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GENETIC ANALYSIS OF ENZYME POLYMORPHISMS IN CARP OF ROPSHA BREED

Electrophoretic methods of the investigation of genetic polymorphism in population genetics are widely used nowadays. With their aid it has been proved that the high level of genetic variability of proteins is characteristic of natural populations.

The number of publications dedicated to the problems of biochemical polymorphism in animal populations (including fish populations) increases continuously, and the number of analyzed animal species and protein systems available for electrophoretic analysis is simultaneously increasing. Biochemical markers are often used to distinguish and identify the populations or subpopulations, to investigate the process of microevolution, to find out the genealogy and degree of relationship of species or animal breed groups. There are many articles on their employment in animal breeding as well as in the investigation of the production biology.

But the genetic foundations of variability detected by means of gel electrophoresis are often unknown since their genetic interpretation is based only on the compliance between the observed frequencies of phenotypes and those expected according to the Hardy-Weinberg law or on the homology with similar systems in animals investigated in greater detail.

Carp *Cyprinus carpio* L. is the most important fish cultivated in ponds in the Soviet Union. It is a comfortable object for genetic analysis of protein polymorphism as there are many polymorphic protein systems in the carp and the individual crosses can be made easily. This study is of some practical importance as biochemical markers are frequently used in carp breeding.

The main purpose of our study was to find out the genetic bases of phosphoglucomutase, slow muscle esterase and liver lactate dehydrogenase polymorphism. Simultaneously there was an opportunity to get some additional information on the genetics of fast muscle esterase and polymorphic myogen as well as to test the linkage of all these loci. By means of detected polymorphic genes we also tried to characterize the gene pool of Ropsha breed carp which is the most prospective one in the northern regions of the Soviet Union.

Material and methods

The offspring from individual crosses of one female Ropsha carp (line *M*) with eight different males (I—IV of line *B*, V—VIII of line *M*), was analyzed. From every cross progeny about 50 fishes of the age of 0+ were taken for investigation. To characterize the gene pool of Ropsha carp,

Segregation of myogen, esterase, phosphoglucomutase and lactate dehydrogenase

Cross	*My*			*Est*$_1$				*Est*$_2$					
	A	*a*	χ^2	1-1	1-2	2-2	χ^2	1-1	1-2	2-2	2-3	3-3	1-3
I	48 (48)			48				15		13		7	12
II	38 (39)	14 (13)	0.10	52				5	15	12		8	9
III	46 (46)	1		46				12 (11.25)	9 (11.25)	24 (22.5)			
IV	36 (33)	8 (11)	1.09	44				14 (10.5)	9 (10.5)	19 (21)			
V	35 (34.5)	11 (22.5)	0.03	29 (23.5)	18 (23.5)		2.57	24 (23)		22 (23)			
VI	53 (50.75)	14 (16.75)	0.55	67				18 (16.25)	17 (16.25)	30 (32.5)			
VII	18 (23.5)	29 (23.5)	2.57	31 (23.5)	16 (23.5)		4.79*	19 (24)		29 (24)			
VIII	21 (20.5)	20 (20.5)	0.02	41				16 (20.5)		25 (20.5)			
Group 10 ♀ × 10 ♂	39	57		60 (63.0)	36 (29.5)	(3.5)	5.07*	33 (32.7)	17 (23.0)	8 (4.0)	6 (7.9)	2 (3.8)	28 (22.4)

* Deviation is statistically significant ($P<0,05$).
** Deviation is statistically significant ($P<0,01$).

96 specimens from a mixed group mating of 10 females with 10 males (all from line *BM*) were also analyzed.

All these crosses were made at the Central Experimental Station «Ropsha» in the spring of 1977 by M. A. Andriasheva-Nikitina. The genotypes of parent fishes were not determined.

Samples of tissues (white skeletal muscles and liver) were taken from every specimen and storaged at −20 °C until required. Tissue samples were homogenized in equal volume of 0.5 M *tris*-HCl buffer to which some drops of phenoxyethanol were added. Homogenate was centrifuged at 19 000 g for 30 minutes. Supernatants were subjected to electrophoresis in 7 (myogens, esterases) or 5% (PGM, LDH) vertical polyacrylamide gel slabs according to Davis (1964) in the apparatus of K. A. Truveller and M. N. Nefyodov (Трувеллер, Нефедов, 1974). Gels were run for about 2 hours (3 hours for LDH) at 180 mA. Myogens were stained with amidoblack, the enzymes by usual techniques (Shaw, Prasad, 1970). For the detection of esterases in some cases, instead of α-naphthylacetate, 4-methylumbelliferylacetate was used to determine esterase *D* zones specific of this substrate.

Results

Myogens. In most progenies of the individual crosses two types of patterns described by K. A. Truveller and collaborators (Трувеллер et al., 1973) were found (Fig. 1). One of them, designed *A*, presents a strong

Table 1

phenotypes in individual and group matings (in parentheses expected numbers)

			Pgm				*Ldh-C*$_1$				*Ldh-C*$_2$			
	0	χ^2	1-1	1-2	2-2	χ^2	2-2	1-2	1-1	χ^2	1-1	1-2	2-2	χ^2
			10 (11.25)	23 (22.5)	12 (11.25)	0.20	25 (23.25)	22 (23.25)		0.11			47	
			23 (25)	27 (25)		0.32	50						50	
		0.60	12 (11)	21 (22)	11 (11)	0.14	44	1					45	
		1.57	21 (19.5)	18 (19.5)		0.13	26 (21.5)	17 (21.5)		1.88			43	
		0.09	13 (12.25)	23 (24.5)	13 (12.25)	0.18	46						46	
		0.42	1	28 (32)	36 (32)	1.00	63						63	
		2.08	19 (11.75)	21 (23.5)	7 (11.75)	6.66*	48						48	
		1.96	9 (10.25)	18 (20.5)	14 (10.25)	1.83	40						40	
	2	8.28*	27 (20.3)	35 (47.7)	34 (28.0)	6.88**	55 (54.3)	29 (30.4)	5 (4.3)	0,20	6 (0.02)	4 (3.8)	85 (85.2)	0,82

band absent in the other type *a*. It is known that this protein is coded by one locus *My*, and type *a* is a homozygote of a recessive null allele. Segregation in our experiment (Table 1) was in good conformity with the expected Mendelian ratios — II, IV, V, VI — 3 : 1; VII, VIII — 1 : 1.

In the group cross of 10 females with 10 males a high frequency of type *a* occurred, indicating the high concentration (0.77) of the recessive allele in the gene pool of the Ropsha carp.

Fast muscle esterase. In the extract of white skeletal muscles of the carp, two polymorphic zones of esterases occur (Московкин et al., 1973). Both of them could be revealed with 4-methylumbelliferylacetate while no specific zone of esterase *D* was detected by us in carp muscles.

The fast esterase *Est*$_1$ seems to be identical with the polymorphic serum esterase. The monogenic determination of this esterase and the epigenetic nature of the additional fast band in this zone has been proved in numerous experiments (Московкин et al., 1973; Щербенок, 1973, 1976; Трувеллер et al., 1974; Черфас, Трувеллер, 1978).

In crosses I—IV (males of line *B*), V and VIII only fast allele homozygotes were found. In crosses V and VII, heterozygotes were present but their frequency was lower than expected (see Table 1). The difference was statistically significant in the latter case.

In the group mating no slow allele homozygote was found while the distribution of phenotypes occurred to be nonequilibrial by Hardy-Weinberg.

Slow muscle esterase. There was a remarkable variability in the slow

esterase zone (see Fig. 1). At all three variants with different mobilities forming six phenotypes were found. Segregation in crosses V, VI, VII can be interpreted only if we assume that males were null allele homozygotes and the allele occurs to be the fourth one in this locus. In crosses III, IV and VI the males had to be null allele heterozygotes, while in matings I and II the third allele, the slowest one, was present. The segregation in these two crosses could not be interpreted genetically as any hypothesis was in conflict with the explanation suggested by the analysis of the other six crosses. So we cannot consider this polymorphism conclusively interpreted.

In the group cross, besides the six expected phenotypes, null allele homozygotes were also found. There were differences in the staining intensity of single bands but they were not distinct enough to distinguish the null allele heterozygotes. As the null allele heterozygotes were counted together with the normal homozygotes, the distribution of phenotypes deviated from the expected one. The deviation was statistically significant.

Phosphoglucomutase. When the carp PGM was electrophoresed in 5% gel, a typical pattern for this enzyme was found (Fig. 2). There were two codominant alleles, presented by single bands in homozygotes. Both of them occurred in heterozygotes. But when we used 7% gel, the homozygotes presented double bands and the heterozygotes a triple one (see Fig. 2). Segregation in individual crosses was in good accordance with the diallelic hypothesis. Only in cross VII significant deviation from the expected Mendelian ratio was found.

In the group mating progeny no more variants of PGM were found but the distribution of phenotypes was nonequilibrial — there was a significant deficiency of heterozygotes.

Lactate dehydrogenase. The liver LDH of the carp gives a complicated pattern (Fig. 2) as our samples were not purified from blood traces, and, beside combinations of liver specific *C* subunits the other isoenzymes, products of genes *A* and *B* were also detected.

We found the most frequent pattern, also described by other authors (Shaklee et al., 1973; Иванова et al., 1973) in the offspring of all individual crosses. This pattern probably corresponds to homozygote of the most widely spread alleles in both liver specific *C* loci of LDH. In crosses I and III patterns of another type were found. Those seem to be heterozygotes of a slow allele in *Ldh-C*$_1$ locus. Segregation of these phenotypes corresponds to the ratio expected if one of the parents was heterozygote, the other homozygote in one locus.

There were more phenotypes in group cross offspring. One of them could be interpreted as a fast variant of *Ldh-C*$_1$ gene (Fig. 2), and another one as double heterozygote, but some patterns could not be explained on the present level of knowledge. More data and better resolutions are needed to interpret them.

Linkage analysis

As the genotypes of parent fishes were not known and the number of fish was rather small, the results of the analysis of gene linkage cannot be very authentic. In many crosses the combination of genotypes of parents did not enable us to test the gene linkage at all, as in the case when the whole progeny consisted of homozygotes. But in some cases there was more than one repeat of test possibility, and as the information on the carp gene linkage in literature is scanty, the results of our experiments are given here.

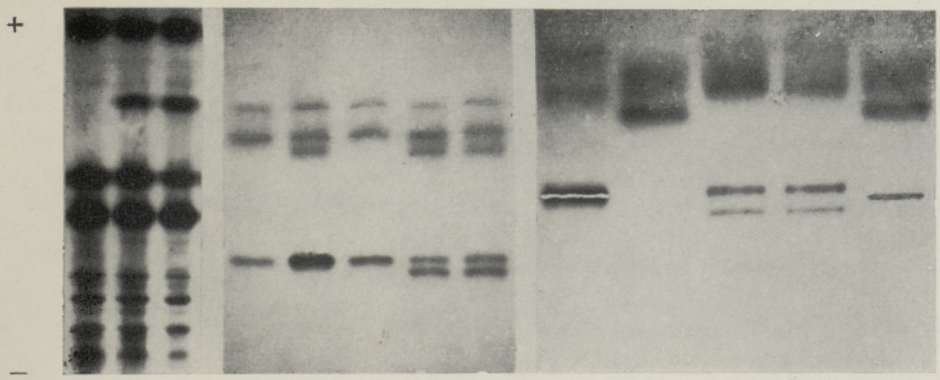

Fig. 1. Polymorphism of carp myogens and esterases: I — myogens, II — fast esterase, III — slow esterase.

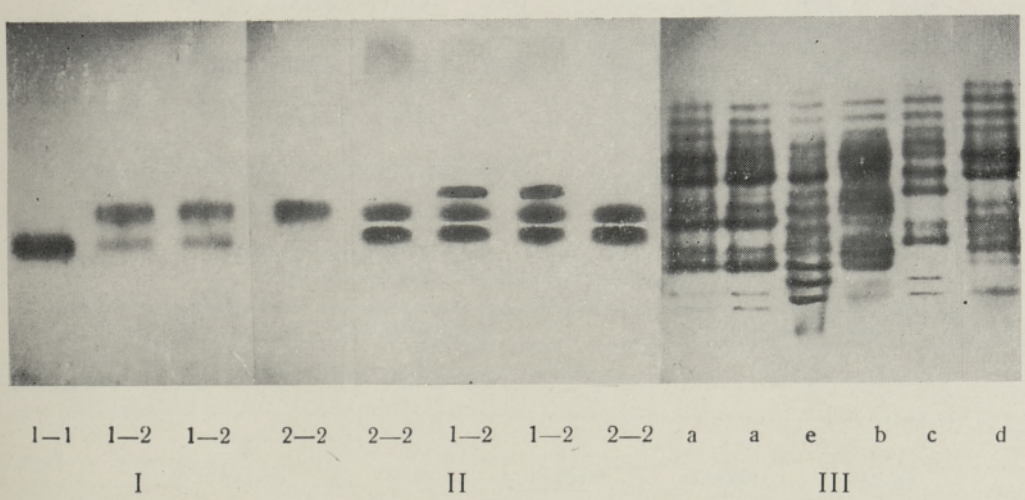

Fig. 2. Polymorphism of carp PGM and LDH: I — PGM, electrophoresis in 5% gel; II — PGM, electrophoresis in 7% gel; III — LDH (*a* — normal pattern, *b* — double heterozygote, *c* — *Ldh-C*$_1$ fast variant homozygote, *d* — unexplained, *e* — *Ldh-C*$_1$ heterozygote).

Table 2

Linkage analysis of genes *My* and *Pgm* (in parentheses expected numbers)

Pgm phenotypes	*My* phenotypes											
	II		IV		V		VI		VII		VIII	
	A	*a*	*A*	*a*	*A*	*a*	*A*	*a*	*A*	*a*	*A*	*a*
1—1	17 (18.375)	5 (6.125)	18 (14.675)	3 (4.875)	7 (8.25)	4 (2.75)	—	—	8 (5.625)	10 (5.625)	6 (5.125)	3 (5.125)
1—2	19 (18.375)	8 (6.125)	15 (14.675)	3 (4.875)	17 (16.5)	5 (5.5)	21 (22.5)	7 (22.5)	6 (11.25)	14 (11.25)	10 (10.25)	8 (10.25)
2—2	—	—	—	—	9 (8.25)	2 (2.75)	26 (22.5)	6 (7.5)	4 (5.625)	4 (5.625)	5 (5.125)	9 (5.125)
χ^2		0.90		2.23		1.09		0.98		9.22		4,46

Table 3

Linkage analysis of genes Est_1, *Pgm* and *My* (in parentheses the expected numbers)

Est_1 phenotypes	*Pgm* phenotypes						*My* phenotypes	
	V			VII			V	
	1—1	1—2	2—2	1—1	1—2	2—2	*A*	*a*
1—1 (*FF*)	7 (5.375)	13 (10.75)	7 (5.375)	11 (5.5)	12 (11.0)	6 (5.5)	23 (16.5)	5 (5.5)
1—2 (*FS*)	3 (5.375)	9 (10.75)	4 (5.375)	7 (5.5)	7 (11.0)	1 (5.5)	10 (16.5)	6 (5,5)
χ^2			3.14			11.2*		5.21

* Deviation is statistically significant ($P<0,05$)

Table 4

Linkage analysis of genes $Ldh\text{-}C_1$, *Pgm* and *My* (in parentheses the expected numbers)

$Ldh\text{-}C_1$ phenotypes	*Pgm* phenotypes			*My* phenotypes	
	I			IV	
	1—1	1—2	2—2	*A*	*a*
1—2	6 (5.25)	9 (10.5)	4 (5.25)	15 (14.625)	2 (4.875)
2—2	4 (5.25)	13 (10.5)	6 (5.25)	19 (14.625)	6 (4.875)
χ^2			1.62		3.37

The linkage of gene *My* with gene *Pgm* could be tested in matings III—VIII, with gene Est_1 in cross V, with gene $Ldh\text{-}C_1$ in cross VIII (Tables 2 to 4). It is evident that genes *My* and *Pgm* occur to be unlinked as in most cases the phenotype distribution corresponds to the expected ratio with a high level of probability. In mating VII the deviation is significant. It can be interpreted as a result of the non-Mendelian

segregation of PGM phenotypes. The deviation from the expected ratio was even greater if the linkage could be supposed. The *Ldh-C*$_1$ gene seems also not to be linked with *My* gene. The genes *My* and *Est*$_1$ can be linked as the distribution of phenotypes differs from the expected one in the case of a total unlinkage more than in the case of linkage with a circa 20% recombination.

The linkage of genes *Est*$_1$ and *Pgm* was analyzed in crosses V and VII. As the esterase phenotypes did not give Mendelian ratios, the linkage test showed a rather high deviation from the expected distribution and we could not make reliable conclusions on the basis of these data. The ratio of phenotypes of *Pgm* and *Ldh-C*$_1$ in cross I reveals that these genes are not linked. As the mode of inheritance of slow esterase *Est*$_2$ is not clear, we could not yet test the linkage of this gene with others.

Discussion

Our results are in good accordance with literature data about the inheritance of carp myogens and fast muscle esterase. Polymorphic myogen systems, similar to those found in the carp, are described in other cyprinids — vimba *Vimba vimba* (L.) (Паюсова, Корешкова, 1973) and Japanese crucian carps (Taniguchi, Sakata, 1977). As the fast esterase is identical with serum esterase, its mode of inheritance is known and there are many publications on the employment of the variants of this gene for the identification and characterization of carp breeds (Московкин et al., 1973; Чугаева et al., 1973; Щербенок, 1973; Starmach, 1977).

Connections of this esterase locus with productivity qualities, such as growth rate or disease resistance of the carp, have also been investigated (Щербенок, 1973; Илясов et al., 1977; Илясов, Шарт, 1978). The deficiency of heterozygotes in crosses V and VII and the lack of 2—2 homozygotes in group mating offspring remains unexplained and needs special investigation. There are not many data on selection against slow allele of this esterase in literature, but in some cases the deficiency of slow allele homozygotes has been described in the Ropsha carp (Щербенок, 1973, 1976).

The mode of inheritance of slow muscle esterase also needs further investigation. Our results enable to assume that it is coded by one locus where at least four alleles occur, one of them being the null allele. The patterns of this esterase have been described in literature (Московкин, 1973; Черфас, Трувеллер, 1978) while the Amur river wild carp revealed a high level of variability in this zone. The assumption that males V, VII, and VIII were null allele homozygotes is probable, as some carp breeds have a high concentration of the null allele (Московкин et al., 1973; Паавер, 1978) and the line *M* of the Ropsha carp has a remarkable content of European cultured carp heredity. In the line *BM* the concentration of the null allele proves to be low indeed.

Genetic interpretation of PGM variation is not difficult as it represents a trivial diallelic codominant system in one locus.

Double bands of homozygotes in the case of electrophoresis in 7% gel can be explained by differences in molecule conformation of reduced and oxidized forms of enzyme, as in *Lepomis cyanellus* (Champion, Whitt, 1976).

The liver specific LDH gene *C* characteristic of cyprinids is duplicated in the carp (Shaklee et al., 1973; Valenta et al., 1976). We could not analyze the inheritance of all detected variants of LDH as most of the

progenies of individual crosses happened to be monomorphic (homozygotes). Segregation in matings I an III shows that *Ldh-C*$_1$ gene alleles are inherited codominantly.

In some crosses single fish presented phenotypes which were not possible theoretically. As the contamination of sample group could not be excluded, these fish were not accounted for. The contamination can also explain the curious phenotype distribution of *Est*$_2$ in cross II but then the question arises why other genes in this cross give normal segregation. In cross VII some factor has affected the gene recombination or survival of different genotypes. Mendelian segregation has been disturbed in every locus while in genes *Pgm* and *Est*$_1$ the deviation is statistically significant.

Up to now there are only some data about the carp gene linkage in literature. A linkage of genes *My* and *Est*$_1$ is supposed (Московкин et al., 1973), and the *My* and *Est*$_2$ genes are shown not to be linked either with each other or with scale cover or transferrin genes (Трувеллер et al., 1974). Our results reveal that the genes *My* and *Pgm* are not linked. There is some evidence that the genes *Ldh-C*$_1$, *Est*$_1$ and *Pgm* as genes *My* and *Ldh-C*$_1$ are not linked either. But our results are not in conflict with the hypothesis of the linkage of genes *My* and *Est*$_1$ with frequency of recombination a circa 20 to 30%. There is nothing surprising in the fact that no linkage of studied loci has been found as the number of chromosomes of the carp is high (n=50).

Our results reveal that, unlike the Estonian aborigene (Antsla) carp, a high level of genetic variability of proteins is characteristic of the Ropsha carp. In the group mating all the investigated proteins were polymorphic. The significant deviations from Hardy-Weinberg equilibrium can be explained by the fact that the 10×10 cross does not correspond to the model of the panmictic population.

The Ropsha carp is characterized by a high concentration of the null allele of myogens and fast allele of *Est*$_1$, as well as by a remarkable variation of *Est*$_2$ and LDH. The gene pool of the Estonian carp lacks the null allele of myogens while it contains a low concentration of *Est*$_1$ fast allele and a high concentration of *Est*$_2$ null allele. The liver LDH of the Antsla carp is monomorphic (Паавер, 1978).

We can suppose that a higher level of variability of the Ropsha carp arises from its hybrid origin. The alleles of polymorphic genes characteristic of the Ropsha carp and absent in the Antsla carp, originate from the Amur wild carp, one of the ancestors of the Ropsha carp. But the possibility that the gene pool of the Estonian carp is pauperized due to inbreeding and genetic drift cannot be excluded, as the stock of the Antsla carp originates from a scanty number of fish.

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ROPŠA KARPKALA ENSÜÜMIDE POLÜMORFISMI GENEETILINE ANALÜÜS

Artiklis on käsitletud ropša tõugu karpkala polümorfsete valgutüüpide pärandumist järglaskonnale (8 individuaalristamist ning 10 emas- ja 10 isaskala segaristamine). Tulemused on kooskõlas kirjanduse andmetega polümorfse lihasvalgu ja kiire lihasesteraasi pärandumisest. Kiire lihasesteraasi osas täheldati aeglast varianti määravat alleeli sisaldavate genotüüpide oodatust väiksemat sagedust. Aeglase lihasesteraasi määrab geneetiliselt üks geen, millel esineb neli alleeli (neist üks null-alleel), fosfoglükomutaasi aga

üks geen, millel on kaks alleeli. Laktaadi dehüdrogenaasi elektroforeetilise spektri varieeruvus nõuab veel uurimist, kuid võib arvata, et maksaspetsiifilistel geenidel C_1 ja C_2 on kummalgi vähemalt kaks alleeli. Aheldatuiks võib uuritud geenidest pidada üksnes lihasvalgu ja kiire esteraasi lookusi, kuid ka see oletus vajab kontrollimist. Erinevalt Eestis kasvatatavast antsla karpkalast on ropša karpkala valgud geneetiliselt väga muutlikud, mis tuleneb selle tõu hübriidsest päritolust.

Тийт ПААВЕР

ГЕНЕТИЧЕСКИЙ АНАЛИЗ ПОЛИМОРФИЗМА ФЕРМЕНТОВ РОПШИНСКОГО КАРПА

Исследовалось наследование полиморфных миогенов, мышечных эстераз, фосфоглюкомутазы и печеночной лактатдегидрогеназы (ЛДГ) в восьми индивидуальных и одном групповом (10♀×10♂) скрещиваниях ропшинского карпа. Результаты подтверждают имеющиеся в литературе данные о наследовании миогенов и быстрой эстеразы. В отношении быстрой эстеразы наблюдался и некоторый дефицит медленного аллеля в потомстве как индивидуальных, так и группового скрещиваний. Медленная эстераза кодируется одним геном, имеющим четыре аллеля (один из них нулевой), фосфоглюкомутаза — одним геном, имеющим два аллеля. Генетические основы изменчивости печеночной ЛДГ требуют уточнения. В обоих печеноспецифичных локусах *C* наблюдаются по крайней мере два аллеля. Из исследованных генов сцепленными могут быть только *My* и Est_1. Для ропшинского карпа в отличие от эстонского беспородного (антслаского) характерен высокий уровень генетической изменчивости белков, связанный, очевидно, с его гибридным происхождением.