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COLONISATION OF WATER BODIES BY THE ZEBRA MUSSEL *DREISSENA POLYMORPHA* (PALLAS) IN THE LIGHT OF GENETIC STUDIES

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ABSTRACT: Five populations of the zebra mussel *Dreissena polymorpha*, from small, isolated, post-glacial water bodies and one reservoir formed in the 50s (all in the Western Pomerania) have been examined. Isoenzyme electrophoresis in starch gel was used in order to estimate their variation and genetic structure. The studied populations are widely variable genetically, and their genotypes are very diverse, in spite of their isolated character. The analysis revealed 86% polymorphic loci, 2.3–3.7 alleles per locus and 2.5–4.2 per polymorphic locus, 2.4–5.4 genotypes per locus and the expected heterozygosity of 0.338–0.487. The genetic similarity between the populations ranged from 0.828 to 0.949 and was somewhat lower, compared to other populations of the species. The level of genetic variability of *D. polymorpha* in the isolated populations was comparable to that found in large populations from the Western Pomerania and with the founder populations from the Great Lakes of North America. Colonisation by *D. polymorpha* is not accompanied by impoverishment of gene pool resulting from founder effect. The species seems to be expanding massively, using all of its genetic potential.

KEY WORDS: bivalve molluscs, zebra mussel, *Dreissena polymorpha*, colonisation, enzymatic polymorphism, heterozygosity, founder effect

INTRODUCTION

The zebra mussel, *Dreissena polymorpha* (Pallas, 1771), is a typical expansive species, whose distribution area for about 200 years has gradually extended from the basins of the Black, Caspian and Azov Seas, the expansion being still in progress (WIKTOR 1969, STAŃCZYKOWSKA 1977).

Based on the analysis of fossil record, it has been demonstrated that *D. polymorpha* was present in Europe in pre-glacial period (NOWAK 1974). Its Tertiary range included the area between the Atlantic Ocean in the west and the Aral Sea in the east, the White Sea in the north and the Black and Caspian Seas in the south. During the Ice Ages, the species became almost completely extinct, its distribution being limited to the coasts of the Black and Caspian Seas. From that area it started to expand again (PIECHOCKI & DYDUCH-FALNIOWSKA 1993). The zebra mussel dispersed mainly along the rivers, the dispersal being associated with the development of inland navigation (URBAŃSKI 1957). The first stage of its expansion covered the European part of Russia, and the expansion route led from the northern part of the Caspian Sea and the delta of the Volga river, upstream of Volga and to its tributaries. The second, more intense, expansion stage started from the coast of the Black Sea and proceeded northward along the Dnieper river and its tributaries. Having invaded Eastern Europe, the zebra mussel penetrated to Central and Western Europe along two main routes: the coast of Northern Europe and the Danube river valley (NOWAK 1974).

In Poland the earliest records of *D. polymorpha* date from before 1824, from the area of the former Eastern Prussia; in the Western Pomerania the species was found in the Gulf of Szczecin as late as 1896 (BRANDT 1896, PIECHOCKI & DYDUCH-FALNIOWSKA 1993). It is suspected that the zebra mussel got to the Baltic Coast along the Nemen river, which, at the end of the 18th

c., was connected with the Dnieper river by the Ogiński Canal.

In 1800–1960 the zebra mussel invaded ca. 1.25 mln km^2 in Europe, which constituted 35% its distribution area. The mean rate of expansion was ca. 7,800 km^2 per year (NOWAK 1974). According to SCHLOSSER (1995), in 1800–1900 the species increased its distribution range in Europe over twice.

Some authors maintain that during the Ice Ages *D. polymorpha* did not become completely extinct in entire Europe, but survived in at least a few isolated areas: the lakes of Schleswig-Holstein in Thüringen (WALZ 1974), in the Kuronian Bay, Ohrida lake in the former Yugoslavia, in some lakes on the Hungarian Lowland (NOWAK 1974) and in the Balkans (PIECHOCKI & DYDUCH-FALNIOWSKA 1993). According to the proponents of this view, the expansion of the zebra mussel, observed for 200 years in entire Europe, was so rapid due to those isolated localities, and the present distribution area is the reconstructed pre-glacial range of the species (NOWAK 1974, STAŃCZYKOWSKA 1977).

Besides the European expansion, the zebra mussel dispersed also to areas located south and north of its endemic distribution range, but the details of the process are unknown (NOWAK 1974).

In 1986, *D. polymorpha* invaded also the Great Lakes of North America, from where it is expected to expand to whole Nearctic (HEBERT et al. 1989, BORCHERDING 1991, STRAYER 1991). In 1991, American authors recorded from the lake Ontario another introduced bivalve species (MAY & MARSDEN 1992). Based on morphological shell studies and allozyme variation it was classified as *Dreissena bugensis* Andrusov, 1897, which occurs in the Dnieper river in Ukraine (MAY & MARSDEN 1992, SPIDLE et al. 1994).

The objective of my studies was to estimate the level of genetic variability and the genetic structure of selected populations of *D. polymorpha* from the Western Pomerania. The studies included populations from four small and isolated lakes (Orzechów, Duże, Płociowe and Marta), and one, also isolated, lake Czarnogłowy formed in the 50s, as a remnant of a chalk quarry. The results have been compared with literature data on the genetic variation in populations of this species from large lakes of Poland and Europe, and with the first founder populations of *D. polymorpha* and *D. bugensis* from the Great lakes in North America.

Enzyme electrophoresis was used in this study, which is commonly applied in genetic-population studies on natural populations of plants and animals. The results make it possible also to draw conclusions on the ecology, life strategies and evolutionary history of plant and animal taxa (HAMRICK et al. 1979, RITTE & PASHTAN 1982, NEVO et al. 1984, SZWEYKOWSKI 1984, SAFRIEL & RITTE 1986, HAMRICK & GODT 1990, WENNE 1993). A low degree of genetic variability (heterozygosity) in a population suggests a loss of variation resulting from genetic drift (NEI et al. 1975, CHAKRABORTY & NEI 1977, PACKER et al. 1991, BERRY 1992). In Europe, where *D. polymorpha* has occurred in masses for nearly 200 years, its populations theoretically should not undergo random events. However, genetic drift can not be excluded when new populations are established in newly formed water reservoirs, when the zebra mussel inhabits isolated lakes or when its population abundance is drastically reduced as a result of water pollution. It should be expected that such populations of *D. polymorpha* should be characterized by a decreased level of genetic variation in relation to the original populations, as a result of founder effect (CARSON & TEMPLETON 1984).

MATERIAL AND METHODS

Specimens of *D. polymorpha* for the studies were collected during diving in 1992–1994 from five lakes in the Western Pomerania: Orzechów, Czarnogłowy, Duże, Płociowe and Marta. The material was collected by Mr. M. ŚWIERCZYŃSKI, M. Sc., who provided also the description of the lakes.

All the lakes are small (surface area from 28 to 66 ha), isolated, located among forests or fields, and fed only by atmospheric precipitation and subterranean waters. Their water level decreases solely as a result of evaporation. The population abundance and the distribution of the mussels in the lakes are varied.

In the lake Orzechów, of 28 ha area, *D. polymorpha* is unevenly distributed in the entire lake, where the substratum is favourable it reaches even the depth of 10–11 m. In the lakes Duże (32 ha) and Marta (66 ha) the zebra mussel occurs on the whole bottom and most often is attached to tree branches. The density of the bivalve in these lakes is considerable, the mean value being 12,345.0 individuals/m^2. In the lake Płociowe (35 ha) the distribution of *D. polymorpha* is insular, depending on the kind of substratum. On favourable, stable substratum (stones, sand) it is found at the depth of 5 m, but because of the bottom being mostly muddy, in most places it reaches only 1.5 m. The zebra mussel occurs most often on hard objects (tree branches, stones) and reeds. Contrary to the remaining lakes, which are post-glacial, the lake

Czarnogłowy (39 ha) is a young reservoir. It came into existence in the 50s, as a result of chalk excavation. Its southern shore is forest-covered, the other shores are woodless. According to preliminary observations, *D. polymorpha* covers all the bottom at the depth of 0–22 m. The distribution of the bivalve is uneven, because of the diversified substratum, i. e. sand, clay, stones and tree branches. The zebra mussel is very numerous at the depth of 17 m, where some individuals attain the length of 40 mm. The huge biomass of *D. polymorpha* in the lake Czarnogłowy concentrates on the branches of fallen trees.

It was assumed that the zebra mussel from each lake formed a population. The assumption was justified by earlier detailed studies on *D. polymorpha* from the lakes Woświn (ZIELIŃSKI et al. 1996) and Ińsko (SOROKA et al. 1997).

Samples from the following number of sites were taken in each lake: 2 on the lake Orzechów, 10 on each of the lakes Marta and Płociowe, and 11 from each of the lakes Czarnogłowy and Duże. From 20 to 50 individuals were collected at each site, and electrophoretic assays were performed on 10 specimens from each site. A total of 440 specimens of *D. polymorpha* have been subject to analysis.

The collected material was kept in the laboratory for about a month, during which electrophoretic analyses were performed. The material retained its enzymatic activity during the whole study period.

Variation of seven enzymes was analysed using starch gel electrophoresis. The list of the enzymes is presented in Table 1. The electrophoresis followed standard procedures (ZIELIŃSKI 1987, PASTEUR et al. 1988, SOLTIS & SOLTIS 1989, ZIELIŃSKI et al. 1996), with some modifications (SOROKA et al. 1997).

Following genetic interpretation, the results in the form of multi-locus genotypes were statistically analysed with the programmes BIOSYS-1 (SWOFFORD & SELANDER 1983) and GENESTAT-PC v. 2.1 (WHITKUS 1988). A programme written by Mr. P. KONIECZNY, M. Sc., was used to analyse the presence of individuals of unique genotypes (GU) in the populations, with respect to seven enzymatic loci.

Table 1. List of analysed enzymes, applied gel and electrode buffers

Abbreviation	Enzyme	E.C. number	Gel and Electrode Buffer
GOT (AAT)	Aspartate aminotransferase	E.C. 2.6.1.1.	Lithium-borate
EST	Esterase	E.C. 3.1.1.2.	Lithium-borate
PGI	Glucose-6-phosphate isomerase	E.C. 5.3.1.9.	Lithium-borate
ME	NADP- dependent malate dehydrogenase	E.C. 1.1.1.40.	Morpholine-citrate
MDH	NAD- dependent malate dehydrogenase	E.C. 1.1.1.37.	Morpholine-citrate
IDH	Isocitrate dehydrogenase	E.C. 1.1.1.42.	Morpholine-citrate
PGM	Phosphoglucomutase	E.C. 2.7.5.1.	Tris-citrate

RESULTS

Seven enzymatic loci have been identified, based on the electrophoretic analysis of seven enzymes in 440 individuals of *D. polymorpha* from five populations from the Western Pomerania. In all the examined populations, variation has been found in six loci, locus Pgm1 being always monomorphic. The percentage of polymorphic loci, at the polymorphism criterion of 0.99, was 85.7 (Table 2). The lowest number of polymorphic loci – 5 – was found in the population from Orzechów (No. 1), at the polymorphism criterion of 0.95, which resulted most probably from the small sample size.

The number of alleles per locus and per polymorphic locus in each population is presented in Table 2. The populations differ with respect to these values. The lowest number of alleles per locus is that in the population from Orzechów (No. 1), and the highest in the population from Duże (No. 3). The values of the number of alleles per polymorphic locus are analogous (Table 2).

The following values of the number of alleles per polymorphic locus have been found: Me1 – 8 alleles, Got1 – 5 alleles, Pgi1, Mdh1 and Idh1 – 4 alleles each, and 3 alleles for locus Est1 (Table 3). In particular populations the number of alleles in each locus ranged: for Me1 from 3 to 6, Got1 from 3 to 5, Pgi1 from 3 to 4 and for Idh1 from 2 to 4, at the maximum number of alleles in the species amounting to 8, 5, 4

Table 2. Parameters of genetic variability in five populations of *D. polymorpha* from the Western Pomerania (N – number of individuals analysed, A_1 – number of alleles per locus (± S.E.), A_2 – number of alleles per polymorphic locus, P – frequencies of polymorphic loci, H_S – the mean expected heterozygosity in a population (± S.E.)

Population number	Population name	N	A_1	A_2	P*	H_S**
1	Orzechów	20	2.29 (± 0.29)	2.50	85.71	0.338 (± 0.085)
2	Czarnogłowy	110	3.14 (± 0.55)	3.50	85.71	0.487 (± 0.090)
3	Duże	110	3.71 (± 0.57)	4.17	85.71	0.461 (± 0.086)
4	Płociowe	100	3.29 (± 0.57)	3.29	85.71	0.362 (± 0.086)
5	Marta	100	3.00 (± 0.62)	3.33	85.71	0.412 (± 0.080)
	Mean	88	3.09 (± 0.52)	3.36	85.71	0.412 (± 0.085)

* polymorphism criterion 0.99
** according to NEI (1978)

Table 3. Number of alleles in 7 enzymatic loci for 5 populations of *D. polymorpha*

Population number	Population name	Got1	Est1	Pgi1	Me1	Mdh1	Idh1	Pgm1
1	Orzechów	3	2	3	3	2	2	1
2	Czarnogłowy	5	3	3	5	2	3	1
3	Duże	4	3	4	6	4	4	1
4	Płociowe	5	3	4	5	2	3	1
5	Marta	4	3	3	6	2	2	1
	Mean	4.2	2.8	3.4	5.0	2.4	2.8	1.0
	Range	3–5	2–3	3–4	3–6	2–4	2–4	1

and 4, respectively. The remaining loci, Est1 and Mdh1, had the same numbers of identical alleles in four populations (Tables 3 and 4).

The populations of *D. polymorpha* differed with respect to the presence of alleles and their frequencies. From 3 to 13 of all the alleles distinguished were absent from the analysed populations (Table 4). In most loci the same, most frequent, alleles were present. Only in locus Est1 in the population from Orzechów the most frequent was allele 2, while in the remaining populations the most frequent was allele 1. In loci Pgi1 and Idh1 two populations had the same, most frequent, alleles, but they differed in this respect from the remaining populations. In all the polymorphic loci, except Me1 in the population from Duże, the most frequent allele had a frequency of at least 0.45.

Rare alleles, of a frequency below 0.01, were found in 3 loci, their total number being 7. Their highest number – 5 alleles – was found in locus Me1, and one in each of loci Mdh1 and Idh1. No rare alleles were found in the populations from Orzechów and Płociowe, while their highest number (4) was found in the population from Duże.

The expected heterozygosity H_S for the analysed populations ranged from 0.338 to 0.487, and the mean value per population was 0.412 (Table 2). In two populations H_S did not exceed the value of 0.40; in another two populations it was high, over 0.46.

The analysed populations show a high diversity in the level of variation of particular loci (Table 5). In three of them the most variable locus was Got1, for which the expected heterozygosity (H) exceeded 0.57. The least variable loci differed between the populations and their H ranged from 0.05 in the population from Orzechów to 0.35 in the population from Duże. The lowest H values were observed in locus Idh1 in the population from Orzechów, and the highest in locus Got1 in the population from Czarnogłowy.

On an average, locus Got1 proved to be the most variable in all the examined populations, with the mean value of H = 0.54; it was followed by loci Pgi1 and Me1, for which H = 0.52 (Tab. 5). Locus Mdh1 was characterised by the lowest mean value of H, amounting to 0.38. Locus Pgm1 was monomorphic in all the populations (H = 0).

The following number of genotypes was found in the analysed loci: Me1 – 12, Pgi1 – 10, Got1 – 9, Idh – 7, Est1 and Mdh1 – 6 and Pgm1 – 1 (Table 6).

The mean number of genotypes per locus per population was 4.5, the values ranging from 2.43 to 5.43 (populations 1 and 3, 4). The number of genotypes in locus Me1 in particular populations ranged from 3 to 9, in Pgi1 from 4 to 10 and in Got1 from 3 to 8, at a

Table 4. Frequencies of alleles in analysed loci in *D. polymorpha* from 5 populations of the Western Pomerania (N – number of individuals analysed)

Loci/ alleles	Orzechów	Czarnogłowy	Duże	Płociowe	Marta
N	20	110	110	100	100
Got1					
1	0.5500	0.4450	0.7910	0.7700	0.4650
2	0.0000	0.0820	0.0360	0.1200	0.1650
3	0.0000	0.2050	0.0000	0.0150	0.3150
4	0.0750	0.1450	0.1550	0.0550	0.0000
5	0.3750	0.1230	0.0180	0.0400	0.0550
Est1					
1	0.4500	0.5090	0.5410	0.8000	0.5000
2	0.5500	0.4590	0.2450	0.1600	0.4900
3	0.0000	0.0320	0.2140	0.0400	0.0100
Pgi1					
1	0.1750	0.4730	0.6770	0.2900	0.0600
2	0.7000	0.2500	0.2410	0.4500	0.8100
3	0.1250	0.2770	0.0680	0.0850	0.1300
4	0.0000	0.0000	0.0140	0.1750	0.0000
Me1					
1	0.8000	0.5590	0.4050	0.7500	0.6150
2	0.1750	0.2450	0.3860	0.1500	0.2300
3	0.0000	0.0000	0.0050	0.0000	0.0000
4	0.0000	0.0050	0.0000	0.0000	0.0000
5	0.0000	0.1000	0.1090	0.0450	0.0150
6	0.0250	0.0910	0.0860	0.0400	0.1300
7	0.0000	0.0000	0.0090	0.0150	0.0050
8	0.0000	0.0000	0.0000	0.0000	0.0050
Mdh1					
1	0.7000	0.7320	0.5450	0.9100	0.7500
2	0.3000	0.2680	0.4050	0.0900	0.2500
5	0.0000	0.0000	0.0450	0.0000	0.0000
6	0.0000	0.0000	0.0050	0.0000	0.0000
Idh1					
1	0.9750	0.5590	0.4360	0.2850	0.6550
2	0.0000	0.0000	0.0050	0.0000	0.0000
3	0.0250	0.4180	0.4730	0.5950	0.3450
4	0.0000	0.0230	0.0860	0.1200	0.0000
Pgm1					
1	1.0000	1.0000	1.0000	1.0000	1.0000

maximum number of genotypes amounting to 12, 10 and 9, respectively. All the populations had their number of genotypes in particular loci lower, compared to the number of genotypes distinguished, except for loci Est1, Pgi1 and Mdh1, which in single populations (respective numbers 2, 4 and 3) had all the possible genotypes.

The frequencies of genotypes in the analysed loci were diverse in all the populations. The differences involved both the presence of the genotypes and their frequency (Table 6). The lowest genotypic differentiation was observed in the populations from Orzechów and Marta, where the respective numbers of genotypes not found were 34 and 21, compared with all the 50 genotypes distinguished. In the remaining populations from 13 to 15 genotypes were absent.

The most frequent genotypes in the polymorphic loci Me1, Mdh1 and Idh1 were present in all the populations, though not always with the highest frequency. In the remaining loci some genotypes, being the most frequent in some populations, were rare or absent in the others. A high diversity between populations and analysed loci was observed in the case of rare genotypes (frequency below 0.05).

The analysis of enzymatic loci with respect to the HARDY-WEINBERG equilibrium revealed that half of them were in the state of equilibrium (Table 7). On an average each population had 3 loci in the state of equilibrium, among 6 loci tested per population. Loci Pgi1 and Mdh1 were always in equilibrium. Locus Got1 deviated from the HARDY-WEINBERG equilibrium in all the populations, while loci Est1 and Idh1 – in four populations. The lack of equilibrium resulted from a high excess of heterozygotes in these loci (Table 7).

An average of 61 unique genotypes was found in the studied populations, which constitutes ca. 69.3% of all genotypes. The unique genotype is here defined as a genotype (multilocus genotype), which was present only once in the population. The proportion of such genotypes in particular populations ranged from 36 to 83% (Table 8) and was observed to depend on the number of analysed individuals. The more numerous individuals were analysed, the higher was the percentage of unique genotypes. An exception is the population from Marta (No. 5), in which the analysis of 100 specimens revealed only 36% unique genotypes.

In the analysed populations of *D. polymorpha* the genetic similarity, calculated according to NEI (1978), was within the range 0.828–0.949 (Table 9). Most populations were within the range of 0.901–0.949. The highest genetic similarity was that between the populations from Orzechów and Marta. The genetic distances between the populations (NEI 1978) were within 0.052–0.189. The population from Duże was genetically the most remote; its respective distances from the populations from Orzechów and Marta were 0.189 and 0.171.

Table 5. Expected heterozygosity in a polymorphic locus (H) in five populations of *D. polymorpha*

Locus	Orzechów	Czarnogłowy	Duże	Płociowe	Marta	Mean
Got1	0.565	0.720	0.351	0.390	0.658	0.537
Est1	0.508	0.531	0.604	0.334	0.512	0.498
Pgi1	0.476	0.640	0.481	0.679	0.325	0.520
Me1	0.337	0.612	0.671	0.413	0.554	0.517
Mdh1	0.431	0.394	0.539	0.165	0.377	0.381
Idh1	0.050	0.514	0.581	0.553	0.454	0.430

DISCUSSION

All the analysed populations of *D. polymorpha* from the Western Pomerania display a high level of genetic variability, high genetic similarity and genotype diversity, in spite of the isolated character of the lakes that they inhabit. Each population had 85.7% polymorphic loci and a monomorphic locus Pgm1. The mean expected heterozygosity per locus per population (H_S) ranged from 0.338 to 0.487, the mean for all populations being 0.412. The analysed populations had 2.3–3.7 alleles per locus, 2.5–4.2 per polymorphic locus, and 2.4–5.4 genotypes per locus.

The genetic variation of *D. polymorpha* from small forest or midfield lakes does not essentially depart from that found in populations from large lakes of the Western Pomerania. The populations of zebra mussel from the lakes Woświn (809 ha), the third largest in West Pomerania, and Ińsko (590 ha), had the following basic parameters of variation: 75.0% polymorphic loci each, the mean number of alleles per locus 3.6 and 4.0, respectively, per polymorphic locus 3.5 and 4.3, the mean expected heterozygosity per locus per population 0.393 and 0.348 (ZIELIŃSKI et al. 1996, SOROKA et al. 1997). With respect to the loci analysed in this study, the coefficient of expected heterozygosity in the lakes Woświn and Ińsko was 0.449 and 0.398, respectively (SOROKA 1996).

In some of the analysed populations some loci displayed the maximum numbers of alleles and genotypes, found in *D. polymorpha* from Poland (SOROKA 1996). Two populations (Nos 2 and 4) had 5 alleles in locus Got1, two populations (Nos 3 and 4) had 4 alleles in locus Pgi1, one population (No. 3) had 4 alleles in locus Idh1. In populations 2 and 4 the highest observed numbers of genotypes were found in loci Est1 i Pgi1, respectively (Table 6). The population from Orzechów (No. 1) was characterized by the minimum number of alleles and genotypes in all the loci. In the remaining populations the distribution of the number of alleles and genotypes was varied (Tables 3 and 6).

The high value H_S=0.487, the maximum numbers of alleles and genotypes in two loci and the highest proportion of unique genotypes (Tables 2, 3, 6 and 8) in the population from the lake Czarnogłowy – a chalk quarry that came into existence in the 50s – indicates the mode of invasion of new water bodies by *D. polymorpha,* not accompanied by a narrowing of the gene pool of the population. On the contrary, colonisation was effected by numerous, genetically diverse individuals, or was a multiple colonisation from populations originating from various water bodies. It should be conjectured that the remaining isolated lakes were colonised in a similar way, as evidenced by similar values of the variation parameters.

The lowest values of all the analysed parameters (Table 2: A_1–2.29, A_2–2.50, H_S–0.338) were observed in the small population from Orzechów, which is associated with the low number of analysed individuals (20), rather than with the isolated character of the population. In the remaining populations, where 100–110 individuals were analysed, the number of alleles per locus was over 3.0, per polymorphic locus over 3.2, and the mean expected heterozygosity per locus per population over 0.36.

The level of genetic variation in the zebra mussel from both isolated and large populations from the Western Pomerania is comparable to that found in the founder populations from the Great Lakes of North America, which have been invaded by the species since 1985 (HEBERT et al. 1989, ZIELIŃSKI et al. 1996, SOROKA et al. 1997). In these American populations, aged from 3 to 6 years (material collected in 1988–1991) the coefficient of expected heterozygosity per locus per population (H) was high and reached values of 0.31–0.50 (HEBERT et al. 1989, GARTON & HAAG 1991, ROSE & ECKROAT 1991, MAY & MARSDEN 1992, BOILEAU & HEBERT 1993, MARSDEN et al. 1995). The high variation of the American populations of the zebra mussel indicates that the colonisation proceeded from abundant original populations, or was multiple and effected by genotypically diverse individuals. For this reason no founder effect was observed in such cases (HEBERT et al. 1989, GARTON & HAAG 1991, MARSDEN et al. 1995, 1996).

The zebra mussel from small, isolated or newly established populations did not show any decrease in its genetic variation, compared to other populations of

Table 6. Frequencies of genotypes of the polymorphic loci analysed and number of genotypes in five populations of *D. polymorpha*

Locus	Genotype	Populations				
		Orzechów	Czarnogłowy	Duże	Płociowe	Marta
Got1	11	0.100	0.227	0.665	0.600	0.040
	12	–	0.055	0.036	0.200	0.220
	13	–	0.182	–	0.010	0.630
	14	0.150	0.109	0.218	0.090	–
	15	0.750	0.091	–	0.040	–
	25	–	0.109	0.036	0.040	0.110
	34	–	0.182	–	0.020	–
	35	–	0.045	–	–	–
	44	–	–	0.045	–	–
Est1	11	–	0.073	0.309	0.630	0.040
	12	0.900	0.864	0.446	0.260	0.910
	13	–	0.009	0.018	0.080	0.010
	22	0.100	0.018	–	0.030	0.030
	23	–	0.018	0.045	–	0.010
	33	–	0.018	0.182	–	–
Pgi1	11	0.050	0.200	0.454	0.060	–
	12	0.250	0.218	0.345	0.310	0.110
	13	–	0.327	0.091	0.060	0.010
	14	–	–	0.009	0.090	–
	22	0.450	0.082	0.046	0.160	0.650
	23	0.250	0.118	0.046	0.070	0.210
	24	–	–	–	0.020	–
	33	–	0.055	–	0.010	0.020
	34	–	–	–	0.020	–
	44	–	–	0.009	0.020	–
Me1	11	0.600	0.373	0.209	0.570	0.480
	12	0.350	0.209	0.282	0.230	0.170
	14	–	0.009	–	–	–
	15	–	0.073	0.045	0.060	0.020
	16	0.050	0.082	0.064	0.050	0.080
	17	–	–	–	0.020	–
	22	–	0.027	0.091	–	0.040
	23	–	–	0.009	–	–
	25	–	0.127	0.173	0.030	0.010
	26	–	0.100	0.109	0.030	0.180
	27	–	–	0.018	0.010	0.010
	28	–	–	–	–	0.010
Mdh1	11	0.400	0.527	0.318	0.820	0.580
	12	0.600	0.409	0.427	0.180	0.340
	15	–	–	0.018	–	–
	16	–	–	0.009	–	–
	22	–	0.064	0.155	–	0.080
	25	–	–	0.073	–	–
Idh1	11	0.950	0.373	0.091	0.090	0.340
	13	0.050	0.373	0.691	0.380	0.630
	14	–	–	–	0.010	–
	23	–	–	0.009	–	–
	33	–	0.209	0.036	0.360	0.030
	34	–	0.045	0.173	0.090	–
	44	–	–	–	0.070	–
Number genotypes/population		2.43	5.14	5.43	5.43	4.29

Table 7. Chi-square statistics for concordance with HARDY-WEINBERG equilibrium and deficiency or excess (D) of heterozygotes for enzymatic loci in five populations of *D. polymorpha*. (* – p < 0.05)

	Chi^2					
Population	Got1	Est1	Pgi1	Me1	Mdh1	Idh1
1. Orzechów	9.5*	11.0*	0.5	0.2	2.3	0.0
2.Czarnogłowy	79.2*	87.3*	2.8	25.6*	0.1	8.2*
3. Duże	82.3*	84.0*	11.9	19.5	4.7	59.1*
4. Płociowe	19.4*	0.7	3.1	3.8	0.2	23.9*
5. Marta	122.1*	69.5*	0.1	33.9*	0.5	14.2*
	D					
1. Orzechów	0.63	0.82	0.08	0.22	0.43	0.03
2. Czarnogłowy	0.08	0.68	0.04	-0.02	0.04	-0.18
3. Duże	-0.17	-0.15	0.03	0.05	-0.02	0.51
4. Płociowe	0.03	0.02	0.11	0.05	0.10	-0.13
5. Marta	0.47	0.82	0.02	-0.13	-0.09	0.39

Table 8. Percentage of unique genotypes (GU) in five populations of *D. polymorpha*

Population number	Population name	Number of individuals	% GU
1	Orzechów	20	60.0
2	Czarnogłowy	110	82.7
3	Duże	110	80.9
4	Płociowe	100	75.0
5	Marta	100	36.0

Table 9. Matrix of coefficients of genetic similarity (below) and genetic distance (above) of NEI (1978) for analysed populations of *D. polymorpha*

	Orzechów	Czarnogłowy	Duże	Płociowe	Marta
Orzechów	———	0.093	0.189	0.167	0.052
Czarnogłowy	0.912	———	0.060	0.082	0.072
Duże	0.828	0.942	———	0.095	0.171
Płociowe	0.847	0.922	0.910	———	0.107
Marta	0.949	0.931	0.843	0.899	———

the species. Such a decrease in small, isolated or newly established populations, resulting from genetic drift, was observed in many animal species (NEI 1987, LEBERG 1992). The absence of this phenomenon in *D. polymorpha* may be accounted for by its mass mode of colonisation of new water bodies and by its great dispersal potential, resulting from numerous biological properties of the species: most of all the high fertility of females (BORCHERDING 1991), external fertilisation and free-swimming veliger larva, which can travel over long distances in the water (LEWANDOWSKI 1982a). Furthermore, the dispersal is favoured also by the possibility of transport of adult individuals attached with byssus threads to boats and barges (LEWANDOWSKI 1982b, BORCHERDING 1991), and movements of adult mussels resulting from dissolving of their byssus threads (ACKERMAN et al. 1994). The expansion of the zebra mussel is further facilitated by the ability to survive a few days without water (WIKTOR 1969, GRIFFITHS et al. 1991), colonisation of waters of varied trophy (WIŚNIEWSKI & DUSOGE 1983, LEWANDOWSKI 1991), and polluted (STAŃCZYKOWSKA et al. 1983, PIECHOCKI & DYDUCH-FALNIOWSKA 1993), heated and brackish waters (WIKTOR 1969, KORNOBIS 1977).

These biological properties of *D. polymorpha* favour intense transport of various development stages, including adult individuals, resulting in a high potential rate of gene flow, which may explain the absence of founder effect in the newly established populations and the reatively poor genetic differences between the Polish, Western European and American popula-

tions of the zebra mussel (MAY & MARSDEN 1992, SPIDLE et al. 1994, SOROKA 1996).

Like populations of *D. polymorpha*, most other introduced species of molluscs in the Great Lakes of North America, especially those with planktonic larvae, display a level of genetic variation similar to that found in the original populations (WARD 1990). The absence of allozyme variation was observed only in the American population of a bivalve *Corbicula fluminea* (O. F. Müller, 1774), also introduced in North America (SMITH et al. 1979).

It is interesting that populations of *D. polymorpha* described in literature, characterized by the lowest level of genetic variation, are located in Europe: in the Netherlands (H<0.30) (SPIDLE et al. 1994), Germany, Hungary and Russia (MARSDEN et al. 1995), where the species has been present for almost 200 years. This may be explained by the low and varied number of individuals analysed for particular loci in the case of Hungarian and Russian populations, in which from 13 to 40 individuals were analysed for 15 loci (MARSDEN et al. 1995). However, in two populations from the Netherlands and one from Germany, where over 40 individuals were examined for 11–15 loci, the expected heterozygosity was 0.29 (SPIDLE et al. 1994, MARSDEN et al. 1995). In other populations from Germany and in those from Great Britain (BOILEAU & HEBERT 1993) and Poland (population from Orzechów in this paper), where the mean number of analysed specimens was 23, and the number of examined loci ranged from 7 to 11, the expected heterozygosity was higher and ranged from 0.34 to 0.51.

The differences in the genetic variation between the European populations are difficult to explain solely based on the varied number of analysed loci and the number of examined individuals. They may reflect an actual genetic diversity, resulting from adaptation of *D. polymorpha* to varied habitat conditions in the lakes. My own studies (SOROKA 1996) indicate that populations of the zebra mussel from heated lakes display a genetic variation higher than those from lakes of normal temperature, while populations from brackish waters display an excess of heterozygotes in some loci, compared to freshwater reservoirs.

In the analysed populations some genotypes were more frequent, and other less so, than would be predicted from the HARDY-WEINBERG equilibrium. Some genotypic combinations in loci Me1, Mdh1 and Est1 did not appear. In all the loci generally an excess of heterozygotes was found, though in single loci and populations a slight excess of homozygotes was observed (Table 7). Only the population from Orzechów was characterized by an excess of heterozygotes in each locus. Because of the potential possibility of various genotypic combinations (high fertility, external cross-fertilisation) the absence of some homo- and heterozygotes in some of the loci is surprizing. One of the explanations may be their low adaptive value.

There are no unequivocal literature data on the HARDY-WEINBERG equilibrium in *D. polymorpha*. In many papers authors either did not consider the problem (MAY & MARSDEN 1992, SPIDLE et al. 1994), or did not cite unambiguous results. The lack of consistent data on the HARDY-WEINBERG equilibrium in *D. polymorpha* may result from an erroneous interpretation of electrophoregrams, which would seriously complicate the whole problem. It can not be excluded that the equlibrium or its lack may also depend on the geographic location of the population, habitat conditions and direction of selection, and involve various loci to various degree.

The genetic similarity (I) and genetic distance (D; NEI 1978) are often used to compare populations on the basis of frequency of alleles. The values of these parameters for the analysed populations of *D. polymorpha* are presented in Table 9. The genetic distance was within 0.052–0.189, while the similarity ranged from 0.828 to 0.949 and was lower compared to other 12 populations from Poland (0.94–0.99) (ZIELIŃSKI et al. 1995). Among the Polish populations, the lowest genetic differentiation (D = 0.013) was that between four populations from the vicinity of Konin, from lakes located close to each other and connected by canals (SOROKA 1996). The presented results indicate somewhat greater genetic differences between populations of the zebra mussel from isolated lakes, as a result of a less free gene flow between them, compared to other, naturally or artificially connected reservoirs.

A low genetic distance was also observed between American and Western European populations of *D. polymorpha*. For six populations from the Great Lakes (naturally connected lakes) and two Dutch populations the values of D were lower than 0.02 (MAY & MARSDEN 1992, SPIDLE et al. 1994). Large continental clusters of the zebra mussel populations were grouped at a genetic distance of 0.068, which, though much higher, is within the range of genetic and geographic variability of the species (SPIDLE et al. 1994).

The data clearly indicate that the high genetic uniformity of populations of *D. polymorpha* results from biological predispositions of the species to dispersal and depends on the geographic distance between the populations, as well as on the presence or absence of connections between the lakes.

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