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# Limited occurrence of the profunda morph of the quagga mussels (*Dreissena rostriformis bugensis*) in the Volga River reservoirs of Russia and limited genetic differences between morphs in Russia and North America

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## ABSTRACT

The quagga mussel *Dreissena rostriformis bugensis* is a highly invasive species. It plays an important role in benthic communities, influencing their structure and functioning. Two morphs of this mussel have been described: a shallow-water (i.e. the typical) morph and a deep-water morph, profunda. Currently, profunda has been found in several water bodies only within the nonnative range of *D. r. bugensis*. In North America, the profunda morph is widespread and abundant in the Laurentian Great Lakes. In Europe, profunda was found for the first time in 2009 in the Cheboksary Reservoir, which is located on the central part of the Volga River. A 2016 search for profunda in the four deepest Volga reservoirs (Cheboksary, Kuybyshev, Saratov and Volgograd) failed to find this morph even at the site where it was found in 2009. Traditional and outline-based morphometric analyses showed that only the shallow-water morph individuals inhabited studied sites at depths of 25–33 m. The present study revealed that morphological differences between the typical and profunda morphs from both the European and North American ranges were accompanied by limited genetic differences. Microsatellite analysis showed only minor differences in allele frequencies between morphs sampled in 2019 from the Cheboksary Reservoir; these differences were not significant after correction for null alleles. High phenotypic and ecological plasticity of *D. r. bugensis* may facilitate its invasion success.

## INTRODUCTION

The quagga mussel *Dreissena rostriformis bugensis* (Andrusov, 1897) (Dreissenidae) is a widespread, highly invasive bivalve species that is native to the estuaries of the northern Black Sea, Ukraine, and has a pelagic veliger larval stage. Its current nonnative range in North America extends from the Great Lakes of Canada and USA to the El Carrizo Reservoir in Mexico (Wakida-Kusunoki, Wakida & Leon-Sandoval, 2015). In Europe, the current range of *D. r. bugensis* extends from Great Britain in the west (Aldridge, Ho & Froufe, 2014) to the Kama Reservoir of the Volga River Basin in Russia (Istomina, Pozdeev & Shcherbina, 2012) in the east, and from the Gulf of Finland (Orlova *et al.*, 2006) in the north to the Crimean Peninsula (Orlova, 2014) in the south. It is a highly morphologically variable species with wide ecological amplitude.

Two morphs have been described: the 'typical' shallow-water morph and a deep-water morph, profunda. The profunda morph is known only from water bodies in the nonnative part of its range. In the American part of the range, the profunda morph was found almost at the same time as the first records of *D. r. bugensis* in 1992 (May & Marsden, 1992; Dermott & Munawar, 1993). To date, the profunda morph has been recorded in four of the five North American Laurentian Great Lakes. It inhabits the deep eastern part of Lake Erie at depths of 13–60 m (Dermott & Munawar, 1993; Roe & Macisaac, 1997; Claxton *et al.*, 1998), Lake Ontario at depths up to 214 m (Mills *et al.*, 1996; Claxton *et al.*, 1998; Birkett, Lozano & Rudstam, 2015), Lake Michigan at depths of 16–196 m (Nalepa, Fanslow & Lang, 2009; Nalepa *et al.*, 2014a, 2020) and Lake Huron (Nalepa *et al.*, 2018). In the European part of its range, this morph was first found in 2009 in the Cheboksary Reservoir, in the middle reaches of the Volga River (Pavlova, 2012; Pavlova & Pryanichnikova, 2016). The Volga Basin is the largest river system in Europe. The construction of reservoirs and ecosystem change has resulted in multiple invasions of nonindigenous species in the second half of the 20th century (Slynko *et al.*, 2011). The first record of *D. r. bugensis* in the Volga was in the middle reaches of the river in 1992 (Antonov, 1993), from where it subsequently spread both upstream and downstream. The discovery of the profunda morph in the deepest part of the Cheboksary Reservoir suggests that it may also inhabit other reservoirs in the Volga River Basin. Our previous research revealed its absence from the reservoirs (Ivan'kovo,

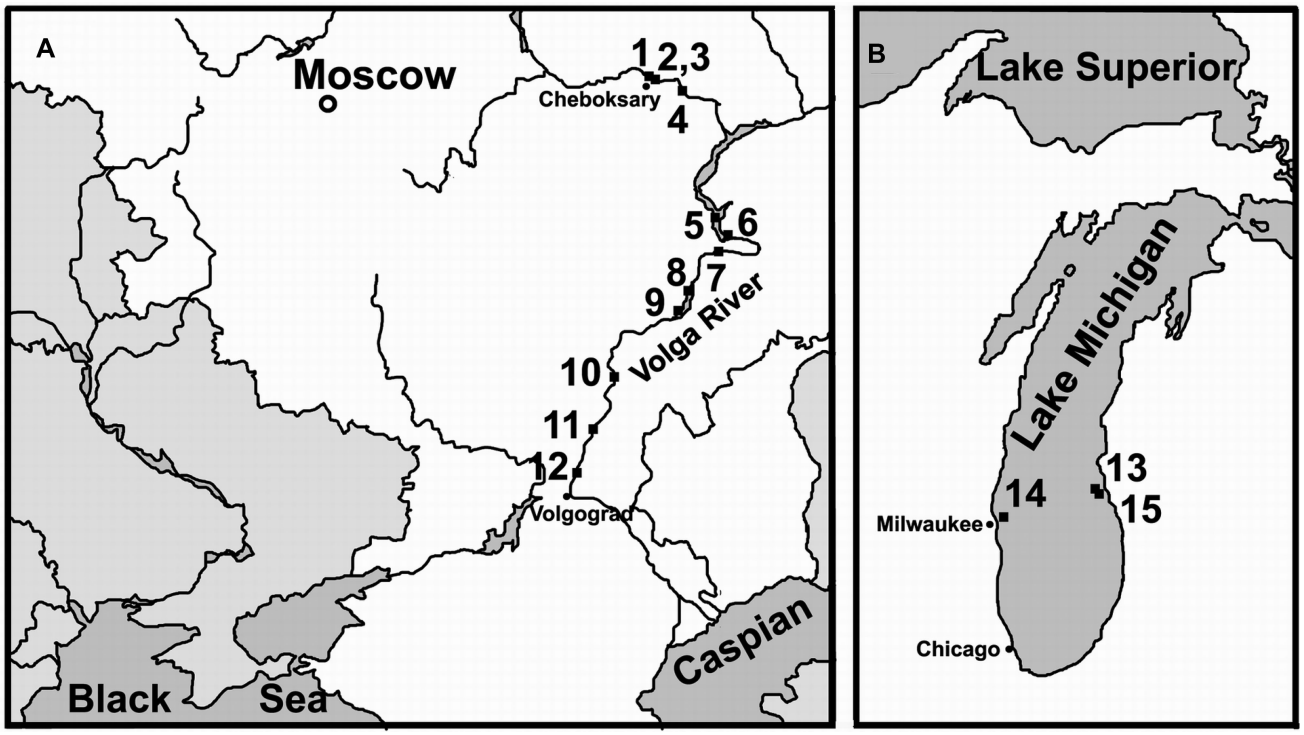


**Figure 1.** Location of the sampling sites in the Volga River, Russia (**A**) and in Lake Michigan, USA (**B**). See Table 1 for geocoordinates, site depths and collection years.

Uglich, Rybinsk and Gorkiy) in the upper reaches of the Volga, where maximal depths do not exceed 21 m (V.V. Pavlova, unpubl.). In 2016, we tried to find profunda morph in the deepest parts of the Cheboksary, Kuybyshev, Saratov and Volgograd reservoirs (maximum depths of 25–33 m).

Compared to the shallow-water morph of *D. r. bugensis*, the profunda morph has a more elongated, lower and less convex shell with rounded ventral edges, weak pigmentation on the outer surface and elongated siphons (Dermott & Munawar, 1993; Nalepa *et al.*, 2014b). The differences between the two morphs are prominent not only at the morphological level but at the physiological level as well. For instance, the profunda morph can commence spawning at lower water temperature (Claxton & Mackie, 1998) than the shallow-water morph, and it has lower levels of oxygen consumption (Tyner, Bootsma & Lafrancois, 2015). However, despite studies based on cytochrome *c* oxidase subunit I (COI; Claxton *et al.*, 1998), 16S rDNA (Stepien, Hubers & Skidmore, 1999), cytochrome *b* (CytB; Stepien *et al.*, 2003), allozymes (Spidle, Marsden & May, 1994) and random amplified polymorphic DNA (RAPD) loci (Stepien, Taylor & Dabrowska, 2002), no genetic differences between the two morphs have yet been detected. In the study presented here, we use more variable microsatellite markers appropriate for revealing the population structure and focus on the profunda morph in Europe (work to date has investigated this morph only from American part of the range of *D. r. bugensis*). The goal of the present paper is to document the distribution of the profunda morph in the reservoirs of the middle and lower reaches of the Volga River and to compare the variability in microsatellite loci of profunda and shallow-water morphs from the American and European parts of the range of *D. r. bugensis*.

## MATERIAL AND METHODS

### *Morphometric analysis*

*Dreissena rostriformis bugensis* was sampled from the Volga River in 2016, with mussels being collected from 12 sites in four waterbodies, the Cheboksary, Kuybyshev, Saratov and Volgograd reservoirs (Fig. 1; Table 1). The deepest sites (25–33 m depth) in these reservoirs were examined. Mussels from shallower sites (5–19 m depth) were collected for comparison. Mussels at each of the sites were collected with a dredge or as a bycatch from fishing bottom trawls. Site 3 (see Fig. 1) is the place where profunda morph was found for the first time in the Volga River Basin in 2009 (Pavlova, 2012); for this site, the data for 2009, 2015 and 2016 are available.

Shallow-water and profunda morph mussels from the American range were also studied (Fig. 1; Table 1). The profunda morph collected in 2004 from a 25-m-deep site in Lake Michigan was considered to be representative of the morph and was used as the reference when describing the profunda morph from the Cheboksary reservoir (Pavlova, 2012).

Morphs were identified using the set of traditional and outline-based morphometric approaches in previous studies (Dermott & Munawar, 1993; Pavlova, 2012; Pavlova & Pryanichnikova, 2016). We used both approaches for a thorough description of morphology. Shell length (*L*) (maximum anteroposterior dimension), shell height (*H*) (maximum dorsoventral dimension) and shell width (*W*) (convexity of both valves closed) were measured with a vernier calliper (Shkorbatov & Starobogatov, 1990). Mussels 11–28 mm in length were measured. Values of *H*/*L* and *W*/*L* were calculated and, for key samples, these values were analysed using the Student's *t*-test.

For the outline-based morphometric analyses of shell shape (Bookstein, 1991), we selected 12–30 specimens measuring 17–24 mm in length (mussels of such size are morphologically mature and were numerous in our samples) from each of the sites we sampled, apart from site 4. This site was not included in our analyses because it yielded too few mussels in the target size range. Scanned images of the left mussel valves were processed using the software SHAPE v. 1.3 (Iwata & Ukai, 2002); this involved an elliptic Fourier analysis of shell shapes and a principal component analysis (PCA) of the Fourier descriptors. All statistical operations were performed in Statistica v. 8.0 (StatSoft Inc.) (Weiss, 2007).

**Table 1.** Sampling sites and morphometrics (mean ± SE) of *Dreissena rostriformis bugensis*.

| Waterbody | Site | Geocoordinates | Depth (m) | Year | *n* | *L* (mm) | *H*/*L* | *W*/*L* | Morph |
|---|---|---|---|---|---|---|---|---|---|
| Cheboksary Reservoir | 1 | 56°09′36″N, 47°09′46″E | 15 | 2016 | 56 | 22.1 ± 0.59 | 0.555 ± 0.004 | 0.424 ± 0.005 | S |
| | 2 | 56°08′53″N, 47°26′40″E | 5–13 | 2016 | 61 | 21.0 ± 0.70 | 0.588 ± 0.005 | 0.456 ± 0.006 | S |
| | 3 | 56°08′24″N, 47°27′01″E | 26 | 2016 | 61 | 20.3 ± 0.74 | 0.573 ± 0.004 | 0.421 ± 0.006 | S |
| | | 56°08′50″N, 47°27′02″E | | 2015 | 89 | 18.6 ± 0.51 | 0.579 ± 0.004 | 0.395 ± 0.005 | S/P (?) |
| | | 56°08′50″N, 47°27′02″E | | 2009 | 115 | 18.7 ± 0.42 | 0.553 ± 0.003 | 0.380 ± 0.003 | P |
| Kuybyshev Reservoir | 4 | 55°57′43″N, 47°58′46″E | 10–14 | 2016 | 23 | 15.7 ± 0.45 | 0.606 ± 0.006 | 0.437 ± 0.008 | S |
| | 5 | 53°49′12″N, 48°57′04″E | 28–32 | 2016 | 77 | 19.0 ± 0.48 | 0.590 ± 0.004 | 0.415 ± 0.005 | S |
| | 6 | 53°25′48″N, 49°25′12″E | 31–33 | 2016 | 29 | 19.8 ± 0.76 | 0.593 ± 0.007 | 0.438 ± 0.007 | S |
| Saratov Reservoir | 7 | 53°14′24″N, 49°04′12″E | 12–16 | 2016 | 56 | 19.6 ± 0.53 | 0.605 ± 0.004 | 0.462 ± 0.006 | S |
| | 8 | 52°30′02″N, 48°07′12″E | 19 | 2016 | 61 | 16.5 ± 0.43 | 0.575 ± 0.003 | 0.457 ± 0.007 | S |
| | 9 | 52°10′12″N, 47°55′48″E | 25–28 | 2016 | 62 | 16.6 ± 0.39 | 0.577 ± 0.004 | 0.454 ± 0.006 | S |
| Volgograd Reservoir | 10 | 50°58′48″N, 45°58′12″E | 13–14 | 2016 | 58 | 17.6 ± 0.46 | 0.582 ± 0.004 | 0.452 ± 0.006 | S |
| | 11 | 49°50′24″N, 45°20′24″E | 27–32 | 2016 | 59 | 17.3 ± 0.40 | 0.567 ± 0.003 | 0.434 ± 0.008 | S |
| | 12 | 49°07′48″N, 44°53′60″E | 25–28 | 2016 | 74 | 17.2 ± 0.46 | 0.573 ± 0.003 | 0.448 ± 0.006 | S |
| Lake Michigan | 13 | 43°12′00″N, 86°22′40″W | 25 | 2004 | 98 | 17.7 ± 0.39 | 0.533 ± 0.003 | 0.335 ± 0.003 | P |
| | 14 | 43°03′43″N, 87°51′50″W | 8 | 2017 | 98 | 20.3 ± 0.45 | 0.574 ± 0.009 | 0.462 ± 0.007 | S |
| | 15 | 43°11′35″N, 86°26′06″W | 45 | 2017 | 116 | 18.2 ± 0.39 | 0.508 ± 0.003 | 0.314 ± 0.003 | P |

Site numbers are those used in Figure 1. Abbreviations: *n*, number of mussels studied; *H*, shell height; *L*, shell length; *W*, shell width; S, shallow-water morph; P, profunda morph.

**Table 2.** Description of the samples for microsatellite analysis.

| Waterbody and year | Morph | Geocoordinates | Depth (m) | Morphometric data |
|---|---|---|---|---|
| Cheboksary Reservoir (2009) | S | 56°09′23″N, 47°26′50″E | 5 | |
| | P | 56°08′50″N, 47°27′02″E | 26 | Site 3 (2009) |
| Cheboksary Reservoir (2015) | S | 56°06′47″N, 45°29′01″E | 12 | |
| | S/P (?) | 56°08′50″N, 47°27′02″E | 26 | Site 3 (2015) |
| Lake Michigan (2017) | S | 43°03′43″N, 87°51′50″W | 8 | Site 14 |
| | P | 43°11′35″N, 86°26′06″W | 45 | Site 15 |

Abbreviations: S, shallow-water morph; P, profunda morph.

### *Microsatellite analysis*

For microsatellite analyses, we used samples collected from the Cheboksary Reservoir in 2009 and 2015, and from Lake Michigan in 2017 (Table 2). The distance between sampling sites at which shallow-water and profunda morphs were found was 1 km in 2009, 150 km in 2015 and 117 km in 2017.

For a preliminary study of genetic variation, we used three microsatellite loci: the tetranucleotide loci Dbu75 and Dbu93, and the dinucleotide locus Dbu110 (Feldheim *et al.*, 2011). Thirty individuals per sample were genotyped. When we subsequently tried to expand the set of loci, we were not able to successfully amplify DNA from the 2009 samples (i.e. due to likely degradation of the DNA; Zimmermann *et al.*, 2008). In order to ensure that sample size would be statistically significant (see number of mussels genotyped in Table 3), we increased the number of genotyped specimens from 30 to 50 for the material collected in 2017 from Lake Michigan. Diatom™ DNA Prep 100 kit (Isogen, Moscow) was used to extract genomic DNA from the gills of the mussels. PCR amplification was carried out using a reaction volume of 25 $\mu$l; this contained 50–100 ng of DNA template, 1.75 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 mM of each primer (forward primer end-labelled with ROX dye) and 0.5 U Taq polymerase. PCR was performed using a T-Personal (Biometra) thermocycler as follows: 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 1 min (annealing) at 56 °C and 30 s at 72 °C; and finally, a 5 min extension at 72 °C (apart from slight changes to the annealing temperature, we followed Feldheim *et al.*, 2011). Amplified products were detected on 7% polyacrylamide gels and stained with ethidium bromide. Alleles were sized using Gel Doc XR+ System (Bio-Rad). For control of allele sizes, some PCR products were subjected to fragment analysis carried out by Syntol Company (Moscow), with subsequent analysis of the results using GeneMarker v. 2.7.0 (SoftGenetics) (Liu *et al.*, 2011).

Expected ($H_E$) and observed ($H_O$) heterozygosity estimates were obtained using GenAlEx v. 6.502 (Peakall & Smouse, 2006, 2012). The inbreeding coefficient ($F_{IS}$), a measure of deviation from the Hardy–Weinberg equilibrium, was assessed with the exact test of Weir & Cockerham (1984); this was implemented in Genepop v. 4.7 (Raymond & Rousset, 1995; Rousset, 2008) and the Markov chain parameters used were 5,000 dememorization steps, followed by 1,000 batches of 5,000 iterations per batch. Null allele frequency was estimated with Microchecker v. 2.2.3 (Van Oosterhout *et al.*, 2004), using Brookfield's (1996) null allele estimator 2. Differentiation among samples ($F_{ST}$) was estimated in GenAlex v. 6.502 (Peakall & Smouse, 2006, 2012). Heterogeneity in allele and genotype distributions between shallow-water and profunda morphs was tested using the exact *G* test as implemented in Genepop v. 4.7 (Raymond & Rousset, 1995; Rousset, 2008) (the Markov chain parameters used were 5,000 dememorization steps, followed by 1,000 batches of 5,000 iterations per batch). This procedure was also applied for null-allele-corrected genotypes obtained from Microchecker. Levels of significance for all multiple comparison tests were adjusted using the Benjamini–Hochberg correction method for false discovery rate (FDR) (Benjamini & Hochberg, 1995).

**Table 3.** Values for number of alleles ($N_A$), expected ($H_E$) and observed ($H_O$) heterozygosity, inbreeding coefficient ($F_{IS}$), null allele frequency (NA) and private alleles (PA).

| Waterbody and year | Morph | *n* | | Locus | | | | Pairwise $F_{ST}$ (= G'st (Nei)) | Genic differentiation (exact *G* test) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Dbu75 | Dbu93 | Dbu110 | All loci | | Prior to null allele correction | After null allele correction |
| Cheboksary Reservoir (2009) | S | 30 | $N_A$ | 11 | 10 | 9 | 10.0 | 0.0136 ($P = 0.091$) | All loci: $P = 0.022^{\dagger}$; | All loci: $P = 0.073$; |
| | | | $H_E$ | 0.770 | 0.775 | 0.764 | 0.770 | | Dbu75: $P = 0.191$; | Dbu75: $P = 0.191$; |
| | | | $H_O$ | 0.667 | 0.267 | 0.633 | 0.522 | | Dbu93: $P = 0.004^{\dagger}$; | Dbu93: $P = 0.018$; |
| | | | $F_{IS}$ | 0.151 | 0.666* | 0.188 | 0.335 | | Dbu110: $P = 0.896$ | Dbu110: $P = 0.919$ |
| | | | NA | 0.06 | 0.29 | 0.07 | 0.14 | | | |
| | | | PA | 175 | 157, 185 | – | | | | |
| | P | 30 | $N_A$ | 8 | 9 | 9 | 8.7 | | | |
| | | | $H_E$ | 0.591 | 0.688 | 0.761 | 0.680 | | | |
| | | | $H_O$ | 0.600 | 0.333 | 0.433 | 0.455 | | | |
| | | | $F_{IS}$ | 0.002 | 0.528* | 0.444* | 0.325 | | | |
| | | | NA | 0.00 | 0.21 | 0.19 | 0.13 | | | |
| | | | PA | – | – | – | | | | |
| Cheboksary Reservoir (2015) | S | 30 | $N_A$ | 8 | 11 | 9 | 9.3 | −0.0049 ($P = 0.674$) | All loci: $P = 0.080$; | All loci: $P = 0.103$; |
| | | | $H_E$ | 0.727 | 0.858 | 0.810 | 0.798 | | Dbu75: $P = 0.038$; | Dbu75: $P = 0.030$; |
| | | | $H_O$ | 0.633 | 0.367 | 0.733 | 0.578 | | Dbu93: $P = 0.228$; | Dbu93: $P = 0.447$; |
| | | | $F_{IS}$ | 0.146* | 0.584* | 0.111 | 0.280 | | Dbu110: $P = 0.409$ | Dbu110: $P = 0.382$ |
| | | | NA | 0.05 | 0.26 | 0.04 | 0.12 | | | |
| | | | PA | – | – | – | | | | |
| | S/P (?) | 30 | $N_A$ | 8 | 11 | 10 | 9.7 | | | |
| | | | $H_E$ | 0.749 | 0.843 | 0.818 | 0.803 | | | |
| | | | $H_O$ | 0.567 | 0.267 | 0.600 | 0.478 | | | |
| | | | $F_{IS}$ | 0.259* | 0.693* | 0.283* | 0.412 | | | |
| | | | NA | 0.10 | 0.31 | 0.12 | 0.18 | | | |
| | | | PA | 207 | – | 192 | | | | |
| Lake Michigan (2017) | S | 50 | $N_A$ | 9 | 11 | 11 | 10.3 | −0.0045 ($P = 0.787$) | All loci: $P = 0.506$; | All loci: $P = 0.658$; |
| | | | $H_E$ | 0.717 | 0.823 | 0.826 | 0.789 | | Dbu75: $P = 0.650$; | Dbu75: $P = 0.656$; |
| | | | $H_O$ | 0.600 | 0.300 | 0.620 | 0.507 | | Dbu93: $P = 0.127$; | Dbu93: $P = 0.218$; |
| | | | $F_{IS}$ | 0.173* | 0.641* | 0.259* | 0.358 | | Dbu110: $P = 0.858$ | Dbu110: $P = 0.883$ |
| | | | NA | 0.07 | 0.29 | 0.11 | 0.16 | | | |
| | | | PA | 215 | 169 | – | | | | |
| | P | 50 | $N_A$ | 8 | 14 | 9 | 10.3 | | | |
| | | | $H_E$ | 0.700 | 0.830 | 0.808 | 0.779 | | | |
| | | | $H_O$ | 0.700 | 0.280 | 0.540 | 0.507 | | | |
| | | | $F_{IS}$ | 0.010 | 0.668* | 0.341* | 0.340 | | | |
| | | | NA | 0.00 | 0.30 | 0.15 | 0.15 | | | |
| | | | PA | – | – | – | | | | |
| Mean/locus | | | $N_A$ | 8.7 | 11.0 | 9.5 | 9.7 | | | |
| | | | $H_E$ | 0.709 | 0.803 | 0.798 | 0.770 | | | |
| | | | $H_O$ | 0.628 | 0.302 | 0.593 | 0.508 | | | |
| | | | $F_{IS}$ | 0.124 | 0.630 | 0.271 | 0.342 | | | |
| | | | NA | 0.05 | 0.28 | 0.11 | 0.15 | | | |

Pairwise $F_{ST}$ and genic differentiation (before and after null allele correction) are given for paired shallow-water (S) and profunda (P) morphs. The number of mussels genotyped is indicated by *n*.

*Samples deviating significantly from the Hardy–Weinberg equilibrium at $P < 0.05$ after FDR procedure.

†*P*-values that were significant in the exact *G* test after the FDR procedure.

## RESULTS

### *Morphometric analyses*

All specimens of *Dreissena rostriformis bugensis* collected from the Volga River in 2016 corresponded with the shallow-water morph. Mean *H/L* and *W/L* values for these mussel samples ranged from 0.555 to 0.606 and from 0.415 to 0.462, respectively (Table 1; Fig. 2). Shallow-water morph mussels from site 14 of Lake Michigan were morphologically similar to those from the Volga River. The lowest values of *H/L* and *W/L* were found in profunda morph mussels from Lake Michigan, with the 2017 mussels having significantly lower *H/L* and *W/L* values (Student's *t*-test: $P = 0.0000001$ and

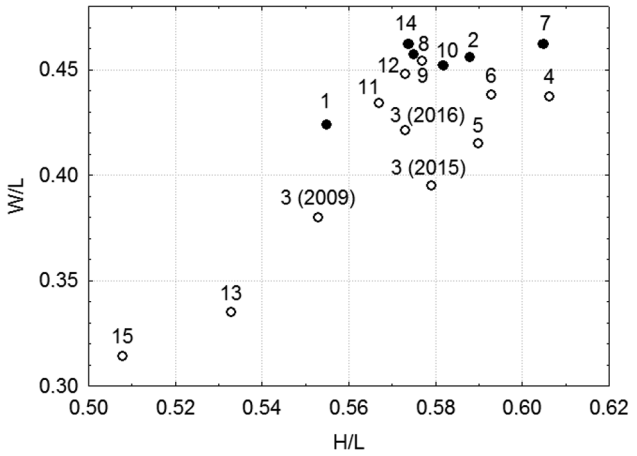


**Figure 2.** Scatterplot of mean *H/L* and *W/L* ratios. Symbols: unfilled circles, deep-water sites (depths of 25–45 m); filled circles, shallow-water sites (depths of 5–19 m).

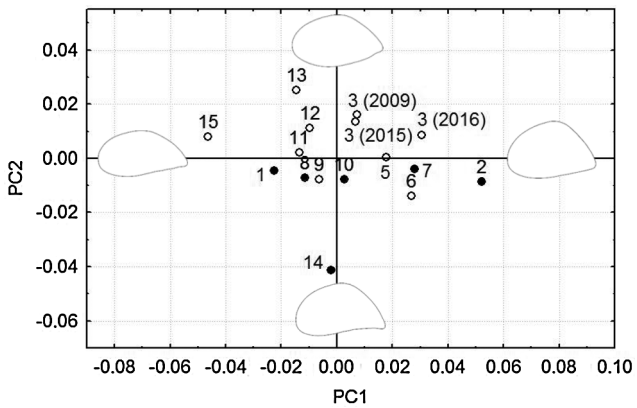


**Figure 3.** Scatterplot of score means of the first two PC axes (based on PCA of Fourier descriptors). Symbols: unfilled circles, deep-water sites (depths of 25–45 m); filled circles, shallow-water sites (depths of 5–19 m). Site 4 was excluded because there were insufficient mussels in the target size range.

0.0000003, respectively) than the 2004 mussels. At the deepest site in the Cheboksary Reservoir (site 3), where profunda was found in 2009, only shallow-water morphs were found in 2016. However, *W/L* values for the mussels collected in 2015 from this site in the Cheboksary Reservoir (0.395) were intermediate to the *W/L* values of the two morphs. This suggests a gradual change in morphology at site 3, from the profunda to the shallow-water morph for the period 2009–2015 (Fig. 2). Differences in mean *W/L* values among the three collection years were statistically significant (Student's *t*-test: $P < 0.05$). For *H/L*, the 2009 values differed from both 2015 and 2016 (Student's *t*-test: $P < 0.05$), but the difference between 2015 and 2016 was not significant (Student's *t*-test: $P = 0.36$).

Correlations between depth and *H/L* and *W/L* ratios for all mussels were strong (Pearson's *r*: −0.36 for *H/L* and −0.52 for *W/L*; $P < 0.05$ for both). Correlation for 11 sites from the Volga River (i.e. except those from the Cheboksary Reservoir) was significant for *W/L* (Pearson's *r*: −0.17; $P < 0.05$) but not for *H/L* (Pearson's *r*: −0.02; $P > 0.05$).

Shell shape variability, as estimated by outline-based morphometrics, is shown in Figure 3. The value of PC1 reflects overall shell shape and elongation, with low values corresponding to lower, elongated shells and high values to higher shells. PC2 reflects ventral edge shape, from concave (low values) to convex (high values).

Both deep- and shallow-water sites are evenly distributed along the PC1 axis. Site 2 exhibits the highest value for PC1 and site 15 the lowest value and this corresponds with the highest and most elongate shells, respectively. All shallow-water sites had negative values for PC2, indicating that the mussels had mainly straight or concave ventral edges to the shells. The concavity of the ventral edge of the shell was most prominent in the shallow-water mussels from site 14 in Lake Michigan. Deep-water sites are distributed along the PC2 axis and are associated with a wide variety of ventral edge shapes. A positive correlation was found between individual values of PC2 and depth (Spearman's *r*: 0.28; $P < 0.05$).

Profunda morph mussels from Lake Michigan are characterized by low values of PC1 and high values of PC2, that is by elongated narrow shells with a convex ventral edge. The PCA suggests a morphological shift away from the profunda morph in mussels collected from the deepest part of the Cheboksary Reservoir for the period 2009–2016. Mussels from other deep-water sites in the Volga River, as sampled in 2016, appeared to either be morphologically identical to the shallow-water morph (e.g. mussels from sites 5, 6 and 9) or show some morphological similarities to the shallow-water morph. In the latter case, for example mussels from sites 11 and 12 exhibit *H/L* and *W/L* ratios that agree with the shallow-water morph (Table 1; Fig. 2) while being close to profunda in shell shape (i.e. shell is more elongate with more convex ventral edges than other mussels).

Both traditional and outline-based morphometrics show that from 2009 to 2016 there has been morphological change in the mussels from the deep region of the Cheboksary Reservoir (site 3) and that this has involved a shift from the profunda morph of Lake Michigan towards the shallow-water morph of the Volga River (Figs 2 and 3). On the basis of *H/L* and *W/L* ratios and shell shape, none of the mussels found in the Volga River in 2016 correspond with the profunda morph. Instead, these mussels correspond with the shallow-water morph, indicating that the profunda morph either is absent in the deepest Volga River reservoirs or persists at densities lower than those that can be detected by the sampling level used in our study.

### *Microsatellite analysis*

All three microsatellite loci were polymorphic for all samples. The number of alleles and values for $H_E$, $H_O$ and $F_{IS}$ for each population are given in Table 3. A total of 42 alleles were scored: 13 for Dbu75, 17 for Dbu93 and 12 for Dbu110. The mean number of alleles per locus varied from 8.7 to 10.3. For all loci among the different sites, $H_E$ ranged from 0.680 to 0.803 and $H_O$ ranged from 0.455 to 0.578. Heterozygote deficiency, as indicated by a positive $F_{IS}$ value, was revealed in all samples. When all loci were taken together, $F_{IS}$ ranged from 0.280 to 0.412. The mean frequency of null alleles was 0.15 (range: 0–0.31). The locus Dbu75 showed the smallest heterozygote deficiency and lowest null allele frequency, while the values of both parameters for Dbu93 were the largest and highest, respectively. The greatest number of private alleles (3) was found in shallow-water mussels from the Cheboksary Reservoir in 2009 (Table 3). Differentiation between shallow-water and profunda morphs collected from the same waterbody in the same year and, as measured by $F_{ST}$, ranged from −0.0049 (mussels collected in 2015 from the Cheboksary Reservoir) to 0.0136 (the 2009 material from the Cheboksary Reservoir); none of these values were significantly different from zero.

Heterogeneity in allele distributions between shallow-water and profunda morphs, as estimated by the genic differentiation tests, showed significant differences between the two morphs only for the Cheboksary Reservoir in 2009. This was observed both for Dbu93 alone and for all three loci combined (Table 3). However, after null allele correction, these differences between the two morphs were no longer significant. Heterogeneity between the two morphs using genotype distribution tests was not significant for any population pair ($P = 0.11$–$0.93$).

## DISCUSSION

The range of *Dreissena rostriformis bugensis* has increased significantly over the last 30 years (Matthews *et al.*, 2014; Lindsay *et al.*, 2018). In the process of range expansion, an invasive species faces new environmental conditions. The consequences of dreissenid invasion for aquatic ecosystems are well studied (e.g. see Nalepa & Schloesser, 2014). Adaptation of nonindigenous species to their new environment is also a problem worthy of attention. In the case of *D. r. bugensis*, intraspecific differentiation arose during the range expansion. *Dreissena rostriformis bugensis* is an estuarine species and its native range consists of the lower reaches of the Ingulets and Yuzhnyi (Southern) Bug rivers and the Dnieper–Bug estuary on the northern coast of the Black Sea, Ukraine. Faced with deep-water conditions (e.g. in the Great Lakes of North America and the Cheboksary Reservoir), the species has produced the profunda morph, which does not occur in the native range.

The profunda morph of *D. r. bugensis* has been found in the North American and European regions of the global range of this species. For North American deep lakes, the impacts of *D. r. bugensis* have been well documented; these impacts include the reduction of spring phytoplankton blooms and the alteration resource pathways for fish (Higgins, 2014). The profunda morph is well adapted to the conditions of the profundal zone and therefore can colonize a large portion of the lake bed, as is the case in Lake Michigan, where the species reaches high densities (Nalepa *et al.*, 2014a, 2020) and has the potential for high levels of collective filtering (Vanderploeg *et al.*, 2010). Indeed, the profunda shell form is well suited for colonizing soft sediments (Claxton *et al.*, 1998). Experimental and modelling data have shown that deep-water dreissenids can alter nutrient cycling and energy flow not only in the bottom layer but also throughout the whole water column. These bivalves can change the ratio of dissolved and particulate nutrients, decrease residence time of nutrients in the water column and accelerate the delivery of nutrients to the benthic zone (Mosley & Bootsma, 2015; Rowe *et al.*, 2017; Shen *et al.*, 2018).

The profunda morph was recorded for the first time from Europe in 2009, from the Cheboksary Reservoir (Pavlova, 2012). This finding suggests that this morph may also inhabit other deep-water areas in the Volga River Basin. In 2016, we tried unsuccessfully to find the profunda morph in the four deepest reservoirs in the Middle and the Lower Volga (i.e. in the Cheboksary, Kuybyshev, Saratov and Volgograd reservoirs). The traditional and outline-based morphometrics used in the present study show that none of the sampled mussels correspond closely with the profunda morph. Even at the site in the Cheboksary Reservoir, where the profunda morph was sampled in 2009, only mussels corresponding to the shallow-water morph were found in 2016.

The reason for the change in morphology of the profunda morph in the deepest region in the Cheboksary Reservoir remains unclear. Most likely, this was related to changes in some ecological conditions. Peyer, Hermanson & Lee (2010) found that temperature plays a significant role in the morphogenesis of *D. r. bugensis*. The rearing of mussels at low temperature (6–8 °C) yielded a morph approaching that of the profunda morph. In contrast, mussels reared at a higher temperature (18–20 °C) exhibited the shallow-water morphology (Peyer *et al.*, 2010). The summer of 2010 was very warm in the western part of Russia. Elevated water temperatures seemed to have a strong impact on deep-water mussels. For instance, the number of adult mussels and veligers in the Rybinsk Reservoir decreased several times, likely due to abnormally high water temperatures (Pryanichnikova, 2013; Sokolova, 2013). Average July air temperature in the Cheboksary region ranged from 16.9 to 22.4 °C in 2006–2016 but was 25.5 °C in the abnormally warm year of 2010 (Raspisanie pogody, 2019). In the sampled portion of the Cheboksary Reservoir, water temperatures at the surface and near bottom differ only slightly due to water mixing driven by the activity of the nearby hydroelectric power station (Okhapkin, 1994). Therefore, deep-water mussels were subjected to unusually high temperatures. One of the effects might be an adaptive adjustment of morphogenesis that resulted in the morphological change. Morphogenesis in bivalves is determined primarily by mantle cells during the process of shell formation (Mann, 2001). Recent studies have shown that expression of biomineralization-related genes is influenced by temperature and other environmental factors (Liu *et al.*, 2012; Moullac *et al.*, 2014; Li *et al.*, 2016). Obviously, the impact of increased temperature, as described above, could affect mussels not just in the Cheboksary Reservoir but also in the whole Volga River. Considering the current increase in average annual temperatures, we hypothesize that the conditions necessary for the appearance and normal functioning of the profunda morph will be unlikely to occur in the Volga River Basin in the near future.

Obvious morphological differences between the two morphs suggest that they are determined by some genetic differences. Multiple researchers have tried to find a genetic marker that separates the two morphs of *D. r. bugensis*. Studies have been carried out using various markers: COI (Claxton *et al.*, 1998), 16S rDNA (Stepien *et al.*, 1999), CytB (Stepien *et al.*, 2003), allozymes (Spidle *et al.*, 1994) and RAPD loci (Stepien *et al.*, 2002). However, all of these have failed to reveal any genetic dissimilarity between the two morphs. In one study (Baldwin *et al.*, 1996), a 4-bp difference in COI sequences was found, but further investigations by Claxton *et al.* (1998) in mussels collected from the same site at the same time did not reveal the specific profundal haplotype discovered by Baldwin *et al.* Microsatellites used in research on population structure could offer a way forward.

Our findings on the variability in microsatellite loci between the two morphs of *D. r. bugensis* from Lake Michigan and the Cheboksary Reservoir are consistent with the results of other studies. Levels of genetic variability ($H_O$) for all loci in the studied samples ranged from 0.455 (profunda morph sampled from Cheboksary in 2009) to 0.578 (2015 shallow-water morph from Cheboksary) and were similar to those published for other populations of *D. r. bugensis* from the European and American parts of the range (Therriault *et al.*, 2005; Imo, Seitz & Johannesen, 2010; Marescaux *et al.*, 2016). The values of $H_O$ for mussels from the Cheboksary Reservoir were similar to those published previously for the samples from the Volga (Therriault *et al.*, 2005: 0.542; Brown & Stepien, 2010: 0.51). Values of the inbreeding coefficient $F_{IS}$ were rather high (0.280–0.412) but similar to published values (Imo *et al.*, 2010: 0.186–0.483; Marescaux *et al.*, 2016: 0.137–0.362). Low observed heterozygosity and high inbreeding coefficients were due to the high frequency of null alleles, which reached 0.31 for one locus. Mean null allele frequency across all loci ranged from 0.12 to 0.18. Possible reasons for the appearance of null alleles are nonamplification (due to failed primer annealing to the template because of variation in the nucleotide sequences of the flanking regions of microsatellites; Callen *et al.*, 1993) and size homoplasy (i.e. when the apparent homozygote is in fact a heterozygote with two alleles of identical size but of different nucleotide sequence; Viard *et al.*, 1998). Despite the generally similar pattern of dispersion of null alleles at loci between all samples, the changes in the specific nucleotide sequences causing them may differ between the European and North American parts of the range of *D. r. bugensis*. The Wahlund effect, where subpopulation structure causes the reduction of heterozygosity, may be another reason for heterozygote deficiency. In dreissenids, individuals originating from different donor populations occur in the same population (Marsden, Spidle & May, 1996; Lewis, Feder & Lamberti, 2000).

Following null allele and multiple testing corrections, no genetic differences were found between the shallow-water and profunda morphs of *D. r. bugensis* in any water body. Studies published in the past also failed to find differences in microsatellite markers between the shallow-water and profunda morphs (C.E. Lee & G.W. Gelembiuk, unpubl.; see Peyer *et al.*, 2010). In our study, no genetic differences were observed between North American representatives

of the two morphs, despite the prominent morphological differences and the two populations being separated by a distance of 117 km, on opposite shores of Lake Michigan (Table 3). This finding is consistent with published studies on dreissenids; these studies have found no correlation between genetic differentiation among populations ($F_{ST}$) and geographical distance (Wilson, Naish & Boulding, 1999; Therriault *et al.*, 2005; Marescaux *et al.*, 2016). Generally, due to high propagule pressures during invasion and multiple introductions, low genetic differentiation is characteristic for populations of *D. r. bugensis* (Marescaux *et al.*, 2016). Moreover, extensive vessel traffic and large-scale water currents and circulation patterns maintain gene flow even between distant populations and, particularly, between settlements of different morphs. We suggest that multiple introductions combined with ongoing high gene flow during the pelagic larval stage may be preventing genetic isolation between the two morphs, despite their ecological and physiological differences.

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