina* Pallas, a transitional form between *D. p. polymorpha* and the next Caspian subspecies *D. p. andrusovi* (Andr)) are found in offshore areas of the northern Caspian Sea, at salinity as high as 3-8 PSU. This subspecies occurs mostly in the eastern part of the northern Caspian Sea up to 7-8 PSU. The third subspecies *D. p. aralensis* (Andr.) is peculiar for lower portions of rivers, draining into the Aral Sea and inhabits small lakes along the sea shore (Mordukhai-Boltovskoi 1974).

4 Shell morphology

The shell of *Dreissena polymorpha* has a typical heteromyarian form with great reduction of the anterior territory and great elongation of the opisthodontic ligament. Ventrally one or both valves bear the byssal notch. The shell is triangle-shaped from anterior view with flattened ventral surface. There is a sharp shoulder ridge ("carina") located ventrolaterally on each valve. Internally there is a well-marked pallial line with large insertions for the posterior adductor and posterior byssal retractor and, correspondingly, small insertions for anterior muscles. These are situated on a conspicuous vertical shelf, also called septum, which occupies the umbonal region. The shell is ordinary coloured. Patterns are diverse and can change in the same mollusc from one growing season to the next (Biochino 1994; Marsden et al. 1996).



Figure 1. Holocene (solid line) and recent (dashed line) range of *Dreissena p. polymorpha* dispersal in Europe; main routes of invasions (dotted lines); relatively recent (1980s-1990s) records (asterisks).

5 Biological peculiarities of *Dreissena p. polymorpha* as a prerequisite of invasion success

5.1 LIFESTYLE AND REPRODUCTION

Dreissena is a sessile byssate bivalve able to inhabit fresh waters, where the niche of sessile filter feeders was vacant before invasion. Occupying this niche *Dreissena* forms dense settlement in all accessible zones and on all kinds of substrates in fresh and oligohaline parts of invaded water bodies. Due to this attached mode of life it can be transferred by shipping as a member of fouling communities on ships' hulls.

Having a remote marine ancestor *Dreissena* has a life cycle with a pelagic larval stage similar to that of marine bivalves. These stages are termed preveliger, D-stage veliger, post-D-stage veliger, and plantigrade. The presence of free-living stages promotes both remote dispersal in ballast water communities between regions as well as rapid colonisation of accessible habitats within and between localities in target water bodies. *D. polymorpha* is a gamogenetic species with equal occurrence of males and females in populations. The age and body length for maturation (at an age of 0+ or 1+) depend on temperature conditions and the time of the year of the juveniles' settlement in each locality. The zebra mussel in Europe is characterised by annual reproduction, with the exception of the most northern populations. *Dreissena* is an r-strategist; mature molluscs are known to produce over 1 million eggs or 10 billion sperm (Sprung 1991). Early maturation and high generative production are two more prerequisites for its invasion success.

Temperature and salinity are the most important environmental abiotic factors limiting the recruitment and development of *D. polymorpha*. The spawning period is extended from late spring to early autumn at temperatures above 12°C. Duration and the time of the year for the breeding season are highly variable and dependant on the geographical position of the locality (Lvova & Makarova 1994; Lvova et al. 1994). Hence further dispersal and establishment of *Dreissena* northward is limited by reproduction, which is successful only above mean summer temperatures of 12°C.

5.2. HABITAT PREFERENCES

The zebra mussel occurs usually on hard and mixed bottoms. At soft and silty bottoms it can also overgrow empty shells and live molluscs of the same and other species, as well as pieces and debris of other hard substrata. Vertical distribution of the species depends first of all on the availability of hard substrata and accessible food resources. The mussel can live from shoreline down to tens of meters. Its maximal depth of occurrence registered for European waters is 60 m (Grim 1971). Maximum abundance is at 1-5 m depth (Liakhnovich et al. 1994). In water bodies with winter ice-cover the distribution of *Dreissena* toward the shoreline is limited by ice abrasion, in lakes and reservoirs it is often limited by water level fluctuations (Liakhnovich et al. 1994). As a rule, *Dreissena* lakes are mesotrophic with relatively high pH, moderate alkalinity, and moderate amounts of dissolved mineral salts in the water (Liakhnovich et al. 1994).

5.3 OTHER ENVIRONMENTAL REQUIREMENTS

5.3.1 Salinity, Ca^{++} , and pH

D. p. polymorpha occurs in freshwater and oligohaline conditions, its expansion to more saline waters ($> 2\text{-}4$ PSU) is restricted by salinity tolerance of larval stages (Kilgour et al. 1994). Similar to other brackish water euryhaline bivalves, the European zebra mussel is capable of hyperosmotic regulation in range from freshwater to 2 PSU (Karpevich 1952). In experiments with step-by-step increase of salinity, the adults (e.g., the Caspian and the Baltic Sea populations) tolerated salinity up to 12-15 PSU (Orlova et al. 1998). In freshwater Belorussian lakes (524 totally studied) *Dreissena* occurs in a range of 164-388 mg l^{-1} total dissolved solid concentrations. It is absent in lakes with values below 64 mg l^{-1} (Liakhnovich et al. 1994). Among inorganic ions calcium is important for *Dreissena* dispersal and early development. *Dreissena* is less tolerant to decrease of calcium concentration in water and low pH than other freshwater molluscs (Unionacea, Sphaeriidae). Minimum Ca^{++} concentration in lakes inhabited by *Dreissena* is < 28.3 mg l^{-1} Ca^{++} at pH 7.3 in Europe, while in North America it occurs at > 15 mg l^{-1} Ca^{++} and forms dense populations at > 25 mg l^{-1} (McMahon 1996). Rearing requires 12 mg l^{-1} , while minimum Ca^{++} concentration for successful development of veliger is 34 mg l^{-1} (Sprung 1987). So far limited dispersal of *Dreissena* in low mineralised lakes and reservoirs of Europe, as well as in dystrophic lakes, may be explained by calcium limitation. Together with ionic composition and dissolved solids concentration, pH is one more important limiting hydrochemical factor, restricting *Dreissena* dispersal in European lakes. The study of 524 Belorussian lakes (pH 3.3-9.6) revealed *Dreissena* occurrence in lakes with pH 6.7-8.9 only (Liakhnovich et al. 1994). In North America the mussel has colonized areas with pH 7.0-9.0; successful development of larvae occurs at pH 7.4-9.7 (Bowman & Bailey 1998).

5.3.2 Temperature and oxygen

The species is considered as low boreal by its origin (Starobogatov 1994) and can thus inhabit accessible waters in temperate climatic zones. Temperature of 0°C is the lower and $30\text{-}32^{\circ}\text{C}$ the higher limit for adult survivorship. Upper limit for cells is $40\text{-}42^{\circ}\text{C}$ (Shkorbatov et al. 1994). As mentioned above 12°C is the lower limit for recruitment.

Capacity to tolerate low oxygen conditions varies strongly between different populations (Shkorbatov et al. 1994). In general *D. polymorpha* can be considered as a species relatively resistant to short-term hypoxia, having the critical saturation level as low as 25-26% at 20°C . Individual mussels are able to tolerate experimental anoxic conditions at 20°C for 3-6 days, while the increase of temperature up to 25°C rapidly accelerates the mortality of mussels (Shkorbatov et al. 1994). In nature, however, the distribution of the zebra mussel is usually limited to littoral and sublittoral zones, and slopes of riverbeds, where oxygen conditions are appropriate.

5.3.3 Exposure to air

Dreissena from different European populations can survive in air, in conditions of high humidity (80-100%) for 3-5 days (Shkorbatov et al. 1994). Consequently, it cannot tolerate recession of the shoreline longer than for this period. Therefore the distribution of *Dreissena* toward the shoreline in lakes and reservoirs is limited by water level fluctuations.

tuations, that do not exceed 0.5 m in the majority of lakes; in reservoirs they can reach 2 m or more. Newly settled individuals only contribute to temporary *Dreissena* settlements in the zone of water level fluctuations (Liakhnovich et al. 1994) in lakes and reservoirs, while populations with normal age-size structure occur deeper.

5.4 FEEDING AND GROWTH

Dreissena polymorpha is a polyphagous seston-feeder. It feeds on particulate organic matter with size 1-500 μm . Content of food consumed is close to the content of seston (Yablonskaya 1967, 1969). Food selectivity is provided by the sorting role of gills and labial palps. Besides of useless inorganic particles *Dreissena* usually avoids eating sticky-looking diatoms, big-sized colonies of Chlorophyta and Cyanophyta (Vanderploeg et al. 1995), emulsions of organic liquids etc. At high concentrations of seston only 10% of the suspension filtered by *Dreissena* was found in its stomach (Mikheev 1964).

Diurnal diet of *Dreissena* depends on the size of molluscs, nutritional value and concentration of seston, and abiotic characteristics of the environment (Mikheev 1964). Diurnal diet can be calculated using the balance equation:

$$C=1/U*(P+R),$$

where C = diurnal diet; P = production; R = rate of metabolism ($R=(0,1396W^{0,63})*24$ (mgO_2 ind h^{-1}), where W is wet weight (g) (Alimov 1981).

When the concentration of seston does not differ sufficiently from natural values (3-15 mg l^{-1}) and the size of particles is 4-50 μm (Mikheev 1967), then the daily diet can be estimated as the rate of filtration multiplied by seston concentration:

$$C=(F*c)*12,$$

where c = is seston concentration (mg l^{-1}); 12 = number of hours per days, when *Dreissena* is usually actively filtering.

Efficiency of assimilation varies from 0.5 to 0.6, being most often close to 0.6 (Alimov 1981). Filtration normally occurs at temperature range 5-30°C (Kondratiev 1962), and pH 8-9 (Morton 1971). Filtration rate is strongly dependent on body weight and can be described by the equation:

$$F=85.5W^{0.6} \text{ (Alimov 1981),}$$

where F= rate of filtration (water clearance) expressed in ml ind h^{-1} ; W = wet weigh of body (g).

Linear growth of *Dreissena polymorpha* can be described by Betralanffi equation:

$$L(t) = L_{\infty} e^{-kt}$$

where L(t) = length to time t, L_{∞} = theoretically maximum length (mm), k = constant of growth (1/year), e-basic of natural logarithm.

Parameters of linear growth for different European populations are calculated by Ali-mov (1981). By his results L_{∞} varies from 29 to 51 mm; Measured L_{\max} from 23.2 to 42 mm, k varies from 0.122 to 0.492 1/year; calculated maximum age varies from 4.2 to 11 years.

5.6 GENETIC VARIABILITY

The review of the data collected has shown high level of genetic variability in the zebra mussel populations both in Europe and North America. The results of the analyse, estimated by the allozyme electrophoresis method (Marsden et al. 1996), confirm that the zebra mussel is able to adapt to a wide variety of environmental conditions with no loss of genetic diversity. Obviously no bottleneck effect is present trough the process of *Dreissena* ntroductions. This peculiarity of invasion is characteristic for molluscs extending their range via free-living planktonic larvae (in ballast water) and/or by repetitive transfers when founder population consists of large number of individuals.

5.7 SUCCESS AND LIMITATION OF *DREISSENA POLYMORPHA* INVASION

Available natural and man-mediated vectors and similarity of environments in donor, transitional and target areas have promoted rapid expansion of the Ponto-Caspian *Dreissena polymorpha* northward at least twice during the known history of the species. According to Kinzelbach (1992) the first event occurred naturally during the Mindel-Riss interglaciation. The history of that natural expansion was the following: Following the rising water level in the Ponto-Caspian rivers *D. polymorpha* colonized the middle and upper portions of them. When the connection appeared between the ancient Pripiat' and Bug Rivers it invaded the Vistula River. From there the zebra mussel continued expansion as far as to the Netherlands and England via interglacial primary stream valleys. In the beginning of the Wurm glaciation the species recessed back to the Ponto-Caspian region.

The second unremitting natural and man-mediated expansion of *D. polymorpha* took place in Europe beginning in the early 19th century. By the end of the century the species colonized most of the inland waters of West and Central Europe and estuaries of the Baltic Sea and the North Sea. For the second half of the 20th century it was reported as the dominant species in bottom assemblages of reservoirs constructed on large rivers in Eastern Europe and was also found in alpine lakes. By 1986 it was recorded in the eastern Gulf of Finland and by 1994 in Ireland and then, in 1995, along the Finnish coast (Nowak 1971; Kinzelbach 1992; Starobogatov Andreeva 1994; Kharchenko 1995; Valovirta & Porkka 1996; Olenin et al. 1999).

Biological peculiarities of the species are the most important prerequisites of either success of transfer or success of the final step of the invasion process the establishment of a population in the target locality. The attached mode of life and free-living stage (remote marine origin) broadens the ways of introduction of *Dreissena*. It can be transferred both in larval (ballast water) and adult (attached to ship bottoms) stages. Invading fresh water lakes, rivers, artificial water-bodies and oligohaline marine environment (e.g. the Baltic Sea) the zebra mussel becomes the dominant species in fouling communities. In some cases it forms communities of Ponto-Caspian type together with other

Ponto-Caspian invaders (Riccardi & MacIsaac 2000). Being an r-strategist and producing annually numerous larvae, which are able to fast dispersal with currents, the zebra mussel colonises fast all accessible habitats within target localities. As *Dreissena* originates from habitats that had wide temporal and spatial variations of environmental characteristics throughout their geological history (first of all salinity, water level and temperature), it can establish populations in a wide range of freshwater and oligohaline habitats in temperate climates.

In both range expansion events mentioned above, whether they are natural or human-mediated, the biological peculiarities of the species are also defining the limits of potential dispersal. Having relatively vulnerable free-living stages in the life cycle and weaker osmoregulatory capacity (Dietz et al. 1994), than many of native freshwater bivalves, the distribution of *Dreissena* is limited by low concentration of dissolved mineral salts in water, especially by low calcium concentration, as well as by low pH values. Temperature requirements are also limiting expansion northward by summer isotherm above 12°C. Being active sessile filter-feeder *Dreissena* requires mesotrophic conditions in the habitat with propitious concentrations of seston.

6 Conclusions

The zebra mussel is a classic case of "neozoans", with a remote marine ancestor. So far the success of its invasion to freshwater has been facilitated, first of all, by unusual biological peculiarities of the species received from "marine past", and secondly by long-term adaptation to oligohaline and freshwater conditions, through the course of evolution in ancient series of the Paratethys Great Lakes – Seas and their estuaries succeeded now by basins of Ponto-Caspian region.

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