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Range expansion of quagga mussels *Dreissena rostriformis bugensis* in the Volga River and Caspian Sea basin

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Abstract

In 1992, we discovered populations of the nonindigenous quagga mussel *Dreissena rostriformis bugensis* (Andrusov 1897) in the middle reaches of the Volga River. The same species was found in samples collected between 1994 and 1997 in the Volga delta and in shallow areas of the Northern Caspian Sea. *D. r. bugensis* always co-occurred with its more widespread congener, the zebra mussel *D. polymorpha* (Pallas 1771). The quagga mussel's contribution to total *Dreissena* abundance increased over time in the middle Volga reservoirs and Volga River delta. *D. r. bugensis* was common in the Volga portion of Rybinsk Reservoir during 1997 and, by 2000, it was in Uglich, Rybinsk and Gorky Reservoirs on the Upper Volga River. *D. r. bugensis* was neither found in Ivankov Reservoir, nor in terminal sections of the Volga-Baltic corridor including the eastern Gulf of Finland. Presently, all but the northern-most regions of the Volga River have been colonized by *D. r. bugensis*. We hypothesize that its introduction into the Volga River and Caspian basin occurred no later than the late 1980s via commercial shipping that utilized the Volga-Don waterway to navigate between the source Black-Azov Sea region and recipient areas on the Volga River. Larval drift likely contributed to establishment of populations at downstream sites, while human-mediated vectors may be responsible for introductions to upstream locations on the Volga River. We anticipate continued northward dispersal in conjunction with shipping activities.

Introduction

The Black and Azov Sea estuaries (Ponto-Azov) and the Northern Caspian Sea are considered key donor regions for recent fresh and oligohaline species invasions to the North and Baltic Sea regions (Leppäkoski and Olenin 2001; Bij de Vaate et al. 2002; Leppäkoski et al. 2002). In addition, species from these donor regions are disproportionately represented among recent invaders to the Laurentian Great Lakes (Ricciardi and MacIsaac 2000; MacIsaac et al. 2001). European dispersal of Ponto-Caspian species has resulted from intentional stocking programs and unintentional transport facilitated by human activities including commercial shipping and canal development (e.g., Zhuravel 1951; Mordukhai-Boltovskoi 1960; Karpevich 1975; Slyn'ko et al. 2002; Pollux et al. 2003). Creation of continental and transoceanic invasion corridors has facilitated dispersal of these species to recipient ecosystems in northern and Western Europe (e.g., Baltic and North Seas) and from these locations to North America (MacIsaac et al. 2001; Bij de Vaate et al. 2002; Slyn'ko et al. 2002). Dispersal and invasion by some Ponto-Caspian taxa is consistent with an 'invasional meltdown' scenario, whereby early arriving species facilitate establishment of subsequent ones (Simberloff and Von Holle 1999; Ricciardi 2001). For example, invasion of the Great Lakes by dreissenid mussels (*Dreissena polymorpha* (Pallas 1771), *D. rostriformis bugensis (*Andrusov 1897*)*) appears to have facilitated subsequent invasions by round gobies (*Neogobius melanostomus* (Pallas 1811)), which prey on the mussels, and by amphipods (*Echinogammarus ischnus* Stebbing 1899), which exploit habitat associated with mussel colonies (Ricciardi 2001). Facilitation of one invading species by an established one has also been reported in Europe (e.g., Van der Velde et al. 2000).

Dreissena polymorpha is one of the best-studied nonindigenous species owing to its prodigious capabilities of dispersal, population growth and biofouling. Its European invasion history is extensive both temporally and spatially, having been dispersed by human vectors during the past two centuries. Dispersal in Europe has been effected primarily by human-mediated mechanisms, including fouling on commercial vessels, ballast water transfer, canal development, and by timber rafting (see Andrusov 1897; Nowak 1971; Karataev et al. 1998; Olenin et al. 1999; Bij de Vaate et al. 2002; Pollux et al. 2003). Most recently, *D. polymorpha* was introduced by a trailered pleasure boat transported by ferry from England to Ireland, where it continues to spread (Pollux et al. 2003).

Dreissena polymorpha and *Mytilopsis leucophaeata* (Conrad, 1831) are the only Dreissenidae that have dispersed into the Baltic Sea area, the latter originating from the Atlantic coast of the United States and the Gulf of Mexico (Marelli and Gray 1983; Darr and Zettler 2000; Leppäkoski and Olenin 2001). Other members of the genus *Dreissena* have much more confined native and introduced ranges. For example, despite the existence of potential invasion corridors from the Ponto-Azov region to continental Europe (MacIsaac et al. 2001; Bij de Vaate et al. 2002), only *D. polymorpha* has been reported from inland Europe and the Volga River basin (Kinzelbach 1992; Starobogatov and Andreeva 1994; Scalskaya 2000; Van der Velde et al. 2000). Differential dispersal of dreissenid molluscs from Ponto-Caspian waters is difficult to comprehend, as invasion corridors available to *D. polymorpha* also should have been accessible to other dreissenids that possess broad environmental tolerances.

The quagga mussel was first recorded in the Bug River in the Black Sea drainage, and described as *D. rostriformis* (Andrusov 1890). Andrusov (1897) later named the species *D. bugensis*. Molecular analyses have revealed that there exist only minor genetic differences between *D. rostriformis* from the Caspian Sea and *D. bugensis* from the Black Sea, raising the possibility that they are a single species (Therriault et al. 2004). Rosenberg and Ludyanskiy (1994) and Starobogatov (1994), however, suggest separate species within the Pontodreissena lineage – *Dreissena rostriformis* and *D. bugensis* due to differences in coloration, morphology, maximum adult size and salinity tolerance. Consistent Therriault et al. (2004), hereafter we refer to *D. bugensis* as *D. rostriformis bugensis,* and *D. rostriformis* from Caspian Sea sample, collected at 12 ppt salinity as *D. rostriformis distincta* (Andrusov 1897).

D. rostriformis bugensis maintained a very restricted distribution within its native region–including the Dnieper-Bug Liman and lower Inguletz River–between the 1890s and 1940s (Zhuravel 1951). Its relatively rapid range expansion within the Ponto-Azov region resulted from construction of irrigation canals and reservoir impoundment in the basin's watershed (Mills et al. 1996). Between the 1940's and 1990's, *D. r. bugensis* extended its range north of the Black Sea into the Dnieper River and lower reaches of the Pripiat River, and west into the Dniester Reservoir and Dniester River estuary (Kharchenko 1995; Mills et al. 1996). The Pripiat River is a component of the central European invasion corridor linking the Black and Baltic Seas via the Dnieper River to the south and Vistula and Nemanus Rivers to the north (Ricciardi and MacIsaac 2000; MacIsaac et al. 2001; Bij de Vaate et al. 2002). No evidence exists that *D. r. bugensis* has dispersed farther north (i.e., beyond the lower Pripiat River) along this corridor. *D. r. bugensis* was first recorded in the Volga River in 1992 (Antonov 1993), 40 years after opening of the Don-Volga canal (in 1952) that linked the Ponto-Azov and Caspian regions. No palaeontological evidence exists that *D. r. bugensis* was ever present in the Caspian Sea, nor in the Volga River or Zymlyansk Reservoir, a deep-water constituent of the Volga-Don waterway.

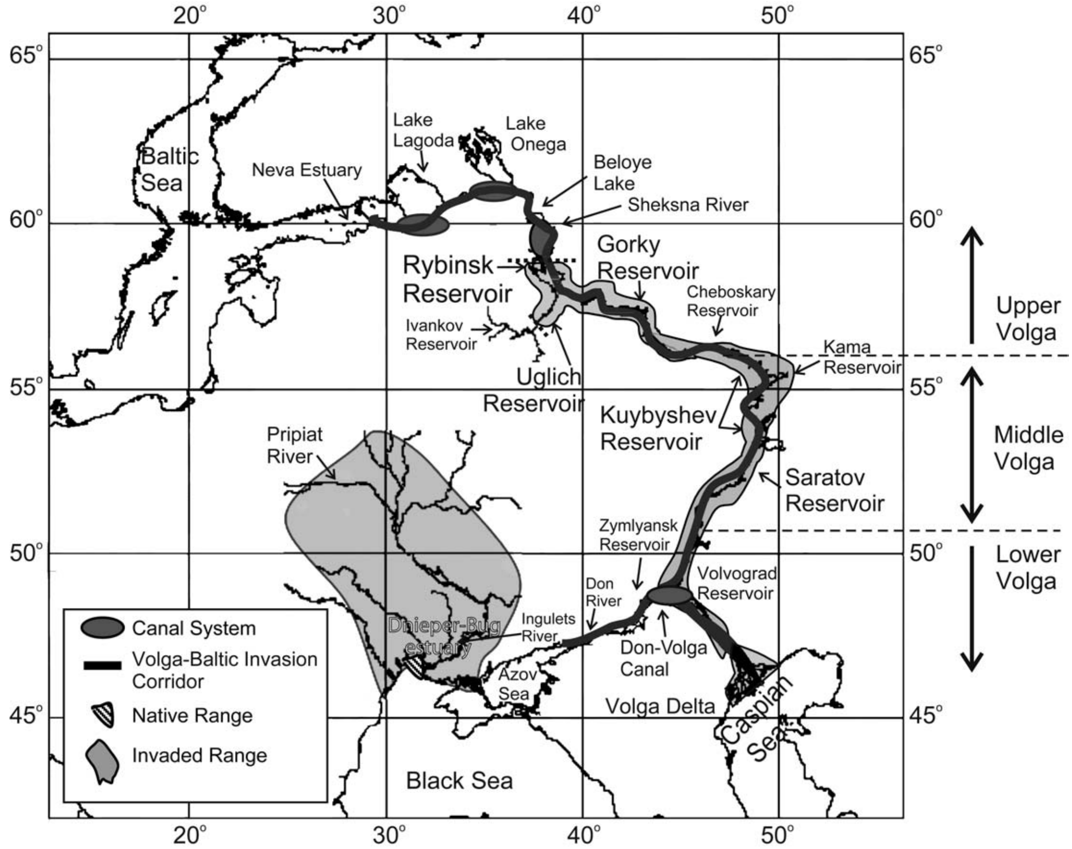

Figure 1. Eurasian distribution of *Dreissena rostriformis bugensis* along the Volga River system. Major reservoirs are indicated by larger letters. Site numbers and *Dreissena* composition are provided in Table 1. Distribution limits in the Upper Volga River (e.g., Rybinsk and Uglich Reservoirs) are indicated by dotted lines.

The objective of this study was to examine the recent invasion history and patterns of dispersal of *D. r. bugensis* within the Volga River and Caspian Sea, and to identify vectors of primary and secondary range expansion.

Study area and methods

Our study area covered three major regions in the Volga-Caspian basin, Russia: 1) the southern region, including the Northern Caspian Sea and the Volga delta; 2) the middle region, including Saratov and Kuybyshev Reservoirs and associated reaches of the Volga River; and 3) the northern region, including Upper Volga Reservoirs and waterbodies of the Volga-Baltic traffic system (see Figure 1).

To establish the presence of *D. r. bugensis*, we collected benthic samples downstream of the Kuybyshev Reservoir dam (area 1) in 1992-1993, and again in 1998 (see Table 1). In 1993, we sampled 100 km upstream of this location (area 2), while in 2001 we sampled the northern stretch of Kuybyshev Reservoir (area 3). Saratov Reservoir (areas 4, 5) was sampled during 1992 and 1998. During 1994–1997 and 2000, samples were collected in the Astrakhan nature reserve in Damchik district (area 6), in the Volga delta, the Volga-Caspian channel, shallow areas of the Caspian Sea adjacent to the Volga delta (area 7), and at Chistaya Banka Island in the transitional zone of the Northern Caspian Sea (area 8). In region 3, we sampled the upper part of the Volga River including Rybinsk Reservoir (1997, 2000 and 2001; areas 9–14), and Uglich, Ivankov and Gorky Reservoirs (2000; areas 15–17, 22). All samples were collected from standardized sampling stations developed by the Institute for Inland Water Biology, Borok, Russia (IBIW), and later examined for presence of *Dreissena* mussels. Additional sampling was conducted at several sites in the Upper Volga system, including at

Table 1. D. rostriformis bugensis records in key areas of the Volga – Caspian basin and Volga-Baltic waterway; contribution of *D. r. bugensis* to total *Dreissena* abundance. For location of sampling areas, see Figure 1 and Material and Methods.

Area	Sampling site		Sampling Date	Site Depth (m)	*D. r. bugensis* and *D. polymorpha* presence (--/--)	*D. r. bugensis* Maximum size (mm)	Contribution of *D. r. bugensis* to total abundance (%)	Source
	Site number	Sampling location						
Kuybyshev Reservoir	1	Above dam, right bank	Sept, 1992	1–12	+/+	23–30	54	Antonov 1993
		Above dam, Togliatti River port	Sept, 2001		+/-	23–30	100	this study
	2	Sengilei city	Sept, 1993	13	+/+	23–30	10	Antonov 1996
	3	Krasnovidovo, riverbed slope	Sept, 2001	9–14	+/+	32	83	this study
		Krasnovidovo, littoral, right bank	Sept, 2001	0.5–1	+/+	7	84	this study
		Krasnovidovo, littoral, island, leftward on the river slope	Sept, 2001		−/+	–	–	this study
Saratov Reservoir	4	Settl. Mordovo	Sept, 1992	10	+/+	23–30	< 1-4	Antonov 1993
		Settl. Mordovo	1998		+/+	No data	92-100	this study
	5	Gusinoe Lake	Sept, 1992	1–2	+/+	No data	< 1	Antonov 1993
		Gusinoe Lake	1998		+/+	No data	55-88	this study
Volga delta	6	Damchik area ABNR, united data*	Sept, 1994	2–5	+/+	1.5	13	Orlova et al. 1999
		Damchik area ABNR, united data*	Sept, 1995		+/+	11	17	Orlova et al. 1999
		Damchik area ABNR, united data*	Sept, 1996		+/+	28	34	Orlova et al. 1999
		Damchik area, ABNR*, stream Bystraya	Sept, 2000		+/+	31	98	this study
Volga avandelta	7	Volga-Caspian canal	Sept, 1996	1.5	+/+	21	56	Orlova et al. 1999
		Gandurinsky canal	Sept, 1996		+/+	20	4	Orlova et al. 1999
		Gandurinsky canal	Sept, 1997		+/+	28	78	Orlova et al. 1999
	8	Chistaya banka	Sept 1997	1.5	+/+	9	79	Orlova et al. 2002
Rybinsk Reservoir (Volga part)	9	Koprino	1997	6	+/+	18	> 50	Dr. Biochino pers. comm.

Table 1. Continued.

Area	Sampling site		Sam-pling Date	Site Depth (m)	*D. r. bugensis* and *D. polymorpha* presence (--/--)	*D. r. bugensis* Maximum size (mm)	Contribution of *D. r. bugensis* to total abundance (%)	Source
	Site number	Sampling location						
		Koprino	Sept, 2000		+/+	29	98	Orlova and Shcherbina 2001
		Koprino	Sept, 2001		+/+	28	97	this study
Rybinsk Reservoir (Mologa part)	10	Breitovo	Sept, 2000	11	−/+	–	–	this study
		Breitovo	Sept, 2001		+/+	16	> 1	this study
	11	Pervomaiskie islands	Sept, 2000	3.5–5	−/+	–	–	Orlova and Shcherbina 2001
		Pervomaiskie islands	Sept, 2001		+/+	18	Single individuals	this study
Rybinsk Reservoir (Central part)	12	Central cape	Sept, 2000	5.5	+/+	34	Single individuals	Orlova and Shcherbina 2001
		Central cape	Sept, 2001		+/+	34	Single individuals	this study
Rybinsk Reservoir (Sheksna part)	13	United data	Sept, 2000	7.5	−/+	–	–	Orlova and Shcherbina 2001
		United data	Sept, 2001		−/+	–	–	this study
Rybinsk Reservoir (downstream of the dam)	14	Volkovo	Sept, 2000	5	−/+	–	–	Orlova and Shcherbina 2001
		Volkovo	Sept, 2001		+/+	17	5	this study
Uglich Reservoir	15	Dubna River	Sept, 2000	6–7	−/+	–	–	Orlova and Shcherbina 2001
	16	Medveditza and Nerl River mouths	Sept, 2000	5.5–8.0	+/+	34	85.3	Orlova and Shcherbina 2001
Ivankov Reservoir	17	United data	Sept, 2000	4.4–7.0	−/+	–	–	Orlova and Shcherbina 2001

Table 1. Continued.

Area	Sampling site		Sampling Date	Site Depth (m)	*D. r. bugensis* and *D. polymorpha* presence (--/--)	*D. r. bugensis* Maximum size (mm)	Contribution of *D. r. bugensis* to total abundance (%)	Source
	Site number	Sampling location						
VBW**, Sheksna Reservoir	18	United data	Sept, 2001	7	− /-	–	–	this study
VBW**, Beloye Lake	19	United data	Sept, 2001	1–5	− /-	–	–	this study
VBW**, Neva Bay	20	United data	Aug, 2001	–	− /-	–	–	N.P. Finogenova pers. comm.
VBW**, Neva estuary	21	United data	1998-2001	1–5	− /+	–	–	Orlova and Panov (unpubl.)
Gorky Reservoir	22	United data	2000	4–11	+/+	33	2–18	this study
Volgograd Reservoir	23	Near city of Volgograd	2000	0.5–1.5	+/?	27	No data	this study
Dnieper Liman (Black Sea basin)	24	Near city of Kherson	Aug, 2001	7			this study	
		Riverbed slope			+/+	27	86	
		Littoral zone			+/+	21	62	

*ABNR Astrakhan Biosphere Nature reserve; **VBW – Volga-Baltic waterway

Sheksna River (area 18), Beloye Lake (area 19) and in the eastern Gulf of Finland (areas 20, 21; see Table 1).

During September 2001, the additional samples were collected along a 450 km stretch of the Middle Volga including the Kama and Volga sections of Kuybyshev Reservoir to evaluate the current species composition of dreissenid mussels (Figure 1). Habitats sampled included riverbed slope, riverbed ridge (*via* collections on fouled unionids collected from trawls) and the littoral zone, where *Dreissena* postveligers settle upon accessible hard substrates (Table 1). One qualitative sample of *Dreissena* was collected from the lower Volga at Volgograd Reservoir in 2000 (area 23). Finally, in August 2001, samples were collected from the native range *D. r. bugensis*, near Kherson, Ukraine.

In the Upper Volga River (between Volga-Baltic Waterway and Gorky Reservoir; Figure 1), and in the lower Volga River (between Volvograd Reservoir and the Volga delta–Caspian Sea) sampling was conducted using ponar grabs or by picking individuals attached to other mollusks. In the mid-Volga stretch, between the Kuybyshev and Saratov Reservoirs (Figure 1), we towed a 30-cm rake over a fixed distance (Shkorbatov and Antonov 1990) to estimate presence/absence and abundance. Samples from the eastern Neva estuary, Gulf of Finland, were collected by SCUBA diving. Finally, sampling of *D. r. bugensis* in the mussels' native region (i.e., in the Dnieper Liman, Black Sea basin) was conducted using a benthic trawl. Basic information for all sampling sites is provided in Table 1.

All *Dreissena* individuals were identified, counted and the percent contribution to total dreissenid abundance calculated. Shell length of all *Dreissena* were measured with calipers to the nearest mm or, for the smallest individuals of 0+ cohort, subdivided into 1 mm classes under a dissecting microscope. Size-frequency distribution histograms were developed and used to assess population size structure.

Results

Dreissena rostriformis bugensis was found at multiple sites in the Middle Volga at Kuybyshev and Saratov Reservoirs during 1992 (Table 1, Figure 1). It was also found in the Lower Volga, in the river delta in 1994, and first appeared in the transitional zone of the Northern Caspian Sea in 1996. It was first recorded in the Upper Volga in the Volga part of Rybinsk Reservoir during 1997. In 2000, *D. r. bugensis* was found in all parts of Rybinsk, Gorky and Uglich Reservoirs. In the entire Volga River cascade, *D. r. bugensis* has invaded seven of nine reservoirs, where it occurs on submerged plants and debris, in addition to ridges and slopes of former riverbeds. Densities in littoral zones are high but temporally variable, subject to occasional water level fluctuations associated with hydraulic regulation. Surveys of Sheksna River revealed the presence of only *D. polymorpha*, and dreissenids were completely absent from Beloye Lake. Thus by 2001, *D. r. bugensis* had an extensive range in Volga-Caspian basin that covered 3000 km, from the Rybinsk and Uglich Reservoirs in the north to the northern Caspian Sea in the south. Salinity in inhabited regions of the Caspian Sea was low, ranging between only 2 and 3‰. All reservoirs and other sampling sites, exclusive of the Neva estuary (0.3 − 1.7 psu, Nikulina 2003), were freshwater.

Despite its relatively recent invasion history in the Volga River system and in the Caspian Sea, *D. r. bugensis* comprised an increasing and often dominant fraction of total dreissenid abundance at many localities. For example, *D. r. bugensis* replaced *D. polymorpha* over time at many localities in the Lower Volga delta and Middle Volga (e.g., Kuybyshev and Saratov Reservoirs; Figure 2, Table 1). In the Volga delta, for example, the contribution of *D. r. bugensis* to total *Dreissena* abundance increased from 0% in 1992 and 1993, to 4%, 24%, 32% and 96%, in 1994, 1995, 1996 and 2000, respectively (Figure 2). Similar patterns were observed at each of the other major reservoirs on the Volga River (e.g., Rybinsk, Saratov, Kuybyshev) (Figure 2). Concurrent with these changes, the size structure of the *D. r. bugensis* population changed dramatically (Figure 3). For example, in 1994 the population in the Volga delta consisted only of small individuals (<2 mm), though the following year mussels as large as 12 mm were observed. In 1996, the distribution encompassed mussels of all size classes (1–30 mm) (Figure 3).

Surveys of dreissenid shells revealed that *D. r. bugensis* was absent from the Upper Volga River (Ivankov Reservoir, site 17) during 2000. Living *D. r. bugensis* dominated dreissenid populations in Uglich Reservoir, immediately downstream of Ivankov Reservoir (Figure 1). However, the shell 'bank' of dreissenid mussels at Uglich Reservoir contained only a very small fraction ($<0.7\%$) of *D. r. bugensis* remains, supporting its recent establishment in the

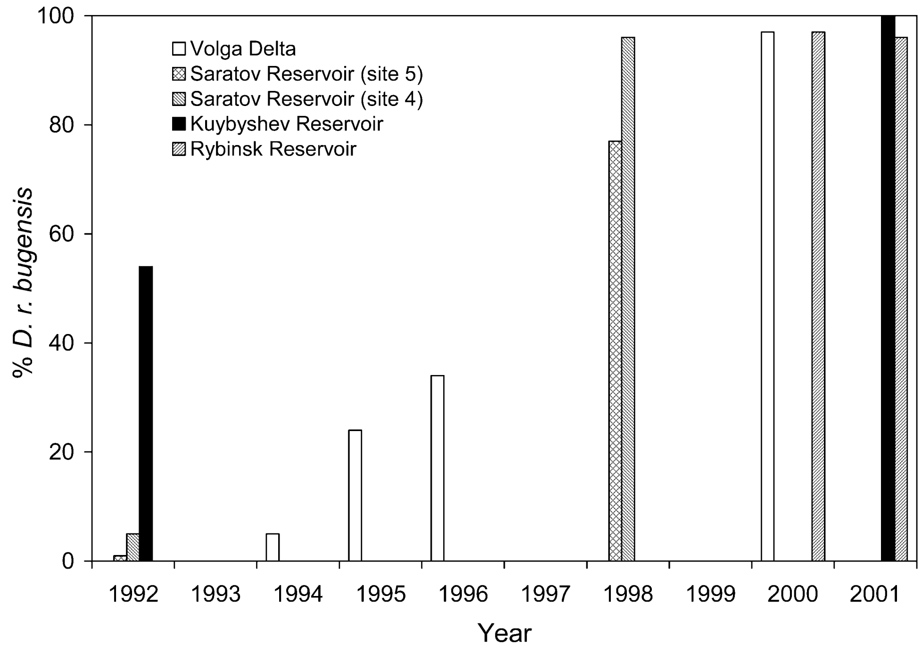

Figure 2. Temporal patterns of *Dreissena rostriformis bugensis* contribution to total dreissenid (*D. polymorpha* and *D. r. bugensis)* abundance at five locations along the Volga River system over time. See Table 1 for sample collection methods.

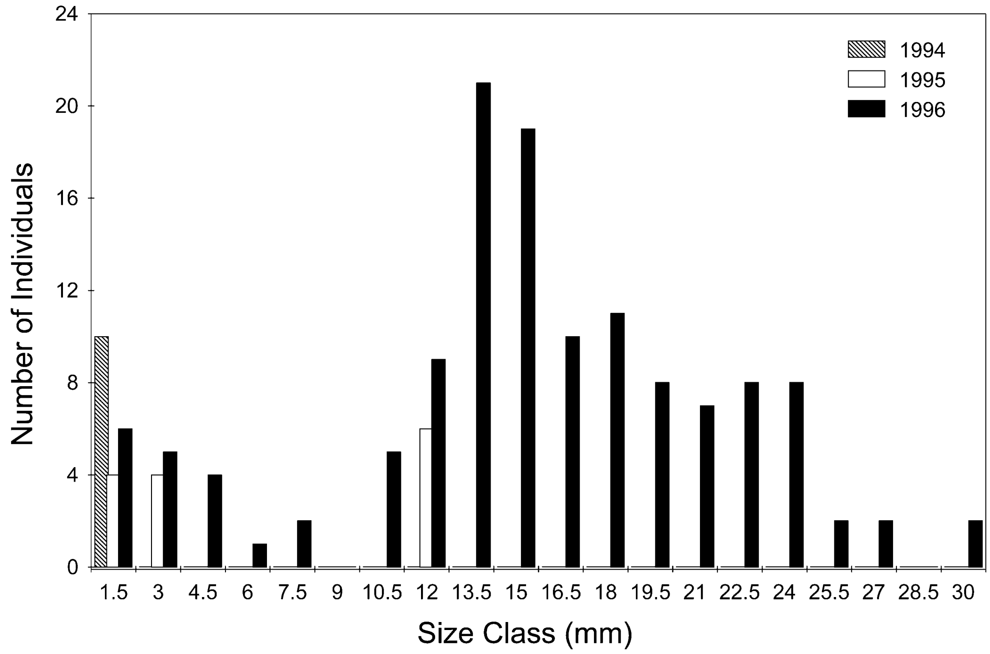

Figure 3. Changes in *Dreissena rostriformis bugensis* size classes over time in the Volga delta showing the rapid establishment of larger, older individuals.

reservoir. Further downstream in Rybinsk Reservoir (Figure 1), only large size classes of *D. r. bugensis* were observed alive, although shell remains at this location included all size classes of mussels. Consequently, it appears that the mussel invaded Rybinsk Reservoir followed by Uglich Reservoir.

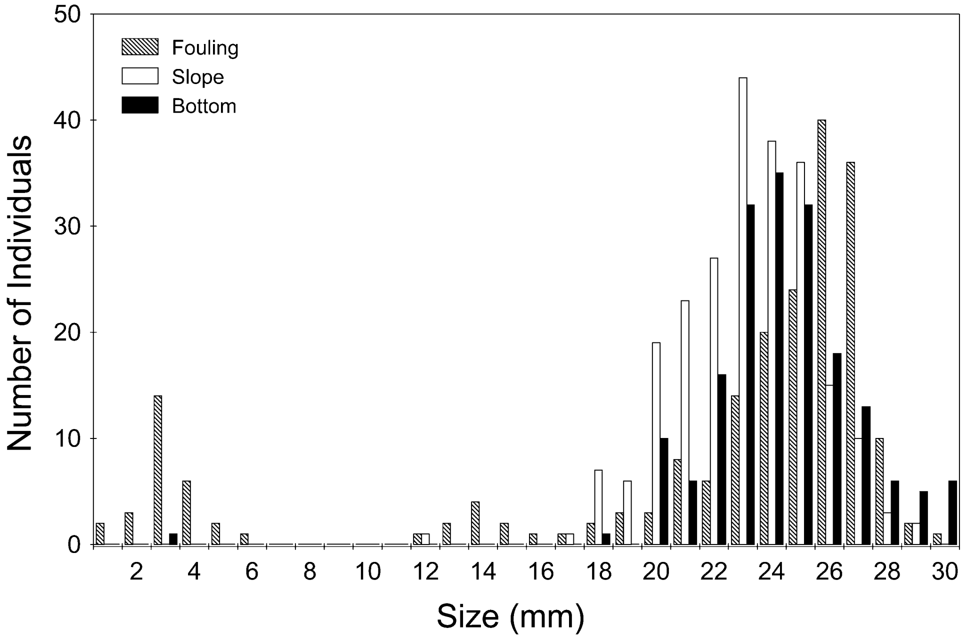

Figure 4. Size structure of *Dreissena rostriformis bugensis* for three habitat types (nearshore fouling community, riverbed slope community, and benthic community) in Kuybyshev Reservoir during 2001.

We assessed the relative abundance of different dreissenid mussels and species composition of young-of-year mussels (shell length < 1 to 13 mm) in Kuybyshev Reservoir during 2001. For riverbed slope populations, the contribution of *D. r. bugensis* was highest in the northern (Svijaga River to Loishevo; site 3) and southern (Togliatti; site 1) regions of the reservoir, and lower in the middle section (i.e., at Bolshoi Tcheremshan River mouth; site 2, Figure 1). The size composition of *D. r. bugensis* differed between riverbed and littoral habitats, with comparatively more small, medium and large individuals in fouling, slope and bottom habitats, respectively.

The size structure of *D. r. bugensis* populations appears to be related to habitat type as well as to the colonization history in the basin (Figure 2, Figure 3, Figure 4). For example, when first discovered in the Volga River, *D. r. bugensis* populations were dominated by small individuals and very few large mussels were present (Figure 2). However, with time, the Volga delta population assumed a size structure comparable to that of co-occurring *D. polymorpha*, and was similar to that of other well-established populations of *D. r. bugensis* in the Kuybyshev Reservoir (sites 1–3) and in the Dnieper Liman (site 24). By contrast, *D. polymorpha* populations that had been present at these sites for longer time periods contained a mixture of large and small size classes. In Kuybyshev Reservoir, size composition of *D. r. bugensis* varied by location (Figure 4). Populations on the reservoir bottom tended to be largest, followed by those residing on the reservoir's slope. A bimodal size distribution was observed among fouling individuals, with both large (20–30 mm) and small (0–6 mm) individuals present. Indeed, except for these individuals, there was scant evidence of mussel recruitment in the Kuybyshev Reservoir during 2001 (Figure 4).

With the exception of observations in 1997, *D. r. bugensis* populations in the upper Volga River cascade were dominated by larger size classes of mussels. For example, the population in the Upper Volga reservoir was dominated by relatively large individuals (i.e., 19 to 34 mm) during 2000, and the maximum average shell length of *D. r. bugensis* was greatest in the uppermost reservoir (i.e., Uglich; sites 15–16). Overall differences in size structure of *D. r. bugensis* populations from the Upper Volga, Rybinsk and Uglich reservoirs were substantial. The absence of juveniles and general paucity of small size classes in each of the populations in the upper reservoirs indicates that autochthonous recruitment of *D. r. bugensis* was low or absent in 1999 and 2000. However, more numerous yearling mussels were present in Rybinsk Reservoir in 2001.

Discussion

This study attempts to reconstruct the invasion history of *D. r. bugensis* in the Volga River and Caspian Sea drainage. Because the sampling regime was not designed with this explicit purpose in mind, different locations were sampled at different times, often with different equipment. These limitations preclude a definitive spatial and temporal analysis of the invasion dynamics. Nevertheless, by analysing presence/absence and population size structure data, it is possible to reconstruct the general pattern of invasion of this important species.

Dreissena rostriformis bugensis is native to the Dnieper-Bug Liman and Lower Inguletz River, the Black Sea basin, and was not found in the Volga River or Caspian Sea until recently. The Middle Volga was likely invaded first, as large individuals (23–28 mm) were observed in Kuybyshev and Saratov Reservoirs during 1992 (Table 1; Figure 1). Growth relationships have been derived principally for *D. polymorpha*. This species typically grows up to ~15 mm in its year of settlement, depending on food and thermal conditions (Mackie 1991; Smit et al. 1992; Dall and Hamburger 1996). Thereafter shell growth is sharply curtailed, typically to less than 7 mm per year (Smit et al. 1992; Dall and Hamburger 1996). Assuming a similar growth rate for *D. r. bugensis*, individuals with shell lengths up to 28 mm may be two to four years old. Consequently, it is possible that invasion of sites in the Middle Volga River occurred between 1988 and 1990.

Based on expected patterns of larval advection and the temporal sequence of establishment of new benthic populations, we propose that the first introduction may have occurred in the middle or upper part of Kuybyshev Reservoir (sites 2 or 3, Table 1). It is less likely that the initial colonization event may have occurred in Cheboksary Reservoir, which is immediately northwest and upstream of the Kuybyshev Reservoir. Shortly thereafter, perhaps by 1994, *D. r. bugensis* established well downstream in the lower Volga River (Figure 1). The initial inoculum of mussels for the Volga River cascade likely originated from a source population in the Dnieper River basin to which the species is native (site 24 or surroundings). This view is supported by microsatellite analyses, which show considerable genetic homogeneity among endemic and introduced populations of *D. r. bugensis* and marked differences in comparisons with the Caspian Sea population, likely *D. r. distincta* (Therriault et al. 2004).

The most probable mechanism for the initial introduction of *D. r. bugensis* into the Volga-Caspian basin is shipping from the Black Sea, via the Volga-Don Waterway (Figure 1). Subsequent invasions in the Volga delta and northern Caspian Sea may have resulted from either shipping activities or advective larval drift. Natural dispersal vectors–including larval drift–contributed substantially to downstream range expansion. Based upon confirmed presence data, the downstream dispersal rate of *D. r. bugensis* in the Volga River system was nearly 700 km/year, far greater than that reported for *D. r. bugensis* in the Laurentian Great Lakes (Mills et al. 1996). The rapid colonization of downstream sites in the Volga River system is, however, consistent with the dispersal pattern of *D. polymorpha* in North America (Johnston and Carlton 1996). The latter species spread through a combination of passive larval drift and 'jump' dispersal to overland sites (Johnson and Padilla 1996; Johnson et al. 2001). However, downstream establishment can be patchy rather than continuous, as was observed along the shore and main channel of Kuybyshev Reservoir and for *D. polymorpha* range expansion in rivers throughout eastern North America and Europe (Johnson and Carlton 1996; Pollux et al. 2003).

An extensive survey of dreissenids in the uppermost Volga reservoirs conducted between 1980 and the1990's did not detect *D. r. bugensis* (Scalskaya 2000). However, small- and large-bodied individuals were observed in Rybinsk Reservoir during 1997 and 2000, respectively, indicating that *D. r. bugensis* has inhabited this region since the mid-1990s.

Horvath et al. (1996) concluded that downstream populations of *D. polymorpha* were highly dependent on production of recruits from upstream sources in lakes. For invasive species with planktonic larvae, downstream drift may facilitate 'stepping-stone' range extensions whereby current colonists will later seed sites further downstream. Conversely, establishment of *D. r. bugensis* in Uglich Reservoir and other upstream locations in the Volga cascade was possible only *via* human-mediated vectors (e.g., shipping, fishing, boating, and scientific expeditions; Orlova and Shcherbina 2002). These forms of assisted 'jump' dispersal result in establishment of non-contiguous populations in upstream destinations, and are less dependent on distance from colonization sources than are natural dispersal modes (MacIsaac et al. 2001).

Terminal populations can establish if furnished with allochthonous supplies of propagules. While not yet invaded, Ivankov Reservoir appears vulnerable to transfer of mussels established in adjacent reservoirs (Uglich, Rybinsk) (Figure 1).

The creation of the Volga River cascade changed the flow regime in the Lower Volga River to a more estuarine environment, resulting in a regime of unpredictable water-level fluctuations. All reservoirs support lacustrine stretches, especially the largest three (Volgograd, Kuybyshev and Rybinsk). Initial invasions of *D. r. bugensis* in the late 1980's correspond with development of seemingly favorable conditions along the entire Volga cascade. Thus, we suggest that invasion of the Volga system required a connection (via the Volga-Don canal) to allow for long-distance transfer of propagules, and alterations of hydraulic conditions. This hypothesis is supported by available evidence from the Black Sea. For example, *D. r. bugensis* began its range extension in the Dnieper River basin and adjacent water bodies following large-scale reconstruction of waterways and irrigation systems in southern Ukraine (Zhuravel 1967; Pligin 1979). By the late 1960's, the species was common in canals and reservoirs, often displacing *D. polymorpha* in swiftly flowing and deep-water habitats (Pligin 1979; Mills et al. 1996). *D. r. bugensis* failed until recently to disperse through corridors linking the Black and Baltic Seas (i.e., waterways from the Pripiat to Nemunas and Vistula Rivers). Its range expansion appears to have required both appropriate dispersal vectors and facilitation by other factors. These facilitating factors may include large-scale transformation of habitats along the invasion corridors in association with river impoundment, including reduced water velocity, increased total dissolved solid content, and stabilized oxygen concentration and temperature (Zhuravel 1951, 1967; Pligin 1979). These environmental changes resulted in conditions more typical of Black Sea estuaries. For example, restoration of conditions amenable to Black Sea estuarine opportunists in the Dnieper River cascade facilitated establishment of numerous species in this basin (Zhuravel 1951). These invasions were also facilitated by enhanced vector (i.e., shipping) activity that allowed upstream movement of propagules and subsequent dispersal west and east via canals from the Dnieper-Bug estuary and Ingulets River (e.g., Kharchenko 1995). It should be noted, however, that quagga mussel range expansion also has been much slower in North America than that of zebra mussels, even though the species seemingly share life histories, dispersal vectors etc. Consequently, much remains to be learned regarding the peculiarities of dispersal of these species.

Future spread and consequences

D. r. bugensis is a Ponto-Caspian endemic that is believed to pose an invasion risk to brackish and fresh waters of Northern Europe and the Baltic Sea region (Gollasch and Leppäkoski 1999; Orlova 2000). Five inland European invasion corridors may facilitate increased dispersal to these regions (MacIsaac et al. 2001). Of these, the deepwater, Volga-Baltic waterway is the most likely to allow future invasions by Ponto-Caspian species to the eastern Gulf of Finland.

Of the106 nonindigenous species that have invaded the Volga River cascade since the 1940's, a significant number (48%) are of Ponto-Caspian origin, particularly so for arrivals over the last three decades (Slyn'ko et al. 2002). Most invasive Ponto-Caspian species do not tolerate low pH or low calcium concentrations (Zhuravel 1951; Karataev et al. 1998), thus their establishment may be impaired in the upper reaches of the Volga-Baltic waterway where these conditions predominate (Alekin 1953; Bylinkina et al. 1982; Bylinkina 2001). However, a number of Ponto-Caspian species have 'skipped' entire sections of the Volga-Baltic waterway and have established farther upstream in the Neva Estuary (Slyn'ko et al. 2002). Successful establishment of *D. r. bugensis* in Rybinsk Reservoir will likely accelerate range expansion in the Upper Volga cascade and in the whole Volga River basin. This population also may serve as a source for expansion to the eastern Gulf of Finland with shipping along the Volga-Baltic waterway. We anticipate that *D. polymorpha* may be replaced by *D. r. bugensis* at sites along the Volga River, as the invasion of the latter species progresses northward. *Dreissena rostriformis bugensis* also is replacing *D. polymorpha* in shallow and deep habitats in Lakes Ontario and Erie in the Laurentian Great Lakes (Mills et al. 1996, 2003), apparently owing to its greater physiological efficiency (see Baldwin et al. 2002; Stoeckmann 2003). Given the history of ecological transformations associated with invasion by dreissenid mussels, establishment of *D. r. bugensis* at novel sites in the Volga-Baltic waterway could facilitate invasion by other Ponto-Caspian species, including the polychaete *Hypania invalida* (Grube 1860) and bivalve *Monodacna colorata* (Eichwald 1829) (Ricciardi 2001).

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