

Regularities of Formation of Diversity of Life Strategy and Genetic Variability of The Kamchatka Rainbow Trout *Parasalmo mykiss* in a Local Population

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Received December 16, 2019; revised January 10, 2020; accepted January 11, 2020

Abstract—The diversity of life strategy, population structure, size, age and sex composition, growth and variability of 11 microsatellite loci in mykiss (rainbow trout) *Parasalmo mykiss* of the Utkholok River (Northwestern Kamchatka) were studied. The mykiss population represents a system of groupings with different types of life strategy: anadromous fish prevail in the population, while river and semi-anadromous (estuarine and riverine–estuarine) fish are less common. Each of the groupings has specific size, age and sex composition, the ratio of the first time-maturing and re-maturing fish. At that, the individuals with different types of life strategy reproduce together on the same spawning grounds and there is no isolation between them. Analysis of the variability of microsatellite loci revealed no significant differences for any locus between the observed genotypic distributions and the theoretical Hardy – Weinberg distributions. The genetic differentiation of mykiss in the Utkholok River relates to the differences between fish with a river–estuarine life strategy and the others in three loci (*Ots3*, *One108*, and *One112*). The results of clustering show the maximum value of the probability of belonging to the same cluster of all mykiss individuals with different life strategies. Significant differences at the some loci are not evidencing their reproductive isolation. It has been found that mykiss population of Utkholok River is an integrated dynamic system of groupings with different types of life strategies, which are formed in each generation because of the cumulative impact of environmental factors and heredity.

Keywords: mykiss *Parasalmo mykiss*, life strategy, migrant, resident, microsatellites, Northwestern Kamchatka

DOI: 10.1134/S003294522006003X

INTRODUCTION

Mykiss (rainbow trout) *Parasalmo mykiss* is one of the few salmonid species exhibiting extremely complex intraspecific organization related to lifestyle: some individuals realize their life cycle in fresh waters (residential or resident), while the others migrate for various distances from fresh waters into brackish and marine waters (migrant or anadromous (Behnke, 1992, 2002; Jonsson and Jonsson, 1993; Quinn and Myers, 2004; Pavlov et al., 1999, 2001; Pavlov and Savvaitova, 2008; Kuzishchin, 2010). Since mykiss inhabits different types of waterbodies located in different natural zones the relationship between resident and anadromous fish varies significantly across the species range (Behnke, 1992, 2002; Waples et al., 2008). In waterbodies of North America, in the case of sympatry between anadromous and resident groups, there is both an extensive exchange of genes between them (Seamons et al., 2004; Olsen et al., 2006; Pearsons et al., 2008) and genetic isolation (Narum et al., 2004). In cases where there is no reproductive isola-

tion between resident and anadromous groupings, both anadromous and resident individuals (McMillan et al., 2007; Christie et al., 2011; Courter et al., 2013; Sloat, Reeves, 2014) may represent the offspring from joint spawning.

At the same time, the question of the relationship between resident and anadromous individuals or groups and the ways of their formation is studied insufficiently (Waples et al., 2008; McMillan et al., 2012; Sloat et al., 2014; Kendall et al., 2015). Such type analysis is considered as an important task for assessing the adaptability and resistance of anadromous and resident fish to the consequences of anthropogenic transformation of the environment and global climate changes (Lehman and Tilman, 2000; Koellner and Schmitz, 2006; Satterthwaite et al., 2010; Schindler et al., 2010; Benjamin et al., 2013).

In the populations of mykiss in Kamchatka, individuals with migrant and resident life strategy (LS) types coexist everywhere, and fish with migrant LS are heterogeneous and differ in the length of their migra-

tion routes and the time spent in the sea or in brackish-water coastal areas (Pavlov et al., 1999, 2001; Pavlov and Savvaitova, 2008). The ratio of fish with different types of LS in local populations is determined by the geomorphology of the river system (Pavlov et al., 1999, 2001, 2008; Kuzishchin, 2010). In addition, even within the same river system, the ratio of fish with different types of LS varies from year to year, and in some rivers, anadromous individuals can produce riverine-type descendants and vice versa (Pavlov et al., 2001; Zimmerman et al., 2003).

It is assumed that the division of a generation into migrant and resident individuals is determined epigenetically, i. e. is the result of a complex, nonlinear interaction of environmental factors and individual characteristics of the early life stage of a particular individual (Pavlov et al., 1999, 2001, 2008; Pavlov and Savvaitova, 2008; Kuzishchin, 2010; Sloat et al., 2014). Studies on the population-genetic structure of Kamchatka mykiss generally confirm this assumption, since in some studied rivers, fish with different types of LS belong to the same gene pool (Pavlov, 2000; Pavlov et al., 2004, 2011, 2019; McPhee et al., 2007, 2014).

However, the problem of the genetic characteristics of fish with different LS types is insufficiently studied, it remains unclear how the genotype of an individual, interacting with environmental factors, affects the formation of either migrant or resident lifestyle in mixed populations (Simpson, 1992; Hendry et al., 2004; Nichols et al., 2008; McMillan et al., 2012; Kendall et al., 2015). The currently available data on Kamchatka mykiss require clarification, especially for those rivers in which a complex composition of fish with different LS types is observed. As one of such rivers is the Utkholok River in the Kamchatka northwest. The mykiss population there has been monitored since 1970 and all types of LSs known for Kamchatka have been identified in the river: typical-anadromous, anadromous-B, estuarine, river-estuarine, river (type names are given after: Pavlov et al., 2001). The ratio between these types changes in different years (Savvaitova et al., 1997, 2003; Pavlov et al., 2001, 2016). For spawning, mykiss widely uses the main channel and different tributaries of the river; everywhere in the spawning grounds, a joint spawning of migrant and resident fish takes place. Thus, the mykiss population in Utkholok River is a convenient object for studying the processes of LS diversity formation.

Taking into the account all mentioned above the present paper sets to study structure of population and genetic variability of mykiss in the Utkholok River, to reveal the regularities of formation of diversity of LS and to assess the importance of genetic factors in this process.

MATERIALS AND METHODS

The materials for the study were collected in 1995–2018 in the Utkholok River basin from the estua-

rine zone to the headwaters and tributaries. The river is located in an area remote from populated regions and does not undergo anthropogenic transformation, there is no economic activity and there have never been any introduction or fish propagation activities. The Utkholok River is of a mountain-tundra character, originates in the spurs of the Medvezhy Ridge, flows in a single channel from the upper reaches to the mouth of the river; many tributaries of different types (mountain and tundra), different lengths and water content inflow the river. The water is brown. The length along the main channel is ~140 km, the area of the drainage basin is 1350 km², and the water discharge at the mouth during the low-water period is 12.3 m³/s. Mykiss spawning grounds are located in the main riverbed from the foothills to the coastal plain and in a number of tundra-type tributaries, mainly confined to the midstream of the river (Pavlov et al., 2016).

The fish were caught using angling gear according the “catch and release” principle; from year to year on the same pits and rapids throughout the daylight time. That is, the material obtained is as standardized as possible in time, place and method of sampling. The movements of fish in the river system and in the estuary were studied by tagging with individual numbered tags (FloyTag or PIT-tag) and recording recaptures (Pine et al., 2003); 1288 specimens were tagged and 66 specimens were recaptured. For all caught fish, the Smith length (*FL*) and body girth were measured, a sample of scales (at least 15 scales) was taken from rows 1–4 above the lateral line in the area between the posterior edge of the dorsal and the beginning of the adipose fin (Pavlov et al., 2001). For genetic analysis, a strip of tissue (15 × 5 mm) was taken from the edge of the anal fin and fixed in 96% ethanol.

The LS type in fish was determined by scales in accordance with original methods (Pavlov et al., 2001). At least three scales with an intact center were taken from each individual and scale prints on acryl acetate plates were produced using a hydraulic press (pressure 200 Pa at a temperature of 85°C. Then, using the image-capture system of digital image processing (Leica DMLS microscope with a set of lenses with magnification from × 2.5 to × 10, digital camera Canon X500-D, Japan), an electronic image of the scales was obtained from the prints in the form of a file in the TIFF format. Analyzing the scale structure (the width of the annual zones and the number of sclerites in the annual zones) such features as the type of life strategy, the age of sexual maturation, the repetition of spawning, the number of years spent in fresh water, in the sea, or in the estuary were determined (Kuzishchin et al., 1999; Pavlov et al., 1999; 2001, 2016; Kuzishchin, 2010). For the reverse calculation of the fish growth, the diagonal radius of the scales (*R*) (Kuzishchin et al., 1999; Pavlov et al., 2001), the width of annual increments (on the basis of which $l_1, l_2, l_3 \dots l + 1$ the increments in body length in 1- 2nd, 2nd, 3rd ...

and in the current years of life were calculated) were measured. The reverse calculation of the body length of fish at different ages was carried out according to Lee's formula (Busaker et al., 1990): $l_i - c = r_i/R(FL - c)$, where l_i is the calculated body length of an individual at the i -th age, r_i is the radius of the i -th annual ring on the scales, R is the scale radius, FL is the observed Smith length, c is the free term calculated by the equation of the relationship between the scale radius and the fish length: $FL = c + bR$, with the correlation coefficient being >0.95 .

Ten meristic characters according to the modified Pravdin's scheme (Pavlov et al., 2001) were studied; all calculations were performed in the field conditions using fresh materials. The morphological materials were processed using the methods of univariate statistical analysis (Lakin, 1990). To assess the phenotypic diversity of the samples, the principal component analysis (PC) was applied (James and McCulloch, 1990), the variation-covariance matrix was calculated, the length of the eigenvector was equated to the square root of the eigenvalue (Rohlf, 1993).

Genetic analysis was performed in the mykiss sampled in 2004, 2017 and 2018. Mykiss group samples of typical anadromous, riverine-estuarine, and riverine LSs were compared. We used 11 microsatellite loci designed to analyze the genetic variability of salmonids: *Ssa197* (O'Reilly et al., 1996), *Ssa20.19* (Sanchez et al., 1996), *One103*, *One104*, *One108*, *One111*, *One112* (Olsen et al., 2000), *Ots3* (Small et al., 1998), *Oki10* (Smith et al., 1998), *Omy1011* (Spies et al., 2005), and *Omm1070* (Rexroad et al., 2001).

Polymerase chain reaction (PCR) was carried out in MJ Research PTC 100 amplifier (USA) using 10 μ L of ready lyophilized mixtures for PCR GenePak PCR Core (IsoGen, Russia) with the addition of 5 μ L of a primer mixture (final concentration 0.5 μ M) and 5 μ L of genomic DNA (100 ng). Amplification was performed in the following regime: denaturation for 2 min at 94°C, then 8 cycles, including 1 min of DNA matrix denaturation at 94°C, 30 s of primer annealing at 50–56°C (depending on the primers) and synthesis of new chains for 30 s at 72°C; then 21 cycles followed, including 30 s at 94°C, 30 s at 50–56°C and 15 s at 72°C; elongation 3 min at 72°C. Annealing temperature for primers: *Ssa20.19*, *One104*, *One108*, *Ots3*, *Oki10*, *Omy1011*, *Omm1070*—50°C; *One103*—52°C; *Ssa197*, *One112* was 54°C; for *One111*, 56°C.

The amplification products were fractionated by electrophoresis in 6% non-denaturing polyacrylamide gel in 0.5 \times TBE buffer at a voltage of 300 V for 2–5 h. The obtained electrophoregrams were stained with ethidium bromide and photographed in ultraviolet light. The pBR322 DNA plasmids treated with *HpaII* restriction endonuclease were used as markers of fragment lengths. Allele sizes for each locus were determined using the 1D Image Analysis Software Version 3.5 (Kodak, United States). The data for all loci were

examined for possible genotyping errors, as well as the presence of null alleles were analyzed using the Micro-Checker 2.2.3 software (Van Oosterhout et al., 2004).

The main indicators of genetic diversity (allele frequencies, allelic diversity (A), expected and observed heterozygosity (HE , HO)) were obtained using the GENEPOP 4.2 program (Rousset, 2008). Deviations from the Hardy - Weinberg equilibrium were tested using the coefficient of inbreeding (F_{IS}), and their significance was assessed using Fisher's exact tests. Allelic diversity estimates (A_R), adjusted for the minimum sample size, were obtained using the FSTAT 2.9.3 software (Goudet, 2001). The differences in A_R , H_O and H_E between *P. mykiss* with different types of LS were assessed using the Mann - Whitney U-test (Lakin, 1990). One-way analysis of variance (ANOVA) was performed in Excel software package in order to assess the differences in A_R , H_O and H_E between mykiss specimens with different LS types. To assess the general and pairwise differentiation of populations, we used the F_{ST} indicator and its analog θ obtained in the GENEPOP and GDA 1.0 programs (Lewis and Zaykin, 2001). The selective neutrality of microsatellite loci was tested using the BayeScan 2.1 software (Foll and Gaggiotti, 2008).

The analysis of the population structure was carried out by the Bayesian method in the STRUCTURE 2.3.4 software (Pritchard et al., 2000). We used a model allowing genetic mixing and correlation of allelic frequencies among clusters, with 400.000 initial (burn-in) and 800.000 MCMC (Markov chain Monte Carlo) iterations, for K (hypothetical number of populations) from 1 to 3, three analyzes for each K value.

RESULTS

Population Structure. Diversity of Life Strategy

In the local population of mykiss in the Utkholok River, in 1970–1971 and 1995–2000, the individuals with different types of LS were identified and described (Savvaitova et al., 1973, 1997; Pavlov et al., 1999, 2001; Savvaitova et al., 1999). There are five following types of groupings.

Typically-anadromous (TA): the fish spend the first 2–4 years of life in the river, where they undergo smoltification. Then they migrate downstream and feed from 1 to 6 years far in the sea until reaching sexual maturity, after which they return to the river for spawning.

Anadromous-B (AB): following 2–4 years of life in the river and smoltification, the fish migrate downstream and exit the river, fatten in the coastal sea zone for about 3 months and return at immature stage back to the river. The next spring, they make a downstream migration from the river, going far into the sea, where, after reaching sexual maturity, they return to

the river for spawning. At the moment of anadromous migration, TA and AB fish are indistinguishable from each other in terms of external habitual features, color, behavior and distribution and can be differentiated only on the basis of an analysis of the recording structures.

The sea period of life in TA and AB mykiss in the Utkholok River is not studied. There are some reasons to believe that these fish are wintering in the region of southern Kuril Islands (Kovalenko et al., 2005).

Estuarine (E): after three-five years of life in the river juvenile specimens undergo smoltification, migrate downstream, leave the river and fatten in the brackish waters of the sea coastal zone for one to three consecutive years until reaching sexual maturity, after which the fish return to the river for spawning. In summer, mykiss with the estuarine LS type feeds not in the estuary, but rather in the sea coastal zone outside the river boundaries (Pavlov et al., 2016). In winter, these fish inhabit a deep section of the estuary (1.5–2.0 m at low tide) above the so-called “gorlo” (throat) separating the river from the sea (Pustovit and Pichugin, 2006).

Riverine–estuarine (RE): these fish alternate living in fresh and brackish waters within the near-mouth zone of the river. Their exit from the river does not relate to smoltification and return to the does not relate to sexual maturation. During the life span of a single specimen may exit the river to the sea near-mouth zone one to three (most often one) time but always winter in the river.

In contrast to the migrant mykiss with other types of LS, the ER fish leaving the river for 1–2 months are large (FL 277–386 mm). The exit of such large fish into the estuary is observed during the period of downstream migration of juvenile Pacific salmon. In spring, part of the river mykiss, pursuing flocks of downstream migrants, follows after them into the estuary and the coastal part of the sea outside the river, where it continues to feed on juvenile pink salmon *Oncorhynchus gorbuscha*, chum salmon *O. keta*, and other Pacific salmonids. The RE fish return to the river at the end of August – September.

The Utkholok River estuary is of the highly stratified polyhaline type with a salt water wedge (Carleton-Rey, 1977; Karpenko, 1998); the coastal area has a third (moderate) surf type (Kusakin, 1977). Owing to this structure, E and RE mykiss lives in the mixing zone of riverine and sea waters in the conditions of sharply changing salinity and temperature: during the day, salinity may vary from 3 to 27‰, temperature from 6 to 12°C in July and from 12 to 20°C in August (Pustovit and Pichugin, 2006). In calm weather, with low sea waves, E and RE mykiss often stays in the upper desalinated (depth 1.5–2.0 m, salinity 7–12‰) river water layer above a saltier seawater layer (2–8 m, salinity 18–24‰) and can move 2–4 km from the mouth. In the estuary and coastal zone of the sea, mykiss feeds on juvenile Pacific salmonids, entering the estuary at high tides and leaving for the sea at low

tides. This type of feeding and migrations has been described for other rivers of Western Kamchatka as well: the Utkha (Dobrynina et al., 1988; Karpenko, 1998) and Kol’ (our observations) rivers.

Riverine (R): is a characteristic of the fish realizing their whole life cycle within river. In the Utkholok River, the distribution of the riverine mykiss is mosaic: it is confined to the areas of deep flow channel pits (area 250–500 m², depth 2.5–5.0 m) in the mid-stream part of the river. Usually, two or four individuals $FL > 300$ mm live in one such pit; they are confined to the edge sections of the pits either at the entrance to it, or at the place where the pit turns into the pool. Based on the tagging and recapture data ($n = 6$), the river mykiss exhibits settled mode of life and moves within the river system on little distances. In autumn (September–October) R and RE individuals stay together in the channel pits; they are similar in appearance, distribution and behavior. In autumn, R ($n = 87$) and ER ($n = 63$) mykiss feed on eggs of Pacific salmonids, amphipods (Gammaridae, Amphipoda) and larvae of amphibiotic insects: caddis flies (Trichoptera), mayflies (Ephemeroptera) and stoneflies (Plecoptera).

In all years of observations in the local population of mykiss in the Utkholok River the individuals with migrant LS types (TA and AB) predominated with the proportion of >60% in sum. At the same time, in different years the ratio of fish with different types of LS varies considerably. The proportion of fish associated with fresh waters (R and RE) is sometimes significant and in some years reaches ~40%. The smallest share is a characteristic of the fish with the estuarine LS type: they were recorded singly or in some years were absent at all. During the observation period, there was a tendency towards an increase in the proportion of fish associated with fresh waters (Table 1).

Mykiss spawns in rather vast areas of the river system. Reproduction of TA and AB-mykiss occurs in the main channel (in the upstream and midstream reaches) and in the Kolkaveem, Oglyamch, Vodorsol’, Kuvshes, etc. tributaries to the river. In these tributaries, large TA and AB fish reproduce together with R, RE and E individuals (Maksimov, 1974; our observations).

Age Composition

The age composition of mykiss of different LS types is very complex and is determined both by the number of complete years lived and by the combination of the duration of freshwater, marine, and estuarine periods of life. In general, the life expectancy of mykiss in the Utkholok River reaches 9–10 years. Among TA fish, the specimens at the age of 4+–9+ are found, with a predominance of individuals at the age of 6+ in all years; sexual maturation occurs mainly at the age of 6+ and 7+ (Table 2). Most TA fish spend three years in the river before downstream migration (Fig. 1) and fatten in the sea for three years (biograph-

Table 1. Proportion of mykiss *Parasalmo mykiss* specimens of different types of life strategy in the Utkholok River in different years, %

Year	Sample size, ind.	Type of life strategy				
		TA	AB	E	RE	R
1971	123	85.0	12.4	—	—	2.6
1995	133	67.2	8.0	6.2	8.0	10.6
1996	169	59.2	11.8	3.5	11.2	14.2
1997	173	55.2	14.5	2.2	13.2	14.9
1998	182	56.3	18.3	4.1	12.2	9.1
2000	198	56.0	15.3	3.1	11.3	14.3
2001	238	55.6	14.1	2.2	10.2	17.9
2002	248	52.3	12.2	4.1	13.2	18.2
2003	192	50.2	11.8	4.6	14.5	18.9
2004	277	60.5	12.6	—	4.2	22.7
2005	283	41.5	14.3	—	13.0	31.2
2006	227	40.9	12.3	7.0	13.2	26.4
2007	315	53.3	11.4	3.2	11.2	20.9
2017	269	63.5	7.1	3.0	11.1	15.2
2018	245	65.7	5.7	3.3	11.4	13.9

Here and in tables 2–8 the abbreviations for life strategy are as follows: TA—typically anadromous, AB—anadromous-B, E—estuarine, RE—riverine-estuarine, R—riverine.

Table 2. Age composition (top) and share of the specimens spawning for the first time (bottom) of mykiss *Parasalmo mykiss* in the groupings with different types of life in the Utkholok River, %

Age, years	Type of life strategy (sample size, ind.)				
	TA (2403)	Ab (265)	E (71)	RE (261)	R(405)
4+	<u>3.3</u>	—	<u>8.5</u>	—	—
	3.4		8.4		
5+	<u>23.4</u>	<u>4.4</u>	<u>36.6</u>	<u>5.4</u>	<u>7.7</u>
	15.6	4.4	45.1	—	—
6+	<u>51.7</u>	<u>25.8</u>	<u>45.0</u>	<u>31.6</u>	<u>26.3</u>
	49.3	36.1	45.1	34.4	26.1
7+	<u>19.2</u>	<u>37.6</u>	<u>9.9</u>	<u>41.5</u>	<u>35.3</u>
	31.7	46.3	1.4	42.8	48.3
8+	<u>1.9</u>	<u>24.9</u>	—	<u>13.5</u>	<u>23.0</u>
	—	13.2		22.8	25.6
9+	<u>0.5</u>	<u>5.4</u>	—	<u>5.4</u>	<u>4.6</u>
	—	—		—	—
10+	—	<u>1.9</u>	—	<u>2.6</u>	<u>3.1</u>
		—		—	—
Weighted average age, years	<u>5.93</u>	<u>7.06</u>	<u>5.56</u>	<u>6.64</u>	<u>6.98</u>
	6.07	6.67	5.38	6.87	6.99

ical group 3.3+). AB fishes have by a longer life span and later sexual maturation (Table 2). E-type mykiss has the simplest age composition and, in general, reaches sexual maturation earlier. The duration of the freshwater period in AB and E fish is generally shorter than in TA: among downstream migrants of AB and E fish >30% are individuals aged 2+ (Fig. 1).

The downstream migrants of these fish are represented by juvenile specimens that have undergone smoltification and migrate downstream at different stages of silvering: light parr and silver parr (Pavlov et al., 2005; Pavlov et al., 2016). In ER and R fish older individuals predominate and reach sexual maturation later (Table 2). In contrast to TA, AB, and E fish,

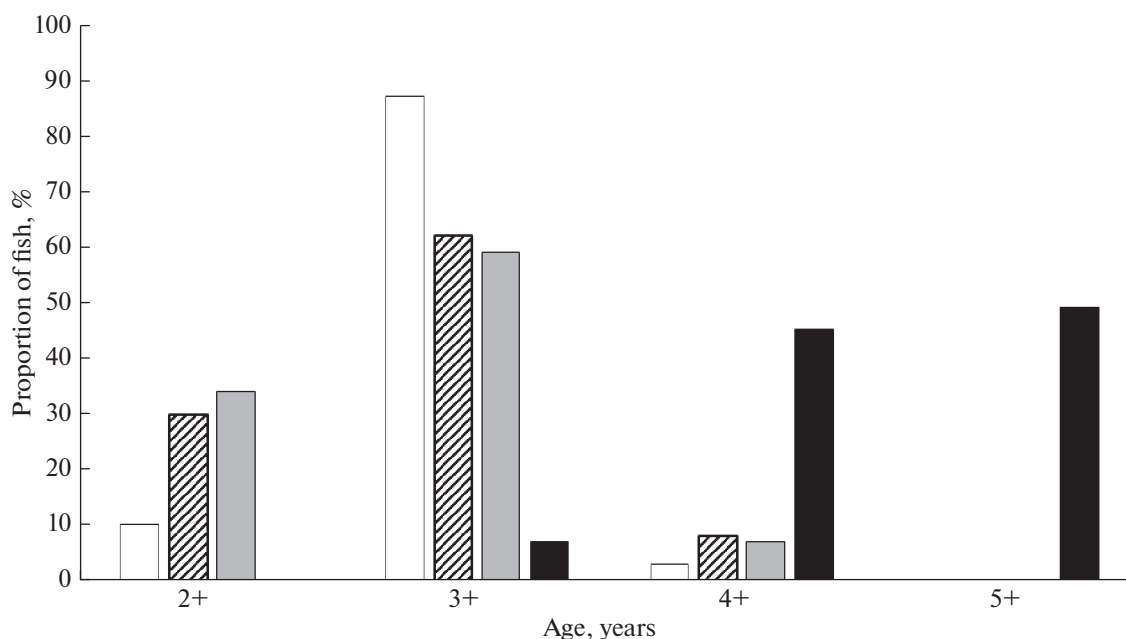


Fig. 1. Age composition of downstream migrants of the Utkholok River mykiss *Parasalmo mykiss* with different types of life strategy: (□)—typically anadromous, (▨)—anadromous-B, (■)—estuarine, (■)—riverine-estuarine.

downstream migration from the river of fish with ES LS occurs at a later age: mainly the fish of age 4+ and 5+ migrate to the estuary and coastal area (Fig. 1) without any signs of smoltification.

The complex age composition of mykiss with different LS types suggests that during joint spawning the fish belonging to several (5–8) generations are crossed, with young individuals being more common among TA and E fish, while among AB, RE, and P, the older specimens prevail. This ensures the integration of different generations and the maintenance of the general gene pool of the population.

Size and Sex Composition, Fecundity of Females

There are two size groups in the Utkholok River mykiss population (Table 3, Fig. 2). TA and AB individuals exhibit the largest sizes. The variation curves of the body length of mykiss with different types of LS overlap: small TA and AB juvenile individuals are similar in length and body weight to large E, RE, and P fish of older ages.

Females prevail among TA and AB specimens of mykiss; in the E fish, the sex ratio is generally equal, with a slight predominance of males; males noticeably predominate among RE and R fish (Table 3). The fecundity of TA and AB females is significantly higher than that of mykiss of other LS types. The Utkholok River mykiss population exhibit a high degree of repetition of spawning: some TA and AB individuals can spawn up to six to seven times in life, and most of the spawners are fish that reproduce two or three times in

life. E, RE, and R individuals spawn up to three or four times in their lives, but most of them are fish that spawn once.

That is, TA and AB females made the greatest contribution to reproduction in terms of total fertility. At the same time, ER and R mykiss males also play an important role in reproduction, participating in the fertilization of eggs of TA and AB females.

Growth

The inverse calculation of growth revealed that in the first years of life, before migration into the sea, s of TA, AB, and E juvenile mykiss grow more slowly than juvenile specimens that later turn to R or RE type (Table 4). Juvenile specimens of R and RE mykiss exhibit a significantly greater increase in body length (age class 1+: $t = 3.08–3.66$, $p > 0.999$ for different comparison pairs; age class 2+: $t = 3.25–4.05$, $p > 0.999$; age class 3+: $t = 4.31–4.82$, $p > 0.999$; age class 4+: $t = 7.13–8.58$, $p > 0.999$). A significant increase in the growth rate of ER and R fish begins at the age of four or more years, which is probably determined by the transition of juvenile mykiss in the Utkholok River to feeding mainly on fish (Kirillova and Kirillov, 2006; Kirillova, 2009). At the same time, the differences in body length between juvenile ER and R mykiss in the first years of life are insignificant ($t = 0.17–1.21$, $p < 0.95$ for different age classes).

At the same time, in groups of the same age, the limits of variation in body length of all juvenile specimens significantly overlap. Therefore, R and RE mykiss

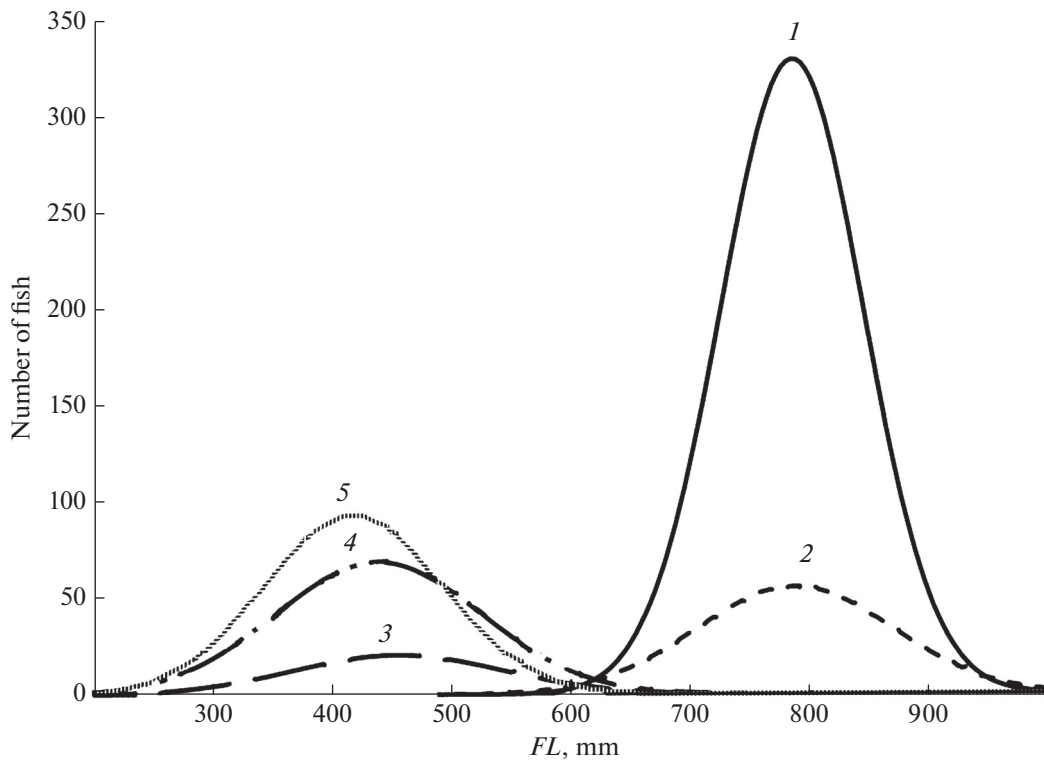


Fig. 2. Body length (*FL*) of mykiss *Parasalmo mykiss* with different types of life strategy: 1—typically anadromous, 2—anadromous-B, 3—estuarine, 4—riverine-estuarine, 5—riverine.

groups are formed from that part of juvenile fish that is not a discrete group, but belongs to the group of the fastest growing individuals and is an extreme variant of the variability range.

Morphometric Characteristics

Groupings of mykiss with different LS types have similar mean values and ranges of variation of meristic

Table 3. Size characteristic, proportion of sexes, fecundity of females and replication of spawning in the Utkholok River mykiss *Parasalmo mykiss* of different types of life strategy

Parameter	Type of life strategy				
	TA	Ab	E	RE	R
Body length (<i>FL</i>), mm	$\frac{783 (2069)}{559-965}$	$\frac{765 (312)}{540-942}$	$\frac{459 (79)}{289-660}$	$\frac{438 (256)}{278-650}$	$\frac{417 (421)}{280-613}$
Body weight, g	$\frac{5450 (2069)}{2013-10656}$	$\frac{5089 (312)}{1650-10020}$	$\frac{1317 (79)}{330-3800}$	$\frac{1271 (256)}{278-3522}$	$\frac{1039 (421)}{250-3718}$
Share of females, %	$\frac{67.5 (1924)}{59-74}$	$\frac{57.2 (288)}{52-70}$	$\frac{45.8 (62)}{40-49}$	$\frac{32.5 (218)}{27-38}$	$\frac{24.1 (334)}{11-28}$
Fecundity, pieces	$\frac{8185 (418)}{4915-13530}$	$\frac{8011 (87)}{4887-12893}$	$\frac{3759 (23)}{1220-4850}$	$\frac{3369 (89)}{1077-4413}$	$\frac{3211 (76)}{1103-4503}$
Replication of spawning	1–7, more often 2: 52% and 3 – 29%	1–6, more often 2: 41% and 3 – 32%	1–3, more often 1: 78%	1–4, more often 1: 63% and 2 – 33%	1–4, more often 1: 82%

Top—mean and (in parentheses) the number of fish studied; bottom—limits of the parameter variation.

Table 4. Body length (*FL*, mm) of mykiss *Parasalmo mykiss* of different types of life strategy during first years of life (according to the data of inverse calculations)

Type of life strategy	Sample size, ind.	Age, years			
		1+	2+	3+	4+
TA	328	92.5 ± 2.11 82–116	133.2 ± 3.12 102–165	176.1 ± 3.76 142–196	221.2 ± 4.77 202–235
AB	168	91.2 ± 2.27 80–111	130.7 ± 3.45 100–160	175.7 ± 3.89 141–200	219.2 ± 5.12 199–230
E	53	90.8 ± 2.89 80–103	131.2 ± 3.55 98–161	175.9 ± 4.01 140–191	220.3 ± 5.44 197–229
RE	119	102.3 ± 2.00 95–123	147.8 ± 3.23 125–175	201.1 ± 4.24 188–223	281.2 ± 5.11 265–301
R	277	101.8 ± 2.08 94–125	151.4 ± 3.76 122–177	203.2 ± 4.18 181–221	272.5 ± 4.89 249–288

Here and in Table 5: top—mean and error of mean; bottom—limits of parameter variation.

Table 5. Meristic parameters of the Utkholok River mykiss *Parasalmo mykiss* with different types of life strategy

Parameter	Type of life strategy (sample size, ind.)				
	TA (227)	AA (106)	E (51)	RE (94)	R (118)
<i>ll</i>	126.42 ± 0.82 123–132	125.73 ± 0.78 121–131	125.68 ± 1.01 118–135	127.00 ± 0.88 120–134	126.88 ± 1.01 121–135
<i>D</i>	9.68 ± 0.1 8–11	9.71 ± 0.11 8–10	9.75 ± 0.13 8–11	9.65 ± 0.14 8–11	9.75 ± 0.11 8–11
<i>A</i>	9.59 ± 0.10 8–10	9.54 ± 0.12 8–10	9.61 ± 0.13 8–10	9.56 ± 0.12 8–10	9.55 ± 0.10 8–10
<i>P</i>	12.65 ± 0.12 12–14	12.77 ± 0.14 12–15	12.72 ± 0.11 12–15	12.70 ± 0.14 11–14	12.68 ± 0.11 12–15
<i>V</i>	8.71 ± 0.10 8–9	8.70 ± 0.12 8–9	8.65 ± 0.09 8–9	8.69 ± 0.11 8–9	8.67 ± 0.09 8–9
<i>rb.1</i>	11.81 ± 0.18 10–13	11.77 ± 0.11 10–13	11.69 ± 0.13 10–13	11.76 ± 0.14 10–13	12.01 ± 0.11 10–13
<i>rb.2</i>	11.32 ± 0.16 10–13	11.24 ± 0.13 10–13	11.31 ± 0.12 10–13	11.27 ± 0.14 10–13	11.30 ± 0.10 10–13
<i>sp.br.</i>	19.60 ± 0.24 18–24	19.48 ± 0.25 17–23	19.77 ± 0.26 18–23	19.55 ± 0.27 18–23	19.69 ± 0.26 18–23
<i>pc</i>	41.22 ± 1.04 31–52	41.42 ± 0.98 32–48	42.80 ± 1.03 30–52	42.07 ± 1.17 31–53	41.50 ± 1.01 30–53
<i>vert.</i>	61.88 ± 0.47 59–64	62.08 ± 0.26 61–65	61.93 ± 0.36 60–64	61.84 ± 0.42 60–65	61.83 ± 0.37 60–64

Here and in Table 6 the following abbreviations for parameters are used: *ll*—number of scales in lateral line; *D*, *A*, *P*, *V*—number of branched rays in the dorsal, anal, pectoral and ventral fins; *rb.1*, *rb.2*—number of gill rays left and right, *sp. br.*—number of gill rakers left, *pc*—number of pyloric caeca, *vert.*—number of vertebrae.

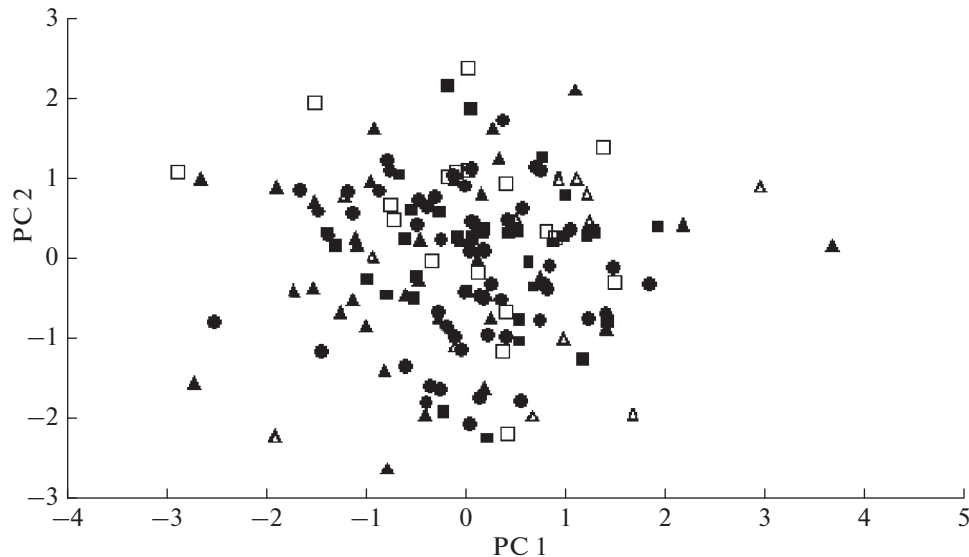


Fig. 3. Phenetic relations of mykiss *Parasalmo mykiss* groupings with different types of life strategy assessed by the method of principal component (PC) by combination of 10 meristic parameters: (●)—typically anadromous, (□)—anadromous-B, (△)—estuarine, (■)—riverine-estuarine, (▲)—riverine.

parameters (Table 5); in all cases a normal distribution of the observed values was revealed. In no one case of pairwise comparison of different samples, significant differences were found as evaluated by the Student's and Mann-Whitney tests. The application of the principal component analysis revealed that all mykiss samples form significantly overlapping factor areas and none of the 10 meristic features contributes significantly to discrimination (Fig. 3, Table 6).

Variability of Microsatellite Loci

Use of Micro-Checker software did not detect possible genotyping errors at any of the studied loci. All samples showed the possibility of the presence of null alleles at loci *One111*, *Omy1011*, and *Omm1070*. In this regard, information on these loci was not used to analyze mykiss differentiation. No significant differences were found at any locus between the observed genotypic distributions and the theoretical Hardy – Weinberg distributions.

The neutrality test revealed no selection for all loci, with the exception of *One112*, which is probably influenced by balancing selection (aposterior probability $p = 0.91$, $\log_{10} BF = 1.02$, where BF is the Bayes factor).

Genotypic Diversity of Mykiss

All studied loci in the Utkholok River mykiss were polymorphic, with the exception of the *One104* locus. Mykiss with river type LS is monomorphic on the *Ssa197* locus (Table 7). The maximum values of the expected H_E heterozygosity, as well as the largest number of A alleles, are in the *One112* and *One108* loci.

The mean estimates of heterozygosity and allelic diversity for all polymorphic loci in the TA, RE, and R fish samples were, as follows, respectively: H_E/H_O , 0.500/0.520, 0.524/0.549 and 0.491/0.474; A_R , 5.4, 4.9, and 5.8. There were no significant differences in the indicators of genetic diversity for the entire set of loci between mykiss with different types of LS ($p > 0.05$ in all comparison pairs). However, when comparing H_O at individual loci in five comparison pairs, significant differences were revealed ($p < 0.05$): between TA and P fish in loci *Ssa197*, *One103*, and *Oki10*; R and RE, in by loci *One103* and *One108*. In four out of five cases, river fish had significantly lower indices of the observed heterozygosity compared with TA or RE ones, and only in one pair of comparison (at the *One108* locus) this indicator was lower in RE fish than in P.

Table 6. Loads of eigenvectors of meristic parameters in the Utkholok River mykiss *Parasalmo mykiss* with different types of life strategy

Parameter	PC1	PC 2
<i>ll</i>	-0.6157	0.0254
<i>D</i>	-0.2142	-0.4314
<i>A</i>	0.4283	0.0656
<i>P</i>	0.5349	0.4513
<i>V</i>	-0.4219	0.6218
<i>rb.1</i>	-0.3716	0.5778
<i>rb.2</i>	-0.0911	0.4821
<i>sp.br.</i>	0.4682	0.1764
<i>pc</i>	0.2985	0.3263
<i>vert.</i>	0.1845	0.1659

PC1 and 2 – principal components 1 and 2.

Table 7. Genetic variability of mykiss *Parasalmo mykiss* of different types of life strategy by polymorphic microsatellite loci

Locus	Index	Type of life strategy		
		TA	RE	R
<i>Ssa197</i>	A/A_R	2/1.98	2/1.95	1/1.00
	H_E/H_O	0.102/0.107	0.054/0.055	0.000/0.000
	n	56	36	46
<i>Ssa20.19</i>	A/A_R	3/2.99	3/3.00	3/3.00
	H_E/H_O	0.568/0.607	0.584/0.617	0.597/0.652
	n	56	34	46
<i>One103</i>	A/A_R	2/2.00	2/2.00	2/2.00
	H_E/H_O	0.468/0.410	0.475/0.638	0.409/0.304
	n	56	36	46
<i>One108</i>	A/A_R	13/11.70	8/8.00	13/12.10
	H_E/H_O	0.814/0.857	0.799/0.785	0.850/0.945
	n	56	28	37
<i>One112</i>	A/A_R	13/11.30	11/10.80	15/12.80
	H_E/H_O	0.800/0.857	0.846/0.888	0.840/0.772
	n	56	36	44
<i>Oki10</i>	A/A_R	8/6.30	7/6.30	8/7.00
	H_E/H_O	0.715/0.767	0.686/0.611	0.675/0.578
	n	56	36	45
<i>Ots3</i>	A/A_R	2/1.70	2/2.00	3/2.40
	H_E/H_O	0.035/0.036	0.221/0.250	0.064/0.065
	n	56	36	46
Среднее	A/A_R	6.14/5.40	5.00/4.90	6.40/5.80
	H_E/H_O	0.500/0.520	0.524/0.549	0.491/0.474
	n	56.0	34.6	44.3

A —number of alleles, A_R —allele diversity, corrected by the sample size; H_E , H_O —expected and observed heterozygosity, n —sample size, ind.

Genetic Differentiation of the Utkholok River Mykiss

Differentiation of mykiss both in allele frequencies and genotypes is significant as assessed based on the entire set of loci ($p < 0.001$). This heterogeneity is mainly associated with highly significant differences at the *Ots3* locus ($p = 0.008$). Differences for the *Ssa197* ($p = 0.044$) and *One108* ($p = 0.022$) loci are also significant; differences for the rest of the polymorphic loci are insignificant ($p > 0.05$).

The overall assessment of mykiss differentiation in terms of θ index is small, but significant: $\theta = 0.006$, with a 95% bootstrap interval (0.002, 0.012). The *Ots3* locus makes the greatest contribution to differentiation ($\theta = 0.053$).

Pairwise comparison (F_{ST}) of mykiss of different LS types revealed significant differences between ER and TA specimens ($p = 0.003$), as well as between R and ER ones ($p = 0.042$) (Table 8). Differences

between TA and P mykiss are insignificant. Pairwise F_{ST} values range from 0.005 to 0.008. Comparisons in terms of genotype frequencies (Fisher's exact test) show similar results: highly significant differences between TA and ER mykiss ($p = 0.001$) and differentiation of R and ER mykiss ($p = 0.048$).

Below diagonal — pairwise values of genetic differentiation F_{ST} ; above diagonal — pairwise comparison by frequencies of genotypes (Fisher's exact test); boldface marks statistically significant differences ($p < 0.05$).

The study revealed that genetic differentiation in the Utkholok River mykiss relates to the differences between fish with an ER-type LS and others. The ER mykiss significantly differs from TA fish in three loci: *Ots3* ($p = 0.007$), *One108* ($p = 0.024$), and *One112* ($p = 0.009$). The ER significantly differs from R mykiss in the *Ots3* locus ($p = 0.009$). In addition, significant differences in one locus *Ssa197* ($p = 0.032$)

were found between TA and R fish, but the analysis of the entire set of microsatellite loci, revealed that the differences between these samples are insignificant (Table 7).

The clustering using the STRUCTURE software show the maximum value of the probability corresponding to the minimum estimate of the log-likelihood $\ln Pr(X/K)$ for $K = 1$. Thus, it is most likely that all mykiss individuals with different LSs belong to the same cluster.

DISCUSSION

The problem of the formation of anadromous and resident individuals in mykiss, elucidation of the role of heredity and environmental factors in this process are in focus of studies by researchers from different countries, but at present the data available are ambiguous. It is known that in a number of cases the maternal origin and genetic characteristics of fish influence formation of LS through the anadromous or resident channel of individual development (Thrower et al., 2004; Carlson and Seamons, 2008). Thus, in some North American mykiss populations, regions of the genome (QTL — quantitative trait loci) have been identified that, at the level of individuals, affect the smoltification process and the formation of anadromous LS in these fish (Nichols et al., 2008; Le Bras et al., 2011; Hecht et al., 2013). At the same time, the authors point out that the revealed genetic differences are not due to isolation and cannot be considered as indicators of the divergence of anadromous and resident fish in the populations studied (Thrower et al., 2004; Nichols et al., 2007, 2008; Le Bras et al., 2011; Hecht et al., 2013).

Some studies showed that the largest proportion of smolts is observed among the offspring of anadromous spawners, while in the offspring of resident spawners, predominantly resident individuals are formed (Hayes et al., 2012; Liberoff et al., 2014). Heritability (the proportion of genetic variability in the total phenotypic variability) for some features associated with anadromia in mykiss is assumed to be rather high (Thrower et al., 2004). However, both in the offspring of anadromous and resident parents, 10–33% of individuals realize alternative LS, which indicates the influence of environmental factors on the formation of either anadromous or resident lifestyle (Ruzycski et al., 2009; Hayes et al., 2012; Berejikian et al., 2014; Liberoff et al., 2014).

At the same time, the results of many other studies show that the formation of LS is not strictly determined by the hereditary factor, i.e., by the genetic structure: over the decades, in mixed populations, 7–20% of anadromous fish originate from resident females, and the proportion of resident fish with anadromous mothers, is even higher (Zimmerman et al., 2003, 2009; Sharpe et al., 2007; Christie et al., 2011; Courter et al., 2013; Sloat and Reeves, 2014; Sloat et al., 2014).

Table 8. Matrix of comparison of genetic differentiation of the Utkholok River mykiss of different types of life strategy

Type of life strategy	Type of life strategy		
	TA	RE	R
TA	—	0.001	0.176
RE	0.008	—	0.048
R	0.005	0.006	—

It was found that during the introduction of mykiss into rivers upstream the waterfalls changes in the genetic structure of the population occur due to gene drift and, probably, selection pressure, but, even after 70 years of isolation, smolts are still produced among the juveniles specimens of resident mykiss (Thrower and Joyce, 2004; Hayes et al., 2012).

Various researchers point out great importance of the influence of the environment on the predetermination of anadromous or resident LS through differentiated growth of fry and fat accumulation processes, which can often neutralize the effect of the genetic component (Dodson et al., 2013; Doctor et al., 2014; Sloat, Reeves, 2014; Sloat et al., 2014).

In view of the ambiguous data on the contribution of genetic variability and environmental factors to the formation of alternative LS, the data of a comparative analysis of the sympatric groups of anadromous and resident mykiss using molecular methods are of special interest. Different situations are described in the rivers of North America. In some cases, the differences between anadromous and resident groups were not revealed: they reproduce together and there is a gene flow between them (Taylor, 1995; Docker and Heath, 2003; Seamons et al., 2004; Olsen et al., 2006; McMillan et al., 2007; Christie et al., 2011). In other cases, significant differences were found in the variability of microsatellite loci, determined by the complexity of the river basin, the timing of spawning of anadromous and resident fish in different tributaries and the resulting assortative crosses (Narum et al., 2004, 2008; Heath et al., 2008; Mills et al., 2012).

Currently, most researchers, when studying the formation of LS diversity at the level of local populations, attach particular importance to a comprehensive analysis of the population structure, genetic variability, and structure of the river basin (Docker and Heath, 2003; Manel et al., 2003; McPhee et al., 2007, 2014; Pavlov et al., 2009, 2016; Kuzishchin, 2010; Fleming et al., 2014). In this regard, in order to understand the relationship of anadromous and resident groups and the ways of their origin, the need for a thorough analysis of each population at the level of individual river systems differing in basin area, geomorphology, localization of mykiss spawning grounds and other is emphasized (Docker and Heath, 2003;

Gomez-Uchida et al., 2009; Dodson et al., 2013; Fleming et al., 2014; McPhee et al., 2014; Sloat et al., 2014).

The Utkholok River is one of the rivers of interest for analyzing the population structure and processes of formation of LS diversity. The mykiss population inhabiting this river is a complex, multilevel system of groupings with different LS, each of which, in addition to the extent of exhibited traits of migratory behavior, is characterized by a specific size, age, sex composition, and the ratio of the first-maturing and re-maturing fish. Large spawning area suitable for mykiss breeding is a specific feature of the Utkholok River: virtually the entire middle and upper reaches of the river and the main tributaries serve as mykiss spawning grounds (Pavlov et al., 2016). Of particular interest the Utkholok mykiss is due to the significant proportion of RE fish in the population, since in the rivers of North America semi-anadromous (brackish-water) groups fattening in the estuary are poorly studied (Busby et al., 1996; Behnke, 2002; Quinn and Myers, 2004; Hard et al., 2007).

The grouping system of the Utkholok Rives mykiss with different types of LS is dynamic, and almost all parameters of the population structure vary temporally (Savvaitova et al., 1997, 2002; Pavlov et al., 2001, 2016). The absence of differences in meristic parameters and the analysis of the variability of microsatellite loci revealed that the Utkholok mykiss is a single, integrated grouping of the population level of organization with a common gene pool. Integration into a single population is provided by high abundance of TA and AB fish, which use for reproduction the entire river system, from the foothills to the downstream reaches, and spawn with individuals of all other LS types. According to our observations, very often in spawning grounds, pairs of spawners are formed from large TA or AB females and small ER and R males. This reduces the likelihood of assortative crossing and isolation between mykiss groups with different LS types.

The revealed significant differences in some loci between TA, on the one hand, and ER and R individuals, on the other, presumably, may not serve as evidence of their reproductive isolation, but mark the influence of heredity on the formation of different types of LS. It is possible that the localization of microsatellite loci that are differentiating for mykiss with different types of LS in the Utkholok River relates to the genomic regions involved in the determination of physiological or morphological traits affecting the formation of LS (QTL regions) (Nichols et al., 2008; Le Bras et al., 2011; Hecht et al., 2012, 2013; Hale et al., 2013).

For instance, for some SNP (Single nucleotide polymorphism) and microsatellite markers demonstrating significant differentiation between the resident and migrant mykiss in North America, a close localization with potentially involved genes and genomic regions in the formation of anadromia has been shown (Martínez et al., 2011; Narum et al., 2011;

Limborg et al., 2012; Hale et al., 2013). Despite the lack of evidence for the effect of selection on most loci in our study, it cannot be ruled out that the revealed genetic differentiation may be determined by the differences arising in fish due to the action of selective forces under specific environmental conditions (Taylor, 1991; Boula et al., 2002; Heath et al., 2008).

One may also assume the influence of heterozygosity on LS formation in mykiss. In some salmonids, sea trout *Salmo trutta* and mykiss, increased level of heterozygosity at allozyme loci was associated with an increase in the growth and maturation rates of individuals, the level of metabolism and adaptability (Leary et al., 1983; Ferguson, 1992; Mitton, 1994; Makhrov et al. others, 1997). However, in contrast to allozymes, microsatellites are noncoding sequences; their structural and functional role in the genome is debatable (Li et al., 2002). It was assumed that microsatellites could exhibit a correlation with phenotypic traits, for example, at linking to allozyme loci, and under the influence of natural selection, which, however, was not confirmed by any empirical data (Thelen and Allendorf, 2001; Hansson and Westenberg, 2002).

Our data on the differences in the observed heterozygosity between mykiss with different types of LS are ambiguous; for a number of loci, river fish have significantly lower values of heterozygosity indices, however, for other loci, their heterozygosity is higher than in TA and ER fish. In addition, the significance of differences across the entire set of loci between mykiss of different LS types was not revealed. Finding of a reliable correlation between heterozygosity and phenotypic traits requires additional research and collection of mykiss with different LS types for many seasons.

It is obvious that the influence of heredity on the formation of TA, ER, and R individuals can be considered as only partial, taking into account the low (<1%) indicators of F_{ST} differentiation and the results of Bayesian clustering.

The results of the present study allow us to propose a hypothetical scheme of intrapopulation differentiation and the formation of LS diversity in the Utkholok River mykiss. Analysis of the age composition and growth of juvenile specimens revealed that this process takes place in several stages during 4–5 years of life of each generation.

The first stage of differentiation in the mykiss fry generation occurs during the first and second summer of life. Reverse calculations of growth by fish scales showed that the fastest growing individuals in a generation retain a high growth rate in the future and switch to feeding on fish by the end of the second summer of life (Kirillov and Kirillova, 2006). A high growth rate in the first years of life directs development strictly towards the formation of a river lifestyle, fish do not undergo smoltification and are settled, being a river-bed predator (Kirillov and Kirillova, 2006; Pavlov et al., 2016). Our data are accords well with the results

of studies on mykiss in the rivers of North America, which showed that rapid growth and the achievement of large sizes largely determine the development towards the formation of resident individuals (Satterthwaite et al., 2010; Sogard et al., 2012).

Earlier we revealed the formation of river residents in this way in another salmonid species, Dolly Varden char *Salvelinus malma*, in the Kol' River population (Gruzdeva et al., 2017). It is likely that the highest growth rate of mykiss in a generation, in addition to environmental factors, may be genetically determined. Thus, in experimental studies on mykiss in North America, a region of the genome in which genes determining many traits, including the growth rate are concentrated, was identified (Nichols et al., 2008).

The second stage relates to smoltification and downstream migration. Juvenile specimens that do not have such high growth rate as juvenile R and RE-fish, during the second to fourth year of life, smoltify and migrate downstream into the sea. The duration of the freshwater phase of the life cycle of such fish is determined by complex processes of growth, fat accumulation (Pavlov et al., 2005, 2007; Pavlov S.D. et al., 2011) and, probably, gametogenesis, as we have shown earlier on the example of Dolly Varden char and cherry (masou) salmon *Oncorhynchus masou* (Gruzdeva et al., 2013, 2017). The number of years that juvenile TA, AB, and E mykiss spend in fresh water before migrating downstream into the sea is determined by their reaching a certain critical age, body size, and fat content (Pavlov et al., 2005, 2007, 2010; Satterthwaite et al., 2009; Beakes et al., 2010).

In the Utkholok River, the overwhelming majority of juvenile specimens are smoltized at the age of 3+ (Fig. 1) (Pavlov et al., 2005). Most likely, AB and E fishes are formed from a part of downstream migrants, in which the degree of development of smoltification-related transformations is less pronounced: from the so-called light parr, which are more often 2+ years old and have to linger in the estuarine zone (Pavlov et al., 2005).

The third stage is the differentiation of the fast-growing fish remaining in the river. Some of them leave the river for fattening in the estuary and the sea coastal part; they subsequently become RE fish. The exit of the large river mykiss from the river is not associated with smoltification and occurs during the downstream migration of juvenile Pacific salmonids. In the first half of summer, a part of mykiss, pursuing flocks of downstream migrants, migrates after them into the estuary and the sea coastal part, where, at low water salinity, favorable conditions are formed for fattening those fish that have not undergone smoltification. The estuaries of some North American rivers are considered a highly productive area for mykiss fattening, but are poorly utilized by other salmonids (Shapovalov and Taft, 1954; Bond et al., 2008). It is possible that some genetic isolation of the ER group is

a reflection of differences in fish that have a more active migratory behavior or an increased level of metabolism that promotes migration into the estuary and exit from the river when chasing schools of downstream salmonids.

As it was shown in the North American mykiss, the individuals with a higher level of energy metabolism are more prone to travels (Forseth et al., 1999; Morinville, Rasmussen, 2003; Garrett, 2013; Sloat and Reeves, 2014; Sloat et al., 2014). It is possible that the ability of ER mykiss to tolerate temperature and salinity changes (so characteristic of the estuarine zone) and to feed efficiently during the summer months in brackish water may also be hereditary in nature. However, in our opinion the availability of food resources is the stimulus for migrating outside the river: according to our observations, ER fish more often enter the estuary in odd years, when there is a mass migration of juvenile specimens of productive generations of pink salmon and chum salmon. The formation of a group of ER-fish is the final stage of intrapopulation differentiation, which, among other factors, may be influenced by heredity, i.e., the genetic component.

Thus, the formation of LS type diversity and the structure of the Utkholok River mykiss population are multistage processes resulting from a complex combination of exogenous (habitat: large areas of spawning grounds, conditions of habitat and feeding of juvenile specimens in the river, food availability in the estuary) and endogenous (hereditary) factors. As a result, due to differences in the state of the habitat, a temporal dynamics of the ratio of fish with different types of LS arises (Table 1), which is an adaptive response to the action of external factors. It is noteworthy that in 1970–1971 E and RE fish were not found. There is reason to believe that this was a consequence of the so-called cold era in the North Pacific, characteristic of this period of the twentieth century (Mantua and Hare, 2002; Overland et al., 2008). It is likely that the low temperature of the sea surface and the coastal zone limited the possibility of summer feeding of fish that did not undergo smoltification. However, the starting of a warmer period at the end of the twentieth century led to significant rearrangements in the ecosystem of the Pacific Ocean and the Sea of Okhotsk, in particular, to a northerly displacement of the feeding area of almost all salmonids, especially in the western part of the Pacific Ocean (Welch et al., 2000; Myers et al., 2007, 2016; Abdul-Aziz et al., 2011; Kaeriyama et al., 2014). As a result, the Utkholok River mykiss population while remaining internally integrated, was able to demonstrate a system of flexible adjustment to large-scale fluctuations of environmental factors for a relatively short period (about 30 years). Appearance in the 1990th of E- and RE groupings as elements of local temporal adaptation, increased the level of population diversity and its stability in space and time. It is known that complexly structured populations are significantly more resistant to any adverse impact (Luck et al., 2003;

Greene et al., 2010; Schindler et al., 2010; Sloat et al., 2014).

In general, the results of the present study support the concept on the epigenetic nature of the LS diversity formation mechanism in the Utholok River mykiss population. There is every reason to consider mykiss from Utkholok River as an integrated population with all the diversity of individuals with different LS types and as an independent unit of biodiversity preservation. The case studied here presumes a differentiated approach to the analysis of the structure of mykiss populations, i.e., an analysis of the patterns and mechanisms of the formation of LS diversity in each individual river. The geomorphology of the river is known to have a direct impact on genetic diversity, reproduction characteristics, LS diversity and the structure of mykiss populations (Pavlov et al., 1999, 2001, 2008; McPhee et al., 2007, 2014; Kuzishchin et al., 2008; Kuzishchin, 2010).

In this regard, it is very likely that the mechanisms of the process of LS diversity formation will be specific for each individual local population. In addition, the materials of the present study assumes the use of other advanced methods of molecular genetic analysis to identify the role of hereditary factors in the formation of diversity at the population level of organization.

ACKNOWLEDGMENTS

We are sincerely grateful to the participants of the expeditions of Moscow State University WSC-TCA (Wild Salmon Center, Portland, USA, The Conservation Angler, Edmonds, USA) in 1995–2018 for sampling the field materials. We are especially grateful to P. Sowerel, J. Miller, G. Kennedy (TCA), M. Sloat (WSC), M. Zimmerman, L. Campbell (Fish and Wildlife Service, State of Washington, USA), N. P. Borodina, S. E. Abramov, A. S. Kustov, P. A. Rukin, (Rosprirodnadzor Directorate in the Kamchatkii Kray, A. A. Andryukhin, D. S. Navrotsky, A. A. Turushev, D. V. Turusheva (Kamchatka Trophy Hunts, Elizovo Town, Kamchatkii Kray) for the tremendous efforts in providing and conducting field studies.

FUNDING

The study was carried out within the frames of Lomonosov Moscow State University “Noah’s Arc” (processing of genetic materials); analysis of long-term data, preparation of summary tables and manuscript were carried out under the support of Russian Scientific Foundation, grant no. 19-14-00015.

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