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Comparative shell morphology of the zebra mussel, *Dreissena polymorpha* in the Drava river (Croatia)

Jasna Lajtner[1], Zrinka Marušić[2], Göran I. V. Klobučar[1], Ivana Maguire[1] & Radovan Erben[1]

[1]*Department of Zoology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, P. O. Box 933, HR–10000 Zagreb, Croatia; tel: +385 1 4877750, fax: +385 1 4826260, e-mail: jlajtn@zg.biol.pmf.hr*
[2]*Institute for Tourism, Vrhovec 5, HR–10000 Zagreb, Croatia*

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We examined the shell morphometrics of the zebra mussel (*Dreissena polymorpha*) collected from the system of the Dubrava hydro-electric power plant on the Drava river (Croatia). Study sites had different sediment types, depth, and physical and chemical conditions. Site 1 was the shallow of the Drava river, while sites 2 and 3 were located in the artificial Dubrava lake at depths of 3 and 8 m, respectively. A total of 1,200 zebra mussels were collected. The following morphological variables were examined: shell length (SL), shell width (SW), shell height (SH) and shell mass (SM). In addition three different ratios were defined: SW/SL, SH/SL and SW/SH. Analysis of variance (ANOVA) and Duncan multiple comparison test were applied to test the differences of the ratios among the three sites and to determine which of them was significantly different from the others. The analysis showed that the ratios SW/SL and SW/SH differ significantly between all three sites ($P < 0.0001$), while the ratio SH/SL did not differ between sites. The log-transformed variables were further analysed using principal component analysis. ANOVA and Duncan test were applied to the resulting principal components to test for differences in component scores among the three sites. The analysis separated the riverine and the lake populations of mussels into two morphological groupings, indicating that considerable phenotypic plasticity exists among the populations of the zebra mussel.

Key words: *Dreissena polymorpha*, shell morphometrics, phenotypic plasticity, river Drava, artificial Dubrava lake, Croatia.

Introduction

The freshwater mussel *Dreissena polymorpha* Pallas, 1771 has become one of the most dominant species in many lakes and rivers of Europe, since it started spreading from the Caspian area at the beginning of the 19th century (Stanczykowska, 1977). In 1985, *Dreissena* even reached the Great Lakes of N America, entering the area via ballast water discharge (Hebert et al., 1989), and has spread rapidly over the neartic continent. This success can be attributed to (i) the ability of the adults to adhere to hard surfaces with their byssus, (ii) development by free-swimming veliger larvae, unique among freshwater bivalves, and (iii) the extraordinary high fecundity (Stanczykowska, 1977; Borcherding, 1991).

D. polymorpha has an epifaunal mode of life in which the shell morphology, particularly the flattened ventral surface, is specialized for byssal attachment to hard substrate such as rock outcrops, stones, and submerged logs. In the absence of hard substrate, the mussels are able to survive as aggregations attached to pebbles, debris, and shells of unionid clams, or as clumps on other mussels (Bij de Vaate, 1991; Mackie, 1991). Populations are greatest in the littoral and sublittoral zones between 2 and 12 m (Stanczykowska, 1977). Although the zebra mussel has been found to a depth of 55 m, growth and reproduction did not occur at that depth in European lakes (Walz, 1973, 1978).

Large populations of zebra mussels play an important role in limnetic ecosystems. Through filter feeding, they reduce high numbers of phytoplankton (Macisaac et al., 1992; Bastviken et al., 1998) and remove suspended matter from the water column (Hinz & Scheil, 1972). The increase in organic content of the sediments by the deposition of faeces and pseudofaeces may benefit some invertebrates (Griffith, 1993; Macisaac & Rocha, 1995). In some places the zebra mussel is the main food source for wintering waterfowl (Stanczykowska, 1977; Cleven & Frenzel, 1993). Benthivorous fish, crayfish, and leeches also prey upon the mussels (Smit et al., 1993; Molloy et al., 1994; Nagelkerke & Sibbing, 1996; Perry et al., 1997).

During the 1980s *D. polymorpha* began to colonize the Drava river ecosystem (Mišetić et al., 1991). Since then, it has been spreading upstream to the town of Varaždin and this process is still in progress (Mrakovčić et al., 2001).

The hydro-electric power plant system on the Drava river, where *D. polymorpha* now occurs, consists of three artificial lakes within 60 km: Varaždin, Čakovec and Dubrava, all situated upstream of the confluence with the Mura river. The artificial lakes were built to supply electricity to NW Croatia, but also play an important role in flood protection and irrigation of agricultural land. The top few metres of the lake banks are covered with asphalt that provides good substrate for the attachment of the mussels, which also settled in the hydro-electric power plant system causing many technical problems (Erben et al., 2000).

The hydrological regime of the Drava river is characterized by high waters in the spring and summer due to the snow melting in the Alps. Nevertheless, the hydropower developments built on the Drava river have radically altered the natural flow rhythms of the water. In 2000 the peak high water (1,306 m^3s^{-1}) in the Dubrava artificial lake occurred in November (Mrakovčić et al., 2001).

Previous researchers have reported that *D. polymorpha*, as implied by its name, can demonstrate considerable phenotypic plasticity, with respect to shell morphology and colour (Pathy & Mackie, 1993; Rosenberg & Ludyansky, 1994). In this study we compared the morphometry of the riverine and lake populations of *D. polymorpha,* and tried to determine if significant differences between them exist. To do this, we used principal components analysis to quantitatively analyse four morphometric variables on three populations. This technique allowed us to analyse differences in mussel shape independently of mussel size and allometry (Reyment et al., 1984; Claxton et al., 1998).

Material and methods

Field sampling

Samples were collected from the artificial Dubrava lake and Drava river. Dubrava lake is the largest artificial lake on the Drava river, with water surface area of 16.6 km^2, and an average volume of 94×10^6 m^3. Current velocity in the reservoir is generally lower than 1.00 m s^{-1} and water turnover occurs in four days. Apart from flushing periods, the water level fluctuations of the reservoir do not exceed 0.50 m. Samples were collected at three sites on March 23, 2000 (Fig. 1). Site 1 (46°18′ N, 16°44′ E) was immediately offshore of the Drava river, approximately 1 km downstream of the dam of the Dubrava hydro-electric power plant, at

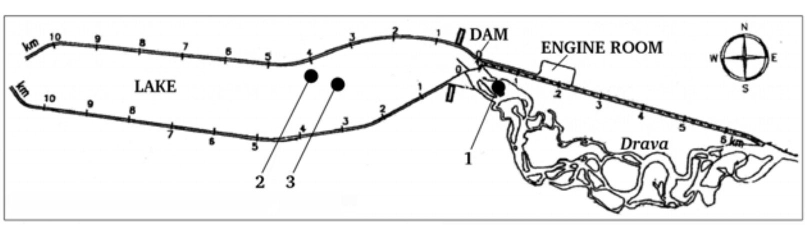

Fig. 1. Site locations in the system of the Dubrava hydro-electric power plant on the Drava river.

Table 1. Environmental variables for the three sampling sites.

Environmental variables	Site 1			Site 2			Site 3			P
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
Chlorophyll-a (mg m^{-3})	0.06	2.52	1.05	0.11	11.35	2.73	0.10	3.34	0.88	0.510
Water temperature (℃)	8.20	22.00	16.19	5.80	22.00	15.00	5.80	21.80	14.37	0.702
pH	7.70	8.15	7.95	7.70	8.69	7.98	7.63	8.37	7.82	0.332
Dissolved oxygen (mg L^{-1})	8.20	16.70	11.41	5.80	14.10	10.89	5.30	11.54	9.66	0.308
Calcium (mg L^{-1})	38.40	46.40	42.06	32.00	44.84	38.17	33.60	48.05	39.55	0.331
Total hardness (mg $CaCO_3$ L^{-1})	132.00	168.00	148.86	120.00	164.00	143.00	120.00	164.00	139.43	0.628
Alkalinity (ml 0.1 N HCl L-m^{-1})	2.30	2.70	2.50	2.00	2.70	2.30	2.00	2.60	2.30	0.292

Key: Minimum, maximum and arithmetic mean of the variables are based on 7 seasonal samplings during the year 2000; P-value (Kruskal-Wallis).

a depth ranging from 0.3 to 0.5 m. Current velocity is generally lower than 0.50 m s^{-1}. Site 2 (46°19′ N, 16°41′ E) and site 3 (46°18′ N, 16°41′ E) were located in the lake, about 4 km upstream from the dam. Site 2 was located on the lake banks at a depth of 3 m, with asphalt as a sediment type, while site 3 was located in the middle of the lake at a depth of 8 m, with fine silt and clay sediments. Mussels from site 1 were scraped from small rocks, collected by wading. A diver collected mussels from sites 2 and 3. A total of 1,200 mussels were collected from all three sites.

Water chemistry samples were collected seasonally during year 2000, by using a 5 L Van Dorn bottle. Water temperature, pH, dissolved oxygen, calcium, total hardness, alkalinity, and chlorophyll-a were determined using routine procedures (Apha, 1985).

Morphometric characters

The following four morphometric variables were measured: shell length (SL), the maximum anteroposterior dimension of the shell; shell width (SW), the maximum left-right dimension with both valves appressed; shell height (SH), the maximum dorsal-ventral dimension of the shell measured perpendicular to the length; and shell mass (SM), the mass of the shell dried for two days at 105℃ after the body was removed. Mussels were measured with callipers, to the nearest 0.1 mm.

Statistical analyses of morphometric characters

The Kruskal-Wallis test was used to determine the difference in environmental variables between the three sites.

Analysis of variance (ANOVA) was applied to test the differences of the three ratios (SW/SL, SH/SL, and SW/SH), among the three observed sites. The Duncan multiple comparison test was used to determine which of the three sites was significantly different from the others for each variable.

The log-transformed variables were further analysed using principal component analysis on 540 shells. ANOVA and the Duncan test were applied on the resulting principal components to test for the differences in component scores among the three sites.

All of the statistical analysis was carried out using SAS® System for Windows. P-values less than 0.05 ($P < 0.05$) were considered statistically significant.

Results

Environmental variables

The minimum, maximum and mean values of environmental variables at three sites in the artificial Dubrava lake and Drava river are shown in Table 1.

All mean values, except the chlorophyll-a and pH are the highest for site 1, but the differences between the sites are not statistically significant (Tab. 1). Notable, but not significant differences between the three sites were recorded only in April, when the maximum value of chlorophyll-a at site 2 was up to 3 times higher than the value from site 3 and 4.5 times higher than the value from site 1. Highest temperatures (around 22℃) occurred in August while lowest temperatures did not fall below 5.8℃. The waters are alkaline, rich in calcium, and well oxygenated except in the summer: minima did not fall below 5.30 mg l^{-1}. Generally, based on all measured environmental variables, the artificial Dubrava lake and the Drava river are oligotrophic to mesotrophic waters.

Morphometric characters

The ratios SW/SL and SW/SH differ significantly among all three sites (Tab. 2). In comparison, SH/SL ratio was not found to be statistically different between sites (Tab. 2).

Table 2. Morphometric characteristics of the collected mussels.

	N	Site 1		Site 2		Site 3		P
		Mean	SD	Mean	SD	Mean	SD	
Ratio SW/SL	400	0.57 a	0.06	0.50 b	0.05	0.49 c	0.04	<0.0001
Ratio SH/SL	400	0.49 a	0.04	0.49 a	0.04	0.50 a	0.03	0.1466
Ratio SW/SH	400	1.17 a	0.15	1.02 b	0.10	1.00 c	0.09	<0.0001

Key: N – sample size; Mean – arithmetic mean; SD – standard deviation; P – value from ANOVA; means followed by the same letter are not significantly different (Duncan test).

Table 3. Loadings of variables on the first three principal components.

	PC1	PC2	PC3
Shell length (SL)	0.506	0.292	−0.802
Shell width (SW)	0.493	−0.644	0.165
Shell height (SH)	0.492	0.645	0.568
Shell mass (SM)	0.508	−0.290	0.089
% of total variance	89.820	6.020	2.230

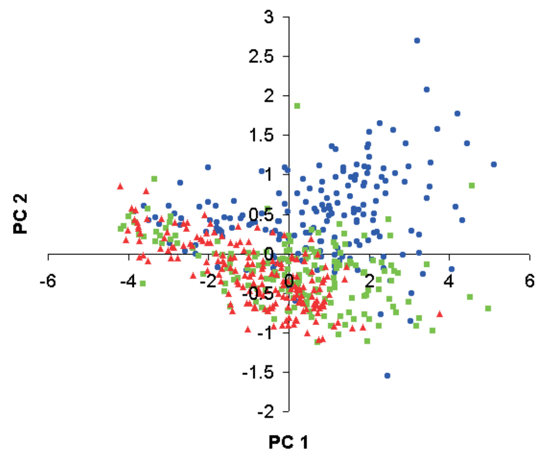

Fig. 2. Relationship between scores on PC1 and PC2. Blue circle represent zebra mussels collected from site 1 (shallow of Drava river). Green quadrate represent zebra mussels collected from site 2 (Dubrava lake at depth of 3 m). Red triangle represent zebra mussels collected from site 3 (Dubrava lake at depth of 8 m).

Principal component analysis resulted in three components explaining 98% of total variance (Tab. 3). The first component explained the majority of the total variation among the data (90%). All of the first component loadings were strongly positive and approximately equal with the respect to the four morphometric variables. It indicates that first component is a measure of shell size. With respect to the high proportion of the explained total variance, it can be concluded that mussel size accounted for most of the variance in the data.

Approximately 6% of total variance was explained by the second principal component. The loadings on the second principal component were positive with respect to shell height and shell length. Negative loadings of the second component were those with respect to shell width and shell mass.

The third principal component explained about 2% of total variance in the data. The highly negative loading of the third component was with respect to length, while the highly positive loading was, as with the second component, with respect to shell height. The unequal loadings' signs on second and third principal components could indicate that those components are the measure of mussel shape.

While the scores of the first component differ significantly among all three sites (Tab. 3), the scores of the second and the third principal components did not differ significantly between sites 2 and 3, while both scores were significantly different from those observed for site 1.

The relationship between scores on the first and second principal components are presented in Fig. 2. The plot of component loadings separated the mussels into two morphological groupings based on the collection sites. Mussels collected from site 1 (river shallow) were separated from those collected from sites 2 and 3 (artificial lake).

Discussion

According to the physico-chemical and biological parameters, which have been measured in the hydro-electric power plant system on the Drava river for a long period (for the Dubrava hydro-electric power plant since 1989 when it was built) artificial Dubrava lake is an oligotrophic to mesotrophic lake (MRAKOVČIĆ et al., 2001). In our research we measured the environmental variables that are important for survival and growth of the zebra mussels (CLAUDI & MACKIE, 1994). The most important variables are temperature, calcium levels, and pH. Of lesser importance, but still significant are annual variations in nutrient levels (which is usually reflected in chlorophyll-*a* levels) and dissolved oxygen (CLAUDI & MACKIE, 1994). All environmental variables measured during the year 2000 at all three sites were favourable for the growth of molluscs. Furthermore, there was no significant difference between the environmental variables from the different sites. The possible reason for this is the complete exchange of lake water every four days (MRAKOVČIĆ et al., 2001).

Many authors (DERMOTT & MUNAWAR, 1993; PATHY & MACKIE, 1993; ROSENBERG & LUDYANSKY, 1994) have compared the ratios of several morphometric variables in mussels (*D. polymorpha, D. bugensis* Andrusov, 1897, *Mytilopsis leucophaeta* Conrad, 1831). In general, the disadvantage of this type of analysis is that ratios are not constant within a group that shows allometry or substantial plasticity (REYMENT et al., 1984). Therefore, we also used principal component analysis to demonstrate differences between sampled populations of zebra mussel.

Our analysis shows that the ratios SW/SL and SW/SH differ significantly between all three sites, while the ratio SH/SL does not differ between sites. Site 1 was the shallow of the Drava river, at a depth of 0.3 to 0.5 m. Mussels from that site had the highest SW/SL ratio, and the SM was higher than in other mussels, as well. There are a few possible explanations for this. Mussels were attached to gravel and small rocks, primarily as separate individuals and the density of the population was intermediate. Site 2 was the artificial lake at depth of 3 m. Population density there was very high which was probably the result of favourable environmental conditions and asphalt as a sediment type. Mussels existed as big clumps, which restricted their growth. Because of this, the ratio of SW/SL was smaller than on the site 1. This result is in accordance with ALUNNO-BRUSCIA et al. (2001). They examined the influence of food availability and population density on the morphometry and shell length-body-mass relationship of *Mytilus edulis* L., 1758. The authors conclude that mussels tended to be narrower at high density. Site 3 was in the lake at the depth of 8 m with fine silt and clay as sediment and with the lowest mussel density. Mussels are primarily attached to debris such as trunks and branches of trees and bushes. As a result of high water in a spring and summer and brief floods in autumn and winter, a significant amount of silt was settled on the bottom and on the mussels. Those mussels, compared to mussels from sites 1 and 2, had the smallest SW/SL ratio. Moreover, their shells were very fragile and easy to break off.

PATHY & MACKIE (1993), and ROSENBERG & LUDYANSKY (1994) have reported that zebra mussels can demonstrate considerable phenotypic plasticity, with respect to shell morphology and colour. This is in agreement with our results. The animals they examined were from different lakes and rivers. DERMOTT & MUNAWAR (1993) who compared the morphometry of the epilimnetic and profundal forms of the quagga mussel, *D. bugensis* in the Lake Erie, came to the same conclusions.

Our results of principal component analysis showed that the mussels collected for this study could be separated into two morphological groupings. We believe that these groups represent phenotypes that are best adapted to different habitats, particularly riverine shallow (site 1) versus artificial lake (sites 2 and 3). Using the same type of analysis CLAXTON et al. (1998) have reported that *D. polymorpha*, in contrast to *D. bugensis*, showed no shell plasticity with respect to depth or site location within Lake Erie. This corresponds with our results, where according to principal component analysis, both populations from two different sites within artificial lake belong to the same group.

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