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GENETIC STRUCTURE OF AN INVASIVE BIVALVE *DREISSENA POLYMORPHA* (PALLAS) FROM POLAND. II. ECOLOGICAL VARIATION

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ABSTRACT: Thirty two populations of *Dreissena polymorpha* (Pall.) from Poland were electrophoretically studied with respect to enzymatic loci *Got1*, *Est1*, *Pgi1*, *Mdh1*, *Me1*, I*dh1* and *Pgm1*. The variation analysis focused on the possible differences between populations inhabiting lakes of different character. Populations from heated lakes displayed a higher genetic variation compared to unheated reservoirs. Populations from brackish waters showed an excess of homozygotes (loci *Got1* and *Pgi1*) compared to freshwaters. Gradual eutrophication of lakes seems to cause no significant changes in the genetic structure of zebra mussel populations.

KEY WORDS: bivalves, zebra mussel, *Dreissena polymorpha*, genetics, ecological variation

INTRODUCTION

The zebra mussel (*Dreissena polymorpha*) is an expansive species whose distribution range has been gradually increasing for ca. 200 years, from the regions of the Black, Caspian and Azov Seas, the expansion still being in progress (WIKTOR 1969, STAŃCZYKOWSKA 1977). The process is favoured by numerous biological properties of the species, among others high fertility (BORCHERDING 1991), external fertilisation and the veliger larva which is capable of long-distance dispersal within water bodies (LEWANDOWSKI 1982a). The expansion is also aided by transport of adult individuals attached with their byssus threads to boats, barges etc. (LEWANDOWSKI 1982b, BORCHERDING 1991) and migration of adult individuals after dissolving their byssus threads (ACKERMAN et al. 1994). Besides, the process is facilitated by the ability to survive a few days outside water (WIKTOR 1969, GRIFFITHS et al. 1991), to colonise waters of various trophic conditions (WIŚNIEWSKI & DUSOGE 1983, LEWANDOWSKI 1991), polluted (STAŃCZYKOWSKA et al. 1983, PIECHOCKI & DYDUCH-FALNIOWSKA 1993), heated and brackish waters (WIKTOR 1969, KORNOBIS 1977).

In Poland the earliest records of *D. polymorpha* date from 1824, from the former Eastern Prussia, while in Western Pomerania it was observed only as late as in 1896 (BRANDT 1896, PIECHOCKI & DYDUCH-FALNIOWSKA 1993). At present in Poland the species occurs mainly in the Mazurian Lakeland, Pomerania and Wielkopolska. It inhabits fresh and brackish waters: slow-flowing rivers, canals, harbours, lakes, ponds, estuaries and dam reservoirs (WIKTOR 1969, STAŃCZYKOWSKA 1972, PIOTROWSKI & OCHMAN 1993). Such diverse conditions testify to a great adaptive potential of the bivalve. The zebra mussel tolerates high chemical pollution, and changes in habitat conditions in water bodies affect it to a lesser degree compared to other molluscs (MOUTHON 1981, STAŃCZYKOWSKA et al. 1983).

Like other expanding species, the zebra mussel displays a wide genetic variation which enables it to spread over large areas and occupy a variety of habitats (WIKTOR 1969, STAŃCZYKOWSKA 1976, 1977, HEBERT et al. 1989, GARTON & HAAG 1991, MAY & MARSDEN 1992, BOILEAU & HEBERT 1993, PIECHOCKI & DYDUCH-FALNIOWSKA 1993, SPIDLE et al. 1994).

The aim of this study was an estimate of genetic variation and genetic structure of Polish populations of *D. polymorpha* in view of the effect of various environmental factors, such as increased water temperature, salinity and the trophy level.

The technique used was isoenzyme electrophoresis on starch gel. The technique is commonly applied in genetic-population and genetic-evolutionary studies (NEI 1972, 1987, HEDRICK 1975, HAMRICK & GODT 1990).

MATERIAL AND METHODS

MATERIAL

D. polymorpha was collected from 32 water bodies in Poland (Fig. 1). The sites were selected in such a way as to represent the areas of Poland where *D. polymorpha* was the most common i.e. Pomeranian, Wielkopolskie, Mazurian and Suwalskie Lakelands, and lakes of S Baltic coast, and the widest possible range of habitat conditions. The studies included populations from lakes of limited or strong eutrophication, from waters that are periodically or constantly brackish and from heated waters. The location and list of the sites are presented in Figure 1 and Table 1, respectively.

It was assumed that *D. polymorpha* from one water body constituted one population. Such an assumption was justified by earlier detailed studies on *D. polymorpha* from the lakes Ińsko (SOROKA et al. 1997) and Dąbie (PIESIK et al. 1998).

Each sample included material randomly collected from many parts of the lake and depths ranging from 0.1 to 20 m. Each sampling point constituted a part of a compact colony of *D. polymorpha*. From 20 to 50 individuals were collected at each point. The number of sampling points depended on the surface area of the water body, the length of shoreline and the size of zebra mussel population. The number of sampling points per population ranged from 2 to 31, the mean being 12 (Table 1). Only in the lake Sitno, where individuals of *D. polymorpha* were scattered over the bottom, 10 specimens were collected from a small area. The material was collected by a diver, Mr. MAREK ŚWIERCZYŃSKI, M. Sc., from the Chair of Animal Ecology, University of Szczecin.

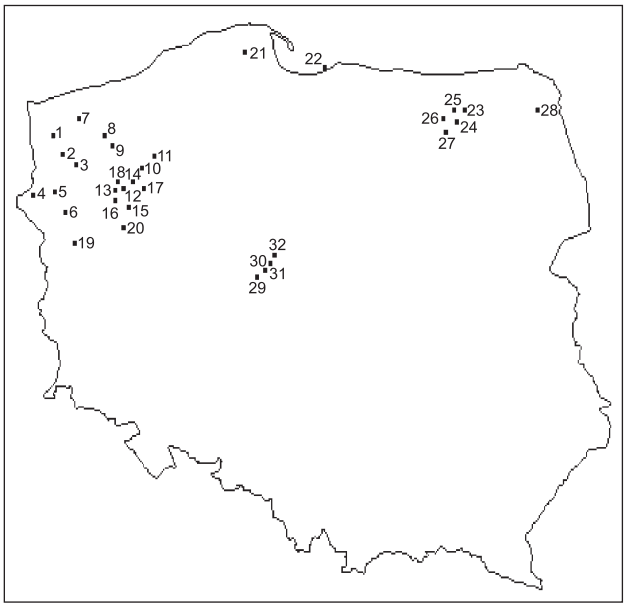

Fig. 1. Sampling sites of *D. polymorpha*

Table 1. List of sampling sites of *D. polymorpha*

No.	Lake	No. of sampling points	Date of collection
1	Dąbie	19	20.04.91, 5.07.91
2	Miedwie	30	28.03.94, 2.04.94, 5.05.94
3	Gardzko	4	12.06.94
4	Orzechów	2	10.01.94
5	Chłop	11	25.09.93
6	Marwicko	11	15.04.93
7	Czarnogłowy	11	8.06.93, 4.02.94
8	Woświn	20	23.09.92, 6.10.92, 16.06.93
9	Ińsko	31	15.09.92, 5.11.92, 7.05.93
10	Lubianka	15	17.04.93
11	Duże	11	11.12.92
12	Raduń	10	28.09.93
13	Adamowo	22	15.04.94
14	Sitno	4	16.04.94
15	Ostrowiec	12	20.04.94
16	Płociowe	10	20.01.94
17	Marta	10	21.04.94
18	Krzywe	16	1.06.93
19	Chycina	11	30.04.94
20	Jaroszewskie	14	9.05.93
21	Łeby-Redy	9	29.09.93
22	Vistula Bay	8	15.05.94
23	Śniardwy	10	16.05.94
24	Mikołajskie	4	16.05.94
25	Wersminia	8	17.05.94
26	Inulec	10	17.05.94
27	Majcz	14	18.05.94
28	Necko	10	19.05.94
29	Gosławskie	10	4.03.95
30	Pątnowskie	10	4.03.95
31	Mikorzyńskie	10	7.03.95
32	Ślesińskie	10	8.03.95

The samples were placed in separate containers and transported, live or deep-frozen, depending on the distance, to the Department of Genetics. The material from Western Pomerania (population samples 1–19) was maintained in laboratory culture. Water in the aquaria was aerated and lit, and the mussels were fed with algal suspension. The remaining samples (20–32) were frozen and stored at –20°C. Thus protected samples were stored for ca. 1 month during which electrophoretic analyses were carried out. The material preserved its enzymatic activity during the whole period of analysis.

The total number of analysed specimens was 3,870 from 32 populations (Fig. 1, Tables 1, 5). The number of analysed specimens per population ranged from 20 to 310, the mean being 121. Ten specimens from each colony were analysed.

Table 2 contains basic morphometric parameters and trophy levels of the water bodies where the zebra mussel was sampled. Since the water bodies differed in their geographical location, temperature, salinity and trophy level, they and their inhabiting populations were divided into groups. With respect to the temperature of the water bodies, the populations

Table 2. Morphometric parameters and trophy levels of water bodies

Number	Lake	Area (ha)	Mean depth (m)	Maximum depth (m)	Trophy level
1	Dąbie	5,600	2.8	4.2	eutrophy
2	Miedwie	3,527	19.3	43.8	eutrophy
3	Gardzko	56	–	–	–
4	Orzechów	28	–	–	β-mesotrophy
5	Chłop	327	10.6	33.0	β-mesotrophy
6	Marwicko	140	3.5	12.4	β-mesotrophy
7	Czarnogłowy	39	–	33.0	β-mesotrophy
8	Woświn	810	9.3	28.1	β-mesotrophy
9	Ińsko	590	11.0	41.7	β-mesotrophy
10	Lubianka	91	7.1	17.8	–
11	Duże	32	11.1	28.8	–
12	Raduń	230	9.5	25.0	β-mesotrophy
13	Adamowo	106	7.3	34.4	eutrophy
14	Sitno	67	4.0	7.0	β-mesotrophy
15	Ostrowiec	388	9.4	28.5	eutrophy
16	Płociowe	35	10.3	25.0	α-mesotrophy
17	Marta	66	7.7	25.0	α-mesotrophy
18	Krzywe	122	5.9	18.1	–
19	Chycina	85	8.5	17.1	β-mesotrophy
20	Jaroszewskie	92	14.2	35.7	β-mesotrophy
21	Łeby-Redy	154	8.0	15.6	–
22	Vistula Bay	83,800	2.6	5.0	–
23	Śniardwy	11,340	5.8	23.4	eutrophy
24	Mikołajskie	498	11.2	26.0	eutrophy
25	Wersminia	88	4.0	8.4	α-mesotrophy
26	Inulec	178	4.6	10.1	eutrophy
27	Majcz	163	6.0	16.4	α-mesotrophy
28	Necko	400	10.1	25.0	eutrophy
29	Gosławskie	454	3.0	5.3	eutrophy
30	Pątnowskie	307	2.6	5.4	eutrophy
31	Mikorzyńskie	245	11.9	38.0	eutrophy
32	Ślesińskie	148	7.5	25.7	eutrophy

were divided into an "Unheated" group including populations from unheated water bodies, and a "heated" group, including those from heated reservoirs. The group Unheated (N 3,470) comprised populations 1–28, the group Heated (N 400) populations 29–32. In respect of water salinity the populations were divided into Fresh- and Brackish water groups. The Freshwater group (N 3,600) comprised populations 2–21 and 23–32, the Brackish water group (N 270) populations 1 and 22. The trophic categories distinguished were meso- and eutrophic water bodies (Table 2). The Mesotrophic group (N 1,670) included populations from α- and β-mesotrophic water bodies, numbers 4–9, 12, 14, 16, 17, 19, 20, 25 and 27. The Eutrophic group (N 1,570) comprised eutrophic and eutrophic/mesotrophic water bodies, population numbers 1, 2, 13, 15, 23, 24, 26, 28–32 (Table 2).

The variation parameters analysed and the statistical methods applied have been described in SOROKA (2002).

BIOCHEMICAL METHODS

Seven enzymes were analysed with starch gel eletrophoresis (Table 3). The electrophoresis followed standard procedures (PASTEUR et al. 1988, SOLTIS & SOLTIS 1989), with some modifications (SOROKA 2002). The protocols for enzyme extraction, gels and buffers used, electrophoresis and enzyme staining have been described in detail by SOROKA (2002).

ESTIMATE OF TROPHIC LEVEL OF THE LAKES

Data on the trophic level of 18 lakes (No. 1, 2, 4, 5, 7–9, 12, 23–32) were obtained from different sources and listed in Table 2. For the remaining lakes the trophy was estimated based on three indices of trophic level WST according to CARLSON (1977), the basic parameters (SD, TP and Chl) were obtained from the Voyvodeship Inspectorates of Environment Protection in Gorzów and Poznań, and from the Centre of Enviroment Studies and Monitoring in Piła. WST indices were calculated with the following formulas:

$$WST_{SD} = 10\left(6 - \frac{\ln SD}{\ln 2}\right)$$

where SD – Secchi's disc visibility in metres,

$$WST_{TP} = 10\left(6 - \frac{\ln \frac{48}{TP}}{\ln 2}\right)$$

where TP – total phosphorus concentration in surface water, in μg l^{-1},

$$WST_{Chl} = 10\left(6 - \frac{2.04 - 0.68 \ln Chl}{\ln 2}\right)$$

where Chl – chlorophyll concentration in surface layers of water, in μg l^{-1}.

WST for each lake was calculated based on all the parameters. Only for lakes Marta, Płociowe and Sitno, because of the lack of data, WST_{TP} index was not calculated. Classification of the lakes follows CARLSON (1977): WST<40 – oligotrophic lakes, 40≤WST<60 – mesotrophic lakes, WST≥60 – eutrophic lakes. The trophy level was not determined for five lakes (Gardzko, Lubianka, Duże, Krzywe, Łeba-Reda) and the Vistula Bay because of the lack of monitoring of water quality in these water bodies.

Table 3. List of analysed enzymes

Abbreviation	Enzyme	E.C. number	Gel and Electrode Buffer
GOT (AAT)	Aspartate aminotrasferase	E.C. 2.6.1.1.	Lithium-borate
EST	Esterase	E.C. 3.1.1.2.	Lithium-borate
PGI	Phosphoglucoisomerase	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

ELECTROPHORETIC PHENOTYPES OF ANALYSED ENZYMES AND THEIR GENETIC INTERPRETATION

Author's own numbering of alleles was used, because of the absence of data on band position and principles of allele numbering in literature describing electrophoretic phenotypes of *D. polymorpha* (HEBERT et al. 1989, MAY & MARSDEN 1992, SPIDLE et al. 1994). Bands and alleles were numbered according to the commonly accepted principles, though the numbers did not always correspond to mobility.

Each enzyme had a few electrophoretic phenotypes which were numbered according to the sequence adopted. The phenotypes were one-, two-, three-, four-, or five-banded and were exclusive within individuals.

In the genetic interpretation it was assumed that exclusive one-banded phenotypes of different electrophoretic mobility were single-locus homozygotes. Phenotypes of 2, 3, 4 and 5 bands were interpreted as heterozygotes for their respective loci.

Seven enzymatic loci were identified, one for each enzyme. For the detailed genetic interpretation of the obtained electrophoretic phenotypes, detailed data on genetic similarity and distance between the populations, and their genetic structure see SOROKA (2002).

GENETIC DIFFERENCES BETWEEN TEMPERATURE-BASED GROUPS OF POPULATIONS OF *D. POLYMORPHA*

Genetic similarity between the groups Unheated and Heated was high and amounted to 0.9788, the genetic distance being 0.0215 (according to NEI 1978). The highest genetic similarity was observed between populations of the group Heated (0.9868), and the range of values was very narrow (0.9801–0.9972). In the group Unheated the range of values of I_N was wide: 0.8277–0.9988 (Table 4).

Table 5 and Figure 2 illustrate allele frequencies in the groups, Table 6 shows values of heterozygote excess (D), Figure 3 presents values of coefficients H, H_T, D_{ST} and G_{ST} for particular loci, considering the division into groups, Figure 4 shows H_S values and mean values of H_T, D_{ST} and G_{ST}.

Table 4. Genetic similarities and distances for six population groups of *D. polymorpha*

Group	Mean genetic similarity	Range	Mean genetic distance	Range
Unheated	0.9542	0.8277–0.9988	0.0473	0.0012–0.1891
Heated	0.9868	0.9801–0.9972	0.0133	0.0028–0.0201
Freshwater	0.9557	0.8277–0.9988	0.0458	0.0012–0.1891
Brackish water	0.9376	0.9376–0.9376	0.0644	0.0644–0.0644
Mesotrophic	0.9499	0.8464–0.9938	0.0518	0.0062–0.1668
Eutrophic	0.9655	0.8933–0.9972	0.0353	0.0028–0.1128

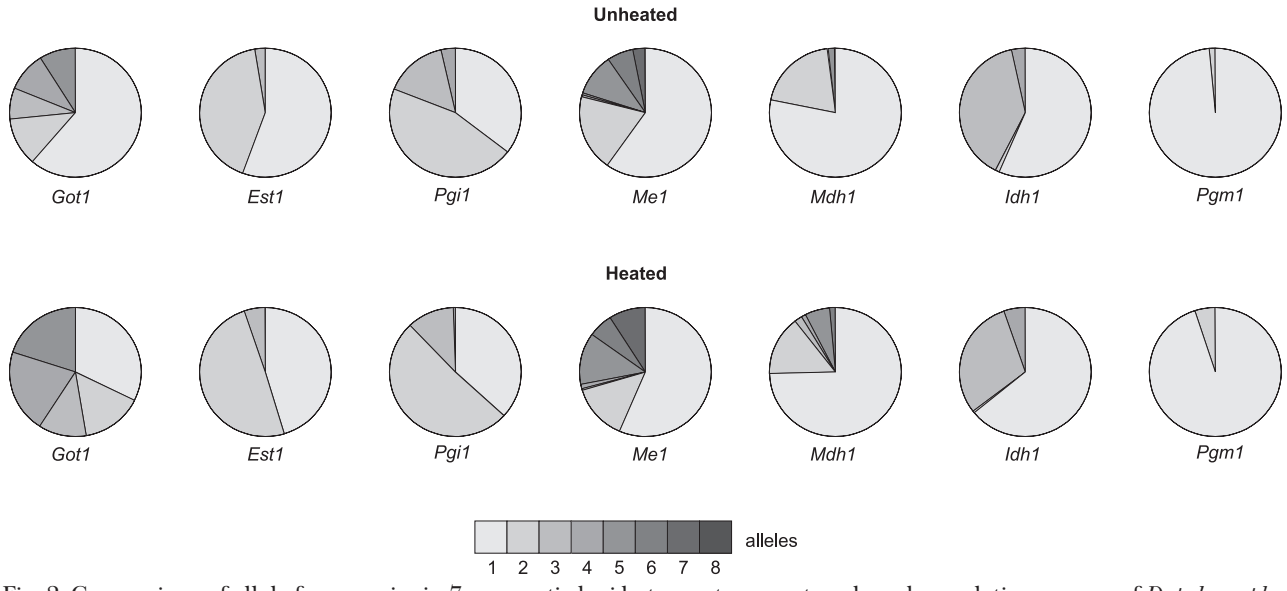

Fig. 2. Comparison of allele frequencies in 7 enzymatic loci between temperature-based population groups of *D. polymorpha*

Table 5. Allele frequencies for temperature-based population groups of *D. polymorpha*

Loci/alleles	Unheated N 3,470	Heated N 400
Got1		
1	0.613	0.323
2	0.121	0.151
3	0.078	0.117
4	0.099	0.209
5	0.089	0.200
Est1		
1	0.556	0.454
2	0.418	0.494
3	0.026	0.051
4	0.000	0.001
Pgi1		
1	0.354	0.368
2	0.456	0.511
3	0.155	0.116
4	0.035	0.005
Pgm1		
1	0.985	0.950
2	0.015	0.050
Me1		
1	0.598	0.564
2	0.192	0.140
3	0.005	0.004
4	0.005	0.011
5	0.105	0.130
6	0.064	0.061
7	0.030	0.090
8	0.001	0.000
Mdh1		
1	0.782	0.746
2	0.198	0.149
3	0.002	0.019
4	0.001	0.011
5	0.015	0.061
6	0.002	0.014
Idh1		
1	0.565	0.641
2	0.010	0.005
3	0.391	0.301
4	0.034	0.053

Table 7. Allele frequencies for salinity-based population groups of *D. polymorpha*

Loci/alleles	Fresh N 3,600	Brackish N 270
Got1		
1	0.569	0.780
2	0.128	0.068
3	0.085	0.039
4	0.115	0.043
5	0.103	0.070
Est1		
1	0.550	0.469
2	0.419	0.516
3	0.030	0.015
4	0.001	0.000
Pgi1		
1	0.357	0.335
2	0.458	0.514
3	0.156	0.081
4	0.029	0.070
Pgm1		
1	0.988	0.888
2	0.012	0.112
Me1		
1	0.583	0.718
2	0.189	0.152
3	0.005	0.006
4	0.005	0.017
5	0.112	0.050
6	0.065	0.050
7	0.039	0.007
8	0.001	0.000
Mdh1		
1	0.782	0.724
2	0.191	0.221
3	0.003	0.020
4	0.002	0.004
5	0.019	0.031
6	0.003	0.000
Idh1		
1	0.570	0.615
2	0.009	0.018
3	0.385	0.335
4	0.036	0.032

Table 6. Heterozygote excess values (D) for particular loci in six population groups of *D. polymorpha*

Group	N	***Got1***	***Est1***	***Pgi1***	***Me1***	***Mdh1***	***Idh1***
Unheated	3470	0.196	0.581	0.000	0.032	–0.011	0.078
Heated	400	0.220	0.680	0.030	0.098	0.058	0.020
Freshwater	3600	0.230	0.577	0.019	0.043	0.000	0.089
Brackish water	270	–0.255	0.835	–0.225	0.000	–0.040	–0.210
Mesotrophic	1670	0.256	0.561	0.013	0.009	0.004	0.103
Eutrophic	1570	0.168	0.576	–0.004	0.070	0.017	–0.065

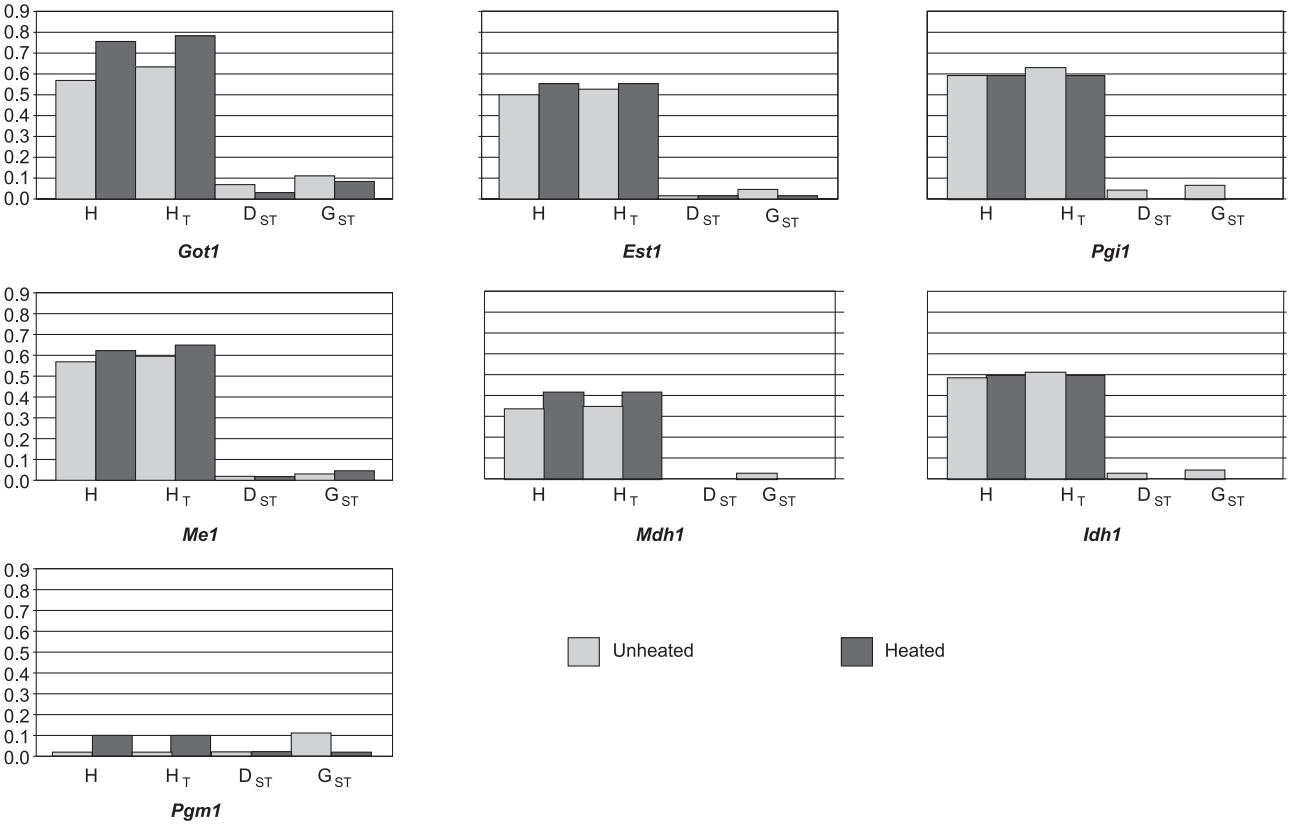

Fig. 3. Comparison of values of coefficients H, H_T, D_{ST} and G_{ST} for 7 loci between temperature-based population groups of *D. polymorpha*

In the studied population groups, the alleles of the highest frequency were the same, and their frequencies were very similar, except locus *Got1* (Fig. 2). In each group one rare allele was absent. The distribution of allele frequency in the two groups showed statistically significant differences in all the loci, the differences being the largest for loci *Got1* and *Mdh1* (Chi-square test, α=0.05).

There were also differences in the values of coefficients H, H_T, D_{ST} and G_{ST} (Fig. 3). The group Heated showed the highest values of H and H_T for 6 loci, in the group Unheated there were the highest values of D_{ST} and G_{ST} in all the loci. Also H_S values and mean H_T values were the highest in the group Heated, the mean values of D_{ST} and G_{ST} being the highest in the group Unheated (Fig. 4).

Values of heterozygote excess (D) in both groups were positive except locus *Mdh1* in the group Unheated (Table 6). D values in particular loci did not differ significantly between the groups (Student t-test).

GENETIC DIFFERENCES BETWEEN SALINITY-BASED POPULATION GROUPS OF *D. POLYMORPHA*

The analysed groups of populations from fresh and brackish waters showed a high genetic similarity of 0.9831 and a small genetic distance (0.0171). The lowest genetic similarity (0.9376) was that between the two Brackish water populations. The mean genetic similarity between the Freshwater group populations was higher (0.9557) and ranged from 0.8277 to 0.9988 (cf. Table 4).

Frequency of alleles varied considerably in the Fresh- and Brackish water groups (Table 7, Fig. 5). In locus *Est1* there were differences even in the most frequent allele: *Est1*-1 in the Freshwater group and *Est1*-2 in the Brackish water group. In the remaining loci

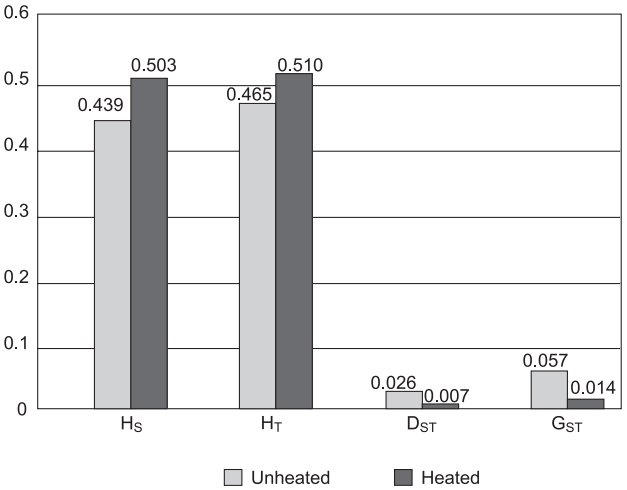

Fig. 4. Values of H_s coefficient and mean values of coefficients H_T, D_{ST} and G_{ST} for temperature-based population groups of *D. polymorpha*

alleles of the highest frequency were the same, but their frequencies differed. In the Freshwater group all the alleles found in the species were present, in the Brackish water group three rare alleles were absent, each in one of the loci *Est1*, *Me1* and *Mdh1* (Fig. 5, Table 7).

Allele distributions showed statistically significant differences between the groups in all the loci (Chi-square test, α=0.05).

H and H_T values were the highest in loci *Got1* and *Me1* in the Fresh water group, and in loci *Mdh1*, *Idh1* and *Pgm1* in the Brackish water group. D_{ST} and G_{ST}

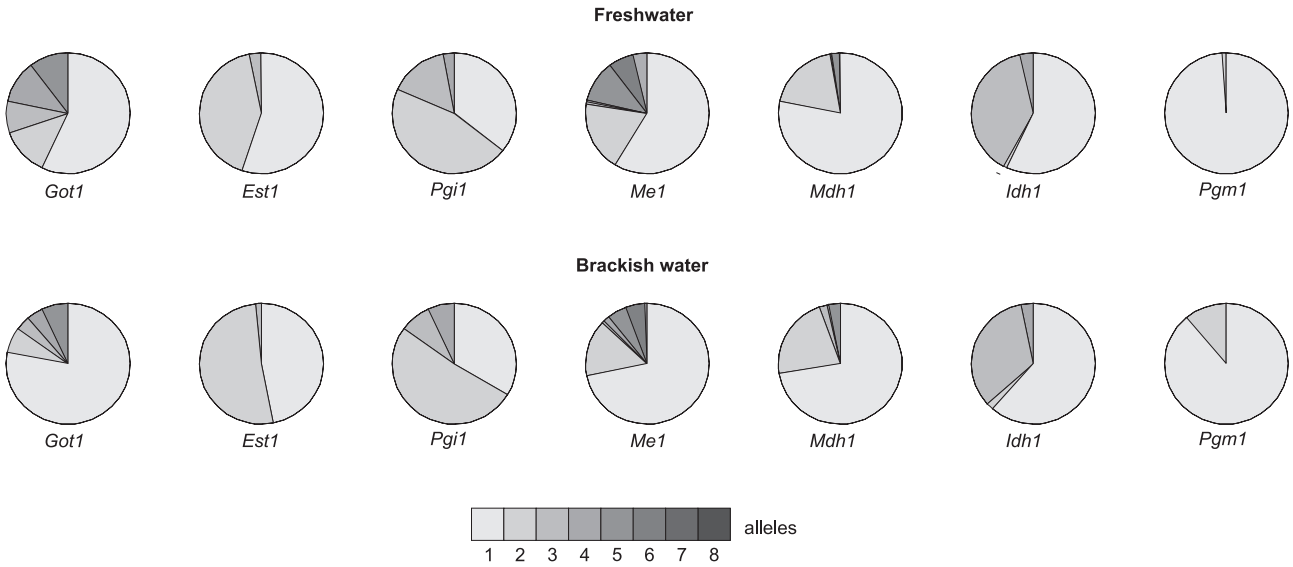

Fig. 5. Comparison of allele frequencies in 7 loci between salinity-based population groups of *D. polymorpha*

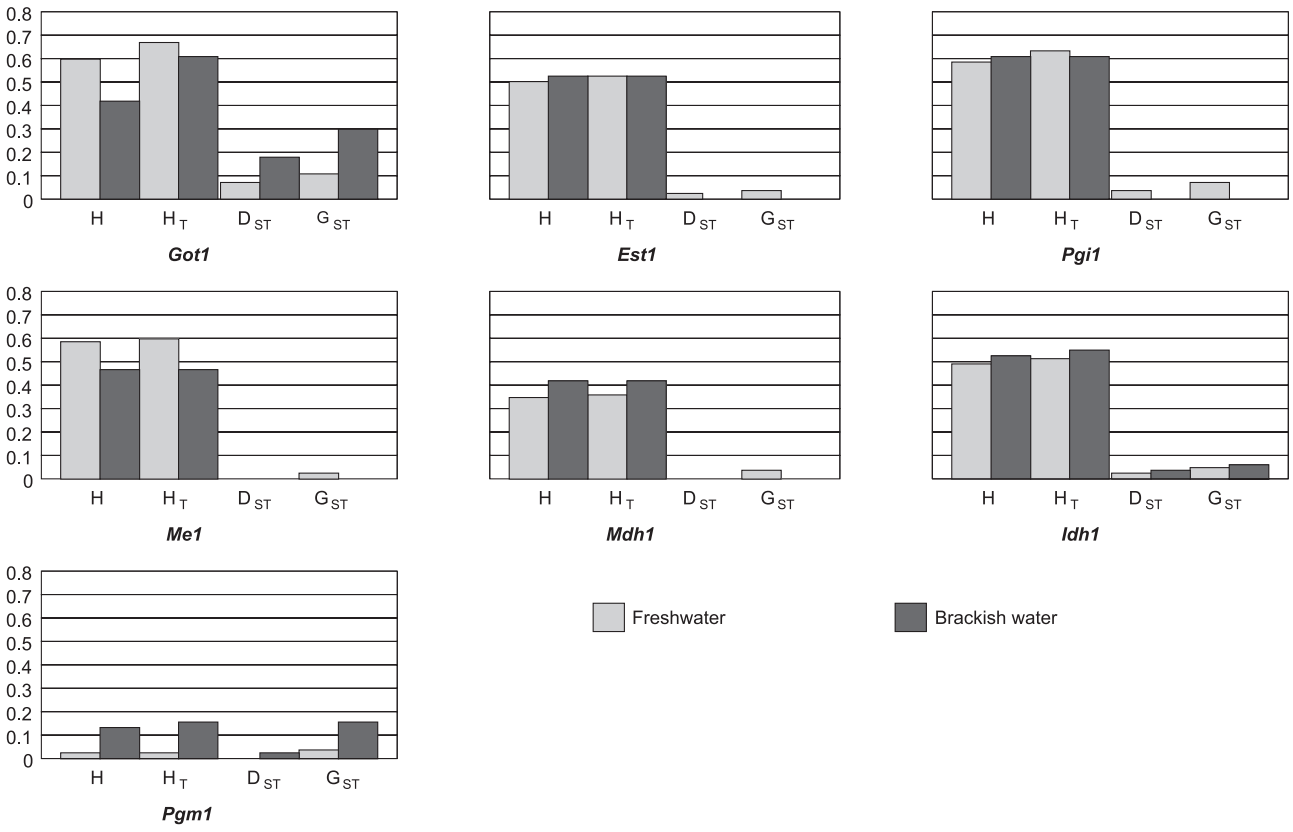

Fig. 6. Comparison of values of coefficients H, H_T, D_{ST} and G_{ST} for 7 loci between salinity-based population groups of *D. polymorpha*

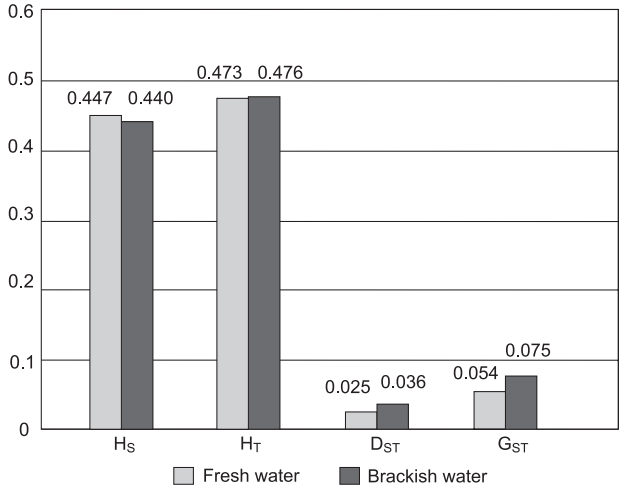

Fig. 7. Values of H_S coefficient and mean values of coefficients H_T, D_{ST} and G_{ST} for salinity-based population groups of *D. polymorpha*

coefficients in loci *Est1*, *Pgi1*, *Me1* and *Mdh1* had higher values in the Freshwater group, and in loci *Got1*, *Idh1* and *Pgm1* in the Brackish water group (Fig. 6). Mean values of coefficients H_T, D_{ST} and G_{ST} were higher in the Brackish water group, of H_S – in the Freshwater group (Fig. 7).

In the Brackish water group there was a deficit of heterozygotes in 4 loci (negative D values), contrary to the Freshwater group where there was an excess of heterozygotes in 5 loci (Table 6). Statistically significant differences in D values between the groups were observed for loci *Got1* and *Pgi1* (Student t-test, α=0.05).

GENETIC DIFFERENCES BETWEEN TROPHY-BASED POPULATION GROUPS OF *D. POLYMORPHA*

Population groups of *D. polymorpha* from meso- and eutrophic lakes showed a high genetic similarity (0.9946) and a genetic distance of 0.0054. Populations in the Eutrophic group were more similar to each other. In the Mesotrophic group the populations differed more with respect to their genetic similarity which ranged from 0.8464 to 0.9938. The mean genetic distance in this group was the highest and amounted to 0.0518 (cf. Table 4).

Table 8 lists frequencies of alleles for the analysed population groups. All the 33 alleles found in the species for 7 loci were present in the Eutrophic group, while in the Mesotrophic group two alleles were absent: *Est1*-4 and *Mdh1*-3, whose frequencies in the species were 0.001 and 0.004, respectively (Fig. 8). In the analysed population groups the alleles of the highest and similar frequency were the same. The differences involved rare and low-frequency alleles. The highest differences were observed for allele *Pgm1*-2 which in the species was present in 38% populations, with a mean frequency of 0.014. In the Mesotrophic group

Table 8. Allele frequencies for trophy-based population groups of *D. polymorpha*

Loci/alleles	Mesotrophic N 1,670	Eutrophic N 1,570
Got1		
1	0.638	0.522
2	0.095	0.163
3	0.081	0.097
4	0.105	0.104
5	0.081	0.114
Est1		
1	0.567	0.535
2	0.407	0.438
3	0.026	0.026
4	0.000	0.001
Pgi1		
1	0.336	0.374
2	0.445	0.484
3	0.180	0.117
4	0.039	0.025
Pgm1		
1	0.999	0.954
2	0.001	0.046
Me1		
1	0.607	0.589
2	0.209	0.152
3	0.008	0.004
4	0.005	0.009
5	0.097	0.107
6	0.055	0.072
7	0.018	0.065
8	0.001	0.002
Mdh1		
1	0.768	0.801
2	0.216	0.160
3	0.000	0.008
4	0.001	0.004
5	0.013	0.022
6	0.002	0.005
Idh1		
1	0.574	0.577
2	0.003	0.020
3	0.381	0.381
4	0.042	0.022

its frequency was 0.001 and it was present in 4 populations (29%) of the group, while in the Eutrophic group its frequency was 0.046 and it was found in 8 populations (67%, Table 8). The distributions of allele frequency in the groups showed statistically significant differences in all the loci except *Est1* (Chi-square test, α=0.05).

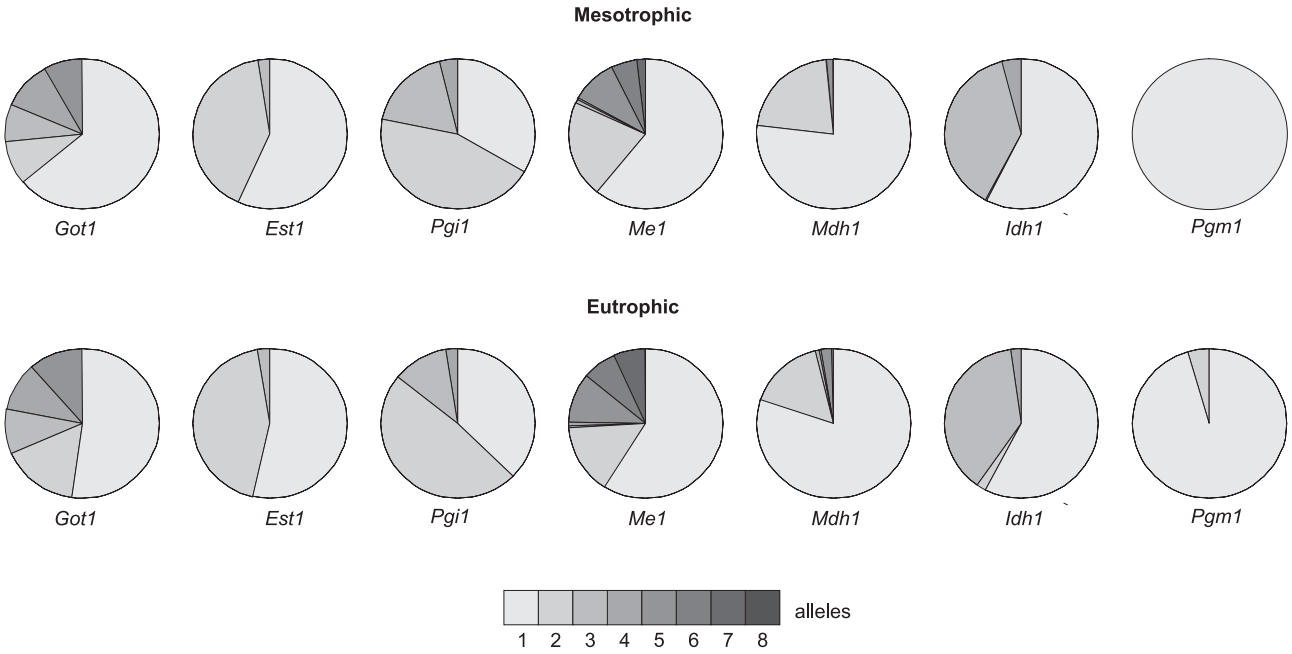

Fig. 8. Comparison of allele frequencies in 7 loci between trophy-based population groups of *D. polymorpha*

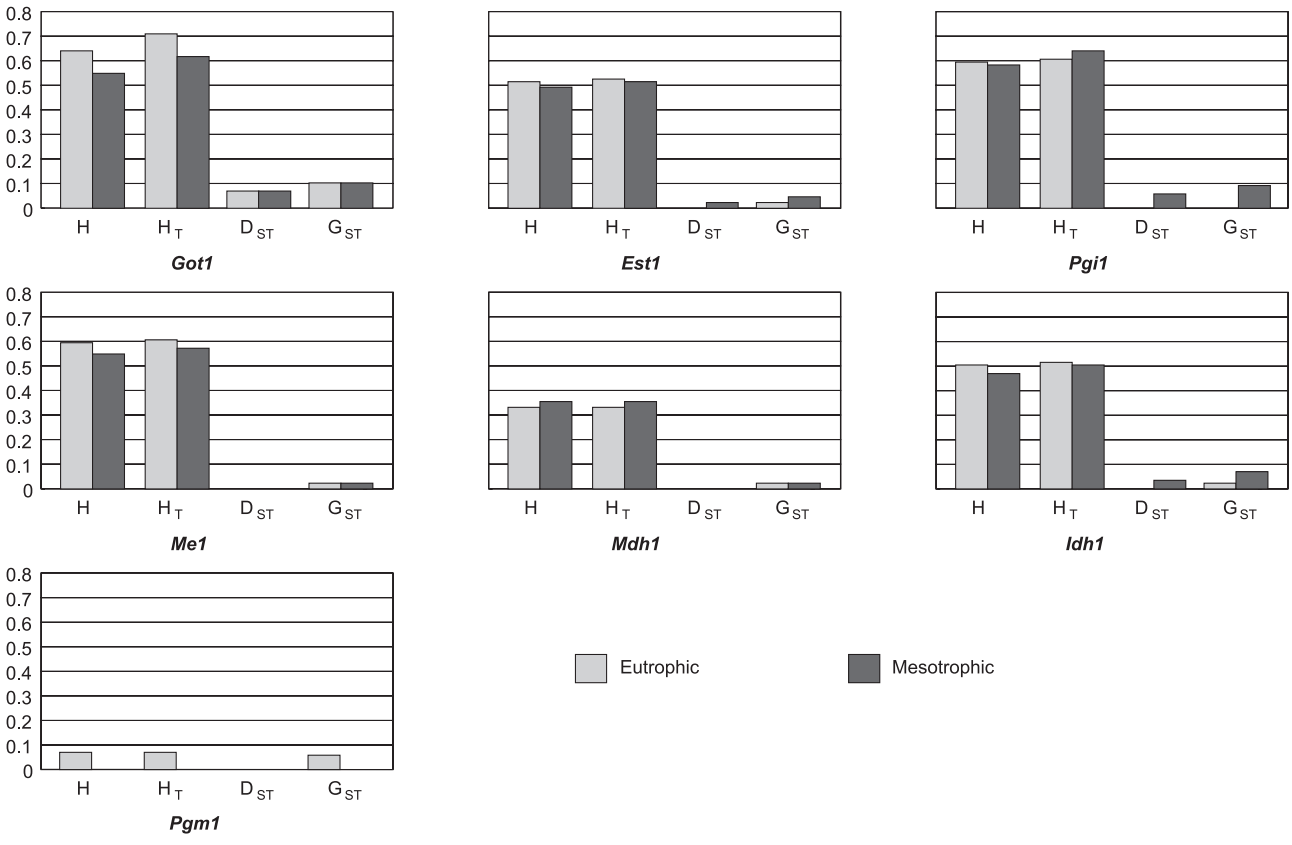

Fig. 9. Comparison of values of coefficients H, H_T, D_{ST} and G_{ST} for 7 loci between trophy-based population groups of *D. polymorpha*

The highest H and H_T values were noted in the Eutrophic group, for 6 and 5 loci, respectively, while genetic diversity as expressed by values of D_{ST} and G_{ST} was the lowest in this group (Fig. 9). In the Eutrophic group there were also the highest H_S and mean H_T values, and the lowest mean D_{ST} and G_{ST} values, compared to the Mesotrophic group and to the whole species (Fig. 10).

In the Eutrophic group a deficit of heterozygotes was observed in loci *Pgi1* and *Idh1*, while in the Mesotrophic group there was an excess of heterozygotes in all the loci (Table 6). No statistically significant differences between the groups in D values were observed in the studied loci (Student t-test).

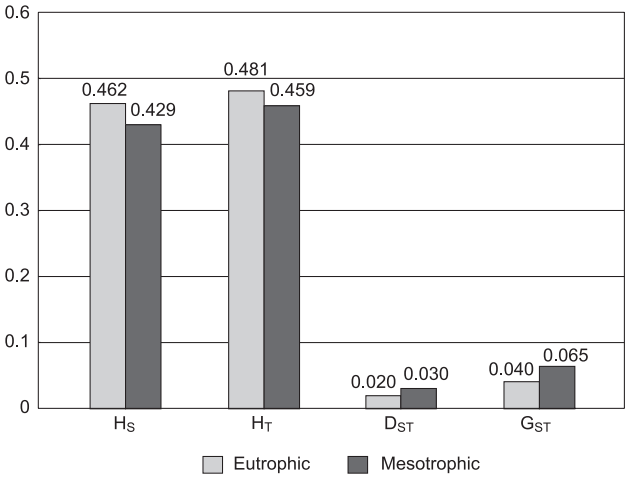

Fig. 10. Comparison of H_S coefficient and mean values of coefficients H_T, D_{ST} and G_{ST} for trophy-based population groups of *D. polymorpha*

DISCUSSION

Marine bivalves are subject to intense studies on the effect of stress factors on the development of life cycle stages, mortality and condition of adult individuals, and their effect on on the genetic structure (CHRISTIANSEN & CASTLOW 1975, MALLET et al. 1987, MORGAN 1987, BLOT & THIRIOT-QUIEVREUX 1989, LAM & CALOW 1990, SCOTT & KOEHN 1990, TEDENGREN et al. 1990, KILGOUR et al. 1994). In this study an attempt was made at determining the effect of stress factors, such as increased temperature, salinity and increased trophy level on the variation and genetic structure of *D. polymorpha*.

Populations of *D. polymorpha* from the Konin lakes, of an increased temperature (summer stagnation temperature ca. 30°C) showed a higher variation as expressed by the mean expected heterozygosity per locus, compared to the populations from unheated water bodies (summer stagnation temperature ca. 20°C, Fig. 4). Nonetheless, the genetic similarity between these populations was very high (I=0.979).

D. polymorpha from the Konin lakes, compared to the Mazurian lakes, shows a decidedly slower growth, shorter life span, longer period of planktonic occurrence of larvae and their higher mortality (STAŃCZYKOWSKA 1976, KORNOBIS 1977, LEWANDOWSKI & EJSMONT-KARABIN 1983, STAŃCZYKOWSKA et al. 1988). A comparison of size and shell and body weight of bivalves from lakes of various degree of heating revealed that the mussels from stronger heated lakes grew faster which was reflected in the body mass rather than the shell size (STAŃCZYKOWSKA 1976). The above data and genetic studies indicate that under thermal stress conditions individuals of *D. polymorpha* of higher genetic variation survive and adapt.

Genetic studies on populations of *D. polymorpha* from lakes of different trophy level are very important because of the rather quick decline of the number of mesotrophic lakes in Poland, as a result of progressing eutrophication. In polluted lakes of high trophy a gradual decrease in abundance and biomass of the zebra mussel is observed (STAŃCZYKOWSKA et al. 1983, PIESIK et al. 1998).

Genetic studies on *D. polymorpha* from lakes of different trophy showed that a higher genetic variation was characteristic of populations from eutrophic water bodies (Fig. 10). The genetic similarity between both groups of zebra mussel populations was high (0.995). Unfavourable habitat conditions in lakes, including their gradual eutrophication, increased phosphorus content and pH, have a limiting effect on the size of zebra mussel populations but do not change the degree of their polymorphism. Similar results were obtained for *Macoma baltica* in regions of increased pollution (WENNE 1993).

Salinity is a very important factor for freshwater organisms. Studies of KILGOUR et al. (1994) demonstrated that *D. polymorpha* adapted very well to slowly changing salinity, especially at low temperatures (3–12°C). The results of the present study on the populations of the zebra mussel from brackish reservoirs (2–3‰) showed that, with respect to genetic variation, they were similar to other populations of the species, inhabiting freshwaters. The genetic similarity between populations of the zebra mussel from these two habitats was also high (I=0.983). In populations from brackish water bodies, however, a deficit of heterozygotes was observed in four loci, and it was statistically significant for two loci (*Got1* and *Pgi1*). On

the contrary, in freshwaters, there was an excess of heterozygotes in 5 loci (Table 6). A deficit of heterozygotes was observed also in some marine molluscs (SINGH & GREEN 1984, ZOUROS & FOLTZ 1984).

Stress environment factors, such as increased water temperature, a slight increase in salinity or increasing trophy level do not limit gene flow between populations of the zebra mussel and most probably will not contribute in the nearest future to the origin of physiological races or subspecies. Populations of *D. polymorpha* show a high genetic homeostasis which, combined with the high polymorphism, provides a basis for wide adaptive possibilities of the species and increases its invasive abilities.

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