A Review of the Biology and Ecology of the Quagga Mussel (*Dreissena bugensis*), a Second Species of Freshwater Dreissenid Introduced to North America[1]

EDWARD L. MILLS

Department of Natural Resources, Cornell Biological Field Station,
900 Shackelton Point Road, Bridgeport, New York 13030

GARY ROSENBERG

The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway,
Philadelphia, Pennsylvania 19103

ADRIAN P. SPIDLE

School of Fisheries HF-10, University of Washington, Seattle, Washington 98195

MICHAEL LUDYANSKIY

Lonaz Inc., Research and Development, P.O. Box 993, Annandale, New Jersey 08801

YURI PLIGIN

Institute of Hydrobiology, Kiev, Ukraine

AND

BERNIE MAY

Genome Variation Analysis Facility, Department of Natural Resources,
Fernow Hall, Cornell University, Ithaca, New York 14853

SYNOPSIS. North America's Great Lakes have recently been invaded by two genetically and morphologically distinct species of *Dreissena*. The zebra mussel (*Dreissena polymorpha*) became established in Lake St. Clair of the Laurentian Great Lakes in 1986 and spread throughout eastern North America. The second dreissenid, termed the quagga mussel, has been identified as *Dreissena bugensis* Andrusov, 1897. The quagga occurs in the Dnieper River drainage of Ukraine and now in the lower Great Lakes of North America. In the Dnieper River, populations of *D. polymorpha* have been largely replaced by *D. bugensis*; anecdotal evidence indicates that similar trends may be occurring in the lower Laurentian Great Lakes. *Dreissena bugensis* occurs as deep as 130 m in the Great Lakes, but in Ukraine is known from only 0–28 m. *Dreissena bugensis* is more abundant than *D. polymorpha* in deeper waters in Dneiper River reservoirs. The conclusion that North American quagga mussels have a lower thermal maximum than zebra mussels is not supported by observations made of populations in Ukraine. In the Dnieper River drainage, quagga mussels are less tolerant of salinity than zebra mussels, yet both dreissenids have acclimated to salinities higher than North American populations; eventual colonization into estuarine and coastal areas of North America cannot be ignored.

INTRODUCTION

North America's Great Lakes have recently been invaded by two species of *Dreissena* (Rosenberg and Ludyanskiy, 1994; Spidle *et al.*, 1994). The zebra mussel (*Dreissena polymorpha*) became established in Lake St. Clair of the Laurentian Great Lakes by 1986 (Hebert *et al.*, 1989) and has spread rapidly from the Great Lakes eastward through the Mohawk and Hudson River systems and southward through the Mississippi River drainage. In August of 1991, specimens of a morphologically and genetically distinct *Dreissena*, termed the quagga mussel, were discovered in the Erie Canal and Lake Ontario where they coexisted with more numerous *D. polymorpha* (May and Marsden, 1992). The quagga mussel, identified as *Dreissena bugensis* Andrusov, 1897 (Rosenberg and Ludyanskiy, 1994; Spidle *et al.*, 1994), has a distinctive shell with convex ventral margin and lacks the carina between the ventral and lateral shell surfaces resulting in a rounded cross-section. *Dreissena polymorpha* has a flat or concave ventral margin and pronounced carina so that the ventral edge of the shell is perpendicular to the lateral, allowing the zebra mussel to remain upright when placed on a flat surface. Although *D. polymorpha* is presently the prevailing species in North America, *D. bugensis* has largely replaced *D. polymorpha* in the Dnieper River drainage system in Ukraine (Pligin, 1979). In North America, the quagga mussel is primarily restricted to Lake Erie, Lake Ontario and the St. Lawrence River although one sighting of *D. bugensis* has been confirmed outside the Great Lakes basin in the Mississippi River near St. Louis, MO (O'Neill, 1995).

This paper summarizes current information about the taxonomy, geographic distribution, genetics, physiology, and ecology of the quagga mussel (*D. bugensis*) and relates this information to other dreissenids in North America and Ukraine when possible.

IDENTIFICATION OF THE QUAGGA MUSSEL AS *DREISSENA BUGENSIS*

At the time of the discovery of the quagga mussel in North America, the systematics of *Dreissena* were poorly understood, with no clear consensus as to the number of species in the genus nor their distributions. As a result, biologists were not immediately able to determine the taxonomic identity of the quagga mussel. The quagga mussel was known to have originated in the Old World, because variation at protein coding loci matched that of tissue samples from the Dnieper River, where only two dreissenid species are present: *Dreissena polymorpha* and *D. bugensis* (Zhadin, 1952). Rosenberg and Ludyanskiy (1994) reviewed the systematic literature on *Dreissena* and examined type material in the Paleontological Institute in Moscow. They found that the quagga mussel corresponds to the original description and type specimens of *D. bugensis* Andrusov, 1897. Thus, genetic analysis and examination of the primary systematic literature firmly established the identity of the North American quagga mussel as *D. bugensis* (see review by Marsden of genetics for *Dreissena* in this volume).

Russian classifications have treated *D. bugensis* as a full species or as a subspecies of *D. rostriformis* Deshayes, 1838. According to Rosenberg and Ludyanskiy (1994), living specimens of *Dreissena bugensis* can be distinguished from *D. rostriformis* by their larger size (reaching 38 mm compared to 23 mm), more pronounced byssal groove, generally less compressed shell, and a distinct color pattern. *Dreissena bugensis* typically occurs in freshwater in Russia in salinities up to 1 ppt (Nevesskaya, 1965) while *D. rostriformis* does not occur in freshwater and is restricted to the middle and southern Caspian Sea, in salinities up to 12.7 ppt (Zhadin, 1952). While Marelli (1991) recently suggested that *D. bugensis* and *D. polymorpha* are synonymous, most recent authors consider them to belong to different subgenera, and their fossil records clearly indicate different lineages (Taktakishvili, 1973; Babak, 1983; Nuttall, 1990).

The creation of putative zebra × quagga mussel hybrids in the laboratory by pooling gametes collected after exposing adults to serotonin has recently been reported, indicating that interspecies fertilization events may be possible (Nichols and Black, 1994).

These putative hybrid larvae have not been successfully reared, however, indicating that their (1) viability may be limited or (2) that these were single species haploid larvae. Evidence for species-specific sperm attractants exists (Miller, 1994) suggesting that interspecific fertilization events may be rare in nature. Further, electrophoretic surveys of loci diagnostic between zebra and quagga mussels have failed to find evidence of adult hybrids in natural populations in Lake Ontario and Lake Erie (Spidle et al., 1995), suggesting that if interspecific fertilization does occur, and if offspring of those fertilization events survive to adulthood, such hybrid individuals do not constitute a measurable proportion of the dreissenid community.
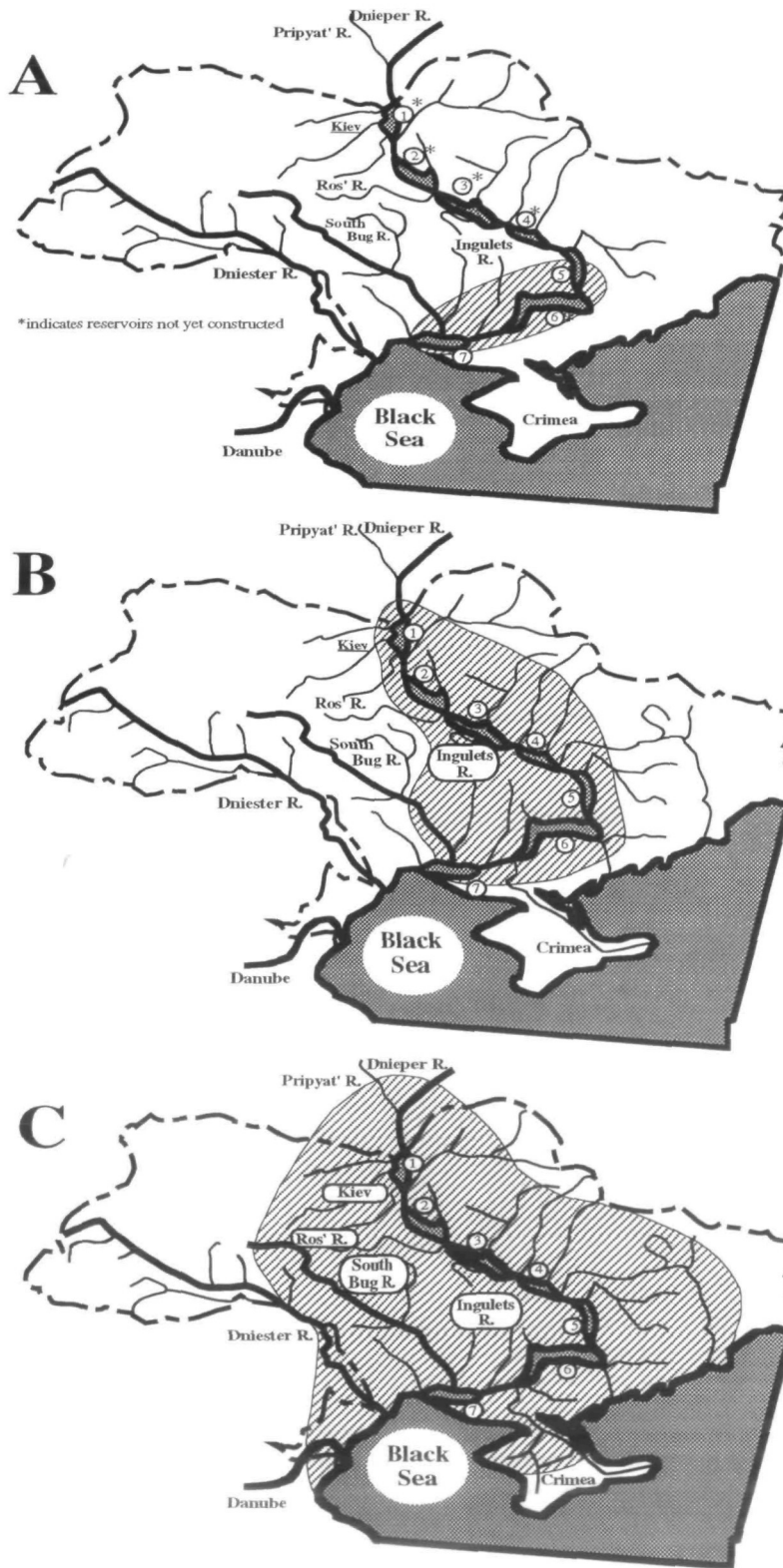
GEOGRAPHIC DISTRIBUTION

Two populations of *D. bugensis* are known to exist in the world today, in the Ukraine and the Laurentian Great Lakes. In the Dnieper River drainage of the Ukraine (Fig. 1), *D. bugensis* was first discovered in the Bug portion of the Dnieper-Bug Estuary near Nikolaev by Andrusov (1890), who named the species in 1897. Since the 1940s, the quagga mussel has spread into the Dnieper River drainage to regions that earlier had only *D. polymorpha*. Fig. 1 illustrates the range expansion of *D. bugensis* in the Dnieper and Bug River systems during the periods of 1950–53, 1970–73, and 1990–1992. Until the 1940s, *D. bugensis* was found only in the South Bug River and the lower Ingulets River (Andrusov, 1890, 1897; Zhadin, 1952; Zhuravel', 1951); it was absent from both the Dnieper portion of the Dnieper-Bug estuary and the lower Dnieper River (Markovskiy, 1954; Olivari, 1971; Moroz; 1993). In 1941, *D. bugensis* was found in the Zaporozh'ye Reservoir, the first reservoir built on the Dnieper River (Fig. 1A). As reservoirs such as the Kakhovka (Markovskiy, 1954), Dneprodzerzhinsk, Kiev, and Kanev (Pligin, 1984, 1985) were built in the 1950s and 1960s, *D. polymorpha* invaded first and *D. bugensis* appeared later (Fig. 1 B). By 1990–92, *D. bugensis* had spread to the Pripyat' River delta which is currently its northernmost range (Fig. 1 C). Between 1964 and

1989, *D. bugensis* spread approximately 500 km northward, as well as east and south through canals; it now occurs in almost all large and medium Dnieper reservoirs in the eastern and southern regions of Ukraine and the deltas of Dnieper River tributaries. Less information is available on the presence of *D. bugensis* in Dnieper River tributaries, but it dominates the macrobenthos of small reservoirs on the Ros' River, 200 km from its confluence with the Dnieper River. *Dreissena bugensis* is absent from the deltas of small rivers and estuaries on the Black Sea to the west of the Dnieper-Bug estuary (Moroz, 1993). The quagga has been reported in the Dniester River basin (Shevtsova, personal communication, 1994) but is absent in the Danube River and its canals (Grossu, 1993).

The first sightings of the quagga mussel in the Laurentian Great Lakes were in September 1989, when one quagga was found near Port Colborne, Lake Erie (Fig. 2) (Mills et al., 1993), although the recognition of the quagga type as a distinct species did not occur until 1991 (May and Marsden, 1992). By the spring of 1993, the distribution of *D. bugensis* in the Laurentian Great Lakes was from the central basin of Lake Erie to the St. Lawrence River at Quebec City. In 1992, quagga mussels were absent in Lake St. Clair, the Detroit River, western Lake Erie, the Erie-Barge Canal, Oneida Lake, the Mohawk River, the Hudson River, and Cayuga and Seneca Lakes of New York's Finger Lakes although these water bodies all contained *D. polymorpha* (Mills et al., 1993; Dermott and Munawar, 1993). In the fall of 1994, however, the first quaggas were sighted on intake structures of electric power generating stations in Cayuga and Seneca Lakes (R. Tuttle, New York State Gas & Electric, Binghamton, NY, personal communication). The first confirmation of quaggas outside the Great Lakes basin was made in the Mississippi River between St. Louis, MO and Alton, Il in 1995 (O'Neill, 1995).

ENVIRONMENTAL LIMITS

The presence of two genetically distinct species of *Dreissena* in the Laurentian Great Lakes and in the Ukraine raises the

A

Dnieper R.
Pripyat' R.
Kiev
Ros' R.
South Bug R.
Ingulets R.
Dniester R.
*indicates reservoirs not yet constructed
Danube
Black Sea
Crimea

B

Pripyat' R. Dnieper R.
Kiev
Ros' R.
South Bug R.
Ingulets R.
Dniester R.
Danube
Black Sea
Crimea

C

Dnieper R.
Pripyat' R.
Kiev
Ros' R.
South Bug R.
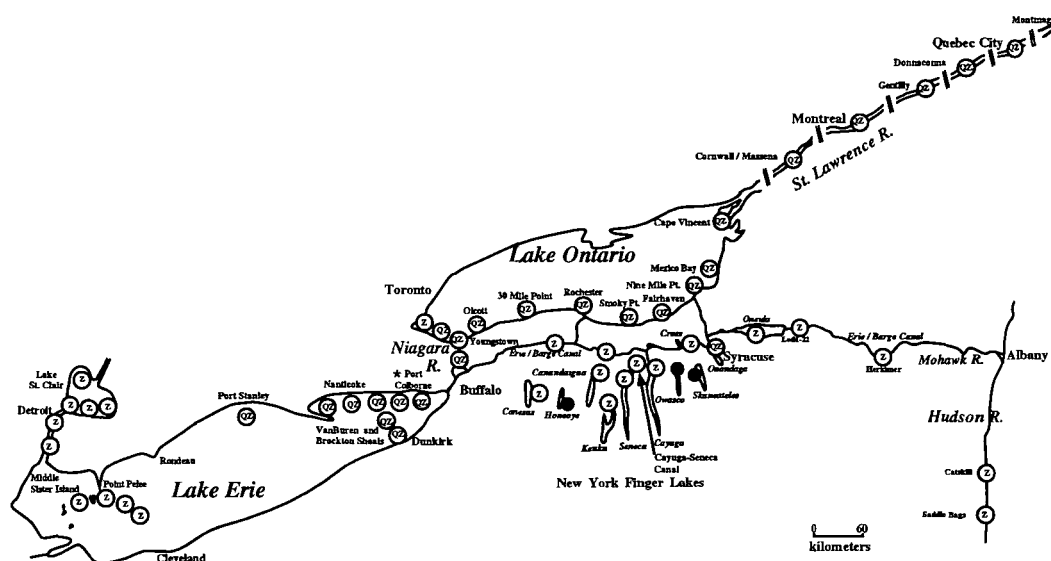Ingulets R.
Dniester R.
Danube
Black Sea
Crimea

FIG. 2. Locations of quagga (Q) (*Dreissena bugensis*) and zebra (Z) (*Dreissena polymorpha*) in the lower Great Lakes and inland waterways of New York State during 1992. ● = quagga and zebra mussel absent; ○ = quagga and/or zebra mussel present. Adapted after Mills *et al.*, 1993.

possibility that they have different habitat preferences and environmental limits leading to differential range expansion. Information about the distribution of both species in North America and Eurasia provides circumstantial evidence that *D. polymorpha* and *D. bugensis* may have different tolerances to salinity and temperature.

Salinity tolerance

The range of salinity levels inferred to limit *D. polymorpha* in Eurasia is quite wide, from 2 to 12 ppt in inland seas, but only 0.5 ppt in estuaries on the Atlantic coast of the Netherlands (see review in Strayer and Smith, 1993). Exposure to 1.6 ppt NaCl for a week was observed to be fatal to zebra mussels in one set of laboratory experiments (Horohov *et al.*, 1992), while other tests have shown perturbations in respiration of *D. polymorpha*, but no mortality, resulting from increasing salinity to 10 ppt (Karpevich, 1947). If either *Dreis-*

sena species exhibits tolerance to salinity they could colonize estuarine and coastal areas. Side by side comparisons of salinity tolerance in North American populations of *D. polymorpha* and *D. bugensis* showed that neither species could survive salinity levels greater than 5 ppt (Spidle, 1994). No interspecific difference in survival time when exposed to salinity was shown (Spidle, 1994). The negative effect of salinity on survival is enhanced at warmer temperatures (5°C to 20°C), with mussels of both species having a much shorter survival time at all salinity levels (Spidle, 1994) compared to Eurasian populations. For North American quagga, there is no evidence that the salinity tolerance of the quagga mussel is any greater than that of the zebra mussel.

The main factor controlling *Dreissena* distribution in the Dnieper-Bug estuary is water salinity (Grigoryev, 1968, Alexenko, 1991, Moroz, 1993). In the lower Dnieper River, salinity is typically about 0.3 ppt,

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FIG. 1. Range expansion of *Dreissena bugensis* (stripe pattern) in the Dnieper River drainage between 1950 and 1992. Panel A: 1950–53; Panel B: 1970–73; Panel C: 1990–92. Numbers identify location of reservoirs: 1 = Kiev; 2 = Kanev; 3 = Kremenchug; 4 = Dneprodzerzhinsk; 5 = Zaporozh'ye; 6 = Kakhovka; and 7 = Dnieper-Bug Liman.

whereas in the Dnieper-Bug estuary, depending on the flow of the Dnieper River, it varies from 0.5 to 10 ppt. *Dreissena polymorpha* is more tolerant of increases in salinity than is *D. bugensis* (Alexenko, 1991; Moroz, 1993; Antonov and Shkorbatov, 1990; and Orlova, 1987).

Dreissena polymorpha in the lower Dnieper was found to have maximum growth at salinities of 1–1.5 ppt, whereas in the Dnieper-Bug estuary maximum growth occurs at 1–3 ppt (Markovskiy, 1954). The maximum salinity in which *D. polymorpha* was found in the early 1950s was 8 ppt. In the lower Dnieper River and the Dnieper-Bug estuary, more than 50% of the mussel population was *D. polymorpha* at salinities ranging between 0.0–1 ppt as Cl⁻, whereas *D. bugensis* dominated at salinities between 0.00–0.02 ppt (Aleksenko, 1991). The maximum total salinities at which each species was found were 7.6 and 4.0 ppt, respectively. These findings contrast with Strayer and Smith (1993) who predicted that the North American distribution of *D. polymorpha* would be limited to a maximum salinity (marine ion composition) of 2 ppt. Apparently populations of *Dreissena* in Ukraine, which have experienced more generations, show greater acclimation to salinity extremes than more recently colonized dreissenids in North America.

Distribution of *D. bugensis* and *D. polymorpha* in the Dneiper-Bug estuary depends on Dnieper River run-off and salinity (Alexsenko, 1991; Moroz, 1993). These two parameters are strongly related: when the annual run-off is high, the estuary becomes less saline; when annual runoff is low, saline water from the Black Sea intrudes freshwater areas, killing off *Dreissena. Dreissena polymorpha* increases in abundance relative to *D. bugensis* as salinity increases. For example, in the low precipitation year of 1984, with high salinity levels, no *D. bugensis* were observed, while in the high precipitation year of 1981, when salinity was low, living *D. bugensis* predominated over *D. polymorpha.* The reverse situation was recorded in 1986–1987.

Laboratory experiments using Ukrainian *Dreissena* show that both species can ac-

climate to higher salinities; at 7–15°C and over a 40-day period, *D. bugensis* acclimated to a salinity of 5 ppt (survival 68%), and *D. polymorpha* to 8 ppt (survival 70%) (Aleksenko, 1991). At the same temperature over a 10-day period, mortality was more than 90% beginning from a salinity of 8 ppt for *D. bugensis* and 11 ppt for *D. polymorpha.* For mussels exposed to temperatures of 18–21°C for over a 40 day period, *D. bugensis* and *D. polymorpha* acclimated to salinities of 4 ppt (survival 91%) and 6 ppt (survival 100%), respectively. Subsequent salinities of 5 ppt and 8 ppt were lethal within 10 days to both species.

Salinity tolerances for *D. polymorpha* from the lower Dnieper River and those from the estuary have been shown to be different (Aleksenko, 1991). These studies concluded that estuarine *D. polymorpha* can survive higher salinities than riverine *D. polymorpha,* apparently because they acclimated to increased salinities in the estuary during years of low flow of the Dnieper River, when the salinity of the estuary was usually 1–3 ppt higher. Similar data were recorded for *D. polymorpha* and *D. bugensis* inhabiting the main flow of the Lower Dnieper River and the Dnieper-Bug estuary (Table 1), concluding that *D. polymorpha* was the more salinity tolerant of the two species (Antonov and Shkorbatov, 1990).

The acclimation of *D. polymorpha* to local ecological conditions has been shown in the Volga River in Russia (Antonov and Shkorbatov, 1983). Here, the effects of temperature and salinity on whole animals and ciliated gill epithelium of *D. polymorpha* taken from six river populations indicated 1) the population most tolerant to salinity and temperature changes was the southernmost, nearest to the Caspian Sea; and 2) the least resistant population was the northernmost, farthest from the sea.

Temperature tolerance

North American populations.—The upper thermal limit of the North American quagga mussel is lower than that of the zebra mussel. Three estimates of temperature tolerance have shown that increasing acclimation temperature will increase the temperature tolerance of individual mussels.

TABLE 1. *Salinity tolerance of* Dreissena bugensis *and* D. polymorpha *when acclimated to freshwater and 4 ppt salinity and tested at four different salinities (after Antonov and Shkorbatov, 1990).*

Acclimation conditions	Dreissenid species	Salinity (ppt)		
		4	6	8
		Percent active		
Freshwater	River *D. polymorpha*	60	23	27
	Estuarine *D. polymorpha*	68	37	29
	D. bugensis	35	13	13
4 ppt salinity	River *D. polymorpha*	79	63	74
	Estuarine *D. polymorpha*	87	73	77
	D. bugensis	63	23	20

The three test techniques included introducing mussels directly into heated water (Domm *et al.*, 1993), comparing survival time at constant elevated temperature following a gradual increase of temperature from ambient (Spidle, 1994), and experimental determination of upper lethal temperature by increasing temperature from ambient at varying rates to a lethal temperature (Spidle, 1994). Results of these experiments indicate that some of the observed depth stratification in the lower Great Lakes between the species may be due to thermal stress in the quagga mussel above certain depths.

The quagga mussel has been shown to have a greater instantaneous mortality rate than the zebra mussel across acclimation temperatures that were eventually lethal to both species (Domm *et al.*, 1993). The zebra mussel has been demonstrated to survive indefinitely at 30°C (McMahon *et al.*, 1994; Spidle, 1994). Conversely, the quagga mussel shows rapid mortality at 30°C (Fig. 3; Spidle, 1994).

In the Great Lakes, an important concern is the susceptibility of the quagga mussel to mechanisms that have been found to successfully control zebra mussels in water intakes. Recirculating hot water through the intake pipe has been shown to be effective in reducing zebra mussel colonization of intake pipes. Models have been generated to predict the effect of different rates of temperature increase on instantaneous mortality rate of zebra mussels for given acclimation temperatures (McMahon *et al.*, 1993). Similar tests conducted with quagga mussels have demonstrated that the LT50 (instantaneous temperature required to cause 50%

mortality) of *D. bugensis* is from 2–5°C lower than that of *D. polymorpha* (Table 2). In spite of the difference in LT50, the LT100 (instantaneous temperature required to cause 100% mortality) predicted from a logistic regression model is not statistically different between the species. The lack of difference in LT100 indicates that even though most quaggas die at lower temperatures than will kill zebra mussels, a few exceptional quagga mussels may be as tolerant of elevated temperature as is the zebra mussel (Fig. 4).

Evolutionary studies suggest that the optimal temperature of an organism will co-evolve with its thermal maximum, and in the same direction (Huey *et al.*, 1991; Martins and Garland, 1991). Because the North American quagga mussel clearly has a lower thermal maximum than the zebra mussel, it is possible to assume that the quagga mussel has a lower optimal temperature for feeding and reproduction than does the zebra mussel, which may explain the depth stratification observed to partially separate *D. bugensis* and *D. polymorpha* in Lakes Erie and Ontario. A lower thermal optimum for the quagga mussel would explain the observation that *D. bugensis* has not been found in large numbers outside of the Great Lakes nor was it observed in the Erie Canal in repeated surveys in 1992 (Mills *et al.*, 1993).

Information is not yet available on the relative response of quagga mussels and zebra mussels to extreme low temperature conditions. Recent theory in the evolution of stress response points out that the critical thermal maximum and minimum appear to evolve independently rather than together
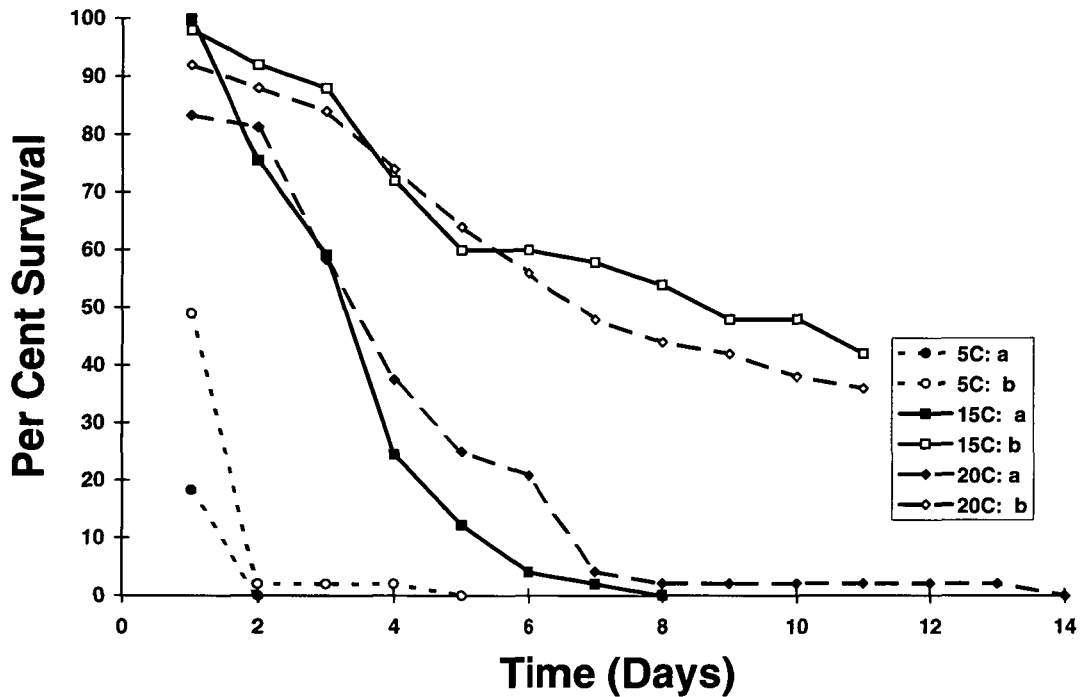
FIG. 3. Percent survival of quagga mussels (*Dreissena bugensis*) through time in replicated trials (a & b) when exposed to water temperatures of 30°C. The numbers 5, 15, and 20 indicate prior acclimation temperature in °C.

(Huey and Kingsolver, 1989; Hoffmann and Parsons, 1991; Huey and Kingsolver, 1993). Even though the zebra mussel is more tolerant of warm water than the quagga mussel, the response of the two species to cold water must be determined in laboratory experiments which test both the critical minimum temperature and the minimum temperature for essential activities such as feeding and reproduction for each species of *Dreissena*.

Ukrainian populations.—The distribution of *D. bugensis* along the Dneiper River is reflective of a north to south gradient with the warmest temperatures occuring in the southern reaches of the basin. The maximum summer temperature in the Dnieper-Bug estuary is usually 24–25°C offshore and 30–32°C in the littoral zone (Zhuravleva, 1988). In the Dnieper reservoirs, the maximum summer temperatures are lower: 23.5°C in Kahovhka Reservoir (the southernmost) and 21°C in Kiev Reservoir (the northernmost) (Shevchenko, 1989). According to Shevtsova (1968), increasing

water temperatures from north to south correlates with the quagga's more southerly occurrence in the Dneiper River basin. This finding contrasts with earlier suggestions in this paper that the North American *D. bugensis* may be a cold deep-water form (Dermott and Munawar, 1993; Mills *et al.*, 1993).

The effects of elevated temperatures on *Dreissena* in Ukraine populations have shown the onset of mortality to be 27–27.3°C for *D. polymorpha* and 28.1°C for *D. bugensis* (Antonov and Shkorbatov 1990). Fifty percent mortality was recorded at 28.2–28.4°C and 29.3°C for each species, respectively (Antonov and Shkorbatov 1990). As the water temperature increased, the first *D. polymorpha* with fully opened shells were observed at 28.6°C, whereas the first *D. bugensis* with fully open shells were observed at 29.7°C. Antonov and Shkorbatov (1990) reported the upper lethal temperature for *Dreissena* as 32–35°C, but did not give separate lethal ranges for each species.

In contrast to the results of Antonov and Shkorbatov (1990), the results of Domm *et al.*, (1993) showed that North American *D. polymorpha*'s upper temperature limit was significantly higher than that of *D. bugensis*. The average survival time of *D. polymorpha* at a constant, eventually lethal, temperature was also significantly longer. Differences in thermal resistance in *D. polymorpha* are commonly reported in the literature; the results depend strongly on length of thermal acclimation and it is difficult to compare temperature resistance data obtained from mussels collected in different geographic locations (McMahon *et al.*, 1994).

ECOLOGY

Depth

The depths at which quagga mussels and zebra mussels have been observed in Lake Ontario are among the deepest (>100 m) ever recorded for the genus *Dreissena* (Mills *et al.*, 1993). In Polish lakes, zebra mussels generally reach maximum densities between 2 and 4 m depth and are sparse at depths >8 m (Stanczykowska, 1977; Stanczykowska *et al.*, 1983; Stanczykowska and Lewandowski, 1993). Similar patterns have been noted for European lakes (Wesenberg-Lund, 1939; Dunn, 1954) although Walz (1973) found adult zebra mussels at a depth of 55 m and zebra mussel larvae at depths between 120 and 140 m. In Lake Ontario, both quagga and zebra mussels coexist at depths of 8–110 m, with only *D. bugensis* found at depths of 130 m. In the eastern basin of Lake Erie, Dermott and Munawar (1993) found *D. bugensis* outnumbered zebra mussels by 14 to 1 in the deeper offshore waters and colonized soft substrata beyond depths of 40 m. In both Lakes Ontario and Erie, the proportion of *D. bugensis* increased with depth and declined as water temperature increased, suggesting that this dreissenid is possibly a cold water form. The dominance by quagga mussel in profundal areas of North American lakes indicates that the impacts on food webs by dreissenids is not limited to shallow near shore regions of lakes.

Dreissena bugensis is much more abun-

TABLE 2. *LT50 and LT100 estimated from logit models, and SM100 observed for each treatment in the acute temperature stress experiment.**

Species	Rate	Acclimation temperature	LT50	SM100	LT100
q	60	5	30.869	35	39.166
z	60	5	35.003	37	39.822
q	60	15	34.056	35	34.335
z	60	15	35.669	37	38.755
q	60	20	35.063	36	35.332
z	60	20	36.201	38	40.276
q	30	5	33.057	36	39.451
z	30	5	36.014	38	39.717
q	30	15	34.815	37	36.931
z	30	15	36.099	37	38.940
q	30	20	35.479*	37	36.961**
z	30	20	36.444*	38	42.276**
q	15	5	34.099	37	38.869
z	15	5	36.306	38	41.005
q	15	15	34.949	39	39.410
z	15	15	37.192	39	39.348
q	15	20	34.634	37	39.793
z	15	20	37.085	38	37.652
q	5	5	33.491	38	42.767
z	5	5	37.001	39	39.261
q	5	15	36.102	39	40.223
z	5	15	37.203	39	40.489
q	5	20	36.442	NA	45.195
z	5	20	x	NA	x

* Species is coded as q = quagga and z = zebra; rate is given as minutes per °C increase; x indicates no mortality occurred within the range of observation. NA indicates 100% mortality was not reached. Quagga and zebra mussels have different predicted LT50 values (p < 0.05) except where indicated by * and similar predicted LT100 values (p > 0.05) except where indicated by ** (From Spidle, 1994).

dant in deep waters in the Dnieper reservoirs than *D. polymorpha* (Zhuravel, 1967*a*) which is consistent with observations in North America. Pligin (1989) confirmed this for the Dneiper River system, showing that *D. bugensis* comprised 99–100% of the mollusks in the deepest areas of reservoirs, while in littoral zones *D. polymorpha* comprised 15–20%. Further, the first sightings of *D. bugensis* in the new Dnieper River reservoirs (Kremenchug, Kiev, and Kanev) in the 1950s to the 1970s were made in the deeper downstream portions near the dams, and only later did expansion occur upstream through the reservoirs (Pligin, 1989).

An analysis of *Dreissena* depth distribution in Dnieper reservoirs indicates that *D. bugensis* inhabits a wider range of
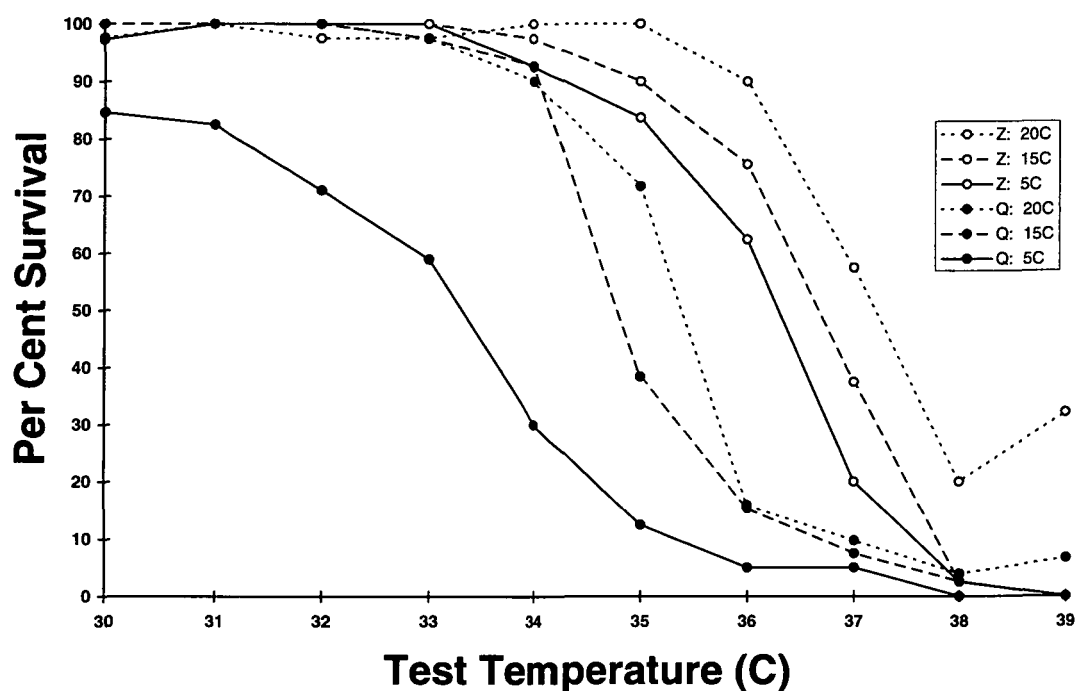
FIG. 4.   Percent survival in zebra and quagga mussels in tests of tolerance to acute temperature stress (averaged across four rates of temperature increase). The key indicates species and acclimation temperature for each test. (Q: 5C represents the treatments of quagga mussels acclimated to 5°C).

depths than *D. polymorpha* (Table 3). The maximum abundance of both species was from 4 to 10 m. Below 12 m, reductions in mussel abundance might be explained by a deficit of favorable substrata due to the siltiness of the deeper sections of the reservoirs, as well as by reduced oxygen concentrations. However, exact data on

TABLE 3.   *Mean abundance of* D. polymorpha *and* D. bugensis *by depth in Kremenchug and Kakhovka Reservoirs, 1985–1992 (Pligin, unpublished).*

Depth (m)	Number of samples	Densities (number per m²)	
		D. polymorpha	D. bugensis
0.0–2.0	146	297	743
2.1–4.0	52	270	656
4.1–6.0	49	880	2,140
6.1–8.0	41	935	2,562
8.1–10.0	53	418	2,791
10.1–12.0	27	131	1,200
12.1–14.0	19	32	179
14.1–16.0	13	+	8
16.1–18.0	5	+	+
18.1–20.0	9	0	+
>20.1	5	0	+

(+ denotes few).

changes in oxygen concentration with depth in Dnieper reservoirs is not available. The deepest record of *D. bugensis* was at 28 m in Kakhovka reservoir, which has a maximum depth of 35 m.

Displacement of D. polymorpha *by* D. bugensis

In the 1960s and 1970s, *D. bugensis* almost entirely displaced *D. polymorpha* in Zaporozh'ye reservoir and had become the dominant form in the Kakhovka Reservoir and other water basins of the Dneiper River (Zhuravel', 1965; Birger et al., 1968; Dyga and Zolotareva, 1976; Lubyanov and Zolotareva, 1976). *Dreissena bugensis* represented 80–90% of the *Dreissena* population in canals and reservoirs, sometimes completely displacing it in deeper waters of some reservoirs (Zhuravel' 1967b). In hydropower plant intake structures on the Dnieper River, *D. bugensis* steadily gained in dominance over *D. polymorpha* (Dyga *et al.*, 1975). In 1964, *D. bugensis* constituted only 7% of the *Dreissena* in fouling intake

structures, in 1966, 15% and by 1973, 98% (Dyga *et al.*, 1975).

Pligin (unpublished) has compiled data on the occurrence of the two dreissenid species in the Kremenchug and Kiev Reservoirs. He found that *D. polymorpha* comprised 43–45% of the benthos in the Kremenchug Reservoir soon after it was created in 1961. The first specimens of *D. bugensis* were found in the lower portion near the dam of this reservoir in 1967, and from 1971 to 1975, *D. bugensis* expanded into *D. polymorpha* habitat. *Dreissena bugensis* was found in the littoral zone only as recently as 1974. In the first two years after the filling of the Kiev Reservoir, *D. polymorpha* comprised 44% and 90% of the benthos (Olivari, 1972). There were no continuous field studies in this reservoir for the next nine years, but the first specimen of *D. bugensis* was found there near the dam in 1971, after which the population of this species expanded. As *D. bugensis* expanded, the ratio of *D. bugensis* to *D. polymorpha* shifted in favor of *D. bugensis* by 1979. In the main flow of the lower Dnieper River near Kherson, *D. bugensis* displaced *D. polymorpha* in four years (Moroz, 1980). In 1975 both species were abundant, with biomasses of 4,952 and 2,797 g/m² for *D. bugensis* and *D. polymorpha*, respectively. In 1976–77 *D. bugensis* (biomass = 9,330 g/m²) began to displace *D. polymorpha* (biomass = 59 g/m²) and in 1978 this displacement was almost complete (*Dreissena bugensis* = 10,900 g/m² and *D. polymorpha* = 18 g/m²).

Recent field work by Rosenberg and Ludyanskiy (1994) verifies the predominance of *D. bugensis* in the Dnieper River basin (Fig. 5). Samples were collected at depths not greater than one meter, except for grab samples which were collected at 2–3 m in the Dnieper Bug estuary. For all sites except the site in the Samara River (#5), the biomass of *D. bugensis* was at least 3.3 times greater than *D. polymorpha*. At the Samara River site, water flow may not have been suitable for *D. bugensis* settlement since it was the highest compared to the other sites. The biomass of *D. bugensis* relative to *D. polymorpha* increased from north to south at low-flow stations (1 and
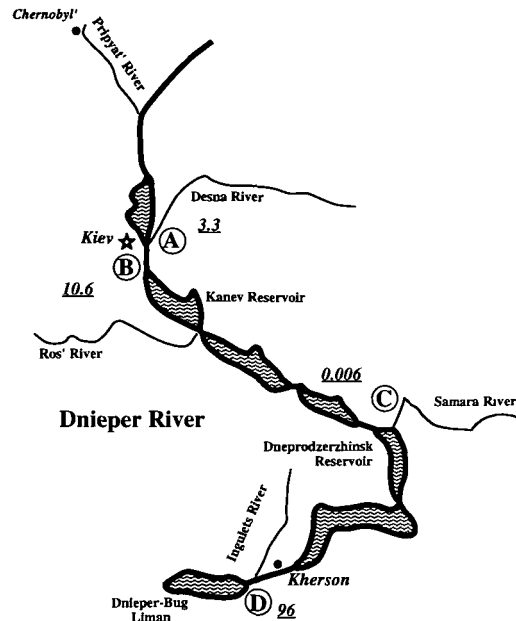

FIG. 5. Ratio of the biomass in grams of *Dreissena bugensis* to *D. polymorpha* (underlined numbers) at four sites in the Dnieper River during August 1993. Letters identify location of sites: A = Desna River delta; B = Dnieper River at Kiev; C = Dnieper River at Dnepropetrovsk; and D = Dnieper River at Kherson.

4) along the Dnieper River. At the Dnieper River sites, specimens of *D. bugensis* were much larger on average than those of *D. polymorpha*.

In the lower Great Lakes, where populations of *D. bugensis* have had less time to develop than in the Ukraine, there is only anecdotal evidence that quaggas may be expanding into habitats once dominated by *D. polymorpha*. In Lake Erie, for example, quaggas are expanding westward into areas known to be dominated by *D. polymorpha* (Culligan, personal communication NYS-DEC, Dunkirk, NY). Similar observations were made in Lake Ontario during the summer of 1994 (R. Owens, personal communication National Biological Survey, Great Lakes Center, Oswego, NY) where *D. bugensis* appeared to dominate at depths >25 m.

Substratum

In the lower Dnieper River and its estuaries, substratum availability may be more

important than water salinity for determining the distribution of *Dreissena* (Aleksenko, 1991). Aleksenko (1991) found *Dreissena* preferred solid substrata but questioned the assumption that they do not live on sand substrata (Mordukhai-Boltovskoi, 1960). In shallow waters where sands were affected by the hydrodynamic activity of waves, *Dreissena* lived only on hard substrata such as unionid bivalves, stones and pieces of wood. However, as turbulence decreased with increasing depth, *Dreissena* colonized sand substrata. In the Dnieper-Bug estuary, *Dreissena* were abundant on sands and silty sands, *D. polymorpha* being more abundant on sands than *D. bugensis* and *D. bugensis* being more abundant on silty sands than *D. polymorpha* (Aleksenko, 1991). Pligin (unpublished) collected similar data in Ukrainian reservoirs, showing *D. polymorpha* dominant on sand and silty sand, and *D. bugensis* dominant on various silty substrata.

In the Great Lakes, *Dreissena* species have been found on all types of hard substrata (Domm *et al.*, 1993). *Dreissena bugensis* colonizes soft substratum in water depths exceeding 40 m and sand and sandy silt between 10 and 30 m (Dermott and Munawar, 1993). By 1992, at least 80% of Lake Erie's bottom substrata were invaded by *Dreissena* and only areas where periodic anoxia occurred were devoid of the genus (Dermott and Munawar, 1993). For Lake Erie and other North American lakes where *D. bugensis* and *D. polymorpha* coexist, it is now clear that both dreissenids will impact not only the littoral shoals but the profundal areas of lakes as well.

DISCUSSION

Historically, *Dreissena* evolved by neotenous retention of the byssus from now extinct infaunal forms such as *Congeria* and *Dreissenomya* (Morton, 1993). *Dreissena polymorpha* is highly derived, having evolved the keeled shape that allows it to anchor tightly to hard substrata. *Dreissena bugensis* lacks this keel, and does not attach as firmly; however, it retains the primitive ability to colonize soft substrata. The ability of dreissenids to colonize both hard rocky nearshore substrata and soft sediments of

lakes (soft substratum often dominates the bottom lake area of lakes) means that these organisms through their filtering activity will impact the ecology of both littoral shoals and the profundal zone. In Lake Erie where quagga mussels occupy the soft substratum (80% of the lake bottom is soft substratum), competition for space and food by *D. bugensis* already has shown signs of negative impact on profundal organisms like the burrowing amphipod *Diporeia* (Dermott and Munawar, 1993).

The finding that quagga mussels occupy deeper, colder waters in the Great Lakes contrasts sharply with observations in the Dnieper River drainage and raises new questions about the optimal depth of this species. No point in the Dneiper River drainage is deeper than 35 m and *D. bugensis* is most abundant in the Dneiper reservoirs between 4 and 10 m, with a maximum recorded depth of 28 m. In Lake Ontario, *D. bugensis* have been found at 110 m (Mills *et al.*, 1993) and in Lake Erie they colonize soft substrata beyond 40 m (Dermott and Munawar, 1993). In the Dneiper River basin, *D. bugensis* initially inhabited the deeper areas of newly colonized waters and appeared later in shallow littoral habitats. As a result, patterns of colonization by Ukrainian quagga mussel populations would suggest that *D. bugensis* is not limited to deep water habitats but could inhabit a wider range of depths in North American waters than once thought. In addition, Ukrainian populations once dominated by *D. polymorpha* have been largely replaced by *D. bugensis*. For the Great Lakes, there is anecdotal evidence that *D. bugensis* is expanding into shallower depths, lending support to the notion that the quagga mussel may be able to occupy a wide range of depths here as well.

The conclusion that North American quagga mussels have a lower thermal maximum than zebra mussels is not supported by observations made on populations in the Ukraine. Laboratory studies have shown that the North American quagga mussel has a higher mortality rate than the zebra mussel across acclimation temperatures that were eventually lethal to both species (Domm *et al.*, 1993). Quagga mussels ex-

hibit high mortality at 30°C (Spidle, 1994) whereas the zebra mussel can survive indefinitely at the same temperature (McMahon et al., 1994; Spidle, 1994). However, Dnieper River populations of D. bugensis spawn at higher temperatures than D. polymorpha (Shevtsova, 1968) and laboratory studies indicate that D. bugensis exhibited lower mortality at elevated temperatures compared to D. polymorpha (Antonov and Shorbatov, 1990). While experience from the lower Laurentian Great Lakes suggests that the quagga is a cold deep water form, findings from the Ukraine suggest otherwise and will need to be taken into account when extrapolating the potential thermal range of the quagga mussel in North America. Furthermore, species closely related to, if not conspecific with, Dreissena polymorpha occur in Greece and Asia Minor (Rosenberg and Ludyanskiy, 1994), regions that are much warmer than Ukraine and Russia, so the potential thermal range of that species might also be higher than recent experiments indicate.

The genus Dreissena which is highly polymorphic and produces millions of larvae has a high potential for rapid adaptation. In a few generations, rare alleles might increase greatly in frequency. This would allow new allelic heterozygote types to be formed, and creation of new alleles by recombination. Consequently, Dreissena could adapt to new environmental conditions after several generations. Strayer and Smith's (1993) prediction of a salinity limit of 2 ppt for North American Dreissena may someday be too low in light of the Ukrainian data. Distribution of Dreissena in the Dnieper-Bug estuary is controlled by salinity and D. bugensis has been shown to survive salinities twice that predicted for North America. While North American quagga populations apparently cannot acclimate to salinities to which Ukrainian populations have, eventual colonization into estuarine and coastal areas of North America cannot be ruled out. Evidence for this possibility comes from D. rostriformis grimmi, a close relative of D. bugensis, which which is known to inhabit the Caspian Sea at salinities up to 12.7 ppt (Rosenberg and Ludyanskiy, 1994).

Dreissena has colonized North American waters for less than a decade and acclimation studies to date have been on a much shorter time scale than seasonal changes or than the 3–5 year life span of Dreissena. In the Ukraine, on the other hand, the response of Dreissena to changing environmental conditions has had a much longer time scale to evolve. The potential for rapid adaptation to extreme environments by a highly polymorphic and fecund species such as D. polymorpha is high. A highly polymorphic, fecund species like D. polymorpha has high potential for adaptation to extreme environments via rapid evolution of allelic frequencies and combinations. Dreissena bugensis has evolved as a more saline and thermal tolerant riverine and reservoir species in the Ukraine compared to North American populations. Although we can speculate about the eventual range expansion of Dreissena in North America and whether Dreissena bugensis will dominate over D. polymorpha, we know that colonization by these dreissenids in freshwater and possibly estuaries will have significant long-term impacts on North American waters.

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