

Aftereffects of Muskrat Introduction in Western Siberia: Morphological and Functional Aspects

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Abstract—The muskrat (*Ondatra zibethicus* L.) allochronic samples at different stages of its introduction in Western Siberia are compared by geometric morphometrics; the comparison demonstrates directed changes in the size and shape of mandible as well as the changes in its morphological and functional characteristics as a feeding organ. As is shown, a rapid initial divergence of the northern (Yamal Peninsula) and southern (Kurgan oblast) muskrat populations, accompanied by emergence of morphological differences between them, is followed by biocenotic adaptation with gradual (over half a century) directed parallel changes in the mandible shape associated with its functional properties in the south and north of the region. The range of morphogenetic transformations of the allochronic samples of the northern group is larger as compared with the southern group, which is explainable by the more severe environmental conditions in the Yamal forest-tundra. Both populations display a statistically significant decrease in the morphological disparity of the mandible shape from the mid-20th century to its end. Leveling of the muskrat mandible size between the northern and southern populations by the end of the last century excludes any allometric effects in the observed geographic and chronographic differences in the mandible shape. Therefore, microevolutionary transformations of the morphogenesis of other invasive species can be implemented on a historical time scale, that is, relatively rapidly. This should be taken into account when forecasting potential local biocenotic crises. The model of the long-term morphogenetic aftereffects of the muskrat introduction in Western Siberia confirms the possibility of rapid adaptive morphogenetic, morphological, and functional changes in invasive mammalian species introduced into new communities.

Keywords: muskrat, introduction, invasive species, variation, geometric morphometrics, morphogenesis, microevolution, Western Siberia

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INTRODUCTION

The biological processes involved in introduction of invasive species represent one of the most topical problems in general biology (Sakai et al., 2001; Pavlov and Bukvareva, 2007; Facon et al., 2008; Pavlov et al., 2009), which is tightly associated with rapid adaptation of invasive species to new cenotic conditions. The introduction of new species inevitably changes the biodiversity of natural communities, interfering with the historically established balance in biocenotic relationships. Another logical consequence of a successful introduction is buildup of new populations of an introduced species (Shvarts, 1959), establishment of its population structure, and differentiation of the emerging populations (Vasil'ev et al., 1999; Bertolino, 2013).

The last decades with an increase in the density and diversity of the transport network brought about mass introduction of new aggressive invasive species in cenoses, resulting in extinction of some species and reduction in abundance of other species in the historically established natural communities (Dgebuadze,

2014). This makes especially topical the evolutionary and ecological insight into the long-term aftereffects caused by the introduction of model species, including assessment of the rates and directions of their morphogenetic rearrangements.

From the evolutionary and ecological standpoint, an efficient introduction is the process of historical adaptation of an invasive species to a new cenotic environment (Vasil'ev et al., 1999; Dgebuadze, 2011; Straye, 2012) associated with their morphogenetic changes, on one hand, and rearrangements in the species components of aboriginal communities, on the other hand. An adequate model for studying these basic processes underlying the adaptation of a species to new abiotic and biotic environments is the intentional muskrat (*Ondatra zibethicus* L.) introduction in Eurasia (Ondatra..., 1993; Chashchukhin, 2007).

The population-level differentiation of this species was accompanied by development of specific adaptations to new habitats (Vasil'ev et al., 1999; Chashchukhin, 2007). That is why the muskrat introduction

Table 1. Historical stages in muskrat expansion and introduction in Western Siberia

Years	Main stage of introduction
1929–1932	Beginning of colonization of the Dem'yanka River basin by Canadian founders
1933–1946	Colonization and increase in the muskrat abundance
1950–1958	Peak of abundance and commercial hunting in Kurgan oblast
1955–1960	Peak of muskrat abundance and commercial hunting in the Yamal Peninsula
1975–1985	Phase of a sheer drop in abundance in both south and north
1990–2015	Stable low abundance without considerable variation

can be regarded as an analog for geographic morphogenesis making it possible to assess at a first approximation the rate and efficiency of the initial stages in microevolution based on morphogenetic changes in populations (Vasil'ev et al., 1999; Panarari-Antunes et al., 2012; Straye, 2012).

The muskrat introduction in Western Siberia (Table 1) commenced in 1929, when the first batch of animals from a northern Canadian population was released in the Dem'yanka River basin (Shvarts, 1959; Pavlov et al., 1973; Vasil'ev et al., 1999).

Later, this species expanded to lakes in Kurgan oblast and to the north of Tyumen oblast both naturally and with the help of game managers. In the middle of the last century, the muskrat abundance in Western Siberia reached its peak with a drastic decrease in both the abundance and variation by the end of the 20th century and continuing so far. The latter was associated with the population transition to the third phase of its introduction (Chesnokov, 1976), which should be correctly referred to as a “population–cenotic” phase. This means not only establishment of local populations and intraspecific divergence but also the regulation of species abundance and its cenotic role by biogeocenoses.

Smirnov and Shvarts (1959) in the 1950s compared the southern and northern muskrat populations at the first stages of their introduction according to a set of morphophysiological characteristics and found no specific population features. However, we later used the same material and revealed significant differences between the northern and southern populations in morphometric and nonmetric cranial characteristics, which were retained to the end of the 20th century (Vasil'ev et al., 1999).

The goal of this work was to study the long-term morphological, morphogenetic, and morphofunctional aftereffects of the muskrat introduction in Western Siberia using geometric morphometrics, GM (Rohlf and Slice, 1990; Rohlf, 1999; Zelditch et al., 2004; Klingenberg, 2011). Several studies demonstrated a high efficiency of GM methods in revealing specific features of morphogenetic processes in different species and intraspecific groups (Zelditch et al., 2004, 2006; Sheets and Zelditch, 2013). Thus, the GM approach applied to assessment of long-term aftereffects of

muskrat introduction allows these aftereffects to be regarded as transformations in the species morphogenesis during its adaptation to a new habitat.

MATERIALS AND METHODS

Age-uniform allochronic muskrat samples from Kurgan oblast and the Yamal Peninsula were the object of this study. The samples were obtained at the initial (1954, 35 individuals; 1955, 59 individuals) and late (1979–1980, 29 individuals; 1989, 42 individuals) stages of muskrat introduction and assayed for the variation in the size and shape of mandible as an ecologically important organ directly associated with the muskrat foraging, feeding function, and cenotic role.

Recall that GM approach makes it possible to strictly partition the variation in size and shape, allowing us to assess the morphogenetic component in the overall variation of the muskrat during its introduction in the south and north as well as to visualize the major morphogenetic transformations (Zelditch et al., 2006; Sheets and Zelditch, 2013).

Electronic images of the mandible right ramus lingual side were digitized (resolution, 1200 dpi) using TPS software (Rohlf, 2015a, 2015b). The variation in shape was characterized using a configuration of 16 landmarks (Fig. 1). Generalized Procrustes analysis (GPA), based on least squares method, was used for superimposing the configurations (Rohlf and Slice, 1990). Between-group differences were estimated by canonical analysis of the Procrustes coordinates, which characterized the variation in the shape of objects.

The functional potential of mandible configurations was assessed using the four following measurements: A, articular–incisor; B, articular–molar; C, temporal–articular; and D, articular–masseter (Fig. 1). These measurements were used to calculate the mandibular indices (Anderson et al., 2014): TI, temporal–incisor; TM, temporal–molar; MI, masseter–incisor; and MM, masseter–molar as $TI = C/A$, $TM = C/B$, $MI = D/A$, and $MM = D/B$.

Within-group morphological diversity was assessed by the technique of mean nearest neighbor distances (MNND) within the variation polygons (Hammer, 2009). MNNDs, expected (μ) distances for a random

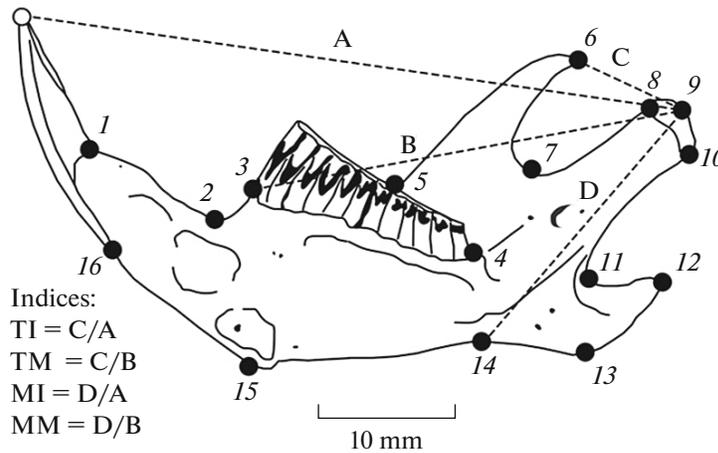


Fig. 1. Location of 16 landmarks (1–16) and measurements (A–D) on the lingual side of the muskrat mandible necessary to calculate the mandibular indices TI, TM, MI, and MM (the corresponding equations are shown to the left). The additional not numbered landmark at the tip of incisor was used only for measuring A.

Poisson distribution, and the other parameters ($R = MNND/\mu$, Z-test, and its statistical significance, p) necessary for assessing the point distribution models within the variation polygon for each sample were calculated. According to this technique, the ratio (R) of MNNDs to the expected mean distance (μ) for the variable polygon obtained using Poisson distribution characterizes the point dispersion model. Correspondingly, clustering of points is observed at $R < 1$; Poisson dispersion, at $R = 1$; and overdispersion, at $R > 1$.

Along with two-way ANOVA, two-way nonparametric multivariate ANOVA (NPMANOVA) utilizing permutation testing for 10000 replicates was used. The main computations and statistical analysis were performed with the help of TPS (Rohlf, 2015a, 2015b), PAST (Hammer et al., 2001), and MorphoJ (Klingenberg, 2011).

The variation in total mandible size was indirectly assessed according to the centroid size (CS), determined as the square root of the sum of squared distances of a set of landmarks from the image center (Rohlf and Slice, 1990).

Preliminary analysis did not show any significant sex differences neither in form nor centroid size (CS), allowing the male and female samples to be pooled.

RESULTS AND DISCUSSION

A comparison of the muskrat allochronic samples from the northern and southern populations demonstrated that both groups statistically significantly differed in the mandible size as early as the first stage of introduction, after 10–12 generations (Table 2). The animals of the northern, Yamal Peninsula, population had a significantly smaller mandible as compared with the representatives of the southern, Kurgan, population. However, the mandible size (proportional to CS) in the samples of these populations became almost the same after 40–50 years of introduction, by the end of the 20th century.

The statistical significance of these differences in CS was assessed by two-way ANOVA according to the factors “natural zone,” Bm (scale: 1, forest-tundra, Yamal Peninsula; 2, forest-steppe, Kurgan oblast), and “introduction stage,” In (scale: 1, initial stage, 1950s; 2, final stage, 1980s). The analysis demonstrated (Table 3) statistical significance of the differences in both factors and their interaction (Bm × In).

The geographic differences in CS, determined by the fact that the animals live in different natural zones, are more pronounced as compared with the chronographic differences, associated with the stage of introduction. Note that the component reflecting the inter-

Table 2. Comparison of the mandible centroid size (CS) with standard errors (SE) between the muskrat allochronic samples from the northern Yamal (1955 and 1989) and southern Kurgan (1954 and 1979–1980) populations

Characteristic	Compared populations			
	Yamal		Kurgan	
Year	1955	1989	1954	1979–1980
Sample size, n	35	59	29	42
CS ± SE	1255.2 ± 11.8	1349.7 ± 9.2	1418.3 ± 15.4	1374.2 ± 11.4

Table 3. Results of two-way ANOVA of the muskrat mandibular ramus centroid size (CS, pixels) in the northern and southern populations at different stages of introduction in Western Siberia

Source of variation	Sum of squares	Number of degrees of freedom, <i>d.f.</i>	Mean square	F	<i>P</i>
Natural zone, Bm	298 200	1	298 200	25.68	0.00001
Stage of introduction, In	130 000	1	130 000	11.2	0.00100
Interaction of factors, Bm × In	177 600	1	177 600	15.29	0.00010
Within-group variation	1 893 000	163			
Total variation	2 517 000	166			

action of both factors (Bm × In) and characterizing the leveling of mandible CS at the second stage of introduction as compared with the first stage is comparable to the chronographic differences (Table 3).

Consequently, the observed trends of leveling of the mandible size at the second stage of introduction are statistically confirmed.

Canonical analysis of the Procrustes coordinates characterizing the variation in shape demonstrated that the mandible shape in northern and southern muskrat populations differed both at the initial stage of introduction and at the end of the 20th century (Fig. 2).

The between-group differences along the first two canonical axes are statistically significant and account for 87.8% of the between-group variation. The maximum mandible transformation in both populations is observed along the first canonical variable, CV1,

which reflects the chronographic variation and accounts for 58.8% of the between-group variance. The range of morphogenetic transformations in the allochronic samples of the northern population is larger as compared with the southern population, which is explainable by specificity of northern biocenoses and more severe environmental conditions in the muskrat habitats of the Yamal forest-tundra. The chronographic changes appear as a decrease in the mandible height with a concurrent increase in incisor part and shortening of the angular and articular processes.

The morphogenetic specificities of the northern and southern populations retained at different stages of introduction and reflecting the geographic variation appear along the second axis, CV2. This variable accounts for 29.0% of the between-group variance,

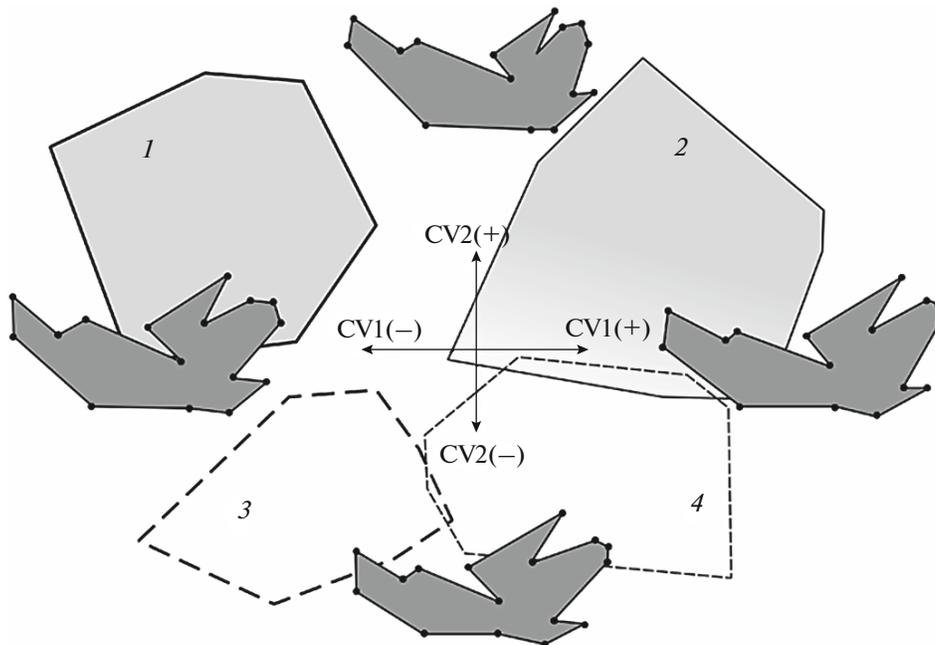
**Fig. 2.** Results of canonical analysis of the mandible shape in allochronic muskrat samples at different stages of introduction in the Yamal (1, 1955; 2, 1989) and Kurgan (3, 1954; 4, 1979–1980) populations (shaded projections show the most pronounced changes along the first and second, CV1 and CV2, canonical axes).

Table 4. Assessment of the correctness in classifying the ordinates of objects using canonical analysis of the muskrat mandible shape in the Yamal and Kurgan populations at different stages of muskrat introduction in Western Siberia

Compared samples	Yamal		Kurgan		Sample size
	1	2	3	4	
Results of classification of objects by canonical analysis					
(1) 1955	35	0	0	0	35
(2) 1989	0	58	1	0	59
(3) 1954	0	0	29	0	29
(4) 1979–1980	0	0	1	41	42
Results of analysis	35	58	31	41	165
Correctness, %	100	100	93.6	100	98.8
Results of cross-validation by jackknifing					
(1) 1955	35	0	0	0	35
(2) 1989	0	54	1	4	59
(3) 1954	0	0	29	0	29
(4) 1979–1980	0	4	3	35	42
Results of analysis	35	58	33	39	165
Correctness, %	100	93.1	87.9	89.7	92.7

being twofold lower than that along CV1. The geographic variation appears as a drastic relative increase in the mandible incisor part and body in the northern population along with a relative elongation of the tooth row and shortening of the coronoid, angular, and articular processes, which reflects the adaptation of northern animals to rougher food (Anderson et al., 2014). The mandible of the southern animals is in general more gracile and displays the opposite traits (Fig. 2).

The interaction of factors (Bm × In), which was rather small in the share of between-group variance (12.2%) and statistically insignificant, appeared along the third axis, CV3. Thus, the effect of interaction is evident according to CS; however, this trend was not statistically confirmed according to the mandible shape.

Note a high level of correctness in classification of the objects according to their sample specificity,

shown by the conducted canonical analysis of the mandible shape (Table 4).

Such a level is usually attained when comparing subspecies and even closely related species rather than geographically distant populations. All this suggests a large scale of the detected muskrat intraspecific differentiation in both the geographic and chronographic aspects and makes it possible to regard these between-group differences as microevolutionary events.

Four mandibular indices were used for assessment of the mandible morphofunctional characteristics (Anderson et al., 2014). We calculated these indices from four measurements of the mandibular ramus (Fig. 1, Table 5). Note that an additional not numbered landmark was set at the tip of incisor for measuring A (not used in the remaining measurements).

Two-way NPMANOVA with permutation testing of 10000 resampling replicates was used to compare allotopic and allochronic muskrat samples according to four mandibular indices. This analysis demonstrates statistical significance of the differences in both factors as well as their interaction (Table 6).

The factor associated with geographic conditions of the habitat is the major contributor to the total variance, while the contribution of chronographic differences is somewhat smaller. The role of interaction of these factors, i.e., different directions of the changes in mandibular indices in the northern and southern muskrat populations at different stages of introduction, is insignificant despite the significance of the interaction itself and can be neglected.

The results of canonical analysis of the mandibular indices for these four compared muskrat samples are shown in Fig. 3. It is evident that the centroids of allochronic samples from the northern and southern muskrat populations shift in parallel along the second canonical variable (CV2), which can thus be interpreted as manifestation of the between-group chronographic variation in the mandibular indices.

In this case, canonical analysis suggests the major role of geographic variation, which is evident along the first canonical axis (CV1), and a lesser role of the chronographic variation, close in the range of between-group differences, evident along the second canonical variable (CV2). Note that the ranges of geographic differences in the mandible shape between the

Table 5. Mandibular indices (±SE) characterizing the morphofunctional properties of the mandible in the Yamal and Kurgan populations at two stages (I and II) of the muskrat introduction in Western Siberia

Sample, stage of introduction	Number of individuals	Mandibular indices			
		TI	TM	MI	MM
Yamal, I	35	0.161 ± 0.003	0.275 ± 0.005	0.724 ± 0.003	1.234 ± 0.004
Yamal, II	59	0.155 ± 0.002	0.267 ± 0.003	0.718 ± 0.002	1.237 ± 0.003
Kurgan, I	29	0.180 ± 0.003	0.307 ± 0.006	0.713 ± 0.003	1.217 ± 0.004
Kurgan, II	42	0.166 ± 0.002	0.277 ± 0.004	0.722 ± 0.003	1.210 ± 0.003

Table 6. Results of two-way NPMANOVA of the mandibular indices characterizing the morphofunctional properties of the mandible in the Yamal and Kurgan populations at two stages of the muskrat introduction in Western Siberia

Source of variation	Sum of squares	Number of degrees of freedom, <i>d.f.</i>	Mean square	F	<i>p</i>
Natural zone, Bm	0.026975	1	0.026975	16.44	0.0001
Stage of introduction, In	0.019481	1	0.019481	11.87	0.0001
interaction, (Bm × In)	0.001779	1	0.001779	1.08	0.0002
Residual	0.264150	161	0.001641		
Total	0.312390	164			

centroids of muskrat northern and southern samples are equal both at the beginning of introduction and at the end of the 20th century. Since the calculations involved mandibular indices, the results of canonical analysis allow for a direct morphofunctional interpretation of the between-group differences in the muskrat mandible in space and time.

Without going into discussion of the contribution of individual mandibular indices to the variation along both first canonical axes, we can infer that the manifestations of geographic variation (accounting for 45.6% of the total variation along CV1) are more important from the functional standpoint. A somewhat smaller share of the between-group variation appeared along CV2 (34.9% of the total variance). That is why the chronographic variation reflects somewhat smaller morphofunctional effects as compared with the geographic variation.

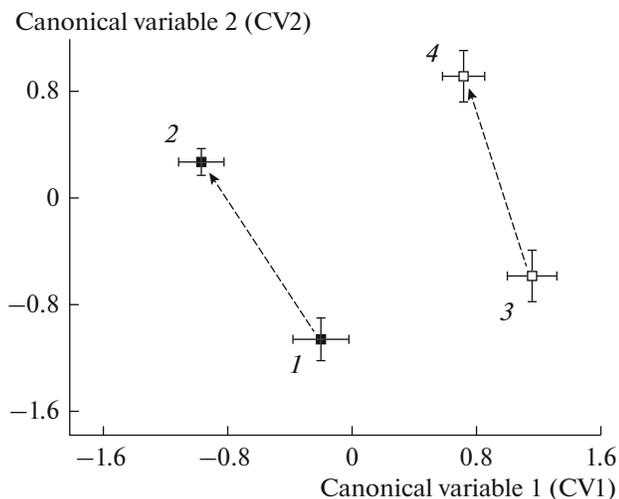


Fig. 3. Results of canonical analysis of the mandibular indices in the compared allochronic northern (1, 1955; 2, 1989) and southern (3, 1954; 4, 1979–1980) muskrat populations in Western Siberia (standard errors are shown for each centroid). Dashed lines denote the directions of chronographic changes in geographically distant populations.

These results suggest that the geographic between-population morphofunctional differences in the mandible structure are rather expectable. Most likely, they are determined by the fact that the feeding objects of the muskrats in the northern and southern populations are a priori different in both the composition and ratio (Ognev, 1950). The values of mandibular indices and shaded projections (Table 5, Fig. 2) suggest that the functional potential of the mandible associated with more intensive grinding of food objects is more pronounced in the southern population as compared with the northern one. As for the animals of the northern population, they display the trend of feeding with coarser food via crushing at both stages of introduction (Anderson et al., 2014). On the other hand, the parallelism in chronographic variation in both populations is a nontrivial phenomenon. First, this suggests a parallel transformation of morphogenesis toward certain specific morphofunctional features. Second, this reflects a direct and to a certain degree unidirectional “pressure” of the biotic communities on both the northern and southern populations leading to selection and strengthening of certain morphogenetic changes common to these two muskrat populations.

Comparison of the trends of the changes in mandibular indices in both populations during the first to second stages of introduction (Table 5, Figs. 2 and 3) suggests that the observed changes in mandible shape are directed toward an equal increase in the morphofunctional potential for food grinding and utilizing hard feed (Anderson et al., 2014). Thus, the cenotic demands over a half-century span have led to a directed change in the mandible morphofunctional properties in both geographically distant muskrat populations.

Note that the most important among the mandibular indices are the temporal–incisor (TI) index, the increase in which reflects an increase in the effort potential during food grinding and chewing, and the masseter–molar (MM) index, indicating better ability to process hard food objects (Anderson et al., 2014). We used these variables (TI and MM) to estimate the within-group morphological disparity in the compared groups by analyzing MNNDs within the varia-

tion polygons (Hammer, 2009). The results of computations are shown in Fig. 4.

It is evident from Fig. 4 that the within-group morphological disparity (MNND) characteristics in the northern and southern populations at the first stage of introduction are higher than at the second stage in a statistically significant manner. Note that both populations at the first stage display a significant overdispersion of ordinates (Table 7). An increase in the MNND value in the analysis of shape variation can be interpreted as an increase in the within-group morphological disparity, i.e., as a fan of morphogenetic trajectories (Hammer, 2009; Sheets and Zelditch, 2013; Vasil'ev et al., 2016).

Thus, the mandible morphogenetic diversity at the first stage of introduction was higher in both populations as compared with the second stage (Table 7). Note that the *R*-ratio in both geographically distant populations is close to unity, i.e., the dispersion of points within the variation polygon of these samples acquired a random Poisson pattern. This means that a drastic widening of the fan of morphogenetic trajectories at the first stage of introduction in both muskrat populations indirectly suggests insufficient regulation of development and, presumably, insufficient fitness of animals to the local conditions. In any case, an increase in morphological disparity and the observed overdispersion suggests that the animals of both populations were stressed. The characteristics of within-population disparity of mandible shape (Table 7) demonstrate not only a decrease in the morphological disparity (MNNDs) but also a random pattern of ordinate dispersion at the second stage of introduction. Thus, it is likely that the adaptation to local conditions took place at the second stage, since the morphogenetic changes in the mandible in both northern and southern populations are in general regulated. This is demonstrated by a random dispersion of the points within a certain narrow range of MNNDs in the variation polygon. Since we consider here the variation of morphofunctional indices, this means stabilization and, possibly, functional optimization of the muskrat

Mean nearest neighbor distances, MNND

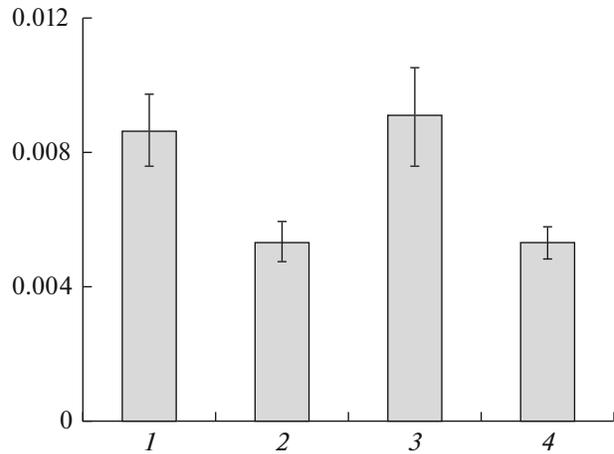


Fig. 4. Comparison of the mean nearest neighbor distances with standard errors (MNND ± SE) within the variation polygons of (1, 2) the northern and (3, 4) the southern populations at different stages of muskrat introduction in Western Siberia (first stage, odd sample numbers; and second stage, even numbers).

mandible shape in both the northern and southern populations after the half-century introduction.

CONCLUSIONS

Thus, considerable morphogenetic and morphofunctional changes in the shape of mandibular ramus took place in the established exclave populations of the muskrat during its introduction in Western Siberia. Similar directions of chronographic changes in the mandible shape in the northern and southern populations suggest that the adaptive transformations in the muskrat morphogenesis also go in the same directions. The initial range of morphological differences between the northern and southern populations was retained, although the mandible shape of their members changed. The initial differences in the centroid size between the northern and southern populations

Table 7. Comparison of the characteristics of within-population mandible shape diversity in the muskrat allotopic and allochronic samples at different stages of its introduction in Western Siberia

Characteristic	Compared populations			
	northern (Yamal)		southern (Kurgan oblast)	
	1955	1989	1954	1979–1980
Number of individuals, <i>n</i>	35	59	29	42
Observed MNND	0.0087	0.0054	0.0091	0.0053
Expected value (μ)	0.0065	0.0048	0.0068	0.0050
<i>R</i> -ratio	1.34	1.13	1.34	1.06
Z-test	3.35	1.66	3.08	0.85
Probability or random distribution, <i>p</i>	0.0008	0.0969	0.0021	0.3923

had leveled by the end of the 20th century, demonstrating that the differences in mandible shape at the second stage of introduction cannot be interpreted as exclusively allometric effects. It is evident that the changes in mandible shape are determined by directed morphogenetic transformations. Therefore, the parallel chronographic transformations of morphogenesis in both populations after a half-century span can be associated only with a gradual integration of the muskrat in new biocenoses and somewhat different trophic functions in the north and south.

Thus, direct modifications within the norm of reaction (different for geographically distant groups) initially emerged at the beginning of introduction against the background of a decrease in the initially high muskrat abundance and subsequent integration of the populations into definitely different biotic communities in the north and south of the region. These modifications were accompanied by an increase in morphological disparity (fan of morphogenetic trajectories). Then the mandible morphogenesis changed in almost parallel directions, which considerably reduced the mandible morphological disparity. The functional mandibular indices also changed in parallel in the northern and southern populations. The last fact indirectly suggests the leading role of selective processes associated with similar cenotic pressures in the intrazonal near-aquatic biotopes. Note that the morphological specificity of the northern and southern populations that initially developed at the first stage of introduction was retained, although the mandible shape changed. Correspondingly, the microevolutionary events associated with emergence of considerable morphofunctional and morphogenetic transformations of mandible shape in space and time took place over the half-century span of the muskrat introduction in analogous biotopes in the south and north of Western Siberia. These results demonstrate a high adaptive potential of this species and its capability of rapid morphogenetic and morphofunctional transformations, which most likely determined the success in muskrat introduction in most Eurasian natural zones. By the analogy to the muskrat, rapid adaptive transformations of morphogenesis on a historical rather than geological time scale are expectable in the cases of uncontrolled introduction of other invasive species (at least, some of them). Thus, the observed long-term morphological and morphofunctional aftereffects of introduction are examples of rapid directed microevolutionary transformation of morphogenesis and morphofunctional changes in invasive mammalian species during their introduction to new communities.

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