Aquatic Invasions (2013) Volume 8, Issue 3: 311–318
doi: http://dx.doi.org/10.3391/ai.2013.8.3.07

Research Article

Relative abundance of two dreissenid species, *Dreissena polymorpha* and *Dreissena rostriformis bugensis* in the Lower Don River system, Russia

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Received: 5 November 2012 / Accepted: 31 May 2013 / Published online: 9 August 2013

Handling editor: Vadim Panov

Abstract

Relative abundance of two dreissenid species, *Dreissena rostriformis bugensis* and *Dreissena polymorpha*, in the total dreissenid community was calculated for 15 sites in the lower Don River system, Russia, between 1977 and 2010 to determine relative trends in their sympatric occurrence. The proportion of *D. r. bugensis* first increased at most stations reaching a maximum by 1999. However, after 1999, this species consistently decreased at 14 of the 15 sites. Degree of decline seems to correlate strongly to calcium content and total mineral content of the water. At sites in the Manych River with a higher Ca^{2+} and total mineral content, the proportion of *D. r. bugensis* in the total dreissenid population declined from 65–75% in 1999 to 14–22% by 2009–2010, whereas at sites in the Don River with lower Ca^{2+} and total mineral content its proportion declined from 25–50% to only 1 %. However, Ca^{2+} and total mineral content cannot explain the synchronous and consistent long-term decrease in relative numbers as observed. *D. r. bugensis* normally displaces *D. polymorpha* over time due to superior physiological characteristics. Reasons for the decline of *D. r. bugensis* in the total dreissenid community are unclear, but given its synchronicity despite different times of invasion and hence species interactions we assume a macroregional factor affecting all the populations examined.

Key words: zebra mussels; quagga mussels; competitive interactions; mussel trends

Introduction

Dreissena rostriformis bugensis (Andrusov, 1897) (*Dreissena bugensis* auctorum) and *D. polymorpha* (Pallas, 1771) (quagga and zebra mussel) are closely related bivalves of Ponto-Caspian origin that have invaded extensive areas beyond their native ranges in both Europe and North America (Orlova and Scherbina 2002; Mills et al. 1996; Karatayev et al. 2007; Zhulidov et al. 2010; Van der Velde et al. 2010). These dreissenid species have attracted great attention not merely because of their invasive potential but also because of profound impacts they have had on aquatic communities, especially in the New World (Ludyanskiy et al. 1993; Vanderploeg et al. 2002; Orlova et al. 2004; Nalepa et al. 2009). Other reasons for the profound interest in these mollusks are their different invasion patterns, population dynamics, and invasion strategies, as well as factors limiting their spread and determining relative numbers within areas of sympatry (Orlova et al. 2005; Nalepa et al. 2010; Zhulidov et al. 2010). Competitive and non-competitive interactions between the two species are of particular interest in this respect (Zhulidov et al. 2010).

Whereas *D. polymorpha* began to spread throughout Eurasia about 200 years ago and has now colonized most of Western Europe (Starobogatov 1994; Karatayev et al. 2007; Van der Velde et al. 2010), *D. r. bugensis* has only recently (from early 1980s on) appeared outside of its primary invasion range within the Black Sea basin (Orlova et al.

2005; Zhulidov et al. 2010). In the Great Lakes of North America, the two species were first reported almost simultaneously in the mid to late 1980s (Hebert et al. 1989; Mills et al. 1993; Carlton 2008). However, while *D. polymorpha* spread rapidly and was found in all five of the Great Lakes in just a few years after discovery, *D. r. bugensis* spread more slowly and was not found in all the lakes until over a decade after discovery (Nalepa et al. 2010).

The overlapping of ranges in these two ecologically similar species places them in direct competition for available resources. In areas where they are sympatric, *D. r. bugensis* generally seems to be competitively superior to *D. polymorpha*, having quickly displaced *D. polymorpha* as the dominant dreissenid in many North American lakes and rivers (Mills et al. 1999; Ricciardi and Whoriskey 2004; Nalepa et al. 2010), and in river impoundments of Ukraine and Russian Federation (Kharchenko 1995; Mills et al. 1996; Orlova and Scherbina 2002). In some areas, however, a partitioning of available substrate, as well as biotopes, has allowed *D. polymorpha* to remain co-dominant with *D. r. bugensis* (Diggins et al. 2004).

Contrary to these observations, we found in our previous studies an unexpectedly low proportion of *D. r. bugensis* relative to *D. polymorpha* in the lower Don River basin despite the former species having sufficient time to gain dominance over the latter (Zhulidov et al. 2004). Further, some evidence suggests that quagga mussels have been present in the lower Don River system much earlier than believed. For instance, we examined empty shells of dreissenids from river drift at some locations in the lower Don River and Tsimyansk Reservoir dating back to approximately the early 1940s and found a certain proportion of *D. r. bugensis* shells (our unpublished data). Continued investigations of relative trends in the two species over a 27-year period in the lower Don River basin revealed an unexpected temporal pattern. Prior to 1999, *D. r. bugensis* increased in abundance and became the dominant species at some locations; however, after 1999 this species declined relative to *D. polymorpha* (Zhulidov et. al. 2006, 2010). This unexpected recent tendency of *D. r. bugensis* to decrease in relative numbers in at least part of its non-native range suggests a closer scrutiny of the data dealing with the relative abundance of the two co-invasive dreissenid species. In this respect, longer time series of observations supported by additional information on the environmental conditions in the dreissenid habitats are certainly of importance.

In earlier papers, we documented relative trends in *D. r. bugensis* and *D. polymorpha* populations in the Don River system over the period between the late 1970s and 2004 (Zhulidov et. al. 2006, 2010). In this paper, we present results of continued sampling of these species between 2005 and 2010 and also reconsider some biotic and abiotic factors affecting relative dreissenid numbers in this river system, especially total mineral content and calcium content.

Materials and methods

Dreissenid samples were collected from 15 sites in the lower Don River system, in the lower part of the Tsimlyansk Reservoir, and also in the Manych River within the western part of the Kuma-Manych depression (Figure 1) (Zhulidov et al. 2004, 2006). A general description of sampling sites is given in Table 1. Samples were collected from a variety of substrates and two water depths at each site. In shallow water (< 2 m) mussels were collected by hand at any accessible substrate along the shore (concrete piles, twigs, macrophytes, etc.). In deeper water (2–6 m) mussels were collected with an Eckman-type box corer (area = 0.01 m^2). These methods were followed throughout the entire study period. At each site and on each sampling date, 90–300 individuals of similar size (15–22 mm) were identified to the species level.

The last year in which data for all 15 sites was presented and discussed was 2004 (Zhulidov et al. 2006). Since then, sampling was continued for Stations 1–11 until 2010, and continued for Stations 12–15 until 2009. As previously, samples were collected once a year, except in 2007 when samples were collected twice, in May and August. Values of total mineral content (the sum of principal ions) and calcium content (Ca^{2+}) (see Table 1) were obtained from the monitoring program, the State Service (Network) of Observation and Control of Environmental Pollution (OGSNK/GSN, see Zhulidov et al. 2000, 2004 for details). Linear regression and the Pearson product-moment correlation coefficient were used to examine relationships between variables. All proportions were arcsine-transformed before analysis. Probabilities of < 0.05 were considered significant. As noted, there were two sampling dates in 2007 and thus for this year an average proportions were determined and used in any statistical analysis. Similarly, average proportions were used when two sampling dates occurred in 2003 (Zhulidov et al. 2006).

Table 1. General location of stations sampled in the Don River and Manych River. Values given for total mineral content (sum of principal ions) and calcium content (mg/L) are the yearly mean (± SD) over the period 1995–2000.

River/Station Number	Location	Latitude; Longitude	Distance from River Mouth	Total Mineral Content	Calcium Content
Don River					
1	Tsimlyansk reservoir, 50 km upstream from dam	47°42′27.34″N; 42°13′40.22″E	373	ND	ND
2	0.3 km downstream from Tsimlyansk Reservoir dam	47°36′26.60″N; 42°06′29.18″E	323	450 ± 80	45 ± 7
3	32 km downstream town of Volgodonsk	47°35′13.66″N; 41°47′46.93″E	291	450 ± 80	46 ± 8
4	downstream Village of Konstantinovs	47°34′31.12″N; 41°01′28.92″E	207	ND	ND
5	Don River, 6.5 km downstream Village of Semikarakorsk	47°32′29.39″N; 40°44′10.10″E	160	590 ± 180	77 ± 19
6	Village of Razdorskaya	47°32′27.71″N; 40°39′23.35″E	150	660 ± 130	76 ± 13
7	15 km downstream Village of Bagaevskaya	47°13′53.57″N; 40°13′29.91″E	97	710 ± 190	75 ± 20
8	1 km upstream Aksay settlement	47°15′03.53″N; 39°53′20.06″E	61	800 ± 230	75 ± 20
9	Don River, Village of Koluzaevo	47°10′14.34″N; 39°33′10.90″E	33	790 ± 230	73 ± 19
10	river delta, B. Kalancha branch, upstream village of Dugino	47°09′15.33″N; 39°27′04.16″E	20	760 ± 210	75 ± 19
11	1 km upstream Azov town	47°07′29.76″N; 39°25′00.40″E	16	810 ± 240	78 ± 21
Manych River					
12	Manych River, Proletarskoye reservoir	46°15′38.73″N; 42°56′41.89″E	258	2220 ± 510	ND
13	Village of Vesyoly	47°08′03.49″N; 40°49′10.42″E	160	2360 ± 360	ND
14	Ust-Manych reservoir	47°14′28.41″N; 40°17′01.15″E	99	1880 ± 270	119 ± 15
15	near Manychskaya village	47°14′28.41″N; 40°17′01.15″E	98	1780 ± 400	ND

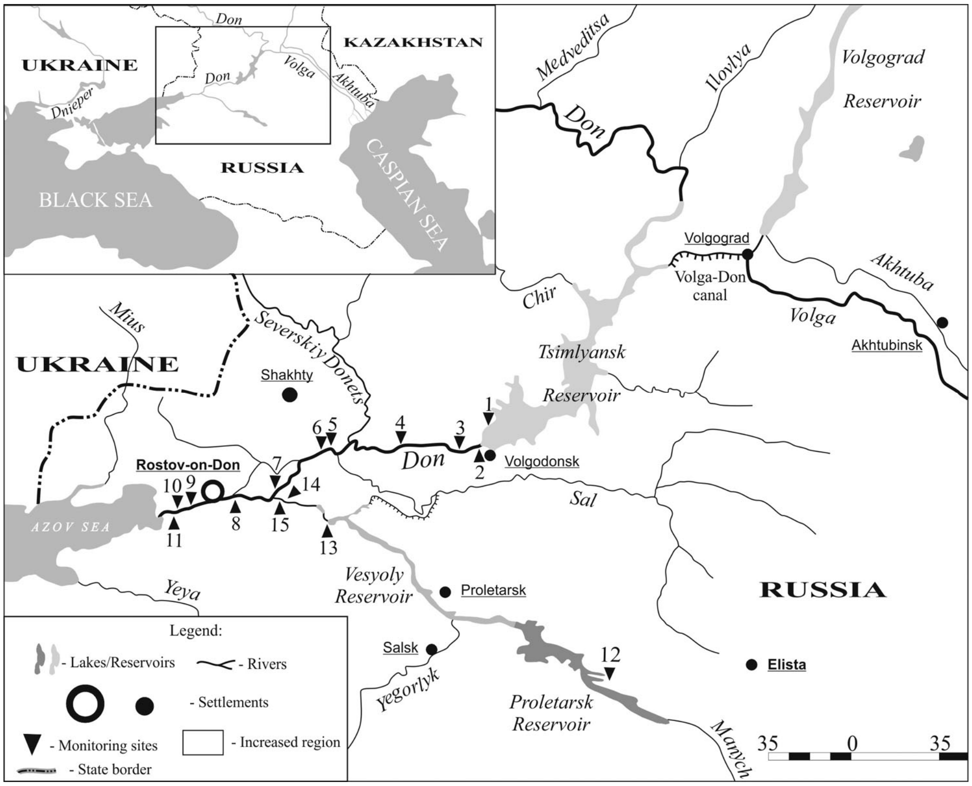

Figure 1. Location of sampling stations in the lower Don River and Manych River systems.

Results

The percentage that *D. polymorpha* and *D. r. bugensis* comprised of all dreissenids collected on each sampling date is given in Appendix 1. As presented in our previous paper (Zhulidov et al. 2006), *D. r. bugensis* was found first in the lowermost portion of the Don River and then spread upstream. For the 5 sites initially sampled in 1977, it was first collected at Station 11 in 1980, at Stations 7 and 8 in 1981, at Station 6 in 1984, and at Station 2 in 1991 (Figures 1 and 2). The percentage of *D. r. bugensis* gradually increased at these and additional monitoring sites over time, reaching a peak of 30–50 % of the dreissenid population in 1999 at most sites. However, starting in 1999, the percentage of *D. r. bugensis* declined at 14 of the 15 sites sampled (Figures 3 and 4). The only location where *D. r. bugensis* did not decline was in Tsimlyansk Reservoir (Station 1) where it consistently comprised only a small fraction of the dreissenid population ($\leq$ 5 %). The percentage of *D. r. bugensis* declined at the 14 other sites through 2004, and the decline was significant (Wilcoxon signed rank test; $P < 0.01$). In 1999, *D. r. bugensis* accounted for 25–50% of total dreissenid numbers at sites in the Don River downstream from the Tsimlyansk Dam and 65–75% in the Manych River. By 2004, percentages dropped to 10–18% and 33–43% in the two rivers, respectively.

In 2005–2010, the percentage of *D. r. bugensis* in the total dreissenid population continued to decrease (Figures 2, 3 and 4). As found previously, this trend occurred at all of the sites examined except at Station 1, where the percentage of *D. r. bugensis* rarely exceeded 5% throughout the whole period of observation. Proportional declines of *D. r. bugensis* in the lower Don River and the Manych River systems were similar despite greater initial abundances of this species in the latter system. From 2005 to 2010, *D. r. bugensis* declined such that proportion values were 8 to 29% lower than found in 2004. By 2009-2010, the percentage of this species in the total dreissenid population declined to only 1–4% at sites in the Don River and to 14–22% at sites in the Manych River.

Unlike Zhulidov et al. (2004) who examined the relationship between percentages of the two dreissenid species and total mineral and calcium content using only one or two years (1999 and 2001 or 2002), we were able to examine this relationship for a longer time series. The percentage of *D. r. bugensis* strongly correlated to total mineral content and calcium content in 1999 when percentages of *D. r. bugensis* peaked (Pearson coefficient = 0.90 and $P < 0.001$ for mineral content; Pearson coefficient = 0.87 and $P = 0.001$ for calcium content), and in 2009–2010 when percentages were minimal (Pearson coefficient =0.92 and $P < 0.001$ for mineral content; Pearson coefficient = 0.70 and $P = 0.02$ for calcium content) (Figure 5). It is interestingly to note that the proportion of *D. r bugensis* was generally more closely associated with total mineral content than calcium content in both 1999 and 2009/2010.

Discussion

The decline of *D. r. bugensis* relative to *D. polymorpha* in the lower Don River basin seems to be a unique occurrence within the entire area where distributions of these two species overlap. Most all previous studies in both Eurasia and North America have shown that *D. r. bugensis,* over time, displaces *D. polymorpha* in a variety of habitats (Kharchenko 1995; Mills et al. 1996; Mills et al. 1999; Orlova and Scherbina 2002; Ricciardi and Whoriskey 2004; Zhulidov et al. 2010; Nalepa et al. 2010). While our previous studies in the lower Don River system indicated that the percentage of *D. r. bugensis* peaked and then declined through 2004 (Zulidov et al. 2010), our continued studies in the same system between 2005 and 2010 indicated percentages continued to decline even further. Presently, *D. r. bugensis* is uncommon but may still be found in the Manych River, but it is now generally a rarely-found species in the lower Don River.

Similar to initial declines observed in 1999–2004, continued declines in 2005–2010 occurred at all sites within the lower Don River and Manych River systems. This spatially consistent trend has now occurred for 11 years over a waterway system of more than 600 km, and across sites that were likely subjected to a variety of local influences. As demonstrated earlier over the 1999–2004 period (Zhulidov et al. 2006), correlation in declining trends between sites (Kendall's coefficient of concordance [W]) was strong and highly significant ($W = 0.81$; $P < 0.001$). This consistent trend between sites was even more evident when recent data (2005–2009) were included in the statistical analysis ($W = 0.98$; $P < 0.001$). If only sites in the lower Don

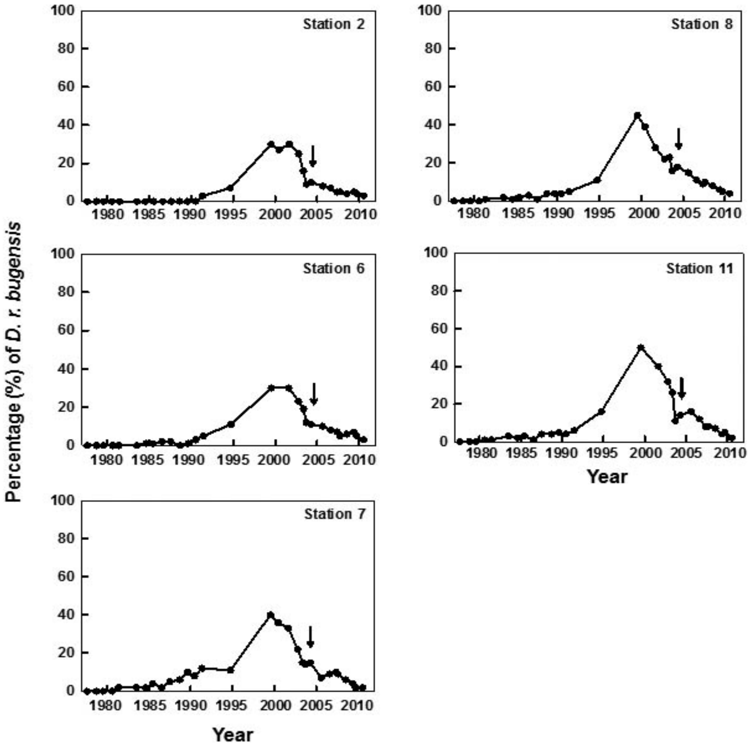

Figure 2. The relative proportion (percent) of the total *Dreissena* population comprised by *D. r. bugensis* at the 5 sampling stations in the lower Don River system that were sampled in 1977–2010. The arrow marks the last year in which data was previously provided (see Zhulidov et al. 2006).

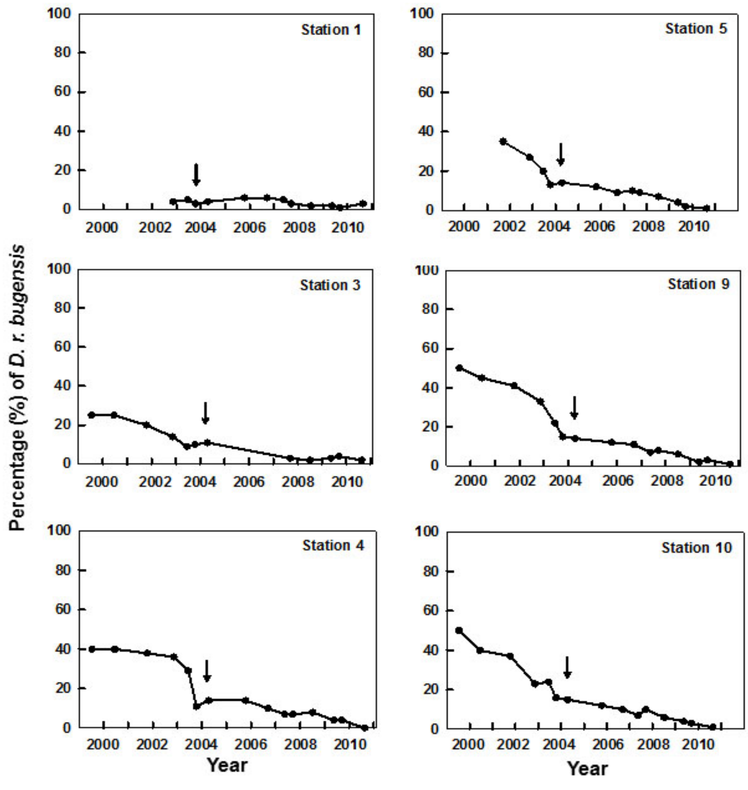

Figure 3. The relative proportion (percent) of the total *Dreissena* population comprised by *D. r. bugensis* at the 6 sampling stations in the lower Don River system that were sampled in 1999–2010. The arrow marks the last year in which data was previously provided (see Zhulidov et al. 2006).

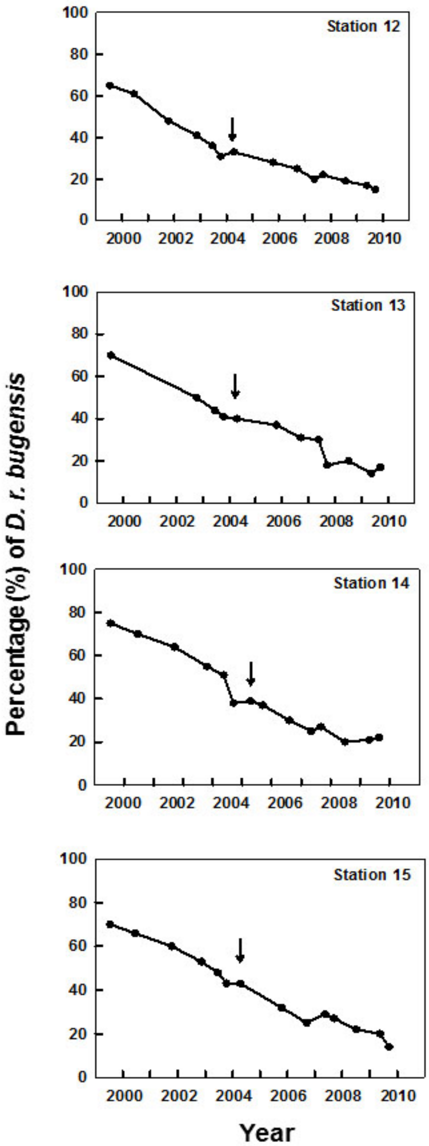

Figure 4. The relative proportion (percent) of the total *Dreissena* population comprised by *D. r. bugensis* at the 4 sampling stations in the Manych River that were sampled in 1999–2009. The arrow marks the last year in which data was previously provided (see Zhulidov et al. 2006).

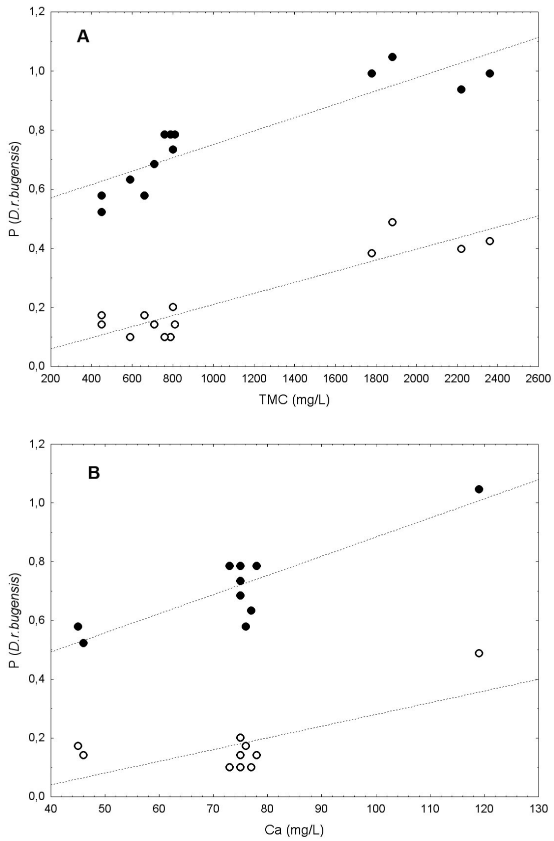

Figure 5. Relationship between arcsin-transformed relative number of *Dreissena r. bugensis* (P) and total mineral content of the water (TMC, top) and calcium content (Ca, bottom). Each point represents a different station; closed circles = values in 1999, open circles= values in 2010 (for Manych River values for 2009 were used).

River were included in the analysis for the period 1999–2010, correlation between sites would be equally apparent ($W = 0.98$; $P < 0.001$). To cause such an extensive and synchronous decline, either a broad, fundamental change in river conditions would have had to occur beginning in 1999, or conditions were unfavourable for *D. r. bugensis* to retain its prevalence in the new habitat after successful initial colonization.

The competitive advantage of *D. r. bugensis* is probably determined by a set of physiological characteristics that promote a higher tolerance to some environmental conditions compared to *D. polymorpha* (Zhulidov et al. 2006, 2010; Nalepa et al. 2010). In particular, *D. r. bugensis* has a higher assimilation efficiency than *D. polymorpha*, especially at low food levels (Baldwin et al. 2002) and a lower respiration rate under different seasonal temperatures (Stoeckmann 2003). These characteristics decrease metabolic costs and allow *D. r. bugensis* to have greater growth and greater allocations of energy to soft body mass than *D. polymorpha* at similar food conditions (Roe and MacIsaac 1997). Furthermore, higher growth rates allow *D. r. bugensis* larvae to settle at a larger size than *D. polymorpha* larvae, giving them additional competitive advantage (Martel et al. 2001).

Less evidence is available to explain possible competitive disadvantages of *D. r. bugensis*. While some laboratory studies found this species to be less tolerant of higher temperatures than *D. polymorpha* (Domm et al. 1993), controlled studies under more natural conditions showed that growth and survival of *D. r. bugensis* was similar to, or greater than, *D. polymorpha* at typical summer-warm temperatures (MacIsaac 1994; Thorpe et al. 2002). *D. r. bugensis* may be more sensitive to low calcium levels than *D. polymorpha* (Jones and Ricciardi 2005), but calcium levels in these river systems are high and far greater than the minimum required by either species. Among possible biotic factors that could contribute to unexpected declines in *D. r. bugensis* is selective predation by molluscivorous fish. This species has a thinner shell as compared to *D. polymorpha* and would therefore more preferred as a diet item by fish (Zhulidov et al. 2006, 2010). However, the prevalence of *D. r. bugensis* in dreissenid communities in other river systems with similar fish species composition would make this hypothesis very unlikely. Likewise, we still have no evidence that another possible biotic factor would be affecting *D. r. bugensis*, via selective infection by pathogen organisms (Karatayev et al. 2003; Zhulidov et al. 2006).

Given these reasons, the abrupt and continued decline of *D. r. bugensis* between 1999 and 2010 is difficult to explain. A fundamental change in river conditions seems unlikely. Based on long term monitoring data, broad changes in hydrochemical conditions such as flow regimes or chemical composition have not occurred in these river systems over the past decade (our unpublished data). In our earlier paper, we speculated that greater numbers of *D. r. bugensis* in the Manych River compared to the lower Don River might be due to differences in total mineral/calcium content (Zhulidov et al. 2004). Indeed, total mineral content was 1780–2360 mg/L in the Manych River, but only 450–810 mg/L in the Don River system; calcium content being 119 mg/L and 45–78 mg/L, respectively. We suggested that higher calcium levels in the Manych River favored *D. r. bugensis* over *D. polymorpha* since these levels were at the upper tolerance limit for *D. polymorpha* exceeding the optimum (70 mg/L; Ludyanskiy et al. 1993). The continued decline of *D. r. bugensis* over the recent 5-year study period was similar in the two river systems, making this original suggestion unlikely (Zhulidov et al. 2006). We believed that if higher total mineral/calcium content in the Manych River system favored *D. r. bugensis* because it was more tolerant of such high concentrations than *D. polymorpha* then declines would likely have been less than those found in the lower Don River system. It is evident, however, that calcium content or total mineral content of water does affect the relative number of *D. r. bugensis* and can account for among-site differences observed. But this factor can hardly be responsible for the temporal trends in dreissenid relative numbers and even seems to have no influence on these trends, e.g. imposing constraints on them through tolerance limits. The trends as such are obviously due to some other factors completely different from water mineralization. We still do not know reasons for the relative decline of *D. r. bugensis* and can only speculate at this point. It is of interest in this respect, that the timing of increase, maximum, and subsequent decline in the relative abundance of *D. r. bugensis* was synchronous at all sites despite different times of first appearance of *D. r. bugensis* and therefore different time periods in which the two species interacted (Zhulidov et al. 2006). Therefore, we feel that the relative decline has nothing to do with competitive interactions. In our view, the synchronicity across all sites provides strong evidence that some macroregional factor affected all populations examined.

Acknowledgements

We thank two anonymous reviewers for their helpful comments We are also grateful to Vadim Panov for his assistance and patience.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Number of *Dreissena polymorpha* and *D. r. bugensis* collected in the lower Don River system during 1977–2010.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2013/Supplements/AI_2013_Zhulidov_etal_Supplement.pdf