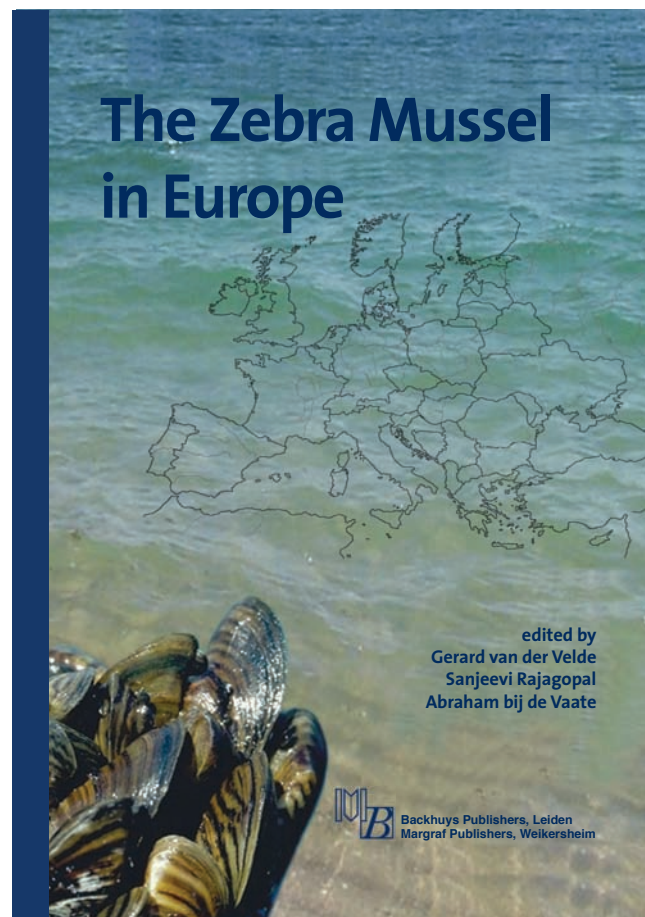


Chapter 4

A PERSPECTIVE ON GLOBAL SPREAD OF *DREISSENA POLYMORPHA*: A REVIEW ON POSSIBILITIES AND LIMITATIONS

Bart J. A. Pollux, Gerard van der Velde and Abraham bij de Vaate

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4. A perspective on global spread of *Dreissena polymorpha*: a review on possibilities and limitations

Bart J. A. Pollux, Gerard van der Velde and Abraham bij de Vaate

Abstract

The zebra mussel is a successful invasive freshwater bivalve that has colonised large parts of Europe and North America. Since in most cases its arrival has had severe economic and ecological consequences, attempts have been made to predict the further spread of the zebra mussel within Europe and especially North America. The aim of this study was to determine the possibilities and limitations for a global range expansion of the zebra mussel based on its biology, ecology and physiology. We propose that a range expansion by the zebra mussel is restricted to fresh- and brackish waters (with salinities ranging 0.007-14 ‰) within the temperature range of the 10°C isotherm of the coldest month and the 14°C isotherm of the warmest month where the environmental conditions meet the requirements for simultaneous reproductive activity within populations. The potential expansion is further most likely restricted to the northern hemisphere where mean dissolved calcium concentrations exceed the 12-15 mg l⁻¹ threshold necessary for egg development and shell growth. Within these regions, ports and harbours within 3-5 weeks of cross-oceanic journey are likely to be colonised in the future.

Introduction

The zebra mussel, *Dreissena polymorpha* (Pallas, 1771), is a successful invasive bivalve that can be found in many temperate fresh- and brackish waters in Europe and North America. Zebra mussels often form dense aggregations that can reach densities of up to 700,000 m⁻². It is this tendency that has led to many adverse socio-economic and ecological consequences after its invasion into new areas (Roberts, 1990; Mackie, 1991; Haag et al., 1993; Ludyanskiy et al., 1993; Nalepa and Schloesser, 1993; Van der Velde et al., 1994; Hushak, 1996; Schloesser et al., 1996; Strayer et al., 1999; Pimentel et al., 2000). Because of these severe economic and ecological consequences following an introduction of the zebra mussel, models were developed to predict its further spread in North America. These were based on substrate availability (Mellina and Rasmussen, 1994), temperature (Strayer, 1991; Allen and Ramcharan, 2001; Drake and Bossenbroek, 2004) and water chemistry parameters such as calcium concentration and pH (Neary and Leach, 1992; Ramcharan et al., 1992b; Mellina and Rasmussen, 1994; Hincks and Mackie, 1997; Allen and Ramcharan, 2001; Drake and Bossenbroek, 2004). Surprisingly, however, despite the obvious capabilities of the zebra mussel to

invade new areas, no attempts have been made to identify potential areas outside of Europe and North America that are suitable habitats for future invasions. Invasions by the zebra mussel (as by many other invasive species) typically follow a multi-step process (Fig. 1) and a deeper understanding of each of these steps is required in order to be able to predict further range expansions by the zebra mussel. Here, we present a thorough review, combining information about its historical range expansion, dispersal mechanisms, biological and ecological features, and physiological requirements, to determine the possibilities and limitations of a global range expansion.

Range expansion in Europe

Representatives of the genus *Dreissena* arose in the late Miocene (Morton, 1970; Kinzelbach, 1992). Nuttall (1990) and Kinzelbach (1992) provide maps of the distribution of this genus during that period. During the Miocene-Pliocene period (23.8 my 1.8 my) *Dreissena* occurred in Central Europe and northern Asia along the Volga River and as far east as the Aral Sea and the Euphrate River (Stanczykowska, 1977; Morton, 1993). The Pleistocene epoch (1.8 my

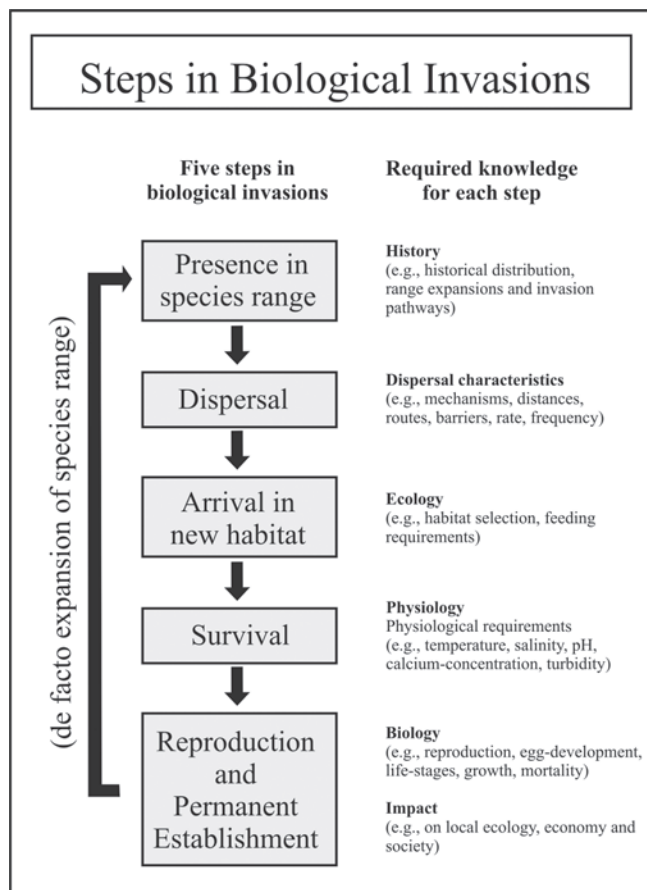


Figure 1. Multi-step process showing the five stages during the spread of the zebra mussel (*Dreissena polymorpha*). For each step, the knowledge required for understanding and predicting potential range expansions is given.

10,500 y) that followed was characterised by a series of glacial periods, averaging about 100,000 years, alternating with interglacial periods lasting 10,000 to 20,000 years. During this Pleistocene period the distribution of *Dreissena* was reduced considerably to small areas including the slightly brackish areas of the Caspian and Aral seas, the freshwater areas of the Azov and Black seas and the Balkan Peninsula (Morton, 1993). Other authors suggested that the zebra mussel did not disappear totally from Europe but survived in a few isolated refuges such as Schleswig-Holstein, Ochryda Lake and some waters of Thuringia and the Hungarian lowland, but these theories cannot be supported by available evidence (Stanczykowska, 1977; Kinzelbach, 1992). The present epoch, the Holocene, began 10,500 years ago when the last glacial period ended and the ice sheets had retreated to the Arctic. For a long time during this post-glacial period the zebra mussel remained confined to the northern Black Sea region. But approximately 300 years ago this situation changed when the zebra mussel started to establish outside the Ponto-Caspian region (Stanczykowska, 1977).

The zebra mussel's pattern of dispersal can be inferred from records of first observation on the occurrence of (prob-

lems caused by) *D. polymorpha* (Kinzelbach, 1992; Van der Velde et al., 1994; Table 1). It was first found in the Ural River and described by Pallas in 1771 (Stanczykowska, 1977). According to most authors the dispersal started from the Black and Caspian seas and was directed northward through the Dnieper and Volga tributaries, respectively (Stanczykowska, 1977; Ludyanskiy et al., 1993; Bij de Vaate et al., 2002). Notably, the beginning of the spread of the zebra mussel during the 18th century coincided with a time when riverine shipping trade increased, and canals were built linking different navigable rivers systems. In 1775 a canal was built linking the Dnieper and Zapadnyi Bug rivers, allowing access from the Black Sea region and in 1804 the Oginskij Canal was completed linking the Dnieper and Newman rivers and the Dnieper and Zapadnaya Drina rivers, subsequently leading to the establishment of zebra mussels in the Curonian Lagoon in the Baltic Sea (Orlova et al., 2000; Minchin et al., 2002a). From ports in the Baltic region, its dispersal was directed further north-eastward along the coasts of the Baltic Sea, to the Neva estuary (1980s) and along the Finnish coast (1995) (Valovirta and Porkka, 1996; Orlova et al., 2000; Orlova and Panov, 2004); and westward to north-western Europe (Great Britain 1824, Netherlands 1826, Germany 1830, Copenhagen 1840s), attached to imported timber transported overseas by ships (Kerney and Morton, 1970). From here, its dispersal was directed further northward to Sweden (1920s), and south-eastward into central Europe by upstream transportation of adult mussels attached to the hulls of boats (Kinzelbach, 1992; see Table 1). Its dispersal even further southward may initially have been impeded by the lack of river connections and by mountain ranges like the Alps and Pyrenees, which remained barriers for the species. However, with the increasing popularity of recreational water sports zebra mussels have been transported to high alpine lakes (attached to recreational vessels transported on trailers), leading to the colonization of the Lake Geneva, Zurich and Constance (Switzerland) around the 1960s. The subsequent transportation of craft to and from high alpine lakes resulted in the relatively late colonisation of South European countries, such as Yugoslavia (1970s), Italy (1970s) and Spain (2001). The transportation of second-hand craft on trailers is also held responsible for the colonisation of the isolated island of Ireland in 1997 (Pollux et al., 2003). In 1986, the zebra mussel was first discovered in North America, where it most likely arrived with the ballast water from an ocean-crossing vessel (Hebert et al., 1989). After its introduction it spread rapidly to major rivers and isolated water bodies east of the Rocky Mountains. Today, the zebra mussel occurs in many lakes, canals and rivers throughout Europe, the eastern part of Canada and the United States, and the European part of the former USSR.

Table 1. First recorded discoveries, in chronological order, of the zebra mussel (*Dreissena polymorpha*) in Russia, Europe and the United States. The likely vectors of introduction have been given for each introduction (vector numbers corresponding to the numbers presented in Table 2). If information about the dispersal vector was not available, suggestions were given for possible vectors of introduction.

Year	Location (Country)	Source	Vector
18th century			
1769	Ural River (Russia)	Ludyanskiy et al. (1993)	14
1771	Volga River (Russia)	Ludyanskiy et al. (1993)	14
1771	Caspian Sea (Russia)	Ludyanskiy et al. (1993)	—
1794	Danube River (Hungary)	Ludyanskiy et al. (1993)	14
19th century			
1800	Dnieper River (Russia)	Ludyanskiy et al. (1993)	14
1804	Curonian Lagoon (Baltic region)	Orlova et al. (2000)	
1824	London (Great Britain)	Kerney and Morton (1970)	16
1826	Rotterdam Harbour (The Netherlands)	Kerney and Morton (1970)	16
1830	Hamburg (Germany)	Kerney and Morton (1970)	14
1830s	Lower reaches of Rhine River (Germany)	Neumann et al. (1993)	14
1831	Goole dock, Yorkshire (Great Britain)	Kerney and Morton (1970)	16
1834	Union canal, Edinburgh (Great Britain)	Kerney and Morton (1970)	14
1835	Meuse River (France)	Kinzelbach (1992)	14-16
1838	Elbe River (Germany)	Minchin et al. (2002)	14-16
1840s	Middle reaches of Rhine River (Germany)	Kinzelbach (1992)	14
1840	Mannheim harbour (Germany)	Kinzelbach (1992)	16
1840	Copenhagen (Denmark)	Kerney and Morton (1970)	14-16
1840	Pärnu Bay (Estonia)	Minchin et al. (2002a)	
1842	Exeter canal, Exmouth (Great Britain)	Kerney and Morton (1970)	14
1845	Dvina River (Russia)	Ludyanskiy et al. (1993)	14
1845	Daugava River (Russia)	Ludyanskiy et al. (1993)	14
1847	Moscow River (Russia)	Ludyanskiy et al. (1993)	14
1855	Don River (Russia)	Ludyanskiy et al. (1993)	14
1855	Main River (Germany)	Thienemann (1950)	14
1855	Seine River (France)	Kinzelbach (1992)	14-16
1860s	Upper reaches of River Rhine (Germany, Switzerland)	Jantz and Schöll (1998)	14
1863	Loire River (France)	Kinzelbach (1992)	14-16
1865	Rhône River (France)	Kinzelbach (1992)	14-16
1866	Garonne River (France)	Kinzelbach (1992)	14-16
1868	Upper Danube River	Thienemann (1950)	14
1875	Kama River (Russia)	Ludyanskiy et al. (1993)	14
20th century			
1920s	Sweden	Minchin et al. (2002a)	16
1932	Lake Balaton (Hungary)	Kinzelbach (1992)	15-16
1936	Lake IJsselmeer (The Netherlands)	Smit et al. (1993)	1, 13
1940s	Scandinavia	Ludyanskiy et al. (1993)	16
1960	Lakes Geneva, Zurich and Constance (Switzerland)	Kinzelbach (1992)	15
1969	Lake Garda (Italy)	Annoni et al. (1978)	15
1970s	Po River (Italy)	Giusti and Oppi (1972)	15
1970s	Yugoslavia	Ludyanskiy et al. (1993)	15
1980s	Neva estuary (Gulf of Finland, Baltic Sea)	Orlova et al. (2000, 2004a)	16
1986	Lake St. Clair (North America)	Hebert et al. (1989)	12
1988	Lake Erie (Canada)	Ludyanskiy et al. (1993)	1, 13-15
1989	Lake Michigan (United States)	Ludyanskiy et al. (1993)	1, 13-15
1989	Lake Ontario (United States)	Ludyanskiy et al. (1993)	1, 13-15
1990	Lake Superior (United States)	Ludyanskiy et al. (1993)	1, 13-15
1990	Lake Huron (United States)	Ludyanskiy et al. (1993)	1, 13-15
1990	Hudson River (United States)	Ludyanskiy et al. (1993)	1, 13-15
1991	Illinois River (United States)	Ludyanskiy et al. (1993)	1, 13-15
1991	Mississippi River (United States)	Ludyanskiy et al. (1993)	1, 13-15
1995	Further northward along the Finnish coast	Valovirta and Porkka (1996)	12,16
1996	Riga Bay (Latvia)	Minchin et al. (2002a)	12,16
1997	Lough Derg and Lower Shannon (Ireland)	McCarthy et al. (1997)	16
21st century			
2001	Ebro River (Spain)	Araujo and Álvarez Halcón (2001)	16

Table 2. Potential natural and human-mediated dispersal mechanisms, and potential direction of dispersal, of larval and adult life stages of the zebra mussel (*Dreissena polymorpha*).

Life stage	Direction	Natural vectors	Human-mediated vectors
Larvae	Downstream	1. Passive dispersal via currents and other hydrodynamic processes	9. Transfer of volumes of water containing larvae (e.g. ships ballast water)
	Upstream	2. Accidental entanglement onto more mobile animals (e.g. fishes, ducks)	10. Transfer of volumes of water containing larvae (e.g. ships ballast water)
	Overland	3. Accidental entanglement onto more mobile animals (e.g. amphibians, turtles, water-fowl, mammals)	11. Transfer of volumes of water containing larvae (e.g. retention of larvae in crevices of recreational craft, transportation of fishes, bait bucket water)
	Overseas	4. –	12. Transfer of volumes of water containing larvae (e.g. ships ballast water)
Adults	Downstream	5. Passive dispersal of adults attached to solid objects (e.g. driftwood and dislodged macrophytes)	13. Transportation of solid objects with adults attached (e.g. attached to hull, anchor chain, rudder, etc. of boats)
	Upstream	6. –	14. Transportation of solid objects with adults attached (e.g. attached to hull, anchor chain, rudder, etc. of boats)
	Overland	7. –	15. Transportation of solid objects with adults attached (e.g. recreational boats, fishing fykes, navigation buoys, bait buckets, nets)
	Overseas	8. –	16. Transportation of solid objects with adults attached (e.g. trade products such as timber wood or imported second hand craft)

Causes of invasion

Natural mechanisms of dispersal

The natural strategy of dispersal could best be described as a ‘*passive drift strategy*’, where the main transportation is the passive transportation by hydrodynamic processes to downstream areas (Table 1).

Larvae. The passive advective transportation of free-swimming larvae is the most important mechanism of natural dispersal. The zebra mussel is one of the few freshwater mussels that possesses this effective mechanism of dispersal (Jenner and Mommen, 1985). The zebra mussel larvae have only limited swimming capabilities and have to rely on currents and other hydrodynamic processes for their dispersal. Therefore their dispersal in this stage is restricted to downstream transportation in rivers and ‘horizontal’ transportation throughout lakes. Studies in river systems have shown that in this way larvae can be transported downstream over considerable distances (Stoeckel et al., 1997; Jantz and Neumann, 1998; Schneider et al., 2003). The spread of larvae by accidental entanglement to animals (e.g., amphibians, fur-bearing mammals and ducks) is not likely to play an important role in the dispersal, because of the high mortality rates

of larvae during atmospheric exposure experienced during animal-mediated transportation (Carlton, 1993; Johnson and Carlton, 1996; Johnson and Padilla, 1996).

Adults. Adult zebra mussels have a benthic life-style. They live attached to hard, submerged substrates by means of their byssus threads. As a result, natural spread during this stage is necessarily limited. Reported transportation of adult mussels is restricted to the incidental downstream transportation attached to driftwood or dislodged macrophytes (Johnson and Padilla, 1996) as well as the accidental entanglement (e.g., in the fur of aquatic mammals or onto the legs of birds) and attachment (e.g., to the hard exterior of turtles and crayfish; Carlton, 1993) onto more mobile animals. But these ‘accidental transportation vectors’ do not contribute a great deal to the dispersal of the species (Carlton, 1993).

Human-mediated mechanisms of dispersal

Over the last decades the number of biological invasions has increased at an accelerating rate (Cohen and Carlton, 1998). Especially the unintentional transportation of species has led to increasing invasion rates as international traffic

became more important. Moreover, technological advances allow greater speed of the transportation vectors (e.g. ships, planes, trucks, etc.), reducing transit time of the organisms leading to higher survival rates during transportation (Everett, 2000). As for many other biological invaders, human-mediated dispersal has been held responsible for the rapid range expansion of the zebra mussel over the last few centuries (Tables 1 and 2). The human-mediated dispersal of the zebra mussels could be characterised as a ‘hitch-hikers strategy’. The biological features of the zebra mussel enable larvae and adults to hitch-hike on human related means of conveyance and some consider the potential human-mediated dispersal of the zebra mussel virtually limitless (Carlton, 1993).

Larvae. Zebra mussels have a free-swimming larval stage lasting approximately 2-5 weeks (Sprung, 1989). This free-swimming stage allows larvae to be taken in with ship’s ballast water and be transported to upstream and overseas areas. This has proven to be an extremely effective mode of long-distance transportation, which allowed the colonisation of other continents (North America in 1986). Johnson and Padilla (1996) further report on the overland transportation of larvae retained in crevices of recreational boats. According to them larvae can stay alive at least 8 days in such ‘pools’ (see also Johnson and Carlton, 1996). Basically, any transportation of large volumes of water can be considered as possible vectors of larval transportation (e.g., water used in transport of fish for stocking programs, bait bucket water, water released from aquariums, water taken up and discharged between lakes and rivers by fire trucks; Carlton, 1993).

Adults. The production of byssus-threads allows adult mussels to attach themselves onto the hull, anchor chain, rudder, etc., of ships allowing passive upstream dispersal in rivers. This way, zebra mussels were able to leave their confinements of the Ponto-Caspian Seas (Kerney and Morton, 1970). Moreover, zebra mussels can attach themselves to any hard substrate, which can then be exported to overseas areas. This way, the zebra mussel was introduced to the United Kingdom (1824) and the Netherlands (1826), with imported timber from the Baltic region (Kerney and Morton, 1970; Bij de Vaate et al., 2002). After introduction to North America another mechanism of dispersal became apparent: the overland transportation of adult mussels attached to recreational boats (or to material snagged by the anchor or boat-trailer such as aquatic plants, woody debris, ropes, etc.). This enabled the colonisation of isolated lakes and ponds that were frequented by leisure boats (Carlton, 1993; Johnson and Carlton, 1996; Johnson and Padilla, 1996) and the Island of Ireland by imported second-hand boats from the United Kingdom (Minchin and Moriarty, 1998a; Pollux et al., 2003). Notably, however, the transportation of attached zebra mussels can essentially happen via any solid object that is transported between water bodies (i.e., fishing equipment, fykes, cages, nets, buoys, bait buckets; Carlton, 1993).

Alteration of habitats

One way in which human-mediated habitat alterations can lead to biological invasions is by the uplifting of physical barriers. The construction of canals for example, connecting rivers, lakes and even complete catchments allows the transportation of larvae and adult mussels to areas that were formerly inaccessible (Kinzelbach, 1992; Van der Velde et al., 2000; Bij de Vaate et al., 2002). The clearest example in Europe is the construction of the Main-Danube channel in 1992. This enabled many Ponto-Caspian species to reach North West European waters and mingle with the native species (Van der Velde et al., 2000; Bij de Vaate et al., 2002).

A second way in which human-mediated habitat alterations can lead to biological invasions is by changing formerly unsuitable habitats into suitable habitats (habitat modification). Alterations in water quality, such as pollution, can have a profound effect on local communities by depressing populations of previously abundant species. This will result in new available niches that can be re-occupied, allowing the rise of new opportunistic species that are more tolerant for the new environmental conditions (Lee and Bell, 1999). This appears to have happened in European rivers when water-chemistry changed from fresh- to slightly brackish water due to increased discharges of industrial, agricultural and domestic sewage and potassium and browncoal mines (Den Hartog et al., 1989; Lee and Bell, 1999). In the Rhine River this resulted in the rise of brackish-water tolerant invaders, among which was the zebra mussel (Van den Brink et al., 1991, 1993). Another example of an alteration in water chemistry that led to colonization by the zebra mussel can be found in the Netherlands. In the 20th century several estuaries in the Netherlands (Lake IJsselmeer in 1932, 3,500 km² and Lake Volkerak-Zoommeer in 1987, 60 km²) were converted into freshwater lakes by damming them from the sea (Smit et al., 1993). Immediately after the damming chloride concentrations decreased rapidly from 6 and 10 g l⁻¹, respectively, to less than 1 g l⁻¹ in both Lakes (Havinga, 1954). The damming resulted in the creation of an enormous fresh- to brackish-water habitat suitable for the zebra mussel and colonization quickly followed (after 4 years in Lake IJsselmeer and 1-2 years in Lake Volkerak-Zoommeer; Van Benthem-Jutting, 1954; Smit et al., 1993).

Biology Reproduction

Dreissena polymorpha is dioecious and reaches sexual maturity at a shell length of 8 to 10 mm. The soft tissue body weight and gonad development follow a distinct seasonal cycle (Borcherding, 1991; Jantz and Neumann, 1998; Fig. 2a). Gametogenesis starts during the winter when water temperatures decrease below 8 to 10°C. The increase in

gonad volume during February to April results mainly from an increase in the number of gametes. The increase in gonad volume during April to May results from the growth and maturation of the oocytes. The beginning of the spawning season at the end of May is marked by a decrease of gonad volume. From June to July, the remaining oocytes will mature while the oocyte number remains unchanged, leading to a slight increase in gonad volume. At the end of August the next cohort of oocytes will be shed leading to another sharp decrease in gonad volume (Borcherding, 1991, 1992c). However, the reproductive cycle itself is strongly related to water temperature and may therefore differ between water bodies (Borcherding, 1991). Moreover, water temperature can influence the length of the reproductive period. Stanczykowska et al. (1988) demonstrated that the reproductive period in lakes receiving heated water from two power plants was twice as long compared to non-heated lakes.

Several studies suggest a 12°C threshold for the start of the spawning season (Kornobis, 1977; Sprung, 1989; Kern et al., 1994; McMahon, 1996). The temperature-rise over the 12°C threshold is an important event imperative for a simultaneous timing of reproductive activity, which is necessary for successful fertilisation within populations (Borcherding, 1991). The oocytes and the spermatozoa are simultaneously released into the water where fertilization will take place (Jenner and Mommen, 1985). Zebra mussels have a high fecundity, with egg production ranging from 10^4 to 1.6×10^6 eggs female⁻¹ year⁻¹ (depending on female size and food availability) and egg size ranging from 30 to 96 µm in diameter (Table 3). For successful development of zebra mussel eggs the temperature must be between 12 to 24°C (optimum 18°C), the pH between 7.4 to 9.4 (optimum pH 8.5) and the calcium concentration must exceed 12 to 15 mg Ca²⁺ l⁻¹ (Sprung, 1987).

The planktonic phase

Authors seem to disagree on the duration of the planktonic phase with estimates varying from 8 days to 5 weeks, most likely depending on the water temperature (Table 3). Notably, the occurrence of larvae at 3.5 to 11°C (i.e., under the 12°C threshold) has been reported, however, these occurrences were most likely not the result of a winter spawning event, but rather of declining autumn water temperatures which arrested larval development and postponed metamorphosis until next spring (McMahon, 1996 and references therein). There are often temporal and spatial differences in larval density (Kornobis, 1977; Stanczykowska, 1977; Bij de Vaate, 1991; Wacker and Von Elert, 2003b), estimates of larval densities in the water column varying from 0 to 500 larvae l⁻¹ (although higher abundances of >1800 up to 9000 larvae l⁻¹ have been reported; Table 3). Larvae show distinct

seasonal abundance peaks during the course of the year, with peak abundances ranging from April to September. Several studies have reported a bimodal peak distribution of larval abundances during this period (Garton and Haag, 1993; Fraleigh et al., 1993), most likely the result of two spawning periods during the reproductive season (Borcherding, 1991). The newly settled mussels, from the first peak at the beginning of the season, may attain sexual maturity and reproduce within a few months, their first spawning period coinciding with the second spawning period of the older generations at the end of the season (Jantz and Neumann, 1998). Zebra mussels may display a distinct vertical distribution of veligers with most veligers pre-dominantly situated within the upper few metres of the water column (Sprung, 1993; Stoeckel et al., 1997; Bially and MacIsaac, 2000; Wacker and Von Elert, 2003a). However, in situations with increased mixing rates or down-welling events in the water column veligers may incidentally be transported to greater depths (Wacker and Von Elert, 2003b) or may show a more homogenous vertical distribution (Kern et al., 1994; Barnard et al., 2003). Zebra mussels may furthermore display a patchy horizontal distribution of veligers, which may either be related to weather conditions (e.g., strength and direction of wind) or to hydrodynamic conditions (e.g., waves and water currents), which can affect the speed and direction of larval dispersal (Jantz and Neumann, 1998).

The growth rate of larvae in nature is highly variable (Table 3), depending mainly on temperature (Sprung, 1989; Smit et al., 1992) and chlorophyll-a content of the water (Jantz and Neumann, 1998). However, although the chlorophyll-a content is generally considered a good indication of the quantity of algal food in the water, Jantz and Neumann (1998) emphasized that the concentration of chlorophyll-a will not always reflect the amount of food available for zebra mussel larvae, for the following reasons: (a) the amount of algal food particles that reach the mussels per unit of time strongly depends on the presence or absence of water currents; (b) particle size may influence filtration efficiency of the zebra mussel larvae, because larvae can only feed on particles larger than 1 µm but smaller than 4 µm in diameter (Sprung, 1989); and (c) the larvae display selective feeding, depending on the 'palatability' of the available planktonic organisms (Sprung, 1989). Therefore, not only the quantitative, but also the qualitative composition of the phytoplankton has to be considered (Jantz and Neumann, 1998). Both, low quantity and low quality of food during the larval stage can result in lower growth rates, leading to irreversible consequences for post-metamorphic mussels and potentially in inferior competitive abilities as a benthic animal (Wacker and Von Elert, 2002).

The larval stage is characterized by high mortality rates, with different rates over the different developmental stages

Table 3. Literature data on various characteristics of the planktonic larval stage.

Egg length (μm)	Time until Trochophore Stage + (Shell length in μm)	Time until D-shaped Stage + (Shell length in μm)	Time until Settlement Stage + (Shell length in μm)	Planktonic Larval Density (# larvae l^{-1})	Veliger Growth Rate ($\mu\text{m day}^{-1}$)	Mortality (in % or % day^{-1})				refs
						From Trochophore to D-stage	From D-Stage to Umbonal Stage	From Umbonal Stage to Settlement Stage	From D-Stage to Settlement Stage	
-	6-20 hours	2-4 days (90-100)	18-33 days (220)	-	20	60-89%	-	-	99.3-100%	1
40-96	2 days (83-95)	2-9 days (70-160)	18-90 (167-300)	-	-	-	-	-	-	2
30-50	-	-	4 wks	-	-	-	-	-	-	3
60-90	-	-	-	-	-	-	-	-	-	4
-	-	(70-80)	18-28 (220)	-	6.0-7.5	-	-	-	-	5
-	-	-	-	315	4-15	-	-	-	-	6
-	-	-	-	0.2-339.5	-	-	-	-	-	7
-	-	-	(195-250)	-	-	-	-	-	-	8
-	-	-	(200-275)	-	-	-	-	-	-	8
-	-	-	-	-	-	-	-	-	-	8
-	-	(270-300)	5 wks	-	-	-	-	-	-	1
-	-	(110-190)	7-16	-	-	-	-	-	-	1
-	-	(225-255)	-	-	-	-	-	-	-	1
-	-	-	8-10	-	-	-	-	-	-	9
-	-	-	5-16	-	-	-	-	-	-	9
-	-	-	-	<500	-	-	-	-	-	9
-	-	-	-	9000	-	-	-	-	-	9
-	-	-	-	10-100	1-4	-	-	-	-	2
-	-	-	-	126-268	4.1-4.5	-	-	-	-	2
-	-	-	-	22-320	6-11	-	-	-	-	2
-	-	-	-	>400	2-24	-	-	-	-	2
-	-	-	7-18	-	17(± 1.9)	-	-	-	-	7
-	-	-	7-63	-	-	-	-	-	-	7
-	-	-	-	0-1850	6.0-11.0	-	-	-	-	11
-	-	-	-	1549	-	-	-	-	-	11
-	-	-	-	>4500	-	-	-	-	-	11
-	-	1-2 days (~70)	-	>50	$L=90.4e^{0.13\text{Days}}$	$8.9\%\cdot\text{day}^{-1}$	$81.5\%\cdot\text{day}^{-1}$	$63.9\%\cdot\text{day}^{-1}$	99.8%	10
-	-	-	-	-	-	$9.6\%\cdot\text{day}^{-1}$	$22.5\%\cdot\text{day}^{-1}$	$9.9\%\cdot\text{day}^{-1}$	94%	10

Sprung, 1989¹; Mackie and Schloesser, 1996²; Mackie, 1991³; Jantz and Neumann, 1998⁴; Neumann et al., 1993⁵; Kern et al., 1994⁶; Stoeckel et al., 2004b⁷; Wacker and von Elert, 2003b⁸; Stańczykowska, 1977⁹; Schneider et al., 2003¹⁰; Borcherdig and de Ruyter van Steveninck, 1992¹¹; and references therein)

(Table 3). Schneider et al. (2003) found that mortality peaked at the transition from the D-stage to the umbonal stage, in both natural and laboratory reared larvae. Stańczykowska et al. (1988) estimated mortality as 20% in the veliger stage to 99% in the post-veliger stage, while Sprung (1989) observed a 60 to 89% mortality during transition from the trochophore-stage to the D-stage, followed by a 99.3 to 100% mortality during transition from the D-stage to the settling stage (Sprung, 1989). Several potential causes for the high mortality rates have been investigated: (a) the effect of predation (e.g., by copepods, adult zebra mussels but especially fish and fish fry) on mortality rates was assessed with exclusion experiments, but all larvae died within 10 days in the absence of predators, indicating that predation was not the cause for mortality (Sprung, 1989); (b) the effect of egg quality on larval mortality was assessed, but there was no evidence for reduced rearing success as a consequence of reduced lipid content or egg weight (Sprung, 1989); and (c) the

effect of food availability on larval mortality was estimated by feeding experiments, showing that even in the presence of apparently abundant food particles (algae, blue-green algae, bacteria, yeast) the filtering selectivity of the larvae (with a particle size of 1 to 4 μm and utilizing only specific food sources) may limit food intake. Starvation experiments further showed that the larvae were not able to survive for a long time without food (approximately 1 to 2 weeks), declining with increasing temperature (Sprung, 1989; Sprung, 1993). Based on his experiments, Sprung (1989) suggested that food limitation is one of the most important causes of high mortality rates among zebra mussel larvae. In addition, Rehmann et al. (2003) studied the effect of small-scale turbulence on mortality. They showed that turbulence increases veliger mortality, suggesting that during downstream transportation in running waters, mortality rates are likely to be very high. Horvath and Lamberti (1999a) showed that the percent of living veligers (y) declined exponentially with

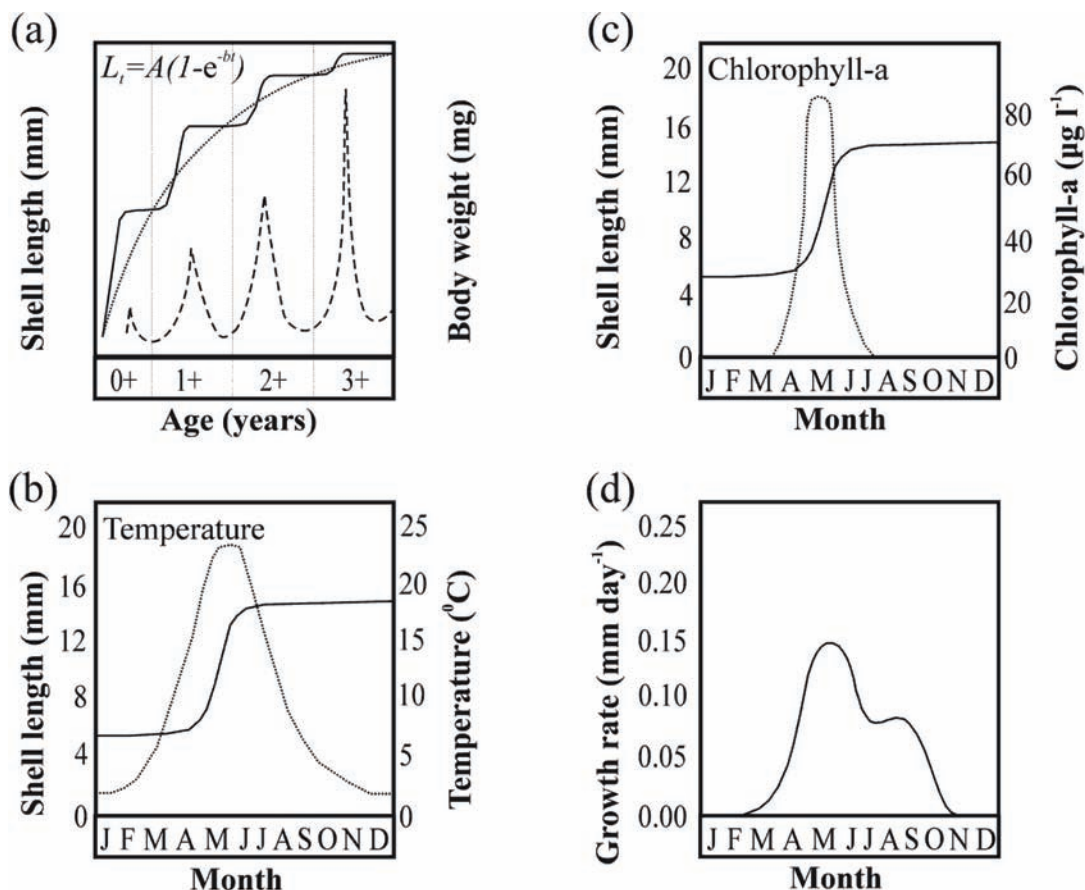


Figure 2. Variation in shell growth and body weight of the zebra mussel (*Dreissena polymorpha*). (a) Seasonal variation in shell growth (black line) and body weight (dashed line) over a period of four successive years (Kornobis, 1977). Life-time shell growth can be approximated by the Von Bertalanffy curve (dotted line). (b) Seasonal increase in shell length in relation to mean water temperatures (Bij de Vaate, 1991). (c) Seasonal increase in shell length in relation to available food, as indicated by chlorophyll-a concentrations (Jantz and Neumann, 1998). (d) Seasonal variation in shell growth rates. The depression in summer is attributed to reproductive activities (Smit et al., 1992).

downstream distance (x), from $90 \pm 3\%$ to $40 \pm 8\%$ over a length of 18 km in Christiana Creek (USA), following the equation: $y = 80.1e^{-0.5x}$. Schneider et al. (2003) estimated the overall mortality of zebra mussel larvae at 99.8% during downstream dispersal over a length of 128 km in 5.3 days in the Illinois River (USA).

Settlement

The transition from the pelagic free-swimming larval phase to the sessile benthic juvenile phase is referred to as settlement. The mussel larva attaches to the substrate by means of byssus threads. Secretion of byssus threads first occurs during the pediveliger larval stage and enables the young juveniles to colonise smooth and vertical surfaces and to withstand considerable water currents (Jenner and Momen, 1985). Settlement success is determined by environmental conditions, such as the physical and chemical properties of the water column (e.g., turbidity, salinity, pH, Ca-concentration, temperature, etc.) and substrate (e.g., hardness, substrate composition), as well as the hydrodynamic condi-

tions near the substrate (e.g., strong currents may prevent settlement or inhibit filtering capacity whereas no current at all may lead to food deprivation) (Stanczykowska, 1977).

Observed settlement densities vary from 0 to 10^6 larvae m^{-2} (Kornobis, 1977; Bij de Vaate, 1991), however, settling stages are very sensitive displaying mortality rates of 90 to 99%. Most larvae die during the process of settlement because of environmental conditions, such as unfavourable near bottom oxygen conditions, lack of suitable hard substrates, continuous strong water currents that prevent settlement and wave action that carries larvae away from the shore (Stanczykowska, 1977; Mackie and Schloesser, 1996). Mean shell length at settlement is approximately 200–220 µm (Table 3). The occurrence of larger settling larvae (270 to 300 µm) has been reported, but these were probably the result of a postponed settlement due to a lack of suitable substrates, stimulating larvae to delay their metamorphosis. In general, the substrate on which larvae can settle is not very specific (Sprung, 1993). In natural ecosystems the only general requirement for settlement substrates is that it has to be hard

and solid. This includes rocks, stones, crayfish, plants and shells of adult Dreissenidae or Unionidae (Sprung, 1993). Mud and sand are generally not considered to be suitable substrates for primary settlement, although studies in several US lakes (i.e., Lake Erie, Lake Champlain) show that zebra mussels can directly colonise muddy and sandy substrates (grain diameter ranging from 0.06 to 0.5 mm; Beekey et al., 2004a) by using their byssus threads to bind sediments into conglomerates (Bially and MacIsaac, 2000; Beekey et al., 2004a). Studies furthermore show that zebra mussel density is higher at moderate depths (approximately 4 to 7 m) than at shallower (< 3.5 m) and greater ones (8.5 to 30 m), despite the fact that zebra mussel larvae and newly settled juveniles were pre-dominantly present in more shallow water (Bially and MacIsaac, 2000; Wacker and Von Elert, 2003b). Bially and MacIsaac (2000) suggested that the absence of mussel colonies at shallower sites (< 3.5 m) was not the result of either recruitment or substrate limitation, but rather of seasonal storms which are more likely to affect the newly settled individual in shallower sites, whereas Wacker and Von Elert (2003b) suggested that the presence of recently settled juveniles in deeper water (at 15 and 30 m) despite the low presence of larvae, was the result of passive transportation of larvae from shallow to deeper water during down-welling events. A study by Yankovich and Haffner (1993) further showed that the zebra mussel displayed microhabitat selection during settlement. Settlement on artificial substrates (i.e., cement blocks) mainly took place in the internal sheltered holes as opposed to the external region (i.e., top and sides of the cement blocks). Block tops had the lowest settlement densities because of the relatively high rates of exposure to water turbulence. Moreover, individuals that initially settled on the block tops displayed post-settlement habitat selection and moved away to more favourable conditions.

Growth

In general, shell growth follows a sigmoid curve throughout the season, starting in spring when water temperature is approximately 3°C (Smit et al., 1992) to 6°C (Bij de Vaate, 1991), reaching an optimum during the summer and declining again to zero in autumn when water temperature decreases below 3 to 6°C (Fig. 2a). After settlement in spring, the juveniles will display a rapid increase in shell length. Reported growth rates range from 0.15 mm week⁻¹ (in 0.9 mm post-veligers), 0.5 mm week⁻¹ (in 4 mm juveniles) to 0.35 mm week⁻¹ and 0.59 mm week⁻¹ (in 5 to 6 mm juveniles) under field conditions (Dorge-lo, 1993). Several studies demonstrate a relation between mussel size at the beginning of the growth season (L) and the shell growth (Li) during the season, which can best be described by either a second-order polynome equation, $Li = aL^2 - bL + c$ (Bij de Vaate, 1991; Smit et al., 1992),

or a negative exponential equation, $Li = ae^{-bL}$ (Smit et al., 1992; Jantz and Neumann, 1992; Neumann et al., 1993). Seasonal shell growth-rates are a combined function of water temperature (Fig. 2b) and chlorophyll-a densities (Fig. 2c), with temperature-dependent bell-shaped curves and chlorophyll-a dependent heights (Jantz and Neumann, 1998). Smit et al. (1992), found that growth rates best fitted the sum of two Gauss shaped functions, with the observed summer depression in growth rates being related to reproductive activities (Smit et al., 1992; Fig. 2d). Regardless of the seasonal sigmoidal growth patterns, the life-time growth pattern can be approximated by the Von Bertalanffy equation: $Lt = A(1 - e^{-bt})$, where Lt is the shell length at age t , b is the growth rate at which the asymptotic length A is approached (Kornobis, 1977; Fig. 2a). The relation between the life-time growth of soft body tissue (AFDW) and shell length can be described by the general equation: $W = aL^b$, in which W is the ash-free dry weight of the soft body and L is the shell length (Bij de Vaate, 1991).

Life span

The average life span of the zebra mussel varies between different water bodies depending on differences in water temperature between the lakes. Stanczykowska (1977) noted that mussels living in warmer waters live shorter than mussels living in cooler waters. This is true for warmer lakes in the south of Europe as well as for 'heated lakes' (due to heated discharge) situated in northern Europe. Estimates of life-span vary from 3 to 4 years (Goslawsko-Slesinskie Lakes, Neusiedler Lake, Balaton Lake), to 5 years (Mazurian Lakes, Hancza Lake), 5 to 6 years (Szczecin Lagoon, Uchinski Dam Reservoir, Constance Lake), to 6 years (in most Volga Dam Reservoirs), 6 to 7 years (Swiss Lakes, Zarnowieckie Lake), up to 6 to 9 years (Pialovski Dam Reservoir).

Physiological requirements

Environmental gradients

The successful colonization by zebra mussels is restricted to environments that have suitable conditions for reproduction, growth and survival. Knowledge about the mussel's physiological requirements is necessary to understand why colonisation of some waters is successful whereas of others is not. Moreover, such knowledge is indispensable for the development of models designed to predict future dispersal of the species (Johnson and Carlton, 1996; Drake and Bosenbroek, 2004).

Environmental conditions are generally present in a geographical gradient. Such gradients exist for almost all environmental factors and are present in all habitats where they affect virtually all species (Cox and Moore, 1980). A species can function efficiently over a limited part of each gradient,

the so-called *range of optimum*. Within this range the species can survive and efficiently maintain a population (i.e., growth and reproduction). Beyond this range of optimum the species will increasingly suffer from physiological stress. It may stay alive but cannot function efficiently. These extreme limits are called *the lower and upper limit of tolerance* and these determine the potential range of occurrence of the species. Beyond these limits the species cannot survive. Three factors complicate the determination of tolerance limits for a given species from laboratory experiments: Firstly, the species can *acclimate* physiologically to some environmental factors. For example the upper tolerance limit for temperature depends on both the temperature of the environment where the animal has been living prior to the experiment and on the length of the time it has been living there. Secondly, tolerance limits for one environmental factor will depend on the levels of other environmental factors. For instance, the pH will affect the temperature tolerances (e.g., at very low pH levels a fish species cannot tolerate high temperatures as well as at normal pH levels). Thirdly, the different stages of a life-cycle may have different limits of tolerance. For example, adult zebra mussels and larval mussels have a different tolerance to salinity.

Temperature

For growth, the zebra mussel is restricted to water temperatures exceeding 3 to 6°C (Bij de Vaate, 1991; Smit et al., 1992). Exposure to lower temperatures will arrest growth. Borcharding (1991) concluded that the temperature rise over the 12°C threshold is an important event that is absolutely imperative for the simultaneous timing of reproductive activity within a population. Since simultaneous spawning is necessary for fertilisation success, water bodies with a maximum daily temperature below 12°C throughout the entire year (i.e., which will lack the temperature-rise over the 12°C threshold), cannot be successfully colonised by the zebra mussel (Borcharding, 1991). Therefore, here, 12°C is considered to be the zebra mussel's *lower* thermal tolerance for maintaining viable populations, rather than the 3 to 6°C lower limit for growth.

The zebra mussel has an *upper* thermal tolerance limit of approximately 30°C. However, there are geographical differences in the upper thermal tolerance limits among populations of the zebra mussel. Northern European populations have an upper thermal tolerance limit of 27 to 28°C as compared to Northern American populations which have a slightly elevated thermal tolerance limit of 30 to 31°C (Spidle et al., 1995). The basis for the elevated upper thermal tolerance limit among North American zebra mussels as compared to the North European zebra mussels has been debated. The zebra mussels in North America are likely to have originated from the warmest part of Europe,

the Black-Caspian sea region (Marsden et al., 1996). The North American mussels may therefore be genetically more thermal tolerant than the North European mussels that are probably more adapted to the colder North European waters (Marsden et al., 1996; McMahon, 1996). This corroborates with a number of studies showing that zebra mussels from the most southern site of the Volga River (Astrahan, near the Caspian Sea) were more tolerant to elevated temperatures than zebra mussels from more northern sites (Rybinsk and Kuibyshev; Smirnova et al., 1993).

Even on a local scale the upper temperature limits mentioned above are not rigid. Seasonal change in temperature will occur gradually throughout the year. During this period mussels will adjust (i.e., acclimate) their upper thermal tolerance limit within certain genetically determined boundaries. Laboratory experiments (subjection of mussels to increased heat over a period of several hours) have shown that the acclimation temperature (in this case the temperature at which the mussels were kept previous to the experiments) has a significant effect on the survival of zebra mussels, which can work in two ways: higher acclimation temperature will either lead to higher tolerance of exposure *temperature* or in a higher tolerance of exposure *time* (Jenner and Mommen, 1985; Spidle et al., 1995; McMahon, 1996).

Two studies (Allen et al., 1999; Mihuc et al., 1999) in sub-tropical rivers (Atchafalaya River Basin, Louisiana and the Lower Mississippi River) at the southern edge of the zebra mussel's distribution in North America, clearly showed that 31 to 32°C is the upper thermal tolerance limit that determines the boundary of its distribution. Zebra mussels progressed from the main channel into the floodplain during the winter and early spring, when minimum daily temperatures dropped below 31°C and shell growth and tissue conditions were highest. However, during summer periods when minimum daily temperatures remained above 32.5°C, tissue conditions declined, shell growth ceased and adult mortality was so high that it eradicated the previously established mussels. These studies show that summer temperatures in the sub-tropical regions prevent the establishment of resident zebra mussel populations at its edge of its distribution and confirm that ~31°C is the upper thermal tolerance limit of the zebra mussel.

Salinity, pH and calcium concentration

Salinity. It is obvious from the available literature that the zebra mussel displays a very wide euryhalinity (Orlova et al., 2000). The *lower* salinity tolerance limit was estimated to be 0.007‰ (Orlova et al., 1998) to 0.4 to 0.5‰ (Strayer and Smith, 1993). Estimates for the *upper* salinity tolerance limit range from 2 to 4‰ (McMahon, 1996 and references therein), 5‰ (Spidle et al., 1995; in their experiments no in-

dividuals survived beyond 18 days in salinities higher than 5‰), 6‰ for successful spawning, fertilization and larval settlement (McMahon, 1996), 7‰ for successful adult colonization (McMahon, 1996) and 8‰ for successful spawning and rearing (Setzler-Hamilton et al., 1996). Despite the relative low tolerance levels found in the above mentioned experimental studies, a viable population has existed in the Aral Sea, which was characterized by salinities of up to 12‰ (Strayer and Smith, 1993; Orlova et al., 2000). In 1976-1977 an increase in the Aral Sea's salinity to 14‰ extirpated its entire zebra mussel population, suggesting that this 14‰ lethal limit may be the zebra mussels' incipient upper salinity limit. Acclimation experiments showed that the zebra mussel is very sensitive to sudden changes in salinity and that the species is much more tolerant to gradual changes in salinity (Strayer and Smith, 1993). This may be the reason why such low estimates for the upper salinity tolerance limits for the zebra mussel are derived from laboratory experiments, whereas under natural conditions it can be found at much higher salinities. This can be illustrated by comparing studies conducted in areas with high mixing rates, such as estuaries, to hydrologically more stable environments, such as the Aral Sea. In the Hudson River Estuary zebra mussels originating from upstream areas are passively dispersed downstream, recruiting and surviving in downstream areas with salinities up to 2 to 5‰ (Walton, 1996). Barnard et al. (2003) found in the St. Lawrence estuary that, although veligers were found up to 10‰, veliger abundance showed a sharp increase at salinities below 2‰, suggesting a threshold salinity of approximately 2‰ for veligers. They suggested that, since the St. Lawrence estuary is characterized by high mixing rates and veligers are extremely sensitive to sudden changes in salinity, these high mixing rates might not allow for a sufficient acclimation period resulting in the observed sharp decline at 2‰. Several laboratory studies have shown that, given an adequate acclimation period, zebra mussels can spawn, be reared and survive at salinities of 8 to 10‰ (Setzler-Hamilton et al., 1996; Wright et al., 1996), suggesting that in more stable saline environments, such as the Aral Sea, zebra mussels can maintain viable populations at higher salinities (Orlova et al., 2000). Notably, Smirnova et al. (1993) reported differences in salinity tolerance between different populations of *Dreissena polymorpha* in the River Volga. Individuals from the site farthest from the Caspian Sea (Rybinsk) which lived in freshwater, typically displayed a higher mortality in relation to increases in salinity than individuals from the site nearest to the Caspian Sea (Astrahan) which lived in brackish water, most likely the result of acclimation (though local adaptation of the populations cannot be entirely ruled out).

pH. There is a narrow range for the successful rearing of eggs and larvae with a lower pH tolerance limit of 7.4 and an

upper pH tolerance limit of 9.4, with an optimum at pH 8.5 (Sprung, 1987; Hincks and Mackie, 1997). This may explain why the zebra mussel does not occur in lakes with average pH values below 7.3 (Ramcharan et al., 1992b).

Calcium concentration. Calcium is essential for the capability of dividing cells in embryos, the growth of the shell valves and many other physiological processes. Zebra mussels cannot survive in the absence of calcium. A study by Hincks and Mackie (1997) showed that there is a negative growth of adult zebra mussel at calcium levels less than 8.5 mg $\text{Ca}^{2+} \text{ l}^{-1}$. Sprung (1987) estimated the lower calcium tolerance limit for zebra mussel survival to be 12 to 15 mg $\text{Ca}^{2+} \text{ l}^{-1}$ necessary for the rearing of eggs (Sprung, 1987). It has even been suggested that, in nature, the zebra mussel is not found in lakes with concentrations below 28.3 mg $\text{Ca}^{2+} \text{ l}^{-1}$ (Ramcharan et al., 1992). According to Sprung (1987) the calcium concentration will cease to be a limiting factor at concentrations higher than 50 mg $\text{Ca}^{2+} \text{ l}^{-1}$.

Turbidity

Several studies have focused on the mechanisms by which zebra mussels respond to (acute) elevated concentrations of suspended sediments (Alexander et al., 1994; MacIsaac and Rocha, 1995; Madon et al., 1998). They found that the primary short-term response was increased production of pseudofaeces, rather than avoidance of sediments by cessation of filtering capacity (closure of valves). Moreover, there appeared to be an increased metabolic cost associated with the pseudofaeces production. The ingestion rates, oxygen consumption rates and assimilation efficiencies are greatly reduced (Alexander et al., 1994; Madon et al., 1998). It was therefore suggested that zebra mussels in turbid rivers may exhibit low growth rates because of the associated metabolic cost of pseudofaeces production. However, turbidity levels in the Lower Ohio River exceed the predicted turbidity levels that should inhibit growth (McMahon, 1996) and zebra mussels nevertheless thrive there. A study by Summers et al. (1996) suggests that zebra mussels adjust their metabolic rate in response to chronic exposure to turbidity. This acclimation to chronic high turbidity may be the reason why the zebra mussel can still thrive in very turbid waters. No clear upper turbidity tolerance limit can be found in the literature.

Aerial exposure tolerance

The aerial exposure tolerance (expressed as survival per unit of time) depends on a number of factors, such as relative humidity, temperature, air movement and mussel size. Studies have shown that the survival of aerially exposed zebra mussels increases significantly with increasing relative humidity (McMahon et al., 1993; Ussery and McMahon, 1994), decreasing air temperature (McMahon et al.,

1993; Paukstis et al., 1999; Ussery et al., 1998), decreasing air movement (Ussery et al., 1998) and increasing mussel size (Ricciardi et al., 1995a). Due to the many factors that can influence survival, it is difficult to define an upper tolerance time limit for zebra mussel survival when subjected to aerial exposure. However, the results show that at conditions considered optimal for survivorship estimates for surviving emersion vary from 10 days of emersion (at 10°C, in 95% relative humidity and no moving air; Ricciardi et al., 1995a), 13 days (at 15°C in high relative humidity, McMahon, 2002) to 18 days (under cool and damp conditions in March, Dan Minchin, personal communication). These studies suggest that, zebra mussels attached to the hulls of boats transported on trailers, and thus exposed to moving air, may not survive long-distance overland transportation during the dry summers, when temperatures are high (Ussery et al., 1998). However, under typical spring/autumn weather conditions, with low temperatures and high humidity, adult zebra mussels can survive overland transport (e.g., on small trailered boats) to any location within 3-10 days' drive of the place of departure (Ricciardi et al., 1995a). Notably, within four to six days driving almost every location in the United States can be reached from any other location in the United States.

Identification of threatened regions in the world

Based on dispersal

The possession of planktonic larval stages allows the intake of larvae with ship's ballast water and subsequent transportation overseas. Ballast water has long been identified as a source of long-distance jump dispersal of non-indigenous species (Carlton and Geller, 1993; Cohen and Carlton, 1998). There is still little known about the biology in ballast water. For instance, it is not clear how long larvae can survive in ship's ballast water. There are two 'natural' factors that may limit survival time in the ballast water. Firstly, depletion of food resources. Zebra mussel larvae have highly specific dietary requirements with regard to the kind and size of food particles and in the absence of food larvae may experience 100% mortality within 11 to 15 days at 12 to 24°C. Secondly, the duration of the planktonic larval stage (approximately 2-5 weeks). If zebra mussel larvae lack suitable substrates for settlement at the end of the larval stage (e.g., because of a toxic surface coating on the ship's interior), they will probably die, although it has been suggested that a lack of suitable substrates may stimulate larvae to postpone their metamorphosis and extend their planktonic larval stage beyond this 2-5 weeks (Sprung, 1989). We therefore suggest that if conditions in the ballast water are optimal, zebra mussels may be successfully transported to ports and harbours within 2-5 weeks (and possibly more) of cross-oceanic journey time (in the northern hemisphere journeys typically take between 1-3 weeks). The recent global range extension of two simi-

lar freshwater bivalve mass invaders, *Corbicula fluminea* (Müller, 1774) and *Limnoperna fortunei* (Dunker, 1857), shows that inter-continental transportation of bivalve larvae via ballast water is very likely to occur. These two species originate from rivers and streams of East Asia. *Limnoperna fortunei* has invaded South America in 1991 (the Rio de la Plata, Argentina), supposedly via ballast water from trading ships arriving from Korea and Hong Kong (South East Asia) (Ricciardi, 1998), while *Corbicula fluminea* has already invaded every continent on earth, spreading from China to South East Asia, Australia, Africa, South America, North America and North and South Europe and is still spreading today (Morton, 1996).

From invaded ports and harbours, the potential for further secondary spread by the zebra mussel is considered to be virtually limitless. Upstream areas in rivers may be colonized through spawning by adult mussels attached to the hulls of riverine ships. Isolated water bodies may be colonized by zebra mussels, attached to various solid objects (e.g., pleasure boats, fishing fykes, buoys, bait buckets, etc.) transported overland from infested waters. Adults can, under ideal conditions (e.g., low temperature, high humidity and low movement of air), easily survive emersion for up to 10-18 days, whereas larvae, retained in pools of water in crevices of recreational boats, can survive overland transportation for up to 8 days. Hence, after the initial colonization of ports and harbours, most rivers, canals, lakes and ponds within 4 to 5 days travel, may under optimal conditions be successfully colonized.

Based on survival and reproduction

For zebra mussel survival the environmental parameters have to meet the physiological requirements. On a global scale, regions for possible zebra mussel survival can be roughly defined by three environmental parameters: salinity, water temperature and calcium concentration. Firstly, the occurrence of the zebra mussel is restricted to freshwater lakes, canals, rivers and brackish water estuaries and seas, with salinities ranging from a lower limit of 0.007 ‰ to an upper limit of 12-14 ‰. Secondly, the zebra mussel is restricted to specific temperature zones, with temperatures ranging from a lower limit of 3-6°C to an upper limit of 31°C. For reproduction however, the zebra mussel is restricted to areas that have a temperature rise over a 12°C threshold, which is an important event that is imperative for the simultaneous timing of reproduction activity within a population. Water bodies that lack this temperature-rise over the 12°C threshold will therefore not be able to maintain permanent populations. On a global scale, suitable areas can therefore roughly be defined as the areas between the 10°C isotherm of the coldest month and the 14°C isotherm of the warmest month (Fig. 3). Thirdly, the zebra mussel survival and reproduction

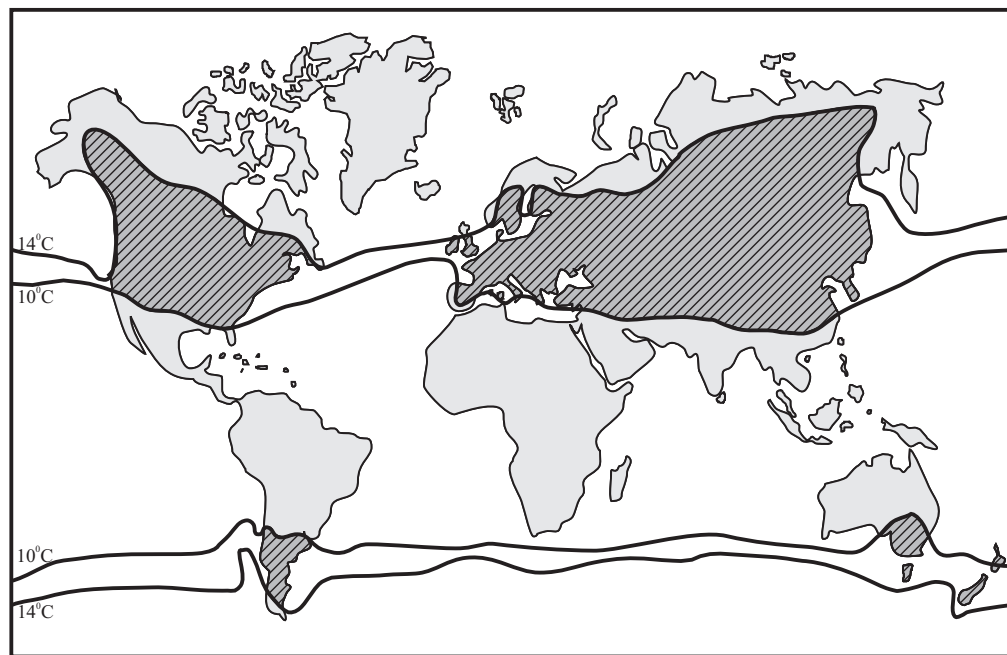


Figure 3. A Map of the world, showing the potential range of occurrence of *Dreissena polymorpha*, between the 10°C isotherm of the coldest month and the 14°C isotherm of the warmest month, based on its temperature requirements for survival and reproduction.

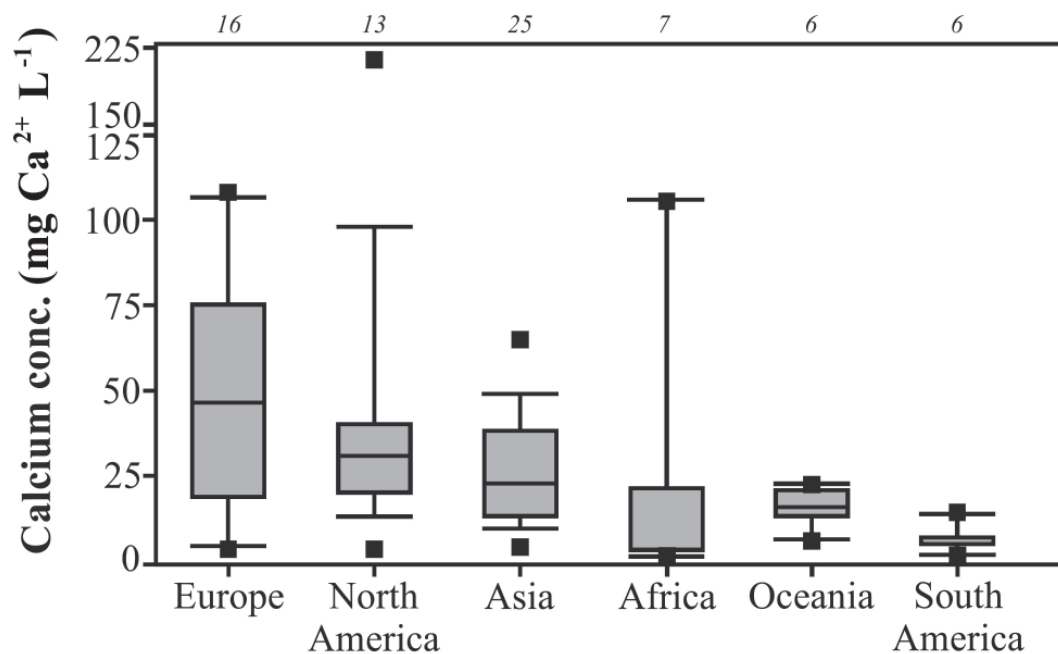


Figure 4. Box- and Whisker-plot representing the statistical distribution of calcium by continent, based upon averages at major river mouths. The numbers on top of the graph indicate the number of studied rivers for each continent. The horizontal lines within each box give the median score, the lower and upper parts of each box the 25th and 75th percentiles, respectively. The whiskers represent scores that lie within 1.5 times the interquartile range (IQR) of the box. The black dots represent the outliers, i.e., scores that lie more than 1.5 times the IQR from the box (redrawn after Meybeck and Helmer, 1989).

is restricted to waters with calcium concentration exceeding 12 to 15 mg Ca²⁺ l⁻¹. Since there are, due to geological processes, large differences in mean composition of river waters between continents (Table 4), particularly dissolved

calcium-concentrations (Fig. 4), these continents may each offer a different likelihood for zebra mussel survival. The continents of the northern hemisphere, Europe, North America and Asia, have the highest mean concentration levels of

Table 4. Mean composition of river waters of the world (Wetzel, 2001).

	Ca ²⁺ (mg l ⁻¹)	Mg ²⁺ (mg l ⁻¹)	Na ⁺ (mg l ⁻¹)	K ⁺ (mg l ⁻¹)	HCO ₃ ⁻ (mg l ⁻¹)	SO ₄ ²⁻ (mg l ⁻¹)	Cl ⁻ (mg l ⁻¹)	NO ₃ ⁻ (mg l ⁻¹)	^a TDS (‰)	^b DIC (mg l ⁻¹)
Europe	31.1	5.6	5.4	1.7	95.0	24.0	6.9	3.7	0.182	18.7
North America	21.0	5.0	9.0	1.4	68.0	20.0	8.0	1.0	0.142	13.3
Asia	18.4	5.6	5.5	3.8	79.0	8.4	8.7	0.7	0.142	15.5
Africa	12.5	3.8	11.0	-	43.0	13.5	12.1	0.8	0.121	8.5
South America	7.2	1.5	4.0	2.0	31.0	4.8	4.9	0.7	0.069	6.1
Australia	3.9	2.7	2.9	1.4	31.6	2.6	10.0	0.05	0.059	6.2

^a Total Dissolved Solids (i.e., Salinity: 1 mg l⁻¹ = 1 ppm = 0.001 ‰)

^b Dissolved Inorganic Carbon

Ca²⁺, suitable for zebra mussel survival, egg development and shell growth. In contrast, the continents of the southern hemisphere, South-America, Africa and Australia, have very low mean calcium concentrations, most likely not allowing survival or reproduction after introduction.

Threatened regions and systems in the world: a synthesis

Based on the physiological requirements of the zebra mussel we conclude that fresh- and brackish waters with salinities ranging within 0.007 to 14‰, situated between the 10°C isotherm of the coldest month and the 14°C isotherm of the warmest month, are suitable areas for zebra mussel survival and reproduction. Considering the calcium requirements, suitable areas for shell growth are restricted to the northern hemisphere, where mean concentrations exceed the 12 to 15 mg Ca²⁺ l⁻¹ threshold. Thus, a range expansion of the zebra mussel is most likely restricted to the northern hemisphere, including Europe, North America and Asia. In Europe, the zebra mussel is still slowly expanding, as evidenced by recent range-expansions in England, Ireland, Spain and Russia (Araujo and Álvarez Halcón, 2001; Karatayev et al., 2003a; Pollux et al., 2003; Aldridge et al., 2004), and it will continue to spread to the few areas where it is, as yet, absent. In North America, the zebra mussel has occupied the major rivers in the east including the St. Lawrence, Hudson, Mississippi, Ohio, Illinois, Tennessee, Susquehanna and

Arkansas. A further range-expansion, to the rivers and water bodies in the western part of North America is likely (Drake and Bossenbroek, 2004). From the west coast of the United States, the potential for introduction to East Asia, via ballast water, is possible (Morton, 1996). Ports and harbours that frequently receive international cross-oceanic vessels are most likely the first to be colonized by long-distance intercontinental cross-oceanic journeys (jump dispersion). After the initial establishment of permanent populations, secondary spread (diffusion dispersion) to downstream, upstream and overland areas is considered to be virtually limitless (Carlton, 1993). Potential major river systems in East Asia are the Yellow River which empties into the Gulf of Chihli (China), the Yangtze and the Pearl rivers (China), Hong Kong City situated in the Pearl River estuary (China), the Amur River (Russia) and the rivers that empty into Tokyo bay (Japan). Finally, we suggest that future studies may benefit greatly from nonparametric analyses (e.g., GARP) to predict potential zebra mussel spread in these areas in more detail, using (high resolution) geographical and ecological data at more local scales (Drake and Bossenbroek, 2004).

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