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Effects of the Habitat and Genotype on Osteological Traits in Landlocked and Anadromous Ecological Forms of Atlantic Salmon *Salmo salar* Linnaeus, 1758

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Abstract: Studies of speciation and intraspecific differentiation in salmonid fishes are traditionally based on analysis of osteological traits. In the current study the variation of osteological traits was compared between two Atlantic salmon forms: anadromous and landlocked. Each form was represented by three samples: one from a wild population, and two from hatcheries; i.e., we studied six samples in total. In total, 45 osteological characters were analyzed. Differences between the forms were found to be genetically determined to a substantial extent. The factor “origin” explained 48% of the total morphological difference between the fish samples; the factor “habitat”, 32%; and their interaction, 14%. Phenotypic plasticity of the anadromous form was observed to be lower than that of the landlocked form. We consider that the higher phenotypic plasticity may compensate for a decrease in genetic diversity which is observed in landlocked forms of the species.

Keywords: arctic; resident; anadromous; salinity; morphology; fish; bone; skull; heredity; phenotypic plasticity

1. Introduction

A number of fishes inhabiting coastal areas of the Arctic seas demonstrate various adaptations in relation to water salinity. Some species can produce both marine and resident freshwater forms, whereas others produce anadromous forms reproducing in freshwaters, but spend the rest of their life in the sea. These adaptations allow fishes to more effectively utilize limited resources of the Arctic seas (for a review, see [1–3]). Moreover, multiple abrupt changes in salinity, which were experienced by Arctic hydrobionts during their evolution [4,5], facilitated formation of species and genera capable of living in both fresh and marine waters [6–8].

The formation of landlocked forms in marine and anadromous northern fish has recently come to be used as an important model to study evolutionary processes (for a review, see [3,9–11]). However, it is rather difficult to associate particular traits with environmental factors and salinity in particular. Difficulties arise because traits, e.g., morphometric ones, of an individual are affected by the environment at all stages of its life cycle, and a study in adults consequently requires knowledge of their life history. Moreover, while the direct effect that the environment exerts on individuals during their ontogeny results in nonheritable phenotypic plasticity, certain alleles of the genes that affect morphological traits are selected through generations via natural selection.

A problem with several unknowns has therefore to be solved to understand the nature of phenotypic changes. When morphological differences are detected between individuals from different populations, it is necessary to understand whether the differences have genetic basis or are due to phenotypic plasticity. Gause [12] has provided a brilliant example of solving the problem in his classical work with ciliates. Two steps have been observed in adaptation to salinity changes in his work: the first one is due to phenotypic plasticity and the next to selection of certain genotypes whose carriers are best fit to live in a given environment.

However, the above problem of estimating the contribution to adaptation for phenotypic plasticity and changes in allele frequencies of various genes is not the only problem to solve in studies of the kind. It is rather difficult to determine whether salinity is the primary factor to which organisms adapt or other factors drive evolution in this particular case. The mechanisms of morphological divergence between freshwater and marine populations have been the focus of many studies in the threespine stickleback *Gasterosteus aculeatus*, which is a “supermodel” of evolutionary biology [13–19]. The conclusion made in the majority of the studies is that a decrease in predation pressure, rather than a change in salinity, is mostly responsible for the morphological changes that arise upon the shift from marine to fresh water. Threespine stickleback, however, is an extremely euryhaline species which is able to spawn both in marine and fresh waters, thus this conclusion should be applied to other fish with a caution.

Morphological differences between landlocked and anadromous forms of one species have been observed in Salmonoidei (for a review, see [20–23]) and Cyprinidae [24]. However, no morphological difference between individuals from freshwater and saltwater lakes of one water system has been detected in the cyprinid Altai osman *Oreoleuciscus potanini* [25]. The finding gives grounds to question the idea that migrations to saltwater during ontogeny are always responsible for the morphological features that distinguish anadromous forms from landlocked ones. There is a possibility that their morphological features are adaptations to long-distance migrations to a greater extent. In fact, morphological differences (hereditary ones) have been observed not only between anadromous and resident forms, but also between resident and potamodromous (migrating from rivers into lakes to feed) forms in the brown trout *Salmo trutta* [26]. The above studies demonstrate convincingly that to evaluate the salinity effect on fish morphology, only migratory populations of the same species should be compared, one population migrating into salt water (anadromous) and the other into fresh water (potamodromous).

In view of the above, the Atlantic salmon *Salmo salar* was chosen as a subject for this study because both anadromous and landlocked forms are known for the species. In turn, the landlocked form subdivides into resident (river and lake) freshwater forms and a potamodromous (lake-river) form, which includes fish that spawn in rivers and migrate into large lakes to feed (for a review, see [27]). Note additionally that Atlantic salmon is a key species in both marine and freshwater Arctic ecosystems, and is broadly farmed in aquaculture, and represents a popular model for evolutionary and genetic studies (see monographs [28–31]). The anadromous form of Atlantic salmon is still a target of commercial and amateur fishing. The landlocked form has disappeared from many water systems or occurs at an extremely low population size. The form is therefore of importance to study in order to develop measures for its preservation [32].

Osteological traits are convenient to use when studying the morphological variation in fish because their bones are numerous and diverse, their shapes are well preserved during storage, and measurement error is relatively small [33–35]. These traits have already been successfully used in population studies in Atlantic salmon (for a review, see [36]). Differences in osteological traits have been described for the anadromous and landlocked forms of Atlantic salmon [28]. There are data that the traits change in response to cultivation [37].

The goal of this study is to evaluate the effect of environmental conditions on the osteological traits in the anadromous and landlocked forms of Atlantic salmon. For that,

we examined juveniles from natural populations and juveniles that belonged to the same two populations, but reared in two hatcheries.

2. Materials and Methods

Brief characteristics of the model populations and specifics of their artificial rearing. Our model populations inhabit rivers of the Republic of Karelia in the northwestern part of Russia. One was a lake-river (landlocked) population that spawns in the Shuya River and feeds in the Lake Onega, which belongs to the basin of the Baltic Sea. The biology of the population has been described in detail [38]. The other was an anadromous population that spawns in the Keret River, which drains into the White Sea, and migrates to the Atlantic Ocean to feed. The biology of the population has been described in [39]. Hybridization between Atlantic salmon and brown trout has been observed in the Keret River [39], but we used only the individuals whose species identification as *S. salar* was verified by molecular genetic testing [40]. Some spawners are annually caught in both rivers for artificial reproduction in the Kem and Vyg hatcheries (Karelia). Fish are grown for two years and then released into their native rivers without mixing the two populations. The salmon samples collected in nature are hereafter designated according to the respective original river, Keret-W and Shuya-W. Juvenile samples obtained from spawners of the two rivers and grown in the Kem (K) and Vyg (V) hatcheries are designated Keret-K, Keret-V, Shuya-K, and Shuya-V, respectively.

Sample collection and processing. In the hatcheries, fish were sampled from several ponds to minimize the uncontrolled factors that might affect the morphological traits. Wild fish were caught by electrofishing. The fork length (FL) was measured in all fish immediately after capture. Basic characteristics of the samples are summarized in Table 1. Because fish of the Shuya population grow far faster in artificial conditions than fish of the Keret population do, we used 1-year-old fish of the Shuya population and 2-year-old fish of the Keret population. Substantial differences in fish size were thus avoided to facilitate interpretation of results of morphological analyses.

Table 1. Characteristics of the juvenile Atlantic salmon samples examined in this work.

River of Origin	Source	Abbreviated Name of Sample	Sampling Date	Sample Size	Fork Length, cm		Age
					Range	Mean \pm SD	
Keret	Vygskiy Hatchery	Keret-V	21.04.2001	30	11.3–16.2	13.81 \pm 1.16	2.
Keret	Kemskiy Hatchery	Keret-K	28.04.2001	31	10.2–20.2	15.61 \pm 2.25	2.
Keret	Keret River, wild	Keret-W	05.10.2001	30	6.1–15.5	9.76 \pm 3.34	0+ and older
Shuya	Vygskiy Hatchery	Shuya-V	19.04.2001	30	6.4–9.6	7.80 \pm 0.78	1.
Shuya	Kemskiy Hatchery	Shuya-K	26.04.2001	30	6.9–14.0	10.81 \pm 1.82	1.
Shuya	Shuya River, wild	Shuya-W	07.09.2001	27	5.5–15.4	10.09 \pm 2.97	0+–2+

Fish heads were fixed with ethanol. In the laboratory, the heads were macerated in 2% KOH at room temperature for approximately 30 h prior to analysis, and bones were washed and dried [37,41]. Images of bone structures were obtained using an Epson Perfection 2450 Photo scanner, and the coordinates of 25 landmarks (Figure 1) were determined using UTHSCSA Image Tool 3.0 by one operator (A.O.Yu.). Forty-five distances between landmarks were used as traits. All traits are listed in Table S1 as distances between landmarks. The bones selected for this study are often used for the studies of *Salmo* genera and show utility in discrimination of relative forms [37,41–43].

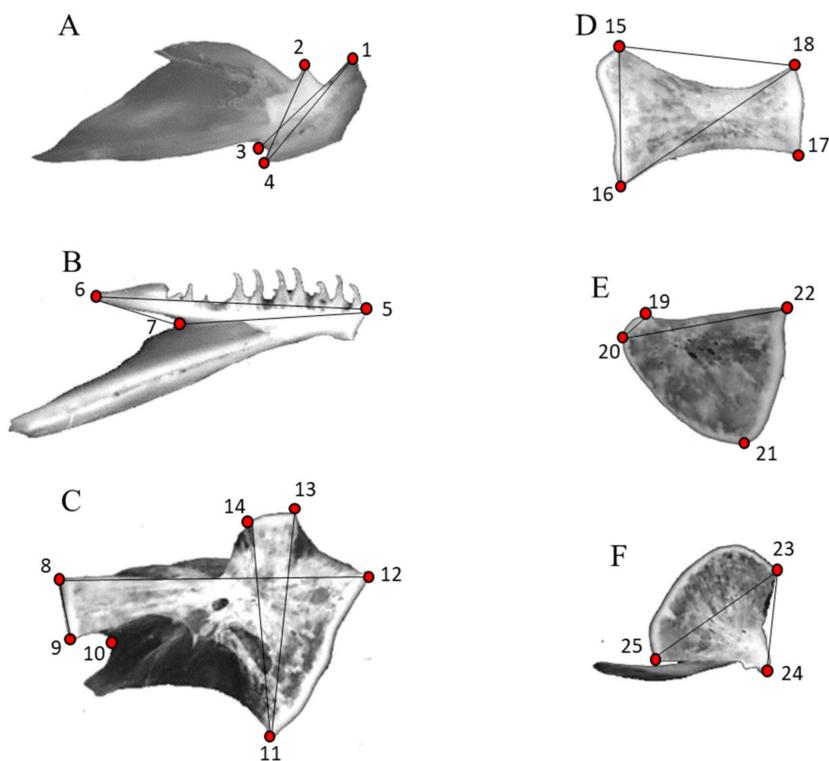


Figure 1. Cranial bones and landmarks used for morphological analysis of Atlantic salmon: (A)—Articulare, (B)—Dentale, (C)—Hyomandibulare, (D)—Ceratohyale, (E)—Epiphyale, (F)—Quadrate. Twenty-five landmarks are designated with red points. Distances between all landmarks in one bone, 45 in total, were used as traits. These traits were used for construction of 39 indices (ratios between traits, see Supplement Table S1). Eleven of these 39 indices, which did not show correlation with size, were selected for further analysis. The lines show traits which were used for construction of these 11 indices (Supplement Table S1).

Statistical analyses. Fish length was compared between samples by ANOVA. Pearson's correlation was used to test the morphological traits for association with the fish length. Totally, 39 morphological indices, based on ratios of all traits of one bone (Supplement Table S1) were used to compare the samples. For the further analysis we used only indices which did not show correlation with body length to avoid a size correction procedure which potentially can result in artifacts because of potential differences in allometry patterns of compared samples. Pairwise comparisons of the indices between samples were performed by one-way ANOVA. A cluster analysis was carried out to visualize the results of the comparisons. Phenotypic plasticity of a population was statistically analyzed by comparing the Euclidean distances between populations in the space of principal components. To evaluate the contributions of environmental conditions and genetic specifics of the populations to the between-population difference, ANOVA was performed using two factors, “habitat” (a comparison of the wild samples with the samples from the Kem and Vyg hatcheries) and “origin” (a comparison of the Shuya and Keret populations). Statistical analyses were carried out using Statistica 8.0 software.

3. Results

An association of cranial bone dimensions with the body length. The mean body length increased in the following sample order: Shuya-V, Keret-W, Shuya-W, Shuya-K, Keret-V, Keret-K (Table 1). The juveniles from the Vyg hatchery were generally smaller than those from the Kem hatchery. The four cultivated samples differed in fish length ($p < 0.01$ in each of the six pairwise comparisons). The wild juveniles from the Shuya River were larger than

the reared juveniles of the same population from the Vyg hatchery (the Shuya-V sample, $p < 0.01$). The juveniles from the Keret River were significantly smaller than the juveniles of the same population from the Kem and Vyg hatcheries (the Keret-K and Keret-V samples, respectively; $p < 0.01$ in both of the cases).

In the pooled sample, the majority (28 of 39) indices significantly correlated with the body length ($p < 0.05$). The 11 indices that did not correlate with the body length were consequently used in further analysis (Table 2, Supplement Table S1).

Table 2. Cranial bone indices that did not correlate with the body length in the six juvenile Atlantic salmon samples examined in this work (see Supplement Table S1 for the full list of traits and indices).

Index	Bone	Indices as a Ratio of Traits (traits Are Distances between Landmarks)
Ind2	Articulare	1–3/1–4
Ind4	Articulare	2–4/1–4
Ind6	Dentale	5–7/5–6
Ind7	Dentale	6–7/5–6
Ind8	Hyomandibulare	8–9/8–12
Ind23	Hyomandibulare	11–13/8–12
Ind24	Hyomandibulare	11–14/8–12
Ind29	Ceratohyale	15–16/15–18
Ind31	Ceratohyale	16–18/15–18
Ind33	Epihyale	19–20/20–22
Ind38	Quadrata	23–24/23–25

Sample comparisons by osteological traits. The mean values and standard deviations of the indices under the study are summarized in Table 3. Each of the samples differed in at least two indices from the other samples in pairwise comparisons (Table 4).

Table 3. Mean cranial bone indices (mean \pm std. dev.) in the six juvenile Atlantic salmon samples examined in this work. The indices are designated as in Table 2.

Index	Keret-V	Keret-K	Keret-W	Shuya-V	Shuya-K	Shuya-W
Ind2	90.1 \pm 3.6	89.4 \pm 4.0	89.4 \pm 3.6	86.6 \pm 3.3	86.3 \pm 2.7	86.2 \pm 3.1
Ind4	72.4 \pm 2.2	71.0 \pm 1.5	70.8 \pm 2.3	72.6 \pm 2.0	71.7 \pm 1.9	72.0 \pm 1.9
Ind6	71.1 \pm 2.6	71.0 \pm 2.0	69.3 \pm 2.1	71.9 \pm 2.0	71.8 \pm 1.9	72.3 \pm 2.0
Ind7	31.6 \pm 2.5	31.5 \pm 2.3	32.5 \pm 2.1	31.1 \pm 1.8	30.8 \pm 1.9	29.6 \pm 2.0
Ind8	17.4 \pm 1.7	18.0 \pm 1.0	17.9 \pm 2.1	19.0 \pm 1.1	17.7 \pm 1.1	19.6 \pm 1.2
Ind23	68.1 \pm 1.2	68.2 \pm 2.1	68.8 \pm 3.5	66.9 \pm 1.4	67.3 \pm 2.0	66.8 \pm 1.3
Ind24	65.5 \pm 1.1	65.6 \pm 2.0	66.4 \pm 2.3	64.1 \pm 1.6	64.4 \pm 1.9	64.4 \pm 1.4
Ind29	68.1 \pm 3.7	68.8 \pm 3.3	69.3 \pm 4.1	69.2 \pm 2.6	68.6 \pm 3.2	67.4 \pm 2.4
Ind31	110.9 \pm 3.0	111.6 \pm 3.7	109.7 \pm 4.1	111.3 \pm 2.3	110.7 \pm 2.9	107.8 \pm 3.6
Ind33	22.3 \pm 1.9	23.7 \pm 2.3	22.3 \pm 2.3	24.8 \pm 1.8	24.8 \pm 2.9	23.8 \pm 2.1
Ind38	68.7 \pm 2.0	69.6 \pm 2.2	70.5 \pm 3.8	68.9 \pm 1.9	72.9 \pm 2.6	70.9 \pm 2.8

Table 4. Significant differences between juvenile Atlantic salmon samples with respect to the cranial bone indices that do not correlate with the body length (results of one-way ANOVA, $p < 0.01$ above the diagonal, $p < 0.05$ below the diagonal). The indices are designated as in Table 2.

Sample	Keret-V	Keret-K	Keret-W	Shuya-V	Shuya-K	Shuya-W
Keret-V	—	Ind 33	Ind 6	-	-	Ind 2, 7, 8, 23, 24, 31, 33, 38
Keret-K	Ind 4	—	Ind 6	Ind 2, 4, 8, 23, 24	Ind 24	Ind 2, 7, 8, 23, 31
Keret-W	Ind 4, 38	Ind 33	—	Ind 8, 38	Ind 23	Ind 4, 29, 33
Shuya-V	Ind 2, 8, 23, 24, 33	Ind 33	Ind 2, 4, 6, 7, 23, 24, 33	—	-	Ind 7, 29, 31, 38
Shuya-K	Ind 2, 24, 33, 38	Ind 2, 38	Ind 2, 6, 7, 24, 33, 38	Ind 8, 38	—	Ind 8, 31, 38
Shuya-W	-	Ind 4, 6, 24, 38	Ind 2, 6, 7, 8, 23, 24	-	Ind 7	—

A distinct clustering by population was observed for the samples. All samples from the Keret population grouped together to form one cluster; all samples from the Shuya population, another cluster. Between-sample similarity in the Keret population was considerably higher than in the Shuya population. Within each of the two clusters, the samples from the hatcheries were more similar to each other than to the wild sample captured in the respective river (Figure 2).

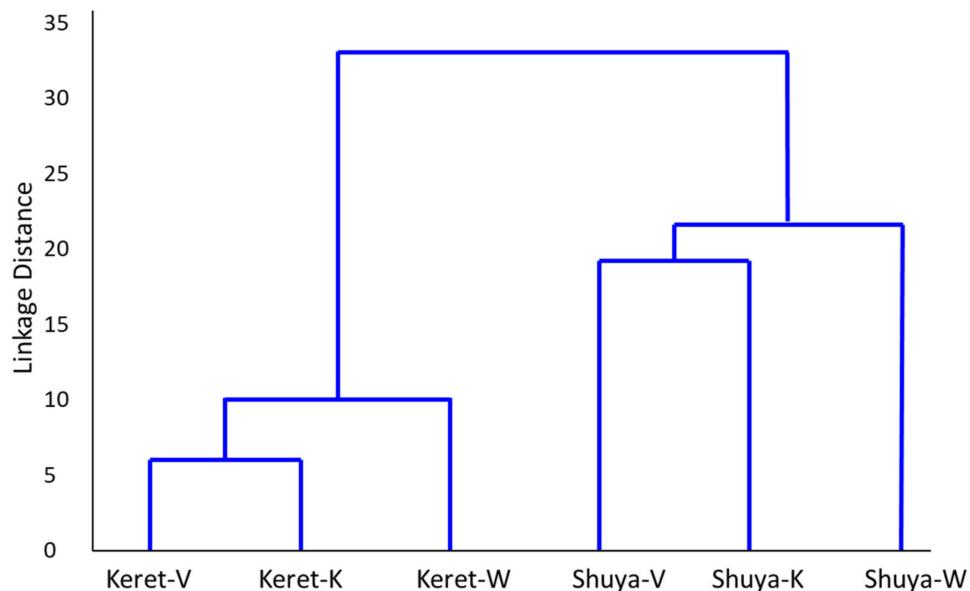


Figure 2. Clustering of the six juvenile Atlantic salmon samples by the 11 cranial bones indices. The measure of similarity is squared Euclidean distance, and the clustering algorithm is unweighted pair-group average.

To statistically evaluate the differences between different populations, we compared within-population pairwise Euclidean distances between three samples from each population in the space of the six first principal components. The principal components were used to prevent duplication of the information that is associated with correlations between the indices. The six first principal components accounted for a substantial portion, 82%, of the total variance in the set of the 11 traits. Student's t -test showed that pairwise Euclidean distances between samples in the Shuya population were significantly greater than those in the Keret population ($p < 0.05$).

Evaluation of the factors explaining differences between the populations. Genetic differences between anadromous salmon from Keret and landlocked salmon from Shuya were found to determine the cranial bone shape in the juvenile samples to a substantial extent (Figure 3, Table 5). The factor “origin” (genetic differences) explained 48%; the factor “habitat” (environmental differences), 32%; and their interaction, 14% of the total morphological difference between the fish samples. The residual variance, which cannot be explained by the effects of the factors and their interaction, accounted only for 6% of the total variance of the traits under study in Atlantic salmon juveniles.

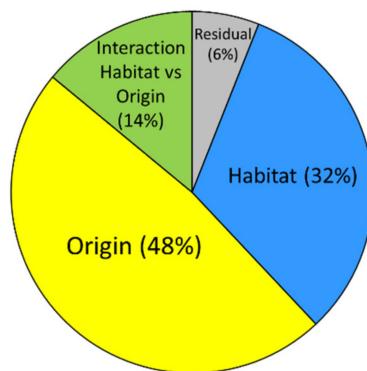


Figure 3. Effects of the genetic (origin) and environmental (habitat) factors and their interaction in the development of cranial bones in the cultivated and wild juvenile Atlantic salmon samples from the Shuya and Keret populations (ANOVA results for the 11 cranial bones indices).

Table 5. Effects of the factors “habitat” and “origin” and their interaction on the development of cranial bones in Atlantic salmon (**, the difference was significant at $p < 0.01$).

Factors	Test	Value	F	Effect—df	Error—df	p	Partial Eta-Squared	Non-Centrality	Observed Power (alpha = 0.05)
Habitat	Wilks	0.460	7.0	22	326	0.000 **	0.322	155	1.00
Origin	Wilks	0.519	13.7	11	163	0.000 **	0.481	151	1.00
Habitat–origin interaction	Wilks	0.733	2.5	22	326	0.000 **	0.144	55	1.00

4. Discussion

Adaptive genetic differences between landlocked and anadromous Atlantic salmon populations. Our findings indicate that genetic factors are responsible to a substantial extent for the osteological difference between the anadromous and landlocked forms of Atlantic salmon. Note that genetic differences in other traits have also been observed between the anadromous and landlocked *S. salar* forms. The relevant data are considered in more detail below.

Based on our data (and many observations at hatcheries), landlocked salmon of the Shuya River grow faster than anadromous salmon of the Keret River do. This agrees, for instance, with the fact that landlocked salmon of the Penobscott strain (Maine, United States) grow faster than anadromous Atlantic salmon from Scotland do [44]. Studies of certain landlocked Atlantic salmon populations have shown that the potential to adapt to saltwater is decreased in their individuals, the extent of the decrease varying among salmon from different water bodies [45–49]. However, no difference in the potential to adapt to saltwater has been observed between the anadromous and landlocked forms in other studies [50–52].

A landlocked population from the Byglands-fjord lake in Norway showed a reduced number of muscle fibers compared with anadromous fish and was found to be genetically fixed [53]. Females reach maturity at an earlier age in landlocked populations compared with anadromous population from Newfoundland [54]. A decrease in female age at maturity has been demonstrated experimentally by modeling the formation of a landlocked

Atlantic salmon strain from an anadromous population at the Vyg hatchery [27]. Unintentional selection for a certain allele of the *mMEP-2** malic enzyme gene has additionally been detected in that experiment [40]. Interestingly, the allele occurs at a high frequency in some wild landlocked Atlantic salmon populations from Northern Europe [55,56]. Thus, ample evidence indicates that genetic differences are observed between the anadromous and landlocked forms in Atlantic salmon and arise as a result of natural selection. This is quite expectable because the anadromous form is exposed to dramatic changes in environmental conditions during ontogeny, while the landlocked form is not.

Comparisons of molecular genetic and genomic characteristics between anadromous and landlocked populations have demonstrated a high similarity of the two Atlantic salmon forms, but substantially lower genetic diversity has been observed in the landlocked form (for a review, see [57–60]). Higher phenotypic plasticity may compensate for a decrease in genetic diversity. For example, fish of a landlocked threespine stickleback population vary in DNA methylation level to a greater extent than fish of a marine population [18]. An increase in phenotypic plasticity is similarly characteristic of the landlocked Atlantic salmon population examined in our study.

Higher phenotypic plasticity in the lake-river Atlantic salmon form. The degree of morphological differences between three samples originating from the same population was used as a measure of phenotypic plasticity in our experiment. Three samples of a common origin differed only in conditions during ontogenesis, both in the case of landlocked salmon of the Shuya River and in the case of anadromous salmon of the Keret River. As Figure 2 and statistical comparisons demonstrate, a higher morphological similarity was observed for the samples of anadromous Atlantic salmon. Phenotypic plasticity has not been compared as of yet between the anadromous and landlocked *S. salar* forms as far as we know, but there are indications that a higher variation is observed in lake forms compared with anadromous forms in salmonids [43]. Our findings support the conclusion based on mathematical modeling [61] that phenotypic plasticity decreases in the populations that change their environment during ontogeny. There are grounds to believe that the regularity has a direct bearing on speciation processes in salmonids.

Atlantic salmon evolved from a predominantly landlocked to a predominantly anadromous lifestyle according to published data. Brown trout is an ancestral species of Atlantic salmon [62,63]. Landlocked forms are more common and phenotypic plasticity is generally higher in brown trout compared with Atlantic salmon (for a review, see [64]). However, although morphological traits of Atlantic salmon become more homogeneous than in brown trout as a result of the transition to a predominantly anadromous lifestyle during evolution, phenotypic plasticity compensates for a decrease in genetic diversity in landlocked forms of the species. An increase in phenotypic plasticity with a decrease in genetic diversity is most likely a widespread regularity in Arctic fishes [3] and needs further investigation.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14100806/s1>, Table S1: List of indices used for morphological analysis of Atlantic salmon. Indices are ratios between traits, which are designated as distances between the landmarks shown at Figure 1.

Author Contributions: All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by A.O.Y., D.L.L., A.A.M., V.A.S., I.L.S. and V.S.A. The first draft of the manuscript was written by A.O.Y. and all authors commented on previous versions of the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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