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Articles

Genetic variability and phenotypic diversity in populations of the Eurasian perch, Perca fluviatilis (Actinopterygii, Percidae)

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The Eurasian perch *Perca fluviatilis* (Linnaeus, 1758) is a common species of fish in northern ecosystems. The species demonstrates high phenotypic diversity when it inhabits various types of water bodies. Here, we investigate whether there is a relationship between the genetic variability and phenotypic diversity in natural perch populations. *Perca fluviatilis* samples (n = 218) were collected from seven localities in the Ob-Irtysh river basin in western Siberia, Russia. We used color morphs and standard morphometric approach to study phenotypic diversity, allozyme and ISSR-PCR markers to study the genetic variability of the perch. In total, 19 types of perch colouration were found. The number of color morphs varied from 4 to 16 in different reservoirs. The sets of colour morphs and prevailing coloration types, as well as some morphometric characteristics, were significantly different in all studied populations. Low allozyme variability was identified in the perch. The average observed and expected allozyme heterozygosity was 0.003 and 0.056, respectively; 13% of the loci were polymorphic. The genetic diversity (h) of the markers (ISSR) was 0.31; from 53% to 96% of the bands were polymorphic. Genetic differentiation in the perch was high, especially in allozyme loci. The FST and GST values were 0.39 and 0.085 for allozyme and ISSR markers, respectively. The genetic variability indices of the perch did not correlate with phenotypic diversity. Our results suggest that the use of different phenotypic or genetic markers can provide extremely different information on the level of variability in the population.

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Keywords

Allozymes, color morph, genetic differentiation, ISSR, *Perca fluviatilis*, polymorphism, Ob-Irtysh basin

Introduction

The Eurasian perch *Perca fluviatilis* (Linnaeus, 1758) is a common species of percid fish that plays an important role in the food chains as a predator and a forage fish. It is the object of commercial and recreational fishing in Europe and Asia. Due to high tolerance, perch can live in water bodies under significant anthropogenic pressure (Ericson et al. 1999; Lucentini et al. 2002; Georgieva et al. 2015). Perch can be an alternative source of food due to the lower number of other, more valuable fish species. Furthermore, it has recently started to be widely used for aquaculture. As a result of acclimatization, the perch has acquired the status of an invasive species in some areas (Closs et al. 2001). After introduction, perch can reach high abundance and have a significant impact on native fish species due to predation (Akin et al. 2011).

Many researchers have studied the environmental and genetic characteristics of the Eurasian perch (Nesbo et al. 1999; Yang et al. 2009; Ben Khadher et al. 2016). The species demonstrates a high ecological plasticity, thus it can inhabit various types of water bodies. There are stationary and anadromous forms of this species that are genetically differentiated (Nesbo et al. 1998b). The perch has an intraspecies structure and can form genetically and ecologically differentiated subpopulations in the same reservoir (Gerlach et al. 2001; Behrmann-Godel et al. 2004).

The study of the genetic diversity of perch is important to assess the adaptive potential of its populations. The greater allelic diversity and the number of gene combinations can be considered as the basis for environmental plasticity. Usually, researchers use the genetic and morphological approach separately and obtain data on some components of variability. As a result, the authors receive diverse data on the variability of the species. On the one hand, a high phenotypic diversity of natural perch populations has been identified, especially with respect to the color polymorphism of perch (Hanel 1990; Pimakhin 2012; Roch et al. 2015). However, some researchers have shown the low allozyme polymorphism in natural populations of this species (Gyllensten et al. 1987; Heldstab and Katoh 1995). Recent studies have also identified a fairly high level of diversity of neutral DNA markers in the perch (Nesbo et al. 1998a; Yang et al. 2009; Fokina et al. 2015). The reason can be that each of the genetic markers reflects the variability of certain parts of the genome and has its own specifics. We suggest combining the methods to get a more complete picture of the variability of the species. We used allozymes and nuclear DNA intersimple sequence repeat (ISSR) assays. Allozymes reflect the variability of structural genes and can sometimes determine the biochemical adaptation to environmental conditions (Watt 1994). ISSR markers are hypervariable and are generally interpreted as being selectively neutral as they usually located in noncoding regions (Pradeep et al. 2007; Nkongolo et al. 2014). Morphometric parameters allow the fish to adapt to the specific environmental conditions – the depth, flow rate, type of ground and others (Olsson et al. 2007; Rowinski et al. 2015; Hopper et al. 2017). Colour morphs are important for camouflage and depend on the habitat conditions – the transparency of water, the abundance of plants (Bartels et al. 2012). They can also be important for the formation of an intrapopulation genetic structure, since they can be used by fish to recognize a partner when mating (Kekalainen et al. 2010). The inheritance of the colour patterns in the perch is still unknown. The question is whether we can use a variety of phenotypes as a marker of the genetic heterogeneity of perch populations.

Here, we investigate whether there is a relationship between the genetic variability and phenotypic diversity in natural perch populations. First, we analysed data on body proportions and colour polymorphism in natural perch populations. Second, we assessed genetic polymorphism in these populations using two types of markers, allozymes and neutral DNA markers. Finally, we tested the correlation between the phenotypic diversity and genetic variability of fish.

Material and methods

Sampling and study area

Specimens of *Perca fluviatilis* were collected from seven localities of the Ob-Irtysh river basin in Western Siberia, Russia, during the period from June to December 2014–2016 (Fig. 1). All the water bodies differ in contrast both in natural conditions and in the level and type of anthropogenic influence. The perch populations are of practical importance in all the studied places.

The Taz River flows among marshes in the north-eastern part of the West Siberian Plain and flows into the Taz Bay of the Kara Sea. The length of the river is 1401 km. The fishing of Coregonus whitefish species is carried out in the river. Perch is a potential commercial species due to a reduction in the number of populations of these species. The Nadym River flows in the north of Western Siberia, flows into the Ob Bay of the Kara Sea. The length of the river is 545 km. In the lower reaches, the river is heavily polluted with oil products and phenols. Yantarnoe Lake is located in the basin of the Nadym River and is extremely polluted by sewage from the Nadym city. The Bolshoe Antyatskoe Lake is located on the swampy land in the Konda River basin in the center of the Ob-Irtysh basin. The lake is a fishing site where industrial fishing is carried out. The water contains a lot of iron (3-4 mg / l, which is 30-40 times higher than the maximum admissible concentration (MAC) and copper (10- 20 times MAC). The thermal regime is characterized by rapid and significant heating of the water masses. Ten species of fish: the perch, the pike *Esox lucius*, the ruff *Gymnocephalus cernuus*, the roach *Rutilus rutilus*, the dace *Leuciscus leuciscus*, the ide *Leuciscus idus*, the russian carp *Carassius gibelio*, the gudgeon *Gobio gobio* and the peled *C. peled* live in the lake. Perch is the most common fish species in the lake. The Pyshma River is in the south-west of Western Siberia. The length of the river is 603 km. The Prussian carp, the bream *Abramis brama*, the perch, the dace and the common carp *Cyprinus carpio* inhabit this river. Perch is used as an object of recreational fisheries here. Kaiskul Lake is located in a marshy area in the south of Western Siberia. The area of the reservoir is 15.8 km2. The lake is eutrophic and heavily overgrown with vegetation. The perch population of this lake is very important for feeding the local people. The Alabuga River is a tributary of the Ishim River, located in the southern part of Western Siberia, near the border of Russia and Kazakhstan. The length of this river is 46 km, the width is 40-170 m, the depth is 1-10 m. The bottom is sandy-silty, the banks are shallow. The name of the river is translated as "perch" from the local dialect. Perch is the most common fish species in the river. This is the southernmost population of perch that we studied.

The fish were captured with fishing nets, rods, and spoon baits. The fish were sampled along the shoreline in all the localities studied except the Taz River, where the fish were mined on the pelagial. A total number of 218 individuals were sampled (see Table 1 for details).

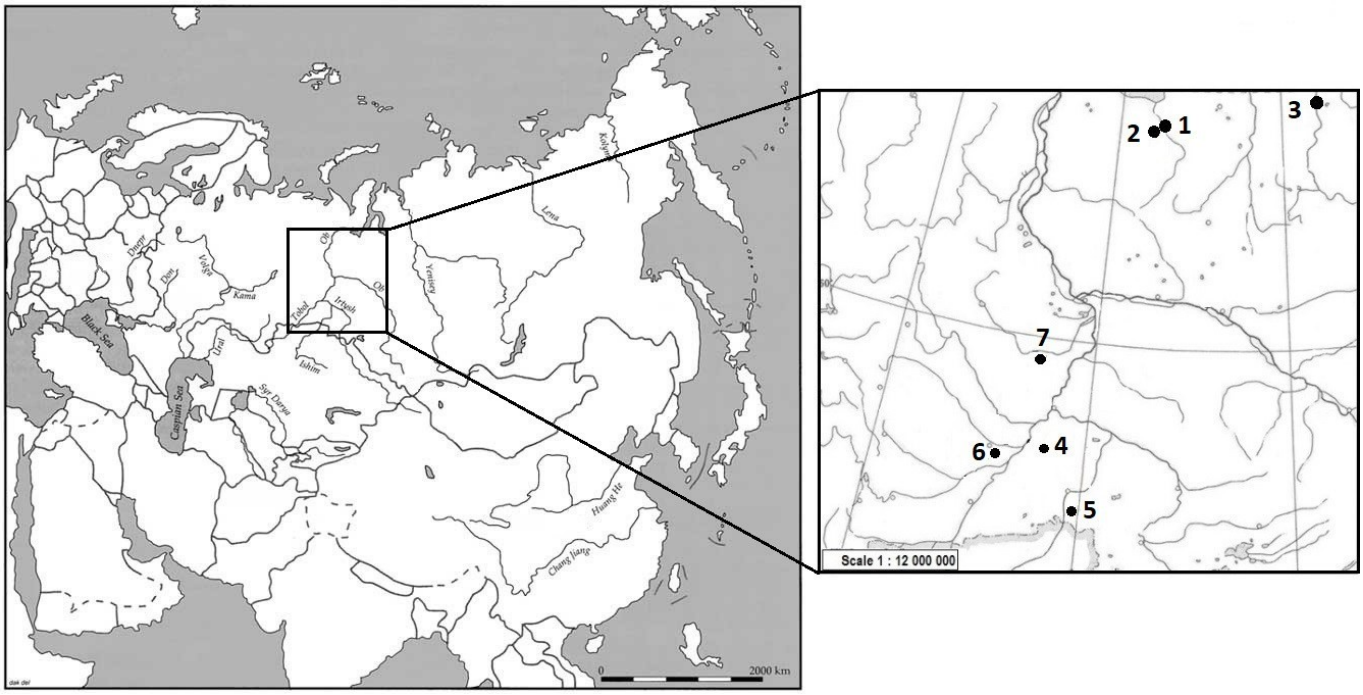

Figure 1. *Places of sample collection:* ***1*** *– the Nadym river,* ***2*** *– the Yantarnoe lake,* ***3*** *– the Taz river,* ***4*** *– the Kaishkul lake,* ***5*** *– the Alabuga river,* ***6*** *– the Pyshma river,* ***7*** *– the Bolshoe Antiatskoe lake.*

Localities	Coordinates	Period	Sample size
The Nadym river	65.5433°N, 72.7153°E	June–August 2014	40
Yantarnoe lake	65.5253°N, 72.5272°E	June–August 2014	40
The Taz river	67.4796°N, 78.7336°E	November 2015	22
Kaishkul lake	56.8348°N, 67.3493°E	September 2015	9
The Alabuga river	55.6856°N, 69.2129°E	June 2016	22
The Pyshma river	56.9695°N, 65.8595°E	December 2016	42
Bolshoe Antiatskoe lake	59.9696°N, 67.5773°E	December 2016	46

Table 1. *The locations of sample collection and the amount of material*

Morphometric studies

The sex of fish was determined by gonads, the age was established by scales, according to the standard procedure (Pravdin 1966). The weight and 15 standard morphometric characteristics of the perch were determined (Fig. 2). All metric traits were corrected for body size before analyses. We used indices in percentages of standard length or in percentages of head length following the methodical recommendations (Pravdin 1966). First, the indices for each individual were determined, then the average values for each sample were calculated.

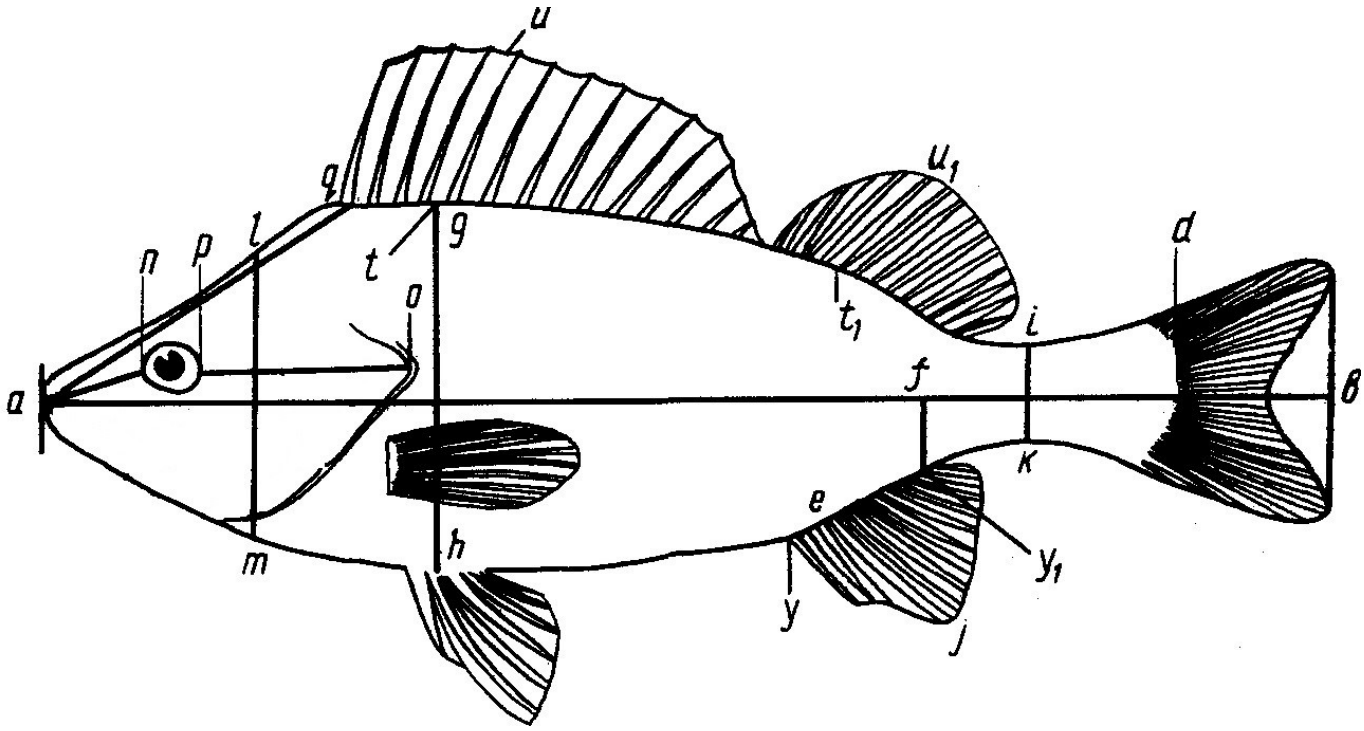

Figure 2. *Scheme of measurement of percid fish: ab – total length, an – snout length, np – horizontal eye diameter, po – postorbital head length, ao – head length, lm – head height, gh – maximum body heights, ik – minimum body heights, aq – antedorsal distance, fd – length of caudal peduncle, tu – first dorsal fin heights, t_1u_1 – second dorsal fin heights, yy_1 – base length of the anal fin, ej – height of the anal fin (by Pravdin 1966).*

Colour polymorphism

We used colour morphs to study the phenotypic diversity in the perch. Each individual perch was photographed, and then the phenotype was described. To reliably evaluate the color morphs, each perch individual was examined twice by two observers. The separate color bands were designated in Latin letters "I", "V", "Y", or "i", depending on the shape of the spot. The morph "I" corresponds to a simple long line, "i" is the short line, "V" and "Y" are two lines connected by the ends or the middle, respectively. The middle of the band was designated for an accurate separation of the bands "I" /"i" and "V"/"Y" (Fig. 3A). Band combinations were considered as colour types and designated in Latin letters according to Hanel’s classification (Hanel 1990) classification of perch colouration.

Figure 3. *Designations of the colouration elements of the perch body.* ***A*** *– types of band;* ***B*** *– variants of band combinations. m – the middle of the bands.*

Allozyme analysis

Muscle tissue samples were kept frozen at – 40 °C for analysis. Allozymic scoring was done utilizing gel electrophoresis and histochemical stains. The proteins were extracted using a standard technique with Tris-HCl buffer, pH 8.0. Proteins were separated by electrophoresis using 7.5% polyacrylamide gel (Maurer 1968). Allozymes used for the analysis were as follows: lactate dehydrogenase (LDH, 1.1.1.27), superoxide dismutase (SOD, 1.15.1.1), aspartate aminotransferase (AAT, 2.6.1.1), esterase (EST, 3.1.1.1), and muscle proteins – myogens (MY). Staining of different proteins was performed according to Richardson (1986). Loci were designated numerically according to increasing electrophoretic mobility.

DNA extraction and ISSR-PCR analysis

Total genomic DNA was extracted from cardiac muscle fixed in 70% ethanol using the alkaline lysis (Bender et al. 1983). ISSR-PCR genotyping was performed with two primers: $(AG)_8G$ (code UBC-809) and $(AG)_8T$ (code UBC-807) (Zietjiewicz et al. 1994). Amplification was set in 25 µL of the reaction mixture containing the PCR buffer (0.01 M Tris-HCl, 0.05 M KCl, 0.1% Triton X-100), 4 mM $MgCl_2$, 0.2 mM of each dNTP, 1 µL of total DNA solution, 2.5 mM primer and 0.2 units µL of Taq-polymerase. The reaction conditions included 7 min at 94 °C; followed by 30 cycles of 94 °C for 30 s, 52(56) °C for 45 s, 72 °C for 2 min; then 72 °C for 7 min. Amplification was carried out using an Mastercycler EP 384 Thermal Cycler (Eppendorf). Although the ISSR-PCR technique has better repeatability compared to other multilocus DNA markers such as RAPD, we repeated genotyping twice to get more reliable results. The PCR products were analysed on a 2% agarose gel. Electrophoretic gels were documented using the VersaDoc system (Bio-Rad).

Data analysis

Allozyme and ISSR data were calculated using POPGEN software (Yeh et al. 1999). We assessed the observed heterozygosity (*H*o), expected heterozygosity (*H*E), the proportion of polymorphic loci (*P*), the average number of alleles per locus (n_a), and Nei's genetic diversity (*h*). The chi-square ($\chi 2$) test (2) was used to compare allele frequencies and evaluate conformity of the genotype frequencies with the Hardy–Weinberg equilibrium. Genetic differentiation between the populations was estimated using Nei's original measures of genetic identity (*I*N), genetic distance (*D*N), and *F*ST and *G*ST values. Correlation coefficient (*r*) between genetic diversity indexes and the number of morphs was calculated using the STATISTICA 10.0 (StatSoft, USA).

Results

Morphometric variability

The number of females was 1.2–1.7 times more than males in all the studied populations. The age of the fish ranged from 1+ to 6+. The age group 3+ was the most numerous in most of the studied populations. To compare the morphologic characteristics in the perch of different reservoirs, morphometric indices of this age group were used. Statistically significant differences were revealed in many morphological features between all perch populations studied (Table 2). There were no significant differences in the total length of the fish from various ecosystems. At the same time, the mean value of head length in the perch of the Nadym river was significantly higher compared to the perch of Alabuga river ($p<0.01$). The perch of the Taz river had a significantly higher value of base length of the anal fin and maximum body height compared to the other populations ($p<0.05$).

Colour polymorphism

We identified 19 color types in the perch (Fig. 3B). The sets of morphs and prevailing phenotypes were different in all the populations studied (Table 3). The highest number of colour morphs (16) was found in the Pyshma River, and the smallest (4) in the Kaishkul Lake. Type B was more

frequent in the Taz and Nadym rivers, B and G – in the Bolshoe Altayskoe lake, B and H – in the Pyshma river, H – in the Kaishkul lake, S – in the Yantarnoe lake, E – in the Alabuga river.

Allozyme polymorphism

We studied five protein systems and identified 15 allozyme loci. LDH1, LDH2, AAT1, MY2, MY4, MY5, SOD2, EST1, EST3, EST4, EST5 loci were monomorphic in all the populations studied. Four loci (SOD1, EST2, MY1, MY3) were polymorphic (Table 4).

Locus EST2 was polymorphic in the Pyshma River and the Yantarnoe lake. Locus SOD1 was polymorphic in perch populations of the Alabuga river and the Yantarnoe lake. Different alleles were dominated in these populations. Loci MY1 and MY3 were polymorphic in populations ofthe Pyshma river and the Bolshoe Antiatskoe lake, respectively. Only single individuals with rare genotypes were encountered in these populations. The proportion of polymorphic loci was 26.7% varying from 6.7% to 13.3% in different perch populations. The observed heterozygosity (*H*o) varied from 0 to 0.04, expected heterozygosity (*H*E) was 0.013–0.076. The mean heterozygosity was low especially in perch from the Alabuga river. A higher value of mean heterozygosity was found in the Bolshoe Antiatskoe lake. Heterozygote deficiency was detected in all the perch populations, excluding the Pyshma river.

Characteristic	The Taz river	The Nadym river	Yantarnoe lake	Bolshoe Antiatskoe lake	The Pyshma river	The Alabuga river
Weight (g)	102.9 ± 6.5	116.0 ± 7.4	82.6 ± 10.9 (1,2)	87.0 ± 5.8 (1,2)	104.8 ± 3.6 (4)	120.6 ± 5.6 (1,3,4)
Total length (mm)	184.7 ± 7.4	183.7 ± 4.2	176.5 ± 7.7	185.1 ± 7.2	190.5 ± 3.8	188.4 ± 2.8
Head length (mm)	46.5 ± 2.7	48.0 ± 1.7	43.3 ± 1.8	43.4 ± 1.5	45.5 ± 1.1	40.0 ± 1.4 (2)
% of standard length						
Head length	25.48 ± 2.00	26.4 ± 0.6	24.59 ± 0.42 (2)	23.53 ± 0.47 (2)	23.93 ± 0.50 (2)	21.17 ± 0.62 (2,3)
Head height	22.18 ± 2.64	18.8 ± 0.6	16.91 ± 0.24 (2)	17.04 ± 0.34 (3)	16.85 ± 0.26 (2)	20.96 ± 3.41 (2-5)
Maximum body heights	27.29 ± 1.67	24.3 ± 0.3	21.70 ± 0.53 (1,2)	21.61 ± 0.55 (1,2)	20.56 ± 0.78 (1,2,3)	24.85 ± 0.97 (3,5)
Minimum body heights	8.19 ± 0.79	7.2 ± 0.2	5.79 ± 0.58 (1)	7.29 ± 0.40 (3)	6.93 ± 0.22	9.73 ± 0.422,3,5
Length of caudal peduncle	19.88 ± 1.90	17.2 ± 0.6	16.93 ± 0.30	16.35 ± 0.97	16.68 ± 0.40	19.92 ± 0.17 (2,3,5)
Antedorsal distance	27.82 ± 1.54	27.6 ± 0.4	25.16 ± 0.50 (2)	25.04 ± 0.64	25.20 ± 0.57 (2)	22.12 ± 1.10 (1,2,4)
First dorsal fin heights	11.79 ± 0.83	12.9 ± 0.4	12.16 ± 0.31	11.72 ± 0.32	11.96 ± 0.28	10.58 ± 0.12 (2,3,5)
Second dorsal fin heights	9.32 ± 0.66	9.9 ± 0.2	9.25 ± 0.19	9.45 ± 0.24	9.44 ± 0.17	10.49 ± 0.18 (3,5)
Base length of the anal fin	12.58 ± 0.66	9.7 ± 0.2 (1)	9.74 ± 0.29 (1)	9.25 ± 0.28 (1)	9.89 ± 0.30 (1)	10.67 ± 0.61
Height of the anal fin	11.06 ± 0.89	11.6 ± 0.2	11.30 ± 0.25	11.50 ± 0.44	10.99 ± 0.29	11.93 ± 0.26
% of head length						
Snout length	33.89 ± 2.42	27.4±1.2 (1)	24.53 ± 0.48 (1)	30.48 ± 1.90 (3)	26.72 ± 0.61 (1,3)	46.92 ± 1.82 (1-5)
Horizontal eye diameter	20.18 ± 0.66	19.1±0.5	20.05 ± 0.70	22.09 ± 0.66 (1,2,3)	20.98 ± 0.46 (2,3)	23.49 ± 0.64 (1-3)
Postorbital head length	46.24 ± 2.85	52.50±1.06	55.43 ± 0.51 (1)	47.92 ± 1.86 (3)	52.31 ± 0.87 (3)	29.59 ± 2.35 (1-5)

Table 2. *Weight and morphometric characteristics of perch in age 3+ (M ± SE)*

M ± SE mean and standard error of mean; 1-6 statistically significant differences between populations at $P<0.05$: 1 compared with the Taz river; 2 compared with the Nadym river; 3 compared with Yantarnoe lake; 4 compared with Bolshoe Antiatskoe lake; 5 compared with the Pyshma river.

Colour type	The combination of bands	Taz river	Nadym river	Yantarnoe lake	Bolshoe Antiatskoe lake	Kaishkul lake	Pyshma river	Alabuga river
A	IIVII	18.0	17.0	6.0	0	33.0	2.5	9.0
B	IYVII	23.0	31.0	13.0	15.0	11.0	14.0	0
C	IIIIIIi	9.0	7.0	0	2.0	0	2.5	5.0
D	IYIIIi	18.0	7.0	6.0	6.5	0	9.5	0
E	IIIIi	0	7.0	0	6.5	0	0	36.0
F	IIIYIi	0	0	0	9.0	0	9.5	0
G	IYYIV	0	7.0	6.0	15.0	0	2.5	0
H	IYYVI	14.0	7.0	6.0	11.0	45.0	14.0	18.0
I	IiIiYIi	0	0	0	0	0	2.5	0
J	VVVVV	0	0	0	2.0	0	4.5	0
K	IYYVV	0	7.0	6.0	9.0	0	12.0	27.0
L	IYIiIII	0	0	0	0	0	2.5	5.0
M	YYYII	4.5	3.0	13.0	6.5	0	2.5	0
O	YYIIIi	0	0	0	6.5	0	12.0	0
P	IIIIVi	4.5	0	6.0	2.0	0	4.5	0
R	YYIIiIi	0	0	0	4.5	0	0	0
S	IiIVIi	0	7.0	25.0	0	11.0	2.5	0
T	IIYIV	0	0	0	4.5	0	2.5	0
U	IiIIVIIii	9.0	0	13.0	0	0	0	0
Number of detected colour morphs		8	10	10	14	4	16	6

Table 3. *Frequency of colour morphs occurrence in perch populations (%)*

Loci	The Alabuga river	Yantarnoe lake	The Pyshma river	Bolshoe Antiatskoe lake
MY1	1.000	1.000	0.800 ± 0 .06	1.000
MY3	1.000	1.000	1.000	0.975 ± 0.02
SOD1	0.895 ± 0.05	0.211 ± 0.07	1.000	1.000
EST2	1.000	0.579 ± 0.08	0.700 ± 0.07	1.000
P(%)	6.7	13.3	13.3	6.7
Ho	0	0.0070	0.0200	0.0400
HE	0.0129	0.0561	0.0183	0.0762

Table 4. *Allele frequencies (± SE) and indices of allozyme variability in perch*

*P*95% – the proportion of polymorphic loci, *H*o – the observed heterozygosity, *H*E – the expected heterozygosity.

ISSR polymorphism

We used two ISSR primers and have received a pattern of 26 bands, which were all polymorphic. The proportion of polymorphic loci varied from 53.9% to 96.2% in various perch populations. The mean Nei's genetic diversity (*h*) was 0.309 and varied from 0.19 to 0.33. The lowest level of DNA polymorphism was in the Alabuga river, but the highest one – in the Pyshma and Taz rivers (Table 5).

Localities	P (%)	h	n_a
The Taz river	96.2 ± 4.08	0.33	1.96

The Nadym river	64.3 ± 7.11	0.24	1.19
Yantarnoe lake	78.6 ± 8.21	0.29	1.19
Bolshoe Antiatskoe lake	92.3 ± 13.33	0.33	1.92
Kaishkul lake	73.1 ± 14.60	0.24	1.73
The Pyshma river	96.2 ± 3.90	0.32	1.96
The Alabuga river	53.9 ± 10.63	0.19	1.54

Table 5. *Indices of genetic variability in perch populations according to ISSR data*

P – the proportion of polymorphic loci, *h* – Nei's genetic diversity, n_a – the average number of alleles per locus.

A high indicator of the genetic differentiation of perch was identified (*G*ST = 0.3109). About 30% of the genetic variability of perch is due to the interpopulation component. Nei's genetic identity indices between perch populations varied from 0.7399 to 0.9957. The smallest genetic distance (*D*N = 0.0043) was between populations from the Nadym river and Yantarnoe lake, 2 km distant from each other. The isolated population from Kaishkul lake and the southernmost population of the Alabuga river were more distant from each other (*D*N = 0.3013) and from other perch populations.

Correlation coefficients (*R*S) between the number of colour morphs and genetic polymorphism indexes in perch populations were + 0.554, + 0.571 and + 0.259 for *P*95, *h*and n_a, respectively ($p>0.05$).

Discussion

We studied fish taken from various types of water bodies (rivers and lakes), from the north to the south of Western Siberia. Perch from the lake populations had lower weight values compared with individuals from the river populations. This can be explained by a wider forage supply and a greater degree of predation of perch in the rivers compared with lakes.

The results of morphometry showed that each perch population has specific morphological traits. The perch from the Alabuga river had the maximum value of horizontal eye diameter and snout length, but minimum value of postorbital head length compared with others populations ($p<0.05$). This can be explained by the low transparency of the water, since the river has a silty bottom. The perch from the Nadym river was characterized by the largest head length ($p<0.05$). This may be due to the predominance of predation in the foraging strategy of perch because the northern rivers are oligotrophic. The perch from the Taz river had the largest value of maximum body heights ($p<0.05$) compared with others populations. In this river fish were sampled on the pelagial while in other localities fish were mined on the shoreline. This fact is confirmed by the data of other authors who found a large body height of the perch in the pelagial than in the littoral (Svanbäck and Eklöv 2004). A significantly higher value of base length of the anal fin in the perch from the Taz river may be due to the high flow velocity in the river.

Morphologic data confirm the high ecological plasticity of the species. Morphology of percid fish plays a key role in adaptation to environmental conditions. It may depend on various abiotic and biotic factors, such as temperature, water transparency, habitat type, variation in resource levels, interspecific competition, predator density and prey abundance (Olsson et al. 2007; Kekalainen et al. 2010; Bartels et al. 2012; Rowinski et al. 2015; Hopper et al. 2017; Leino and Mensinger 2017). Morphometric characteristics can determine a swimming activity and a foraging strategy of perch (Faulks et al. 2015; Baktoft et al. 2016). At the same time, we have not revealed evidence that variations of body size and weight were associated with adaptation to climatic conditions. The specific set of habitat conditions and the species composition of the biological community might be more significant for perch.

The sets of colour morphs and prevailing phenotypes were different in all the studied populations. The diversity of morphs can be a consequence of a variety of habitat conditions, especially in large reservoirs with a variety of habitat types. Unfortunately, inheritance of the colour patterns in perch is still unknown. Partially, morphological variations can be inherited. Differences in the colouration of perch in different water bodies can be caused, in addition to adaptation and natural selection, by the history of colonization and genetic drift in isolated lakes.

Our data indicate that the perch from Siberia has a low level of allozyme polymorphism. Some researchers pointed to a low allozyme polymorphism in the Eurasian perch from the waterbodies of Europe (Gyllensten et al. 1987; Heldstab and Katoh 1995). Almost complete absence of allozyme variability was found in perch populations from eight freshwater localities in Sweden, Ireland and Scotland, five brackish water localities in the Baltic Sea (Gyllensten et al. 1987), and four Swiss lakes (Heldstab and Katoh 1995). The perch has the lowest level of allozyme polymorphism in comparison with other freshwater fish species from the region studied (Zhigileva et al. 2010). The low allozyme variability seems to be the characteristic of the Eurasian perch, regardless of the habitat of the species.

Indicators of DNA polymorphism in the perch were higher – the proportion of polymorphic loci was 100%, Nei’s genetic diversity (h) was 0.309. These data are consistent with the variability data of the same markers in other freshwater fish species of the Ob-Irtysh basin (Zhigileva et al. 2013; Zhigileva and Kulikova 2016). The proportion of polymorphic loci and Nei's genetic diversity were larger in larger rivers (the Taz river, the Pyshma river) and lakes (Bolshoe Antiatskoe lake) than in small water bodies such as the Alabuga river. This may be due to the larger effective size of the population and the lower probability of the loss of genetic diversity as a result of a genetic drift in large populations compared to small populations. Previously, it was found that the genetic diversity of ISSR markers in population of the silver crucian carp *Carassius auratus gibelio* was positively correlated with a lake area (Zhigileva et al. 2017).

Indices of genetic variability in perch populations according to ISSR data did not correlate with the number of colour morphs in perch populations. Population genetic characteristics mainly depend on phylogeographic history, gene flow and effective population size. Evidently, the variability of neutral genetic markers such as the ISSR does not directly affect adaptation to environmental conditions. Similar findings were obtained by other researchers who did not find any significant coupling of morphology and genetic divergence (Faulks et al. 2015). The morphological divergence in the perch populations can be stem mainly from a plastic response to different environmental conditions (Heynen et al. 2010).

Conclusion

To summarise, we found that every population of perch contains a unique gene pool and a set of colour morphs. Each population has a small range of heterozygosity, but all the populations are different from each other in morphology and genetic variability. We also found that the level of genetic variability does not correlate with phenotypic diversity. These findings are important for the rational organization of the fishery and protection of genetic resources of the species. We can not assess the genetic diversity of the perch, based only on the variety of observed phenotypes such as color morphs and body proportions. Phenotypically homogeneous populations can contain unique alleles. Conversely, morphologically diverse populations may have small genetic differences. A combination of morphological and genetic methods should be used to adequately assess genetic diversity and adaptive potential of perch populations.

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References

Akin S, Sahin C, Verep B, Turan D, Gözler AM, Bozkur A, Çelik K, Çetin E, Aracı A, Sargın Đ (2011) Feeding habits of introduced European perch (*Perca fluviatilis*) in an impounded large river system in Turkey. African Journal of Agricultural Research 6 (18): 4293–4307. https://doi.org/10.5897/AJAR11.397

Bartels P, Hirsch PE, Svanback R, Eklov P (2012) Water transparency drives intra-population divergence in Eurasian perch (*Perca fluviatilis*). Plos One 7 (8): e43641. https://doi.org/10.1371/journal.pone.0043641

Baktoft H, Jacobsen L, Skov C, Koed A, Jepsen N, Berg S, Aarestrup K, Svendsen J (2016) Phenotypic variation in metabolism and morphology correlating with animal swimming activity in the wild: relevance for the OCLTT (oxygen- and capacity-limitation of thermal tolerance), allocation and performance models. Conservation Physiology 4: cov055. https://doi.org/10.1093/conphys/cov055

Behrmann-Godel J, Gerlach G, Eckmann R (2004) Postglacial colonization shows evidence for sympatric population splitting of Eurasian perch (*Perca fluviatilis* L.) in Lake Constance. Molecular Ecology 13 (2): 491–497. https://doi.org/10.1046/j.1365-294X.2003.02082.x

Jain BP, Goswami SK, Pandey S (2021) Chapter 8 – Nucleic Acid. In: Jain BP, Goswami SK, Pandey S (Eds) Protocols in Biochemistry and Clinical Biochemistry. Academic Press, 69–100. https://doi.org/10.1016/B978-0-12-822007-8.00010-6

Ben Khadher S, Fontaine P, Milla S, Agnèse J-F, Teletchea F (2016) Genetic characterization and relatedness of wild and farmed Eurasian perch (*Perca fluviatilis*): possible implications for aquaculture practices. Aquaculture Reports 3: 136–146. https://doi.org/10.1016/j.aqrep.2015.12.003

Closs GP, Ludgate B, Goldsmith RJ (2001) Controlling European perch (*Perca fluviatilis*): lessons from an experimental removal. In: Managing invasive freshwater fish in New Zealand. Proceedings of a workshop hosted by department of conservation, Hamilton, 37–48. https://www.researchgate.net/publication/253494712_Controlling_European_perch_Perca_fluviatilis_lessons_from_an_experimental_removal

Ericson G, Liewenborg B, Lindesjöö E, Näf C, Balk L (1999) DNA adducts in perch (*Perca fluviatilis*) from a creosote contaminated site in the River Ångermanälven, Sweden. Aquatic Toxicology 45 (2&3): 181–193. https://doi.org/10.1016/S0166-445X(98)00100-3

Faulks L, Svanback R, Eklov P, Ostman O (2015) Genetic and morphological divergence along the littoral-pelagic axis in two common and sympatric fishes: perch, *Perca fluviatilis* (Percidae) and roach, *Rutilus rutilus* (Cyprinidae). Biological Journal of the Linnean Society 114 (4): 929–940. https://doi.org/10.1111/bij.12452

Fokina O, Grauda D, Rashal I (2015) Genetic diversity of two perch *Perca fluviatilis* populations of the Latgale region. In: Environment. Technology. Resources. Vol. II. Proceedings of the 10th International Scientific and Practical Conference, Rezekne, Latvia, Rezekne Higher Education Institution (Rēzeknes Augstskola), 96–98. http://dx.doi.org/10.17770/etr2015vol2.280

Georgieva E, Yancheva V, Velcheva I, Becheva M, Stoyanova S (2015) Histological alterations under metal exposure in gills of European perch (*Perca fluviatilis* L.) from Topolnitsa Reservoir (Bulgaria). Archives of Biological Sciences 67 (2): 729–737. https://doi.org/10.2298/ABS141020034G

Gerlach G, Schardt U, Eckmann R, Meyer A (2001) Kin-structured subpopulations in Eurasian perch (*Perca fluviatilis* L.). Heredity 86: 213–221. https://doi.org/10.1046/j.1365-2540.2001.00825.x

Gyllensten U, Ryman N, Stahl G (1987) Monomorphism of allozymes in perch (*Perca fluviatilis* L.). Hereditas 102: 57–61. https://doi.org/10.1111/j.1601-5223.1985.tb00465.x

Hanel L (1990) The variability of the coloration in the perch (*Perca fluviatilis*, Pisces, Perciformes) from the riverine lake Slapy (Central Bohemia). Acta Societatis Zoologicae Bohemoslovacae 54: 161–163.

Heldstab H, Katoh M (1995) Low genetic variation in perch (*Perca fluviatilis* L.) from three major European drainage systems in Switzerland. Aquatic Sciences 57 (1): 14–19. https://doi.org/10.1007/BF00878023

Heynen M, Hellstrom G, Magnhagen C, Borcherding J (2010) Does morphological variation between young-of-the-year perch from two Swedish lakes depend on genetic differences? Ecology of Freshwater Fish 19: 163–169. https://doi.org/10.1111/j.1600-0633.2009.00400.x

Hopper GW, Morehouse RL, Tobler M (2017) Body shape variation in two species of darters (Etheostoma, Percidae) and its relation to the environment. Ecology of Freshwater Fish 26: 4–18. https://doi.org/10.1111/eff.12245

Kekalainen J, Kahkonen J, Kiviniemi V, Huuskonen H (2010) Morphological variation of perch *Perca fluviatilis* in humic lakes: the effect of predator density, competition and prey abundance. Journal of Fish Biology 76: 787–799. https://doi.org/10.1111/j.1095-8649.2009.02475.x

Leino JR, Mensinger AF (2017) Interspecific competition between the round goby, *Neogobius melanostomus*, and the logperch, *Percina caprodes*, in the Duluth-Superior Harbour. Ecology of Freshwater Fish 26: 34–41. https://doi.org/10.1111/eff.12247

Lucentini L, Lorenzoni M, Panara F, Mearelli M (2002) Effects of short- and long-term thermal stress in perch (*Perca fluviatilis*) determined through fluctuating asymmetry and HSP70 expression. Italian Journal of Zoology 69 (1): 13–17. https://doi.org/10.1080/11250000209356432

Maurer HR (1968) Disk-Elektrophorese: Theorie und Praxis der diskontinuierlichen Polyacrylamidgel Elektrophorese. De Gruyter and Co., Berlin, 221 pp.

Nesbo CL, Mohammed OA, Jakobsen KS (1998a) Heteroplasmy, length and sequence variation in the mtDNA control regions of three percid fish species (*Perca fluviatilis*, *Acerina cernua*, *Stizostedion lucioperca*). Genetics 148: 1907–1919. https://doi.org/10.1093/genetics/148.4.1907

Nesbo CL, Mohammed OA, Jakobsen KS (1998b) Genetic differentiation among stationary and anadromous perch (*Perca ftuviatilis*) in the Baltic Sea. Hereditas 129: 241–249. https://doi.org/10.1111/j.1601-5223.1998.00241.x

Nesbo CL, Fossheim T, Vollestad LA, Jakobsen KS (1999) Genetic divergence and phylo-geographic relationships among European perch (*Perca fluviatilis*) populations reflect glacial refugia and postglacial colonization. Molecular Ecology 8: 1387–1404. https://doi.org/10.1046/j.1365-294x.1999.00699.x

Nkongolo KK, Gervais S, Michael P, Zhou Y (2014) Comparative analysis of Inter Simple Sequence

Repeats and Simple Sequence Repeats markers: genetic analysis of *Deschampsia cespitosa* populations growing in metal contaminated regions in Canada. American Journal of Biochemistry and Biotechnology 10: 69-80. https://doi.org/10.3844/ajbbsp.2014.69.80

Olsson J, Svanback R, Eklov P (2007) Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. Oecologia 152 (1): 48–56. https://doi.org/10.1007/s00442-006-0588-8

Pimakhin A (2012) Color variability of Eurasian perch (*Perca fluviatilis* L.): a review. In: Proceedings in ARSA – Advanced Research in Scientific Areas, 1, 1563–1569. https://www.semanticscholar.org/paper/Color-variability-of-Eurasian-perch-(Perca-L.)%3A- a-Pimakhin/19273aca6f0e8a82319c0966422da82285e0ef75

Pradeep AR, Jingade AH, Urs RS (2007) Molecular markers for biomass traits: association, interaction and genetic divergence in silkworm *Bombyx mori*. Biomarker Insights 2: 197–217. https://doi.org/10.4137/BMI.S0

Pravdin IF (1966) Guide to the study of fish. Food industry, Moscow, 146 pp.

Richardson BJ (1986) Allozyme electrophoresis. A handbook for animal systematics and population studies. Academic Press, London, 410 pp.

Roch S, Behrmann-Godel J, Brinker A (2015) Genetically distinct colour morphs of European perch *Perca fluviatilis* in Lake Constance differ in susceptibility to macroparasites. Journal of Fish Biology 86 (2): 854–863. https://doi.org/10.1111/jfb.12608

Rowinski PK, Mateos-Gonzalez F, Sandblom E, Jutfelt F, Ekstrom A, Sundstrom LF (2015) Warming alters the body shape of European perch *Perca fluviatilis*. Journal of Fish Biology 87 (5): 1234–1247. https://doi.org/10.1111/jfb.12785

Svanback R, Eklov P (2004) Morphology in perch affects habitat specific feeding efficiency. Functional Ecology 18: 503–510. https://doi.org/10.1111/j.0269-8463.2004.00858.x

Watt WB (1994) Allozymes in Evolutionary Genetics: Self-Imposed Burden or Extraordinary Tool? Genetics 136: 11–16. https://doi.org/10.1093/genetics/136.1.11

Yang XX, Wang CH, Wang J, Ma YQ, Yin JG, Wu HX (2009) Isolation and characterization of 12 polymorphic microsatellite loci in Eurasian perch (*Perca fluviatilus* L.). Conservation Genetics Resources 1: 229. https://doi.org/10.1007/s12686-009-9056-1

Yeh FC, Yang R, Boyle T (1999) POPGENE. Version 1.31. Univ. Alberta and Centre Int. Forestry Res. Retrieved from http://www.ualberta.ca/~fyeh/popgene_download.html