J. Appl. Genet. 37(1), 1996, pp. 105-120

Genetic variability in selected Polish population of *Dreissena polymorpha* (Pallas) (*Bivalvia: Dreissenidae*)

Roman ZIELIŃSKI, Marianna SOROKA, Małgorzata WACHOWIAK-ZIELIŃSKA

Department of Genetics, Faculty of Biology and Marine Sciences, University of Szczecin

Abstract. Genetic variability of a selected population of *Dreissena polymorpha*, an invasive species playing a significant role in aquatic ecosystems, was studied. Starch gel electrophoresis was used to analyse 8 enzymatic loci in 200 individuals collected from 20 sites in a lake. The population was found to have 75.0% of polymorphic loci, 2.8 alleles per locus, 3.5 alleles per polymorphic locus, 0.393 coefficient of expected heterozygosity, and 149 genotypes. Zebra mussel clumps were strongly polymorphic; almost every individual had a different genotype. The high polymorphism observed in the *D. polymorpha* clumps had most likely resulted from external cross-fertilisation and the presence of free-swimming veliger larvae as well as from a considerable heterozygosity of individual bivalves. Genetic variability of the population studied was found to be similar to that of populations inhabiting other Western Pomeranian lakes, including both highly polluted ones and those formed as recently as about 40 years ago. This provides evidence for a mass colonisation of freshwater reservoirs effected by very polymorphic parent populations of *D. polymorpha*. The literature data on North American zebra mussel populations which invaded that continent about 10 years ago show them to be polymorphic, too, but not as much as European ones.

Key words: *Bivalvia, Dreissena polymorpha*, enzymatic polymorphism, population.

Introduction

The zebra mussel (*Dreissena polymorpha*) (Pall.) has been recorded in Polish inland waters since the beginning of the 19th century. The bivalve is

Received: July 1995. This study was supported by Grant No. 6 P204 101 06 of the State Committee for Scientific Research.

Correspondence: R. ZIELIŃSKI, Department of Genetics, Faculty of Biology and Marine Sciences, University of Szczecin, Łukasińskiego 43, 71-215 Szczecin, Poland.

a typical invader whose range, while centred in the Caspian, Black, and Azov Seas, has been gradually broadening over the last 200 years (WIKTOR 1969, STAŃCZYKOWSKA 1977,). In Poland, the zebra mussel is common in natural and man-made lakes, estuaries, and dam reservoirs (KORNOBIS 1977, STAŃCZYKOWSKA 1977). The bivalve occurs also in those lakes and lagoons which experience salt water intrusions (Lakes Dąbie and Dłużno; the Szczecin, Vistula, and Kamieński Lagoons) and tolerates salinity of up to 4‰ (WIKTOR 1969, STAŃCZYKOWSKA 1972, ŚWIERCZYŃSKI et al. 1986, PIOTROWSKI, OCHMAN 1993). *D. polymorpha* inhabits waters differing in trophic conditions and shows high individual variability. Numerous authors have emphasized the bivalve's important ecological role involving biofiltration of water, bioaccumulation, and biosedimentation (STAŃCZYKOWSKA 1968, LEWANDOWSKI 1982, STAŃCZYKOWSKA et al. 1983).

According to estimates by STAŃCZYKOWSKA (1968), *D. polymorpha* population is capable of filtering the whole volume of lake during a few days, a month or a summer, depending on the bivalve's population size. The zebra mussel is also responsible for some undesirable effects due to its habit of settling on underwater constructions, docks, and waterways (SZLAUER 1974, HEBERT et al. 1989).

D. polymorpha is a dioecious species with no sexual dimorphism. A female produces 30.000 eggs a year. The fertilisation is external (BORCHERDING 1991). The initially pelagic larvae settle on hard substrata to form aggregations (clumps) of few to several hundred individuals (STAŃCZYKOWSKA 1964). In areas of high abundance, zebra mussel clumps occur in dense beds of widely varying densities, reaching up to several hundred individuals per 1 m^2 substratum (STAŃCZYKOWSKA 1961, LEWANDOWSKI 1983). In many eutrophic water bodies, *D. polymorpha* populations have dwindled, which is regarded as an adverse symptom. For this reason, methods are being developed to use artificial substrata in order to increase the area offered to *Dreissena* larvae for settlement and thus to enhance the zebra mussel population increase (PIESIK 1992).

Little is known about the genetics of European populations of *D. polymorpha* (BOILEAU, HEBERT 1992). Genetics of the zebra mussel populations inhabiting Polish waters has been treated in reports by ZIELIŃSKI, WACHOWIAK-ZIELIŃSKA (1992), SOROKA, ZIELIŃSKI (1994), ZIELIŃSKI et al. (1994a, b, c) who demonstrated an extensive isoenzymatic polymorphism of the bivalve in Polish waters.

In the mid-80's, *D. polymorpha* invaded the North American continent. Its occurrence there is perceived as a threat to the natural equilibrium of water bodies. The rapid propagation of the bivalve has brought about certain unde-

sirable effects, resulting predominantly from the bivalve's settling on underwater constructions. The American populations of *D. polymorpha* have already been a subject of a number of electrophoretic studies (HEBERT et al. 1989, GARTON, HAAG 1991, MAY, MARSDEN 1992). A milestone in the *Dreissena* research was the finding of the "quagga" form, identified as *D. bugensis*, in the Great Lakes (MAY, MARSDEN 1992, SPIDLE et al. 1994).

The present paper is aimed at elucidating genetic variability of *D. polymorpha* inhabiting Lake Woświn in Western Pomerania, based on starch gel electrophoresis of 8 enzymes. The study was carried out at the sub-population level to identify the degree of genetic variation of clumps. An additional objective was to highlight the genotypic variation in the population and in clumps by examining separate individuals in terms of all enzymatic loci. The results were compared with data on other *D. polymorpha* populations from Poland and North America.

Material and methods

A *D. polymorpha* population inhabiting Lake Woświn, the third largest lake in Western Pomerania, was studied. The Woświn area is 809 ha; the lake is 9.5 km long with a maximum depth of 28 m. It is α-mesotrophic and its water purity was classified to class 1 to 2. The lake is located in the Ińsko Landscape Park and a natural (floral, faunistic, and landscape) reserve is planned around it. *D. polymorpha* is abundant in the lake, its population being stable in terms of size. For this reason, the population was regarded by the present authors as a good model for genetic studies and a good source of data for comparisons with *D. polymorpha* populations undergoing strong variations and dwelling in polluted, brackish, and heated reservoirs. In Lake Woświn, the bivalve is the most abundant in the southern part, the lowest densities being recorded in the northern and north-western parts of the lake.

Individuals for this study were sampled in such a way as to give a good representation of the whole Woświn population and provide sufficient information on genetic variability of individuals in various clumps. The bivalves were collected by SCUBA diving in September and October 1992 and in June 1993 from 20 randomly selected sites (0.1-3.0 m depth range) located in different parts of the lake (Fig. 1). At each sampling site, 20-40 individuals were picked up from a cohesive clump, spatially separated from other clumps.

Each sample was placed in a separate container and transported to the laboratory of the Department of Genetics, University of Szczecin. The bivalves

were kept live in aquaria throughout the period of the assays; water in the aquaria was aerated and lit and the bivalves were fed algal suspensions.

Electrophoresis was run on 10 live bivalves picked out of each of the 20 clumps collected. A 20 mg muscle tissue sample was dissected out from each individual with a scalpel and ground separately in 200 µl 0.1 M Tris-HCl extraction buffer (pH 7.5) in a cooled mortar (ZIELIŃSKI 1987). The tissue extract obtained was refrigerated for 15 min. at 4°C. Subsequently, 3.5 × 8 mm pieces of Whatman 3 MM filter paper were soaked in the extract; each piece was inserted into a different 10% Sigma electrostarch gel. Electrophoresis was run in three buffer systems, following ZIELIŃSKI (1987) and ZIELIŃSKI, SOROKA (1994). The following enzymes were separated in lithium borate buffer (pH 8.0): aspartate aminotrasferase (GOT: EC 2.6.1.1.); esterase (EST: EC 3.1.1.2.); phosphoglucoisomerase (PGI: EC 5.3.1.9.). Tris-citrate (Poulik) buffer (pH 8.0 of electrode buffer and pH 9.1 of gel buffer) was used to separate phosphoglucomutase (PGM: EC 2.7.5.1.) and sorbitol dehydrogenase (SDH: EC 1.1.1.14.). Morpholine citrate buffer (pH 6.1) was applied in separation of NAD-dependent malate dehydrogenase (MDH: EC 1.1.1.37.), NADP-dependent malate dehydrogenase (ME: EC 1.1.1.40.) and isocitrate dehydrogenase (IDH: EC 1.1.1.42.).

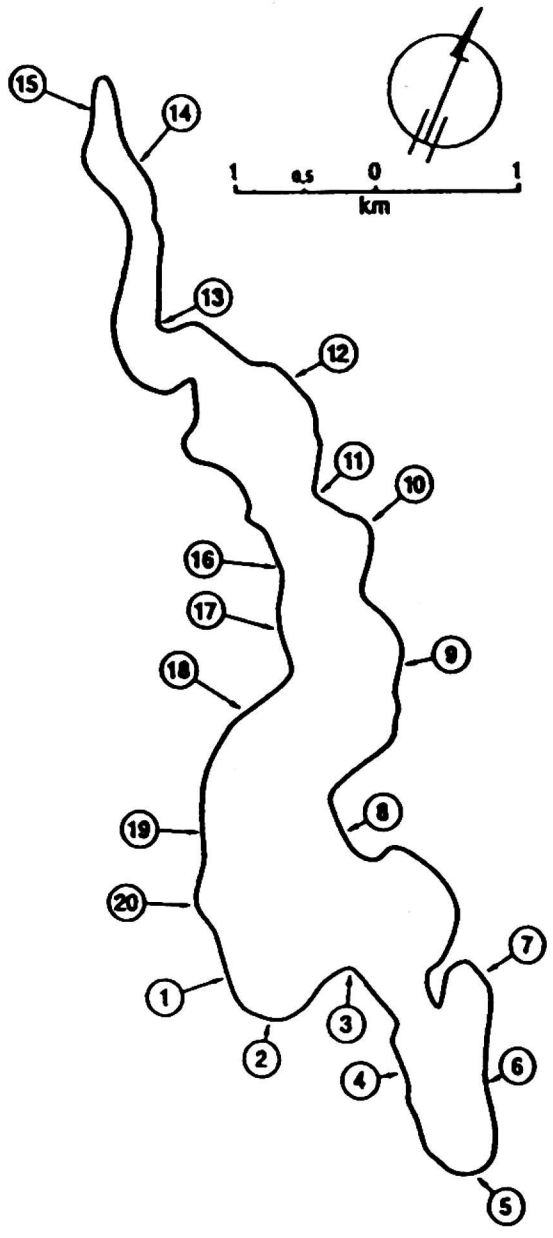

Fig. 1. *Dreissena polymorpha* collecting sites in Lake Woświn

Except for SDH, all the enzymes studied in this work were used in previous genetic and populational studies on *D. polymorpha* (HEBERT et al. 1989, MAY, MARSDEN 1992). In this paper, the authors' allele numeration was used because the authors mentioned above presented no pattern of band location or principles

of allele numbering. In this work, band numbers were not always coincident with their mobility. Band numbers used in this study follow the standard practice used in our laboratory, according to which the lack of some bands and alleles was caused by their absence in the population analysed. The polymorphism criterion adopted was 0.99, which means that the polymorphic allele frequency was equal to or higher than 0.01. This polymorphism criterion was considered when determining the number of alleles per locus, the number of alleles per polymorphic locus and the expected heterozygosity.

The assays were run at 4°C. Following separation, the enzymes were developed with standard procedures with some modifications (PASTEUR et al. 1988, SOLTIS, SOLTIS 1989). Except for GOT and EST, which were stained with the incubation mixture, all the enzymes were stained using the agar-overlay technique (ZIELIŃSKI 1987, SOLTIS, SOLITS 1989). Staining, performed at 37°C, took about an hour. All the enzymes examined migrated in the anodal part of the gel.

Genetic interpretation of the electrophoretic phenotypes obtained was based on the analysis of band patterns. The simplest one-band phenotypes were interpreted as homozygotes, while phenotypes with two or more bands were interpreted as heterozygotes (PASTEUR et al. 1988).

Since each individual yielded 8 enzymes to be analysed, multi-enzyme phenotypes and genotypes could be described for each bivalve used in the assays. The degree of polymorphism in the clumps could be estimated, too. The coefficient of the mean expected heterozygosity was calculated using the BIOSYS-1 software (SWOFFORD, SELANDER 1983).

Due to a low number of individuals picked up from each clump, the inter-clump variability was not assessed. When analysing 10 individuals from each of the 20 clumps collected, an attempt was made to get a *D. polymorpha* sample representative of the Lake Woświn population and to find out whether the clumps analysed were polymorphic or not.

Results

The Lake Woświn *D. polymorpha* population showed polymorphism of 6 out of the 8 enzymes analysed. The highest number of electrophoretic phenotypes was recorded for ME (11 phenotypes), followed by MDH (8), IDH (7),

PGI (6), GOT and EST (5 each), and PGM (2) (Table 1). Monomorphic enzymes were PGM and SDH. A total of 8 enzymatic loci, one for each enzyme analysed, were identified (Table 2). The average numbers of alleles per locus and per polymorphic locus were 2.8 and 3.5, respectively. The highest number of alleles was recorded with respect to Me (7 alleles), followed by Mdh (5), Got and Idh (4 each), Est and Pgi (3 each), Pgm (2), and Sdh (1). Polymorphic loci made up 75.0% of all loci in the population studied. At least two alleles at these loci occurred at a frequency exceeding 10%. Rare alleles (frequency lower than 1%) were detected at the Pgm, Idh, Mdh, and Me loci. High-frequency alleles occurred both in homo- and heterozygotes, while low-frequency alleles were present mainly in heterozygotes.

The coefficient of the mean expected heterozygosity for the 8 loci analysed was 0.393 (Table 2). Idh showed the highest h value (0.599), followed by that of Me (0.580), Pgi (0.564), Est (0.525), Mdh (0.491), and Got (0.382). Of the 6 polymorphic loci found, Pgi and Mdh showed the Hardy-Weinberg equilibrium (Table 2).

Based on the combined analysis of the 8 enzymatic loci, a total of 149 genotype categories were distinguished in the population studied, 123 genotypes occurring only once. The unique

Table 1. Frequencies of electrophoretic phenotypes of the enzymes analysed in the Lake Woświn *Dreissena polymorpha* population

Enzyme	Phenotype	Frequency
GOT	11	0.63
	12	0.14
	15	0.13
	15	0.02
	25	0.08
EST	11	0.08
	12	0.82
	13	0.03
	22	0.02
	23	0.05
PGI	11	0.07
	12	0.25
	13	0.06
	22	0.36
	23	0.20
	33	0.06
ME	11	0.44
	12	0.15
	14	0.01
	15	0.09
	16	0.03
	22	0.11
	25	0.09
	26	0.05
	27	0.01
	34	0.01
	55	0.01
MDH	11	0.48
	12	0.29
	14	0.01
	15	0.04
	16	0.01
	22	0.11
	25	0.05
	55	0.01
IDH	11	0.14
	13	0.63
	14	0.07
	22	0.01
	33	0.01
	34	0.13
	44	0.01
PGM	11	0.99
	12	0.01
SDH	11	1.00

Table 2. Frequencies of alleles, index of expected heterozygosity at each locus, h, and Chi-square test (degree of freedom in parenthese) for the enzymatic loci analysed in the Lake Woświn *Dreissena polymorpha* population

Loci / allele		Frequency	h	χ^2
Got	1 2 4 5	0.775 0.110 0.063 0.052	0.382	102.63* (6)
Est	1 2 3	0.526 0.447 0.027	0.525	109.02* (3)
Pgi	1 2 3	0.225 0.595 0.180	0.564	3.78ns (3)
Me	1 2 3 4 5 6 7	0.586 0.262 0.005 0.007 0.093 0.040 0.007	0.580	186.67* (21)
Mdh	1 2 4 5 6	0.655 0.280 0.005 0.055 0.005	0.491	11.89ns (10)
Idh	1 2 3 4	0.490 0.005 0.385 0.120	0.599	108.02* (6)
Pgm	1 2	0.998 0.002	0.005	–
Sdh	1	1.000	0.000	–

* $p<0.05$, ns – non-significant

genotype index, GI, was 0.61 (123/200), while the frequency of each unique genotype was 0.5%. Other genotypes occurred at the frequencies of 1; 1.5; 2; 2.5; 3.5, and 5.5% (Fig. 2).

Each of the 20 clumps analysed proved to be polymorphic with respect to 5-6 enzymes. The average numbers of alleles per locus in a clump and per polymorphic locus in a clump were 2.45 and 2.92, respectively. The percentage

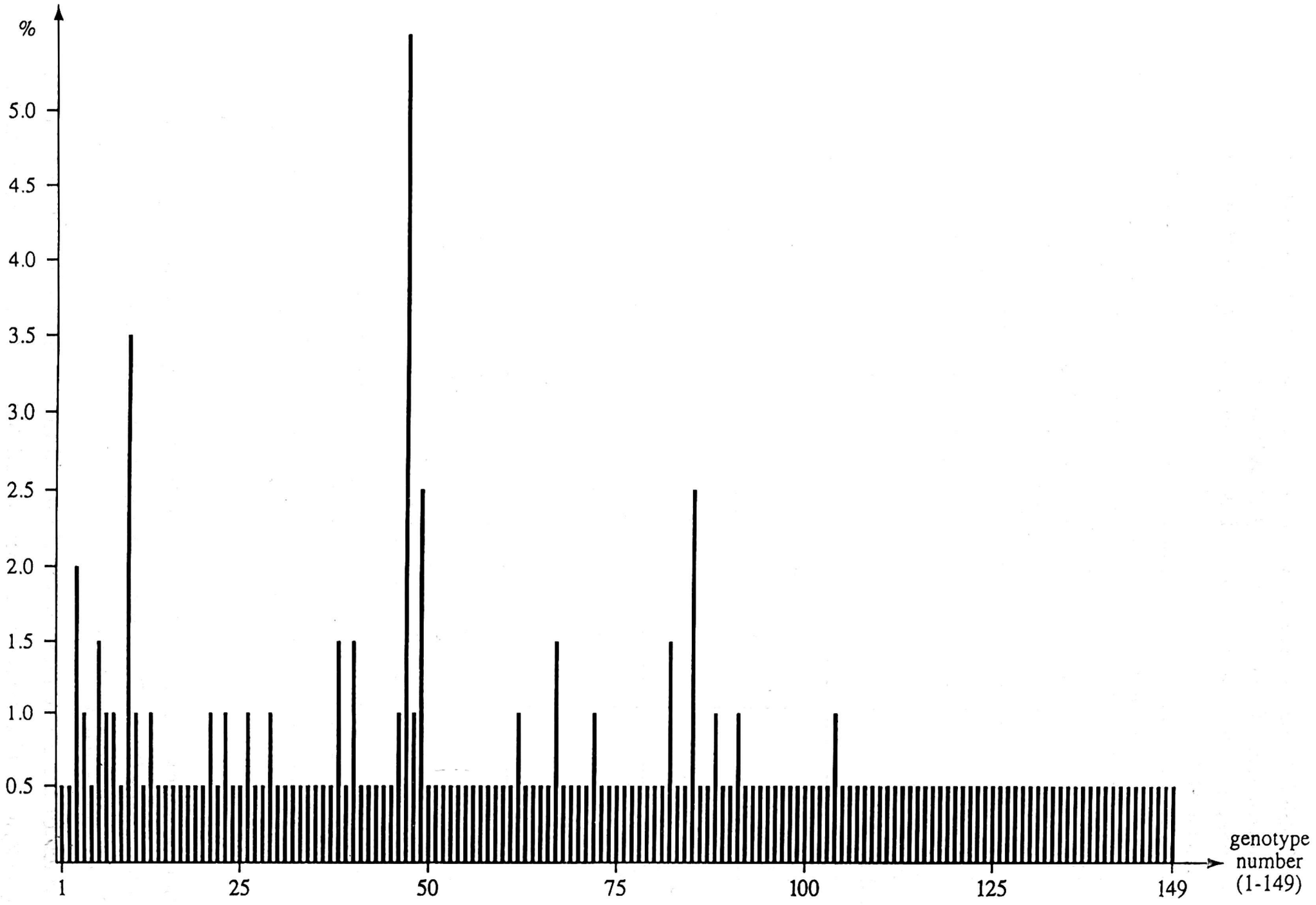

Fig. 2. The genotypes detected and their frequencies in the *Dreissena polymorpha* population analysed

Table 3. Average number of alleles per locus, average number of alleles per polymorphic locus, percentage of polymorphic loci and number of genotypes in the Lake Woświn *Dreissena polymorpha* clumps analysed

Clump No.	Average number of alleles per locus	Average number of alleles per polymor-phic locus	Percent of polymorphic loci	Number of genotypes
1	2.25	2.67	75.0	10
2	2.63	3.17	75.0	10
3	2.38	2.83	75.0	9
4	2.88	3.50	75.0	10
5	2.63	3.17	75.0	10
6	2.38	2.83	75.0	10
7	2.63	3.17	75.0	10
8	2.63	3.17	75.0	10
9	2.75	3.33	87.5	10
10	2.38	2.83	75.0	10
11	2.13	2.50	75.0	10
12	2.38	2.83	75.0	10
13	2.25	2.50	62.5	10
14	2.25	2.67	75.0	10
15	2.38	2.83	75.0	10
16	2.13	2.50	75.0	10
17	2.38	2.83	75.0	10
18	2.38	2.83	75.0	10.
19	2.38	2.83	75.0	10
20	2.75	3.33	75.0	10
Mean	2.45	2.92	75.0	9.95

of polymorphic loci per clump was 75.0%. Most frequently, a clump showed 10 different genotypes to be found in 10 individuals analysed per clump (Table 3). High-frequency alleles were recorded in all the clumps. On the other hand, the clumps differed from one another by the presence of rare low-frequency alleles (Table 4).

Table 4. Allele frequencies in 20 *Dreissena polymorpha* clumps studied in Lake Woświn

Loci / alleles		Clump No.																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Got	1	0.90	0.80	0.65	0.50	0.85	0.95	0.75	0.70	0.40	0.90	0.90	0.95	1.00	0.90	0.75	0.80	0.95	0.65	0.55	0.60
	2	–	0.10	0.05	0.25	0.10	–	0.15	0.15	0.30	–	0.10	0.05	–	–	0.20	0.15	0.05	0.20	0.25	0.15
	4	0.10	0.10	0.25	0.20	–	–	0.15	0.10	0.05	0.10	–	–	–	0.10	–	0.05	–	0.05	–	0.10
	5	–	–	0.05	0.05	0.05	0.05	0.05	0.05	0.25	–	–	–	–	–	0.05	–	–	0.10	0.20	0.15
Est	1	0.50	0.50	0.50	0.75	0.75	0.45	0.55	0.60	0.45	0.50	0.50	0.65	0.55	0.55	0.45	0.45	0.45	0.45	0.45	0.45
	2	0.50	0.50	0.50	0.25	0.25	0.50	0.45	0.40	0.55	0.45	0.50	0.20	0.35	0.45	0.50	0.55	0.55	0.50	0.50	0.50
	3	–	–	–	–	–	0.05	–	–	–	0.05	–	0.15	0.10	–	0.05	–	–	0.05	0.05	0.05
Pgi	1	0.35	0.20	0.35	0.20	0.15	0.35	0.35	0.05	0.25	0.15	0.25	0.10	0.20	0.25	0.20	0.25	0.30	0.15	0.20	0.15
	2	0.55	0.60	0.50	0.55	0.80	0.50	0.55	0.70	0.55	0.60	0.55	0.80	0.55	0.55	0.65	0.60	0.40	0.80	0.65	0.55
	3	0.10	0.20	0.15	0.25	0.05	0.15	0.10	0.25	0.20	0.25	0.20	0.10	0.25	0.20	0.15	0.15	0.30	0.05	0.15	0.30
Me–	1	0.70	0.55	0.60	0.35	0.45	0.70	0.60	0.45	0.55	0.85	0.75	0.60	0.80	0.40	0.35	0.70	0.60	0.55	0.60	0.55
	2	0.25	0.20	0.40	0.25	0.20	0.25	0.15	0.30	0.30	0.10	0.25	0.30	0.05	0.40	0.45	0.30	0.20	0.35	0.25	0.30
	3	–	–	–	0.05	0.05	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	4	–	0.05	–	0.05	0.05	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	5	0.05	0.20	–	0.20	0.25	0.05	0.20	0.15	0.15	0.05	–	0.05	0.10	–	0.20	–	0.05	0.10	–	0.10
	6	–	–	–	0.10	–	–	0.05	–	–	–	–	0.05	0.05	0.20	–	–	0.15	–	0.15	0.05
	7	–	–	–	–	–	–	–	0.10	0.05	–	–	–	–	–	–	–	–	–	–	–
Mdh	1	0.60	0.55	0.65	0.60	0.55	0.65	0.70	0.65	0.70	0.70	0.80	0.75	0.90	0.30	0.50	0.90	0.65	0.60	0.75	0.55
	2	0.30	0.25	0.35	0.35	0.25	0.30	0.15	0.30	0.25	0.20	0.15	0.25	0.10	0.60	0.50	0.10	0.25	0.40	0.25	0.40
	4	–	0.05	–	–	–	–	–	–	0.05	–	–	–	–	–	–	–	–	–	–	–
	5	0.10	0.15	0.05	0.05	0.20	0.05	0.15	0.05	–	0.10	0.05	–	–	0.10	–	–	–	–	–	0.05
	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.10	–	–	–
Idh	1	0.62	0.55	0.60	0.55	0.40	0.45	0.50	0.45	0.35	0.45	0.50	0.45	0.40	0.30	0.60	0.50	0.45	0.70	0.50	0.50
	2	–	0.10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	3	0.35	0.35	0.35	0.35	0.45	0.50	0.45	0.45	0.50	0.30	0.40	0.50	0.40	0.35	0.30	0.45	0.40	0.30	0.45	0.35
	4	0.05	–	0.05	0.10	0.15	0.05	0.05	0.10	0.15	0.25	0.10	0.05	0.20	0.35	0.10	0.05	0.15	–	0.05	0.15
Pgm	1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	2	–	–	–	–	–	–	–	–	0.05	–	–	–	–	–	–	–	–	–	–	–
Sdh	1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5. Parameters of genetic variability in *Dreissena polymorpha* from five Western Pomeranian lakes

Lake	Percent of polymorphic loci	Average number of alleles per locus	Average number of alleles per polymorphic locus	Mean expected heterozygosity H
Czamogłowy	75.0	2.75	3.30	0.426
Dąbie	87.5	3.00	3.83	0.359
Duże	75.0	2.88	3.50	0.403
Ińsko	75.0	3.25	4.00	0.348
Miedwie	87.5	3.25	4.17	0.417
Mean	80.0	3.03	3.75	0.391

Table 6. Parameters of genetic variability in *Dreissena polymorpha* from North American lakes

Lakes (number of loci)	Percent of polymorphic loci	Average number of alleles per polymorphic locus	Mean expected hete-rozygosity H	References
St. Clair (23 loci)	73.9	3.1	0.306	HEBERT et al. 1989
Erie (7 polymorphic loci)	100.0	3.4	0.307	GARTON, HAAG 1991
St. Clair, Erie, Michigan, Erie Canal, Huron, Ontario (12 polymorphic loci)	100.0	3.6	0.347	MAY, MARSDEN 1992
St. Clair, Oneida (11 polymorphic loci)	100.0	3.3	0.441	BOILEAU, HEBERT 1992
Mean	93.5	3.35	0.350	

Discussion

Genetic variability of the Lake Woświn *D. polymorpha* population was high, which places the bivalve among 11 animal species of the highest variability (BOILEAU, HEBERT 1992).

A high degree of polymorphism within individual clumps was detected in this work as well. Among the polymorphic loci, the presence of all alleles in each clump was recorded only at the Pgi locus (Table 4). The pattern of low-frequency allele occurrence was irregular.

The high variability, observed both in individual clumps and in the whole *D. polymorpha* population could have resulted from external cross-fertilisation and from the presence of free-swimming veliger larva in the species' life cycle.

Genetic variability in the Lake Woświn *D. polymorpha* population resembled that found in populations inhabiting other Polish lakes (ZIELIŃSKI, WACHOWIAK-ZIELIŃSKA 1992, ZIELIŃSKI et al. 1994a, b, c). Table 5 summarises and compares selected genetic variability parameters of *D. polymorpha* populations from the Lake Woświn and five other Western Pomeranian lakes (all these populations were studied using methods identical to that employed in the present work). Values of the parameters compared are very close in all populations. It is noteworthy that two of the lakes sampled (Czarnogłowy and Dąbie) were environmentally quite different than the remaining three, similar to one another and to Lake Woświn. A small lake, Czarnogłowy is a remnant of a clay pit abandoned about 40 years ago, while the Lake Dąbie is one of the largest Polish lakes and shows a high degree of pollution. The data allow to conclude that factors such as pollution in the Lake Dąbie and the young age of the Lake Czarnogłowy have produced no changes in the genetic structure of their respective *D. polymorpha* populations.

Table 6 presents data on genetic variability of North American zebra mussel populations. It is evident that the variability of those populations is much lower than that observed in *D. polymorpha* inhabiting Polish lakes. As only polymorphic loci were analysed in most of the American studies referred to, the actual variability might have been overestimated. In the Polish populations, the percentage of polymorphic loci and the number of alleles per locus were determined on the basis of 0.99 as a polymorphism criterion, disregarding the rare cases of frequencies lower than 0.01. It is not known whether parameters of the American populations were calculated in the same way. If every allele, regardless of its frequency, was included in the analyses, the variability of the American populations would be additionally increased. Different electrophoresis methods used for studying the Polish and American zebra mussel populations make a comparative analysis of genetic variability difficult. Despite this factor, the present authors are of the opinion that, in reality, the variability in the Polish populations, as compared to the American populations, is still higher than that shown actually by the data.

Three other European populations studied by BOILEAU, HEBERT (1992), two from Great Britain and one from Germany, had an average of 3.3 alleles per polymorphic locus, the coefficient of expected heterozygosity amounting to 0.461. Hence, these populations also showed, a higher variability than the American zebra mussel.

Geographic aspects of polymorphism requires further research on both the American and European populations. Such a research would lead to a more accurate identification of differences in genetic variability between both separate populations in North America and in Europe and between American and European populations. The data thus obtained would contribute to the knowledge of pathways and modes of zebra mussel invasion to different water bodies. Differences in individual allele frequencies could help to formulate plausible hypotheses about an adaptive significance of the detected polymorphism (NEVO 1983). The data obtained so far demonstrate the populations analysed to exhibit such differences. For example, 3 and 2 alleles were detected in this study for Pgi and Est-2, respectively, while HEBERT et al. (1989) reported 4 alleles for each of the loci and GARTON, HAAG (1991) found 5 and 6 alleles, respectively. The polymorphic Me locus in this study showed 7 alleles, while 2 and 3 alleles were reported by HEBERT et al. (1989) and GARTON, HAAG (1991), respectively.

The increased genetic variability of *D. polymorpha* inhabiting European lakes may have resulted from the fact that the history of invasion of Europe and North America by the species was different.

As shown by the data produced by electrophoresis on populations from 30 Polish lakes, the nature of genetic variability is similar throughout the Polish zebra mussel populations and is restricted to a single genetic type, taxonomically equal to *D. polymorpha* (Pall.). *D. bugensis* described by SPIDLE et al. (1994) from the River Dnieper and from three North American lakes (Erie, Ontario, and St. Lawrence) showed a considerably lower genetic variability than North American and European populations of *D. polymorpha*.

Conclusions

The Lake Woświn *D. polymorpha* population is genetically highly variable, as evidenced by a high degree of polymorphism shown by individual loci and by a high degree of genetic variability in zebra mussel individuals. The following values of genetic variability parameters have been obtained: 75.0% of polymorphic loci; 3.5 alleles per polymorphic locus; 0.393 coefficient of expected heterozygosity; and 74.5% of different genotypes in the population. The zebra mussel clumps showed the presence of 99.5% of different genotypes. Genetic variability of the *D. polymorpha* population analysed was similar to

that exhibited by other Western Pomeranian populations. Polymorphism of European *D. polymorpha* populations is higher than that of North American zebra mussel populations.

Acknowledgements. The authors wish to thank Mr M. Świerczyński, M.Sc. of the Chair of Ecology, University of Szczecin, for collecting material for this study.

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