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Morphological Diversity and Variability of Sympatric Populations of Crucian and Prussian Carps in Radionuclide Contaminated Lakes in the Southern Urals

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Abstract—The variation in the body shape of crucian and prussian carps has been studied by methods of geometric morphometrics in sympatric populations from two geographically close lakes in the Southern Urals subjected to different degrees of contamination with anthropogenic radionuclides. Along with particular interspecies features, interpopulation differences have been detected as multidirectional reorganization of cyprinid morphogenesis under different ecological conditions of adjacent lakes. The morphogenetic divergence of crucian carp from adjacent lakes is almost two times smaller than that of the prussian carp coexisting with them. The increased intragroup morphodiversity in prussian carp indicates incomplete adaptation of the fish to anthropogenic radionuclide contamination of the lakes and their high morphogenetic plasticity and high adaptive potential than in crucian carp.

Keywords: variation, morphological diversity, crucian carp, prussian carp, radioactive contamination, geometric morphometrics, Southern Urals

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INTRODUCTION

Sympatric and taxonomically close species and intraspecies groups of fish display different morphogenetic responses in the gradient of environmental conditions [1–5]. Similar morphological variations in the environmental gradient may be associated with the long-term coexistence of species under conditions of sympatry and are accompanied by the generation of similar morphogenetic responses to variations in local ambient conditions. The higher are the observed similarity and parallelism of morphogenetic responses of sympatric species to changing environmental conditions, the higher is their coevolutionary potential [6, 7]. Different morphogenetic responses of the species to a changing environment may be induced by recent secondary sympatry at their initial allopatry. The realization of morphological diversity patterns in taxonomically close species is the matter of interest [8]. Of the hydrobionts in freshwater ecosystems, fish are the most sensitive to radioactive contamination [9]. Since ecologically contrasting environmental conditions, including anthropogenic radioactive contamination, are a rare phenomenon, the morphogenetic response of sympatric fish species inhabiting waterbodies exposed to different radiation levels may be accompanied by quick exhaustion of the coevolutionary potential, as well as the detection of species-specificity of morphogenesis of sympatric species under stressful environmental conditions and variation in morphological diversity.

The search for cases of the quick emergence and manifestation of morphogenetic variations in populations of taxonomically close sympatric species in homogeneous communities and geographically close habitats is an important evolutionary and ecological task; its solution is important for the assessment of potential plasticity and polyvariance of morphogenesis and the comparison of the mobility levels of the epigenetic system of population of compared forms [10].

Their wide distribution, high ecological plasticity, and complex genetic structure of cyprinid populations made them the objects of many ecological and morphological, biological, and genetic studies [11–16]. Using geometric morphometric methods [17–19], it is possible to perform multidimensional analysis of the body shape of cyprinids and, indirectly, to estimate their population morphogenetic variations under conditions of long-term radiation and to solve the abovementioned problems. The goal of this work is to study the body shape variation in sympatric species of crucian and prussian carps from the adjacent lakes Bolshoy Igish and Maly Igish in the Southern Urals with different levels of anthropogenic radionuclide contamination by geometric morphometric methods.

MATERIALS AND METHODS

The study was performed on populations of the prussian carp *Carassius auratus gibelio* (Bloch, 1782) and crucian carp *Carassius carassius* (Linnaeus, 1758)

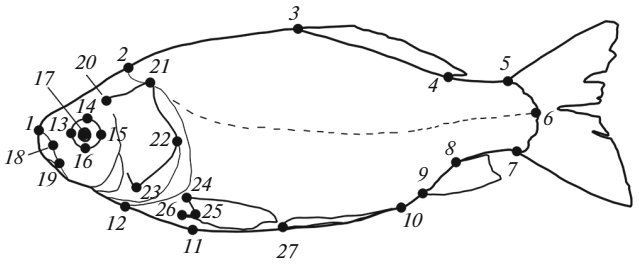

Fig. 1. Scheme of homological landmarks (*1–27*) on the lateral projection of the body of the compared cyprinid species.

inhabiting closed eutrophic lakes in the Southern Urals. The specimens were collected in two neighboring lakes, Bolshoi Igish and Maly Igish, located in the zone of the Eastern Ural Radioactive Trace at the distance of 2 km from each other and 60 km from the epicenter of the accident at the Mayak Production Association in 1957. Only two cyprinid species were recorded in control catches; prussian carp were dominant. The depression of Lake Maly Igish occupies a higher hypsometric position and has a smaller surface area (0.68 km^2) as compared to Lake Bolshoy Igish (1.6 km^2); its maximum depth is 3.1 m, the average depth is 2.6 m, and the maximum depth is 3.3 m and the average depth is 2.7 m in Lake Bolshoy Igish [20]. Despite the close location of the lakes and some similarity of habitats [20], Lake Maly Igish is a fresh body of water and Lake Bolshoy Igish becomes brackish in dry years and at present it is more mineralized waterbody. In 2000–2005, the content of ^{90}Sr was 6.40 ± 0.30 Bq/L, ^{137}Cs—0.067 ± 0.020 Bq/L in Lake Bolshoy Igish, whereas these values for ^{90}Sr and ^{137}Cs reached 0.50 ± 0.03 Bq/L and 0.020 ± 0.003 Bq/L, respectively, in the water of Lake Maly Igish [21]. Therefore, the concentration of anthropogenic strontium ^{90}Sr in water of Lake Bolshoy Igish was by an order higher than in Lake Maly Igish, and the concentration of ^{137}Cs was 2.5 times higher in Lake Bolshoy Igish. According to hydrobiological indexes of saprobity, Lake Maly Igish is a waterbody with a high degree of water pollution; Lake Bolshoy Igish is slightly polluted [22]. Overall, ecological conditions in cyprinid habitats in Lake Maly Igish were somewhat better compared to Lake Bolshoy Igish.

Fish were taken with fixed gill nets in August 2008. Fish specimens were carefully removed from nets so as not to deform the outer structures. Fresh fish specimens were used in our study (not fixed). The biological analysis, length measurements, and age determination of fish were made according to the common ichthyological methods [23]. Males and females were present in samples with crucian carp and only females were found in samples with prussian carp. All specimens, with few exceptions, were adult but were subdivided into two subsequent age groups I and II. Specimens at the age of 3 and 4 years, i.e., mainly mature, were considered as conventionally young fish (group I) and 4- to 5-year-old specimens were attributed to the old age group (group II).

Geometrical morphometrical analysis of the body shape of cyprinids was made according to 27 landmarks recorded with the tpsDig2 digitizing program [24] in homological points on the lateral projection of the body and outer structures of fish (Fig. 1). A total of 174 digitized images of lateral projections of cyprinid specimens with the resolution of 1280 × 960 pixels were made using Nicon CoolPix 4500. The pattern of the body shape variation was analyzed by the method of the principle components of the Procrustes coordinates and relative warps were estimated; intergroup comparisons by the method of discriminant analysis in the canonical coordinate system were made with these values.

Based on the method of principle components, it was preliminary established that dispersion describing age variation in the body shape of cyprinids was only 2.88% of the total dispersion, which is associated with increased body transformation at late age stages, i.e., the age factor makes a minor contribution to body shape variation in the both species. Therefore, the comparison of samples was performed based on combined samples of specimens of different age groups. The presence of specimens of different sex in crucian carp populations did not affect the manifestation of intergroup morphogenetic divergence, which made it possible to use combined samples of crucian carp with both male and female sexes.

Intragroup morphological diversity was estimated by analysis of the nearest neighbor distance within the variation polygons [25]. The mean nearest neighbor distance (*MNND*), expected nearest neighbor distance (*ExpNND*) at random Poisson distribution and other parameters ($R = MNND/ExpNND$; Z-test and its significance level, p) were calculated for assessment of the models of point distribution within the variation polygon of each sample. Aggregation of ordinate dispersion was observed at $R < 1$, Poisson dispersion at $R = 1$, overdispersion at $R > 1$, which, in the case of significant deviation of R from 1, indicates a nonrandom increase in morphodiversity.

Calculations were made with the TPS [24, 26] and PAST 2.17c [27] software packages.

RESULTS AND DISCUSSION

First of all, it is necessary to define the variable forms, the variation in which is associated with ecological environmental differences between adjacent waterbodies and do not depend on sample parameters. Based on the matrix of values of principle components (PC) estimated with the use of Procrustes coordinates, we determined the correlation between the components and the effect of stressing factors, which were formally given as ranks 1 and 2: rank 1 for speci-

mens of the both species in Lake Maly Igish with lower background radiation under conditions of low contamination of aquatic environment with organic substances and low water mineralization; rank 2 is given for specimens from Lake Bolshoy Igish with high level of radioactive contamination under polysaprobic conditions of the lake with high water mineralization. According to Jolliffe cut-off, 14 principal components were analyzed. Of them the effect of only the pollution factor was established for the shape variation along PC6 ($F = 7.20$; d.f. = 1; $p = 0.0080$) and PC7 ($F = 44.96$; d.f. = 1; $p < 0.0001$). Therefore, we considered coupled variation of these components, which explains 7.46% of the total dispersion of the body shape of cyprinids and correlates with the level of pollution in the waterbodies (Fig. 2). Parallelism of the variability of the body shape of crucian and prussian carps associated with a different degree of waterbody contamination is distinctly manifested along PC6 and PC7 (Fig. 2). The trend towards interaction of body shape variation in different lakes is negligible along the axes.

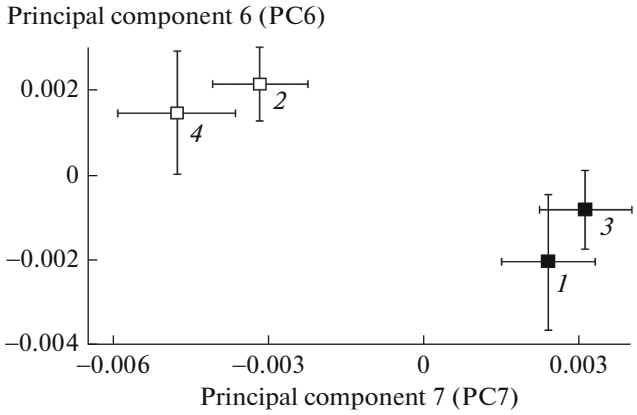

Fig. 2. Ordination of centroids of the samples of prussian carp (*1*, *2*) and crucian carp (*3*, *4*) from lakes Bolshoy Igish (*1*, *3*) and Maly Igish (*2*, *4*) with standard errors (*SE*s) in the plane formed by PC6 and PC7 principal components characterizing the body shape of cyprinids and correlating with the contamination level.

Intragroup morphodiversity was estimated based on polygons of variation of the compared four samples in the PC6 and PC7 plane (Table 1). Random rarefaction of sample composition was preliminarily performed to reduce their size to a similar number of observations. Comparison of the nearest neighbor distances in samples of crucian and prussian carps based on the Kruskal-Wallis test showed significant intergroup differences ($H = 17.1$; $n = 174$; $p < 0.01$). The highest morphodiversity (*MNND*) was manifested in samples of prussian carp in Lake Bolshoy Igish. The *MNND* values were similar in the other three samples. It is important to note that a significant effect of superdispersion of ordinates ($R > 1$) was observed in prussian carp samples from both neighboring lakes. A significant effect of overdispersion was found only in samples of crucian carp from Lake Bolshoy Igish; in Lake Maly Igish, the dispersion of ordinates was of random character ($R = 1$).

Thus, morphodiversity increases in syntopic populations of crucian and prussian carps from Lake Bolshoy Igish with a high-level impact of stressing factors that indirectly indicates destabilization of morphogenesis caused by disturbance of the developmental regulation and the manifestation of a wider spectrum of morphogenetic trajectories, leading to particular phenotypes with frequent deviations from the norm. Such an effect is observed in prussian carp in both waterbodies, demonstrating a high species vulnerability in respect to the effect of contamination on morphogenesis of the species. Morphogenesis of crucian carp is more resistant to the contamination effect. The species develops stably at a lower degree of contamination in Lake Maly Igish.

The high morphodiversity of prussian carp in Lake Bolshoy Igish and significant effect of ordinate overdispersion for polygons of variation in both waterbodies indicate, on one hand, incomplete adaptation to habitat conditions in the both waterbodies and, on the other hand, high morphogenetic plasticity of the species as compared to crucian carp. The increase in the fan of morphological trajectories of prussian carp under the impact of environmental conditions probably enhances its adaptive potential. Some morphoge-

Table 1. Estimation of the model of ordinate dispersion in polygons of the variation of the body shape of fish along PC6 and PC7 associated with the contamination level of waterbodies for four Southern Ural samples of crucian and prussian carps based on the method of mean nearest neighbor distance (*MNND*)

Species and waterbody	Mean distance *MNND*	Expected distance *ExpNND*	*R*	Z	Level of significance (*p*)
Prussian Carp					
Lake Bolshoy Igish	0.0046 ± 0.0008	0.0030	1.52	4.33	<0.0001
Lake Maly Igish	0.0026 ± 0.0005	0.0019	1.32	2.70	0.0069
Crucian Carp					
Lake Bolshoy Igish	0.0027 ± 0.0005	0.0021	1.28	2.35	0.0186
Lake Maly Igish	0.0025 ± 0.0004	0.0022	1.12	0.99	0.3175

Table 2. Results of discriminant analysis of relative warps (RWs) of the body of cyprinids and values of centroids of samples (upper part of the table) from populations of Lake Bolshoy Igish and Maly Igish, the Southern Urals

Compared samples and statistical parameters	Discriminant canonic functions (DCF)		
	DCF1	DCF2	DCF3
Prussian Carp			
Lake Bolshoy Igish	3.669	1.818	0.053
Lake Maly Igish	1.561	−2.570	0.004
Crucian Carp			
Lake Bolshoy Igish	−3.633	0.494	1.287
Lake Maly Igish	−3.329	0.539	−2.799
Eigenvalues	10.1224	3.0275	1.5941
Wilks'Λ-criterion	0.00860	0.09571	0.38548
Number of degrees of freedom	117	76	37
Portion of dispersion, %	68.65	20.53	10.81
Significance level, *p*	< 0.0001	< 0.0001	< 0.001

netic trajectories may be taken up and fixed by selection, which allows the species to adapt quickly to a changing environment. These properties probably ensure a high abundance of the species in both lakes; this can also lead to a high reproduction rate of prussian carp, which are represented in the lake only by females [15].

Discriminant analysis of relative warps (RWs) of the shape with transition to the canonical system of coordinates was performed to reveal stable changes in morphogenesis that differentiate, to the greatest degree, the compared fish groups (Table 2). All three discriminant canonical functions (DCFs) were statistically highly significant. DCF1 constitutes 68.65% of intergroup difference. According to the values and signs of centroids of the compared samples along DCF1, the maximum differences in the body shape were determined along this axis between populations of different carp species. The greatest differences between centroids of the compared species were found in Lake Bolshoy Igish, and the maximum range of intraspecies differences between centroids of samples was found along DCF1 in prussian carp.

Populations of prussian carp from lakes Bolshoy Igish and Maly Igish differ drastically in the value and sign of the centroid along DCF2. The axis amounts to 20.53% of the intergroup dispersion. The centroids of populations of crucian carp inhabiting these lakes occupy an intermediate position. The differences along DCF3, which explain 10.81% of the intergroup dispersion, are due to the body shape divergence of crucian carp from geographically close lakes. Centroids of populations of prussian carp occupy the middle position. Therefore, the value of morphogenetic differences associated with population characteristics of prussian carp from adjacent lakes is almost twice as high as the differences caused by specific characteristics of crucian carp populations in these waterbodies. The morphogenesis of prussian carp is more labile and can be modified under different environmental conditions.

The differences between localities are expressed along DCF2 in prussian carp and along DCF3 in crucian carp. The directions of ecotopic intraspecies interpopulation variation of the body shape in carp do not coincide in common morphospace in a comparison of samples from Lake Bolshoy Igish with unfavorable ecology with samples from the less polluted Lake Maly Igish. In different waterbodies cyprinid species differ in the direction of the morphogenetic response.

Hierarchical cluster analysis of the morphological similarity of the four compared samples of cyprinids was performed with the matrix of the generalized Mahalanobis distance (D) based on the Hover distance (Fig. 3). As a result, two groups corresponding to the different species, crucian and prussian carps, were distinguished. Samples of the corresponding localities were combined within the species. The length of branches in the dendrogram representing local samples of prussian carp was larger than for crucian carp, indicating a higher range of morphological differences between the samples of prussian carp. A high level of support of branching of species clades upon bootstrap testing of the dendrogram (this value is higher in crucian carp and is close to 100%) indicates a high level of intraspecies differentiation in the both cyprinid species.

According to the data obtained by geometric morphometric methods, the cyprinid samples differ significantly; the reliability of the determination of the species group reaches 98.9%, and the analysis of the results of the initial classification by jackknife test confirmed a high level of correctness, 93.7% (Table 3). A high degree of discrimination of different species is quite expected, but it was unexpected for geographically close populations. Only single cases of erroneous identification were found in samples of crucian and

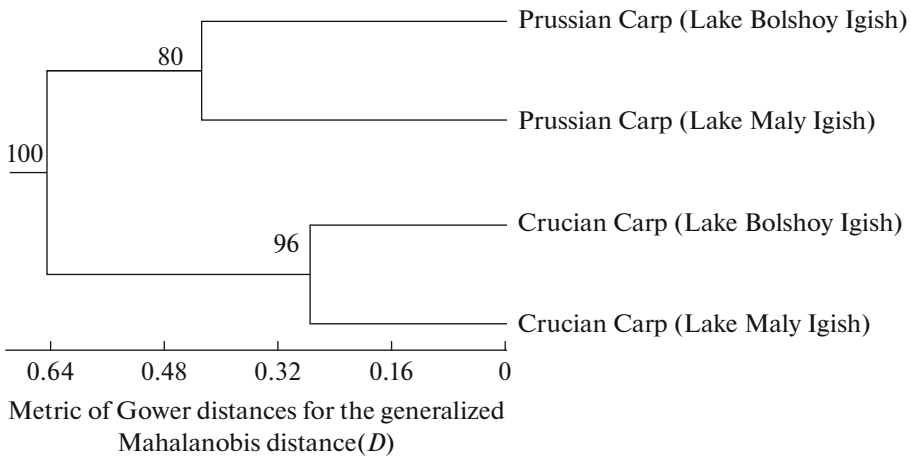

Fig. 3. Results of cluster analysis (UPGMA) of the matrix of the generalized Mahalanobis distance (*D*) between samples of crucian and prussian carps of the Southern Urals populations from adjacent lakes Bolshoy Igish and Maly Igish (bootstrap support of clusters is given, %). The choice of the metric was made on the basis of the maximum value of the cophenetic correlation coefficient (Coph. corr. = 0.98).

prussian carps when specimens were assigned to the populations from neighboring waterbodies. Since the lakes are close to each other, similar variants of morphogenesis causing similar phenotypes may be expected in many specimens of the species, but this is not observed. Practically all samples from neighboring populations of each species are morphologically differentiated, which indicates the presence of considerable morphological differences between them. Erroneous identification of cyprinids is rarely observed only within the species.

This manifestation of intragroup morphological diversity and morphogenetic variability of populations of taxonomically close cyprinid species living in adjacent waterbodies for a long time may be associated with ecological and biological specific characters of the species. Crucian and prussian carps have similar requirements for habitats and mode of life, but the range of prussian carp habitats is wider [11]; prussian carp usually live in open habitats, and crucian carp prefer vegetation stands [28]. Males are absent or few in the Ural populations of prussian carp. We did not record them in our catches. The presence of specimens of different sex in crucian carp populations did not affect the manifestation of intergroup morphogenetic differences. Triploidy and gynogenesis are distinctive features of unisexual populations of prussian carp that promote their high fecundity and well-being under stable living conditions [15].

We may suggest that the gynogenetic triploid form of prussian carp and bisexual diploid form of crucian carp have different ecological preferences and differ in the species morphogenetic response to various ecotopes (lake conditions). The other reason may be the relatively recent (about half a century) anthropogenic radionuclide contamination of waterbodies after the accident at the Mayak Production Association and the different degrees of chronic exposure to low-dose radiation. Such an atypical effect on fish may cause the emergent induction of species-specific morphogenetic responses based on epigenetic reorganizations caused by environmental stress and their further fixation by selection [29]. We consider the scenario to be highly probable, because neighboring populations of similar species had a strong morphological differentiation. Some specimens may be assigned with a high probability to their own local population. As shown in our previous studies [30] the body shape of river perch from the population in the Techa cascade of reservoirs

Table 3. Estimation of the reliability of object discrimination in comparison of body shapes of crucian and prussian carps from populations of two adjacent waterbodies in the Southern Urals

Compared samples*	1	2	3	4	Reliability of identification, %
Results of classification of objects according to groups					
1	49	1	0	0	98
2	0	50	0	0	100
3	0	0	50	0	100
4	0	0	1	23	95.8
Total	49	51	51	23	98.9
Jackknife test of initial results of classification					
1	45	5	0	0	90
2	1	49	0	0	98
3	0	0	47	3	98
4	0	0	2	22	91.7
Total	46	54	49	25	93.7

*(1, 2) prussian carp, lakes Bolshoy Igish and Maly Igish; (3, 4) crucian carp, lakes Bolshoy Igish and Maly Igish.

subjected to a 50-year radioactive impact and from adjacent control waterbodies differs considerably. These differences correlate with the concentration gradients of ^{90}Sr and ^{137}Cs in fish tissues, and specimens of the Techa population are accurately discriminated.

In addition to radionuclide contamination, Lake Bolshoy Igish is characterized by high water mineralization and heavy pollution with organic substances and their decay products, which may initiate species-specificity of morphogenesis in different fish or modify their effects upon the combined impact including radionuclide contamination [31–33]. Meanwhile, inhomogeneity of the lakes with respect to water mineralization and saprobity, unlike the specific character of anthropogenic radionuclide contamination, is common for the living conditions of cyprinids. Both species coexist in fresh and brackish waters, as well as in eutrophic waterbodies at different concentrations of nutrients in water [11, 34, 35].

We propose that the change in epigenetic profiles of DNA to be a probable mechanism of rapid morphogenetic reorganization in cyprinid populations, which may initially be associated with a chronic stress impact of external and internal low-dose radiation. Such rapid directed changes in morphogenesis in response to strong thermal stress and radiation exposure, as well as preservation of these reorganizations in offspring in the temporal aspect, were detected in laboratory lines of *Drosophila* [36]. In recent years, rapid epigenetic reorganizations of the genome structure and their transgenerational inheritance associated with morphogenetic effects were established in many representatives of the biota [29, 37, 38].

Epigenetic changes may be fixed in the fish genome by natural selection, and specific characters of morphogenesis are formed in a particular species in a sequence of generations in each waterbody, which results in different phenotypes of cyprinids in a particular lake. The higher intergroup variation of the body shape in prussian carp is apparently associated with less regulation of their morphogenesis and higher susceptibility to epygenetic reorganizations as compared to crucian carp. The chronic radiation exposure of lake fish can stimulate epigenetic reorganizations, in particular, reorganization of the structure of mobile elements within the genome. The use of comparative molecular data on population epigenomic differences in these cyprinid species may elucidate the problem.

Thus, based on geometric morphometric methods, a specific character of variation in the shape and directions of morphogenesis was detected in crucian and prussian carps in uniform communities and geographically close adjacent lakes in the Southern Urals. Different cyprinid species are well discriminated according to variables characterizing the shape variation: interspecies differences constitute about 69% of dispersion. The level of morphogenetic differences associated with population specificity of crucian carp from adjacent lakes is two times smaller than morphological characteristics of coexisting populations of prussian carp. High intragroup morphodiversity and the effect of overdispersion of ordinates within polygons of variation in prussian carp indicate incompleteness of their adaptation to anthropogenic radionuclide contamination of the lakes. This simultaneously indicates their high morphological plasticity and higher adaptive potential than in crucian carp.

A high level of discrimination of specimens of crucian and prussian carps from different populations makes it possible to conclude that a directed reorganization of morphogenesis occurs in both species under different environmental conditions of adjacent lakes, leading to a certain phenotype of fish of each species in a particular lake. The directions of variation of the body shape elements neither coincide nor interact according to most characteristics, which indicates different morphogenetic responses to the same living conditions manifested in species in different waterbodies. It is possible that different degrees of anthropogenic radionuclide contamination that not characteristic of the lakes ensure morphogenesis reorganization. This indirectly demonstrates a wide range of interspecies divergence of cyprinids in more heavily radionuclide-contaminated Lake Bolshoy Igish and a significant effect of overdispersion in polygons of the shape variation in both lake species. If it is true, the morphogenesis reorganization in the both species in local lakes occurred for a relatively short semicentennial period after an accidental discharge of anthropogenic nucleotides at the Mayak Production Association.

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