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Genetic Differentiation and the Problems of Conservation of Masu Salmon (*Oncorhynchus masou* Brevoort, 1856 (Pisces: Salmonidae)) Populations

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Abstract—This study focuses on the strategy for the conservation of masu salmon, *Oncorhynchus masou*, in the northern part of the species range (via the masu populations in Sakhalin Oblast), based on data of its population structure. It is shown that masu populations that inhabit different rivers genetically differ from each other in allele frequencies at microsatellite markers. In the Naiba River basin, at least two genetically distinct masu populations exist: in the upper reaches and in a tributary, the Bolshoy Takoy River. The masu populations on Iturup Island significantly differ from those on Sakhalin Island; within Sakhalin, the masu salmon from the Chernaya River in the southwestern part of the island is genetically distinct from the southeastern Sakhalin and Aniva Bay populations. The genetic diversity of Iturup populations is substantially lower than that on Sakhalin, probably due to their small sizes. The measures for the conservation and recovery of masu salmon populations should be based primarily on their own genetic resources, or, in the case of a lack of spawners, on the base populations of their ecological/geographical region. In the latter case, masu populations of large rivers can be considered as base ones: for southeastern Sakhalin, this is masu salmon of the Naiba River; for Aniva Bay, this is masu salmon of the Lyutoga River. Transplantation of fish, fertilized eggs, or any other genetic material from a population that is different genetically and inhabits the waters with different ecological gradients should be strongly restricted. The formosan masu salmon from Taiwan Island is studied as an example of a strict genetic isolate.

Keywords: masu salmon, population, nature conservation, Sakhalin, Iturup, formosan isolate, genetic resources

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INTRODUCTION

Of the six Pacific salmon species, the masu salmon, *Oncorhynchus masou* Brevoort, 1856, is the only one that inhabits the Asian Pacific, mainly the basins of the Sea of Japan and Sea of Okhotsk; the other members of this salmon genus spawn in rivers of both the American and Asian coasts of the northern Pacific Ocean [2, 23]. Spawning grounds of masu salmon are found in rivers of the Korean Peninsula, in the northern part of Kyushu Island to the Tatar Strait, and in the lower reaches of the Amur River; on the ocean side, in rivers of the islands of Honshu, Hokkaido, and on the Kuril Islands; the most abundant masu stocks have been recorded from Hokkaido Island [2, 14, 23]. Masu salmon also inhabits the rivers of western Kamchatka; in small numbers, it occurs in eastern Kamchatka; the species is almost absent from

the Sea of Okhotsk coast of the mainland [10, 18]. The area of the ecological optimum for this species is the Sea of Japan basin, where a masu refugium probably existed during the last glaciation [26]. In Sakhalin Oblast, masu salmon is found on the southern Kuril Islands and all over Sakhalin, mainly in the southern part of the island [3, 5, 8, 9]. Systematically, the masu salmon is considered as a Pacific salmon, despite the fact that many of its traits make it closer to the Pacific trout [7].

The abundance of masu salmon has been declining all over the main regions of its reproduction for the past three-quarters of a century. Thus, since 1943, the stocks of this species in Primorsky krai have decreased ten times; the reproduction rate of masu salmon in Khabarovsk krai has also decreased [16]. In the middle of the 1950s, a dramatic decline in the masu abun-

dance began on the islands of Hokkaido, Honshu [23], and Sakhalin, where half a century ago it was of commercial value [4, 5]. The reduction in the masu abundance was largely caused by overfishing, first, with drift nets along the major salmon migration routes. However, overfishing is currently also observed in the coastal zone and in rivers. As an example, the size of the officially permitted masu catch for the Lyutoga River (Aniva Bay, Sakhalin Island) in the previous years, according to the licenses sold, was greater than the total abundance of the masu salmon that entered this river [1]. Angling for juvenile masu in rivers has also contributed to this trend.

Masu salmon spawn in shallow parts of the headwaters of rivers and tributaries, which makes it a conspicuous and easy prey [17]. Kawamura et al. [24] showed that due to the anthropogenic impacts on the rivers (dams, water pollution, and landscape degradation), the subspecies *O. m. ishikawae* on Honshu Island has reached the verge of extinction; therefore, masu fishing is prohibited here. For the same reason, a ban on masu fishing was introduced in Primorsky krai from the late 1950s (Antipina, 1978, cited by [16]). Other anthropogenic factors also contribute to the degradation of masu stocks. As an example, mature masu have not occurred in the Rudnaya River (Primorsky krai) since 1972 because of discharges of boron-containing waste [16]. The abundance of masu salmon on Iturup Island, being low due to natural causes, has decreased even more as a result of measures on elimination of predators prior to release of juvenile chum and pink salmon from salmon hatcheries [9]. Thus, three main anthropogenic threats to masu salmon populations can be identified: overfishing in the sea, fishing pressure in rivers, and habitat degradation.

The importance of the study of the masu salmon population structure was recognized long ago [2, 36, etc.]. This is due to the fact that masu salmon is the only species of Pacific salmon that is differentiated into subspecies [23]. The Russian Far East is inhabited by populations of the main, most common form of masu, *O. masou masou*. The intraspecific differentiation of the masu salmon is rather complex, with a variety of life strategies [3, 16, 23]. Krykhtin [10] indicated at least four geographically isolated groups of masu salmon in the Russian Far East, which were also characterized by a significant intrinsic differentiation [16]. The masu populations of Hokkaido have been well studied genetically: according to the published data, during the last glaciations in the refugium area (in the southern part of the island), the masu populations were probably connected via migratory flows; thus, the masu of southern Hokkaido is poorly differentiated [26]. As these authors note, the temperature limit for masu salmon ran through northern Hokkaido at that time. Rivers of the Sea of Okhotsk coast of Hokkaido were populated by masu only in the Holocene; thus, the populations of northern Hokkaido differ much more genetically, they are relatively small and

more isolated from each other. The only study on the masu in the northern part of its range [40] showed genetic differences between masu samples from the rivers of Sakhalin, western Kamchatka, and Primorsky Krai, but did not reveal any structure due to the lack of representativeness of the samples. At the same time, developing a strategy for the conservation of masu populations requires genetic data and more representative samples from populations of various regions and various rivers within the region, as well as from subpopulations within river basins [6].

The goal of this work was to study the population structure of masu salmon on southern Sakhalin and Iturup Island and assess its population/genetic parameters associated with the problem of conservation and recovery of its populations. Samples from other geographic regions are used for comparison.

MATERIALS AND METHODS

Masu Salmon Samples

A total of 509 specimens from 16 masu samples collected on Sakhalin Island, Iturup Island, and in Primorsky Krai, as well as formosan masu specimens from Taiwan Island were analyzed in the study (Fig. 1). For a more detailed analysis of population structure, re-samples from the same river basins were also taken. The masu populations that spawn in the rivers of the Sea of Okhotsk coast of Sakhalin Island, particularly in the Naiba River basin, were examined most comprehensively. Designations of the rivers from which samples were taken (the numerals 1 and 2 following the names of the rivers mean sampling and re-sampling from the same river basin; n is the sample size) are as follows: (1) Naiba River, samples "Naiba-1" ($n = 31$) and "Naiba-2" ($n = 36$) in the upper reaches of the main river channel, spawners, 2013; (2) Bolshoy Takoy River (the Naiba tributary), spawners, 2013, B. Takoy-1 ($n = 6$), and a sample of juveniles B. Takoy-2 ($n = 48$) in its tributary, Belaya River, 2008; (3) Ochepukha River, juveniles, 2008, Ochepukha-1, $n = 40$; (4) Znamenka River (the Ochepukha tributary), juveniles, 2008, Ochepuha-2, $n = 40$; (5) Lyutoga River (spawners, 2013), samples Lyutoga-1 ($n = 7$, until June 5) and Lyutoga-2 ($n = 41$, June 7); (6) Kura River (spawners, 2013), samples Kura-1 ($n = 34$, June 13) and Kura-2 ($n = 14$, June 14); (7) Chernaya River (spawners, 2014, $n = 48$); (8) Viakhtu River, spawners, 2010, $n = 4$; (9) Samarga River, spawners, 2013, $n = 48$; (10) Slavnaya River, spawners, 2009, $n = 35$; (11) Lake Lebedinoe (connected with the Kurilka River via a channel), juveniles, 2009, $n = 20$; (12) Kurilka River, juveniles, 2009, $n = 27$; (13) Tachia River (Taiwan Island), spawners, samples Tachia-1 (2004, $n = 12$) and Tachia-2 (2014, $n = 10$).

Analysis of Microsatellite DNA

In order to study the population structure we used 15 microsatellite markers suggested by various authors for salmon studies (Table 1). Isolation of total DNA, the polymerase chain reaction, fractionation of the amplification products in a non-denaturing polyacrylamide gel, and determination of the size of alleles were performed according to Rubtsova et al. [15]. Depending on the method, loci with small amplifiable DNA fragments were selected, or primers of large loci were modified to obtain shorter fragments (Table 1). To assess the allelic variability, the level of significance P in tests for the Hardy–Weinberg equilibrium, the differentiation of populations θ_p (F_{ST} -statistics), the number of detected alleles (A_p), and the expected and observed heterozygosities (H_e and H_o), we used GDA software [27] in accordance with the instructions by Weir [37]. The test for the Hardy–Weinberg equilibrium was performed for each sample individually with sequential Bonferroni correction according to the number of loci (15) and the total number of locus tests in all of the samples. Allelic richness was estimated in each sample. The retrospective dynamics of effective reproductive size of population N_e were tested using three indices: $\ln \hat{\beta}$ [25], S_k [41], and M [19]; a negative sign of an index indicates a decline of N_e in the historical past of the population; a positive sign indicates its growth.

RESULTS AND DISCUSSION

Polymorphism of Markers and the Results of Genetic Tests

All the microsatellite loci used in this study proved to be polymorphic (Table 1). The frequencies of the genotypes were in Hardy–Weinberg equilibrium in all the samples; additional tests for the ratio of homo- and heterozygotes [27] revealed a deviation at the *OtsG85* locus in the sample from the Slavnaya River, which proved to be of low significance ($P = 0.037$) with the Bonferroni correction by the total number of locus tests. Re-samples from the same populations insignificantly differed across the considered markers. The genetic differences between the masu populations from different rivers of Sakhalin, Iturup, and Primorsky krai were significant (Table 2). This can probably be explained by the fact that the masu salmon, which is associated with inland bodies of water to a greater extent, has a pronounced homing instinct and each population shows site fidelity to its river basin. The genetic data indicated a decrease in the effective reproductive size of all the populations that were studied (Fig. 2).

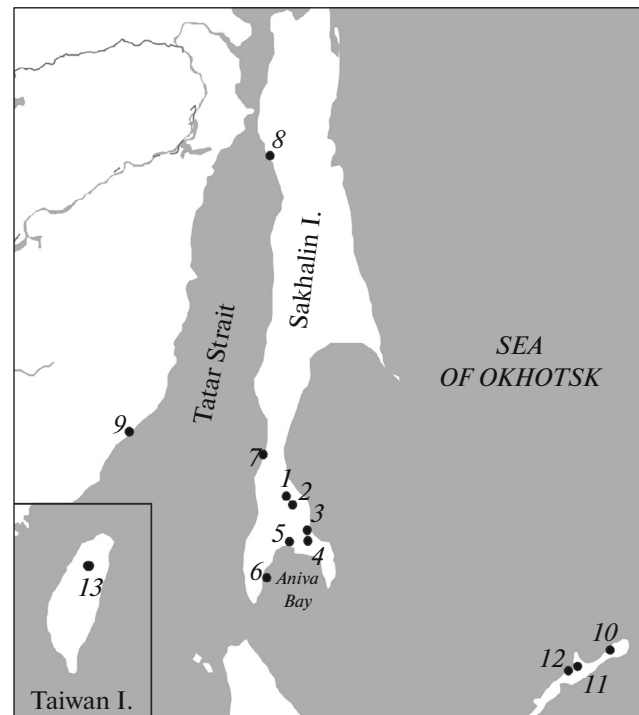


Fig. 1. The locations of masu salmon sampling: (1) Naiba River; (2) Bolshoy Takoy River (a tributary of the Naiba); (3) Ochepukha River; (4) Znamenka River (a tributary of the Ochepukha); (5) Lyutoga River; (6) Kura River; (7) Chernaya River; (8) Viakhtu River; (9) Samarga River; (10) Slavnaya River; (11) Lake Lebedinoye (connected with the Kurilka River via a channel); (12) Kurilka River; (13) Tachia River (Taiwan Island).

Masu Salmon in the Southern Part of the Sea of Okhotsk Coast of Sakhalin

In the Naiba River basin, we identified two genetically distinct populations: the masu salmon from the upper reaches of the Naiba River and the population that inhabit its tributary, the Bolshoy Takoy River (Table 2; Fig. 3). The population structure of the masu salmon in the Naiba River basin is probably even more complicated: only a small sample of the masu (six specimens) from the confluence of the Lebyazhya River into the Naiba, which also differed from the masu of the Naiba River, was available to us; we did not include this sample in the analysis until re-sampling in order to avoid hasty conclusions.

It is an interesting fact that the masu populations in major rivers: the Lyutoga, the Naiba, and even in the more remote Samarga River, are genetically closer to each other than to the neighboring populations of small rivers (Table 2; Fig. 3). Apparently, this can be explained by the following events in the evolutionary past of the species. After the last glaciations, masu salmon began to enter the territories north of southern Primorsky krai and Hokkaido [26]. The above-mentioned major rivers, which were located almost at the same latitude, were probably colonized at the same

Table 1. The characteristics of the studied microsatellite loci in masu salmon *Oncorhynchus masou*

| Locus | References | Motif length, bp ¹ | Allele size interval, bp | Statistics | | |
|-----------------------------|------------|-------------------------------|--------------------------|------------|----------------------|----------------------|
| | | | | <i>n</i> | <i>A_p</i> | <i>H_e</i> |
| <i>Oki1</i> | [34] | 4 | 98/186 | 475 | 20 (1) ⁴ | 0.703 |
| <i>Oki6</i> | [34] | 2 | 68/160 | 491 | 29 (1) | 0.879 |
| <i>Oki10</i> | [34] | 4 | 90/210 | 489 | 29 (2) | 0.942 |
| <i>One103</i> | [31] | 4 | 109/149 | 496 | 11 (1) | 0.779 |
| <i>One109G²</i> | [31] | 4 | 85/125 | 471 | 12 (1) | 0.728 |
| <i>One111</i> | [31] | 4 | 168/184 | 485 | 5 (1) | 0.560 |
| <i>One112</i> | [31] | 4 | 120/280 | 498 | 36 (3) | 0.835 |
| <i>Ots68</i> | [38] | 4 | 108/228 | 492 | 24 (3) | 0.898 |
| <i>Ots85</i> | [38] | 4 | 136/332 | 473 | 37 (1) | 0.958 |
| <i>Ots107</i> | [28] | 4 | 135/307 | 489 | 42 (1) | 0.939 |
| <i>Ogo2G1³</i> | [29] | 2 | 101/119 | 497 | 8 (1) | 0.672 |
| <i>Ogo2G2³</i> | [29] | 2 | 77/83 | 497 | 3 (1) | 0.409 |
| <i>Ssa197</i> | [30] | 2 | 113/137 | 496 | 9 (1) | 0.772 |
| <i>Omm1037G²</i> | [33] | 4 | 173/229 | 484 | 15 (1) | 0.743 |
| <i>Omm1070</i> | [32] | 4 | 111/281 | 466 | 40 (2) | 0.922 |

¹ Determined on the basis of the genotyping results, as the difference between the allelic variants.

² Loci are amplified with modified primers [15], which reduce the size of the PCR product.

³ Primers were modified to reduce the size of the PCR product: F: 5'-caccataagcatgcacacaattgt, R: 5'-gtattgtaaaatgtcttaccctct; in masu salmon, two loci *Ogo2* are amplified by them.

⁴ The number of detected allelic variants in formosan masu salmon is indicated in parentheses.

Statistical indices are as follows: *n*, number of genotyped individuals; *A_p*, number of detected allelic variants among all the individuals; *H_e*, expected heterozygosity.

time (Fig. 1). Among them, the largest masu stocks inhabit southeastern Sakhalin and Aniva Bay, particularly the Naiba and Lyutoga rivers, while the sizes of the rest of the populations in these areas are much smaller [3, 12, our observations]; the masu stock in the Samarga River is one of the largest for this species on the mainland coast [16]. At the time of colonization, all the masu populations (both in large and small rivers) probably differed insignificantly from each other genetically; however, after hundreds and thousands of generations the processes of random genetic drift “separated” them by allele frequencies. In this case the genetic drift should have had a stronger effect on the masu salmon in smaller rivers (Fig. 4), because masu abundance is known to markedly vary in the basins of small rivers [17] and according to the theory of population genetics the intensity of genetic drift depends on the effective size of a population, which, in turn, is determined mainly by the lower abundances in the sequences of generations.

It can be concluded from the above that the masu from the Naiba River should have retained more traits of the ancestral population than the masu from neighboring waterbodies on southeastern Sakhalin; therefore, it can be considered the base population for the area. Similarly, the masu of the Lyutoga River can be referred to as the base population for Aniva Bay. Measures for the recovery of masu populations in each river

basin should be based on the genetic resources of the basin proper, or, in case of a lack of spawners, on the base population of the corresponding ecological/geographical region.

Masu Salmon of Western Sakhalin

In our study, this region was represented in fact by a single sample from the Chernaya River, southwestern Sakhalin; another sample, from the Viakhtu River, was too small. The masu from the Chernaya River is significantly different genetically from the masu of the Sea of Okhotsk coast of Sakhalin, both in the southeastern part and in Aniva Bay (Table 2). These genetic differences can be related to the difference between the river ecosystems of the southeastern and southwestern Sakhalin, as they have different discharge basins (Sea of Okhotsk and Sea of Japan) and different characteristics of the drainage networks, which determine the size of the populations and the direction of their adaptation to the conditions of the river basins. These differences, along with genetic drift, could lead to associated changes at microsatellite loci. Another possible cause of these genetic differences is the different origins of the masu salmon from the Sea of Japan and Sea of Okhotsk coasts of Sakhalin Island; nevertheless, the shorter genetic distance from the Sea of Okhotsk masu to the Sea of Japan masu of the Samarga River, compared to distance to the masu of the Chernaya River

Table 2. The genetic differences (θ_p) between the studied samples of masu salmon, *Oncorhynchus masou*, from the Russian Far East

| Population | Naiba-1 | Naiba-2 | B. Takoy-2 | Ochepukha-1 | Ochepukha-2 | Lyutoga-2 | Kura-1 | Chernaya | Samarga | Slavnaya | Lebedinoye |
|-------------|---------|---------|------------|-------------|-------------|-----------|--------|----------|---------|----------|------------|
| Naiba-2 | 0* | — | — | — | — | — | — | — | — | — | — |
| B. Takoy-2 | 0.016 | 0.011 | — | — | — | — | — | — | — | — | — |
| Ochepukha-1 | 0.012 | 0.013 | 0.015 | — | — | — | — | — | — | — | — |
| Ochepukha-2 | 0.012 | 0.008 | 0.021 | 0.003* | — | — | — | — | — | — | — |
| Lyutoga-2 | 0.010 | 0.007 | 0.009 | 0.010 | 0.009 | — | — | — | — | — | — |
| Kura-1 | 0.013 | 0.008 | 0.017 | 0.013 | 0.011 | 0.007 | — | — | — | — | — |
| Chernaya | 0.031 | 0.029 | 0.030 | 0.033 | 0.032 | 0.020 | 0.033 | — | — | — | — |
| Samarga | 0.017 | 0.014 | 0.021 | 0.014 | 0.013 | 0.011 | 0.015 | 0.024 | — | — | — |
| Slavnaya | 0.054 | 0.051 | 0.048 | 0.043 | 0.047 | 0.033 | 0.044 | 0.061 | 0.040 | — | — |
| Lebedinoye | 0.077 | 0.071 | 0.073 | 0.082 | 0.081 | 0.060 | 0.085 | 0.093 | 0.072 | 0.053 | — |
| Kurilka | 0.067 | 0.062 | 0.071 | 0.067 | 0.065 | 0.050 | 0.061 | 0.074 | 0.046 | 0.040 | 0.073 |

The presented genetic differences are for samples with a size of at least 20 individuals. All the estimates are significant ($P < 0.05$), except for the ones between the re-samples from the rivers Naiba and Ochepukha (indicated by asterisk).

(Table 2), does not allow one to accept this explanation as the major one.

Masu Salmon of Iturup Island

The masu salmon of Iturup Island is significantly different genetically from the masu of Sakhalin. The value of differentiation θ_p between these islands is higher than 5–7%; the differences between the masu

populations inhabiting the southern part of the Sea of Okhotsk coast of Sakhalin Island are much smaller, 1–2% (Table 2), despite the fact that the masu of Iturup is similar to the Sakhalin masu in the biological parameters (body length and weight) [8]. The masu populations of Iturup also differ considerably from each other (4.0–7.3%) and this difference is much greater than that between all the studied populations of Sakhalin, including the masu from the Samarga River

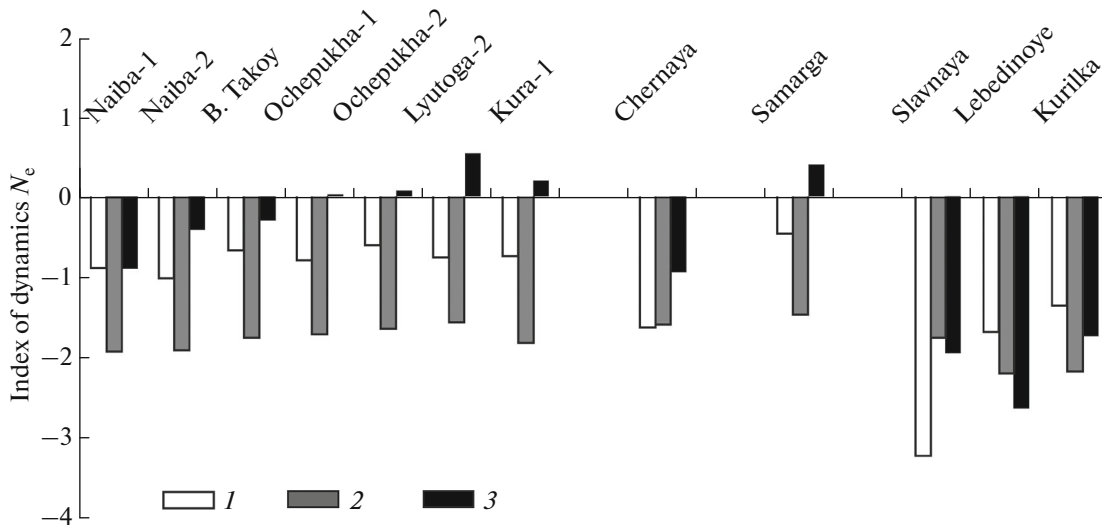


Fig. 2. The indices of the retrospective dynamics in the effective reproductive size of a population, N_e : (1) M , (2) $-\ln \hat{\beta}$, and (3) S_k ; small-size samples are not shown. The index M is modified to $(M - 0.68) \times 10$ for a convenient comparison with the other indices (0.68 is the critical value of M , according to the method by [19]). The negative values of the indices mean a decrease in N_e .

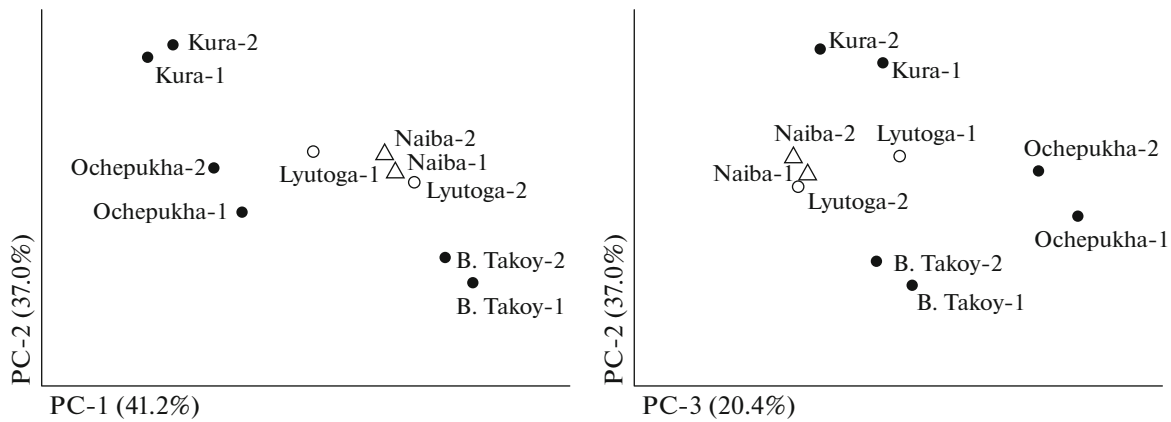


Fig. 3. The arrangement of masu samples from the rivers of the Sea of Okhotsk coast of Sakhalin Island over the three main components (PC-1, PC-2, PC-3), based on microsatellite markers.

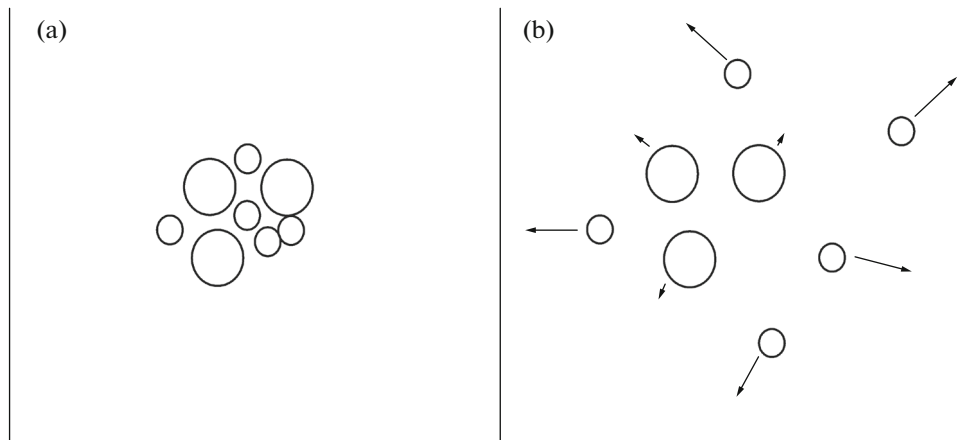


Fig. 4. The pattern of genetic differentiation of populations that have a large or small reproductive size under the effect of genetic drift, which simulates differentiation of large (Naiba and Lyutoga rivers) and small populations. (a) Hypothetical initial differentiation of populations of the northern masu salmon shortly after separation from an ancestral population: the differences between all the newly formed populations are small, regardless of their size; (b) differentiation that occurs over many generations after the separation from an ancestral population, caused by genetic drift: within this time, the genetic differences between populations with small reproductive sizes increased more than those between large populations.

(Table 2). In this case, all the three indices of N_e dynamics show a more significant regression of the effective size of the masu population on Iturup than that of the masu populations on Sakhalin and in Primorsky krai (Fig. 2). The allelic diversity of the masu on Iturup Island also proved to be much lower than that of the masu in the regions above (Table 3).

The genetic features of the masu salmon on Iturup Island are probably related to the fact that its abundance in short rivers of the island such as the Kurilka River is low [8]. Moreover, in the rivers where chum and pink salmon are reared in hatcheries the masu abundance has declined as a result of the measures taken for destruction of predatory fish [9]. All these factors contributed to a strong genetic drift in the masu populations on Iturup, which caused a substantial

reduction in their effective size and genetic diversity, as well as a significant genetic differentiation.

Formosan Masu Salmon

As was noted earlier [21], the formosan masu salmon of Taiwan Island is largely monomorphic (Table 3) due to its low abundance and the long-term reproductive isolation. Surprisingly, the tests for M and S_k dynamics indicate an increase in the genetic variability in the formosan masu, while the $-\ln \hat{\beta}$ index changed sign, which is characteristic of the beginning of differentiation if the initial population was monomorphic [25, p. 1925]. This could happen due to heavy overfishing of masu salmon during many generations (<https://www.youtube.com/watch?v=a5KXIXc7L0Q>). After the pressure on the population eased and the

Table 3. The average estimates of allelic diversity in the samples of masu salmon, *Oncorhynchus masou*

| Population | Parameters of allelic diversity | | |
|----------------------------------|---------------------------------|-------|------|
| | R | H_e | V |
| Sea of Okhotsk coast of Sakhalin | | | |
| Naiba-1 | 9.8 ± 1.3 | 0.77 | 25.5 |
| Naiba-2 | 9.4 ± 1.2 | 0.76 | 26.8 |
| B. Takoy-2 | 9.4 ± 1.2 | 0.77 | 25.2 |
| Ochepukha-1 | 10.1 ± 1.3 | 0.78 | 26.7 |
| Ochepukha-2 | 9.6 ± 1.3 | 0.77 | 23.2 |
| Lyutoga-2 | 10.9 ± 1.4 | 0.79 | 25.8 |
| Kura-1 | 10.2 ± 1.4 | 0.77 | 29.1 |
| Tatar Strait | | | |
| Chernaya | 8.7 ± 1.1 | 0.78 | 22.9 |
| Samarga | 10.9 ± 1.5 | 0.8 | 25.5 |
| Iturup | | | |
| Slavnaya | 7.6 ± 1.0 | 0.74 | 19.9 |
| Lebedinoye | 6.2 ± 0.8 | 0.67 | 17.9 |
| Kurilka | 7.2 ± 1.0 | 0.69 | 20.3 |
| Taiwan | | | |
| Tachia-1 | 1.5 ± 0.2 | 0.12 | 0.19 |
| Tachia-2 | 1.5 ± 0.2 | 0.15 | 0.23 |

R , allelic richness (determined for the minimum sample size of 19 individuals, i.e. 38 alleles); H_e , expected heterozygosity; V , variance of the number of repeats. All parameters are averaged across loci.

reproductive size began to recover, the allelic diversity also began to increase due to newly emerging mutations. Apparently, this evolutionarily slow process is still ongoing, as is seen via the indices above. To determine the time when the pressure on the population decreased, the approach proposed by Zhivotovsky et al. [42] can be applied. By estimating the variance of the number of microsatellite repeats at $V \sim 0.17$ and assuming the mutation rate to be 1.4×10^{-3} per locus per generation [35], we can find that the time constitutes approximately 121 generations. If we assume that the average lifespan of a masu salmon generation is 3–4 years, the estimate will be approximately 360–480 years, which is the approximate time since the relief of the pressure on the formosan masu population.

To understand the origin of the formosan masu [20], it is necessary to study samples from rivers of Korea, southern Primorsky krai, and other watersheds to the Amur River.

CONCLUSIONS

As the genetic data show, the decline in the masu salmon abundance has apparently reached the limit, beyond which the effective reproductive size N_e of all

the studied populations on Sakhalin, Iturup, and in northern Primorsky krai began to decrease (Fig. 2). The reduction of this parameter does not mean that this masu population will disappear, as is shown by the example of the formosan masu, which lost almost all of its genetic variability at the studied selectively neutral markers but has existed in this state for hundreds or thousands of years. However, a decrease in N_e is an indicator of a reduction in the reproductive potential of the studied masu populations compared to the potential in the historical past of these populations. It is therefore necessary to develop measures to support and recover the masu stocks in the Russian Far East.

Artificial reproduction of masu salmon has been of little success. A decrease in genetic diversity and a degradation of hatchery-reared populations of masu salmon have been observed in Japan and China [22, 39]. The hatchery-based reproduction of masu salmon in Primorsky krai also proved to be inefficient [13]. However, even in case of successful hatchery reproduction, the natural (base) populations of masu salmon should be preserved; for this purpose, it is necessary to know the population-genetics organization of the species. Accordingly, conservation of the habitat of the masu salmon as a key element of salmon ecosystems [11], including protection of the upper reaches of rivers and their tributaries, where the masu salmon breeds, is crucially important.

This study considered only a part of the masu species range in the Russian Far East. These results show that many of the masu populations are genetically unique. Therefore, the recovery and maintenance measures applied to each population should be based on their own genetic resources or, in the case of a lack of spawners, on the resources of the base population of masu salmon in each ecological/geographical region. The transfer of fertilized eggs or fish collected from a genetically very different donor population living in different environmental conditions should be restricted in order to prevent further destruction of the gene pools of the populations. The existence of several masu subpopulations within the same river system and their difference from populations of other rivers indicate the necessity of detailed population-biology and genetic research to identify the base populations of masu salmon as a resource for the conservation and recovery of endangered groups of this Pacific salmon species.

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