

Phenotypic Plasticity of the Amur Sleeper (*Perccottus glenii*) Invasive Populations during the Colonization of Water Bodies

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Abstract—The variability of the body shape in invasive fish species—Amur sleeper (*Perccottus glenii*)—from natural and anthropogenic water bodies of the Middle Urals, with different completeness of the species composition, was studied by the use of geometric morphometric methods. We compared samples of Amur sleepers from adjacent water bodies—Lake Shitovskoye and two peat quarries filled with water. Samples of different seasons and years of collection were taken in the lake, which allowed us to correlate the influence of climate and season on the morphogenesis of the Amur sleeper. According to the control catches, the fish community of the lake is represented by ten species; i.e., it is a species-rich community: six native species (roach, river perch, ruff, tench, crucian carp, and pike) and four alien species (bream, beluga, Amur sleeper, carp). The share of Amur sleepers in the control catches in the lake was no more than 3–5%. In the water bodies of peat quarries, species-poor communities of two species were formed (Amur sleeper and crucian carp). Discriminant analysis of the body shape of fish from the lake and peat quarries allowed us to reveal the origin of 93–98% of specimens. Comparing the samples of the younger (2+–3+ years) and older (4+–7+ years) age groups of fish divided by sex and biotope, different directions of changes in the shape of the Amur sleeper's body in ontogenesis were revealed between the biotopic groups. The range of age variability was almost 5 times lower than the intergroup biotopic differences of fish from ecologically contrasting water bodies. The seasonal and interannual intrapopulation variability of body shape in Amur sleepers in the lake is significantly less pronounced than the intergroup differences between samples from the lake and peat quarries. Sex differences accounted for only 6% of the intergroup variance (3 times lower than the level of age differences), and in the species-rich lake community, sex differences decrease with age, and in the water bodies of quarries, on the contrary, they increase. Intragroup morphological disparity (*MNND*) was significantly higher in samples from peat quarries. The data obtained are of a key character, since they characterize a high degree of phenotypic plasticity of the Amur sleeper and a rapid adaptive restructuring of its morphogenesis to different conditions of natural and anthropogenic water bodies of the Middle Urals.

Keywords: *Perccottus glenii*, Amur sleeper, alien species, invasion, variability, morphological disparity, geometric morphometrics, the Middle Urals

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INTRODUCTION

Penetration and distribution of alien fish species outside their range is widespread and is a factor leading to changes in the composition and structure of autochthonous fish communities, impairing the balance of historically established biocenotic relations (Sakai et al., 2001; Facon et al., 2008; Panarari-Antunes et al., 2012). The invasion of new species can lead to changes in the functioning of communities and disruption of ecosystem functions (Zherikhin, 2003; Pavlov and Bukhareva, 2007; Stray, 2012). Since alien species fall into different ecological conditions, they rearrange morphogenesis in accordance with new environmental requirements, including a new biotic environment. Therefore, with a successful invasion,

the formation of new stable populations of the introduced species begins, which is accompanied by the formation of its population structure and further differentiation of newly emerging populations (Zelikova et al., 2013; Vasil'ev et al., 2017a). At this stage of penetration, selective processes of adaptive rearrangement of individual development are carried out, the rate of which should be largely determined by the initial phenotypic plasticity and genetic diversity of the populations of the alien species (Reshetnikov, 2013). In this regard, the evolutionary-ecological study of the long-term consequences of the invasion of alien species, including the assessment of the rates and directions of their morphogenetic rearrangements, becomes especially relevant.

Deliberate and accidental introduction of the Amur sleeper *Perccottus glenii* Dybowski, 1877 (Odonotobutidae, Perciformes) into the water bodies of Northern Eurasia and subsequent intense independent dispersal outside the native range (Primorye, Northern China, northeast of the Korean Peninsula) allowed this Far Eastern fish species to increase the range several times over a relatively short historical period (100 years) (Elovenko, 1981; *Atlas...*, 2002; Reshetnikov, 2009). It can be assumed that the invasion of the Amur sleeper into the water bodies of the Sverdlovsk oblast (Middle Urals) originated from the territory of neighboring southern and southwestern regions (Perm krai, Republic of Bashkortostan, Chelyabinsk oblast, Kurgan oblast). The distribution of the Amur sleeper in the water bodies of these regions of the Southern Urals, Cis-Urals and Trans-Urals was noted in the early and mid-1980s; approximately in the same period, it appeared in the south of the Middle Urals (Zinoviev et al., 1989; Shaigorodsky and Reshetnikov, 1994; Baklanov, 2001; Mikhailov, 2002; Dyachenko, 2013). The expansion of Amur sleeper across the territory of the Sverdlovsk oblast occurs from south to northeast. Since the mid-1990s, the appearance of the invader was recorded in all major large river basins of the region—the Sylva and Chusovaya rivers (Volga-Kama basin) and the Pyshma, Iset, Tura, and Tavda rivers (Ob-Irtys basin) (Lugaskov, 2008; Reshetnikov and Chibilev, 2009; Reshetnikov and Ficetola, 2011). The northern part of the region is currently not inhabited by Amur sleeper. Amur sleeper distributed in the territory of the Middle Urals penetrated into species-rich and species-poor ichthyological complexes and occupied its characteristic habitats with developed vegetation in stagnant or slow-flowing, often swampy reservoirs. Usually, these are lakes, floodplain oxbow lakes, small overgrown ponds, and city ponds filled with quarry water.

The Amur sleeper has high ecological plasticity and survival and is able to suppress or displace native species (*Biologicheskie invazii...*, 2004). Thus, this leads to a significant ecological transformation of local aquatic communities of water bodies, often to a simplification of the biocenosis structure and a decrease in its resistance to external influences (Alimov et al., 2000). On the other hand, new biocenotic relationships in the community and living conditions may turn out to be atypical for an alien species in the acquired area, and a long inhabitation under these conditions may lead to ecological and morphological changes (Shvarts, 1967, 1980; Nikolsky, 1974; Mina, 1986; Lucek et al., 2012). In this regard, it was interesting to study the patterns of morphological variability of Amur sleeper under conditions of ecologically contrasting adjacent water bodies of a single river system in communities with different species richness. The Amur sleeper, as an alien fish species, has become widely distributed over the past 30–40 years in small and large water bodies of the Middle Urals and can serve as a model object in

assessing the degree of phenotypic plasticity of the invader under new environmental conditions far beyond its original range.

Geometric morphometry methods can be applied for the solution of such problems (Rohlf and Slice, 1990; Zelditch et al., 2004; Klingenberg, 2011), since these methods make it possible to separately analyze the variability in the size and shape of objects and perform morphogenetic interpretation of the revealed differences (Sheets and Zelditch, 2013; Vasil'ev et al., 2018).

The purpose of the study was the investigation of the variability of the body size and shape of invasive micropopulations of Amur sleepers in ecologically contrasting adjacent water bodies of the Middle Urals on the basis of a comparison of samples of species from species-poor and species-rich ichthyocenoses using geometric morphometry methods.

MATERIALS AND METHODS

In the study, samples of Amur sleepers from Lake Shitovskoye with a species-rich fish community and two small two peat quarries filled with water territorially close to the lake with species-poor ichthyocenoses were used. Samples of fish were taken on the territory of Sverdlovsk oblast (Middle Urals) from geographically adjacent water bodies—Lake Shitovskoye (57°07'41" N, 60°28'23" E) and peat quarries filled with water. Samples differing in season and year of collection were taken in the lake, which made it possible to assess the possible influence of interannual conditions and phenology on the morphogenesis of the Amur sleeper. Sampling sites in peat quarries were conventionally designated as quarry no. 1 (57°08'03" N, 60°32'41" E) and quarry no. 2 (57°05'46" N, 60°30'07" E). Samples were selected from Lake Shitovskoye in early summer on June 15 (25 specimens) and late autumn on November 16, 2009 (22 specimens), as well as in the summer on June 28, 2010 (25 specimens). Two samples were taken on June 22 and 23, 2011, from quarries no. 1 (55 specimens) and no. 2 (19 specimens) (Fig. 1). A total of 146 specimens (75 males and 71 females) were studied.

Lake Shitovskoye belongs to the system of lakes and swamps of the upper reaches of the Iset River (basin of the Tobol River). The area of the reservoir is 7.8 km², the mean depth is 1.3 m, and the degree of overgrowth is 35%. The coastline is indented, the bottom is covered with sapropel, in some places with sandy soil with an admixture of organic residues; there are numerous remains of wood. The lake is a fresh eutrophic water body (Lugas'kova, 2003), highly nutritive in terms of zoobenthos and above average in terms of zooplankton. Winter and summer mass fish mortality are periodically observed. The quarries are a system of cuts (ditches) and channels filled with water after the cessation of peat extraction (late 1960s—early

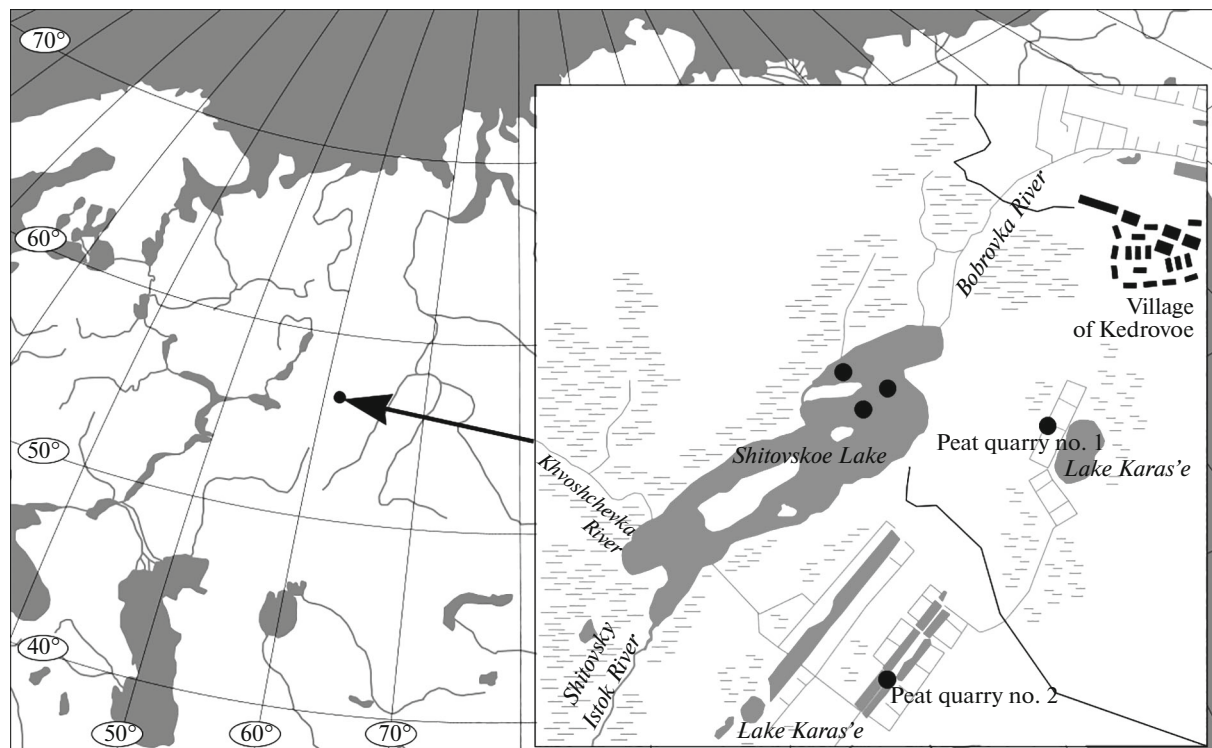


Fig. 1. Schematic map of the location of Lake Shitovskoye and peat quarries (no. 1 and no. 2), indicating the locations of catches of Amur sleepers.

1970s) and streams flowing into the lake. Their depths reach 0.2–2.0 m. Now, the lake and peat quarries filled with water are not subjected to significant anthropogenic impact.

The fish population in Lake Shitovskoye, according to the control net and seining catches, is represented by ten species. Six native species were found (roach *Rutilus rutilus* (Linnaeus, 1758), river perch *Perca fluviatilis* Linnaeus, 1758, ruff *Gymnocephalus cernuus* (Linnaeus, 1758), tench *Tinca tinca* (Linnaeus, 1758), crucian carp *Carassius carassius* (Linnaeus, 1758), pike *Esox lucius* Linnaeus, 1758) and four alien species were found (bream *Abramis brama* (Linnaeus, 1758), belica *Leucaspis delineatus* (Heckel, 1843), Amur sleeper, carp *Cyprinus carpio* Linnaeus, 1758). Earlier, burbot *Lota lota* (Linnaeus, 1758) and ide *Leuciscus idus* (Linnaeus, 1758) were noted in catches. Recently (starting from 2010), the alien pikeperch *Stizostedion lucioperca* (Linnaeus, 1758) started to enter the lake from the cooling pond of Lake Isetskoye. The share of Amur sleepers in the control catches in the lake was not more than 3–5%. In the quarries, one or two species were found, Amur sleepers predominated, and crucian carp was observed singly. In the spring flood from the lake along the canal, temporary entry of other fish species into the peat quarries is possible.

The invasion of Amur sleepers into Lake Shitovskoye and peat quarries filled with water took place, probably, in a close period of time. The first capture of

an Amur sleeper was registered in 1995 in the northern part of the lake near the mouth of the Bobrovka River (Elin, 1999). In the first half of the 2000s (by 2004), Amur sleepers completely occupied the northeastern peat sections (village of Kedrovoe). Probably, by this time, the eastern quarries, in which samples were taken, were also colonized by the invaders. At the same time, until the second half of the 2000s, Amur sleepers were hardly recorded in the control catches in Lake Shitovskoye. The population of the invader in the lake began to grow after the mass fish mortality in 2007–2008. At the same time, over the next few years, a low abundance of pike was noted in the lake. By the end of the 2000s, Amur sleepers were regularly encountered in control catches in the lake, especially near biotopes with developed aquatic vegetation, but the relative abundance of the invader did not exceed 5% in the catch.

Amur sleepers were captured using a set of fixed gillnets with a mesh of 20, 25, 30, and 35 mm, 30–50 m long, as well as traps with a mesh of 6–10 mm. The biological analysis and determination of the age of fish were carried out according to the generally accepted method (Pravdin, 1966). The age of the fish was determined on basis of the scales. The length of the fish was measured from the tip of the snout to the end of the scale. Fish samples were represented by specimens from 2+ to 7+ years old. The fish were subdivided into two conditional age groups: specimens 2+–3+ years old

and specimens 4+–7+ years old for accounting and the analysis of age-related changes in body size and shape. Samples of males and females were considered both separately and as a single set for each of the compared population groups.

The variability of digitized images of the lateral projection of the body of Amur sleepers was analyzed using geometric morphometry methods (Rohlf and Slice, 1990; Zelditch et al., 2004; Klingenberg, 2011). The photographing of fish was carried out with a zoom bar using a Canon EOS 450D digital single-lens reflex camera with a resolution of 1280 × 960 PPI, mounted on a tripod. Images were digitized using the TPS software package (tpsUtil, tpsDig2) developed by Rohlf (2013a, 2013b). Using the on-screen digitizer program (tpsDig2), 22 landmarks were placed on photographs of fish to further characterize the variability of their shape at homologous points of the lateral projection of the body and external structures (Fig. 2a). For the assessment of the actual size, two scaling landmarks (23–24) were placed additionally on the central divisions of the ruler, 1 cm apart from each other. An indirect assessment of the variability of the body size of Amur sleepers was carried out according to the centroid size (CS), which is the square root of the sum of the squared distances from the center of the image to each of the landmarks (Rohlf and Slice, 1990). Two landmarks in the region of the anus and the beginning of the ventral fin (the base of its first ray) were initially placed, which are not shown in the diagram (see Fig. 2a). They were excluded because of a significant variation in their localization with different degrees of intestinal filling. Amur sleepers have a cylindrical body shape; therefore, the stability of the size and configuration characteristics was also preliminarily assessed according to the 2D lateral projection of the left and right sides. The Pearson correlation coefficients in the model sample for the values of the centroid sizes of the left and right sides were $r = 0.997$ ($p \leq 0.0001$), and for the values of the first relative warp (RW1), they were $r = 0.916$ ($p < 0.0001$). The measurement error estimated on the basis of the ratio of the within-group component to the sum of the intra- and between-group components of variability in a one-way analysis of variance taking into account repeated measurements (Yezerinac et al., 1992; Claude, 2008) was 3.15% for the centroid dimensions, and for the body shape of the Amur sleeper, characterized by the first relative strain, it was 5.89%. Thus, despite the cylindrical shape of the Amur sleeper, the estimates obtained showed high accuracy of measurements and reliability of comparison of fish configuration. For 2D modeling of the variability of the body shape of fish, wireframe contour models, which are outlines, were used (Fig. 2b).

For geometric morphometry, the superimposition procedure was performed using the generalized orthogonal least squares Procrustes analysis method (GPA) (Rohlf and Slice, 1990). For the assessment of

intergroup differences, we used the methods of estimating the principal components (PC) and discriminant (DA) and canonical (CVA) analyses of Procrustes coordinates characterizing the variability of the fish body shape. For the assessment of the hierarchy of intergroup relationships, cluster analysis based on the UPGMA and Ward algorithms with the calculation of bootstrap supports for clade branch nodes was used (the choice of the clustering algorithm was made based on the value of the cophenetic correlation coefficient, *Coph. R*, reflecting the degree of association of the final matrix with the original matrix).

Intragroup morphological disparity was estimated on the basis of the ordinates of the two principal components using the nearest neighbor point pattern analysis method within the variability polygon—convex hull (Davis, 1990; Hammer, 2009). In accordance with this method, the *R* indicator was calculated as the ratio of the mean nearest neighbor distance (*MNND*) to the expected nearest neighbor distance (*ExpNND*) obtained for the variability polygon based on the Poisson distribution. Donnelly's method (Donnelly, 1978) was used to remove the edge effect of ordinate variance within a limited variability polygon. The method for analyzing the pattern of nearest neighboring points was implemented by K. Hammer in PAST 4.06 (Hammer et al., 2001; Hammer, 2009).

Index *R* characterizes the ordinate variance model: if $R < 1$, the aggregation of ordinates is manifested; if $R = 1$, random Poisson scattering is observed; and if $R > 1$, then the overdispersion effect is expressed. Increase in *MNND* when analyzing the variability of the shape of objects can be interpreted as an increase in intragroup morphological disparity (Hammer, 2009), and in the case of using geometric morphometry methods, it can be interpreted as an increase in the fan of morphogenesis trajectories (Vasil'ev et al., 2015, 2018). Partial disparity within groups (*PDW*) and partial disparity between groups (*PDB*) (Zelditch et al., 2004) were estimated using the DisparityBox7 program of the IMP package.

In the case of detection of heterogeneity, using Levene's test for homogeneity of variance based on means, its nonparametric analog, the Kruskal–Wallis test, was used along with the one-way ANOVA. For the estimation of Cohen effect size in multiple intergroup comparisons, the ω^2 criterion was used. The linear regression models and correlation analysis were used according to generally accepted recommendations for the assessment of the possible impact of allometric effects (Zelditch et al., 2004; Klingenberg, 2011). The Mantel test was used for the evaluation of matrix correlations. The main calculations and statistical analysis were performed using the TPS (Rohlf, 2013a, 2013b), PAST 4.05 (Hammer et al., 2001), IMP (Zelditch et al., 2004), and MorphoJ 1.07a (Klingenberg, 2011) programs.

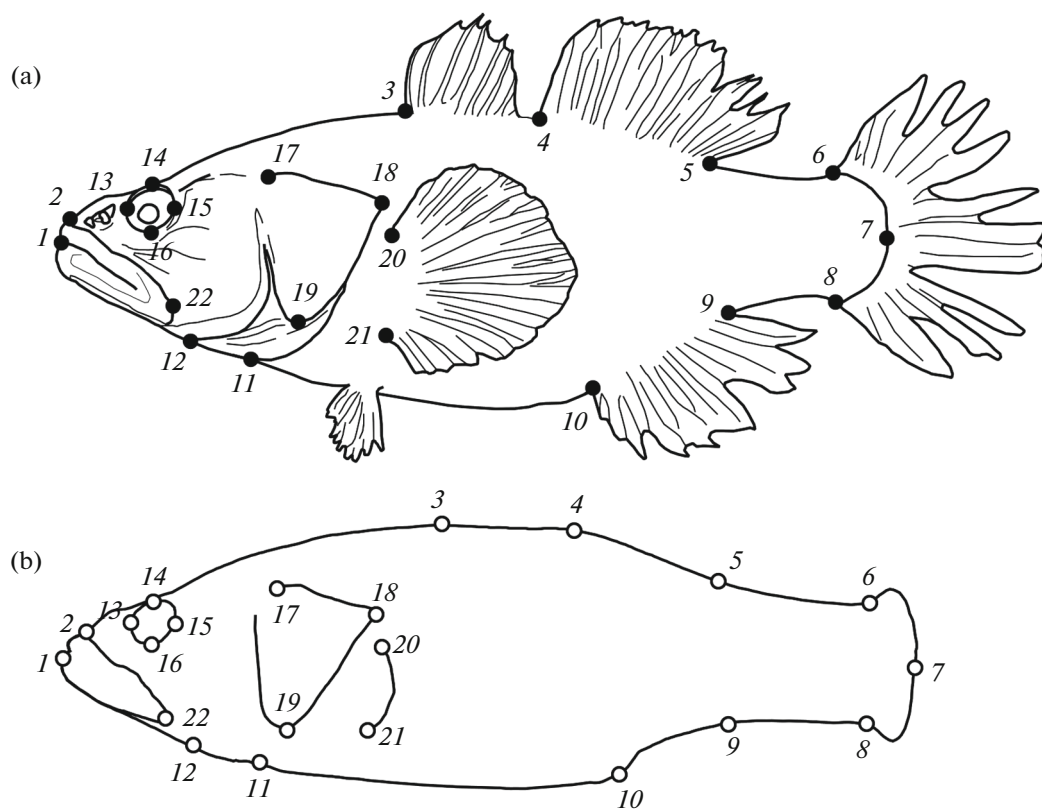


Fig. 2. Scheme of placement of landmarks (1–22) on the lateral projection of the body of an Amur sleeper (a), 2D wireframe model of the landmark configuration for visualization of shape variability (b). Landmarks: (1) tip of the snout; (2) anterior upper edge of the upper jaw; (3) beginning of the first dorsal fin (base of the first ray); (4) tip of the second dorsal fin (base of the first ray); (5) end of the second dorsal fin (base of the last ray); (6) tip of the upper outer ray of the caudal fin; (7) middle of the aboral margin of the caudal peduncle; (8) tip of the lower outer ray of the caudal fin; (9) end of anal fin (base of last ray); (10) tip of the anal fin (base of the first ray); (11) ventral border of the head and trunk; (12) posterior lower edge of the lower jaw; (13) anterior margin of the eye; (14) upper edge of the eye; (15) posterior margin of the eye; (16) lower edge of the eye; (17) upper front edge of the operculum; (18) upper aboral margin of operculum; (19) lower edge of operculum; (20) tip of the pectoral fin (base of the first ray); (21) end of the pectoral fin (base of the last ray); (22) posterior upper edge of the upper jaw.

RESULTS AND DISCUSSION

The principal component (PC) analysis was used for the ordination of Procrustes coordinates, built for the combined sample of Amur sleepers. On the basis of the values of the Jolliffe coefficient, which characterizes the cumulative contribution of shape variation, the first 13 principal components were established and these components were further considered as significant and interpretable. In total, 90.16% of the total variance of the body shape was described. The calculation of Spearman's rank correlation coefficients between the values of the principal components and the biological characteristics of specimens in the samples (age, body size, sex) revealed a significant relationship for individual variables. An estimate of the correlation of PC with the species richness of ichthyocenoses was also obtained, which was formally given in the form of ranks 1 and 2. Rank 1 was used for Amur sleepers from peat quarries, in which, in addition to Amur sleepers, large specimens of crucian carp were found sporadically. Rank 2 was used for Amur sleepers

from Lake Shitovskoye, which was inhabited by ten fish species.

The highest values of the of Spearman's rank correlation coefficients, characterizing the relationship of the principal components with body dimensions ($r_s = -0.64$) and fish age ($r_s = -0.56$) were revealed for the second principal component PC2, along which a regular change in body shape was observed with age. The size-age variability of shape accounts for 14.77% of the total variance. There was a weak but significant relationship with gender ($p < 0.05$) for three principal components—PC5 ($r_s = 0.14$), PC8 ($r_s = 0.17$), and PC11 ($r_s = -0.12$). With the “species richness” factor of communities of adjacent water bodies, significant correlations were established for variability along the first principal component PC1 ($r_s = 0.61$), which explains 26.94% of the total variance, and the third component PC3 ($r_s = -0.32$), which describes 10.62% of the variance (Fig. 3). As can be seen from the figure, the centroids of the samples of adjacent years from Lake Shitovskoye were close, and the centroids of the

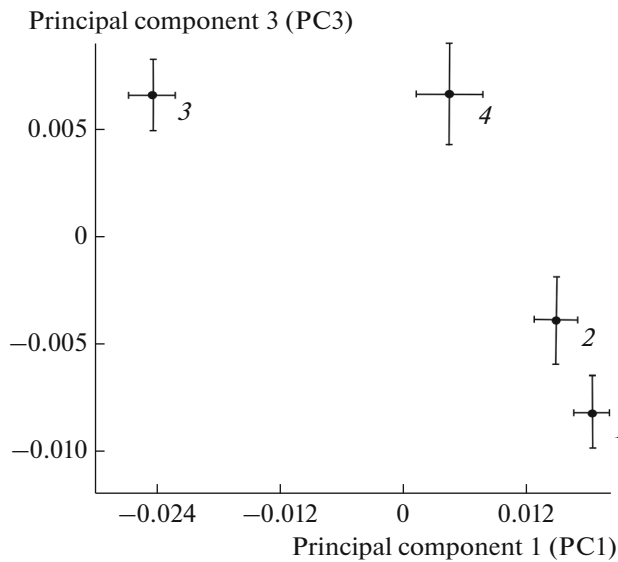


Fig. 3. Ordination of centroids of Amur sleeper samples from Lake Shitovskoye ((1) 2009, (2) 2010) and peat quarries ((3) quarry no. 1; (4) quarry no. 2) taking into account standard errors ($\pm SE$ —standard error) in the plane formed by the main components PC1 and PC3, which characterize the body shape of Amur sleepers and correlate with the species richness factor of the communities.

Amur sleeper samples from quarries no. 1 and no. 2 were not only distant from them but also distant from each other. A significant influence of this factor on the variability along PC1 ($H = 132.19$; $df = 3$; $p < 0.001$) and PC3 ($H = 40.39$; $df = 3$; $p < 0.001$) were deter-

mined. Differences between samples of Amur sleepers from Lake Shitovskoye of different years in 2009 and 2010 were statistically insignificant.

For the assessment of the most stable intergroup differences, a canonical analysis of eight samples of male and female Amur sleepers of two age groups from two adjacent reservoirs, the lake and quarry no. 1, was carried out according to Procrustes coordinates. The results of the centroid ordination of the compared samples taking into account the standard errors ($\pm SE$) are shown in Fig. 4. As a result of the calculations, statistically significant intergroup differences were revealed along all canonical variables (Table 1, Fig. 4). For plotting mean ontogenetic trajectories, which characterize the transformation of the Amur sleeper's body between male and female groups, the centroids of the corresponding samples belonging to different age groups were connected by arrows directed from fish 2+ and 3+ years old (j) to the older ones (a) according to the age in the figure.

Along the CV1 axis, more than 65% of the intergroup variance characterized biotopic variability and was associated with intergroup differences in the body shape of Amur sleepers from the lake and quarry, with the maximum differences between groups of males. Differences between younger age groups from adjacent water bodies turned out to be higher than between older age groups, the convergence of which was mainly due to age-related changes in the body shape of males and females from quarries.

Despite the wide age range, including fish from 2+ to 7+ years old, it was found that the general tenden-

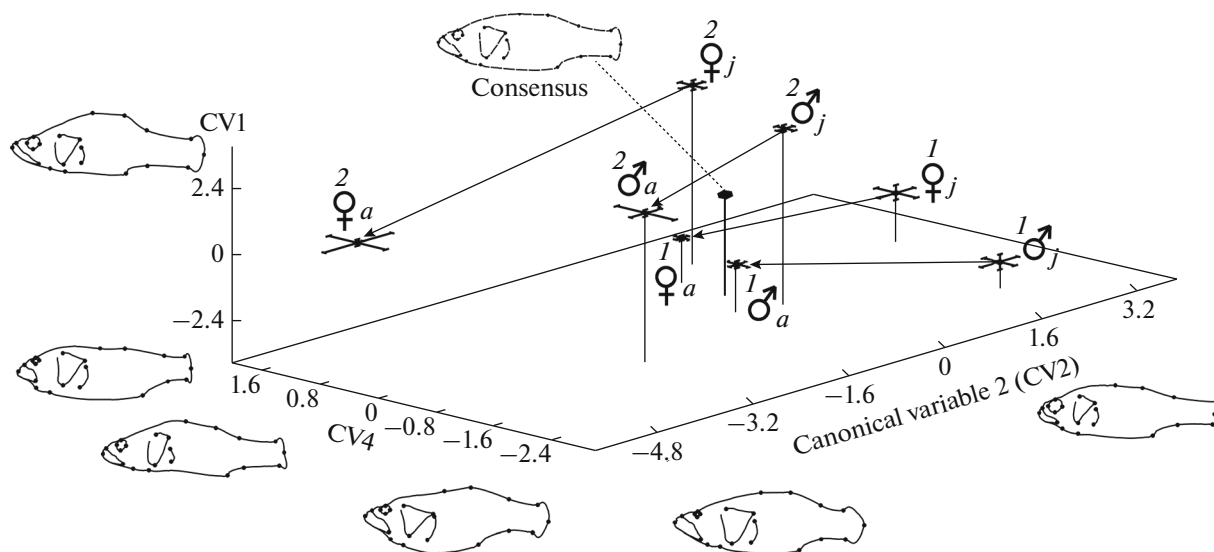


Fig. 4. The results of ordination of centroids of samples of Amur sleeper males and females of two age groups (subscripts: j —fish 2+–3+ years and a —fish 4+–7+ years) from adjacent water bodies of the Middle Urals (superscripts), Lake Shitovskoye (1) and quarry no. 1 (2), along three canonical variables (CV1, CV2, and CV4). Arrows indicate the directions of age-related changes in the body shape of Amur sleepers. Sample centroids and standard errors are shown ($\pm SE$). Schematic contour configurations of landmarks visualizing changes in the body shape of Amur sleepers corresponding to the minimum and maximum values along the canonical variables are presented. The consensus and its ordinate are shown.

Table 1. The results of the canonical analysis of the Procrustes coordinates, reflecting the variability of the body shape of two age groups of male and female Amur sleeper samples from Lake Shitovskoye and quarry no. 1 and centroids of these samples with standard errors ($\pm SE$)

Compared samples and statistical criterions	Canonical variable (CV)			
	CV1	CV2	CV3	CV4
	Sample centroids			
Lake, males 2+–3+ years	-3.164 ± 0.168	2.346 ± 0.306	2.655 ± 0.316	-1.845 ± 0.212
Lake, females 2+–3+ years	-2.268 ± 0.124	3.000 ± 0.296	1.297 ± 0.182	0.155 ± 0.276
Lake, males 4+–7+ years	-2.278 ± 0.132	-0.368 ± 0.140	0.147 ± 0.118	-0.431 ± 0.155
Lake, females 4+–7+ years	-2.015 ± 0.116	-0.173 ± 0.105	-0.664 ± 0.132	0.475 ± 0.110
Quarry, males 2+–3+ years	3.042 ± 0.142	0.093 ± 0.136	-0.439 ± 0.132	-0.725 ± 0.124
Quarry, females 2+–3+ years	2.980 ± 0.166	0.776 ± 0.195	0.500 ± 0.168	1.111 ± 0.169
Quarry, males 4+–7+ years	1.960 ± 0.251	-2.704 ± 0.132	0.337 ± 0.284	-1.105 ± 0.397
Quarry, females 4+–7+ years	1.049 ± 0.553	-5.036 ± 0.060	2.936 ± 0.288	0.919 ± 0.391
Eigenvalues	6.5568	1.4314	0.6767	0.5617
Wilks' Λ -test	0.0099	0.0748	0.1819	0.3049
χ^2 criterion	1056.93	593.79	390.33	271.98
Degrees of freedom	280	234	190	148
Share of variance, %	65.07	14.21	6.72	5.57
Significance level, p	<0.0001	<0.0001	<0.0001	<0.0001

cies of variability of the body shape of Amur sleepers with age in population groups manifested along CV2 were lower by 4.6 times than the level of intergroup biotopic differences of fish from the lake and the quarry. With age, the relative size of the head, the relative length of the snout (jaws), and the relative height of the body of Amur sleepers increased, while the relative size of the eye and the relative length of the caudal peduncle decreased. Separate directions of the size-age transformation of the elements of the body shape of Amur sleepers were in good agreement with the patterns of age-related changes in the shape previously identified for the Amur sleeper (Spanovskaya et al., 1964; Baklanov, 2001; Mandritsa, 2010) and other fish species (Alev, 1963; Vasil'ev et al., 2007; Baranov, 2013).

The general differences in body shape between male and female Amur sleepers account for about 6% of the intergroup variance along CV4, which was 2.6 times lower than the variance of the shape associated with the age. The body shape of males was characterized by a large body gradually expanding caudally, a small protrusion in the frontal part of the head, large triangular gill covers, large pectoral fins and jaws, and a large caudal peduncle. Females had a narrow body tapering caudally, a flat frontal-dorsal region of the head, narrow almost rectangular gill covers, and relatively small pectoral fins. In the ontogenesis of Amur sleepers from the lake and a quarry, special directions of biotopic variability of body shape along CV3 were revealed, which explained about 7% of the

intergroup variance and caused a reversion of morphogenetic changes in age groups of Amur sleepers from adjacent water bodies. Specimens of younger age from quarries were similar in body shape to older fish from the lake and, conversely, older fish from quarries became similar to younger fish from the lake. This effect of the "genotype \times environment" interaction is still unclear in nature and requires further analysis and explanation. Nevertheless, some reversal of morphogenesis in different environments can also be considered as a special manifestation of biotopic variability and a probable adaptive ontogenetic mechanism of the phenotypic plasticity of the alien species.

Cluster analysis of the matrix of generalized Mahalanobis distances (D^2) revealed a low degree of morphological similarity between Amur sleeper age groups of different sexes from the lake and the quarry, which were grouped into separate intrapopulation clusters (Fig. 5).

Two large clusters of samples related to different biotopes were distinguished: Lake Shitovskoye and peat quarry. Each of these clusters was subdivided into samples of younger and older specimens, which, in turn, were divided by sex. Therefore, the hierarchical structure of the cluster in descending order of aggregation rank is presented in the sequence: the highest level of differences is the biotope (micropopulation), the mean level of differences is the age group, and the lowest level of differences is the sex of specimens.

It has been established that, in the multispecies fish community of the lake, under conditions of competi-

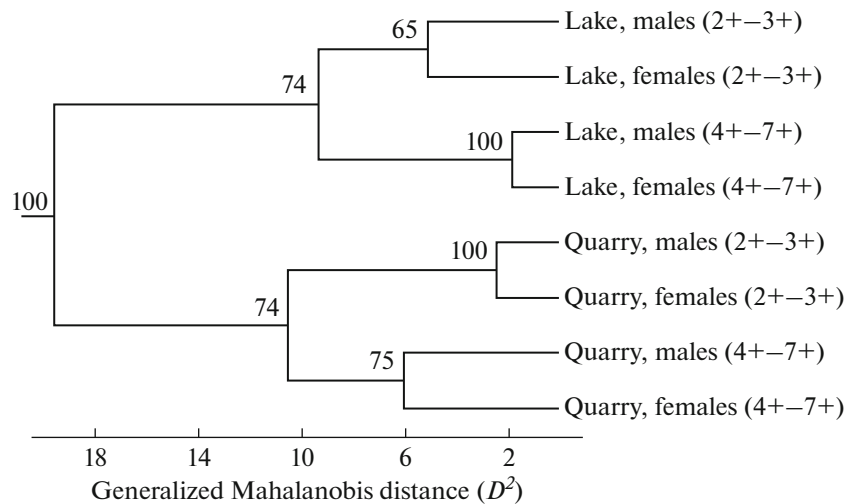


Fig. 5. The results of cluster analysis (Ward's method) of the matrix of generalized Mahalanobis distances (D^2) between the samples of Amur sleeper males and females of two age groups from Lake Shitovskoye and quarry no. 1 (bootstrap support at cluster nodes is indicated, %).

tion and under pressure from predators, the differences in the body shape between male and female Amur sleepers decreased in ontogeny. In the micropopulation of the Amur sleepers of the peat quarry, with a low species diversity of the community and a low level of interspecific competition, in the absence of other ichthyophagous species, on the contrary, sex differences in the body shape of Amur sleepers increased with age (see Fig. 5). At the same time, the level of age differences in the micropopulations of both biotopes was approximately the same.

For fish of the same age (3+), we compared the values of the centroid size (CS), which indirectly characterizes their overall size, as well as the body length measured in millimeters. Multiple comparison of CS of these samples using the Kruskal–Wallis test revealed statistically significant differences ($H_c = 12.98$; $p = 0.0015$). The same results were obtained using one-way ANOVA analysis of the body length of fish in three water bodies (Table 2, Fig. 6). At the same time, the Levene's test did not reveal significant differences between the intragroup variances ($p = 0.2811$), which makes the use of one-way ANOVA valid.

In Lake Shitovskoye, the mean size of fish was significantly lower than in both quarries (nos. 1 and 2),

the differences between which were not significant. It should also be noted that the Cohen effect size in this case was $\omega^2 = 0.35$, which, according to the criteria adopted by Cohen, was significantly higher than the mean level of intergroup differences. Therefore, it can be concluded that the differences in the body length of fish of the same age from the lake and quarries is high, and they also indicate some inhibition of growth in the bodies of Amur sleepers in the lake, but the absence of such in both quarries, where growth processes proceed similarly. The same intergroup differences in body length were also found in fish aged 4+ (these results are not presented here), which indicates the general nature of this phenomenon.

Different growth rates of different body parts can potentially lead to allometric effects, which can influence the manifestation of differences in body shape. Therefore, we evaluated the potential allometric effects using, in accordance with the recommendations of Zelditch et al. (2004), an estimate of the linear regression between the centroid size and the values of the first principal component. The regression analysis was performed separately for each sample. As a result of the calculations, it was found that, in the compared samples of Amur sleepers, the share of the explained regression dependence ranged from 0.47 to 4.86%,

Table 2. Results of one-way analysis of variance of body length (mm) of same-age (3+) groups of Amur sleepers in three compared reservoirs

Source of variability	Sum of squares (SS)	Degrees of freedom (df)	Mean square (MS)	F	Significance level (p)
Between group	3320.69	2	1660.35	13.57	0.000027
Within group	5282.18	43	122.38		
Total	8582.97	45			

and in all cases, it was statistically insignificant (p value ranged from 0.2916 to 0.7478). Thus, it can be concluded that, when interpreting the revealed intergroup differences in the body shape of fish in this case, allometric effects should be excluded as a possible cause.

Since the sex and age differences reflected in the body shape of Amur sleepers were, on the whole, significantly less than the intergroup biotope differences, we carried out a generalized canonical analysis of the body shape in five compared samples without taking into account the sex and age of the fish. The calculation was carried out using Procrustes coordinates. The results of the canonical analysis are shown in Fig. 7. Along the first two canonical axes, biotopic and chronographic (interannual and seasonal) differences in the body shape of Amur sleepers were noted (see Fig. 7), which accounted for 73.85% of the total intergroup variation.

The matrices of generalized Mahalanobis distances calculated as a result of the canonical analysis (D^2) and Procrustes distances (D_p) between the samples were proportional to each other and statistically significant in all pairs of comparisons ($p < 0.0001$). The comparison of distance matrices based on the Mantel test revealed a high level of their correlation ($R_M = 0.922$; $p = 0.0056$).

The hierarchical relationships of the samples are well illustrated by the results of cluster analysis (UPGMA) of the Procrustes distance matrix (Fig. 8). It follows from the figure that biotopic differences in body shape were more expressed than interannual and seasonal differences. It can also be concluded that the level of seasonal changes in Lake Shitovskoye was comparable with interannual changes.

The greatest differences were revealed between the samples of two ecologically contrasting water bodies—the lake and a peat quarry. Therefore, completing the comparison of the body shape of Amur sleepers, we carried out a discriminant analysis of the Procrustes coordinates between the specimens inhabiting these two biotopes. The results of the discriminant analysis are presented in Fig. 9. The body shape of Amur sleepers from the lake and the quarry differed significantly ($D^2 = 28.73$; $T^2 = 1791.76$; $p < 0.0001$), which allowed us to diagnose specimens of each group with high accuracy (97.95%). The results of the cross-validation test revealed almost the same pattern of discrimination (93.15%). Thus, as a result of discrimination, about 98% of specimens were unmistakably classified as belonging to their own biotopes, regardless of the age and sex of the fish. The use of the method of constructing contour configurations allows us to characterize the detected intergroup differences in the shape of the body of Amur sleepers.

Amur sleepers from the quarries were distinguished by a conical head, large eyes, long narrow jaws, a short high body, a relatively longer caudal peduncle, and a

Body length of the Amur sleeper (3+), mm

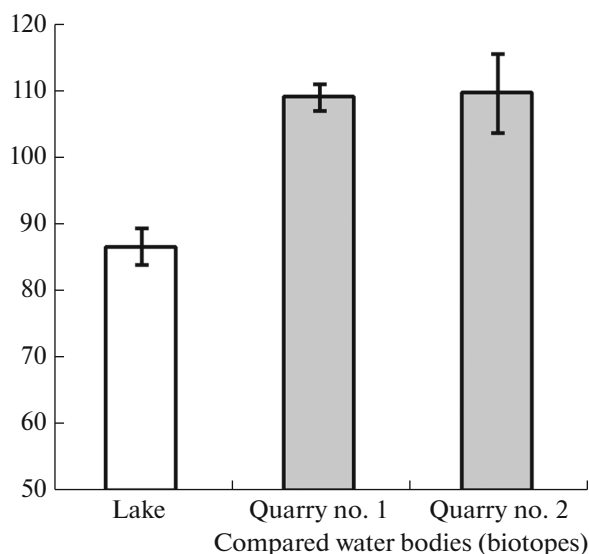


Fig. 6. Comparison of body length (mm) with standard errors ($\pm SE$) in samples of coeval Amur sleeper specimens (3+) in three water bodies.

vertical orientation of the pectoral fin. The hump-backed (convex) shape of the Amur sleeper's body makes it possible to perform quick maneuvers at a small angle and more easily capture food (Webb, 1984) in habitats with a complex structured environment formed by dense thickets of aquatic plants in flooded quarries. Larger eyes, mouth size, and head shape suggest a predatory, piscivorous nature of these fish. Fish from the lake have a massive high head with wide short jaws, as well as dorsally displaced gill covers and small eyes, a low, relatively elongated and almost rectangular body, a short caudal peduncle, and a large pectoral fin inclined backward. The low body profile of Amur sleepers reduces water resistance, allowing to move efficiently and maintain speed with little energy consumption. The location of the pectoral fins suggests that the fish are capable of rapid and abrupt movement (Webb, 1984). For the maintenance of body stability during movement and turns, fish have relatively large unpaired fins. The massive head and subterminal mouth of fish from the lake may be associated with a predominantly benthic feeding strategy (Wainwright and Richard, 1995).

Now, it cannot be argued that the differences between the two biotopic micropopulations of Amur sleepers are solely due to the anthropogenic origin of quarries.

The incompleteness of the composition of the fish community in the peat quarry, where the micropopulation of sleeper inhabits, also can enhance the diversity of morphogenetic trajectories.

Assessment of intra- and intergroup morphological disparity. The levels of intra- and intergroup disparity were compared using the DisparityBox7 program of

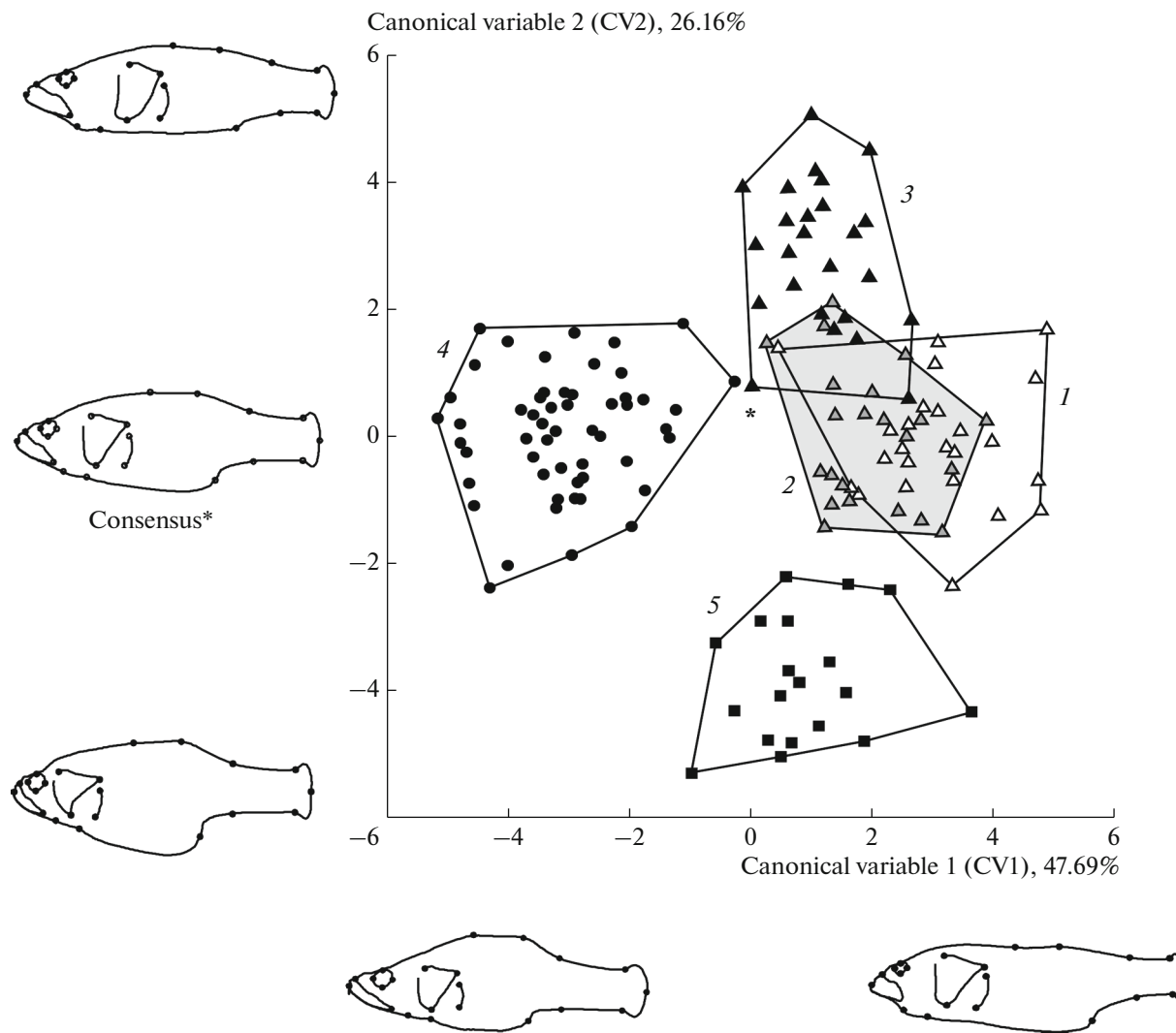


Fig. 7. The results of the canonical analysis of the Procrustes coordinates characterizing the variability of the body shape in Amur sleeper samples combined by sex and age in the Middle Urals: Lake Shitovskoye (1) 2009 (June), (2) 2009 (November), (3) 2010 (June); peat quarries (sections) (4) no. 1, 2011 (June), (5) no. 2, 2011 (June).

the IMP package for two samples of different years from the lake and two samples of the same year from peat quarries using the method of partial morphological disparity *PD* (Zelditch et al., 2004). The results of the comparison are shown in Fig. 10.

As can be seen from the figure, the levels of partial disparity between groups (*PDB*) in the micropopulations of Amur sleepers inhabiting the biotopes of the lake and the peat quarry coincide, and the corresponding level of partial disparity within groups (*PDW*) was significantly higher in the peat quarry micropopulation ($t = 2.8$; $df = 144$; $p < 0.01$).

It is appropriate at this point to recall that $PD = PDB + PDW$ (Zelditch et al., 2004), and therefore *PD2* of samples from the quarry is significantly higher than *PD1* of samples from the lake. Thus, biotopic groups of Amur sleepers differ not only in body shape

but also in the level of its intragroup morphological disparity, which is significantly higher in micropopulations from species-poor peat quarry reservoirs of anthropogenic origin.

We also used another method—estimation of the pattern of distances between the nearest neighboring ordinates for assessing intragroup morphological disparity. For this purpose, in each group of Amur sleepers, variability polygons of the compared samples were constructed in the plane of the first and third principal components PC1 and PC3 (see Fig. 3), which account for 37.56% of the body shape variability and are significantly related to the rank of species richness of communities.

Preliminarily, using the rarefaction procedure, the sample volumes, identical by the number of observations, were formed. As a result of comparison of mean

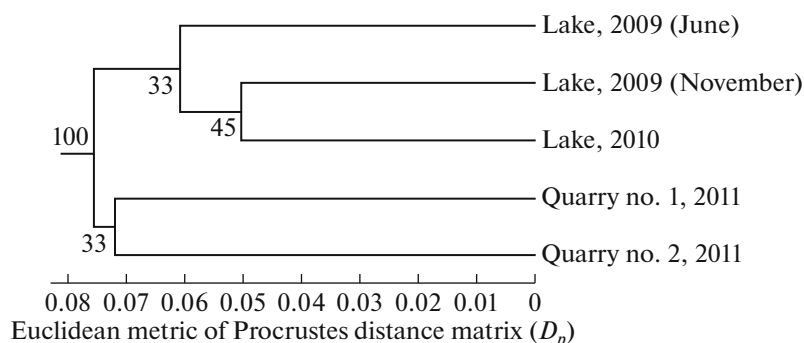


Fig. 8. The results of cluster analysis (UPGMA) of the Procrustes distance matrix (D_p) between Amur sleeper samples of different years and seasons from ecologically contrasting water bodies (Lake Shitovskoye and peat quarries) of the Middle Urals.

nearest neighbor distance ($MNND$) for Amur sleeper samples, on the basis of the Kruskal–Wallis test, significant intergroup differences were revealed ($H = 17.23$; $p < 0.001$). Relatively high levels of morphological diversity ($MNND$) appeared in samples of Amur sleepers from quarries, especially from quarry no. 1 (Table 3).

In two samples of different years from Lake Shitovskoye, the $MNND$ values were close, but had low values. It should be noted that, in the samples of Amur sleepers from all adjacent water bodies, a significant effect of nonrandom ordinate aggregation was observed, since $R < 1$. The latter indicates that, in each water body, an extremely narrow range of developmental trajectories characteristic of most specimens of this water body was selectively implemented. In other words, under the specific conditions of a given reser-

voir, certain paths of morphogenesis are realized, which form a typical phenotype in most specimens (each reservoir has its own special phenotype), while the random component of the intragroup variability of the fish body shape remains minimal. Such an effect is unexpected, since it was assumed that the random component of variability should increase in Amur sleepers that had entered new habitat conditions outside the native species range and increase even more in anthropogenic water bodies (peat quarries filled with water); i.e., overdispersion of ordinates should be observed, but this was not detected. On the contrary, the opposite effect of nonrandom implementation and “replication” of a certain phenotype (a narrow set of phenotypes) in a water body was revealed. Therefore, the observed increase in the $MNND$ of fish from quarries could theoretically be even higher if we compare it

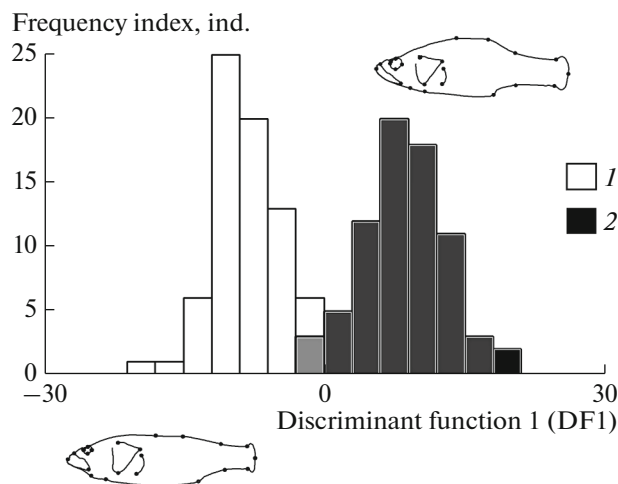


Fig. 9. The results of the discriminant analysis of Procrustes coordinates characterizing the body shape of invasive Amur sleeper micropopulations in two types of biotopes: (1) lake and (2) peat quarry in the Middle Urals. Contour models of fish body shape correspond to the minimum and maximum of the discriminant function.

Partial disparity of Amur sleepers (PD —partial disparity)

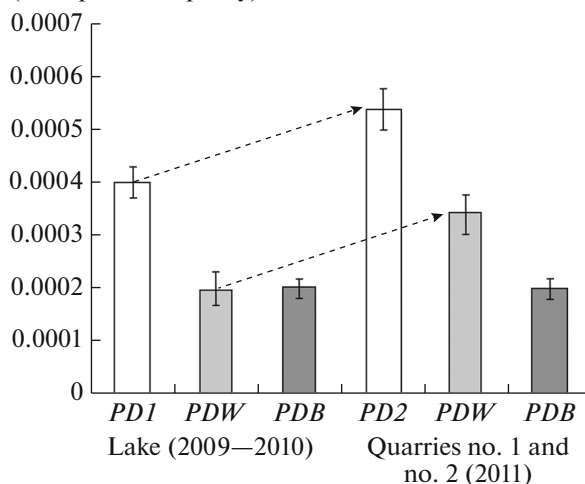


Fig. 10. The ratio of the hierarchical structure of particular morphological disparity ($PD \pm SE$) of the body shape of Amur sleeper from the species-rich fish community from Lake Shitovskoye ($PD1$) and a species-poor community of a peat quarry ($PD2$) taking into account their intragroup (PDW) and intergroup (PDB) component.

Table 3. Estimation of the ordinate variance model in the variability polygon of the body shape of Amur sleepers along PC1 and PC3 for four samples based on the method of the mean nearest neighbor distance (*MNND*)

Sample, year	Mean nearest neighbor distance <i>MNND</i>	Expected nearest neighbor distance <i>ExpNND</i>	<i>R</i>	<i>Z</i>	Significance level (<i>p</i>)
Lake Shitovskoye, 2009	0.0019	0.0031	0.61	−4.08	<0.001
Lake Shitovskoye, 2010	0.0019	0.0036	0.54	−4.85	<0.001
Quarry no. 1, 2011	0.0034	0.0050	0.68	−3.44	<0.001
Quarry no. 2, 2011	0.0029	0.0046	0.63	−3.97	<0.001

with the corresponding *ExpNND* values for random implementation of morphogenesis (see Table 3). It could be assumed that this is the result of the well-known genetic “bottleneck” effect due to the limited number of founder specimens, but the phenotypes (body shape) of Amur sleepers from two spatially distant but ecologically similar peat quarries were closer to each other than between the nearest micropopulations of the lake and quarry no. 1 (see Figs. 1 and 5). The action of directional strict selection also could be proposed, but such an efficiency with the possibility of annual mutual genetic mixing of fish populations from different water bodies, even taking into account the low mobility of Amur sleepers, seems unrealistic (it is known that 3% of exchange per generation should theoretically ensure genetic leveling of adjacent populations—(see Sheppard, 1970; Timofeev-Ressovsky et al., 1973)). Now, we can explain this paradox only by the fact that, probably, the native populations of the species in their original natural habitat acquired a large set of potential adaptive modifications to a wide range of biotopes, which can be easily implemented as one of the possible ways of morphogenesis under certain biotopic conditions. In other words, the conclusion about the existence of a pre-adaptation of Amur sleepers to habitation and development in a wide range of water bodies of the Middle Urals, including flooded peat quarries, suggests itself.

When the specimen enters certain conditions, for example, stress-inducing epigenetic systems (Jablonka and Raz, 2009; Duncan et al., 2014; Burggren, 2016), threshold epigenetic mechanisms (DNA methylation, transposition of mobile elements of the genome, etc.) are activated, and these mechanisms switch morphogenesis in a certain way in accordance with the necessary adaptive modification. Subsequently, the altered epigenetic DNA profile, “tuned” to the replication of a certain group of phenotypes, as shown by many recent studies of epigenetics, is able to be transgenerationally inherited in a stable manner owing to the soft inheritance phenomenon (Dickins and Rahman, 2012; Bonduriansky, 2012; Duncan et al., 2014). Further molecular genetic analysis of microsatellite DNA loci of spatially isolated adjacent micropopulations of Amur sleepers in the Middle Urals can help clarify this issue.

Thus, the results indirectly indicate that the system of morphogenetic trajectories of fish in peat quarries

of anthropogenic origin is indeed wider than in the lake and is consistent with the above estimates of intragroup morphological disparity. The nature of this phenomenon is still unclear. It can be assumed that the high local density of the micropopulation and the almost complete absence of other fish species promotes a threshold “trigger” mechanism for changing morphogenesis based on a special stress-induced effect on the epigenetic system. Such rapid switching of morphogenesis is known, for example, as the “group effect” in locusts and some other species in response to high density and the presence of certain bioinformatic chemical signals in the environment (Shvarts et al., 1976). A certain change in the epigenetic system, for example, rearrangement of transposable elements of the genome, as occurs under the influence of severe heat shock (SHS) on the development of the structure of the wing veins of *Drosophila* (Vasilyeva et al., 1995), provides a characteristic switch in morphogenesis that can have transgenerational inheritance (Bonduriansky, 2012; Burggren, 2016; Bošković and Rando, 2018). Therefore, it is possible that such a density-dependent stress which occurs in Amur sleepers in a low-species ichthyocenosis can quickly switch development toward certain modification and preserve it in future generations if the ecological situation does not change.

CONCLUSIONS

The most successfully and primarily, the alien species was distributed in shallow water bodies, sparsely populated by other fish species, including quarries filled with water of anthropogenic origin. The relative abundance of the species turned out to be higher in peat quarries, where it completely dominated and formed species-poor and single-species ichthyocenoses. The species-rich fish community of the lake prevented an increase in the abundance of Amur sleepers; however, its micropopulation in Lake Shitovskoye was steadily maintained from year to year.

As a result of the morphometric study, it was shown that, in different years in the same water body with a high density of species composition (Lake Shitovskoye), Amur sleepers were characterized by minimal changes and steadily retained their body shape. It is interesting that the seasonal changes of the shape

were generally less expressed or comparable to the interannual chronographic component of variability. Sex and age differences were relatively low and significantly less than the biotopic differences found between representatives of the two studied biotopes: the lake and a peat quarry. The variability polygons of the three compared Amur sleeper micropopulations from the lake and quarries no. 1 and no. 2 were clearly separated; they formed phenotypically differentiated groups, each of which had its own appearance. Using canonical and discriminant methods of analysis, this provides high diagnostic reliability and stable correctness of assigning specimens of any sex and age to their own micropopulation. Such a high level of morphological differences and their reliability (98%) is very rare in the practice of intraspecific comparisons of fish populations, especially those inhabiting adjacent water bodies.

At first glance, it seems that the species, as a result of strict natural selection, has dramatically changed the shape of the body in just a decade and a half of inhabiting the new environment, since this differentiation of the morphogenesis of local micropopulations of Amur sleepers clearly has an adaptive nature. Previously, we already suggested that such a mechanism of differentiation is unlikely owing to the lack of spatial isolation and the possibility of genetic exchange between adjacent micropopulations. On the other hand, the assessment of the intragroup morphological diversity in all water bodies revealed the effect of non-random aggregation of the ordinates of specimens within the variability polygons. This means that all specimens in each micropopulation form a very narrow and specific set of phenotypes, e.g., they exhibit a certain variability (according to Charles Darwin). The traditional interpretation in line with the synthetic theory of evolution (STE) about the strict selection of genotypes and the subsequent close relationship between genotype and phenotype is also unlikely in this case. For such cardinal rearrangements in each population based on the creative synthesis by selection of new adaptive genotypes and, accordingly, phenotypes, there simply would not be enough time (number of generations) or local abundance for effective directional selection. Another version of these adaptive changes, which we discussed above, associated with the pre-adaptation of the species to a wide range of biotopic conditions in the original part of the range and the presence of a potential spectrum of adaptive modifications available for the implementation determined by epigenetic rearrangements in each of specimens is much more possible. The creative role of selection is also present in this model (West-Eberhard, 2003), but the substratum and mechanism of change in this case is different.

Features of the body shape of Amur sleepers in the peat quarries can be associated with the probable cannibalism of the species inhabiting the species-poor community in the absence of other ichthyophages.

Such a modification of development, which allows the restructuring of morphogenesis, providing the possibility of forced cannibalism, could also have been historically formed in the original natural part of the species range and became in demand in species-poor fish communities and in the Middle Urals.

All approaches used for the analysis of intragroup morphological disparity in micropopulations of Amur sleepers indirectly indicate that in species-poor peat quarries, morphological diversity was significantly higher than in Lake Shitovskoye with a species-rich composition of ichthyocenosis. The expansion of the system of morphogenetic trajectories in the micropopulation of Amur sleepers, leading to an increase in intragroup morphological diversity, as we already emphasized, usually indirectly indicates destabilization of development under pessimal conditions. Therefore, we could assume that in peat quarries the habitat and development conditions were more pessimal than in the lake. Probably, this is partly true, but another interpretation of this effect is also possible. Since we found that the growth of specimens in two coeval groups of Amur sleepers (3+ and 4+) in the lake was inhibited compared to peat quarries, another explanation can be assumed. The slow growth of Amur sleepers in the lake may be associated with the competitive influence of the local species-rich fish community and the presence of ichthyophages, which may trigger a certain path of morphogenesis leading to the characteristic lake phenotype. However, this does not affect the diversity of body shape, and development is generally stable. In quarries, the situation is different. It is possible that, on the contrary, a higher growth rate may indicate more favorable conditions for the species in peat quarries, and the increase in morphological diversity may be due to a consequence of the manifestation of the compensation principle formulated by Yu.I. Chernov (2005) both at the community level and at the population level. Usually the principle of Yu.I. Chernov appears as a compensatory increase in the diversity and abundance of representatives of one of the taxonomic groups that is part of a taxon-poor community. This principle can also be manifested at the population level (Vasil'ev et al., 2017a, 2017b, 2018; Baranov, 2020). Sometimes sexual dimorphism in the structure of foraging structures in a compensatory manner increases during the depression or low abundance phases for the reduction of the trophic competition, but it decreases or it is not manifested during the peak of abundance under favorable conditions and excess of food.

In the case of the Amur sleeper, morphological diversity can also in a compensatory manner increase in species-poor or single-species communities of peat quarries in accordance with the principle of Yu.I. Chernov. It should also be noted that sex differences of Amur sleepers decreased with age in the species-rich fish community of Lake Shitovskoye, and in the peat quarry, on the contrary, these differences increased.

This can also be interpreted as a manifestation of the principle of Yu.I. Chernov for the reduction of the probable trophic competition between the sexes.

Thus, the obtained results indicate a high phenotypic plasticity and morphogenetic pre-adaptation of Amur sleepers, which allows the quick transformation of the development and adaptation to various hydrobiological, interannual, and synecological changes in new water bodies, including anthropogenic ones.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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