ABSTRACT Dreissena polymorpha, the zebra mussel, originated in the Caspian and Black Sea basin, and has invaded waterbodies of the former Soviet Union (FSU), eastern, and western Europe during the last 200 years. Since 1771 more than 2,000 papers on the distribution, taxonomy, biology, ecology, and control of species and subspecies of Dreissena were published in Russia and FSU, however, this work has not been generally available. We review work conducted in the FSU over the last 100 years on the tolerance of D. polymorpha to different abiotic conditions in waterbodies of various types in order to provide non-Russian-speaking scientists access to this rich body of literature. D. polymorpha is one of the few bivalve mollusks well adapted to live from entirely freshwater to brackish waters. Different subspecies appear to have different salinity tolerances, ranging from completely freshwater to 18.5%. Zebra mussels require at least 25% oxygen saturation, although they can survive several days in anaerobic conditions. The quagga mussel, D. bugensis, however, is much more tolerant of low oxygen conditions. The upper temperature limit for zebra mussels is around 32-34°C. Zebra mussels are most abundant on hard surfaces, particularly rocky surfaces, and on macrophytes. Water motion, aerial exposure, freezing, and the other physical factors including temperature, salinity, and oxygen affect the distribution of zebra mussels among and within waterbodies. Many of these factors are expected to covary, or differ predictably among waterbodies, driving distribution and abundance patterns as well as patterns of invasibility that we see both within and among waterbodies.

KEY WORDS: Zebra mussels, salinity, oxygen tolerance, temperature, substrate

INTRODUCTION

Invading exotic species are presently considered to be one of the greatest threats to native ecosystems throughout the world (Vitousek 1994). One of the best known recent aquatic invaders to North America is the zebra mussel, Dreissena polymorpha and to a lesser extent, the quagga mussel, Dreissena bugensis. Because of the large environmental and economic impacts of the D. polymorpha invasion in the Great Lakes region and major rivers of eastern USA and Canada, scientists and natural resource managers across Canada and the USA, as well as other countries that have not yet been invaded, are attempting to prevent and plan for likely further invasion of this bivalve. Although Dreissena species have recently invaded North America (Hebert et al. 1989), D. polymorpha has been an aggressive invader in freshwater across countries of the former Soviet Union (FSU), and eastern and western Europe for 200 years, following the activities of humans, especially the building of canals, shipping, and commercial fishing (Starobogatov and Andreeva 1994, Karatayev et al. 1997). Given this long history, there has been a great deal of research in eastern and western Europe on species and subspecies of Dreissena. Due to language and political barriers, however, work performed and published in the FSU has only recently become available to western and English-speaking scientists (listed in Schloesser et al. 1994, reviewed in Karatayev et al. 1997).

In a recent review, Karatayev et al. (1997) summarized work conducted in eastern Europe and the FSU on the effects of D. polymorpha invasion on aquatic communities, and where possible, contrasted these results with current and ongoing research in North America. In this review, our goal is similar. We review work that has been conducted in the FSU addressing physical factors that influence the presence and abundance of dreissenid mussels and how those factors could affect distribution in different types of waterbodies. We present this review to familiarize scientists with this body of work and, where possible, contrast this work with work conducted in North America. This should not, however, be considered a comprehensive review of North American literature. We hope that familiarity with past work from the FSU will help science progress faster; using an existing body of research and literature allows more sophisticated questions to be addressed than would be possible if we knew nothing about the biology of Dreissena. In addition, comparing and contrasting results of research from the FSU with work from North America is valuable. If findings are similar, it strengthens our ability to make generalizations, and if findings are different, we can begin to determine what environmental or other factors are responsible for such differences.

In this review we examine several specific physical factors, including salinity, oxygen, and temperature, that are known to affect the presence and abundance of dreissenids. We then address how these factors affect the differences in abundance of dreissenids among different types of waterbodies. Although we present these factors individually, they are not necessarily independent. Many factors will covary, and there are likely to be interactions among factors that have a much greater impact on dreissenids than would be seen by examining factors individually. In addition, some factors may be more common in certain environments, contributing to between-habitat differences observed. However, to date there is no dataset available in a form where multifactor analysis can be used to address the impacts of all of these specific factors (Ramcharan et al. 1992a). Hopefully, as attention is drawn to the need for such data and as work progresses, specific data will become available allowing this type of analysis.

Because of differences between English and Russian language
D. polymorpha obtuscarinata
D. polymorpha aralensis
D. polymorpha andrusovi
D. polymorpha polymorpha

aralensis (Andr.) are widespread in the Aral Sea (Khusainova and
andrusovi populate the Caspian Sea (Logvinenko and Starobogat-
(1992, Lyakhnovich et al. 1994, Rosenberg and Ludyanskiy 1992, Kinzel-
there are several subspecies of D. polymorpha, each with a more
narrow but different tolerance to salinity (Logvinenko and Star-
obogatov 1968, Galperina and Lvova-Kachanova 1972, Kinzel-
bach 1992, Lyakhnovich et al. 1994, Rosenberg and Ludyanskiy 1994, 1996, Shkorbatov et al. 1994, Starobogatov and Andreeva 1994) (Table 1). Thus, D. polymorpha polymorpha and D. polymorpha andrusovi populate the Caspian Sea (Logvinenko and Staroboga-

TABLE 1.
Upper salinity limit for different subspecies of Dreissena polymorpha found in various waterbodies.

<table>
<thead>
<tr>
<th>Waterbody</th>
<th>Upper Salinity Limit (%)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. polymorpha polymorpha</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dnieper-Bug Liman</td>
<td>5</td>
<td>Markovskiy 1954</td>
</tr>
<tr>
<td>Netherlands estuaries</td>
<td>4</td>
<td>Wolff 1969</td>
</tr>
<tr>
<td>Vistula lagoon</td>
<td>4.8</td>
<td>Klimovich 1958</td>
</tr>
<tr>
<td>Rhine estuaries</td>
<td>5</td>
<td>Remane and Schlieper 1958</td>
</tr>
<tr>
<td>North-Baltic Sea Canal</td>
<td>6.2</td>
<td>Reshoft 1961</td>
</tr>
<tr>
<td>Northern part of the Caspian Sea</td>
<td>5</td>
<td>Karpevich 1964</td>
</tr>
<tr>
<td>Azov Sea</td>
<td>5</td>
<td>Karpevich 1955b</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Kruglova 1957</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Shkorbatov et al. 1994</td>
</tr>
<tr>
<td>D. polymorpha andrusovi</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caspian Sea</td>
<td>11</td>
<td>Karpevich 1952a</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>Ivanova 1973</td>
</tr>
<tr>
<td></td>
<td>12-14</td>
<td>Shkorbatov et al. 1994</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Logvinenko 1965</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Livova 1988</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Livova and Makarova 1990</td>
</tr>
<tr>
<td>D. polymorpha aralensis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aral Sea</td>
<td>17.6</td>
<td>Khusainova 1958</td>
</tr>
<tr>
<td>D. polymorpha obtuscarinata</td>
<td>18.4</td>
<td>Lyakhnovich et al. 1994</td>
</tr>
</tbody>
</table>

D. polymorpha polymorpha has been the most successful invader in the FSU, Europe, and North America, and has the lowest salinity tolerance of any of the subspecies of Dreissena (Lvova 1977, Kinzelbach 1992, Starobogatov and Andreeva 1994). In the Caspian Sea (Karpevich 1964, Shkorbatov et al. 1994) and the Taganrog Gulf of the Azov Sea (Karpevich 1955b, Kruglova 1957 Shkorbatov et al. 1994) D. polymorpha polymorpha populates the least saline areas, from fresh water up to 5% (Table 1).

Several examples illustrate the link between salinity tolerance and the distribution of D. polymorpha polymorpha. The highest densities and standing biomass (up to 1–2 kg m⁻²) of D. polymorpha polymorpha in the Azov Sea are found below 2.5% (Karpevich 1955b, Stark 1955, Yablonskaya 1955, Nekrasova 1971, Lyakhnovich et al. 1994). Prior to 1950 the Don River flowed directly into the Azov Sea resulting in large areas of low salinity, and zebra mussels were widespread (Mordukhai-Boltovskoi 1937, Nekrasova 1971, Lyakhnovich et al. 1994). After construction of the Tsimlyanskoe Reservoir (1952) on the Don River, and the subsequent reduction of the water flow to the Azov Sea, salinity increased, and in low-water years D. polymorpha polymorpha is only found near the Don River Delta. In high-water years the salinity is lower, and zebra mussels occupy the whole eastern part of the Taganrog Gulf of the Azov Sea (Nekrasova 1971, Nekrasova 1973, Lyakhnovich et al. 1994).

Even within D. polymorpha polymorpha, different populations can have different salinity tolerances. For example, Markovskiy (1954) concluded that there were different populations of D. polymorpha polymorpha with different salinity tolerances within the Dnieper Bug Liman (a salty coastal lake). One population lives in salinities of 0.2–3.0% and the other in areas with salinity 0.5–5.0%. For other populations, the maximum density (up to 100,000 m⁻²) and biomass (up to 3 kg m⁻²) of D. polymorpha polymorpha and D. bugensis are in areas with low salinity (average 0.8, maximum 2.0–3.5%) (Grigoryev 1965).

Similar patterns have been found in the Netherlands. Lake IJsseelmeer was formed in 1932 by closing its connection to the Baltic Sea (Smit et al. 1993). Chloride concentrations gradually dropped from 6% in 1932 to 0.6% in 1935, and to 0.4% in 1936. D. polymorpha polymorpha was first recorded in Lake IJsselemeer in 1936, and by 1937 were found in the northern (lower salinity) part of the lake, and by 1938 were distributed throughout the whole lake. The same pattern was observed in Lakes Volkerakmeer and Zoommeer (Smit et al. 1993). These lakes were dammed from the Eastern Scheldt Estuary in April 1987, and chloride concentrations dropped from 10‰ to 0.8‰ by September 1987. The first adult mussels were found in Lake Volkerakmeer in October 1987. In January 1988, D. polymorpha polymorpha had spread throughout Lake Volkerakmeer. Lake Zoonmeer has higher chloride concentrations (0.7‰) than Lake Volkerakmeer (0.3–0.4‰), and was colonized 2 years later. The higher chloride concentration is suggested to be the reason for slower invasion in this lake (Smit et al. 1993).
An experimental study of the salinity tolerance of *D. polymorpha* polymorpha in the upper reaches of the Volga River (Kuibyshev and Kostroma reservoirs) showed that the salinity threshold at which 50% of animals are physiologically stressed and stop filtering, is about 1% (Antonov and Shkorbatov 1983). In contrast, the 50% stress threshold for zebra mussels from the Volga River Delta is 4.7–4.8%. (Antonov and Shkorbatov 1983). Salt tolerance of populations decreases with increasing distance from the Caspian Sea, and has been suggested to be based on genetic differences (Antonov and Shkorbatov 1983, Antonov and Shkorbatov 1984, Shkorbatov 1986, Shkorbatov and Antonov 1986, Shkorbatov et al. 1994). However, definitive long-term experiments to determine if these populations level differences are due to acclimation or acclimatization still need to be conducted. In laboratory experiments to test the effects of rapid changes in salinity on *D. polymorpha polymorpha* it was found that rate of salinity change affects salinity tolerance; lower salinities are lethal when change is rapid than when there is a gradual increase in salinity (Karpevich 1947a, Karpevich 1947b, Karpevich 1952a, Karpevich 1955a, Shkorbatov et al. 1994).

Thus, in Europe, *D. polymorpha polymorpha* can live in salinities up to 6% (Table 1). North American studies have found similar salinity limitations (Kilgour et al. 1994, Walton 1996). Given the salinity tolerances of this subspecies, it should be able to spread widely into estuaries and brackish waters in North America as has been predicted by Strayer and Smith (1993). However, a salinity limit of 10–14%, suggested by these authors, is high. Only *D. polymorpha andrusovi*, *D. polymorpha obtusicarinata* and *D. polymorpha aralensis* have been found at such high salinities in other parts of the world.

*Dreissena polymorpha andrusovi*

*D. polymorpha polymorpha* and *D. polymorpha andrusovi* are both found in the Northern Caspian Sea (Logvinenko and Starobogatov 1968, Galperina and Lvoova-Kachanova 1972, Lyakhnovich et al. 1994, Shkorbatov et al. 1994, Starobogatov and Andreeva 1994). For both subspecies, benthic distribution and biomass are inversely correlated with salinity (Vinogradov 1959, Osadchik 1963, Lyakhnovich et al. 1994). The salinity of the Caspian Sea increased more than 10% from 1937 to 1940 and, as a consequence, the biomass and distribution of both *D. polymorpha polymorpha* and *D. polymorpha andrusovi* were dramatically reduced (Karpevich 1947a, Karpevich 1952a, Karpevich 1955b, Vinogradov 1959, Osadchik 1963, Lyakhnovich et al. 1994). Subsequently, when the salinity was reduced, abundance increased and reached previous levels by the end of the 1960s. The salinity of the Northern Caspian increased again, and by the end of the 1970s was >10%, causing another drastic decrease in the biomass and cover (Lyakhnovich et al. 1994).

Although both subspecies occupy similar habitats, they differ in some of their habitat requirements. Especially high densities of *D. polymorpha andrusovi* are found on silty-shell sediments in the eastern and southern areas of the Northern Caspian Sea (Starobogatov and Andreeva 1994), and *D. polymorpha andrusovi* has a higher salinity tolerance than *D. polymorpha polymorpha*, up to 11–13% (Table 1). Different field studies have found different salinity optima for *D. polymorpha andrusovi*, ranging from 5 to 10% (Karpevich 1947b), 3 to 7% (Vinogradov 1955), and 3 to 8% (Lyakhnovich et al. 1994).

In laboratory experiments, optimal salinities for *D. polymorpha andrusovi* was the same for mussels from either low (4%) or high (10%) salinity habitats and ranged from 2 to 12% (Shkorbatov et al. 1994). *D. polymorpha andrusovi* can survive for a short time at salinities from 0 to 17%, and even at extremes of 19 to 20%. However, *D. polymorpha andrusovi* cannot form stable populations in waters <2% or >12–14% (Shkorbatov et al. 1994).

Interestingly, the distribution of *D. polymorpha andrusovi* in other regions of the Caspian Sea has sharply decreased due to the invasion of another mussel, *Mytilaster lineatus* (Gm.). This mussel was accidentally introduced into the Caspian Sea from the Black Sea in the 1920s with motorboats transported by train during the Russian Civil War (Logvinenko 1965). *M. lineatus* has a greater tolerance of hypoxia and appears to have out competed *D. polymorpha andrusovi* (Starobogatov and Andreeva 1994).

*Dreissena polymorpha obtusicarinata* and *Dreissena polymorpha aralensis*

*D. polymorpha obtusicarinata* and *D. polymorpha aralensis* have higher salinity tolerance than other subspecies of *D. polymorpha*, and at the end of the 1950s were the dominant benthic animals in the Aral Sea (Khusainova 1954, Khusainova 1958, Yablonskaya 1960a, Yablonskaya 1960b, Zenkevich 1963, Mordukhai-Boltovskoi 1972, Yablonskaya et al. 1973, Starobogatov and Andreeva 1994). *D. polymorpha obtusicarinata* was found in salinities up to 18.4% (Lyakhnovich et al. 1994). According to Zenkevich (1963), the average historic salinity of the Aral Sea during natural hydrological conditions was 10.2%. Intensive use of water from rivers (Amu-Darya and Syr-Darya) flowing into the Aral Sea for irrigation caused a dramatic increase (up to 28%) in the salinity (Kodyakov 1991). Subsequent to increased water salinity since the 1960s, the abundance and density of all subspecies of *Dreissena* has decreased (Mordukhai-Boltovskoi 1972, Yablonskaya et al. 1973). An especially dramatic reduction in *D. polymorpha obtusicarinata* was observed in the mid-1970s, and now this subspecies is believed to be completely extinct (Andreeva and Andreev 1990b, Bekmuraeva 1991, Starobogatov and Andreeva 1994).

*D. polymorpha aralensis* was found near estuaries of the Amu-Darya and Syr-Darya Rivers and in waterbodies of the Aral Sea drainage basin (Starobogatov and Andreeva 1994). Experimental studies and field observations demonstrated that adult *D. polymorpha aralensis* can survive in salinities from 0.6 to 17.6%, and its larvae can survive from 2.0 to 17.6% (Khusainova 1958). By 1980, after an increase in salinity, *D. polymorpha aralensis* disappeared from the Aral Sea (Andreeva and Andreev 1990b, Starobogatov and Andreeva 1994); however, it may still be found in other waterbodies of the Aral Sea drainage basin (Starobogatov and Andreeva 1994).

Unfortunately, the effects of physical factors other than salinity on the different subspecies of *D. polymorpha* have not been extensively studied, and the majority of research has been conducted on *D. polymorpha* from freshwater habitats, and therefore, *D. polymorpha polymorpha*. Unless otherwise indicated, the remainder of the literature we review is research on *D. polymorpha polymorpha*.

**Temperature**

The lower temperature limit for *D. polymorpha* is 0°C; zebra mussels cannot survive freezing (Lufener 1965). Mikheev (1967a) studied the filtering activity of zebra mussels from the Pyalovskoe Reservoir (Russia) at low water temperatures. He found that latero-
frontal cilia of gill filaments are completely motionless at 0.5°C, and the lateral cilia barely move at that temperature. The activity of the cilia increases with rising temperatures. At 2°C some of the latero-frontal cilia become active, but not all; active rows of latero-frontal cilia are adjacent to nonmoving cilia on the same gill. At 3°C all of the cilia become active (Mikheev 1967a). Reeder and Bij de Vaate (1990) also reported an increase in filtering rate at 3°C.


In contrast to spawning, European and North American studies have found that veligers can be found in the plankton when temperatures exceed 12°C (Shevtsova 1965a, Wiktor 1969, Slota 1969, Kornobis 1977, Sprung 1987, Sprung 1989, Borcherding 1991, Sprung 1991, Borcherding 1992, Neumann et al. 1993, Sprung 1993, Ram et al. 1993), and some authors report finding larvae at 8–9°C (Yuroshenko and Naberezhny 1971, Kachalova and Slota 1964). However, spawning of _D. polymorpha_ at temperatures lower than 10°C is doubtful, particularly as zebra mussels do not appear to grow or develop below 10°C. Karatayev (1983) suggested that veligers observed at low temperatures might have been carried downstream by currents from warmer parts of reservoirs or connected waterways.

Natural field experiments on the effects of temperature on the growth and reproduction of zebra mussels have been provided by research conducted in the cooling reservoirs of thermal and nuclear power plants. Heating can increase the growth rate and productivity of _D. polymorpha_ (Stanczykowska 1976, Elagina et al. 1978, Karatayev 1983, Karatayev 1984, Karatayev 1990, Lvova et al. 1994). The density and biomass of _D. polymorpha_ are usually higher in areas of cooling reservoirs where water temperatures are 2–6°C above natural temperatures (up to 30°C) than they are in areas where temperatures are not elevated (Pigdaiko 1974, Morukh-Boltovskaii 1975, Oszka and Oszka 1976, Korgina 1978, Karatayev 1983, Grigelis and Raciu纳斯 1984, Karatayev 1988). For example, the production/biomass coefficient for zebra mussels in areas heated 1.5–5°C above normal by the Lukomskaya Thermal Power Station is 50% higher, and the average seasonal growth is 57–100% higher than for zebra mussels grown in unheated waters (Karatayev 1983, Karatayev 1984, Karatayev 1990, Lvova et al. 1994). In addition, _D. polymorpha_ starts spawning earlier in the season in waterbodies warmed by cooling waters (Karatayev 1981, Lewandowski and Ejsmont-Karabin 1983). Thus, in the heated zone of the Konin Lakes, _D. polymorpha_ reproduction begins in April, but not for another 2 months in the unheated zone (Lewandowski and Ejsmont-Karabin 1983). In heated areas of cooling reservoirs larvae are also found in the plankton longer than in unheated areas (Kornobis 1977, Lewandowski and Ejsmont-Karabin 1983, Stanczykowska et al. 1988), suggesting that spawning takes place over a longer period.

Numerous studies have been conducted in both the field (in cooling reservoirs of thermal and nuclear power stations) and laboratory to determine the upper temperature limit for adult _D. polymorpha_ (Shkorbatov 1981, Shkorbatov and Antonov 1980, Karatayev 1983, Protasov et al. 1983a, Protasov et al. 1983b, Antonov and Shkorbatov 1984, Shkorbatov and Antonov 1986, Shkorbatov 1986, Afanasiev and Protasov 1987, Antonov and Shkorbatov 1990, Afanasiev and Shatokhina 1993, Shkorbatov et al. 1994, Antonov 1997). Laboratory studies conducted by Shkorbatov et al. are the most detailed. They carried out long-term studies of zebra mussel tolerance to high temperatures from different regions of the FSU (Shkorbatov and Antonov 1980, Shkorbatov 1981, Antonov and Shkorbatov 1984, Shkorbatov 1986, Shkorbatov and Antonov 1986, Antonov and Shkorbatov 1990, Shkorbatov et al. 1994, Antonov 1997). In the laboratory they found that the temperature threshold where 50% of the population is stressed (does not filter, but effects are reversible, P < 50%) for different populations of _D. polymorpha_ from Volga River varied from 24.8 to 28.1°C, and the 100% thermal stress threshold (P = 100%) is between 28–31°C. Lethal temperatures for the populations studied, where 50% of mussels die (L50) and where 100% of mussels die (L100) are 30.7–33.0°C and 33.5–36.0°C, respectively (Shkorbatov et al. 1994). These authors found that the upper temperature limit for zebra mussels depends on the climatic zone from which they were collected. The highest thermal tolerance has been observed for _D. polymorpha_ from the Volga Delta (46°N), and the lowest for zebra mussels from the Rybinskoe Reservoir (59°N) (Antonov and Shkorbatov 1984, Shkorbatov and Antonov 1986, Shkorbatov 1986, Shkorbatov et al. 1994). Within a waterbody, higher thermal tolerance (41°C) was found for _D. polymorpha_ from heated areas as compared with unheated areas of the Kostromskaya Thermal Power Station (Russia) cooling reservoir (Shkorbatov and Antonov 1986, Shkorbatov et al. 1994).

Upper temperature limits for zebra mussels observed in the field rather than the lab might be a better predictor of geographic limits to _D. polymorpha_ spread. Afanasiev (1986) found that zebra mussels can be inhibited by temperatures higher than 27°C, and even short exposure to 29°C can eliminate more than 70% of a _D. polymorpha_ population (Afanasiev et al. 1988). However, many authors have shown that _D. polymorpha_ can live at 30°C (Karatayev 1983, Protasov et al. 1983b, Vladimirrov 1983, Karatayev 1984, Afanasiev and Protasov 1987, Lyakhovich and Karatayev 1988, Karatayev 1992, Afanasiev and Shatokhina 1993, Karatayev and Lvova 1993, Protasov and Sinitsina 1993, Sinitsina and Protasov 1993, Lyakhovich et al. 1994, Aldridge et al. 1995), and can survive in cooling reservoirs at temperatures up to 32–34°C (Table 2).

The most detailed field studies of thermal tolerance of zebra mussels in FSU were conducted in Lukomskoe Lake, a cooling reservoir for the Lukomskaya Thermal Power Station. Experiments were conducted using caged zebra mussels placed in three different areas: the unheated area of the reservoir (zone III), the area with moderate heating (1.5–4.9°C above normal, zone II), and...
### Table 2.
Upper temperature limit for *Dreissena polymorpha* in various waterbodies.

<table>
<thead>
<tr>
<th>Waterbody</th>
<th>Temperature (°C)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult zebra mussels</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lukomskoe Lake</td>
<td>32</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td>Zaporozhske Reservoir</td>
<td>31.5</td>
<td>Lyakhnovich et al. 1994</td>
</tr>
<tr>
<td>Canal of the Pridnieprovskaya Power Station</td>
<td>32</td>
<td>Lyakhnovich et al. 1994</td>
</tr>
<tr>
<td>Kuchurganskiy Liman</td>
<td>32</td>
<td>Vladimir 1983</td>
</tr>
<tr>
<td>Cooling reservoir of the South-Ukrainian Nuclear Station</td>
<td>33</td>
<td>Sinitsina and Protasov 1993</td>
</tr>
<tr>
<td>Cooling reservoir of the Chernobyl Nuclear Station</td>
<td>34</td>
<td>Protasov et al. 1983b</td>
</tr>
<tr>
<td>Veligers</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Konin Lakes</td>
<td>29</td>
<td>Lewandowski and Ejsmont-Karabin 1983</td>
</tr>
<tr>
<td>Canal Dnieper-Krivoi-Rog</td>
<td>30</td>
<td>Shetvsova 1968a</td>
</tr>
</tbody>
</table>

the area with the highest degree of heating (4.8–10.8°C above normal, zone I) (Karatayev 1983, Karatayev 1984, Karatayev 1992) (Table 3). Mortality was greatest when temperatures exceeded 32°C (Tables 2, 3). In general, zebra mussels survived temperatures up to 31–34°C (Table 2). In North America, zebra mussels from rivers have been shown to have thermal limits of around 30–32.5°C (Aldridge et al. 1995). Zebra mussel larvae appear to be less tolerant of high temperature than adults (Shevtsova 1968a, Lewandowski and Ejsmont-Karabin 1981) (Table 3).

*D. bugensis* appears to be less tolerant of high temperatures than *D. polymorpha* (Dyga and Zolotareva 1976, Antonov and Shkorbatov 1990, Domn et al. 1993). Dyga and Zolotareva (1976) found that in the heated zone of the Zaporozhske Reservoir, quagga mussels can survive up to 30.5°C, lower than the tolerance of *D. polymorpha* (Table 2).

### OXYGEN

The tolerance of dreissenids to low oxygen conditions has been the focus of many field and laboratory studies (Ovchinnikov 1954, Feigina 1959, Mikheev 1967a, Mikheev 1967b, Spiridonov 1971, Shkorbatov 1981, Antonov and Shkorbatov 1984, Shkorbatov and Antonov 1986, Shkorbatov et al. 1994). Initially, Zhadin (1946) suggested that *D. polymorpha* do not occur in habitats where the oxygenation falls below 91.7% of full saturation. Later Ovchinnikov (1954) found, in the Rybinskoe Reservoir, that *D. polymorpha* live in areas with oxygen content higher than 70–80%, and Feigina (1959) found that *D. polymorpha* can survive in waters with oxygen concentration not less than 50% of full saturation. More recent work has shown a critical threshold of 25% oxygenation for *D. polymorpha* (Mikheev 1961, Spiridonov 1972, Shkorbatov et al. 1994). However, zebra mussels can survive for several days in anoxic conditions, depending on the temperature. Mikheev (1964) found that 100% of *D. polymorpha* in anaerobic conditions died on the sixth day of exposure at 17–18°C, on the fourth day at 20–21°C, on the third day at 23–24°C, and that small mussels were more sensitive to the lack of oxygen, Karpevich (1952a) found that *D. polymorpha* in anoxic conditions at 17–18°C can survive 4–5 days. Spiridonov (1972) reported 100% mortality of zebra mussels in anoxic conditions at 20°C after 6–7 days. Similar results have

### Table 3.
Mortality of *Dreissena polymorpha* in experimental cages in the most heated (I), medium heated (II), and unheated (III) zones of Lukomskoe Lake (from Karatayev 1983).

<table>
<thead>
<tr>
<th>Zone</th>
<th>Size range (mm)</th>
<th>Initial sample size (May 9)</th>
<th>June 9</th>
<th>July 28</th>
<th>August 6</th>
<th>September 8</th>
<th>October 28</th>
<th>Monthly mortality</th>
<th>Number of individuals</th>
<th>Total mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>8–10</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td>19</td>
<td>2</td>
<td>1</td>
<td>22</td>
<td>96</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14–16</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td>3</td>
<td>0</td>
<td>24</td>
<td>89</td>
<td></td>
</tr>
<tr>
<td></td>
<td>20–22</td>
<td>28</td>
<td>1</td>
<td>1</td>
<td>25</td>
<td>1</td>
<td>0</td>
<td>28</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25 &amp; &gt;</td>
<td>24</td>
<td>1</td>
<td>2</td>
<td>20</td>
<td>1</td>
<td>0</td>
<td>24</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>T °C</td>
<td>16.6</td>
<td></td>
<td>29.2</td>
<td>26.8</td>
<td>32.4</td>
<td>25.8</td>
<td>16.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>8–10</td>
<td>26</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14–16</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>20–22</td>
<td>27</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25 &amp; &gt;</td>
<td>20</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>T °C</td>
<td>9.8</td>
<td></td>
<td>22.8</td>
<td>23.5</td>
<td>24.9</td>
<td>18.3</td>
<td>12.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>8–10</td>
<td>25</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14–16</td>
<td>27</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>20–22</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25 &amp; &gt;</td>
<td>28</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>T °C</td>
<td>8.0</td>
<td></td>
<td>21.0</td>
<td>22.0</td>
<td>21.6</td>
<td>16.0</td>
<td>8.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
been obtained for *D. polymorpha* from the Kuibyshevskoe Reservoir (Shkorbatov et al. 1994).

*D. bugensis* appears to be more tolerant of low oxygen conditions than *D. polymorpha*. Although Shkorbatov et al. (1994) found that all *D. polymorpha* died under anoxic conditions at the fourth day of exposure, all *D. bugensis* survived through the fourth day. Birger et al. (1975) also showed that *D. polymorpha* requires higher oxygen concentrations than *D. bugensis*.

Observations in the field of the distribution of *D. polymorpha* support laboratory findings. In the Zaporozhskoe Reservoir, zebra mussels are never found in deep waters, where the oxygen content near the bottom decreases to 3–5% of full saturation during the summer season (Lyakhnovich et al. 1994). Because of high oxygen requirements, *D. polymorpha* cannot survive in or above silts, near the bottom decreases to 3–5% of full saturation during the day. Birger et al. (1975) also showed that *D. polymorpha* requires four days of exposure, all *D. bugensis* survived through the fourth day. Shkorbatov et al. (1994) observed (Shkorbatov et al. 1994).

In the Kuibyshevskoe Reservoir (Russia), *D. polymorpha* grows on 5.5 m submerged dead trees that were stranded when the reservoir was created by flooding a forest. It does not grow on the bottom 1 m of trees over the silty sediment (Lyakhov and Mikheev 1964). High densities of zebra mussels overgrow trees to the very bottom at another site in the same reservoir with a constant water current and oxygenation (Lyakhov and Mikheev 1964).

Construction of a cascade of reservoirs on the Dnieper River (Ukraine) changed the hydrological regime in the Zaporozhskoe and Dnieproprovskoe reservoirs, increasing siltation and decreasing oxygen levels. *D. bugensis* replaced *D. polymorpha* as the dominant species in these reservoirs because it has a higher tolerance for silt and low oxygen, and now 80–90% of the mussels in these two reservoirs are *D. bugensis* (Zhuravel 1967, Birger et al. 1968, Lubyanov and Zolotareva, 1976). The density and biomass of quagga mussels in the Zaporozhskoe Reservoir are as high as 100,000–130,000 m\(^{-2}\) (10–12 kg m\(^{-2}\)) (Dyga and Zolotareva 1976). Similar patterns were observed in other reservoir cascades in the Ukraine, where *D. bugensis* displaces *D. polymorpha* as the dominant species (Zuravel 1965, Zhuravel 1967, Birger et al. 1968, Zagubizhenko and Lubyanov 1971, Birger et al. 1975, Pugin 1979).

**SUBSTRATE**


Similar results have been found in North America. Although *D. polymorpha* has been reported to colonize areas dominated by silt in the Laurentian Great Lakes (Hunter and Bailey 1992, Dermott and Munawar 1993), Hunter and Bailey (1992) found that *D. polymorpha* colonized soft substrates in Lake St. Clair by lateral extension of druses which originated from attachment to small pieces of hard substrate, usually live unionid mussels, unionid shells, or clusters of zebra mussels.

High densities of zebra mussels may also be found in newly constructed reservoirs where the bottom is covered with only a thin layer of silt (Kovalova 1967, Kovalova 1969, Spiridonov 1971, Mikheev and Novik 1971, Kirpichenko and Lyakhov 1976, Kovalova 1973). As reservoirs age and silt builds up, zebra mussel densities decline (Lyakhov and Mikheev 1964, Kirpichenko 1968, Mikheev and Novik 1971, Lvova 1977). After the construction of the reservoir for the Kaunas Hydroelectric Power Plant (Lithuania) in 1961, rocky areas were abundant and zebra mussels were found at high densities. By 1972, 80% of the bottom was covered by silt, resulting in a dramatic decrease in zebra mussel density (Bubinas
TABLE 4.
Density and biomass of *Dreissena polymorpha* on various substrates in different types of waterbodies.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Waterbody</th>
<th>Density mean ± SE (m⁻²)</th>
<th>Biomass mean ± SE (g·m⁻²)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stones</td>
<td>Sara Lake</td>
<td>1,580</td>
<td>642</td>
<td>Lyakhnovich et al. 1994</td>
</tr>
<tr>
<td></td>
<td>Naroch Lake 1997</td>
<td>2,396 ± 469</td>
<td>548 ± 107</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Myastro Lake 1995</td>
<td>1,644 ± 698</td>
<td>1,024 ± 491</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Reservoir Drozdy 1995</td>
<td>5,540 ± 1,729</td>
<td>2,154 ± 568</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td>Sand</td>
<td>Volgogradskoe Reservoir</td>
<td>118</td>
<td>5</td>
<td>Kovalova 1969</td>
</tr>
<tr>
<td></td>
<td>Lukomskoe Lake</td>
<td>1,374</td>
<td>527</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td></td>
<td>Naroch Lake 1997</td>
<td>2,11 ± 42</td>
<td>57 ± 11</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Myastro Lake 1995</td>
<td>1,911 ± 683</td>
<td>969 ± 448</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Batorino Lake 1995</td>
<td>474 ± 382</td>
<td>85 ± 58</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Reservoir Drozdy 1995</td>
<td>977 ± 326</td>
<td>409 ± 151</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td>Silty sand</td>
<td>Volgogradskoe Reservoir</td>
<td>870</td>
<td>32</td>
<td>Kovalova 1969</td>
</tr>
<tr>
<td></td>
<td>Lukomskoe Lake</td>
<td>3,930</td>
<td>967</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td>Shells</td>
<td>Lukomskoe Lake</td>
<td>2,607</td>
<td>854</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td></td>
<td>Sara Lake</td>
<td>1,585</td>
<td>825</td>
<td>Lyakhnovich et al. 1994</td>
</tr>
<tr>
<td></td>
<td>Naroch Lake 1997</td>
<td>1,018 ± 218</td>
<td>251 ± 62</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td>Semisubmerged macrophytes</td>
<td>Lukomskoe Lake</td>
<td>2,577</td>
<td>684</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td>Submerged macrophytes</td>
<td>Batorino Lake 1995</td>
<td>2,276 ± 1,023</td>
<td>1,163 ± 314</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td>Clay</td>
<td>Lukomskoe Lake</td>
<td>3,545</td>
<td>369</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td></td>
<td>Sara Lake</td>
<td>1,248</td>
<td>309</td>
<td>Lyakhnovich et al. 1994</td>
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<tr>
<td></td>
<td>Myastro Lake 1995</td>
<td>1,523 ± 294</td>
<td>193 ± 70</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td>Silty soil</td>
<td>Volgogradskoe Reservoir</td>
<td>72</td>
<td>19</td>
<td>Kovalova 1969</td>
</tr>
<tr>
<td>Pure silt</td>
<td>Volgogradskoe Reservoir</td>
<td>657</td>
<td>25</td>
<td>Kovalova 1969</td>
</tr>
<tr>
<td></td>
<td>Lukomskoe Lake</td>
<td>2</td>
<td>0.1</td>
<td>Karatayev 1983</td>
</tr>
<tr>
<td></td>
<td>Naroch Lake 1997</td>
<td>64 ± 64</td>
<td>15 ± 15</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Myastro Lake 1995</td>
<td>0</td>
<td>0</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td></td>
<td>Batorino Lake 1995</td>
<td>65 ± 61</td>
<td>20 ± 20</td>
<td>Burlakova 1998</td>
</tr>
<tr>
<td>Flooded forests</td>
<td>Kuibyshevskoe Reservoir</td>
<td>3,150</td>
<td>1,860</td>
<td>Lyakh and Mikheev 1964</td>
</tr>
<tr>
<td></td>
<td>Sylvenskiy bay of Kamskoe Reservoir</td>
<td>60,803*</td>
<td>21,605</td>
<td>Gubanova 1969</td>
</tr>
<tr>
<td></td>
<td>Volgogradskoe Reservoir</td>
<td>22,000</td>
<td>4,000</td>
<td>Spiridonov 1967</td>
</tr>
<tr>
<td></td>
<td>Volgogradskoe Reservoir</td>
<td>—</td>
<td>1,480</td>
<td>Spiridonov 1971</td>
</tr>
<tr>
<td></td>
<td>Volgogradskoe Reservoir</td>
<td>4,660*</td>
<td>—</td>
<td>Konstantinov &amp; Spiridonov 1977</td>
</tr>
</tbody>
</table>

*Not including yearling mussels.

1980). A pronounced decrease of *D. polymorpha* density with increasing silt was also found in lakes of Volga River Delta (Pokrovskaya 1966). Zebra mussels were the dominant species in these lakes in the 1920s, but completely disappeared by the end of the 1950s due to a dramatic increase in bottom siltation. Tseyeb et al. (1966) found in Dnieper River reservoirs that *D. bugensis* is more adapted to live on silt sediments than *D. polymorpha*. Low densities of zebra mussels can also be found on clay (Kovalova 1969, Dyga and Lubyanov 1975, Lyakhnovich et al. 1994).

**WATERBODIES OF DIFFERENT TYPES**

**Lakes**

Zebra mussels can be found in a wide range of types of waterbodies, however, most work has focused on factors affecting their presence and abundance in lakes. These have included the importance of factors such as nutrients, pH, and calcium (Stanczykowska 1977, Ramcharan et al. 1992a, Ramcharan et al. 1992b, Lyakhnovich et al. 1994, and references there in), biotic factors (Molloy et al. 1997, and references there in), as well as lake morphometry (Strayer 1991). Using data from European lakes, Ramcharan et al. (1992a) found apparent thresholds of calcium carbonate and pH that determine the presence or absence of zebra mussels, and that high nutrient levels are associated with lower population densities. Ramcharan et al. (1992b) also found that lake size and flushing rate had an impact on population fluctuations of zebra mussels in European lakes. Based on data from Europe, Strayer (1991) suggested that small warm lakes are more suitable for *D. polymorpha* than deep and cold lakes.

Research in the FSU has found that trophic type affects the probability of finding zebra mussels in a lake (Ovchinnikov 1933, Deksbakh, 1935, Karatayev 1989, Lyakhnovich et al. 1994, Karatayev and Burlakova 1995a, Karatayev and Burlakova 1995b). Ovchinnikov (1933) and Deksbakh (1935) suggested that eutrophic lakes are the best habitat for *D. polymorpha*. Using data from 553 Belarussian lakes, Karatayev and associates (Karatayev 1989, Karatayev and Burlakova 1995a, Karatayev and Burlakova 1995b, A. Karatayev, L. Burlakova, L. Johnson and D. Padilla,
unpublished data) have shown that zebra mussels are found most
often in mesotrophic lakes, are found less often in oligotrophic and
meso-oligotrophic lakes, least often in eutrophic lakes, and do not
inhabit dystrophic lakes. However, as Karatayev et al. (1997) point
out, the presence of zebra mussels in a lake will decrease chloro-
phyll levels, lowering the trophic status of a lake subsequent to
invasion. Better information about the trophic status of lakes when
they are initially invaded will help answer this question.

Studies on the effects of trophic status on zebra mussels have
shown that the maximum density of D. polymorpha shifts to shal-
lower depths with increasing lake eutrophication (Karatayev and
Burlakova 1995a, Burlakova 1998). Moreover, the maximum
depth of zebra mussels within a lake increases with decreased
trophic status. One possible mechanism for this pattern is that the
decline in water clarity, with increased eutrophication, reduces
the depth of submerged macrophytes, which are an important sub-
strate for zebra mussels. In addition, increased eutrophication leads
to increased siltation in lakes, reducing the area of suitable sub-
strates. This results in shifting the D. polymorpha distribution to
shallower parts of lakes (Karatayev and Burlakova 1995a, Burla-
kova 1998). These hypotheses can be tested as we gather more
comparable information for more lakes with different trophic status.

Reservoirs

In reservoirs formed by the damming of rivers, D. polymorpha
colonizes all suitable substrates, often at high densities (Zhravel
1973, Mordukhai-Boltovskoi et al. 1974, Lyakhov and Mor-
et al. 1994). For example, D. polymorpha colonized the
Dnieprskove Reservoir, formed by damming the Dnieper River,
during the first few years after its construction in 1932 (Zhravel
1952). During the Second World War the dam was removed when
the Soviet army retreated in 1941, and the density of D. polymor-
pha in the former reservoir portion of the Dnieper River dramati-
cally decreased. After reconstruction of the reservoir, D. polymor-
pha again attained high densities (Zhravel 1952).

Especially high densities of D. polymorpha form in reservoirs
created by flooding forested areas, because zebra mussels colonize
flooded stumps, trunks, and branches of trees and brushwood (Zhravel
1952, Luferov 1963, Lyakhov and Mikheev 1963, Lya-
khov and Mikheev 1964, Gromov 1965, Mordukhai-Boltovskoi
donov 1971, Andronova et al. 1976, Kirpichenko and Lyakhov
1976, Konstantinov and Spiridonov 1977, Lvova 1977, Spiridon-
ov 1978, Lyakhnovich et al. 1994) (Table 1). In the flooded
areas of the Kuiyshivskoe Reservoir (Russia) which did not have
trees, D. polymorpha was found in 46% of samples at an average
density of 518 m⁻², whereas in the areas that were flooded forests,
zebra mussels were found in 80% of samples at an average density
of 3,150 m⁻² (Lyakhov and Mikheev 1964). In the Volgogradskoe
Reservoir (Russia) the highest density (22,000 m⁻²) and biomass
(4 kg m⁻²) of D. polymorpha are also found in flooded forest areas
(Spiridonov 1967, Spiridonov 1970), and in the Sylvenskyi Bay of
the Kamskoe Reservoir, the density of D. polymorpha in flooded
forest areas was as high as 371,703 m⁻² with a biomass of 11.4 kg
m⁻² (Gubanova 1968).

In reservoirs that are drawn down during the winter, D. poly-

morpha disappears from the shallow areas (Kachanova 1963,
Mikheev 1964, Gromov 1965, Kirpichenko 1968, Mikheev and
Novik 1971, Konstantinov and Spiridonov 1977, Lvova 1977,
attached to large invertebrates, such as unionid mussels, that mi-
grate to deeper waters survive (Mikheev and Novik 1971, Lyakh-
novich et al. 1994). Thus, the shallow areas of reservoirs subject
to draw downs or fluctuating water levels are usually inhabited only
by yearling mussels. In the Uchinskoe Reservoir (Russia) this area
extends to a depth of 1.5 m (Lvova 1977, Lvova 1978), and, in the
Kremenchuskoe Reservoir (Ukraine), down to 2 m, and covers
18% of the reservoir area (Lyakhnovich et al. 1994). However,
Mikheev and Novik (1971) found that zebra mussels can survive in
the shallow drained areas under ice for long periods at tempera-
tures near 0°C, but not lower. They found that zebra mussels died
only in the parts of reservoirs that drained in the autumn, before ice
cover.

Extremely high densities of D. polymorpha have also been
found on various artificial substrates in reservoirs (Protasov et al.
1983a, Afanasiev and Protasov 1987, Toderash and Vladimirov
1990, Lyakhnovich et al. 1994). For example, on the concrete
walls of the cooling reservoir of the Chernobyl Nuclear Power
Station (Ukraine), the density of D. polymorpha was 248,000 m⁻²,
and biomass was 12 kg m⁻² (Protasov et al. 1983a). This extremely
high density of zebra mussels formed due to both the presence of
suitable artificial substrate and constant water currents.

Rivers

In rivers, zebra mussels are most affected by unidirectional
water flow, disturbance due to water flow, suspended sediment,
and minimal suitable substrates for attachment. Frequently, large
molluscs (bivalves and gastropods) will be the most abundant hard
substratum for zebra mussel attachment in rivers, and are some of
the most often used substrates for attachment in any type of water-
body (Sebestyen 1937, Zhadin 1948, Zhravel 1957, Zhravel
1959, Lubyanov 1956, Zhadin and Gerd 1961, Wiktor 1963,
Kachalova and Sloka 1964, Kuchina 1964, Butenko 1967, Wolff
1994, Karatayev and Burlakova 1995a, Ricciardi et al. 1996,
Karatayev et al. 1997). Often, unionid mussels are the only suitable
substrata for zebra mussel attachment in rivers (Zhadin 1948,
Lubyanov 1956, Lubyanov 1960, Kachalova and Sloka 1964,
Kuchina 1964, Tischikov 1984, Lyakhnovich et al. 1984, Lyakh-
novich et al. 1994). For example, in the Severnaya Dvina River the
density of zebra mussels is low (<10 m⁻²), and zebra mussels are
found on various artificial substrates in reservoirs (Protasov et al.
1983a, Afanasiev and Protasov 1987, Toderash and Vladimirov
1990, Lyakhnovich et al. 1994). Zebra mussels are found only on unionid mussels and occasional stones (Kuchina 1964).
Similarly, zebra mussels are found most frequently on unionid mussels in the Daugava River (Kachalova and Sloka 1964) and Berezina River (Lyakhnovich et al. 1984).

Other factors preventing zebra mussels from attaining high
densities in rivers are the movement of bottom sediments and high
concentrations of suspended matter, especially during periodic
flooding (Zhadin 1946, Zhadin 1959, Lubyanov 1956, Lubyanov
ainova (1954, 1958), and Mordukhai-Boltovskoi (1960) found that zebra mussels are rare in rivers with constant high concentra-
tions of suspended matter, as it inhibits filtering activity.
Unidirectional water flow makes it difficult for local populations of zebra mussels in rivers to increase in density, as larvae are swept downstream. However, high densities of *D. polymorpha* can form in rivers flowing from lakes or reservoirs populated by zebra mussels (Lubyanov 1957, Kirpichenko 1963, Lyakhnovich et al. 1984, Clevlen and Frenzel 1993, Karataev and Burlakova 1995a) which provide a supply of larvae and colonizing juveniles.

High densities of zebra mussels can also form in the lower courses of rivers and deltas because of very slow flow, and reduced movement of bottom sediments (Kuchina 1964, Grigoriev 1965, Kharchenko and Shevtsova 1983, Lyakhnovich et al. 1994). In the lower Danube River the average density of *D. polymorpha* is 1,000 m⁻² and the biomass is 185 g m⁻² (Kharchenko and Shevtsova 1983). Extremely high densities of zebra mussels are also found in the South Bug Liman (Ukraine) (Grigoriev 1965), where in the shallow areas the density of zebra mussels on semisubmerged macrophytes (*Phragmites communis*) is 169,000 m⁻², and biomass is 3–5 kg m⁻², but at other sites without macrophytes, the density is 1,730 m⁻², and biomass is 1,240 g m⁻².

**Canals**

Canals are distinct from lakes and reservoirs because there is a constant, unidirectional water current, and differ from rivers because bottom sediments are much more stable and the concentration of suspended matter is much lower (Karataev 1983, Burlakova 1998). Extremely high densities of zebra mussels form in canals (Kachanova 1962, Kachanova 1963, Puchkova and Polivanova 1967, Shevtsova 1968b, Lvova-Kachanova 1971, Kafantikova 1975, Kornobis 1977, Lvova 1977, Stanczykowska 1977, Karataev 1983, Sokolova et al. 1981, Shevtsova and Kharchenko 1981, Kharchenko and Shevtsova 1983, Afanasiev 1987, Lyashenko and Kharchenko 1988, Lyakhnovich et al. 1994). The average biomass of zebra mussels in the Uchinskoe Reservoir (Russia) was 117–1,044 g m⁻², in the canal outflowing from this reservoir, the average biomass was 3–5 kg m⁻² (Lvova 1977). In canals connecting the Konin Lakes (Poland), which are heated, the average density of zebra mussels was 40,000 m⁻², in the lakes the densities varied from 100 to 1,100 m⁻² (Kornobis 1977). In Lukomskoe Lake (Belarus) the average density of zebra mussels in 1978 was 758 m⁻², with a biomass of 124 g m⁻², whereas in the canal outflowing from this lake the average density of zebra mussels was 58 times, and biomass was 55 times higher (Karataev 1983). The maximum density of *D. polymorpha* in the North-Crimean Canal was 19,899 m⁻², and biomass was 4.7 kg m⁻² (Shevtsova and Kharchenko 1981). Extremely high densities (30,000 m⁻²), and biomass (50 kg m⁻²) of zebra mussels were found on the walls of the Dnieper-Dnibass Canal as well (Kharchenko and Shevtsova 1983).

**DISCUSSION AND GENERAL FINDINGS**

Physical factors affect the distribution and abundance of zebra mussels among and within waterbodies, often in predictable patterns (Table 5). Important driving factors affecting the distribution of zebra mussels include suitable substrate, oxygen content, salinity, and temperature extremes. Factors affecting population density and growth are temperature and suitable substrate for attachment. Lethal temperatures (below 0°C and above 30°C) control zebra mussel distribution, as do critical temperatures for growth and spawning.

Abiotic factors such as desiccation, salinity, and oxygen can set limits to the distribution of *D. polymorpha* and its many subspecies. Some of these factors vary in a predictable fashion. Desiccation can happen at the surface of waterbodies whose water level fluctuates, either naturally as with rivers and lakes, or due to human control as with reservoirs and canals. Salinity in a liman, estuary, or small sea is greatly affected by the influx of fresh water either through rainfall (climatic conditions) or the control of rivers and canals. Increases in salinity decrease *D. polymorpha* abundance and survivorship. Oxygen content of waters can be affected by many factors. Oxygen content will decrease with increased temperature and metabolic activity of living organisms, including microbes. High rates of primary productivity or decomposition and low rates of water flow can create bottom waters with very low oxygen content as is seen in eutrophic lakes and reservoirs. Oxygen content can also be affected by sediment type, as some sediments...
ments such as silts can actively adsorb oxygen, reducing its content in surrounding waters.

As a result of the abiotic factors discussed, the minimum depth where zebra mussels are found is from 0.1 to 0.5 m, depending on local water level fluctuations and the probability of freezing (Stanczykowska 1976, Karatayev 1983, Karatayev 1988, Lyakhnovich and Karatayev 1988, Lyakhnovich et al. 1994, Burlakova 1988). The abundance of suitable substrate for attachment also affects depth distributions of zebra mussels. Many studies have found that in lakes and reservoirs zebra mussels have a maximum density at depths from 1 to 5 m (Kachanova 1963, Lvova-Kachanova 1971, Lvova-Kachanova and Izvekova 1973, Vishnewski 1974, Stanczykowska 1975, Stanczykowska et al. 1975, Lvova 1976, Stanczykowska 1977, Lvova 1978, Karatayev 1983, Stanczykowska et al. 1983b, Karatayev 1988, Lyakhnovich and Karatayev 1988, Lyakhnovich et al. 1994, Karatayev and Burlakova 1995a). However, when suitable substrate and water oxygen conditions occur deeper, as in Bodensee (Germany), the maximum density of <i>D. polymorpha</i> was recorded between 5–15 m depth (Grim 1971), and at 18 m in Lake Garda (Italy) where the density was 24,000 m⁻² (Franchini 1978). In Lake Erie, maximum density (3.443 m⁻²) and total wet biomass (340.9 g m⁻²) of zebra mussels were found at 10–20 depth (Dermott and Munawar 1993).


In the Laurentian Great Lakes, diereisensids occur at extreme depths. In Lake Erie, <i>D. polymorpha</i> and <i>D. bugensis</i> are relatively abundant in the profundal zone (Dermott and Munawar 1993). In general, the proportions of quagga mussels, which are more tolerant of low oxygen conditions, increase with depth whereas zebra mussels decrease (Zhuravel 1957, Zhuravel 1959, Zhuravel 1967, Mackie 1991, Mills et al. 1993, Dermott and Munawar 1993). In Lake Ontario, both quagga and zra mussels coexist at depths of 8–110 m in varying proportions, with only the quagga mussel found at 130 m (May and Marsden 1992, Mills et al. 1993). Because there are no similar lakes to the Laurentian Great Lakes in the FSU, we have no similar data to compare.

In shallow parts of large lakes and reservoirs zebra mussels can be limited by movement of consolidated sand or stone sediments and high concentrations of suspended matter (Lvova 1977, Lyakhnovich et al. 1994). <i>D. polymorpha</i> seems unable to survive in waterbodies with constant concentrations of suspended matter greater than 10–40 g m⁻³ (Mikheev 1967b). However, zebra mussels can live where the concentration of suspended matter is periodically greatly increased, such as in the Taganrog Gulf of the Azov Sea, where the content of suspended matters periodically increases (during storms) up to 500 g m⁻³ (Lyakhnovich et al. 1994).

Physical factors are important in determining both the distribution and abundance of zebra mussels. Many of these factors, acting alone or in combination, are responsible for the patterns that we see in nature, both within and among waterbodies. Further research is required to determine how these factors may covary or act in concert to affect the biology, distribution, and abundance of zebra mussels. Our goal has been to facilitate access to the large body of scientific research that has been conducted over several decades in the FSU on zebra mussels and physical factors that affect their distribution and abundance. Hopefully, access to this research will allow us to move forward to find generalizations, and where appropriate, determine differences in the causal factors affecting the distribution and abundance of zebra mussels.

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