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# Recent trends in relative abundance of two dreissenid species, *Dreissena polymorpha* and *Dreissena bugensis* in the Lower Don River system, Russia

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With 3 figures and 1 table

**Abstract:** We sampled sites in the lower Don River system, Russia between 1977 and 2004 (5 sites) or between 1999 and 2004 (10 sites) to determine relative trends in two dreissenid species, *Dreissena bugensis* and *Dreissena polymorpha.* The sites were located in the main river, in connecting reservoirs, and in a major tributary, the Manych River. For sites sampled beginning in 1977, *D. bugensis* was first found in the lower river in 1980 and then more upstream in 1991. The relative proportion of *D. bugensis* increased to reach a maximum of 30–50 % of the dreissenid population by 1999. After 1999, this species decreased at 14 of the 15 sites. At sites in the Don River, the proportion that *D. bugensis* comprised of the total dreissenid population after 1999 declined from 25–50 % to 10–18 %, whereas at sites in the Manych River the proportion declined from 65–75 % to 33–43 %. The decline of *D. bugensis* relative to *D. polymorpha* is unique; in most other water bodies *D. bugensis* displaces *D. polymorpha* over time because of its superior physiological attributes. Reasons for the relative decline of *D. bugensis* are unclear, but we speculate that selective predation by fish may be a potential factor.

**Key words:** distribution, displacement, predation, competition.

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## Introduction

*Dreissena polymorpha* (Pallas 1771) and *Dreissena bugensis* (Andrusov 1897) also known as zebra mussel and quagga mussel, respectively, are species of Ponto-Caspian origin that have invaded areas far beyond their native ranges to both Europe and North America (Starobogatov 1994, Mills et al. 1996, Orlova & Scherbina 2002). Their expansion has had diverse ecosystem-wide effects, heavily impacting aquatic communities, especially in North American lakes (Ludyanskiy et al. 1993, Vanderploeg et al. 2002). Whereas *D. polymorpha* began to spread intensively throughout Eurasia about 200 years ago and has now colonized most of western Europe (Starobogatov 1994), *D. bugensis* has only recently (late 1980 s/early 1990 s) begun to spread outside of its native range within the Black Sea basin (Orlova & Scherbina 2001). In North America, the two species were first reported almost simultaneously in the late 1980 s (Hebert et al. 1989, May & Mardsen 1992).

The recent range expansion of these two ecologically similar species places them in direct competition for available resources. In areas where they are sympatric, *D. bugensis* is competitively superior to *D. polymorpha*, having displaced *D. polymorpha* as the dominant dreissenid in North American lakes and rivers (Mills et al. 1999, Ricciardi & Whoriskey 2004), and in rivers and reservoirs of Ukraine and Russia within 9 years (Kharchenko 1995, Mills et al. 1996, Orlova & Scherbina 2002). In some areas, however, a partitioning of available substrate has allowed *D. polymorpha* to remain co-dominant with *D. bugensis* (Diggins et al. 2004).

In a previous study, we unexpectedly found low abundances of *D. bugensis* relative to *D. polymorpha* in the lower Don River system despite the former species having colonized the region for over a decade (Zhulidov et al. 2004). Our primary focus in this previous study was to document distribution patterns of the two species over a broad range of conditions. It was not possible, therefore, to ascertain whether relative abundances of the two species were stable and conditions were not favorable to *D. bugensis*, or whether relative abundances were in fact changing, but displacement was occurring at a slower rate than found in other studies. In this paper, we examine relative trends in *D. bugensis* and *D. polymorpha* populations by presenting temporal patterns over a 27-year period in the same lower Don River system.

## Material and methods

Samples of *Dreissena* 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 system

**Table 1.** Location of sites sampled in the lower Don River (Stations 1–11) and in the Manych River system (Stations 12–15) in July 1999–April 2004.

| Station Designation (see Fig. 1 A) | Station Location | Distance from Don River mouth (km) | Times Sampled, 1999–2004 |
|---|---|---|---|
| 1 | Tsimlyansk Reservoir, 50 km upstream from dam | 373 | 4[a] |
| 2 | Tsimlyansk Reservoir, 0.3 km downstream from dam | 323 | 7[b] |
| 3 | Don River, 32 km downstream from town of Volgodonsk | 291 | 7[b] |
| 4 | Don River, downstream Village of Konstantinovsk | 207 | 7[b] |
| 5 | Don River, 6.5 km downstream Village of Semikarakorsk | 160 | 5[c] |
| 6 | Don River, Village of Razdorskaya | 150 | 6[d] |
| 7 | Don River, 15 km downstream Village of Bagaevskaya | 97 | 7[b] |
| 8 | Don River, 1 km upstream Aksay settlement | 61 | 7[b] |
| 9 | Don River, Village of Koluzaevo | 33 | 7[b] |
| 10 | Don River delta, B. Kalancha, upstream village of Dugino | 20 | 7[b] |
| 11 | Don River, 1 km upstream of Town of Azov | 16 | 6[d] |
| 12 | Manych River, Proletarskoye Reservoir | 258 | 7[b] |
| 13 | Manych River, Village of Vesyoly | 160 | 5[e] |
| 14 | Manych River, Ust-Manych Reservoir | 99 | 7[b] |
| 15 | Manych River, near Village of Manychskaya | 98 | 7[b] |

[a] Oct 2002, May 2003, Sep 2003, Apr 2004.
[b] Jul 1999, Jun 2000, Sep 2001, Oct 2002, May 2003, Sep 2003, Apr 2004.
[c] Aug 2001, Oct 2002, May 2003, Sept 2003, Apr 2004.
[d] Jul 1999, Aug 2001, Oct 2002, May 2003, Sep 2003, Apr 2004.
[e] Jul 1999, Sep 2002, May2003, Sep 2003, Apr 2004.

within the western part of the Kuma-Manych depression (Table 1, Fig. 1) (Zhulidov et al. 2004). The lower Don River was defined as the river section from the Tsimlyansk Dam to the delta at Taganrog Bay of the Azov Sea. Some of the sites were located near the continuous monitoring stations of the State Service (Network) of Observation and Control of Environmental Pollution (OGSNK/GSN) of the Federal Service of Russia for Hydrometeorology and Environmental Monitoring (Roshydromet) (see: Zhulidov et al. 2000, 2001). The initial year of sampling varied between the sites. Five sites were sampled beginning in 1977 (Sites 2, 6, 7, 8, and 11), eight sites were sampled beginning in 1999 (Sites 3, 4, 9, 10, 12, 13, 14, and 15), one site was sampled beginning in 2001 (Sites 5), and one site was sampled beginning in 2002 (Site 1). Samples were usually collected once a year during the ice-free season (April to October) except in 1995–1998 when no samples were collected. The last sampling date for all sites was in April, 2004. Dreissenids were collected as part of a biomonitoring program under the supervision of the Hydrochemical Institute. On each sampling date, care was taken to collect

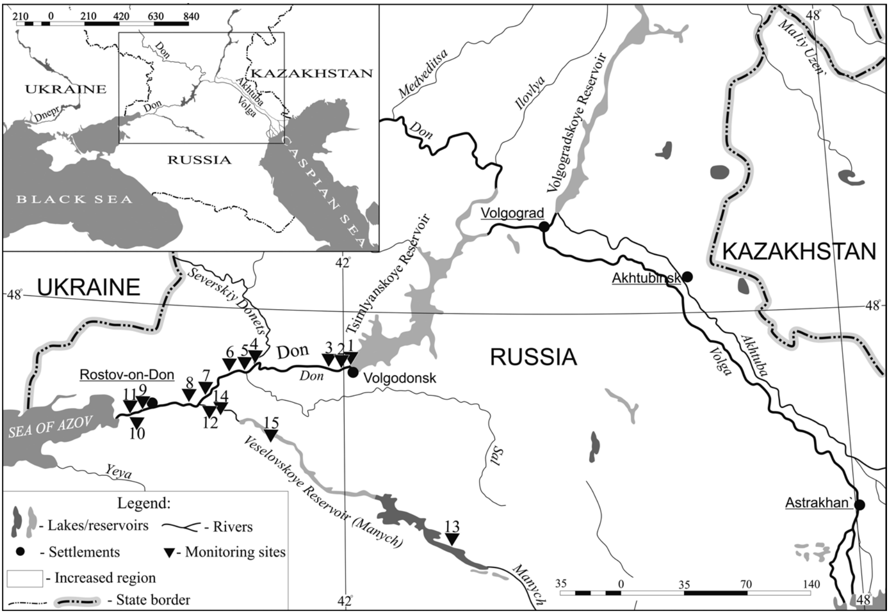


**Fig. 1.** Location of sampling sites in the lower Don River and Manych River systems.

representative specimens (90–300 individuals) from each site. Since our purpose was to document relative abundances of the two species over a wide area, we focused on collecting specimens from a variety of substrates and water depths. At each site, mussels were collected from two depths. In shallow water (<2 m), mussels were collected by hand from 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. Maximum water depths are 10–12 m in the lower Don River and 2–3 m in the Manych River so our sampling depths well-characterized habitats in each river system. All specimens were dried whole (shell and soft tissue) and stored in doubled polyethylene bags. Subsequently, only large individuals of similar size (15–22 mm) were identified to species. Identifications were based on shell morphology as described by May & Mardsen (1992). Specimens identified as *D. polymorpha* had a well-developed carina (i. e., acute angle) between the ventral and dorsal surfaces, while specimens identified as *D. bugensis* did not have a carina. Approximately up to 62 % of *D. bugensis* generally fit the description of the "profunda" form as found in the North American Great Lakes (Dermott & Munawar 1993, Claxton et al. 1998). However, because of uncertainties in shell morphology, these individuals were not considered separately from the typical form of *D. bugensis*.

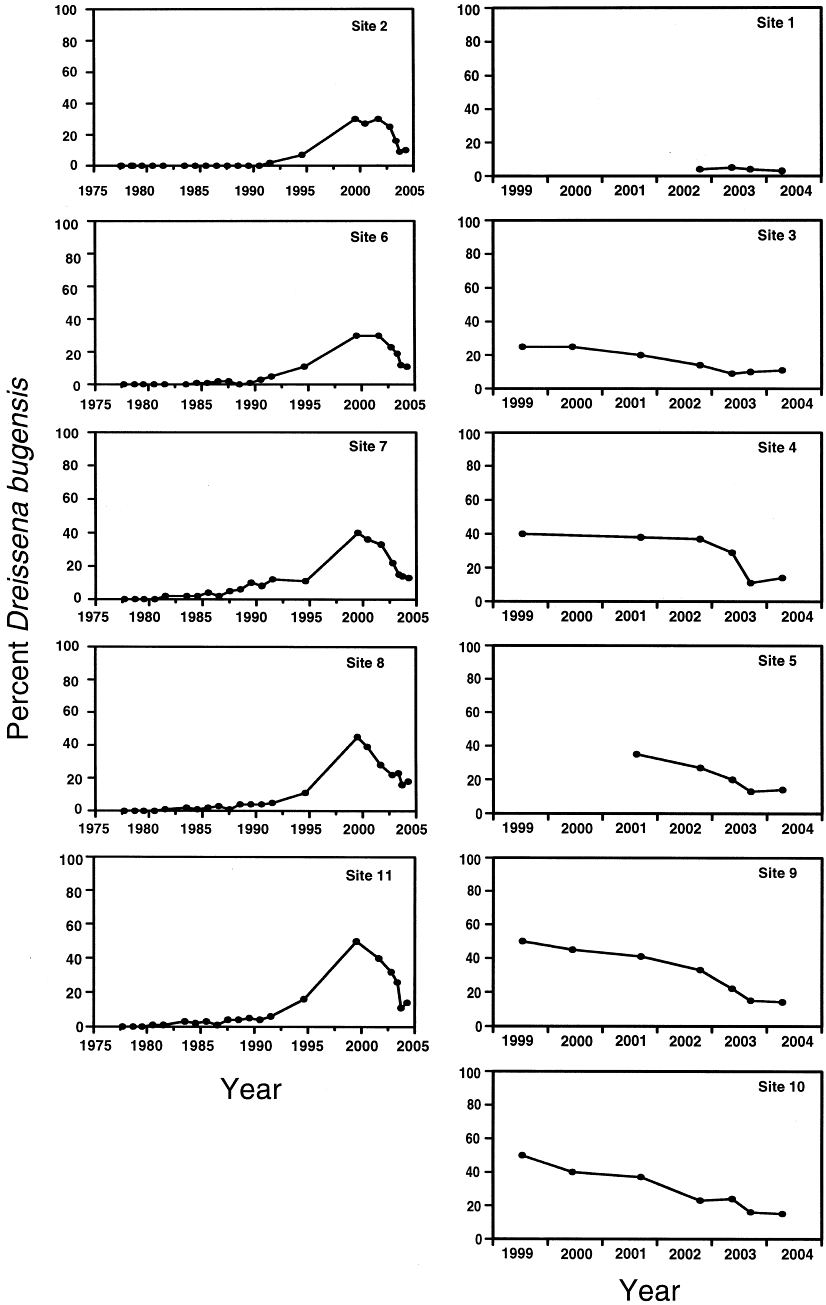


**Fig. 2.** The relative proportion (percent) of the total *Dreissena* population comprised by *Dreissena bugensis* at the 11 sampling sites in the lower Don River system. Sites in the left column were sampled 1977–2004, while sites in the right column were sampled 1999–2004.

# Results

## Trends in dreissenid distribution

For the five sites that were initially sampled in 1977, *D. bugensis* was found first at sites in the lower portion of the Don River system and then at sites in the upper portion. It was found at Site 11 in 1980, at Sites 7 and 8 in 1981, at Site 6 in 1984, and at Site 2 in 1991 (Figs. 1 and 2). The relative proportion of *D. bugensis* gradually increased at each of these sites, reaching a peak of 30–50 % of the dreissenid population in 1999. However, beginning in 1999 and through 2004, the relative proportion of *D. bugensis* declined at 14 of the 15 sites sampled (Figs. 2 and 3). The only location where *D. bugensis* did not de-

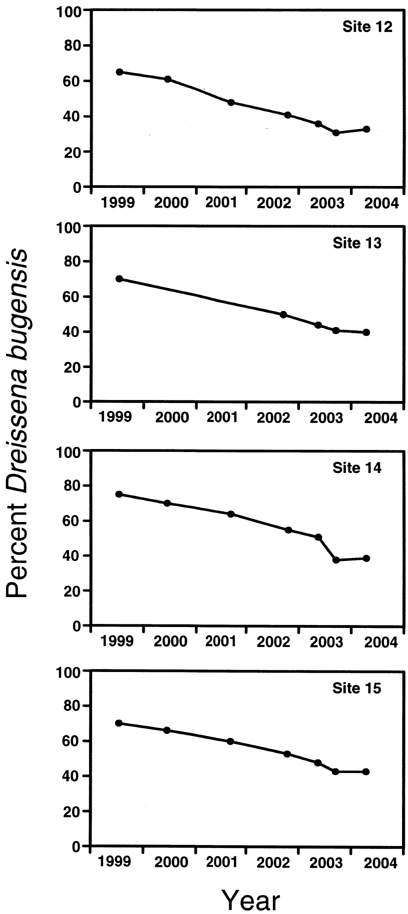


**Fig. 3.** The relative proportion (percent) of the total *Dreissena* population comprised by *Dreissena bugensis* at the 4 sampling sites in the Manych River, 1999–2004.

cline was at the site in Tsimlyansk Reservoir (Site 1) where it comprised only a small fraction of the dreissenid population ($\leq 5\%$). For the 14 other sites, the mean decline between 1999 (13 sites) or 2001 (1 site) and 2004 was 24 % (range 14 to 36 %), and this difference was significant (Wilcoxon signed rank test; $P < 0.01$). Proportional declines of *D. bugensis* in the lower Don River and the Manych River systems were similar despite greater initial abundances of this species in the latter system. Over the 6-year period, the association in trends between the stations was highly significant (Kendall's coeffi cient of concordance = 0.81; $P < 0.001$; excluding Station 1). In 1999, *D. 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, relative proportions decreased to 10–18 % and 33–43 % in the two rivers, respectively.

## Discussion

To our knowledge, this is one of the few records of *D. bugensis* declining relative to *D. polymorpha* in an area of overlapping distributions. Most all previous studies in both Eurasia and North America have shown that *D. bugensis*, over time, displaces *D. polymorpha*. Displacement has occurred in a variety of different habitat types, ranging from warm-shallow and deep-cold lakes, to rivers and reservoirs (Kharchenko 1995, Mills et al. 1996, Mills et al. 1999, Orlova & Scherbina 2002, Ricciardi & Whoriskey 2004). Reasons for the competitive advantage of *D. bugensis* seem to lie in species-specific differences in physiological characteristics. *D. bugensis* has a higher assimilation efficiency than *D. polymorpha* so that at low food levels it maintains higher growth and fecundity rates (Baldwin et al. 2002). Also, *D. bugensis* has a lower respiration rate under different seasonal temperature regimes (Stoeckmann 2003). Lower respiration rates decrease metabolic costs, allowing *D. bugensis* to have greater growth and greater allocations of energy to soft body mass than *D. polymorpha* at similar food conditions (Roe & MacIsaac 1997). These attributes give *D. bugensis* a strong competitive advantage during periods of low food and high temperatures. Also, because of higher growth rates, *D. bugensis* larvae settle at a larger size than *D. polymorpha* larvae, giving them a competitive advantage (Martel et al. 2001). While some laboratory studies found *D. bugensis* 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. bugensis* was similar to, or greater than, *D. polymorpha* at typical summer-warm temperatures (Mac Isaac 1994, Thorp et al. 2002).

All sites within the lower Don River and Manych River systems displayed a similar decline in *D. bugensis*. This consistent decline occurred over a waterway system of more than 600 km, and across stations that were likely subjected to very different local influences. To have such an extensive decline, either a broad, fundamental change occurred in river conditions beginning in 1999, or conditions were marginal for *D. bugensis* to begin with. In the latter case, possibly an initial colonization period was followed by the observed decline as the population failed to acclimate to an unfavorable habitat. At sites in the lower Don River that were sampled beginning in 1977, *D. bugensis* increased gradually to reach a maximum of 40–50 % of the dreissenid population within 18–19 years. This rate of population increase relative to *D. polymorpha* is considerably less than the 71 % within a 4–9 year period found in the lower Dnepr (Dnieper) River (MILLS et al. 1996). Yet the abrupt decline beginning in 1999 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 (ZHULIDOV, unpubl. data). In our previous paper, we speculated that the greater dominance of *D. 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). 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 was 119 mg/L and 45–78 mg/L, respectively. We suggested that higher levels in the Manych River favored *D. bugensis* over *D. polymorpha* since levels exceeded the optimum for *D. polymorpha* (70 mg/L; LUDYANSKIY et al. 1993). However, the decline of *D. bugensis* over the 5-year study period was similar in the two river systems making this original suggestion unlikely. If higher total mineral/calcium content in the Manych River system favored *D. bugensis*, then declines would likely have been less than those found in the lower Don River system.

One possible explanation for the widespread decline of *D. bugensis* is selective predation by the fish community. *D. bugensis* has a thinner, more fragile shell than *D. polymorpha* (NICHOLS [http://www.nsgo.seagrant.org/funding/zmlifehistory.html], TYUTIN & MEDYANTSEVA 2004 a, b, our unpubl. data). A thinner shell allows fish to more efficiently crush and digest even large individuals. Unlike the Great Lakes region in North America, where few native fish species are able to efficiently feed on *D. polymorpha* and *D. bugensis* (JUDE 2003), in Eurasia these bivalves are important food items for a variety of fish. Most of them are cyprinids including roach (*Rutilus rutilus* L.), common bream (*Abramis brama* L.), silver bream (*Blicca bjoerkna* L.), ide (*Leuciscus idus* L.), carp (*Cyprinus carpio* L.), and black carp (*Mylopharingodon piceus* RICHARDSON). Some species from other families are also active consumers of dreissenids, especially round goby (*Neogobius melanostomus* (PALLAS), sterlet (*Acipenser ruthenus* L.) and some whitefish species (STARO-

BOGATOV 1994, RESHETNIKOV 2003). Each of these fish species can be highly selective of its molluscan prey (STAROBOGATOV 1994), and thus influence both the absolute and relative number of dreissenid species.

We believe that the recent expansion of *D. bugensis* into areas previously inhabited only by *D. polymorpha* can lead to shifts in food preferences of some common Eurasian fish species that previously did not feed intensively on dreissenids. KASYANOV & IZYUMOV (1995) indicated that the dreissenid invasion into Volga River reservoirs resulted in a divergence of roach populations into molluscivorous and herbivorous forms, with different growth rates and different morphological and ecological characteristics. We speculate that after an initial colonization period and abundances of *D. bugensis* peak, the fish community adapts to this new food source, contributing to subsequent declines. *D. bugensis* has only recently invaded the Rybinskoye Reservoir, but it has now become the dominant prey item of bream (G. K. SCHERBINA pers. comm.). It has been suggested that colonization of a given water body by dreissenids would increase local populations of molluscivorous fishes, further contributing to the selection process (TYUTIN & MEDYANTSEVA 2004 b).

Selective fish predation, besides explaining the widespread decline of *D. bugensis* relative to *D. polymorpha* in the two river systems, may also explain the proportionally greater abundance of *D. bugensis* in the Manych River. The relationship between shell thickness and calcium content in dreissenids is not known but, because of greater calcium content of the river water, the shells of *D. bugensis* in the Manych River may be thicker than in the lower Don River, leading to a diminished level of selective predation.

Although *D. bugensis* usually displaces *D. polymorpha* as the dominant dreissenid, the latter can remain dominant in certain types of habitats. A recent study found that *D. polymorpha* was more prevalent on macrophytes than on adjacent benthic substrates (DIGGINS et al. 2004). On macrophytes, *D. polymorpha* comprised 30–61 % of all dreissenids, while on benthic substrates *D. bugensis* comprised 92–100 %. An increase in macrophytes in the Don River and Manych Rivers could have occurred during our study period, leading to a proportional increase in *D. polymorpha*. However, we sampled a variety of different substrates and all displayed a similar decrease in *D. bugensis*. Habitat partitioning was also observed vertically along a canal wall (RICCIARDI & WHORISKEY 2004). *D. polymorpha* dominated biomass at an upper wall location (1.5–2.0 m), but *D. bugensis* dominated at lower locations (> 2.5 m). At the former location, *D. bugensis* decreased from comprising 60 % of total dreissenid biomass to 20–30 % in one year. The authors offered no explanation for the *D. bugensis* decline. While a comparison of changes on such a small scale to changes in a large river system may not be justifiable, it does illustrate that abrupt shifts in relative abundances do occur.

While unlikely, selective infection by an unknown pathogen may also have been the cause of the decline of *D. bugensis* relative *D. polymorpha*. Even though spatial distributions overlap and metabolic functions of the two species are similar, differential infection rates have been documented (KARATAYEV et al. 2000). Again, whatever the cause of the proportional decline of *D. bugensis* relative to *D. polymorpha*, the abrupt change in 1999 would indicate some threshold tolerance level had been exceeded.

Our results contrast to most all previously documented trends for these two species in areas of overlapping ranges. In this regard, relative trends in the lower Dnepr (Dnieper) River, Ukraine are of particular interest. *D. bugensis* replaced *D. polymorpha* as the dominant dreissenid in 4–9 years in this river system (KHARCHENKO 1995). Since the Dnepr River study was conducted in the early to mid-1990 s, further surveys should be conducted to determine if *D. bugensis* is still the dominant species. If *D. bugensis* is still dominant, then a detailed comparison of environmental conditions within the lower Dnepr and lower Don/Manych River systems may provide insights into factors influencing relative abundances of these two species. It should be noted that *D. bugensis* was first described in the Yuzhny (Southern) Bug River at the turn of the century, but this species was not found (ALIMOV & BOGUTSKAYA 2004) or was rare (ZHULIDOV, unpubl. data) in this region of the river in the early 1990 s. A survey in the late 1990 s found that *D. polymorpha* was 10 times more abundant than *D. bugensis* in the Southern Bug River Estuary (I. A. GRIGOROVICH, pers. comm.), further demonstrating that under some conditions *D. bugensis* does not replace *D. polymorpha.*

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