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Features of Spatial Structure of Mikizha *Parasalmo mykiss* in the Kol River, Western Kamchatka: On the Problem of the Population Integration in the Complex River System

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Abstract—The features of within-river migrations, biological and morphological characteristics, and allozyme variation are studied in mikizha *Parasalmo mykiss* in the Kol River basin, Western Kamchatka. In this river system with a complex geomorphology, mikizha spawns in tundra-type tributaries, and each tributary is characterized by a certain combination of size, water content, hydrological, and thermic regime. Therefore, the spawning conditions, as well as spatial distribution and biological characteristics of the progeny, are variable. Based on the mark-recapture data, mikizha intensively migrates within the river system, and it does not show any fidelity to certain sites; the spawners can enter different tributaries in various years. Based on the variation of morphometric characters, the difference between the juveniles from various tributaries is absent. The results of allozyme variation show that, despite a mosaic structure of the habitats, mikizha of the Kol River is represented by a single population with a common genofond. Based on the results of this study, it is concluded that mikizha of the Kol River is a single and highly integrated population despite the factors facilitating the diversity. A mechanism of a stable population unity is connected with the within-river migrations, and the spawners are redistributed in different tributaries of the river during each year. This redistribution is directed against the founder effect and gene drift.

Keywords: mikizha *Parasalmo mykiss*, population structure, mosaic habitats, spawning tributaries, river system, allozyme variation

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INTRODUCTION

The investigation of the structure and spatial and temporal variation of the species is one of the most important fundamental problems of microevolution and population biology of fishes (Nikol'skii, 1980; Mina, 1986; Savvaitova, 1989; Waples, 1991; Bernatchez, 1995). The attention of researchers is focused on salmonid fishes (Salmonidae), and the analysis of their diversity at the species and intraspecific levels is conducted in many studies. At present, a significant amount of data shows that the variation in fishes has a mosaic pattern, and it is displayed both in geographic structuring caused by large-scale historical events and at a level of certain water systems due to the occurrence of sympatric intraspecific forms and groups (Nielsen and Sage, 2001, 2002; Taylor et al., 2001; Castric and Bernatchez, 2003; Klemetsen et al., 2003; Hendry and Stearns, 2004).

Recently, the problem of variation of salmonid fishes within a single river basin is intensively studied. In these conditions, the appearance of local isolated groups and intraspecific structuredness of the stock is possible. The final result is the formation of a so-called metapopulation with a high expression of local adaptations, which are adequate to habitat mosaicity (Cooper and Mangel, 1999; Dunham and Rieman, 1999; Hanski, 1999; Young, 1999; Rieman and Dunham, 2000; Sultan and Spencer, 2002; Neville et al., 2006). According to some investigations, the occurrence of the elements of the catchment basin structure (e.g., riverbed branching or the difference in the location of the sites above sea level) can reduce gene flow between certain spawning groups (Angers et al., 1999; Hebert et al., 2000; Castric et al., 2001; Costello et al., 2003). Most often, the factors leading to the fragmentation of a single population are connected with the occurrence of waterfalls and rapids preventing fish migrations. These structures represent the filters or barriers for the penetration of the fish from lower to upper reaches of the river (Currens et al., 1990; Griswold et al., 1997; Carlsson et al., 1999; Carlsson and Nilsson, 2001). Nevertheless, in several salmonid species, the metapopulation appears in the absence of physical barriers as a result of different geomorphology of riverine sites and spawning grounds located in the tributaries of different types (Hebert et al., 2000; Costello et al., 2003; Taylor et al., 2003; Guy, 2005; Massa-Gallucci et al., 2010; Pracheil et al., 2013). However, the fragmentation degree can be variable in different salmonid species and in various river basins (Young, 1999; Costello et al., 2003; Meka et al., 2003; Nielsen et al., 2003; DeHaan et al., 2011; Walsh et al., 2013). Despite a large number of publications devoted to the differentiation of local fish stocks within a river basin, the effect of the basin structure on the intraspecific diversity is poorly studied (Angers et al., 1999; Hebert et al., 2000; Castric et al., 2001; Torgersen et al., 2006; Budy et al., 2014).

Mikizha *Parasalmo mykiss* from Kamchatka is a good model object for the investigation of the problem. This species is characterized by a high level of variation, and individuals with different life strategy types and different expression of anadromous or resident life styles can be found in the population (Pavlov et al., 1999, 2001a, 2009, 2016). As is known, the ratio between the individuals with different life strategy types in Kamchatka is different in the rivers of various types and length. This ratio depends on the geomorphology of the river basin: anadromous mikizha is numerous in short constrain tundra-type rivers, and resident mikizha is the most abundant in braided-anastomosus piedmont rivers (Pavlov et al., 2001b, 2008; Kuzishchin, 2010; Kendall et al., 2015). Nevertheless, genetic separation of the fish with different life strategy types is not revealed in several rivers: the spawning of anadromous and resident mikizha occurs jointly (Kuzishchin et al., 2007; McPhee et al., 2007, 2014).

In Kamchatka, the spawning of mikizha is observed exclusively in the tundra-type rivers or in their tributaries. In these watercourses, a favorable temperature regime facilitating reproduction of the species in the severe climate conditions of the peninsula is observed during the spring and summer (Kuzishchin et al., 2002, 2008). Owing to the spawning pattern, the spawning of mikizha is spatially segregated in several piedmont-type rivers: it occurs exclusively in the tundra-type tributaries. Thus, a situation leading to the separation of the spawning grounds of mikizha and the appearance of conditions facilitating population fragmentation is observed in several river basins (Kuzishchin et al., 2008; Kendall et al., 2015). The Kol River, Western Kamchatka, is one of the complex piedmont-type river systems. In this river, mikizha spawns in six tundra-type tributaries distributed over the entire river basin (Kuzishchin et al., 2008; Pavlov et al., 2009). However, detailed structure of this population, including biological and morphological characteristics of the young, distribution of juveniles within the river system, migrations of the progeny and riverine spawners, and genetic composition of the fish, have not been studied.

The goal of this study is the investigation of the spawning conditions, within-river migrations, and spatial and genetic structure of mikizha in the Kol River basin.

MATERIALS AND METHODS

The material was collected from 2002 to 2006 in the Kol River basin, Western Kamchatka. The river head is located in the spurs of the Sredinny Range of Kamchatka, and the river flows into the Sea of Okhotsk. The river parameters are as follows: approximately 130 km length and 70 m width in the mouth; river discharge in the mouth is 111 m^3/s during the flood and 56 m^3/s at low water; and the total catchment area is 1580 km^2. The river is characterized by a mountain and piedmont pattern all the way from the source to the mouth, it includes several parallel riverbeds (tributaries), and the slope of the bed is more than 5 m/km. Many tributaries of different types, lengths, and water contents flow into the river (Fig. 1). The mountain-type tributaries are located mainly in the upper reaches of the river, and the tundra-type tributaries are usual for the middle and lower reaches (Pavlov et al., 2009). The structure of the tributaries, water current speed, river discharge, water temperature and hydrochemical parameters, as well as fraction composition of the grounds, were analyzed according to the methods applied for the integrated assessment of salmonid habitats. The comprehensive descriptions of the methods are given in our previous studies (Kuzishchin et al., 2008, 2009, 2010; Pavlov et al., 2009, 2016).

The spawners were collected at the spawning grounds in the spring, and their number was assessed visually from the bank of the river and during underwater observations. The spawning ground areas were measured with a tape measure, and they were mapped. The fishes were caught with hook and line (catch-and-release fishing), and sex was determined based on external characters. To determine the life strategy and age of the fish, the scales were obtained from the first to fourth rows above the lateral line in the area between the posterior edge of the dorsal fin and anterior edge of the adipose fin (Pavlov et al., 2001a). The juveniles were collected using electrical fishing (Smith-Root, model 15-A, modification 20316; alternating pulse current, voltage 350–400 V, frequency 40–60 Hz, and pulse duration 2 ms) during low water in the summer (August). A method of three-fold catches of each site was applied (Zippin, 1956), and the distribution of the fishes in the spawning tributaries, as well as their density and biomass, were assessed. In total, 576 catches were conducted on the sites (each not less than 150 m^2 in area) from the heads to the mouths. For the morphological and genetic analyses, the juvenile samples of the age class 2+ were used for each tributary. The morphometric analysis was conducted by an operator on fresh exemplars based on the modified scheme of Pravdin (Pavlov et al., 2001a).

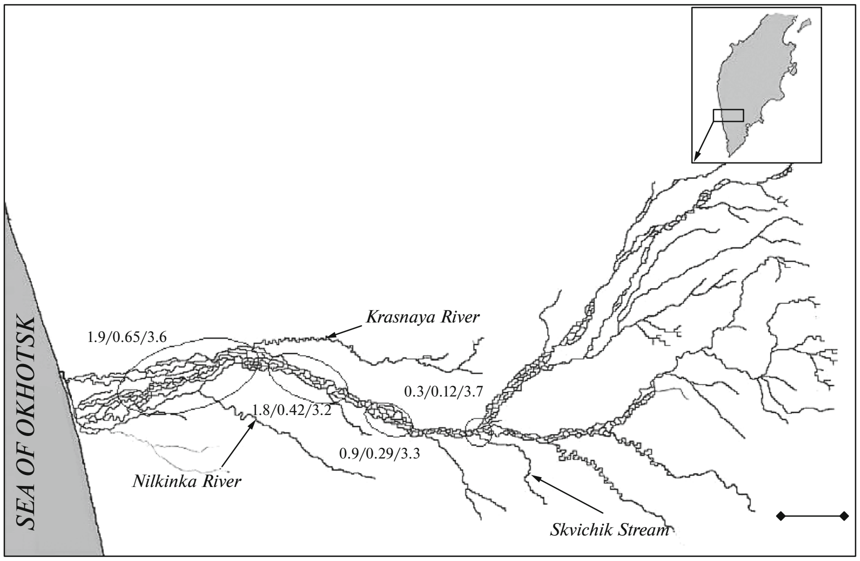

Fig. 1. Kol River and location of spawning tributaries of mikizha *Parasalmo mykiss*; the samples from these tributaries are used in this study. Ovals indicate the areas of the river with the largest wintering holes of mikizha. The numbers are as follows: mean number of the holes per 1 km of the main riverbed/mean area of the hole, ha/mean depth of the hole, m. Scale bar: 5 km.

To study fish migrations, the fishes were tagged by individual numbered marks, and recaptures were registered. The fishes were caught both in the spawning tributaries and in the main riverbed from the mouth to 93 km upstream. The external hydrostatic marks (floy tags) were applied for the fishes larger than 300 mm fork length (*FL*), and microchip marks (PIT tags) (Prentice et al., 1990; Castro-Santos et al., 1996; Pine et al., 2010) were used for the juveniles 100–300 mm *FL*. During the tagging, the sampling sites were registered with a GPS navigator. The fishes were collected by expeditionary groups during the period of open water and by local fishermen in the winter. These especially trained fishermen sampled the fish in strict accordance with the methods used during the period of open water.

The ratio between the progenies of anadromous and resident females was assessed by the microchemical otolith analysis (quantitative analysis of bivalent metal ions, calcium, and strontium). Based on this method, in addition to a presence of marine or freshwater ontogenetic periods of the individual, the life strategy type of the mother can be assessed. It is supposed that, if strontium content in the nuclear zone (primordium) of the otolith is high (1.5–2.0 times higher than in the adjacent layers), the individual originates from an anadromous female; however, if this content is similar to that in adjacent otolith layers, the individual represents a progeny from a resident female (Radtke, 1989; Kalish, 1990; Secor et al., 1995; Radtke et al., 1997, 1998; Volk et al., 2000; Doubleday et al., 2014). The content of microelements in otoliths was determined by X-ray fluorescence (XRF) microanalysis with a Tornado M4 (Bruker AXS, Germany) spectrometer (Pavlov et al., 2013). Mikizha juveniles at the age 2+ (subjected also to morphometric and genetic assessments) were used for this analysis.

For the investigation of allozyme and genetic diversity and heterogeneity of local spawning groups, the samples collected at the spawning grounds of three tributaries of the Kol River (Nilkinka River, Krasnaya River, and Skvichik Stream) were used (Fig. 1). Based on the standard methods of electrophoretic analysis (Davis, 1964; Peacock et al., 1965), the variation in 18 enzymatic systems encoded by 43 allozyme loci was studied (Pavlov, 2000; Pavlov et al., 2001a).

The amount of the material used for different types of the analysis is given in the tables and figures. The material is processed by the methods of variation statistics. The significance of differences was assessed by Student's *t*-test (t_{st}) and nonparametric tests (Mann–Whitney test, *M–U*). Statistica 8.0 software was used for the calculations and preparation of the graphs. For the assessment of allele frequencies, allele variation (*A*), predicted and observed heterozygosity (H_E, H_o), and degree of population differentiation (θ), GDA 1.0 program (Lewis and Zaykin, 2001) was applied. The statistical package GENEPOP 3.4 (Raymond and Rousset, 1995) was used for the pairwise differentiation of the samples F_{ST}.

RESULTS

Biological characteristics of mikizha groups from different tributaries. Mikizha spawns in six of eleven tundra-type tributaries located in the Kol River basin. Each spawning tributary is characterized by a unique combination of size, water content, and hydrological and thermic regimes (Kuzishchin et al., 2008; Pavlov

Table 1. Characteristics of three tundra-type spawning tributaries of mikizha *Parasalmo mykiss* in the Kol River basin

Parameter	Nilkinka R.	Krasnaya R.	Skvichik Stream
Distance between the tributary mouth and Kol River mouth, km	6.4	21.5	45.6
Length, km	28.3	31.6	18.2
Width in the mouth, m	15.4	14.2	12.2
Depth in the mouth, m	1.1	0.7	0.5
River discharge in the mouth, m^3/s	0.5109	0.7449	0.1372
Conductivity, mS	66.3	59.3	56.3
Oxygen content, mg/L	11.14	10.82	10.32
pH	6.95	7.03	6.97
Current speed at low water, cm/s	$\frac{36.3 \pm 2.2}{17.5–63.2}$	$\frac{20.2 \pm 1.9}{16.0–24.2}$	$\frac{24.6 \pm 2.9}{13.8–63.2}$
Weight-average size of ground particles, cm*	$\frac{7.33 \pm 0.101}{3.30–10.21}$	$\frac{4.54 \pm 0.088}{1.30–8.76}$	$\frac{7.65 \pm 0.230}{2.30–34.76}$
Distance between the spawning grounds and tributary mouth, m	1240	840	925
Area of the spawning grounds of mikizha, m^2	380	448	238
Number of the spawners, individuals/year (2003–2006)	$\frac{75 \pm 4}{55–95}$	$\frac{94 \pm 3}{81–112}$	$\frac{42 \pm 4}{32–60}$

Above the line is mean value and standard error; below the line is range of the values; *summing average size of the particles of each fraction in relation to weight proportion of this fraction.

et al., 2009). The mikizha samples from three spawning tributaries (Nilkinka River, Krasnaya River, and Skvichik Stream) were studied (Table 1, Fig. 1). These tributaries were selected based on the differences in their structure and features of mikizha reproduction. The Krasnaya River is the largest tributary of the whole water system of the Kol River, and the largest number of mikizha spawns in this tributary. The Skvichik Stream is characterized by the smallest size and the smallest number of the spawners. Similar to the Krasnaya River, the Nilkinka River is a large tributary. However, owing to the influence of cold phreatic ground waters, the latter river is characterized by a lower temperature regime. Because of this situation, mikizha does not annually spawn in the Nilkinka River: spawning was observed during the years with warm spring (2004 and 2006), but it terminated during the cold spring 2005 (Kuzishchin et al., 2008; Kuzishchin, 2010).

In the spring, the mikizha spawners migrate to the spawning tributaries from the main riverbed 3–5 days before spawning, and they return back to the main riverbed just after spawning. Only juveniles and precocious males live in the spawning tributaries over the entire year. Thus, the tundra-type tributaries of the Kol River basin are the typical spawning and nursery sites of the water system. The phenotypic composition of mikizha spawners is different in various tundra-type tributaries. Typical anadromous, estuarian, resident estuarian, and resident individuals spawn in the Nilkinka and Krasnaya rivers, while only resident fishes spawn in the Skvichik Stream (Table 2).

In the Nilkinka River, the body length and weight of the typical anadromous mikizha ($n = 16$) is 602–813 mm (737 mm on average) and 2.6–6.1 kg (5.2 kg on average), and these parameters in the resident fishes ($n = 44$) are as follows: 412–533 (502) mm and 0.73–2.1 (1.33) kg. In the Krasnaya River, the typical anadromous fishes ($n = 21$) have the body length and weight 594–854 (735) mm *FL* and 2.5–6.8 (5.3) kg, and these parameters in the resident fishes ($n = 96$) are as follows: 403–605 (501) mm and 0.72–2.51 (1.41) kg. The body length and weight of the estuarian and resident estuarian individuals are similar to those in the resident fishes. In the Skvichik Stream, the body length and weight of the resident mikizha ($n = 18$) is 376–501 (392) mm and 0.76–1.74 (0.78) kg.

The substantial differences in age composition of the spawners with a resident type of life strategy are observed in different tributaries. In the Nilkinka and Krasnaya rivers, the majority of the spawners are at the age of 7–8 years (Table 3), and repeat spawners prevail (Table 4). In the Skvichik Stream, the reproduction of the younger fishes (at the age of 5–6 years) is observed, and the first spawning individuals prevail.

In the Nilkinka and Krasnaya tributaries, the average proportion of the spawners with typical anadromous life strategy is approximately 10% (Table 2).

Table 2. Phenetic diversity of mikizha *Parasalmo mykiss* spawners in the Kol River basin, %

Tributary	Number of fishes	Phenotype			
		typical anadromous	estuarian	resident-estuarian	resident
Nilkinka R.	68	10.3 (7.7–11.1)	4.4 (3.2–7.1)	8.8 (6.9–12.1)	76.5 (65.6–84.1)
Krasnaya R.	122	10.6 (9.4–12.7)	3.3 (1.2–6.4)	7.4 (6.5–9.3)	78.7 (70.2–82.1)
Skvichik Stream	75	–	–	5.3 (3.4–6.8)	94.6 (93.2–96.6)

Before the parentheses is mean value; in the parentheses is range of the values.

Table 3. Age composition of resident mikizha *Parasalmo mykiss* spawners in the Kol River basin, %

Tributary	Number of fishes	Age, years						
		5+	6+	7+	8+	9+	10+	11+
Nilkinka R.	65	3.1	20.0	27.7	26.1	10.8	9.2	3.1
Krasnaya R.	105	4.8	14.3	20.9	25.7	18.1	13.3	2.8
Skvichik Stream	71	36.6	31.0	22.6	9.8	–	–	–

Nevertheless, a substantial part of the progeny originates particularly from the anadromous females. For example, based on the analysis of Sr^{2+}/Ca^{2+} ion ratios in the nuclear zones of otoliths, approximately 25% of the juveniles at the age 1+ are the progeny of the anadromous females in the Nilkinka River; the proportion of juveniles with anadromous origin is even larger (~30%) in the Krasnaya River (Figs. 2a, 2b). The large proportion of the juveniles originating from anadromous females is connected with a high fecundity level of anadromous females in comparison to that in riverine resident females. Absolute fecundity of the anadromous females ranges from 8780 to 12730 eggs (9120 eggs on average), and absolute fecundity of the resident females is 1020–4850 (3660) eggs. In addition, the females substantially prevail (with a 10 : 1 ratio between the females and males) in the typical anadromous fishes. Among the resident fishes, the sex ratio is close to 1 : 1. In the Skvichik Stream, the progeny of only riverine resident females is registered (Fig. 2c).

Table 4. Repeatability of resident mikizha *Parasalmo mykiss* spawning in the Kol River basin, %

Tributary	Number of fishes	Number of spawnings				
		1	2	3	4	5
Nilkinka R.	65	19.3	23.5	27.4	25.5	4.3
Krasnaya R.	105	20.8	25.0	25.0	25.0	4.2
Skvichik Stream	71	90.1	9.9	–	–	–

The habitat conditions of mikizha juveniles are different in various tributaries. The juveniles are distributed within the largest areas in the Krasnaya River. They are observed from the mouth to the distance of 20–21 km upstream (at the total length of the tributary 31 km) and characterized by a large density and biomass throughout the whole habitat (Table 5). In the Nilkinka River, which is similar to the Krasnaya River in the length and water content, the juvenile habitat zone is notably smaller reaching 11 km at the total tributary length 28 km. In the former river, mikizha juveniles are distributed only in the lower reaches, and both density and biomass of the fish in different sites are substantially lower than those in the Krasnaya River. In the Skvichik Stream (despite its small size), mikizha juveniles are widely distributed showing a large density and biomass in the middle and lower reaches.

In the Kol River basin, the distribution of mikizha juveniles depends on temperature regimes of the sites of the river and presence of suitable biotopes. Based on the data of control catches, mikizha was not observed in the tributary sites with average daily water temperature in August below 8.5°C and at degree days sum below 950 from May 15 to September 15.

All tributaries described in this study begin from the sources of cold and deep (phreatic) ground waters.

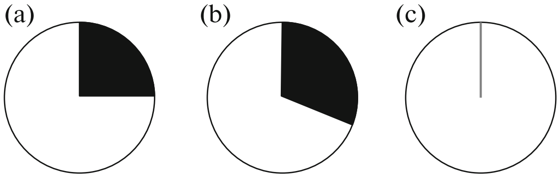

Fig. 2. Ratio between the progenies from (■) anadromous and (□) resident females of mikizha *Parasalmo mykiss* in different spawning tributaries of the Kol River basin in the juveniles of the age class 1+ (based on microchemical analysis of the Sr^{2+}/Ca^{2+} ratio in otolith primordiums): (a) Nilkinka River, $n = 30$; (b) Krasnaya River, $n = 40$; (c) Skvichik Stream, $n = 20$.

Table 5. Habitats, density, and biomass of juvenile mikizha *Parasalmo mykiss* (all age classes) in three tributaries of the Kol River

Tributary	Habitat size		Density, individuals/10 m^2/biomass, g/10 m^2 of juveniles in different parts of the tributary, km from the mouth			
	length, m	area, m^2	1	5	10*	15
Nilkinka R.	10760	144180	5.75/24.23	5.22/21.55	1.35/3.42	–
Krasnaya R.	20380	248640	10.33/56.76	9.36/50.24	6.39/32.21	5.74/23.41
Skvichik Stream	9120	93024	7.54/35.11	7.07/32.76	2.66/11.54	–

* 9 km in the Skvichik Stream.

Therefore, the water temperature in their upper reaches remains low (4–5°C) in the summer and fall, and the temperature rises up to 8.5°C and above in the lower reaches. In the Krasnaya River, the water warming begins not far from the head due to the flattened profile of the riverbed, low current speed, and opened surrounding area. The Nilkinka River is located at the edge of the river valley, and it is supplied by cold deep waters (the initial temperature of the springs is 2.5–3.0°C) throughout its entire length. The water becomes warmer only in the lower reaches of the tributary, and, therefore, the habitat areas of mikizha juveniles are smaller in the Nilkinka River than in the Krasnaya River. A small zone used by mikizha juveniles in the Skvichik Stream is determined by the size of this tributary (Tables 1, 5).

The lower density of mikizha juveniles in the Nilkinka River in comparison with that in the Krasnaya River and Skvichik Stream is connected with a smaller number of suitable biotopes in the former river. Mikizha juveniles prefer to live in the places of accumulation of wooden material and soddy hummocks within the riverbed and in the sites with eddy currents, often under the "roof" formed by branches and trunks of trees. Such habitats are numerous in the Krasnaya River and Skvichik Stream, but the amount of wooden material is lower in the Nilkinka River. The banks of the Nilkinka River are covered by low shrubby willows (*Salix*), but the banks of the Krasnaya River and Skvichik Stream include ripe forest composed of alder (*Alnus*), long-boled willow, and *Chosenia*. Therefore, the amount of wooden material in the riverbed of the Nilkinka River is substantially lower than that in other tributaries.

Table 6. Age composition of juvenile mikizha *Parasalmo mykiss* in three tributaries of the Kol River, %

Tributary	Number of fishes	Age, years			
		0+	1+	2+	3+
Nilkinka R.	933	68.2	19.2	9.5	3.1
Krasnaya R.	2234	59.4	21.3	12.5	6.8
Skvichik Stream	1002	76.2	15.3	7.3	1.2

Despite the differences in the size of the tributaries and habitat areas, the age composition of the juveniles is similar: the young of the current year prevail, and the age of the juveniles does not exceed 3+ (Table 6). The growth rate of mikizha juveniles is the highest in the Krasnaya River and the lowest in the Nilkinka River (Table 7).

Morphometric description of mikizha juveniles from different tributaries. Based on meristic characters, the differences between mikizha juveniles of the same age from different tributaries are absent. Based on several morphometric characters, only the juveniles from the Nilkinka River differ significantly from the juveniles from two other tributaries (Table 8).

The fishes from the Nilkinka River at the age 2+ differ from the fishes from the Krasnaya River and Skvichik Stream of the same age in the larger eye diameter, larger postorbital and interorbital distances, deeper head, longer pectoral fins, and position of the dorsal fin (slightly more displaced to the head in the individuals from the first tributary). However, owing to less favorable environmental conditions in the Nilkinka River in comparison to those in two other tributaries, the dispersion (the values of standard variation and standard error) of morphometric and meristic characters in the Nilkinka River is higher.

Migrations of mikizha in the Kol River basin based on the tagging data. In total, 1022 juveniles of different age (1+–3+) 100–220 mm *FL* (867 and 155 individuals in the tributaries and main riverbed, respectively) and 454 individuals of sexually mature resident mikizha at the age 4+–10+ 360–600 mm *FL* (225 and 229 individuals at the spawning grounds of the tributaries and in different parts of the main riverbed, respectively) were tagged. The total recapture rate was equal to 6.7% (69 individuals) in the juveniles and 4.6% (21 individuals) in adult mature fishes.

Migrations of resident mature fishes. In the Nilkinka River, three individuals (from 44 spawners tagged at the spawning grounds) were recaptured. An individual was caught 15 km upstream from the Krasnaya River mouth in May of the following year, and two other individuals were collected in the main riverbed at a distance of 9–15 km upstream from the Nilkinka River mouth in August of the current year of the tagging. In the Krasnaya River, 6 of 113 spawners tagged

Table 7. Body length (*FL*) and weight of juvenile mikizha *Parasalmo mykiss* in three tributaries of the Kol River, August, from 2002 to 2006

Age, years	Nilkinka R.			Krasnaya R.			Skvichik Stream		
	FL, mm	weight, g	*n*	*FL*, mm	weight, g	*n*	*FL*, mm	weight, g	*n*
0+	30–43 35.9	0.2–1.0 0.5	388	32–45 38.9	0.3–1.2 0.8	502	32–42 37.2	0.3–0.9 0.6	319
1+	72–94 82.1	6.0–9.5 8.0	113	81–105 92.5	6.8–16.4 9.9	305	74–104 87.5	6.3–10.2 8.7	158
2+	98–132 114.5	14.5–26.7 20.1	68	101–160 127.8	34.2–55.8 32.9	195	110–148 119.7	15.8–29.8 24.6	88
3+	102–180 150.3	23.1–89.2 42.2	18	136–201 186.7	57.1–104.4 89.8	97	118–192 159.2	26.9–100.2 50.2	27

Above the line is range of the values; below the line is mean value; *n* is number of studied exemplars.

at the spawning grounds were recaptured. Four fishes were collected in the main riverbed at a distance of 22–47 km upstream from the spawning tributary mouth (two individuals in the winter of the current year of the tagging and two individuals in two years after the tagging). The two other individuals were recaptured in the main riverbed at a distance of 5–13 km downstream of the spawning tributary mouth (an individual was recaptured 1 year after the tagging and another individual was collected in the second winter after the tagging). In the Skvichik Stream, 4 of 42 spawners tagged at the spawning grounds were recaptured. An individual was collected at the spawning ground of the Krasnaya River at a distance of 24 km from the tagging area in May, exactly 1 year after the tagging. Three other individuals were recaptured in the main riverbed at a distance of 11–42 km downstream of the Krasnaya River mouth in the summer of the current year of the tagging. In addition, 26 individuals of resident mature mikizha were tagged in the fourth spawning tributary, the Glinistyi Stream. From these fishes, an individual was recaptured in the main riverbed 9 km downstream from the tributary mouth in the winter of the current year of the tagging.

Among 229 individuals of mature mikizha collected and tagged in the main riverbed of the river, eight fishes were recaptured. Two individuals (a fish was tagged in a site of the main riverbed 35 km from the mouth, and another fish was tagged at a distance of 27 km from the mouth in September) were recaptured in the Nilkinka River mouth in March of the following year. These fishes migrated downstream at a distance of 20–27 km for 5–9 months. Three spawners were recaptured in the main riverbed almost at the sites of the tagging during the current year of the tagging in 1–2 months. Three other individuals tagged from July to September were recaptured in the main riverbed at a distance of 3–9 km from the tagging site in February.

Migration of juveniles. In total, 58 individuals from 867 tagged juveniles were recaptured during the current year of the tagging or in the following year. In the majority of cases, the juveniles remained at the same sites: they migrated at a distance of 100–500 m from the tagging areas. In 2–3 years after the tagging, nine individuals were recaptured in the main riverbed at a distance of 0.5–27 km from the tributary mouth. The fishes tagged in the lower spawning tributaries were recaptured upstream of their initial capture in the upper parts of the riverbed. However, a part of the fish from the upper tributaries (Skvichik Stream) migrated downstream.

Two individuals from 155 juveniles tagged in the main riverbed were recaptured downstream of the tagging site (at a distance of 3 and 10 km) a year after the tagging.

Thus, based on the mark-recapture experiments, resident mikizha representing the main part of the spawning population shows active migrations within the river system moving both upstream and downstream and widely distributing over the entire Kol River basin.

Allozyme variation of mikizha groups from different tributaries. Seven alternative alleles (*est-1*90*, *est-3*92*, *est-4*88*, *est-5*95*, *ssod-1*73*, *smdh-A1, 2*88*, and *smep-1*135)* were registered in 18 ferment systems encoded by 43 gene loci, and two of these alleles (*est-3*92* and *smep-1*135)* were unique. Two loci, *sSOD-1** and *EST-1**, were highly polymorphic. In each of the loci *sMEP-1** and *MDH-1,2**, a single heterozygote was revealed for all material. Therefore, these data were excluded in the subsequent statistical analysis. In other polymorphic loci, a low frequency of occurrence of alternative alleles was observed. All studied ferment systems are characterized by codominant inheritance in salmonid fishes (Altukhov, 2003), and, therefore, they can be used for population analysis.

Table 8. Morphometric characteristics of juvenile mikizha *Parasalmo mykiss* at the age 2+ in three tributaries of the Kol River

Character	Nilkinka R. ($n = 52$)			Krasnaya R. ($n = 67$)			Skvichik Stream ($n = 50$)			Differences, $t_{st}/M{-}U$		
	lim	$M \pm m$	SD	lim	$M \pm m$	SD	lim	$M \pm m$	SD	N. R. : K. R.	N. R. : S. S.	K. R. : S. S.
FL, mm	102–128	116.1 ± 2.9		101–130	122.3 ± 2.1		101–131	118.1 ± 2.8		1.73/0.101	0.49/0.657	1.20/0.422
% *FL*												
c	21.8–25.1	22.93 ± 0.15	1.11	21.3–24.5	22.76 ± 0.09	0.72	21.0–24.8	22.83 ± 0.11	0.79	0.97/0.757	0.54/0.758	0.49/0.842
ao	3.2–6.0	4.60 ± 0.12	0.88	3.3–5.9	4.69 ± 0.07	0.57	3.2–6.0	4.68 ± 0.09	0.61	0.64/0.447	0.53/0.839	0.09/0.965
o	5.0–7.5	6.19 ± 0.10	0.73	4.8–7.3	5.92 ± 0.06	0.49	4.9–7.4	6.05 ± 0.07	0.53	**2.31/0.004**	1.14/0.606	1.41/0.277
po	11.2–13.8	12.58 ± 0.13	0.97	10.6–13.0	12.03 ± 0.06	0.49	10.9–12.8	12.22 ± 0.08	0.55	**3.84/0.003**	**2.35/0.005**	1.90/0.142
io	4.9–7.9	6.56 ± 0.11	0.79	4.1–7.1	6.24 ± 0.05	0.44	4.3–7.2	6.39 ± 0.08	0.56	**2.64/0.005**	1.25/0.013	1.59/0.322
cH	14.4–21.0	15.88 ± 0.19	1.37	14.0–20.4	15.49 ± 0.12	1.07	13.8–20.8	15.52 ± 0.14	0.98	1.73/**0.007**	1.52/**0.007**	0.16/0.901
lmx	10.0–12.8	11.22 ± 0.12	0.83	9.8–12.3	11.02 ± 0.07	0.57	9.9–12.1	11.20 ± 0.10	0.69	1.44/0.376	0.12/0.885	1.47/0.118
mx	8.8–11.1	9.14 ± 0.08	0.58	8.2–10.5	9.07 ± 0.05	0.42	8.4–10.3	9.13 ± 0.08	0.56	0.74/0.658	0.09/0.971	0.63/0.864
hmx	2.0–3.2	2.38 ± 0.03	0.23	2.1–3.1	2.41 ± 0.02	0.19	2.0–3.0	2.44 ± 0.03	0.20	0.83/0.642	1.41/0.415	0.83/0.855
lmd	11.6–17.2	13.79 ± 0.14	1.06	11.7–16.7	13.53 ± 0.10	0.86	12.0–16.2	13.62 ± 0.13	0.92	1.51/0.112	0.89/0.845	0.55/0.913
H	17.6–24.0	20.11 ± 0.23	1.69	17.5–25.5	20.26 ± 0.16	1.31	17.9–24.1	20.20 ± 0.21	1.48	0.53/0.765	0.29/0.917	0.23/0.975
h	7.1–9.2	8.13 ± 0.09	0.68	7.2–9.5	8.29 ± 0.05	0.45	7.3–9.2	8.21 ± 0.08	0.59	1.55/0.212	0.66/0.905	0.85/0.905
lpc	15.0–23.5	17.73 ± 0.24	1.75	14.9–22.6	17.28 ± 0.13	1.05	14.7–20.3	17.42 ± 0.16	1.17	1.65/0.351	1.07/0.548	0.67/0.899
lD	10.2–13.2	12.01 ± 0.13	0.92	10.3–13.8	12.06 ± 0.08	0.64	10.8–13.9	12.08 ± 0.11	0.81	0.32/0.784	0.41/0.879	0.14/0.992
hD	12.6–17.1	14.79 ± 0.18	1.33	11.8–17.4	14.53 ± 0.13	1.08	12.2–16.7	14.66 ± 0.18	1.29	1.17/0.100	0.51/0.893	0.58/0.939
lA	7.6–12.6	9.08 ± 0.24	1.76	7.7–12.4	9.12 ± 0.15	1.27	7.9–11.2	9.10 ± 0.20	1.42	0.14/0.883	0.06/0.997	0.08/0.997
hA	10.4–14.5	12.49 ± 0.18	1.32	10.6–14.1	12.26 ± 0.10	0.81	11.1–14.0	12.37 ± 0.14	0.97	1.11/0.144	0.52/0.917	0.64/0.887
lP	13.1–16.7	15.10 ± 0.27	1.92	12.8–16.8	14.44 ± 0.10	0.84	13.2–16.5	14.59 ± 0.12	0.89	**2.29/0.005**	1.72/0.648	0.96/0.105
lV	10.2–13.9	11.84 ± 0.18	1.33	10.0–13.8	11.69 ± 0.09	0.72	9.8–13.6	11.72 ± 0.12	0.83	0.74/0.759	0.48/0.897	0.15/0.992
aD	43.0–46.2	45.15 ± 0.25	1.82	43.1–47.8	45.69 ± 0.13	1.07	43.9–46.4	45.82 ± 0.17	1.22	1.92/**0.007**	**2.21/0.007**	0.61/0.864
pD	34.2–39.0	37.01 ± 0.25	1.79	32.1–38.8	36.63 ± 0.15	1.22	32.7–38.8	36.73 ± 0.19	1.36	1.30/0.206	0.89/0.818	0.41/0.922
aV	45.4–52.1	50.47 ± 0.28	2.01	45.2–53.8	50.81 ± 0.17	1.37	44.6–54.3	50.57 ± 0.24	1.68	1.04/0.428	0.27/0.938	0.82/0.915
aA	66.1–73.5	67.72 ± 0.32	2.28	66.4–73.0	67.87 ± 0.21	1.78	65.6–73.4	67.79 ± 0.27	1.93	0.39/0.769	0.17/0.977	0.23/0.986
P–V	24.8–31.5	28.75 ± 0.26	1.86	24.1–30.7	28.46 ± 0.17	1.39	23.7–31.2	28.42 ± 0.20	1.42	0.93/0.774	1.00/0.773	0.15/0.999
V–A	16.1–22.3	18.43 ± 0.22	1.59	15.7–20.8	18.13 ± 0.13	1.08	16.2–21.1	18.38 ± 0.16	1.13	1.17/0.122	0.18/0.854	1.21/0.105
Meristic characters												
ll	120–133	128.2 ± 0.54	3.96	119–134	127.3 ± 0.45	3.32	120–134	127.4 ± 0.54	3.88	1.28/0.354	1.05/0.103	0.14/0.920
D	9–11	9.91 ± 0.07	0.55	9–11	9.84 ± 0.07	0.49	9–11	9.85 ± 0.08	0.58	0.70/0.583	0.56/0.701	0.09/0.989
A	9–11	9.55 ± 0.07	0.52	9–11	9.58 ± 0.07	0.53	9–11	9.52 ± 0.08	0.57	0.30/0.718	0.28/0.826	0.56/0.764
P	12–15	13.37 ± 0.13	0.94	12–15	13.28 ± 0.10	0.72	12–15	13.31 ± 0.14	1.02	0.55/0.695	0.31/0.811	0.17/0.876
V	7–9	8.24 ± 0.08	0.62	7–9	8.30 ± 0.07	0.54	7–9	8.27 ± 0.08	0.59	0.56/0.707	0.26/0.773	0.28/0.808
*r.rb.*1	11–14	12.12 ± 0.12	0.89	10–14	11.96 ± 0.10	0.76	11–14	12.10 ± 0.12	0.83	1.02/0.112	0.11/0.867	0.89/0.593
*r.rb.*2	10–13	11.58 ± 0.11	0.82	10–13	11.47 ± 0.09	0.67	10–13	11.42 ± 0.12	0.87	0.77/0.688	0.98/0.554	0.33/0.725
sp.br.	17–22	19.29 ± 0.17	1.23	17–22	19.28 ± 0.16	1.18	17–22	19.28 ± 0.18	1.29	0.04/0.964	0.04/0.970	–
pc	38–60	45.72 ± 1.09	7.88	36–63	47.69 ± 0.84	6.15	37–61	48.33 ± 1.02	7.23	1.43/0.189	1.74/0.105	0.48/0.802
vert.	61–66	63.67 ± 0.18	1.34	61–66	63.47 ± 0.16	1.18	61–65	63.54 ± 0.18	1.25	0.83/0.694	0.51/0.723	0.29/0.799

FL, fork length; *c*, head length; *ao*, snout length; *o*, horizontal eye diameter; *po*, postorbital distance; *io*, interorbital distance; *cH*, head depth at level of occiput; *lmx*, upper jaw length; *mx*, maxilla length; *hmx*, upper jaw width; *lmd*, lower jaw length; *H*, largest body depth; *h*, caudal peduncle depth; *lpc*, caudal peduncle length; *lD*, length of dorsal fin base; *hD*, dorsal fin depth; *lA*, length of anal fin base; *hA*, anal fin depth; *lP* and *lV*, pectoral and pelvic fin length; distances: *aD*, antedorsal; *pD*, postdorsal; *aV*, anteventral; *aA*, anteanal; *P–V*, pectoventral; *V–A*, ventroanal; *ll*, number of scales in lateral line; *D*; *A*; *P*, and *V*, number of branched rays in dorsal, anal, pectoral, and pelvic fins; *r.rb.*1 and *r.rb.*2, number of branchiostegal rays on left and right sides; *sp.br.*, number of gill rakers on first branchial arch; *pc*, pyloric caeca number; *vert.*, vertebral number; N. R. and K. R., Nilkinka and Krasnaya rivers; S. S., Skvichik Stream; lim, range of values; $M \pm m$, mean value and standard error; SD, standard deviation; t_{st}, Student's *t*-test; *M–U*, Mann–Whitney test; test values with significant differences ($p < 0.05$) are in bold.

Table 9. Frequencies of polymorphic loci, genotype distribution, and basic assessment of genetic variation of the loci in the samples of mikizha *Parasalmo mykiss* from the tributaries of the Kol River

Tributary (number of exemplars)	Locus	Alleles	Frequency of main allele	Genotypes: observed/expected			X^2	P	H_O	H_E	n_e
				SS	*SF*	*FF*					
Nilkinka R. (30)	*sSOD-1**	100, 73	0.467	8/8.4	16/15.2	6/6.4	0.089	>0.05	0.53	0.49	1.99
	*EST-1**	100, 90	0.583	6/5.1	13/14.8	11/10.1	0.474	>0.05	0.43	0.48	1.94
	*EST-3**	100, 92	0.983	0/0	1/1	29/29	–	>0.05	0.03	0.03	1.03
	*EST-4**	100, 88	0.867	23/22.5	6/7.1	1/0.5	0.751	>0.05	0.20	0.23	1.30
	*EST-5**	100, 95	0.933	0/0.1	4/3.8	26/26.1	0.113	>0.05	0.13	0.12	1.14
Krasnaya R. (30)	*sSOD-1**	100, 73	0.483	9/7.9	13/15.2	8/6.9	0.669	>0.05	0.43	0.50	1.99
	*EST-1**	100, 90	0.483	9/7.9	13/15.2	8/6.9	0.669	>0.05	0.43	0.49	1.99
	*EST-3**	100, 92	1.000	0/0	0/0	30/30	–	–	–	–	–
	*EST-4**	100, 88	0.983	29/29	1/1	0/0	–	>0.05	0.03	0.03	1.03
	*EST-5**	100, 95	0.850	1/0.6	7/7.8	22/21.6	0.334	>0.05	0.23	0.25	1.34
Skvichik Stream (30)	*sSOD-1**	100, 73	0.533	9/6.4	10/15.2	11/8.4	3.621	>0.05	0.33	0.50	1.99
	*EST-1**	100, 90	0.367	14/11.9	10/14.2	6/3.9	2.702	>0.05	0.33	0.46	1.86
	*EST-3**	100, 92	0.933	1/0.1	2/3.8	27/26.1	**8.816**	**<0.05**	0.07	0.12	1.14
	*EST-4**	100, 88	0.900	25/24.3	4/5.5	1/0.3	2.616	>0.05	0.13	0.18	1.22
	*EST-5**	100, 95	0.917	1/0.2	3/4.7	26/25.2	**4.689**	**<0.05**	0.10	0.15	1.18

Here and in Table 10: *SS*, homozygotes on a slow allele; *SF*, heterozygotes; *FF* homozygotes on a rapid allele; *P*, probability of the correspondence of the distribution of genotypes to the theoretical distribution of Hardy–Weinberg; H_E, expected heterozygosity; H_O, observed heterozygosity; n_e, effective allele number; significant deviations from the Hardy–Weinberg equilibrium ($p < 0.05$) are in bold.

Table 10. Frequencies in the polymorphic loci, genotype distribution, and basic assessments of genetic variation for these loci in the combined sample ($n = 90$) of mikizha *Parasalmo mykiss* from three tributaries of the Kol River

Locus	Alleles	Frequency of main allele	Genotypes: observed/expected			X^2	P	H_O	H_E	n_e
			SS	*SF*	*FF*					
*sSOD-1**	100, 73	0.494	26/23.2	39/45.6	25/21.2	1.73	>0.05	0.43	0.49	1.99
*EST-1**	100, 90	0.478	29/24.9	36/44.2	25/20.9	3.74	>0.05	0.40	0.50	1.99
*EST-3**	100, 92	0.978	1/0.1	2/3.9	87/86	3.27	>0.05	0.02	0.04	1.04
*EST-4**	100, 88	0.917	77/75.8	11/12.8	2/1.4	2.59	>0.05	0.12	0.15	1.18
*EST-5**	100, 95	0.900	2/0.9	14/16.2	74/72.9	1.87	>0.05	0.15	0.18	1.22

Allele frequencies, genotype distribution in the polymorphic loci, and general assessments of variation for each polymorphic locus in the three samples are given in Table 9. The sample from the Svichik Stream had a nonequilibrium or almost nonequilibrium genotype distribution for the majority of polymorphic loci due to the lack of heterozygotes (the assessments of H_O in relation to H_E). A low effective allele number (n_e) in many loci was explained by the same feature. Significant differences (Fisher's F-test) in allele frequencies of polymorphic loci between the samples from the three studied tributaries were not revealed. Thus, these groups could be combined into a single population of the Kol River. In addition, the genotype distributions for all polymorphic loci in the combined sample had become equilibrium (Table 10).

In the heterogeneity tests with the use of *G*-statistics (Nei et al., 1975), the distribution normality was tested again for each of the analyzed loci. In the combined sample, the differences between expected and observed estimates of heterozygosity and polymorphism (H_s and J_s vs. H_o and J_o) were not significant in all polymorphic loci, and the heterogeneity estimates (D_{ST}, CD_{ST}, G_{ST}, and CG_{ST}) were low and insignificant (Table 11).

In addition, in the heterogeneity test, we used generalized estimates for all polymorphic loci both in each analyzed sample and between the samples. All three samples had zero values of heterogeneity, and the

Table 11. Heterogeneity test for combined sample of mikizha *Parasalmo mykiss* by polymorphic loci

Locus	H_S	J_S	H_T	J_T	D_{ST}	G_{ST}
*sSOD-1**	0.5068	0.4932	0.5008	0.4992	0.0000	0.0000
*EST-1**	0.4916	0.5084	0.5067	0.4933	0.0151	0.0299
*EST-3**	0.0552	0.9448	0.0557	0.9443	0.0005	0.0081
*EST-4**	0.1505	0.8495	0.1552	0.8448	0.0047	0.0300
*EST-5**	0.1804	0.8196	0.1813	0.8187	0.0009	0.0050

Here and in Table 12: H_S, genetic variation inside the population; J_S, genetic identity inside the population; H_T, common genetic variation; J_T, common genetic identity; D_{ST}, interpopulation genetic variation; G_{ST}, genetic differentiation (Nei, 1972).

Table 12. Heterogeneity test for the samples of mikizha *Parasalmo mykiss* by all polymorphic loci

Samples	H_S	J_S	H_T	J_T	D_{ST}	G_{ST}
Nilkinka R.	0.2897	0.7103	0.2897	0.7103	0.0000	0.0000
Krasnaya R.	0.2618	0.7382	0.2618	0.7382	0.0000	0.0000
Skvichik Stream	0.2793	0.7207	0.2783	0.7207	0.0000	0.0000
Combined	0.2769	0.7231	0.2799	0.7201	0.0030	0.0109

Table 13. Pairwise F_{ST} values (below the diagonal) and *p* values of exact test calculated based on all polymorphic loci of mikizha *Parasalmo mykiss* (above the diagonal)

Samples	Skvichik Stream	Nilkinka R.	Krasnaya R.
Skvichik Stream	–	0.131	0.221
Nilkinka R.	0.0393	–	0.840
Krasnaya R.	0.0161	–0.0047	–

combined sample, including the fish from the three tributaries, had low and nonsignificant values of the test.

The degree of mikizha genetic differentiation was not significant: $\theta = 0.023$ with 95% confidence bootstrap interval, CI (–0.007, 0.054). All pairwise estimates of genetic differentiation obtained based on the analysis of all polymorphic loci were not significant; and the F_{ST} values ranged from –0.0047 to 0.0393 (Table 13).

Thus, the analysis of allozyme variation shows that the samples from the Nilkinka, Krasnaya, and Skvichik tributaries do not significantly different, and mikizha from the Kol River is represented by a single population with a common gene pool.

DISCUSSION

In the complex and bifurcated Kol River basin, the local mikizha population exists and reproduces mainly due to the fishes with the resident life strategy type; the contribution of anadromous fishes is substantially lower, and it is registered only in certain spawning tributaries (Kuzishchin et al., 2008; Pavlov et al., 2008). During the larger part of the year, the large sexually mature fishes are distributed in the main riverbed, and the tundra-type tributaries are used as the spawning and nursery areas of the water system. Exactly the same features of the spatial distribution are usual for mikizha from different water systems of North America, from Alaska to California (Northcote, 1992, 1997; Dunaway, 1993; Palmer, 1998; Adams, 1999; Heath et al., 2001; Meka et al., 2003; Falke et al., 2013). In addition, in the river systems of North America, the migrations of mikizha from the main riverbed to the tributary and back are observed even in the cases when the tributaries are comparatively large with the size and water content similar to those in the whole Kol River basin from Kamchatka (Wenger et al., 1985; Brown, 1994; Swanberg, 1997; Nelle and Lisac, 2001; Schmetterling, 2001; Meka et al., 2003; White and Rahel, 2008; Falke et al., 2013).

According to several researchers, the spawning of mikizha in the tributaries of a large river is associated with the appearance of certain adaptations and formation of local and specialized within-river groups of a population level (Stacey et al., 1997; Kingsolver and Huey, 1998; Sultan and Spencer, 2002; Nielsen, 2003). This opinion is supported by several investigations of mikizha spatial distribution in the complex river systems conducted with the use of molecular genetic methods. In particular, a well-defined discontinuity is observed in the branched river systems of Alaska, British Columbia, and California with different areas: each tributary supports a small mikizha population that passed through the "bottleneck" (Gall et al., 1990; Nielsen, 1998, 2003; Heath et al., 2001; Nielsen et al., 2003). Because of such spatial distribution of the fish, the researchers consider mikizha of a large river basin as a population system or metapopulation, and the groups from distinct tributaries are described as subpopulations (Narum et al., 2006, 2008; Neville et al., 2006; Fraser et al., 2011; Walsh et al., 2013; Budy et al., 2014; Winans et al., 2014).

Based on our data on mikizha from the Kol River basin, Kamchatka, the results obtained for mikizha from North America are not supported. In the Kol River basin, each of the studied spawning tributaries is characterized by unique combination of size, water content, and thermic regime. Therefore, the features of mikizha reproduction, spatial distribution, and biological characteristics of the juveniles are different, and the disconnection of the spawning tributaries and their various abiotic conditions facilitates a separation of the fish into the groups. However, based on the morphometric and population genetic analyses, the opposite situation is observed: the separation of mikizha within the Kol River basin is absent. Certain nonequilibrium allele frequencies in the sample from the Skvichik Stream can be connected with a low number of the first spawning fishes that migrated to this tributary (Tables 1, 4). As is known, genetic variation is lower in mikizha populations represented by mainly first spawning individuals than in the populations where reproduction is supported by mainly repeat spawners (Narum et al., 2008).

The tagging data also support the within-river unity of mikizha: mature individuals do not show a preference to a certain tributary, and they migrate to any tributary depending on current environmental conditions. The spawning of the same individuals in different tributaries leads to a stable gene flow between the groups, and, thus, population panmixia is supported within the river basin. It is important to note that the presence of anadromous spawners in the groups of the Nilkinka and Krasnaya rivers does not lead to heterogeneity of genetic structure: the juvenile samples represented by the progenies of anadromous and resident females show equilibrium allele frequencies. Thus, based on the data of this study, at present, mikizha of the Kol River is represented by a single population despite a high degree of habitat mosaic.

What are the reasons for a high integration degree of the mikizha population of the Kol River basin despite the effect of environmental factors, which can induce the spatial divergence? In our opinion, this integration is connected with the features of the river basin structure and climate of Kamchatka.

The spawning tributaries of the Kol River basin are comparatively small, and the biotopes suitable for the presence of mature individuals of mikizha are absent. Therefore, the period of their occurrence in the tributaries is strictly restricted by the spawning time. In fact, adult fishes appear in a tributary for less than a week per year, in the second half of May, and they sometimes remain in a tributary for only 1–2 days (Kuzishchin et al., 2008). After the spawning, resident mikizha is widely distributed along the riverbed, and the fishes select specific habitats located from the river mouth to mountain sources (Kuzishchin, 2010; Kuzishchin et al., 2013). According to our observations, the distribution of resident mikizha in the river system occurs before the end of spring flood, and the fishes are located in summer habitats already in the second half of June where they demonstrate a more or less settled way of life until the late fall. Similar features of postspawning behavior and distribution of mikizha are described in the water bodies of North America: after the spawning, the fishes migrate until they find a suitable biotope (Heggenes et al., 1991; Dingle 1996; Meka et al., 2003). However, their movements are restricted in the summer, and they do not exceed 50 m (Soloman and Templeton, 1976; Young, 1994, 1996; Swanberg, 1997; Hilderbrand and Kershner, 2000; Schmetterling, 2001). In the Kol River basin, mikizha migrates both upstream and downstream; however, the representatives of a similar species in North America, cutthroat trout *Oncorhynchus clarkii*, move mainly downstream after the spawning, (Varley and Gresswell, 1988; Hughes, 2000; Meka et al., 2003; Schrank and Rahel, 2004; Mellina et al., 2005; White and Rahel, 2008).

In the winter, mikizha distribution is substantially different from that during the period of open water. In North America, mikizha migrates from the shallows of the river with the onset of cold weather and beginning of ice formation, sometimes, even if the ice is still absent (Chapman and Bjornn, 1969; Fausch, 1984; Brown and Mackay, 1995). During the winter, mikizha moves to deep sites of the main riverbed and selects the habitats with the most rapid appearance of the ice cover (Lewis, 1969; Baltz et al., 1991; Brown and Mackay, 1995; Meka et al., 2003). Owing to this behavior, resident mikizha of North America is capable of extended migrations (more often, downstream, at a distance of 2–3 to 100 km) along the river searching the wintering holes (Bjornn and Mallet, 1964; Bjornn, 1971; Cunjak and Power, 1986; Clapp et al., 1990; Meyers et al., 1992; Brown and Mackay, 1995; Meka et al., 2003).

In the Kol River basin, Kamchatka, the movement of mikizha to deep riverbed holes during the cold time of the year is also observed. The ice cover is established in the deep reaches and riverbed holes in mid-December, but the shallows sometimes remain opened until mid-January. A large concentration of mature individuals in the deep reaches is already observed in December, and they remain in these sites until April. At the same time, the cases of mikizha catches are not registered at the shallow reaches (less than 1.5 m deep) along the whole river from the lower to upper reaches (up to 90 km from the mouth) after the formation of the ice cover, from mid-January to late March. In the Kol River, the majority of deep riverbed holes are located in the areas of the lower and middle reaches, from the mouth to 36 km upstream (Fig. 1). Therefore, the migration of resident mikizha from the whole basin to the wintering holes is directed downstream, similar to this direction in mikizha from North America. Thus, the wintering concentration of adult fishes that spawn in different tributaries is observed at a restricted part of the river. After the wintering, the selection of a spawning tributary by the spawners depends on spring temperature regime and flood situation. For example, the cold and prolonged spring 2004 led to the absence of spawning migration to the Nilkinka River, and the spawners redistributed over other spawning tributaries. In the spring, mikizha can quickly overcome the distances reaching 80 km in all environmental conditions and it sometimes moves against a strong current during a flood (Varley and Gresswell, 1988; Meka et al., 2003; Fraley et al., 2016). Thus, mikizha of the Kol River basin (based on its migration pattern over the entire year) belongs to the reodromous group, sensu Pavlov and Skorobogatov (2014). This means that the fish migrate widely within the river basin, and their preference to any area is absent. Therefore, mikizha individuals can select suitable habitats within a wide range in the summer and, in particular, during the spawning season in the spawning tributaries.

In our opinion, mikizha population of the Kol River system with a complex geomorphology is characterized by the adaptations directed to exploitation of spawning properties of the tributaries, which differ in their structure, hydrological, and thermic regimes. In addition, mikizha of the Kol River basin is represented by a single highly integrated population. The mechanism of maintaining population unity is connected with comparatively extended within-river migrations within the whole basin. Because of these migrations, the spawners are redistributed in different tributaries of the river during each year. We suppose that observed integration of the population is a consequence of small sizes of the spawning tributaries, which are able to support the reproduction of a very small number of spawners. Thus, their redistribution in different tributaries is directed against the founder effect and gene drift.

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