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ARCTIC CHARS

(The Structure of Population Systems and
Prospects for Economic Use)
by K.A. Savvaitova

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An idea is given of ecotypes as the main structural units of fish population systems living in high latitude bodies of water. Numerous populations of Arctic chars are described, as is their systematic position. The importance of developing measures of managing fishing and artificial breeding of Arctic chars is shown.

For fish industry researchers. 33 tables. 53 illustrations. Bibliography - 410 titles.

Editor: S.B. Makarova

INTRODUCTION

Recently, Arctic chars of the genus *Salvelinus* have been attracting more and more attention from researchers both in our country and abroad. This interest is determined on the one hand by the great economic importance in a number of regions of these highly numerous, valuable salmonid fishes and, on the other hand, by the fact that these fish are an excellent model subject for the study of microevolution and the emergence of forms. The study of chars is also extremely interesting because chars are the most typical representatives of northern ecosystems and can serve as indicators of the condition of these ecosystems and as a very important subject of ecological monitoring. 3*

The large phenetic variety of chars and their wide distribution make researching them difficult. In the literature there was until recently only casual, fragmentary information on chars living in different regions; moreover, the information was obtained by different authors who were often not specialists in these fish.

Chars of the genus *Salvelinus* have a circumpolar distribution and are found beginning from Iceland and the west coast of Norway to the east to Greenland. Their natural habitat also extends to the south (the lakes of Swedish Lapland and the Alps, the Tumen'-Ula River and the states of Oregon and California in the United States) [24]. They are featured to the *Salmonidae* family. Until 1832, researchers involved in systematizing salmons included chars in the genus *Salmo* and did not study them as an independent group of fish [282]. In 1832, Nilsson separated the chars into a *Salvelini* group and, in 1836, Richardson described the subgenus *Baione*.

Chars were separated into an independent group on the basis of the absence of teeth on the manubrium of the vomer (unlike the *Salmo* genus). Chars have teeth only on the head of the vomer; they are separated from the teeth on the palatine bones by a space and are retained for the entire life of the fish. In subsequent years, many authors started to use the name given by Richardson as a genus name [21, 315, 367, 368, 369 et al]. At the present time, the independence of the genus *Salvelinus* may be considered as generally accepted. A few Scandinavian scientists, 4
who feature the chars to gēnus *Salmo* [354, 355 et al], are an exception.

The study of the systematization of chars in Europe and North America began a very long time ago and it is possible here to separate two main points of view and trends which, sometimes prevailing concurrently and sometimes alternatively, have been exhibited over the entire period of study of this group of fishes. Some authors thought that only one or two types of char existed and

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* The figures in the right-hand margin indicate page numbers of the original (Tr.).

their diversity was viewed as a manifestation of variability [280, 290, 312, 382]. Other authors featured all diversity of chars to the existence of different species [302, 316, 367, 368, 371]. These authors described many species of chars without reference to their sexual, seasonal, age and ecological variability. As a rule, new species were described with little information, without taking into account biological features or the ecological forms they belonged to. This point of view gradually became predominant. As a result, the following began to be featured to the genus *Salmo*: *S. umbla, S. salvelinus, S. alpinus, S. nivalis Günther, S. killinensis Günther, S. wilughbii Günther, S. perisii Günther, S. rutilus Nilsson, S. carbonarius Strom, S. grayi Günther, S. colii Günther, S. salmarinus L, S. schrenkii Fotzinger, S. monostrictus Heckel et Kner, S. distichus Heckel, S. ventricosus Nilsson, S. salvelini-stagnalis Smitt, S. lepechini Gmelin, S. autumnalis Pallas, S. struanensis Gibson-Maitland.* The following began to be featured to the genus *Salvelinus: S. gracillimus Regan, S. inframundus Regan, S. maxillaris Regan, S. mallochii Regan, S. lonsdalii Regan, S. trevelyani Regan, S. fimbriatus Regan, S. charfii Regan, S. obtusus Regan,* i.e., 29 species of anadromous and lake chars from the waters of the British Isles, Spitzbergen, Iceland and Europe. In North America, the following were described in a similar manner: *S. lordii Günther, S. campbelii Suckley, S. hearnii Richardson, S. alipes Richardson, S. nitidus Richardson, S. hoodi Richardson, S. fontinalis Mitchill, S. hudsonicus Suckley, S. oquassa Girard, S. parkei Suckley, S. alpinus L, S. malma Walbaum, S. namaycush Walbaum, S. siscowet Agassiz, S. aureolus Bean,* etc. [302, 316, 367, 368, 371]. However, as data was collected on the biology of chars and their variability and as new knowledge on the species emerged, the point of view that chars belonged to a few polymorphous species began to win out. Even the advocates of opposite viewpoints began to doubt the validity of the system they had created [369].

More and more researchers began to come to the conclusion that the majority of the species described earlier were synonymous [262, 288, 289, 366, 406].

This period may be considered to some extent as completed for the chars of Europe where the abundance of species described is mainly reduced to one species, *S. alpinus (L)*,
represented by a few forms, or to three species: *S. alpinus, S. salvelinus and S. stagnalis*, the 5
status of which is under discussion. In America and Canada, most researchers today recognize as independent species only *S. alpinus, S. malma, S. fontinalis and S. namaycush* [268].

In the waters of Siberia and the Far East 12 species were once described: *S. alpinus, S. drjagini Logaschov, S. taimyricus Michin, S. boganidae Berg, S. tolmachoffi Berg, S. jacuticus Borisov, S. cherskii Drjagin, S. neiva Taranetz, S. andriaschevi Berg, S. taranetzi Kaganovsky, S. malma, S. leucomaenis (Pallas)*. In the waters of Japan, the following are known: *S. miyabei Oschima, S. malma sachalinensis Oschima, S. leucomaenis, S. leucomaenis fluvialis Oschima, S. pluvius (Hildendorf) and S. japonicus Oschima* [361, 362].

The taxonomic position of chars is the subject of constant ongoing discussions. They have become particularly lively of late. The reason for this lies mainly in the fact that, as a result of more serious and in-depth study of chars, researchers have run into the fact that differentiated sympatric forms exist and the necessity of interpreting this; new methods have appeared revealing a high level of polymorphism and allowing ambiguous conclusions to be made. At the same time, the study of populations was continued from typological positions. All of this led to the revival of systematize and subdivide viewpoints. The number of species started to increase once again.

The disagreements go beyond taxonomic issues; they touch upon problems of the emergence of forms, microevolution and systematization in a broad sense. Therefore, it is expedient to first examine the morphological features of char groupings and their interrelation within separate regions, in order to then compare them in the geographic sense, evaluate the systematic position, and study the processes of the emergence of forms and microevolution.

For an in-depth study of chars, it is very important to have research conducted throughout their entire natural habitat and based on unified approaches and methods. Related in the monograph is a complex hierarchy of population systems in many widely settled, ecologically plastic genera and species of animals. Between the components of these systems is a different degree of phenetic divergence, reproductive isolation and phenetic isolation. Some groupings are on an intraspecies level and are only occurring forms of the species; others have occupied the intermediate position of semispecies or diverged significantly and reached a species or superspecies class [65, 132].

These structures have still not been studied much in fish, although learning about them is
extremely important. Data on the structure of different class groupings and their variability should 6
be the basis of taxonomic research, the knowledge of the processes of speciation and phylogeny of fishes, the description of species composition of ichthyofauna, the structure of faunae and the principles of the emergence of forms of faunistic complexes and the structure of ecosystems at different latitudes. The study of the structure of population systems of fish and their variability is important for the evaluation of the adaptive properties which ensure their existence now and in the future. In relation to the intensifying anthropogenic effect on fish, the importance of such a prediction is not in doubt. Without similar research, it will be impossible to: rationally use schools of commercial fish and determine commercial loads on individual groupings, design the most efficient ecosystems using natural feed, represent individual groupings or conduct selection work [163].

The problems involved with studying the structure of population systems should be classed as key problems in modern ichthyology. The structure of population systems is determined first of all by the development of adaptations by populations to complexes of biotic and abiotic factors, in other words, by the formation of certain ecological groupings. These groupings may differ in growth rate, food, places and periods of reproduction, habitat, morphology, etc. They are characterized by a different level of isolation and divergence; they are distributed allopatrically and sympatrically.

In the monograph, the results of the author's work and that of his students are generalized. In processing materials, generally accepted, traditional methods which are employed in ichthyology were used. However, concurrently with them, on the same materials, a study was conducted of the osteology and karyology of chars and Kamchatka noble salmons [34, 36]; related interrelations of forms and populations were studied by molecular hybridization methods [56] and methods of immunoelectrophoresis and the reaction of precipitation and agglutination [35, 88]. For the differentiation of forms a method of parasite-indicators was used in a number of cases [114]. Materials on the morphometry of chars and the Kamchatka steelhead were processed with the help of methods of multi-test statistical analysis [154]. In this way a comprehensive study was made of chars and steelheads with various methods.

It should be emphasized that an analysis of the "char problem" is offered for the reader's attention within certain concepts which themselves are sufficiently under discussion and the use of which has known limitations.

The author is deeply grateful to all ichthyologist colleagues, without whose help this work 7
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Chapter 1 8

PROCEDURAL ASPECTS OF RESEARCH

PRINCIPLES AND IDENTIFICATION CRITERIA OF GROUPINGS OF A DISTINCT HIERARCHICAL LEVEL IN SALMONS

In studying salmons, there are two most clearly demonstrated trends in solving the "char problem": one which considers the detected differences as subspecies or species [43, 57, 58, 61, 244, 245, 247, 267, 268, 281, 337, 346, 347] and explains the diversity of forms as belonging to separate, independent species, and the other, according to which the existence of a diversity of forms is more often a manifestation of intraspecies variability [18, 19, 71, 72, 148, 149, 197, 198, 205, 206, 217, 218].

At the present time a significant increase in species subdivision is being observed. To a large extent, this has been facilitated by the noncritical recognition of the concept of biological species of E. Mair [132] and the use of so-called "new methods".

In recent studies of salmons, including chars, side by side with traditional methods of morphometric and biological analysis, osteological [38, 39, 57, 32, 138, 139, 140, 141, 195, 216, 217, 250, 366, 403], karyological [34, 42, 43], biochemical [5, 35, 88, 164, 197, 291, 308, 358, 360, 377], genetic (DNA-DNA molecular hybridization) [56, 145, 146, 242] methods and the parasite-indicators method [32, 57, 58, 111, 113, 114, 136, 153, 307] are being employed more and more frequently. Methods of numerical taxonomy [9, 13, 15, 57, 91, 154, 292, 346] are also being employed fairly extensively.

The assessment of criteria put forth on the basis of these methods gives rise to significant discussions.

At the basis of the use of the osteological and, more precisely, the craniological method are the representations of a number of authors concerning the exclusive value of osteological tests for purposes of species diagnostics due to their supposedly greater stability in comparison with any other tests. However, there is another point of view relying on extensive actual material according to which the variability of osteological features of salmons is highly significant and is on a par with and sometimes even exceeds the variability of other features [138, 139, 140].

As the result of a number of works [36, 108, 195, 250, 348 et al], it has been shown that
osteological features in chars are subject to various forms of intraspecies variability; in particular 9
the char's skull changes significantly in ontogenesis and its features may depend on the ecology of the populations [36].

Recently there have been more frequent attempts to impart special weight to karyological data as a criterion of species independence and extent of closeness of one form of chars with another [43]. In this case the karyotype features have contrasting morphological features. In reality, it not the analysis of genotypes that is being discussed, but the analysis of phenotypes according to karyological features. S.S. Shvarts [252], in our opinion, correctly indicated that the karyological procedure may be used only as an additional procedure. Numerous cases of inter- and intrapopulation polymorphism within species in the salmons are described according to the number of chromosomes and chromosome arms [34]. Undoubtedly a karyological analysis may provide valuable information, but only in a group with other methods.

Among the biochemical methods, the following has gained considerable ground: the analysis of electrophoretic mobility of proteins with the aim of studying the genetic structure of populations within a species and close species.

One should bear in mind that the assessment of the genetic relationship of fish on the basis of results of electrophoresis and the assessment of their phenetic and taxonomic relationship may not be in agreement. R. Levontin [151] considers that the differences between populations and species according to quantitative features are not comparable with the differences according to gene frequency in separate loci. However, these methods are extremely useful first of all in assessing the level of genetic independence of sympatric populations. In this case, the different freqency of occurrence of variants of polymorphous protein molecules in cohabiting phenones serves as a criterion for noncrossing, or rather the limited frequency of gene exchange within a population. Side by side with polymorphous proteins, monomorphous proteins are known. Yu.P. Altukhov [5] and Yu.G. Rychkov [3] consider that their electrophoregrams are identical in all individuals of one species, but differ in different species and, therefore, may serve as an absolute species criterion. If that were so in all cases, the phenomenon of monomorphism could be of great use. Unfortunately, this problem is not so simple. One and the same protein may be polymorphous in one species, but monomorphous in another. Thus the hemoglobins are polymorphous in far eastern chars and, apparently, monomorphous in the Atlantic char *S. alpinus*. According to the hypothesis of V.T. Omel'chenko [164], serous esterase is monomorphous in *S. malma and O. nerka*, but it is polymorphous (with clinal variability) in *S. alpinus* [359]. Lactate
dehydrogenase is monomorphous in pink salmon and herring, but polymorphous in lake char 10
[408].

Matters are even more complicated because, in the systems forming the species of populations, it is possible to find populations that are monomorphous according to any gene at all. But monomorphism may be established only having outlined the boundaries of the species, i.e., this criterion is suitable only when it becomes unnecessary. It is important to emphasize this since, for example, data on the hemoglobins of chars obtained by V.T. Omel'chenko [164] were used as grounds for the species independence of recently described species of char.

Features mentioned earlier may be characterized from a genetic point of view. V. Iogansenn [87] formulated the concept of "phene", treating it as an feature determined by the action of one gene.

Recently the concept of "phene" has been extended by new content; it is viewed as an feature inherited discretely according to Mendel's laws. A new trend has appeared: phenetics [254].

Many features according to which char phenones are distinguished may be featured to a group of phenes. Various alleles of proteins and some osteological features are inherited discretely and they may be called phenes. Apparently, a number of comparative-morphological characteristics, on the basis of which a description is given of the char populations presented in our book, may also be featured to phenes. The growth of fish, rate of maturity, level of development of breeding colours, etc. depend on the action of a few hormones which are inherited discretely. And these indicators determine the features of the skeleton's external morphological features. The analysis of many morphological features allows us to conclude that there is no clear borderline between the concept of "phene" and the standard concept of "feature". This is pointed out by A.V. Yablokov and N.I. Larina [256] who cite examples of transferring from discrete features to average values which are constantly varying. Modern methods of biological statistics allow us with sufficient certainty to judge concerning the presence of differences between phenones. Even features where the distributions overlap, but which are statistically different, are suitable for identifying phenones. Therefore, it is possibly to use both discrete and overlapping features.

One should pause on another group of features, the study of which was begun recently and the analysis of which has a fundamental significance. In 1969, G. Mair wrote that the newest and most interesting trend was the attempt to approach the basis of the relationship: the genetic
programme itself. Currently a highly promising procedure for establishing the homology of 11
primary DNA structures is being developed.

A positive feature of the method of molecular hybridization is the possibility of completely excluding convergence and parallel development, as well as the phenomenon of homological variability. The DNA sequences of those forms between which there is no gene exchange may only diverge. The similarity here is the relationship.

The advantage of the molecular hybridization method consists in the fact that, over the long run of its use, it is possible to obtain an integral characteristic of the similarity of many millions of individual nucleotide sequences, the divergence of which proceeds independently of one another. However, as with all previously used methods, the molecular hybridization method does not provide an absolute species criterion. But, in a significant way, it allows research to be supplemented as complex hierarchical population systems are revealed. Insufficient work on fish is being conducted using this method. However, interesting results have already been obtained on whitefishes, graylings and salmons [56, 145].

The parasite-indicator method is undoubtedly valuable; it is used for identifying different groupings [111, 112]. Recently there have been attempts to make this method absolute and to replace the study of important ecological features of fish with an analysis of their parasites alone. The use of this method to solve taxonomic problems is also possible only as part of a set with other methods.

The so-called methods of numerical taxonomy play a special role in describing new species [234]. These methods of answering questions concerning the separation and determination of the status of some forms of char according to osteological features were used by M.K. Glubokovskii [57, 58], and according to external morphology features, V.L. Andreev and V.V. Volobuev [8], S.Sh. Bagaryan [15] and E.E. Borisovets [28, 29]. On the basis of the analysis of similar phenograms, M.K. Glubokovskii drew conclusions concerning the taxonomical position of chars.

A mass attraction to numerical and phenetical methods where, according to E. Mair's accurate expression [133], it was suggested that intellect and theory were becoming nonessential and that we could simply trust the computer, is now already in the past. However, reasonable use of methods of numerical taxonomy side by side with other methods is fully justified and essential. The main task consists in studying first of all the correlational connections of features. The analysis of the structure of feature connections should precede the study of the interrelationship of subjects. Unfortunately, in the literature on chars, not all authors present corresponding data, 12
sometimes restricting themselves to assertions concerning the absence of a correlation [57, 58] or, on the contrary, overestimating the correlation without substantiation.

Among certain researchers the concept has taken a foothold that the use of traditional, particularly plastic features in comparing different populations makes no sense, since a close connection exists between them and a large amount of excess information is being created. However, V.L. Andreev and Yu.S. Reshetnikov [193] (for whitefishes), S.Sh. Bagaryan, A.T. Terekhin [15] and S.Sh. Mikhailova [154] (for chars and Kamchatka noble salmons), showed that a close connection is observed only when the absolute meanings of features are used. If the plastic features are expressed (as is done in ichthyology) in relative quantities (% of body length according to Smitt), the connections between them break down. A system of weakly connected features is formed by which the duplication of information is eliminated and the assignment of equal weight to all features used is justified.

Research conducted using any of the methods listed is preceded by the separation of sympatric and allopatric populations into phenones. If the separation is done incorrectly, the conclusions will be false and, in particular, a polymorphism may be discovered where it does not exist and, on the contrary, if the sample is small and selected tendentiously, there is a danger of overestimating the significance of the revealed diversity. Therefore, however disdainfully some classifiers may relate to features of external morphology, they first of all, although not obviously, proceed from them and all subsequent conclusions in the final analysis are determined by that set of plastic features which characterizes the external appearance of an organism, now elusive, according to which it can reliably distinguish different forms of practice, but which are very difficult to describe. The closest to a detailed description of external appearance is the comparative-morphological characteristic which includes both meristic and plastic features of body proportions adding the main features of colours of living specimens, preferrably during the reproduction period and during the feeding period, including the frequency of occurrence.

In the systematization of fish and in studying intraspecies structure, data on the sizes and structure of eggs are widely used, as are data on embryonal development [264].

In ichthyology it is considered absolutely essential to study growth, reproduction and the nature of food of allopatric and sympatric groupings. These biological features are often at the basis of their differentiation, but afterwards an analysis of groupings should be conducted with the help of the above-listed methods, since each of these methods alone cannot give criteria of either a taxonomic class or related relationships of the forms being studied. Overestimation of any 13
criterion may lead and does lead to serious errors. Conclusions obtained with the help of different methods are often contradictory; on the basis of the same results, diametrically opposed conclusions are sometimes made.

A different interpretation of results is apparently a reflection of differences in approach. If, on the whole, starting at the end of the last century, a population approach is characteristic for ichthyology, then research using "new" methods is so far, as a rule, in progress on separate individuals. Even in those cases where numerous samples from different populations are being studied, researchers' thinking remains typological; they try to ascribe the value of absolute species criteria to the differences discovered. This is caused by the fact that similar research is often conducted not by ichthyologists, but by geneticists, biochemists, parasitologists and others who ignore the growth, sexual, seasonal and other variabilities. Most "new" methods are very labour-intensive and it is not always possible to obtain representative material with their help. For this very reason, we considered it expedient to base this work mainly on results obtained with methods of usual ichthyological research, permitting the analysis of various forms of morphoecologicial diversity in populations throughout the entire natural habitat of species and their comparison with data from the literature. We think that, with the help of traditional "classical" methods, it is possible to obtain extensive material containing a large quantity of information. It is not out of place here to recall the observed underestimation of "old" methods.

FEATURES OF HABITAT SURROUNDINGS

The groups of fish being studied live in the non-tropical part of the Northern Hemisphere, in arctic, subarctic and, to a lesser degree, boreal areas. They are characteristic mainly of the Arctic Ocean and Pacific Ocean provinces of the circumpolar subregion [25]. In these zoogeographical regions, chars populate diverse lakes (table 1), rivers and streams.

The lakes that the chars inhabit are differentiated by genesis of the basins and coincide in time with certain forms and types of relief. Since the formation of the latter occurred at different times, the ages of the lake basins are not the same. However, with few exceptions, they are cut into pleistocene and holocene deposits and they are relatively young in age. The history of their coming into being and their development is closely related to quaternary history [125, 135].

With respect to climate, the regions where these lakes are located are characterized by a 15
harsh winter, a short cold summer, relatively low temperatures, heavy cloud, strong winds, small amounts of precipitation and permafrost.

The overwhelming majority of bodies of water which chars inhabit are catergorized as oligotrophic. Oligotrophic lakes are characterized by the low entry of biogens; they contain little phytoplankton, bacterio- and zooplankton, benthos or fish. Usually they are located on crystalline rock; hypolimnion exceeds epilimnion in volume; they are rich in oxygen; the water is very clear (up to 40 m); very few humin substances; slightly developed littoral; bottom sediments poor in organic chemicals. Water oxidability is 1-2 mg of oxygen per liter [115].

In Europe and along the Arctic Ocean coast of Asia chars predominantly inhabit lakes. In the Far East, where the role of rivers increases greatly in the hydrographic network, chars coincide in their distribution with relatively uniform alpine, semi-alpine and tundra-alpine rivers, which differ in extent and degree of branching of the river basins.

1. Characteristics of lakes inhabited by Arctic chars

Region	Lake	Type of lake	Age, in thousands of years	Length, in kilometres	Width, in kilometres	Depth (max.), in metres	Source of information
Kola Peninsula	Elovoe	glacial-tectonic, oligotrophic	~10	7	0.1-0.3	25	our data
	Enozero	same	~10	~10	~7	>50	237
Taimyr	Khantaiskoe	alpine, oligotrophic	20-9	121	18	up to 420	121, 172
	Keta	same	20-9	97	14.2	200	121, 172
	Lama	"	20-9	82	9.5	228	121, 172
	Glubokoe	"	20-9	44.5	7.4	185	121, 172
	Kapchuk	"	20-9	12	3	50-70	121, 172, our data
Chukotka	Arakam-chechen	alpine, oligotrophic	holocene	1.5	0.5	26	our data
	El'gygytgyn	same	late pliocene	17	12	169	17, 55
	Svobodnoe	thermokarst	-	3	1,5	1.5-2.5	53
Materikovoe coast of the Sea of Ohotsk	Ueginskoe	alpine, oligotrophic	-	3.5	1-1.5	25	50
	Korral'	same	-	1	0.8	10	50
Lena River Delta	Dal'nee	thermokarst	hundreds, dozens of years	~1.5	~1	5-10	220
	Perekhodnoe	same	same	~1.5	~1	15	our data
	Zolotye chiry	"	"	1.5	0.8	5-10	our data
	Forelevoe	alpine, oligotrophic	a few thousand years	1.5-2	0.5-0.7	7	220
Zabaikal'e	Frolikha	alpline, oligotrophic	~10	~12	~3	>25	104
	Leprindokan	same	~10	7	-	-26	241
	Davatchan	"	~10	5.5	1.7	>50	241
	Maloe Leprindo	"	~10	6	2	>50	241
	Bol'shoe Leprindo	"	~10	9	-	>50	241
	Gol'tsovoe	-"	~10	1.5	1	>50	222
Kamchatka	Azabach'e	alpine, oligotrophic	10	12	9	35	123
	Ushkovskoe	limnokrene	-	-	-	-	118
	Kronotskoe	alpine, oligotrophic	30	30	18	128	43
	Dal'nee	same	-	2.5	0.54	60	43
	Nachikinskoe	"	-	1.5	0.8	60	our data

CHAPTER 2
CHARS FROM THE WATERS OF THE EUROPEAN PART OF THE USSR

THE KOLA PENINSULA

It is known that in the rivers of the Barents Sea coast of the Kola Peninsula lives the anadromous Arctic char *S. alpinus* [24], and in some of these rivers its numbers are very high.

There has been almost no research done on the systematization of the lake char of this region. L.S. Berg [24] attributed them to *Salvelinus sp.*, and M.V. Vladimirskaya [45] attributed them to *S. alpinus*. A.I. Kolyushev [105, 107, 108], G.G. Galkin et al [54] view them as a subspecies of *S. lepechini*. With the exception of the works of E.D. Vasil'evaya [40] and V.K. Mitenev [155], there is no information on the chars from the lakes of the Murmansk coast. The anadromous char has also not be researched at all.

Together with Yu.I. Tsarev we studied chars from the basin of the Varzina River (table 2) and the research and description were carried out as follows: length, mass, age, growth, reproduction, food, morphological features, qualitative features.*

Anadromous and lake chars from the basin of the Varzina River different in length and 16
body mass. The former are much larger. In turn, lake chars from Enozero Lake are larger than those from Elovoe Lake.

The maximum age is noted in the population of anadromous chars and the minimum age is among the chars of Elovoe Lake. All populations differ from chars from other bodies of water of the Kola Peninsula in their sluggish growth [54]. However, anadromous chars and chars from Enozero Lake grow more quickly. Anadromous chars and chars from Elovoe Lake mature late and those from Enozero Lake mature earlier. In other bodies of water of the Kola Peninsula, the life span of chars is shorter (6+) and they mature early (3+) [54]. According to meristic features, there are a few reliable and minor differences between the anadromous and lake populations (table 3). Thus, in comparison with the chars from Elovoe Lake, there are more scales on the lateral line and rays on the anal fin in the chars from the Varzina River, but in comparison with the chars from Enozero Lake, there are more rays on the dorsal and anal fins.

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* In the Elovoe and Enozero Lakes of the Varzina River basin, the local population divides chars according to the colouring of the so-called chars and lake chars. Due to the fact that we did not manage to differentiate them clearly, a description is made from combined materials.

2. Biological indicators of chars from the basin of the Varzina River

Feature	Varzina River	Lake Elovoe	Lake Enozero
	Form		
	anadromous	lake	lake
Body length (cm)	30-65* / 49.4	29-33 / 31.7	25-46 / 35.5
Weight (gm)	400-2500 / 1200	200-320 / 275	280-1000 / 628
Maximum age (in years)	16	12	14
Time to mature (in years)	7	8-9	5-6
Spawning period	late autumn	end of August-September	End of September and later
Spawning frequency	not annually	not annually	not annually
Fecundity, number of eggs	3882	-	-
Ratio of the sexes (males to females)	3 : 1	4 : 1	3 : 1
Feeding	does not feed while moving	benthic	benthic and predatory
Growth rate	relatively fast	very slow	reduced

* The variation limits are given in the numerator and the average values are given in the denominator.

True differences according to plastic features also show up between lake populations having relatively similar body sizes. Thus, chars from Elovoe Lake have shorter dorsal and anal fins, a shallow body, a long and low caudal peduncle and a large postdorsal distance. However, the greatest difference is observed in body depth.

3. Meristic features of chars from the Varzina River basin

Feature	Population	lim	$\bar{x} \pm m$	s	Student's test (T_{st})			Coefficient of variation (CD)		
					I/II	I/III	II/III	I/II	I/III	II/III
Number of scales on the lateral line	I	120-155	134.0 ±0.73	6.1	-	5.8	3.1	0.11	0.50	0.34
	II	125-145	132.7±1.10	5.7						
	III	120-140	129.7±0.11	3.0						
Number of rays on dorsal fin	I	9-11	10.3±0.06	0.5	7.7	3.3	4.5	0.9	0.37	0.7
	II	9-10	9.4±0.10	0.5						
	III	9-11	10.0±0.07	0.3						
Numbers of rays on anal fin	I	8-10	9.2±0.06	0.5	10.0	7.6	2.5	1.1	0.7	0.3
	II	8-9	8.2±0.08	0.4						
	III	8-9	8.5±0.07	0.5						
Number of rays on thoracic fin	I	11-13	12.0±0.05	0.5	1.79	-	-	0.2	0.1	0.1
	II	11-13	12.2±0.10	0.5						
	III	11-13	12.1±0.06	0.5						
Number of branchiostegals, on the left	I	9-12	10.6±0.07	0.6	-	-	1.16	0.08	-	-
	II	9-12	10.7±0.14	0.7						
	III	8-12	10.5±0.10	0.7						
on the right	I	9-11	10.2±0.07	0.5	-	3.3	2.10	-	0.3	0.3
	II	9-12	10.2±0.12	0.6						
	III	9-11	9.9±0.06	0.5						
Number of gill rakers	I	22-27	23.8±0.15	1.2	-	2.1	1.0	-	-	-
	II	22-27	23.6±0.40	2.3						
	III	21-26	23.1±0.29	2.1						
Number of pyloric caeca	I	30-55	42.5±0.70	5.1	1.31	-	-	0.15	-	-
	II	30-55	40.0±1.00	5.2						
	III	30-55	41.1±0.60	4.4						
Number of vertebrae	I	61-66	62.7±0.12	0.9	-	-	-	-	-	-
	II	61-64	62.5±0.15	0.6						
	III	60-64	62.8±0.25	1.2						

Note: I - Varzina River (*n* - 72); II - Lake Enozero (*n* - 27); III - Lake Elovoe (*n* - 51); T_{st} - values through which true variations were revealed.

4. Plastic features of chars from the Varzina River basin 18

Feature	Popu-lation	lim	$x \pm m$	s	Student's test (T_{st})			Coefficient of variation *(CD)*			
					I/II	I/III	II/III	I/II	I/III	II/III	
Body length (Smitt) (cm)	I	30-65	49.4								
	II	25-43	37.5								
	III	24-37	32.7								
Head length, %	I	17-23	19.3±0.11	1.0	5.3	5.4	1.4	0.6	0.5	-	
	II	18-24	20.7±0.24	1.2							
	III	17-23	20.3±0.15	1.1							
Length of snout, %	I	4-7	5.2±0.06	0.5	-	2.8	2.1	-	0.2	-	
	II	3-6	5.2±0.11	0.6							
	III	3-7	4.9±0.09	0.7							
Eye diameter, %	I	1-4	2.5±0.03	0.3	12.0	13.7	3.1	1.2	-	-	
	II	2-4	3.1±0.04	0.2							
	III	2-4	3.3±0.05	0.4							
Head height, %	I	11-17	13.0±0.10	0.8	1.9	4.0	4.6	-	0.4	0.3	
	II	11-16	13.4±0.19	1.0							
	III	11-15	12.4±0.11	0.8							
Distance between the eyes, %	I	5-8	6.7±0.05	0.4	0.9	9.0	5.1	-	0.8	-	
	II	5-8	6.6±0.10	0.5							
	III	5-7	6.0±0.06	0.5							
Distance behind the eye, %	I	9-13	10.9±0.07	0.6	3.0	1.9	1.8	0.4	-	-	
	II	9-13	11.4±0.15	0.8							
	III	10-13	11.1±0.08	0.6							
Maxillary bone length, %	I	5-10	7.6±0.08	0.7	3.5	1.7	2.3	0.4	-	-	
	II	6-10	8.2±0.15	0.8							
	III	6-10	7.8±0.09	0.7							
Maxillary bone width, %	I	1-2	1.4±0.03	0.2	4.0	-	-	-	-	-	
	II	0.9-2	1.6±0.04	0.2							
	III	1-2	1.4±0.02	0.2							
Mandible length, %	I	10-16	12.0±0.11	0.9	3.1	4.1	-	-	0.4	-	
	II	10-16	12.8±0.23	1.2							
	III	10-16	12.9±0.19	1.4							
Greatest body height, %	I	18-25	21.4±0.19	1.6	-	14.1	10.3	-	-	1.19	19
	II	17-24	21.4±0.29	1.5							
	III	12-21	17.4±0.21	1.6							
Smallest body height, %	I	5-9	6.8±0.07	0.6	4.7	-	4.3	-	-	0.6	
	II	6-9	7.3±0.08	0.4							
	III	5-8	6.8±0.06	0.5							

4. Plastic features of chars from the Varzina River basin (cont'd.)

Feature	Population	lim	$x \pm m$	s	Student's test (T_St)			Coefficient of variation *(CD)*		
					I/II	I/III	II/III	I/II	I/III	II/III
Length of caudal peduncle, %	I	14-20	16.8±0.11	1.0	1.3	12.9	3.4	-	1.1	0.5
	II	15-20	17.4±0.14	1.0						
	III	16-22	18.9±0.12	0.9						
Postdorsal distance, %	I	35-44	39.4±0.21	1.8	2.0	13.1	8.1	-	1.8	1.1
	II	37-44	40.1±0.29	1.3						
	III	39-46	42.7±0.14	1.0						
Anteventral distance, %	I	45-51	48.0±0.13	1.1	2.8	-	-	0.3	-	-
	II	46-51	48.7±0.21	1.1						
	III	45-51	48.1±0.15	1.1						
Anteanal distance, %	I	64-72	68.3±0.18	1.4	1.3	1.2	-	-	-	-
	II	67-72	68.7±0.24	1.3						
	III	66-70	67.4±0.73	1.4						
Dorsal fin length, %	I	9-13	10.8±0.07	0.6	3.1	3.8	6.2	-	-	0.6
	II	10-13	11.2±0.11	0.6						
	III	8-12	10.4±0.08	0.6						
Dorsal fin height, %	I	11-17	14.0±0.12	1.0	7.8	6.5	3.2	1.9 6	-	0.4
	II	13-20	16.3±0.27	1.4						
	III	12-19	15.3±0.16	1.2						
Anal fin length, %	I	5-10	7.7±0.08	0.7	6.9	3.0	5.2	0.8	-	0.7
	II	7-11	8.7±0.12	0.6						
	III	7-9	8.0±0.06	0.4						
Anal fin height, %	I	9-15	12.2±0.12	1.0	9.3	4.9	5.0	1.0 5	0.4	0.6
	II	11-17	14.3±0.19	1.0						
	III	11-15	13.1±0.14	1.1						
Thoracic fin length, %	I	12-18	14.6±0.13	1.1	5.6	6.1	-	0.5	-	-
	II	12-21	16.8±0.37	1.9						
	III	14-20	16.1±0.21	1.5						
Abdominal fin length, %	I	8-16	11.6±0.12	1.0	6.2	5.6	-	0.7	-	-
	II	11-16	13.2±0.23	1.2						
	III	10-16	12.9±0.20	1.5						

Note: I - Varzina River (*n* - 72); II - Lake Enozero (*n* - 27); III - Lake Elovoe (*n* - 51); $T_S t$ - values through which true variations were revealed.

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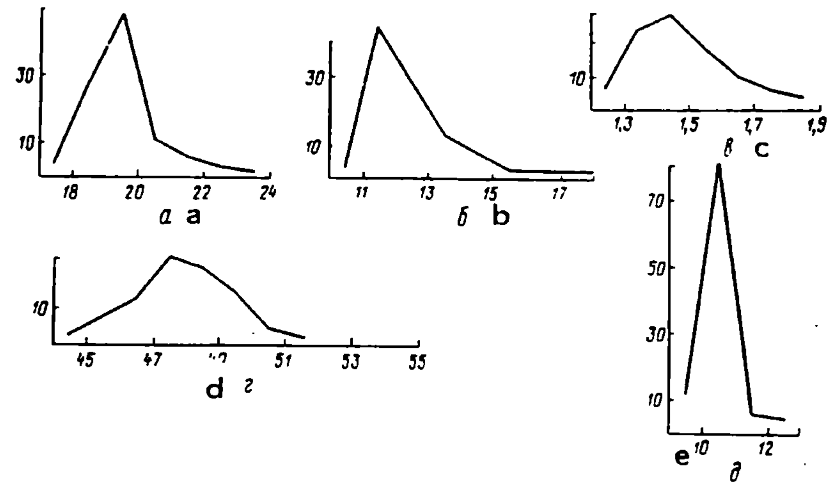

Figure 1. Distribution of features of chars from Lake Noskovoe (Kola Peninsula). % of body length according to Smitt (on the horizontal axis) and frequency of occurrence (on the vertical axis):
a - head length; b- mandible length; c - maxillary width; d -anteventral distance; e - base length of dorsal fin

Anadromous chars truly and sometimes significantly differ from one another according to a series of plastic features (table 4), but all differences are due to their large size and faster growth rate (diagram 1). As T.N. Lyaginaya [130] showed, body proportions depend on the rate of growth of the fish. Individuals from fast-growing populations have shortened heads and paired fins, smaller eye diameter, shorter unpaired fins and a deeper body. Slow-growing individuals, on the other hand, are characterized by a large head and large eyes, with longer paired and unpaired fins and a shallow body. This is related to the different rates of growth of body parts in ontogenesis. The differences that we revealed in body proportions between char populations from the Varzina River basin are confirmed on the whole by these points.

All populations are basically similar in colouring. Anadromous chars are distinguishable only by a silvery background of the body which is characteristic of fish coming from the sea. The chars of all populations also do not differ in the shape of the head and the location and form of the maxillary bone. On the whole, according to a set of features, the level of interpopulation 21
differences is the same as that within a population: between the females and males and between individuals of the same sex at different levels of maturity.

In this way, chars from different bodies of water of the Varzina River basin are similar and represent a single grouping in the taxonomical sense. Differences between them are exhibited in the way of life (anadromous or freshwater habitat) and the growth rate associated with it. The latter is apparently determined to a significant degree by differing availability of food.

Chars of the lakes of the Kola Peninsula and Karelia stem from the original anadromous form [24, 107, 182]. At the same time, the reverse change from freshwater to anadromous form is

observed [237]. It is also possible that some modern lake populations came from lake forms. Many freshwater populations are relics of the ice age, particularly those populating the huge, coldwater and deep lakes of Karelia and the Alps. Their age is approximately 12-15 thousand years [107]. It is known that these relic populations are not uniform. Groupings of large and small chars live throughout the lakes and differ in growth rate, type of food, colouring and morpholoy. Sometimes they are reproductively isolated according to spawning locations and times; sometimes there is no such isolation. Isolation is brought about due to an increase in size of the body of water, volume of water mass, depth, and the presence of various ecological niches. Thus, there are two forms of lake char in the immense Lakes Ladoga and Onega. They occupy different biotypes (one of the forms is deepwater); they differ in growth rate, time of sexual maturity, fecundity, spawning times and locations, morphological features, etc. [24, 44, 228, 229, 230, 231, 232] and they represent rather isolated, self-reproducing groupings. In the lakes of the Kola Peninsula, groupings of so-called chars and lake chars are distinguished [36, 40, 105, 106, 107, 108]. These groupings are widely distributed and may be found both sympatrically and allopatrically. In some bodies of water they also differ in growth rate, type of food, fecundity, colouring and in some morphological features [40, 107]. There are insignificant osteological differences between them [36, 108]. In Lake Noskovoe they are due to a different physiological condition of the fish [36]. However, the relationship between them has not been completely cleared up. Thus, according to the work of A.I. Kolyushev [107], it is difficult to judge the degree of their reproductive isolation, but it is possible to suppose that in the large Umbozero and Kovdozero Lakes and others, they are isolated to a certain extent. There is another stage of
differentiation in small bodies of water. According to the data of E.D. Vasil'evaya [40], in Lake 22
Noskovoe of the basin of the Zarubikhi River, which flows into the Barents Sea, chars and lake chars are not reproductively isolated. The lake chars represent here the part of a single population which is faster growing, sexually mature, preparing for spawning, and has well-developed breeding colours. Evidence of this is the nature of the total distribution curves for chars and lake chars, curves which we created according to the materials of E.D. Vasil'evaya (see diagram 1). According to many features, the distribution deviates somewhat from the norm. However, true indicators of the excess and asymmetry are noted only in a few cases (table 5). There are no multiple-peak curves. All of this indicates, on the one hand, the nonuniform populations from Noskovoe Lake, but, on the other hand, gives no basis for judgements on the significant isolation of groupings of chars and lake chars.

5. True indicators of asymmetry and excess of some features of chars and lake chars from the waters of the Kola Peninsula

Feature	t_A	T_E	Feature	t_A	T_E
	Lake Noskovoe			Varzina River	
C	2.13	3.84	1*md*	4.69	3.34
1*md*	4.95	4.65	*r*	3.58	-
o	-3.30	-	*hm*	-	-3.33
hm	-	-5.10	H_{r3}	4.16	5.24
*l*D	4.24	6.85	*l*V	3.97	-
AV	2.50	3.42	*vt*	3.78	-
	Lake Elovoe				
lv	-	-4.38			
*h*D	-	-3.76			

The question of the existence of chars and lake chars in Lakes Enozero and Elovoe is still an open one. Fishermen, as in other places, differentiate them according to colouring. Such a division coincides to a certain extent with the condition of their gonads. They are more mature in lake chars. However, a separation into chars and lake chars in these waters creates certain difficulties.

Attempts to separate populations according to colouring did not allow the emergence of clear differences. Some differences are observed only in the frequency of occurrence of the same features in chars and lake chars.

The nature of the distribution curves of plastic and meristic features in these waters is the same as in Lake Novskovoe. The indicators of asymmetry and excess are reliable only in some cases. This gives a basis for examining all chars in each lake within a single population.

In this way, in different bodies of water of the Kola Peninsula, there is apparently a different level of differentiation of forms of chars and lake chars - from those who are isolated to a
significant degree to those who are reproductively not isolated, combined within one population 23
(diagram 2). It is probable that the realizatition of different paths of the origin of two sympatrically residing forms of chars depends on the ecological conditions in specific bodies of

water. It is possible that the state of the forage and the presence of areas suitable for spawning influence the origin of forms. In a case where a body of water does not have sufficient forage and spawning grounds are limited, the divergence of forms is severely hindered. A similar picture is observed, for example, in Lake Novskovoe where the forage is rather meagre and there is almost no specialization in foods.

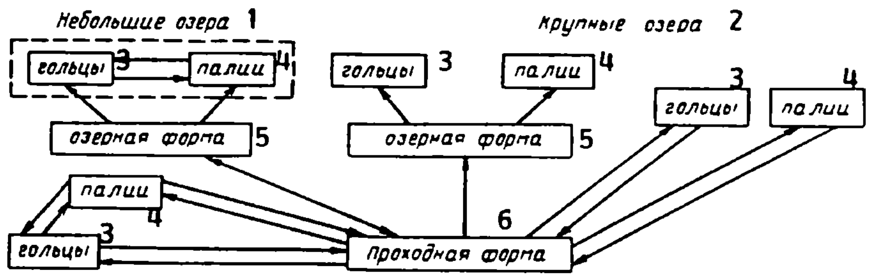

Figure 2. Diagram of the emergence of char forms in the lakes of the Kola Peninsula
1 - small lakes; 2 - large lakes; 3 - chars; 4 - lake chars; 5 - lake form; 6 - anadromous form

The origin of chars and lake chars is not clear. However, it is possible to suppose that individuals with phenotypes of chars and lake chars appeared directly in lakes, although it cannot be ruled out that there were primogenitors of these forms in ancestral populations of anadromous char. Evidence of this is the discovery of fish similar in phenotype to chars and lake chars in the anadromous char population of the Varzina River while swimming to the river to spawn. Chars swimming to the Varzina River to spawn are not uniform in colouring. In addition to silvery individuals, there are black ones with black heads, mouth cavities and backs. They constitute 19% of the females and 42% of the males. Similar colouring is observed only in fish with gonads in the second stage of maturity, of differing ages - from 6 to 12 years and a length of from 43 to 54 cm. The overwhelming majority of chars of the same age and size where such colouring is not observed have mature gonads in the third to fourth stage of maturity. It is curious that the nonuniformity of the anadromous char population is confirmed by the true asymmetry and excess indicators in some features, in particular according to proportions of the snout, mandible and head, by which chars and lake chars are differentiated.

Judging by information in the literature [36, 40, 105, 107, 108] and our data, chars and lake chars of the Kola Peninsuala should be combined within one species.

CHESHSKAYA GUBA OF THE BARENTS SEA 24

In the literature there is only fragementary information on the distribution and biology of anadromous chars of the Cheshskaya Guba. They are sometimes found in rivers of this region even in commercial quantities; moreover, they always select bodies of water with clear water. They are extremely rare in the rivers of the tundra [183]. Their systematic position is unclear. A relatively complete description of chars in the Indiga River is given in the work of V.D. Nesterov and K.A. Savvaitova [160], where a high growth rate is noted and, correspondingly, small head and eye sizes, shorter paired fins, lower height of the dorsal and anal fins and a deeper body. In this respect, chars living in this river are similar to chars from other bodies of water of the Cheshskaya Guba, Novaya Zemlya and Kara Guba [183] as well as the Varzina River.

The high growth rate of chars in the Cheshskaya Guba is likely related to the specific temperature pattern in this region. In winter, the water in the Cheshskaya Guba is subjected to long and severe cooling, and in summer it warms up to $14^{o}C$ at a depth of 15 m and up to $5^{o}C$ at a depth of 38 m. Strong seasonal temperature fluctuations, a harsh winter and comparatively warm summer gave rise to the composition of fauna in the Cheshskaya Guba, which consists mainly of heat-loving and eurytopic forms of invertebrates. Some of these forms found themselves separated from the main natural habitat and can be viewed as warm-water relics [89].

R. Behnke [267, 268] proposes that the chars of the Cheshskaya Guba are a relic grouping which deserves to be separated into an independent subspecies of the Arctic char *S. alpinus*. He bases his conclusion on the number of gill rakers in some char samples from the Cheshskaya Guba and the Kanin Peninsula, kept at the Zoological Institute of the USSR Academy of Sciences. He noted fewer rakers in these fish in comparison with chars of the European North and Siberia. E.K. Suvorov [236] and A.N. Probatov [183] also report a smaller number of gill rakers in chars from this region.

In our research, chars from the Zoological Institute's collection had from 18-21 gill rakers. E.K. Suvorov [236] indicated that, according to the number of gill rakers and extension of the maxilla beyond the posterior margin of the eye, chars of the Cheshskaya Guba approach the Pacific Dolly varden char which has few rakers. In the post ice age warming period, there was apparently a close link with the fauna of the seas of the Far East, a link which found its way right to the White Sea. In modern White Sea fauna, there are fish such as the following that have moved in from the Pacific: *Clupea harengus pallasi maris albi* herring, *Lampetra japonica*
septentrionalis lamprey, *Osmerus eperlanus dentex* smelt and *Scalibregma robusta* polychaeta 25
[25, 89]. It is therefore possible to suppose that even Pacific Dolly varden char came through to the Barents Sea. Plankton and benthos are highly endemic in the White Sea and the Cheshskaya Guba, mainly on the level of subspecies and varieties, but sometimes also on the level of clearly

isolated species [89]. In the Cheshskaya Guba, an endemic form of *Clupea harengus pallasi natio suworovi* herring has been discovered and described [25]. Consequently, it is quite acceptable to propose that the chars of this region are also truly relics and currently an endemic form. However, in our sample from the Indiga River (47 specimens), the number of rakers was higher (21-28) than in the collection's material, although on average lower than in the neighbouring char populations of Novaya Zemlya and the Kara River [85, 86, 184]. The data on the number of gill rakers are not definitive and, using the data, it is difficult to draw conclusions on the taxonomical position of chars of this region. The significance of all meristic and plastic features of chars of the Cheshskaya Guba overlaps the significance of these features in other populations; neither are substantial differences in osteology detected [36, 160].

One should also not completely exclude the possibility of the existence in this region of European (few rakers) and Siberian (many rakers) char populations, since this region is the zone where European and Siberian ichthyofauna join [25, 193].

CHAPTER 3
CHARS FROM THE WATERS OF SIBERIA
TAIMYR PENINSULA

Four endemic species of char of the genus *Salvelinus* have been described in the waters of the Taimyr Peninsula: *S. tolmachoffi* (Yessey lake char from Lake Yessey in the Khatanga River basin), *S. boganidae* (Boganida lake char from Lake Boganida in the Khatanga River basin), *S. drjagina* (Dryagin's char from Lake Melkoe in the Pyasina River basin) and *S. taimyricus* (taimyr char from Lake Taimyr) [24, 127, 129, 155]. Dryagin's char is also in Lakes Taimir, Makovskoye and Khantayskoye [126, 155, 179 et al]. More widely distributed are Boganida lake chars (lakes of the Pyasina River basin and the Gydanskiy Peninsula on Yamal) [20, 168, 196] and taimyr char. Two other forms live in the Norilo-Pyasina lakes: deepwater char and black lake char [217, 222]. In Lake Ayan lives a small dwarf char [225]. In addition, the anadromous Arctic char *S. alpinus* is distributed in the rivers of the Taimyr coast [10, 24, 155, 183].

The vast majority of char species from this region is described on little, sometimes
recorded material. L.S. Berg [24] also paid attention to the provisional state of the *S. tolmachoffi* 26
and *S. boganidae* species. The information in the literature is of a fragmentary nature.

Chars are widely distributed in the waters of Taimyr and quite numerous. They make up the majority of forms and are characterized by high plasticity. The number of forms and species of chars, the level of their isolation from one another, and the structure of separate species have not yet been sufficiently studied.

Those which have been studied in most detail are: Boganida lake char, Dryagin's char, deepwater char, black lake char and taimyr char from Norilo-Pyasina lakes and the anadromous chars from the Gulf of Minin [222]. With the exception of deepwater char and black lake char, all forms of chars from the lakes of this system are close in body length, and the deepwater char differs in small body size (table 6). The age composition of these fish is similar and the life span is long. Individuals from the deepwater chars of Lake Lama live up to 18 years.

All forms of char studied are characterized by a slow growth rate. Anadromous chars grow the most quickly; to a certain degree they are resembled by the Dryagina char and Boganida lake char, the growth rate of which is very similar. The deepwater chars lag behind the most in growth [222]. After reaching sexual maturity, they practically do not increase in length. It is possible that the energy expended on obtaining food in the conditions of ultraoligotrophic bodies of water is so great that, after maturity, all energy obtained from food is expended on reproduction and not on the linear growth of the fish.

Judging by the condition of the gonads, all forms do not spawn each year, but mature late: at the age of 7-12 years. Their fecundity is low and the reproductive ability of each form is rather low.

It is not possible for us to judge the spawning times and locations of all forms. However, based on our data, it is possible to indicate that, in sympatric distribution in Lake Lama, the spawning locations and times of the Dryagina char, the black lake char and the deepwater char are probably not the same. The Dryagina char reproduces in rivers flowing into the lake in late autumn and winter and, possibly, in early spring. The black lake char spawns in rivers in July-August and the deepwater char spawns in the lake itself, in a heap, from August through the first half of September. There is nothing known about how the Dryagina char and the black lake char lay eggs; it is possible that they build nests. The deepwater char apparently does not build nests, but lays eggs on the ground.

The reproductive features of the Boganida lake char remains an open question. We did not manage to catch fish with mature sexual products. Even the very large specimens had gonads at the second stage of development. Individuals with sexual products at this stage of maturity were caught in different seasons and in different bodies of water: in Lakes Keta and Glubokoe in July, 28
in Lake Lama in August and the beginning of September. All adult Boganida lake char were caught in lakes and only a few young specimens with a length of 12-15 cm were caught in the Bunisyak River, which flows into Lake Lama, 5 km from the mouth. All this time, the movement of Dryagina char to spawn was observed. Not one Boganida lake char was found among the char situated above the nests.

6. Biological characteristics of chars from the waters of the Taimyr Peninsula

	Lake Lama				Lake Keta	Minin Gulf
Feature	Boganida lake char	Dryagina char	deepwater char	black lake char	taimyr char	anadromous char
Body length (cm)	24-70	24-79	24-45	36-57	47-77	22-86
Weight (gm)	300-2700	400-5000	100-300	400-1800	900-4800	300-6500
Maximum age (years)	16	16	18	12	11	16
Time to mature (years)	-	12-17	10	-	-	-
Spawning season	-	autumn, winter, possibly spring	end of August - first half of September	July-August	autumn	-
Spawning frequency	-	not annually	annually	-	-	-
Fecundity (quantity)	-	2255-9078	-	1806-2016	-	-
Food	euryphage, predominantly fish	euryphage, predominantly fish	benthophage	euryphage	-	euryphage
Growth rate	fast	fast	very slow	-	-	fast

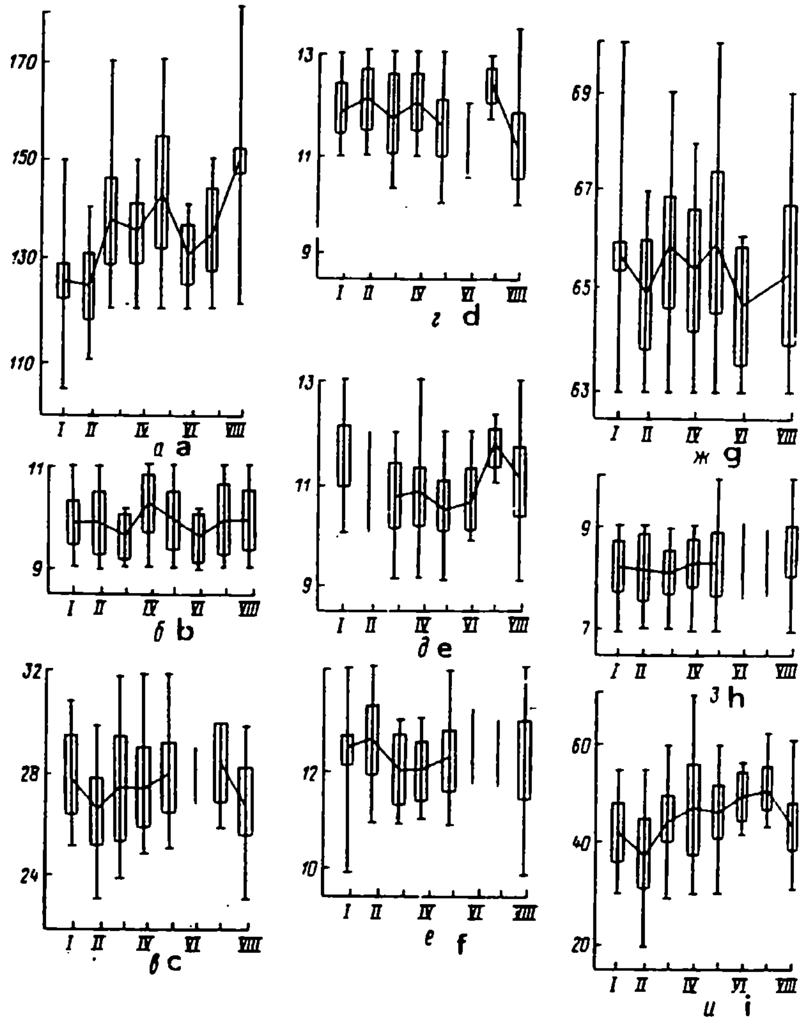

Figure 3. Meristic features (counted values) of chars inhabiting the bodies of water of the Taimyr Peninsula: 29

a - scales on the lateral line; b - rays on the dorsal fin; c - gill rakers; d - branchiostegals on the right;
e - branchiostegals on the left; f - rays on the thoracic fin; g - vertebrae; h - rays on the anal fin; i - pyloric caeca;
I - deepwater char of Lake Lama; II - deepwater char of Lake Kapchuk; III - Boganida lake char of Lake Lama;
IV - Boganida lake char of Lake Keta; V - Dryagina char of Lake Lama; VI - black lake char of Lake Lama;
VII - taimyr char of Lake Keta; VIII - anadromous char of the Gulf of Minin

The studied forms chars in the Taimyr Peninsula differ in meristic features in a number of cases (diagram 3). However, these differences are usually small and we found them in one case only: deepwater char differs noticeably from the anadromous char in the number of scales on the lateral line.

According to plastic features, large differences are revealed in a number of features in comparing deepwater char with all forms. Substantial differences in the eye diameter of the black lake char and the anadromous char have also been established. Between the remaining forms, the differences in some features are reliable, but insignificant [222].

The anadromous char is characterized by a relatively small head, snout, eye, jaws, distance beyond the eye, body height, height of the anal and dorsal fins, length of the dorsal, thoracic and abdominal fins and a wider space between the eyes. The deepwater char, in contrast, has a longer head and jaws; large eye diameter; greater height of the anal and dorsal fins, base length of the dorsal fin, length of the thoracic and abdominal fins, and a lesser postdorsal distance. The Dryagina char and Boganida lake char are similar to one another in head and snout length, eye diameter, distance between the eyes, distance beyond the eyes, jaw length, postdorsal distance and, in most cases, they occupy an intermediary position [222].

The observed differences in plastic features are apparently determined by the nonuniform growth rate of forms of char. Slow-growing chars, as with other species of fish, have a longer head, eye diameter, long thoracic and abdominal fins and a high dorsal fin. In more rapidly growing fish, the head and fins are shorter and the eyes smaller. The location of the dorsal fin is also determined by the growth rate: in slow-growing fish the dorsal fin is set farther back.

Deepwater char are noticeably different in colouring, body shape and head shape, whereas the other forms are similar (diagram 4).

Thus, an analysis of meristic and plastic features, as well as of ecological features and colouring, do not allow us to indicate species separation in the forms we are examining.
E.D. Vasil'eva [36, 39], K.A. Savvaitova et al [217] came to a similar conclusion based on a study 30
of osteological features. All lake chars from Norilo-Pyasina lakes differ in skull morphology from anadromous char from the Gulf of Minin. The closest to it is Dryagina char and Boganida lake char from Lake Keta. It is possible to treat as evidence of the isolation of lake chars the nature of detected osteological differences in the features by which all lake forms differ from anadromous char (greater significance of the supraethmoideum width and praemaxillare height and less distance to the articulare notch). It is also possible that they are explained by the features of a given local school of anadromous chars belonging to the basin of another river [39]. In comparing the ostelogical features of freshwater forms, the smallest differences are found between Boganida lake char and Dryagina char. Taimyr lake char differs to a greater degree from Boganida lake char and to a lesser degree from Dryagina char. It should be emphasized that one is able to note small differences only in the case where forms from different lakes are compared. Forms do not differ in sympatric distribution. In this respect, they cannot be viewed as different species on the basis of osteological data. To a significant degree, deepwater char differs from all forms; two groupings of deepwater char differentiated by skull structure were found in Lake Kapchuk [217]. One group is

made up of individuals with a normal skull structure and the other of individuals, so-called "pugs", with accelerated chondocranium. It is interesting that, in the case of coexistence of all forms of chars, the ostelogical differences turn out to be greater than in the case of allopatry [36, 39].

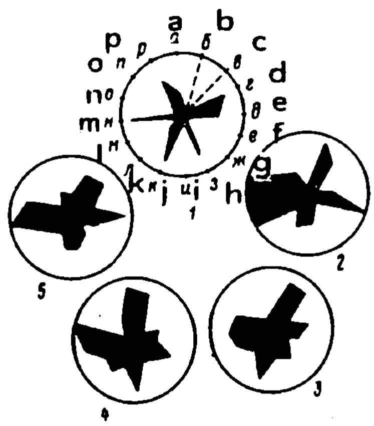

Figure 4. Frequency of occurrence of various elements of colouring, shape of body, head and caudal fin in different forms of chars inhabiting the waters of the Taimyr Peninsula, %:
1 - deepwater char; 2 - Dryagina char; 3 - Boganida lake char; 4 - Taimyr char; 5 - anadromous char; a - rounded head; b - large head; c - maxilla extends far beyond the posterior margin of the eye; d - straight maxillare; e - wide maxillare; f - maxilla overhangs mandible; g - hook on lower jaw and notch on maxilla present; h - deep body; i - long caudal peduncle; j - wide caudal peduncle; k - numerous spots above lateral line; l - grey fins; m - grey lips; n - white belly; o - marble-like back; p - notched caudal fin

Deepwater chars living in different regions are similar in colouring, food and growth; 31
however, they differ in some meristic features, and in the form and proportions of the head [6, 24, 102, 217, 267, 268, 285]. It is curious that here they bear more similarity to sympatric forms of non-deepwater chars than to allopatric deepwater populations.

The systematic position of deepwater chars is debatable. Thus, P. Schillinger [24, 267, 285], being the first to describe deepwater chars from alpine lakes, considered that this char was most likely an ecotype of a sympatric "normal" char from the Bodensee. Therefore, he named it a variety of the main form *Sālmo salvelinus profundus var.* Currently, chars from these lakes are attributed to the species *Salvelinus alpinus*. L.S. Berg [24] separated the deepwater char into an independent species *Salvelinus profundus (Schillinger)*. R. Behnke also tends toward species isolation of this form [267, 268]. Nevertheless, the question remains open concerning the taxonomic rank of deepwater chars from the Bodensee and a number of other alpine lakes. Researchers refrain from assigning species status to this group. Some of them suggest that the observed differences between the "normal" form of char and the deepwater form emerge comparatively easily; in addition, intermediate forms are found in the lake. "Normal" and deepwater chars occupy different niches in a body of water; their differences are the result of adaptation to different living conditions [285]. Char from Lake Shchuch'e in the Polyarnyi Urals are also viewed as part of the species *S. alpinus* [6], but the Labynkyr deepwater char is attributed to a separate subspecies of *S. alpinus* by F.N. Kirillov [102].

There is no doubt that a few forms of char exist in the waters of Taimyr (figure 5) and apparently not one of the forms now living is ancestral. Most likely the lakes of Taimyr were once populated by anadromous char, from which, in the specific conditions of the lakes of the peninsula, arose a magnificent bouquet of forms that became acclimatized to different ecological niches. Modern populations of chars probably have a secondary origin and are semi-anadromous. V.S. Mikhin's data [155] and the results of our research are evidence of the non-uniformity of anadromous chars. They are characterized by a large variety of phenotypes. Among them are noted individuals that recall the Dryagina char, the Boganida lake char, the taimyr char (the curved jaw characteristic of this char was found in two specimens) and even the deepwater char. Moreover, this is apparently first and foremost the result of differences in individual growth rate. Reliable indicators of asymmetry were obtained for features closely related to growth (the greatest body height was $t_A = -3.65$). Also supporting this is V.S. Mikhin's [155] indication of the 32
existence in the anadromous char population of large-headed and small-headed individuals differing in time of entry into the river for spawning and, possibly, representing a spring and winter race. Different proposals may be made with respect to the origin of fast- and slow-growing chars. Slow-growing chars are derivatives of lake populations of different forms, a segment of which regularly swims out to sea for feeding. There is such evidence for the Dryagina char of Lake Taimyr [155]. Fast-growing chars are formed at the expense of their own anadromous chars It is also possible that the division into fast- and slow-growing chars occurs within one population due to extended periods of movement, spawning, downward movement and feeding. Undoubtedly, deepwater char is separated from the other forms to a great degree. Formally it serves as a separation into an individual taxon; however, it is not known whether the changes are reversible. It is noteworthy that, although rarely, relatively large fish are found among deepwater chars (up to 45 cm and a weight of 800 g). It is possible that some of the individuals in the population become predatōrs at some point and begin to grow and mature at different intervals than the majority of deepwater chars. In other words, it is highly likely that the situation described by R. Skreslet [386] for the char from the lakes of Jan Mayen exists. In this case, the isolation barrier between forms will not be so great. The Dryagina char and the Boganida lake char, or the brown trout are closest to one another. Difficulties arose in a number of cases in separating these phenones according to individuals with gonads in stage II of maturity. It is possible that some of the differences obtained reflect features of samples. The absence in the catches of different seasons of sexually mature Boganida lake chars also alerts us. By the way, according to 33
fishermen's statements, they do not know of brown trout with mature gonads. It is possible that

the Dryagina char and the Boganida lake char are two phenones of one and the same form, in a sexually mature and a sexually immature condition. Usually among sexually immature fish the brown trout predominates heavily in numbers; at the same time, the sexually mature fish that we caught always turned out to be Dryagina chars. L.S. Berg [24] wrote that the local name for Dryagina char was brown trout. However, the local residents actually refer to fish with a phenotype similar to Boganida lake char as brown trout. L.S. Berg [24] classified the *S. boganidae var.* that was described by F.I. Belykh [20] as a synonym of Dryagina char.

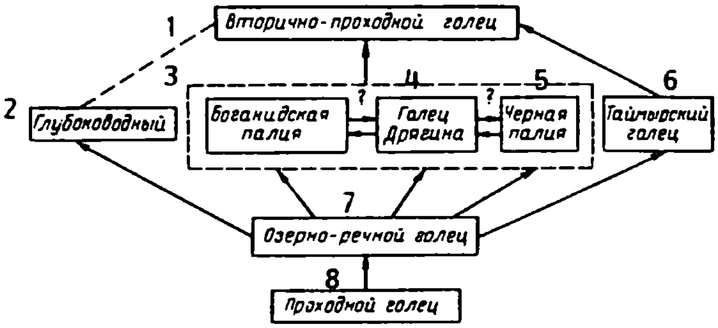

Figure 5. Diagram of emergence of char forms inhabiting the waters of the Taimyr Peninsula.
1 - secondary-anadromous char; 2 - deepwater; 3 - Boganida lake char; 4 - Dryagina char; 5 - black lake char; 6 - taimyr char; 7 - lake-river char; 8 - anadromous char

The results of a multi-test analysis also do not confirm a clear morphological separation of Dryagina and Boganida lake char. These fish form an unbroken series of phenotypes, the extreme variants of which differ significantly [154]. According to DNA molecular hybridization data, the Boganida lake char and the Dryagina char behave similarly with respect to the bench mark *S. malma* [342] and *S. alpinus s. str.* [56]. The deepwater char differs to a great degree. The black river char is very close to the Dryagina char. Apparently this is its melanistic form.

Our material does not permit a judgement concerning the level of separation of the taimyr char. But it is interesting to note that A.V. Podlesnyi and A.A. Lobovikova [179] classified this char among the Dryagina char and they considered the Dryagina char a taimyr char. Disagreements among different authors in defining these forms may be caused by their great similarity.

Forms analogous to chars living in Lake Lama are also known in other Taimyr bodies of water. In different lakes they usually occur independently. The following may serve as an example: the populations of deepwater char from Lake Kapchuk, the populations of Boganida lake char or Dryagina char from Lakes Kapchuk, Glubokoe and Keta which are similar to the chars from Lake Lama, but not identical to them. We do not have at our disposal material on the

Yessey lake char *S. tolmachoffi*. In describing it, L.S. Berg [24] speaks of a small head and a short maxilla which does not extend beyond the posterior margin of the eye. However, in the diagram that he presents, the head is rather large and the maxillary bone extends far beyond the margin of the eye.

It is likely that the following are at the basis of the processes of the emergence of forms in Taimyr chars: extended spawning [225], nonuniform growth rate and different times of sexual maturity. The divergence in type of food by viture of the short vegetation period is revealed here to a lesser degree. All chars are omnivorous; however, the role of fish in the food of large forms is very great, while at the same time, as the only exception, deepwater chars apparently do not eat fish.

The processes of the emergence of forms apparently take place quickly. The large 34
variability allows chars to fill different ecological niches, to form groupings differing in ecology and morphology which can exist in one body of water, almost not mixing until the conditions of their existence are disrupted. The age of Taimyr lakes is young (about 10-20 thousand years) [121]. There has always been and there is still observed now some form or other of connection between the bodies of water. The hydrological network was reconstructed more than once: during the pleistocene-holocene, the lakes migrated actively; the transgression and regression of the sea are noted [121, 126, 172, 173, 174]. It is likely that in such conditions the char groupings were either isolated from one another or in contact with one another. All of this did not likely bring about the completion of irreversible processes of speciation. In other groups of fish living in the bodies of water, endemic species are not known.

BODIES OF WATER IN THE MOUNTAINOUS REGION TO THE EAST OF LAKE BAIKAL

Small forms of chars from Lakes Leprindokan, Davatchan and Gol'tsovoe differ from large forms in their small body size, small mass, shorter life span, period of sexual maturity, low fecundity, annual autumn spawning, the predominance of plankton in the diet and a slow growth rate (figure 6) [221]. Upon reaching sexual maturity, they almost do not grow at all in length and all energy derived from food is apparently used for gonad maturation. However, there are no populations of this form completely identical in features of biology. Each has features particular only to it (table 7).

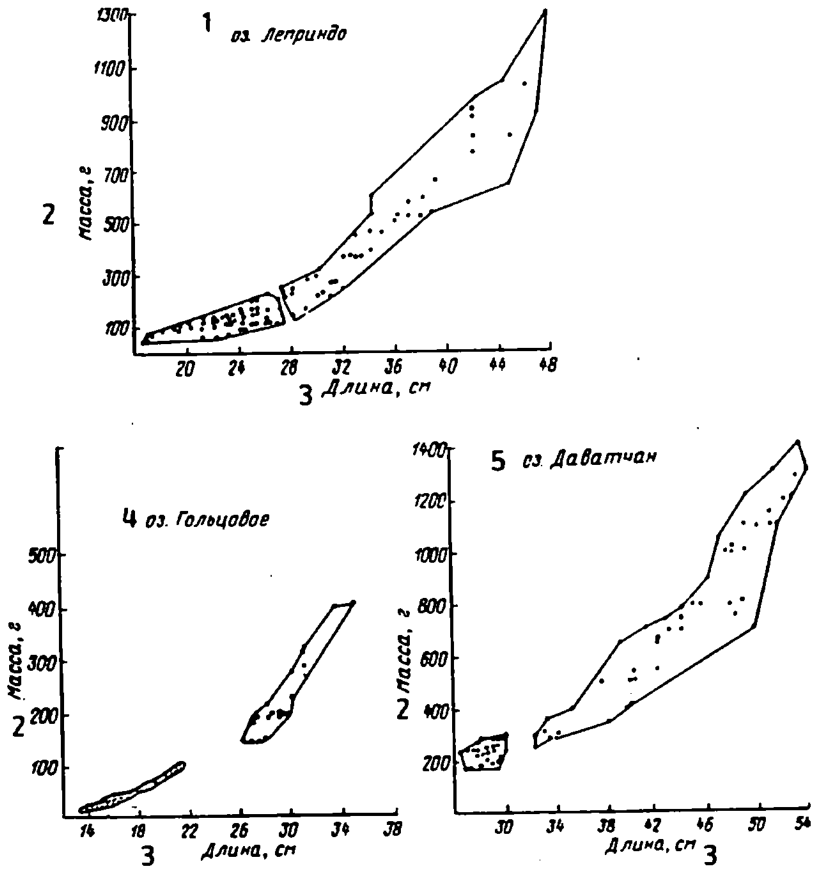

Figure 6. Relationship of length and weight in chars inhabiting the lakes of the Zabaikal'e region.
1 - Lake Leprindo; 2 - weight (gm); 3 - length (cm); 4 - Lake Gol'tsovoe; 5 - Lake Davatchan.

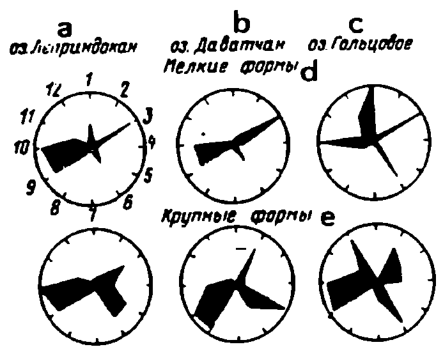

Figure 7. Frequency of occurrence of some features in chars inhabiting the lakes of the Zabaikal'e region, %:
1 - head rounded or conical; 2 - maxillary bone extends or does not extend beyond the eye; 3 - maxillary bone straight or curved;
4 - hook and notch present or not; 5 - caudal fin truncated or notched; 6 - many or few spots; 7 - spots white or brightly coloured;
8 - fins grey or brightly coloured; 9 - sides of the body silvery or olive; 10 - lips grey or brightly coloured; 11 - belly white or brightly coloured; 12 - marble-like stripe pattern on the back or absent.
a - Lake Leprindakan; b - Lake Davatchan;
c - Lake Gol'tsovoe; d - small forms; e - large forms

Individuals of small form populations from different lakes have some similarity in phenotype between them. They have a short and straight maxillary bone; there is no hook or notch on the jaws; shallow body, bright fins and belly, grey lips. However, they differ from one another as follows: in the shape of the head, the location of the jaws, the shape of the caudal fin, the colouring of the sides of the body, the number of spots and the design on the back (figure 7). The dwarf population from Lake Gol'tsovoe is particularly distinctive ; it is an uncoloured form and has features characteristic of young fish (fry spots, a large rounded head, strongly-notched caudal fin).

In a number of cases, these populations differ in meristic features (figure 8), but the differences are small.

The large form populations from different lakes also differ from small forms in their
greater life span, late maturity, fecundity, non-annual spawning, nature of diet and faster growth
rate [221]. At the same time, individuals from different populations differ significantly from one 36
another (see table 7). Thus, large chars from different lakes differ in phenotype; moreover, these
differences are manifested to a greater degree than in small form populations and each population
has combinations of features characteristic for it alone.

According to the majority of meristic features, populations of large chars do not differ substantially. Only in one case does the coefficient CD exceed 1.28. Chars from Lake M. Leprindo have larger branchiostegals on the right than chars from Lake Leprindokan (see figure 8).

With the exception of differences in the number of gills on the lateral line and pyloric
caeca both in small and large chars, significant differences have not been established in meristic
features between populations of small and large chars in one lake or between small and large 38
forms from different lakes, although the differences may be true.

Differences in plastic features and in colouring of char populations are apparently connected with the growth rate and features of sexual maturity (figures 9 and 10). It should be noted that the most obvious is the connection manifested in populations from Lake Gol'tsovoe. In accordance with known patterns in slow-growing dwarf individuals in comparison with large ones, they are longer, have a deeper head, greater eye diameter, greater mandible length, longer paired and unpaired fins, and smaller postdorsal and anteanal distances [221].

7. Biological characteristics of small and large forms of chars living in the lakes of the mountainous region to the east of Lake Baikal (Zabaikal'e region)

Feature	Lake Leprindokan	Lake Davatchan	Lake Gol'tsovoe	Lake Maloe Leprindo	Lake Frolikha
Body length (cm)	24.6 / 36.0	28.5 / 44.0	15.6 / 27.3	- / 47	24-38
Weight (gm)	134 / 750	255 / 800	48 / 300	- / 1750	250-500
Maximum age (years)	10 / 13	13 / 17	12 / 12	- / 14	11
Time to mature (years)	4-5 / 7	8 / 13-15	7 / 8	- / 9	6-7
Spawning season	autumn / autumn	autumn and spring / autumn and spring	autumn / autumn	- / autumn	autumn
Spawning frequency	annually in 85% / not annually	annually in 75% / not annually	annually in 92% / not annually	- / ?	- / ?
Fecundity (quantity)	- / -	170 / -	58 / 600	- / 2935	- / 536
Ratio of the sexes (males : females)	1 : 1 / 1 : 1	3 : 1 / 1 : 1	2 : 1 / 1 : 4	- / 2 : 1	1 : 1
Food	plankotophage / predator	plankotophage / predator	plankotophage / benthophage, predator	- / predator	plankotophage / benthophage, predator

Note: the numerator is the small form of chars; the denominator is the large form.

As regards the small and large chars from Lakes Davatchan and Leprindokan, here the nature of allometry is often the opposite. Small chars from these lakes are larger than dwarf ones from Lake Gol'tsovoe and are characterized by a faster growth rate, while the growth of the large ones is severely retarded.

A study of morphological features of sympatric char groupings of the lakes of the Kuando-Charsk watershed by means of multi-test statistical methods, conducted by S.Sh. Bagiryan-Mikhailova [16], also indicated that large and small forms from Lake Gol'tsovoe differ sharply in body proportions from the chars of other lakes which are rather similar among themselves. The chars of Lake Davatchan occupy an intermediary position. The differences between populations are weak according to the aggregate of meristic features.

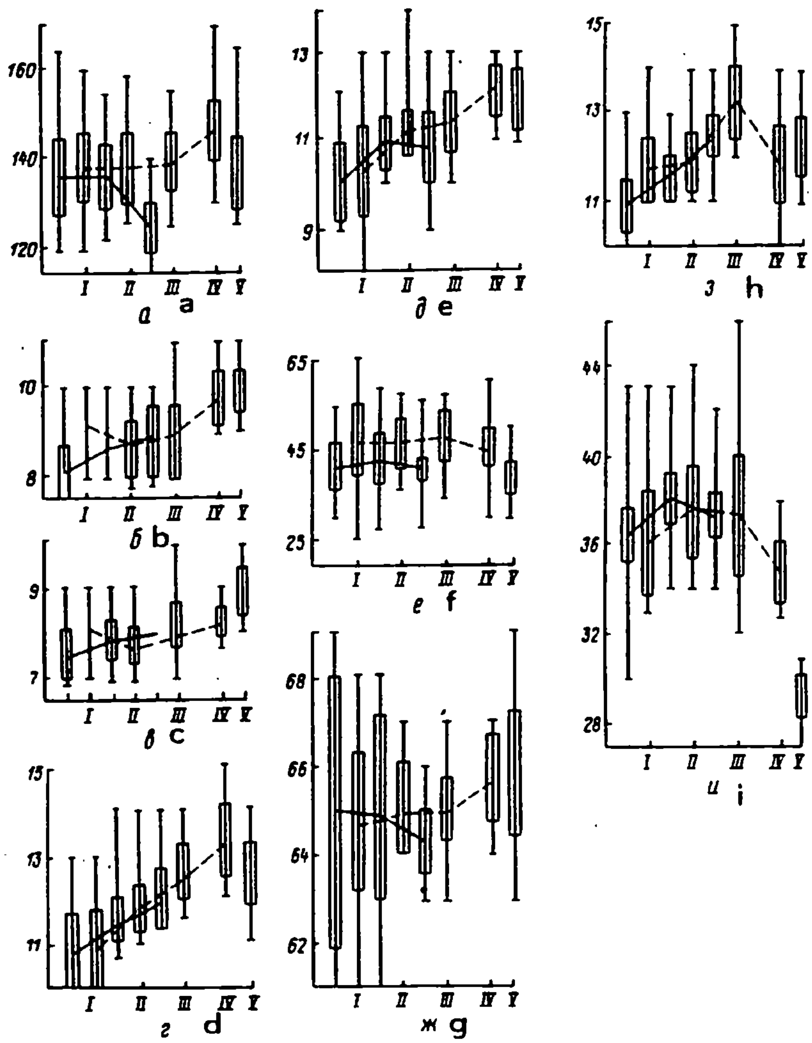

Figure 8. Meristic features (numerical values) of small and large forms of chars inhabiting the lakes of the Zabaikal'e region:
a - scales on the lateral line; b - rays on the dorsal fin; c - rays on the anal fin; d - branchiostegals on the right; e - branchiostegals on the left; f - pyloric caeca; g - vertebrae; h - rays on the thoracic fin; i - gill rakers; I - Lake Leprindokan; II - Lake Davatchan; III - Lake Gol'tsovoe; IV - Lake Maloe Leprindo; V - Frolikha. The solid line indicates the large form of chars and the dotted line indicates the small form.

It is known that fish are capable of forming sympatric ecological groupings, differing in rate of growth, periods of sexual maturity, nutritional state, colouring, sexual relations and type of food.

B.M. Mednikov [143] suggests a system of breakdown of the original uniform population into coexisting ecological forms where extended spawning leads to a situation where the developing eggs fall into nonuniform conditions and this brings about unequal growth. Even after the onset of sexual maturity, dwarfish fish retain the juvenile type of diet and others become capable of eating larger animals, including the young of their own species. In many populations, females grow more quickly, mature later than the males and replenish the composition of the large form. If spawning of the large and small form occurs at different times, seasonal races emerge that strengthen the changes that have taken place in the population. This entire process has an adaptive nature and allows the fuller use of the forage of the species as a whole. A similar process of divergence on ecological forms is observed only in fish that are omnivorous and optional predators. This system is suitable to explain the processes of the emergence of the char forms we 40
are studying in the Zabaikal'e region.

Is is likely that in connection with the presence of a planktophage niche in the lakes of the Kuando-Charsk watershed one observes a clearly expressed differentiation of chars into two forms differing in food composition. The existence of large and small chars, as with other species of fish, is apparently related to a change in qualitative food composition. In the process of ontogenesis, qualitative food composition changes and the absolute and relative sizes of food organisms increase. If the fish, due to size, cannot shift to larger and aggregate foods, their growth is slowed. In those cases where a shift to larger organisms is possible, the rate of growth does not decrease and maturity occurs at a greater age and sizes [143].

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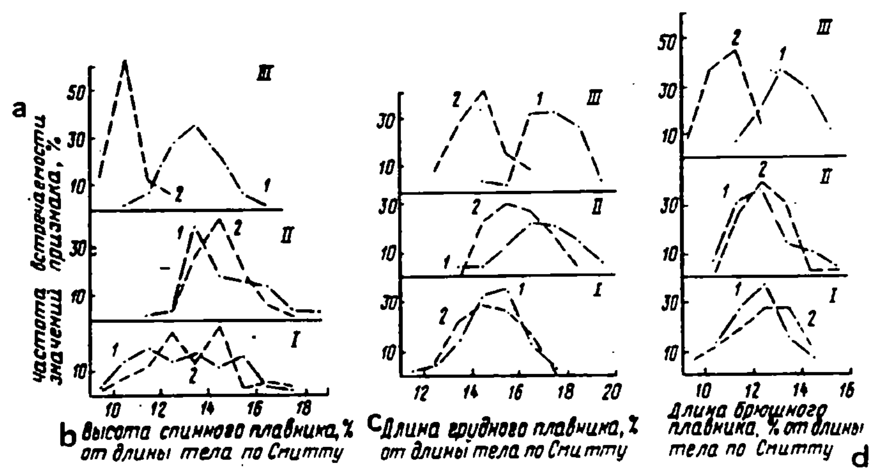

Figure 9. The distribution of features of sympatric groupings of chars inhabiting the lakes of the Zabaikal'e region:
I - Lake Leprindokan; II - Lake Davatchan; III - Lake Gol'tsovoe; 1 - small form; 2 - large form; a - frequency of occurrence of feature values, %; b - depth of dorsal fin, % of body length (Smitt); c - length of thoracic fin, % of body length (Smitt); d - length of abdominal fin, % of body length (Smitt).

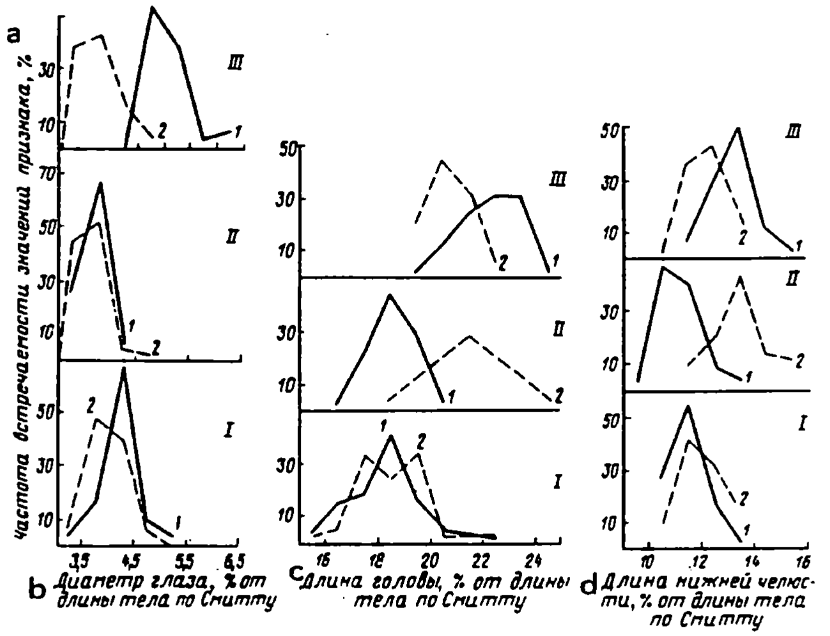

Figure 10. The distribution of features of sympatric groupings of chars inhabiting the lakes of the Zabaikal'e region:
I - Lake Leprindokan; II - Lake Davatchan; III - Lake Gol'tsovoe; 1 - small form; 2 - large form; a - frequency of occurrence of feature values, %; b - eye diameter, % of body length (Smitt); c - head length, % of body length (Smitt); d - mandible length, % of body length (Smitt).

It is apparent that the differences in periods of sexual maturity and life span, form and body proportions, colouring, etc. of different forms and populations of Kuando-Charsk chars are associated with a nonuniform growth rate and type of diet.

Between the large and small forms in the lakes studied, there is apparently a different level of isolation. On the basis of the relationship of the sexes and the spawning periods, it is possible to suppose that in Lake Leprindokan the populations of large and small forms are rather isolated. In Lake Davatchan the isolation is less clear and the spawning of both forms is extended from spring to late autumn and the males dominate among small form fish. It is possible that they take part in the spawning of large fish. There is apparently no isolation in Lake Gol'tsovoe since the spawning times and locations of fish of different forms coincide and among the large fish the females strongly predominate, whereas among the small fish, the males predominate. In the Lakes of Bol'shoe and Maloe Leprindo there is a very large predatory form that is apparently formed in the ontogenesis of one generation.

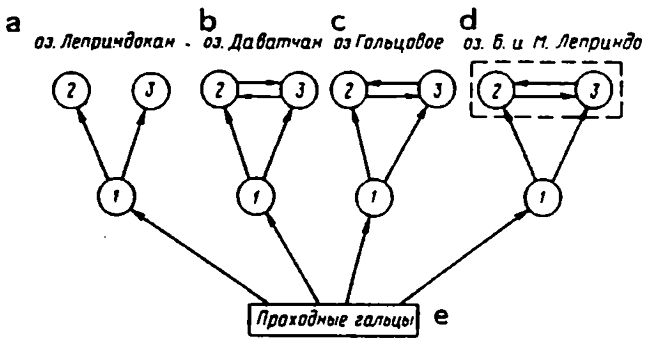

Figure 11. Diagram of possible routes of the emergence of forms of chars inhabiting the lakes of the Zabaikal'e region:
1 - lake char; 2 - large form; 3 - small form; a - Lake Leprindokan; b - Lake Davatchan; c - Lake Gol'tsovoe; d - Lakes Bol'shoe and Maloe Leprindo; e - anadromous chars

A different level of divergence of sympatric groupings is possibly the result of the influence of different conditions in lakes. Although the small and large forms in each lake occupy their preferred niche, the level of this preference is not identical. The small and large chars of Lake Gol'tsovoe differ the least in diet. This lake is very poor in forage. In Lake Davatchan, the possibility of having a separate diet amongs chars is greater; in Lake Leprindokan, with a well-expressed shallow-water segment, a wealth of water vegetation and sandstone-silt bottom [186, 241], these possibilities are more fully realized and, possibly, lead to an even greater divergence in forms.

Thus, it is possible to suppose that in the lakes of the Kuando-Charsk watershed there are different levels of the emergence of forms observed in chars: from groupings arising in the ontogenesis of one generation and sympatric groupings, complementing one another and 41
reproducing jointly, to reproductively isolated, self-reproducing groupings (figure 11). It is difficult to say what the level of divergence is for groupings of large and small chars. It is known that body sizes, length of growth period and growth rate have an evolutionary significance and establish themselves in the process of evolution of the group [152].

It is likely that the existence of char groupings differing in growth rate increase the assortment of crossing, restricts panmixia and also encourages an even greater divergence in forms in existing conditions. However, the very fact of reproductive isolation of groupings, even when the fact is established, still does not evidence the irreversibility of changes. As concerns assortative crossing, as M.V. Mina [150] and B.M. Mednikov [144] correctly indicate, it is more widespread than panmixia. Moreover, apparently the non-accidental crossing betwen individuals is characteristic of a normally exisiting population and does not necessarily have to lead to irreversible processes of speciation. It is more likely that this is an essential precondition for the latter, which is rarely realized.

Similar examples of ecological emergence of forms in chars occur in the alpine lakes of Europe [272, 285, 370, 374, 379, 380]. In the alpine and high-alpine lakes of the region, large and small forms of chars which differ in growth rate live everywhere. These chars are found separately or sympatrically. Four forms are isolated: small, dwarfish; normal, average-growing; large, fast-growing and predatorial; deepwater [264, 275, 285, 370, 378, 379, 380]. In the opinion of researchers, these forms originate from anadromous Arctic char *S. alpinus* and are relics of the ice 42
age. The division between them in many bodies of water is arbitrary and they can move from one form to another [370, 380]; this is directly confirmed by experiments on the migration of chars and, accordingly, their transformation into dwarfish or fast-growing forms under new conditions [370].

R. Buresh [275] and E. Reisinger [370] studied chars from 12 alpine lakes situated at an altitude of 465-1762 m above sea level and 18 high-alpine lakes situated at an altitude of 1763-2990 m above sea level. In all of these lakes, they found chars differing first and foremost in size and weight. R. Buresh considered that the existence of fast- and slow-growing forms was caused by reasons of heredity, but E. Reisinger, O. Steinbock [393], N. Schulz [380] et al suggest that the nature of growth is first and foremost determined by such external interrelated conditions as the existence of appropriate forage, the duration of ice cover, altitude and volume of water mass. They also suggest that the level of manufactured hormones [370, 393] influences the occurrence of fast- and slow-growing forms as well. Thus, hyperfunction of the thymus leads to late maturity and slow growth.

Between the chars of the lakes of the Zabaikal'e region and the alpine lakes of Europe, a similarity is observed not only in the nature of emergence of forms, but in phenotypes [275, 285, 370, 379, 380]. However, there are no completely identical forms. And in this we see the manifestation of parallel variability [33], i.e., in different areas of the natural habitat, in similar conditions, char phenotypes are formed which are similar in separate features, but not identical. The nature of the variability of many features is similar in the first place; this is attributed to the colouring of the belly, lips, fins, spots, shape of the body and head, length of the maxillary bone, etc. In this respect, there is no basis to consider the studied forms and populations of chars living in the lakes of the Zabaikal'e region as individual taxa. In spite of some morphoecological differences between them, they are taxonomically unified. However, under the influence of specific conditions of existence of these chars, they differed noticeably from chars from other regions. Thus, in the bodies of water studied, lives a char with a large number of gill rakers (up to 46) previously unknown for the genus *Salvelinus*. There is no doubt that this is connected to the increased development of plankton in the alpine bodies of water of the Zabaikal'e region. Thanks to winters with little snow and strong winds blowing the snow, the ice cover on these lakes is sometimes clear and extreme isolation permits the development of plankton even in the

ice-covered period [186, 221, 241]. In connection with the poor forage, the chars are fairly omnivorous and the size of the food items varies from small plankton organisms to large fish. Selection is done on expansion of the niche and assimilation of plankton in deep lakes. Therefore, 43
it is likely that the role of plankton in the food of large and small forms of chars in different periods of ontogenesis is very great here.

All chars discovered in the Zabaikal'e region were attributed to the subspecies *S. a. erythrinus* [96, 185, 186, 241]. However, the chars of the Kuando-Charsk lakes differ noticeably from the typical davatchan from Lake Frolikha (see table 7) [159, 216]. Bearing this in mind, it is not likely possible to attribute the chars of the Kuando-Charsk lakes to subspecies *S. a. erythrinus*. The chars we studied also differ, although to a lesser degree, from the chars from Lakes Oron, Namarakit and Bezymyanoe at the source of the Davatchanda River (Vitim River basin) [96].

As indicated by L.S. Berg [25], M.M. Kozhov [104] and N.M. Pronin [186], the Zabaikal'e region chars likely have a common ancestor, anadromous Arctic char, and are relics of the ice age, but differences between the populations of different lakes apparently arose due to living conditions.

The char could penetrate the lakes of the Baikal mountainous region through the basin of the Lena River, through Yenisei and Angara or through the basin of the Amur River. There is indisputable proof of the fact that, at the end of the pliocene - beginning of the pleistocene, Lake Baikal was hydrographically connected with the basin of the Lena River. Waters from the Baikal during this period flowed in the direction of the Lena River through rivers connecting Baikal with other large lakes occupying tectonic depressions of the Baikal system (Bagruzin, Tsipinskaya, Muisko-Charsk, etc.). Remains of Baikal type fauna were are found in large running lakes of the Vitim basin [104, 126, 238, 241]. Some Baikal *Cottogobius Koumans* are found throughout the Lena and are infected with the parasite *Salmincola*, which is characteristic of endemic Baikal gobies. The ancestors of modern chars of the Zabaikal'e region, among other inhabitants of the tertiary non-tropical part of the Northern Hemisphere, populated these bodies of water during the pliocene and post-pliocene periods of the climate cold spell of Siberia and during the retreat of fauna from the northern regions to the south [104]. These data agree with the reasoning of G.U. Lindberg [126] concerning the support of the waters of the Lena River by waters of a 180-meter transgression of the sea, the formation of a vast body of fresh water in the Vitimo-Aldan depression and the connection of Lake Baikal with the ocean through the Tsipo-Tsipikan lakes in the late pliocene - quaternary period.

The second possible route of char penetration into the Baikal basin could be the artery of the Yenisei-Angara. This artery originated in the Quaternary period when the waters of the Baikal broke through the depression at the location of the modern valley of the Angara River and flowed

to the Yenisei [104]. And now these rivers are a distribution route of some elements of Baikal fauna to the north, right to the polar coastline. In their turn, during the period of maximum transgression of the sea and onset of the glaciers, some northern elements were able to actively 44
penetrate Lake Baikal and other lakes of the Baikal mountainous region. Among these elements are seals, Arctic cisco, and possibly whitefishes and char [25, 104].

It is possible to assume even a third path of char penetration into the Baikal basin - through the Amur. D.N. Taliev [238] suggests that the ancestors of Baikal Cottidae stemming from coldwater gobies of the northern part of the Pacific Ocean reached Lake Baikal apparently through the Amur basin. In the past, there were links between Lake Baikal and the Amur River and between the Amur and Lena Rivers. This is evidenced by the presence of some representatives of Amur fauna in the basin of Lake Baikal and the Lena River (for example, Lagowski's minnow) and of Baikal fauna in the Amur River basin (the Baikal multi-bristled worm *Lycodrilus* and the crustaceon *copepoda Epishura*), as well as by the genetic similarity of upper Amur and black Baikal graylings [226]. In the tertiary and quaternary periods in the area of the depression of the Baikal system and in the upper reaches of the Paleolena and the Paleoamur, the lake-river systems played a very substantial role in migrations of individual elements of fauna and entire complexes of fauna [238]. Therefore, it is possible to suppose that among them ancestors of modern Kuando-Charsk chars could enter by this route.

THE LENA RIVER DELTA

In most bodies of water of the Lena River delta, chars of the *S. alpinus* species are found [24, 149, 220]. In Lake Aranastakh in the region of the Neelov Gulf, P.G. Borisov [28] provisionally described the endemic species *S. jacuticus*.

F.N. Kirillov [102] considers that the Dryagina char is in the lakes of the delta. Directly in the Lena River delta itself were found repeatedly anadromous *S. alpinus* [24]. Chars from thermokarst lakes - Lakes Dal'nee and Perekhodnoe - and from the alpine lake, Lake Forelevoe, were studied by K.A. Savvaitova and V.A. Maksimov [220]. Two sympatric groupings differing in growth rate were discovered in the latter lake (figure 12).

The small form of chars in comparison with the large form is characterized by small body size and low weight, a shorter life cycle, earlier sexual maturity, unequal ratio of the sexes and slow growth rate. Spawning in the majority of individuals occurs slightly earlier. The majority of fish of this form apparently reproduce annually (table 8). 45

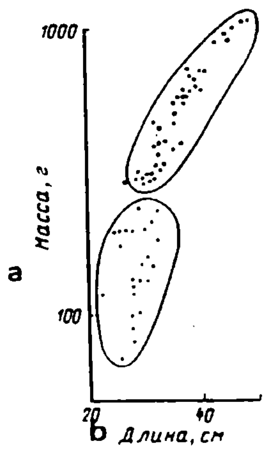

Figure 12. Relationship of body length and weight in chars from Lake Forelovoe
a - weight (gm); b - length (cm)

In contrast to large chars, the head of small chars is more often rounded in shape; the maxillary bone is straight and the maxillary bone overhangs the mandible. There are the lateral fry stripes on the body. A marble-type design is often found on the back; the lips are grey and the belly white. Differences in colouring are probably related to the differences in growth rate and rate of maturity [220].

The distribution of a number of exterior features in a combined population of small and large chars from Lake Forelovoe deviates from the normal distribution; the variation curve is irregular or multi-peaked. The following are observed: true, right asymmetry along the length of the head; left asymmetry along the width of the head, the length and width of the maxillary bone, the length of the thoracic fin, and the shallowest part of the body (figure 13). As V.S. Kirpichnikov indicates [103], the former is a result of the strong dependence of the growth rate on the initial weight of the individual and, to an even greater extent, on the advantages which 47
large fish have in the competition for food. The negative asymmetry is most often related to the presence in the population of poorly-growing individuals. In some cases excessive distributions are noted. Positive excessive distributions have the shape of an acute pyramid with a wide base and are evidence of the fact that some reasons promote a predominant occurrence of average and extreme values of an feature. True positive excess is noted for the length and width of the head, length and height of the maxillary bone, the length of the posterior eye distance, length of the caudal peduncle, the shallowest part of the body, antedorsal distance, length of the thoracic fins. Negative excess in all cases is not certain, although multi-peak and extended curves are noted in a deeper body, postdorsal, anteventral and anteanal distance, height of the dorsal and anal fins and number of scales on the lateral line [220].

8. Characteristics of chars inhabiting the bodies of water of the Lena River Delta

Feature	Lake Dal'nee	Lake Perekhodnoe	Lake Forelevoe large form	Lake Forelevoe small form
Body length (cm)	30-60 / 43-2	22-55 / 43.8	25-50 / 36.9	23-34 / 28.6
Weight (gm)	300-1900 / 847	200-2000 / 1000	200-1300 / 565	70-160 / 125
Maximum age (years)	17	23	15	15
Time to mature (years)	7	9-10	8-10	6-8
Spawning season	August	August-September	August-beginning of September	end of August
Spawning frequency	not annually	not annually	not annually	annually for most
Fecundity (in 1000's)	-	2.2-4.3 / 2.9	0.88-1.9 / 1.3	-
Ratio of the sexes (males : females)	1 : 1	1 : 1	1 : 1	1 : 2
Food	benthos, plankton	benthos, rarely plankton	benthos, flying insects	benthos
Growth rate	fast	fast	lower than previous ones	very slow

Note: the numerator is the variation limits; the denominator is the average value.

The presence of excessive distribution points to the trend to formation of variations deviating from the norm in a given population of chars. This may be related to the displacement of nonuniform groupings or to genetic distribution according to a small number of genes influencing the growth rate [103]. The latter is more probable in this case.

Thus, the large and small chars of Lake Forelevoe represent a single population. The process of the emergence of forms in this lake is in the early phase.

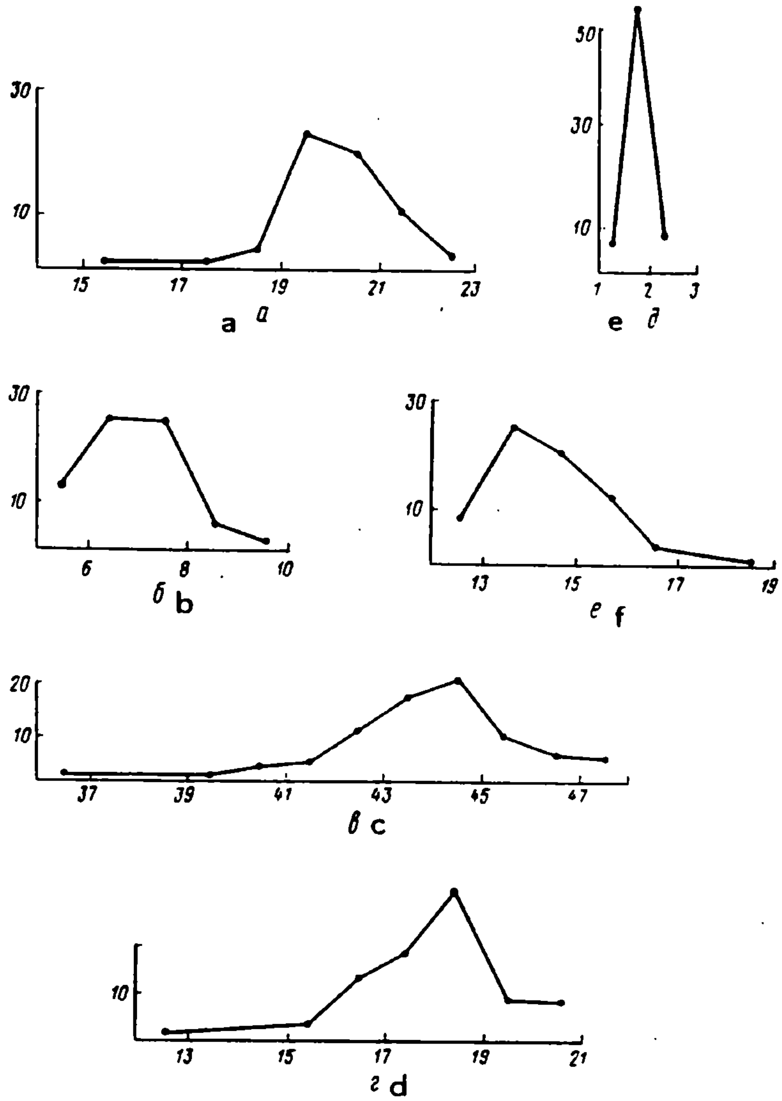

Figure 13. The distribution of features in chars from Lake Forelevoe. % of body length according to Smitt (on the horizontal axis) and frequency of occurrence (on the vertical axis):
a - head length; b - distance between the eyes; c - antedorsal distance; d - caudal peduncle length; e - width of maxillary bone; f - length of thoracic fin.

Chars from Lakes Dal'nee and Perekhodnoe are close in length and body weight, although on average the weight of the former is less. Chars from Lake Forelevoe (a comparison is made only with the large form) differ in smaller sizes and weight (see table 8). The life span of chars from all lakes is long, but not identical. The maximum age (up to 23 years) is noted in a population from Lake Perekhodnoe and the minimum age (up to 15 years) is among the chars from Lake Forelevoe. Their spawning is not annual. They mature at an age of from 7-10 years. Fecundity is low and the lowest is noted among the chars from Lake Forelevoe. The spawning of all populations occurs in the lakes within short periods: in August in Lake Dal'nee and at the beginning of September in Lakes Perekhodnoe and Forelevoe.

Chars from Lakes Dal'nee and Perekhodnoe are similar to one another according to the majority of plastic and meristic features, but they differ from the chars from Lake Forelevoe. The latter have shorter maxillary and mandible bones, shorter antedorsal, anteventral, anteanal and pectoventral distances, a longer caudal peduncle, a higher dorsal fin, longer anal, thoracic and abdominal fins, fewer scales on the lateral line and fewer pyloric caeca, more scales on the anal and thoracic fins (figure 14) [220]. It should be noted that for a number of features (length and proportions of the head, length and location of fins) there is no connection with the growth rate.

In all populations the distribution of exterior features is close to normal (figure 15). Elongation and multi-peaking are noted only for the maximum body depth, which is probably related to the nonuniformity of populations in this feature due to differing gonad maturity in 49
separate individuals. In colouring, body and head shape, the chars from Lakes Dal'nee and Perekhodnoe are similar. Differences are observed only in the shape of the jaws and the pattern on the back. Chars from Lake Forelevoe differ markedly from these populations (figure 16). Mainly they differ in a very short and curved maxillary bone, which in many cases does not even extend beyond the posterior margin of the eye; in a longer and lower caudal peduncle and in bright body colouring: the sides are olive-red without spots or almost without spots; the fins are bright red and orange; the swimbladder is light pink.

Thus, there is no doubt that in the bodies of water studied two different groupings of chars exist: to one belong the chars from thermokarst lakes in the region of the Olenek channel of the Lena River delta; to the other belong chars from an alpine lake located in the spurs of the Kharaulakh' Range.

The study of chars living in the Lena River delta using multi-test methods of statistical analysis indicates the existence of mixed clusters in populations from Lakes Dal'nee and Perekhodnoe and the independence of a cluster in the population of Lake Forelevoe, i.e., it is evidence of the similarity of the former and the isolation of the latter grouping. However, the distance of this cluster from the others is small [154].

Chars from Lakes Dal'nee and Perekhodnoe do not differ from chars from the lakes of the Olenek and Tumatskaya channels studied by M.V. Mina [149], V.D. Lebedev and K.A. Savvaitova [126] and they should be attributed to *S. alpinus*. Chars from the alpine lake, Lake Forelevoe, can be identified, as can *S. jacuticus* from Lake Aranastakh [28]. M.V. Mina, V.D. Lebedev and K.A. Savvaitova viewed the latter as a small, dwarfish form of chars living in the waters of the Lena River delta. However, in Lake Forelevoe we discovered not only small, but large chars with the features of Yakutsk char, as well as with a small number of pyloric caeca. Previously [149] it was suggested that the number of pyloric caeca in chars described by P.G. Borisov [28] changes little with age in connection with the fact that they retained a juvenile type of diet in the specific conditions of Lake Aranastakh where the bottom fauna is scarce, but the plankton is developed. However, in Lake Forelevoe, adult chars similar to the Yakutsk char feed on a variety of bottom fauna; therefore, it is possible to suggest that the number of pyloric caeca is apparently determined early.

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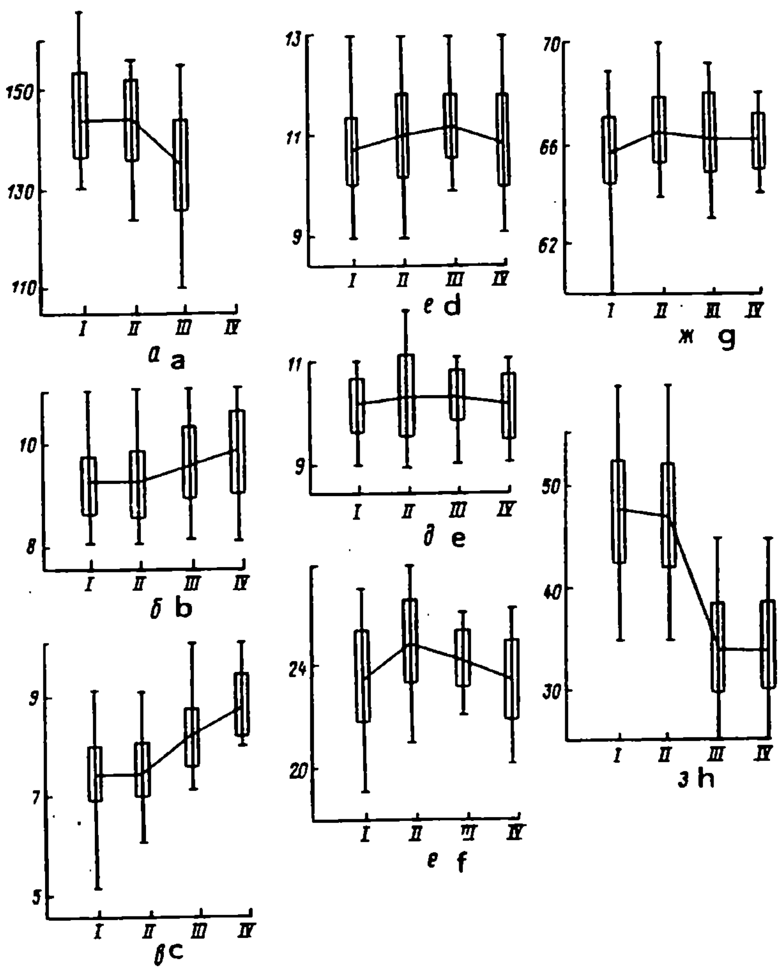

Figure 14. Meristic features (numerical values) of chars inhabiting the Lena River delta.
a - scales on the lateral line; b- rays on the dorsal fin; c - rays on the anal fin; d - branchiostegals on the right; e - branchiostegals on the left; f - gill rakers; g - vertebrae; h - caeca; I - Lake Dal'nee; II - Lake Perekhodnoe; III - Lake Forelevoe (large form); IV --Lake Forelevoe (small form).

The type of food in chars of all populations studied, in spite of the sharp differences in the number of pyloric caeca is basically similar; they are benthophages. The chars of Lakes Perekhodnoe and Dal'nee have an average number of gill rakers, many pyloric caeca and are similar to the Arctic char's shape which has a circumpolar distribution and is found in the waters of the Lena River delta [218]. The Yakutsk char from Lake Forelevoe has the same number of gill 51 rakers and the number of pyloric caeca comes close to the number in certain populations of Far Eastern chars (for example, lake-river chars from Lake Dal'nee in Kamchatka) [200]. They are brought together with the Far Eastern chars by certain elements of colouring, particularly by bright orange and not grey lips, by a light pink and not a violet swimbladder, as well as by a slightly notched or truncated caudal fin.

Thus, the Yakutsk char has features of these two groups of fish and, at the same time, has a number of features peculiar to it alone, in particular a very short and usually curved maxillary bone which does extend to the vertical line of the posterior margin of the eye, a complete lack of spots on the body, or a very few of them, and fleshy lips.

The question arises: how is it possible to explain the combination of so many different features in this form of char? The following premises are feasible. It is known that the hydrologic regime of the Arctic basin is subject to significant fluctuations and the periods of maximum ice cover alternate with the periods of warming when the arrival of pink salmon and chum salmon in the Lena River delta is noted [24]. It is possible to assume that during such periods the natural habitat of the Far Eastern form of chars expanded west and the introgression of genes into the gene pool of local populations could take place. With the onset of a cold spell, the intensity of introgression was reduced and local forms came into being; they had features of all groupings as well as new features, the appearance of which is completely possible in hybrid forms. In order for a new form to come into being, stable conditions are essential, as is a certain level of isolation over the life of the generations. These conditions do not exist in short-lived thermokarst lakes. They are short-term formations; their development depends on the melting of soil ice. Expanding and deepening, the lakes approach the shores of the channels of the delta which, in turn, break down further. As a result, they nearly always joing with the arms of the Lena River; in a high flood they pour in with water from melted snow. Apparently this instability of the system of thermokarst lakes explains the fact that Yakutsk char is found only in alpine lakes of this region, where conditions appropriate for the emergence of forms are found. The conditions in these lakes are more stable and they are geographically very old. As S.G. Parkhomenko [175] points out, there are ice cover remains in the region of the Lower Lena River. They are in the foothills of the Kharaulakh' Range and on the shore of Tiksi. Between the hills made up of dark grey fissile shale are numerous lakes where, possibly, not only a new form appeared, but, as our observations show, there was the next stage in the process of the emergence of forms consisting in the 52
divergence of emerged forms into groupings, differing in growth rate, duration of life cycle and time of sexual maturity.

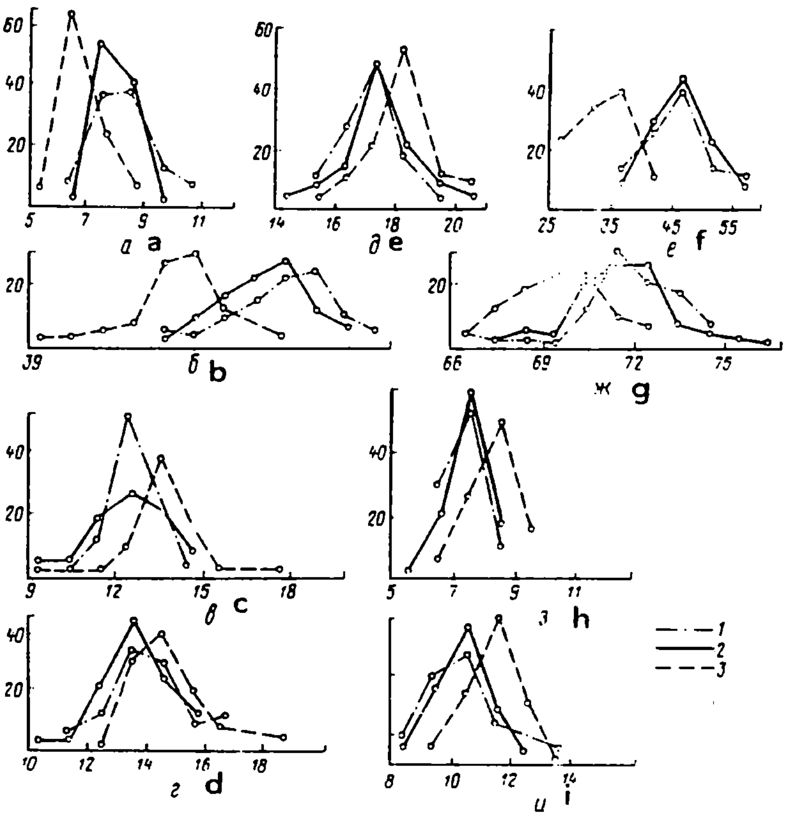

Figure 15. The distribution of features in chars inhabiting the lakes of the Lena River delta. % of body length according to Smitt (on the horizontal axis) and frequency of occurrence (on the vertical axis):
a - maxillary bone length; b - antedorsal distance; c - dorsal fin height; d - thoracic fin length; e - caudal peduncle length; f - number of pyloric caeca; g - anteanal distance; h - base length of anal fin; i - distance between the eyes;
1 - Lake Perekhodnoe; 2 - Lake Dal'nee; 3 - Lake Forelevoe.

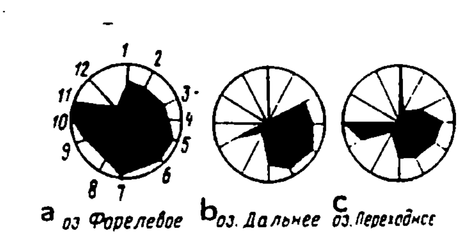

Figure 16. Relationship of features in chars inhabiting the lakes of the Lena River. % of occurrence:
1 - head conical; 2 - maxillary bone does not extend beyond the eye; 3 - maxillary bone curved; 4 - jaws of equal length; 5 - no hook or notch on jaws; 6 - caudal fin slightly grooved; 7 - uniform or nonexistent spots; 8 - bright lips; 9 - bright belly; 10 - no marble-like design on the back; 11 - thick teeth; 12 - fry stripes on the body.
a - Lake Forelevoe; b - Lake Dal'nee;
c - Lake Perekhodnoe

In thermokarst lakes the processes of emergence of forms in chars are manifested less clearly and lead to the emergence of populations which differ very slightly from one another. The differences between them are apparently brought about by genetic-automatic processes. These bodies of water, which exist for a short period and are constantly changing, are populated by populations small in number originating from a few founders. In these conditions the contribution of chars to the variability of the population should be substantial. Chars of thermokarst lakes are probably constantly changing autochton populations. However, there are no conditions to secure this variability and the possibility of new species appearing among them seems unlikely. On the contrary, in alpine lakes the formation of strongly deviating forms, including forms species, is basically feasible (figure 17).

At the present time, it is difficult to determine with certainty the taxonomic status of the Yakutsk char. All of the features characterizing it fall within the variability of *S. alpinus* complex as a whole. However, their combination is unique in a number of cases. It is difficult to say definitively what served as the cause of the appearance of such a combination of features: hybridization or homological variability. Most likely both processes took place, but the contribution of each remains unclear. It is also not known what the level of isolation is at the present time of the Yakutsk char from anadromous chars and chars from thermokarst lakes that are populating the waters of the Lena River delta. Lakes where the Yakutsk char lives are joined with the Neelov Gulf by channels through which these chars can enter. Therefore, it is difficult to decide whether the isolation of the Yakutsk char was completed at the species level. Its further study is essential. It is possible that a form similar to it is found further east. G.Kh. Shaposhnikov [250] describes the skull of a similar char from Lake Darpir in the basin of the Kolyma River.

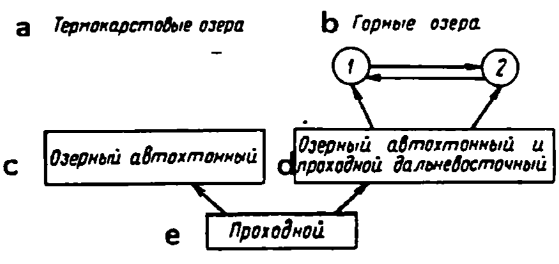

Figure 17. Possible courses of the emergence of forms in chars from the waters of the Lena River delta:
1 - large form; 2 - small form
a - thermokarst lakes; b - alpine lakes;
c - lake autochthonous; d - lake autochthonous and anadromous Far Eastern;
e - anadromous

THE BASIN OF THE INDIGIRKA, ALAZEYA AND CHUKOCH'YA RIVERS

Chars from the lakes of the basins of the Indigirka, Alazeya and Chukoch'ya Rivers were described as *S. czerskii* [24, 101]. M.K. Glubokovskii [60] points to the frequency of lake ecotypes *S. czerskii* in the basins of the Lena, Yana and Kolyma Rivers, as well as the Okhota and Viliga Rivers. Information on the Cherskii char is very sparse. However, an overview of chars of the waters of the USSR would be incomplete without some mention of this group.

The Cherskii char populates only tundra lakes situated higher than river level and having a small run-off. This char is small in numbers. In the lakes of the basin of the Indigirka and Chukoch'ya Rivers its body length is 51.7-55.3 cm [24]; in the lakes of the basin of the Alazeya River its body length is 30-45 cm. The weight of this char is 350-1060 gm; its life span is about 14 years. Its growth rate is slower than normal. Spawning takes place in August-September on the silt bottom and peat. Fecundity is 630-1450 eggs. This fish is a benthophage; it feeds on water insects and other insect larvae [101]. The maxillary bone in adult individuals (but not mature ones) does not extend beyond the eye, but in sexually mature males it does extend beyond the eyes [24]. The maxillary bone extends beyond the vertical line of the posterior margin of the eye [101]. The mandible is flat. Breeding colours are clearly manifested in the males. The hook and notch on the jaws, as well as the teeth in the jaws are well developed. The snout and jaw bones are elongated. The caudal fin is notched.

In comparison with *S. alpinus* from the Kolyma River, Cherskii char has a shallower body, abdominal fins set towards the caudal peduncle, long thoracic fins and a wide maxillary bone [24].

The limited and somewhat contradictory information in the literature hinders the definition of the status of these chars. There are no data in the descriptions presented that prove their species independence.

Chapter 4

CHARS FROM THE WATERS OF THE FAR EAST

THE CHUKOTKA PENINSULA

Until recently in the literature there was only fragmentary information concerning the chars of the Chukotka Peninsula. Along the shores of the Bering Sea, L.S. Berg [24] described an endemic species *S. andriaschevi* from Lake Estikhet near Provideniya Bay; A.G. Kaganovskii [95] described *S. taranetzi* from Lake Achchen. It was also considered that in many bodies of water of the Bering Sea coast of the Chukotka Peninsula, starting from the Bering Strait and even a little further north, lived *S. malma* [24]. In 1960 all Chukotka Peninsula chars known in the literature were reported by V.V. Barsukov [19] who had studied chars from the Provideniya Bay area and conducted a preliminary review of the genus *Salvelinus* synonymously with the arctic char *S. alpinus*. K.A. Savvaitova [198] and Yu.A. Shilin [253] also attributed to this species anadromous and lake chars from the waters of Chaunskaya Bay on the Arctic shore of the Chukotka Peninsula.

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Recently interest in researching Chukotka chars has increased sharply. I.A. Chereshnev discovered sympatric groupings of anadromous chars. Originally he suggested that they be considered two different species: *S. alpinus* and *S. malma* and then, after M.K. Glubokovskii, considered it possible to attribute the grouping he previously viewed as *S. alpinus* to the species *S. taranetzi* [244, 245]. Yu.F. Kartavtsev et al [98] refer to the species independence of the Taranets char and the Dolly varden char. Sympatric chars were discovered by I.A. Chereshnev on the Bering Sea and Arctic coasts of the Chukotka Peninsula [246]. He considers that in the waters of the Provideniya Bay area and in the basin of the Erguveyem River there is a third species of char: the Chukotka char *S. andriaschevi* (V.V. Barsukov [19] pointed to the inaccuracy of its description by L.S. Berg) and in the basin of the Amurema River there are relic lake populations of the arctic char *S. alpinus*.

Thus, in the opinion of I.A. Chereshnev [244, 245, 247], 4 species of char live in the waters of the Chukotka Peninsula: *S. malma, S. taranetzi, S. andriaschevi* and *S. alpinus*. To these may be added chars from Lake El'gygytgyn; R.M. Viktorovskii et al attribute them to the species *S. elgyticus Viktorovsky et Glubikovsky* and *S. boganidae*. Previously the latter was considered endemic to the waters of the Taimyr Peninsula. According to M.K. Glubokovskii, the species *S. andriaschevi* should be viewed as a subspecies of *S. alpinus andriaschevi* [60].

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* The figures in the right-hand margin indicate page numbers of the original (Tr.).

It is impossible to solve the question of the status of Chukotka chars without examining the entire situtation in the genus *Salvelinus*. Therefore, in this section we will pause on the data of the literature and the characterization of our materials on the chars of the Arctic and Bering Sea shores of the Chukotka Peninsula.

Chars from the waters of the Arctic shore of the Chukotka Peninsula. The Dolly varden and Taranets char from the Chaun River, according to the data of M.K. Glubokovskii and I.A. Chereshnev [62] are clearly different in the following aspects: number of pyloric caeca (in the Taranets char there are 39-52 and in the Dolly varden there are 18-36); shape of the caudal fin (in the Taranets char it is strongly emarginate and in the Dolly varden it is truncated); location of the dorsal and anal fins (in the Dolly varden they are closer to the head); depth of the caudal peduncle (it is deeper in the Dolly varden), colour of the mouth opening (in the Dolly varden it is green and in the Taranets char, white); number and size of spots on the sides of the body (in the Dolly varden they are small and numerous and in the Taranets char they are large and few in number); caudal fin colour (in the Taranets char there is a red border, but not in the Dolly varden). To this are added differences according to a set of 60 uncorrelated craniological features [62]. 55

As concerns the chars we studied earlier from the waters of the basin of Chaunskaya Bay [199] and the same chars that we viewed again in the collections of the Moscow State University Zoological Museum, it is difficult for us to identify them completely with *S. malma* and *S. taranetzi*. We were undoubtedly dealing with a phenotypically single-species grouping. There are no chars among them similar to Taranets chars. To a greater degree the chars studied are similar to anadromous Far Eastern Dolly varden. However, unlike the Far Eastern Dolly varden, they have a shortened maxillary bone; there is no hook or notch on the jaws and there is a greater number of pylorica caeca. Therefore, the status of the chars of Chaunskaya Bay cannot be considered definitively clarified.

According to the data of I.A. Chereshnev [224, 245, 246, 247], the Taranets char is widely distributed along the Arctic and Bering Sea shores of the Chukotka Peninsula. Moreover, in its natural habitat it exhibits a surprising morphological stability. Taranets char populations from different bodies of water do not differ in meristic features, body proportions or colouring [62, 245]. There are some differences in biological indicators: fecundity, maturity of gonads, nutritional state, periods of movement (they enter southern rivers at the beginning of July and peak in August; they enter northern rivers at the end of July and peak in the middle of August). All chars spawn in lakes at a depth of 1-5 m and the spawning extends until spring. It is possible that there are seasonal races [246]. At the same time, Taranets char differs sharply from the Dolly varden which is sympatric with it. I.A. Cheresnev indicates that, among the chars studied, there was not one where there were any doubts in its classification [244]. M.K. Glubokovskii and I.A. Chereshnev emphasize the fact that in not one of the studied areas were there any examples of chars discovered where the phenotypes would occupy an intermediate position between segregated phenones [62]. However, if these affirmations were correct in all cases, the so-called "char problem" would simply be removed from the agenda.

There is a different level of isolation between groupings of chars, particularly sympatric ones. According to the data of some authors, sympatric phenones designated as *S. taranetzi* and *S. malma* or forms A and B [29, 30] are clearly separated in all bodies of water where they are encountered and there are no intermediate phenotypes at all [98, 247]. According to the data of other authors, in some bodies of water the isolation between forms is apparently incomplete [53, 146, 154]. It would be improper to have errors in method of different authors account for these discrepancies. Apparently nature is complex and ambiguous. In this respect it is important to examine the features of populations studied anew, particularly in areas where different forms are sympatric.

Chars from the waters of the Bering Sea coast of the Chukotka Peninsula. In the brackish Uelenskii Gulf we discovered two sympatric groupings (A and B) of anadromous char [29]. Both forms are similar in average dimensions, although char A is larger than char B (Table 9). Both forms differ in a comparatively fast growth rate (Table 10); however, form B individuals of the same age grow more quickly. Both forms feed in the lagoon on benthos and fish. However, form A chars are highly infected with parasites, whereas form B chars are almost uninfected.

9. Biological indicators of chars inhabiting the waters of the Chukotka Peninsula

Indicator	Uelenskii Gulf anadromous form A	Uelenskii Gulf anadromous form B	Kurupkan River anadromous form A-B?	Kukekkuyum River anadromous form A	Kukekkuyum River anadromous form B	Lake Varapilen lake form	Lake Gornoe, chechen Arakam-Island, lake form
Body length (cm)	35-75	30-60	30-75	up to 70	up to 77	41-50	12-40
Weight (gm)	200-4000	300-1600	400-3500	up to 3400	up to 4000	up to 1500	100-450
Maximum age in years	9	7	9	9	9	9	12
Maturation time in years	-	-	4	-	-	-	6-7, rarely in 4 years
Spawning time	-	autumn	from August	late autumn	autumn	from August	from August
Spawning frequency	-	not annually	not annually	not annually	not annually	not annually	not annually
Fecundity (number of eggs)	-	-	1500-7000	4325	5846	1700-2500	240-600
Ratio of sexes (males to females)	-	-	-	-	-	-	3:1
Food	benthos, fish	benthos, fish	does not feed during migration	does not feed during migration	does not feed during migration	benthos	Notostraca, rarely fish

10. Growth rate of chars from the waters of the Chukotka Peninsula (cm)

a Район	b Форма	c Возраст, лет											
		2	3	4	5	6	7	8	9	10	11	12	13
Уэлен d	i Голец Таранца (n — 30)	—	—	—	39	43	47	55	61	-			
	j Мальма (n — 10)	—	—	--	42	48	51	--	--	·			
р. Курупкан e	Голец (мальма?) k (n — 54)	--	34	40	46	56	56	56	68				
оз. Горное f	Голец (n — 154) l	17	16	19	27	28	30	30	30	31	32	32	
р. Кукеккуюм g	Голец Таранца (n — 24) i	—	--	38	43	48	52	57	61	·			
	Мальма (n — 36) j	--	—	42	52	54	57	64	77	·			
оз. Варапилен h	Озерный голец (n — 31) m		-		--	44	47	46	49				

a - region; b - form; c - age in years; d - Uelen; e - Kurupkan River; f - Lake Gornoe; g - Kukekkuyum River; h - Lake Varapilen; i - Taranets char; j - Dolly varden; k - char (Dolly varden?); l - char; m - lake char

Between the char forms compared there are differences in the number of gill rakers and pyloric caeca (Figure 18). There are also some differences in body proportions. Char form A differs as follows: slightly smaller snout, shallower head, shorter jaws, shallower body, shorter and shallower caudal peduncle; the dorsal, abdominal and anal fins are located towards the tail area; the dorsal, anal and abdominal fins are slightly shorter (Figures 19-22).

Both forms differ as follows: head shape (in form B it is more often more triangular and pointed); in length and location of the maxillare (in form B it often extends beyond the posterior margin of the eye and is positioned horizontally; in char A it is shorter and usually points downward). On the body of form A chars, as distinct from form B, there are always few spots and they are very large; the caudal fin is emarginate, whereas in form B it is truncated. The body of form A chars is dull silvery and in form B chars it is bright silvery; the body of form A chars is covered by coarser scales.

Strong overlapping was observed in almost all features, but there was never any difficulty in attributing fish caught in this gulf to one form or the other due to the differences in body shape and colouring.

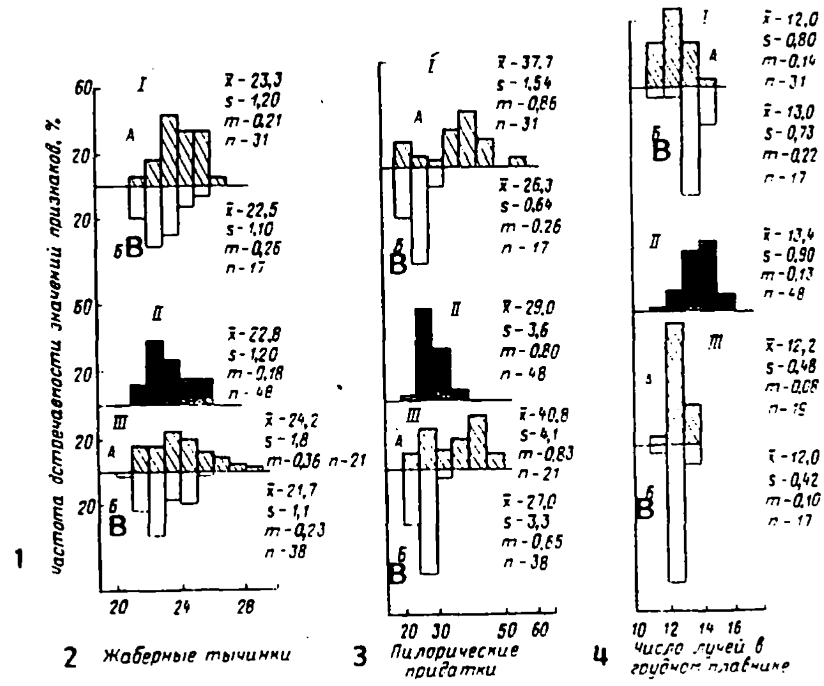

Рис. 18. Сравнение меристических показателей у форм гольцов Чукотки: I — Уэленская лагуна; II — р. Курупкан; III — р. Кукеккуюм; А — голец Таранца; Б — мальма

Figure 18. Comparison of meristic counts in char forms of the Chukotka Peninsula:

I - Uelenskaya lagoon; II - Kurupkan River; III - Kukkekkuyum River; A - Taranets char; B - Dolly varden char; 1 - frequency of occurrence of feature values, %; 2 - gill rakers; 3 - pyloric caeca; 4 - number of rays on thoracic fin.

We noted another situation in the Kurupkan River. I.A. Chereshnev [246] refers to the fact that the sympatric Taranets char and the Dolly varden char (forms A and B) are in this river. In our material, collected at the beginning of September while the fish were migrating to spawn, we were unable to differentiate them. There were many fish in the sample (about 50%) which it was impossible according to phenotype to attribute with certainty to form A or B. It is curious that in many individuals in the most diverse combinations there are features inherent in both forms. This refers particularly to features characteristizing body shape and colour. Great phenotypical divergence is generally characteristic for the males. Some large males, particularly those caught in the spawning-ground area, are similar to the Pacific salmons of the genus *Oncorhynchus* in body and head shape and in the nature of hook and notch development, but in body shape and colour they are similar to the Taimyr chars, Dryagin's char and Boganida lake char; some are reminiscent of the East Siberian char. According to our observations, a typical Dolly varden char (form B), together with clearly different fish, reproduce jointly in the spawning-grounds.

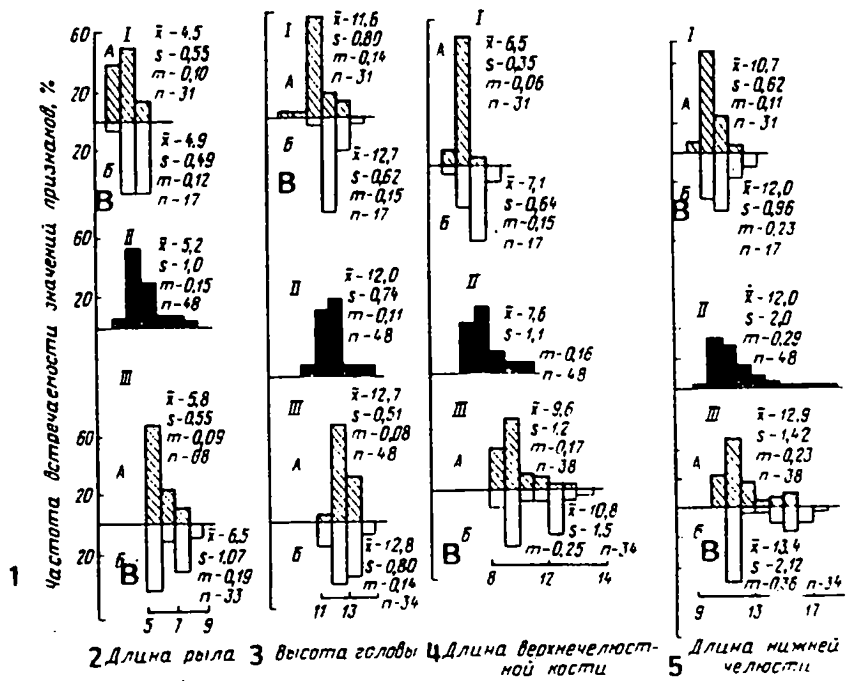

Рис. 19. Сравнение относительных пропорций головы у форм гольцов Чукотки:

I — Уэленская лагуна; *II* — р. Курупкан; *III* — р. Кукеккуюм; *А* — голец Таранца; *Б* — мальма

Figure 19. Comparison of relative proportions of chars in Chukotka char forms:

I - Uelenskaya lagoon; II - Kurupkan River; III - Kukkekkuyum River; A - Taranets char; B - Dolly varden char; 1 - frequency of occurence of feature values, %; 2 - snout length; 3 - depth of head; 4 - maxillary bone length; 5 - mandible length.

Further south, in the Kukekkuyum River (Krest Gulf), live two forms of anadromous chars that are connected to one another in their movements. Their morphological features were studied by V.V. Volobuev et al [53]. These forms are noticeably different from one another in the number of pyloric caeca and, to a lesser degree, in the number of gill rakers. Differences in body proportions are related to a nonuniform growth rate in these fish [53].

The differences in skull morphology are not great in fish with different numbers of pyloric caeca [36]. Form A chars retain features characteristic of young, immature individuals, but usually characteristic of resident salmon populations [138, 139]. The young of both forms do not differ in these features and, as V.V. Volobuev [53] proved, the differences between forms are not absolute and are the result of a different level of development of breeding colours. It is possible to differentiate the forms according to external features only while the fish are migrating to spawn, i.e., when breeding colours are developing. Silvery chars of both forms are difficult and sometimes even impossible to differentiate. Differences in the number of pyloric caeca are significant, but there is no hiatus between forms A and B.

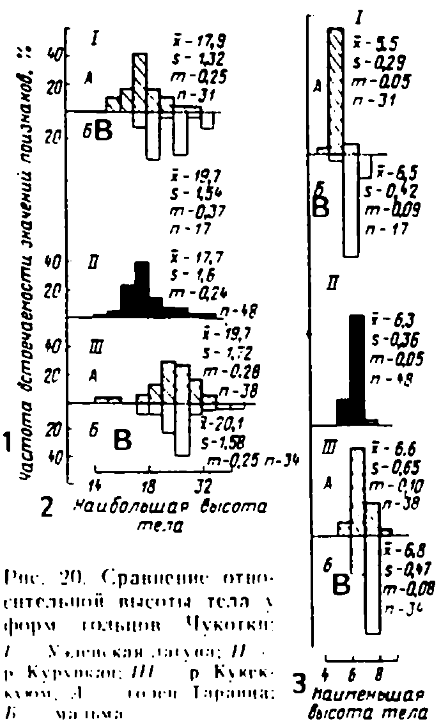

Figure 20. Comparison of relative body depth in forms of Chukotka chars:

I - Uelenskaya Lagoon; II - Kurupkan River; III - Kukkekkuyum River; A - Taranets char; B - Dolly varden char; 1 - frequency of occurence of feature values, %; 2 - greatest body depth; 3 - smallest body depth.

Thus, despite the affirmation by a number of authors [62, 98, 247] that there are definite boundaries between species, particularly between *S. taranetzi* and *S. malma*, the level of isolation of phenones A and B in the waters of the Chukotka Peninsula is apparently not the same [53, 154]. The nature of distribution of the frequency of occurrence of values of many features in phenones A and B is evidence of this. In a number of features, the distributions of sympatric northern Uelen forms A and B differ. However, southern populations of the same phenones are similar in the nature of distributions of features.

The frequency distributions of analogous groupings vary in different regions. A stable similarity is exhibited only in the nature of distribution curves by the number of gill rakers and pyloric caeca. Although there is a great deal of overlapping, in combination with certain features of colour and pattern (spot sizes), these features, although not always, permit the discrimination of phenones. Frequency distributions of the values of features of Kurupkan River char have a known intermediate character between phenones, sometimes coinciding with the distribution of form A and sometimes with the distribution of form B from Uelen or from the Kukekkuyum River. However, in frequency distribution and in number of gill rakers, these chars are closer to form B, whereas in number of pyloric caeca they occupy an intermediate position between two phenones. It should be noted that in this work we did not artificially isolate the intermediate form as we did earlier in accordance with the variation boundaries of the attribute according to I.A. Chereshnev [244] for *S. taranetzi* and *S. malma*, but we examined a series for sampling as a whole; moreover, in both cases the boundaries of the series turned out to be much wider. In body shape, colour, etc. chars from this river are also more varied than separate phenones in different areas of the natural habitat.

The different stages we noted of sympatric isolation of forms A and B in the waters of the Chukotka Peninsula do not permit a uniform definition of the status of these fish. With the aid of only formal taxonomic criteria, it is not likely possible to fully describe this situation. Unfortunately, in this case even the idea of biological species has limited use. Apparently we have an example here of a so-called "dumb-bell structure" where there can be more extreme individuals in a population than average ones. Such a structure can change in the direction of breaking up into species or remain "evolution stable" where the population may remain unchanged for an unlimited amount of time [110, 319].

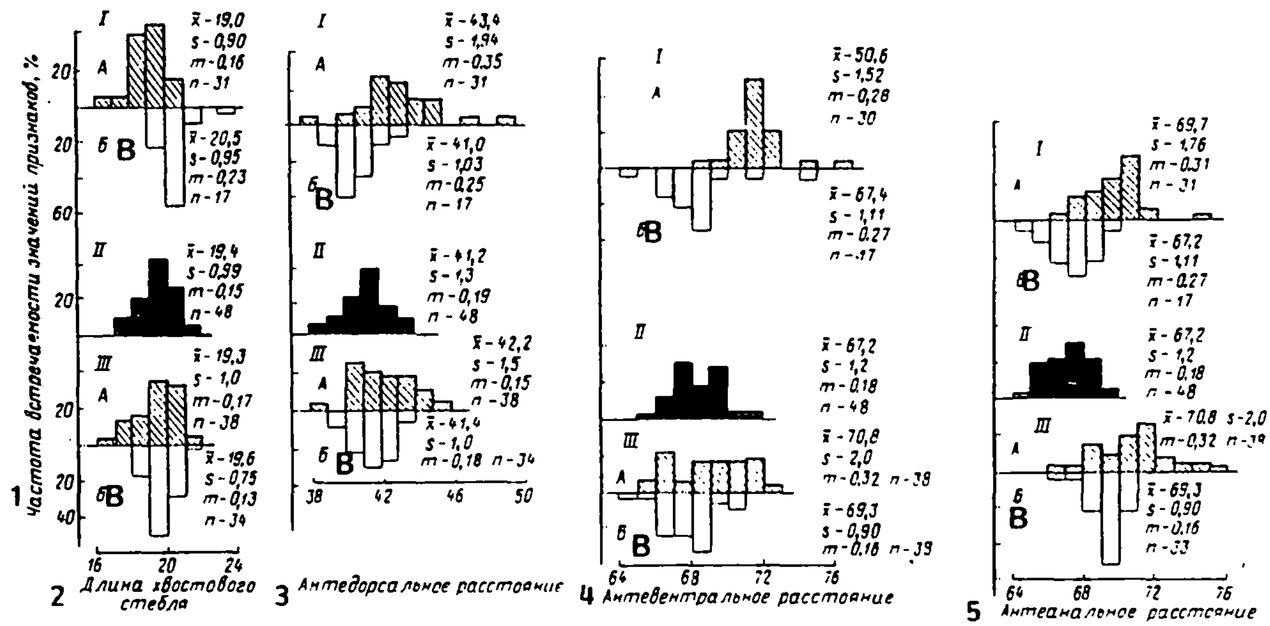

Figure 21. Comparison of certain body proportions in Chukotka char forms:

I - Uelenskaya Lagoon; II - Kurupkan River; III - Kukkekkuyum River; A - Taranets char; B - Dolly varden char; 1 - frequency of occurence of feature values, %; 2 - caudal peduncle length; 3 - antedorsal distance; 4 - anteventral distance; 5 - anteanal distance.

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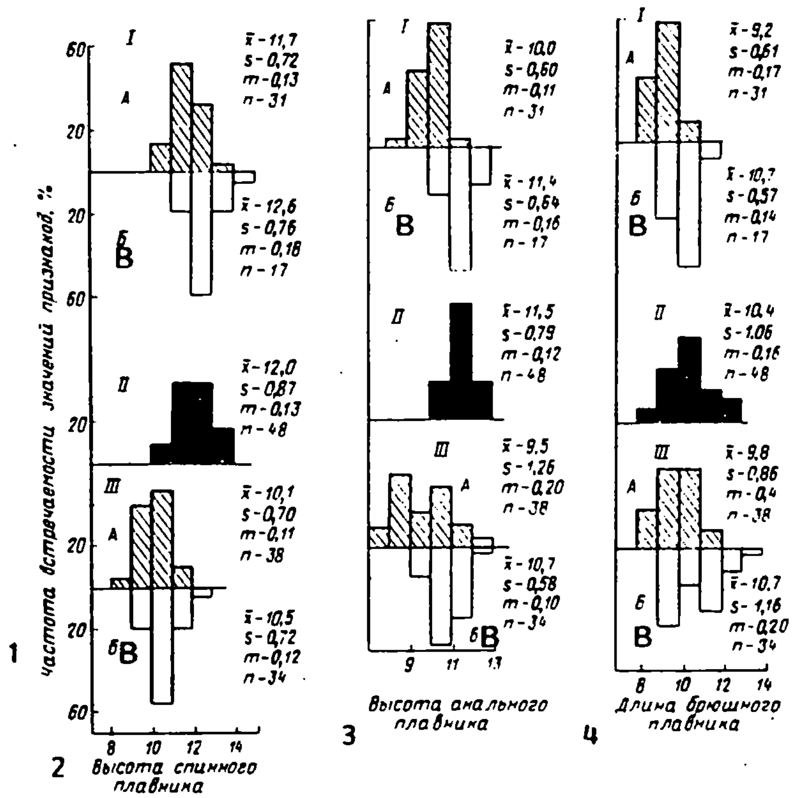

Рис. 22. Сравнение относительной длины плавников у форм гольцов Чукотки:

I — Уэленская лагуна; II — р. Курупкан; III — р. Кукеккуюм; А — голец Таранца; Б — мальма

Figure 22. Comparison of relative fin length in Chukotka char forms:

I - Uelenskaya Lagoon; II - Kurupkan River; III - Kukkekkuyum River; A - Taranets char; B - Dolly varden char; 1 - frequency of occurence of feature values, %; 2 - dorsal fin depth; 3 - anal fin depth; 4 - abdominal fin length.

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The existence of dumb-bell structures is possible under the following conditions: reproductive isolation between extreme genotypes is incomplete and, in spite of strong disruptive selection, intermediate individuals constantly emerge as the result of crossing; reproductive isolation is complete, but disruptive selection is not strong enough to provide the final stages of sympatric speciation; apart from two resources that divergent extreme individuals have the advantage of using, there is a third, which is better used by average individuals. If the capacity of this resource is not great, then disruption selection will act in a population far from speciation, which will give way to stabilizing selection when the number of average individuals becomes small enough [110]. The direction of selection in this case will depend on the nature of assortative crossing. If the assortativeness is poorly expressed, then there will be more intermediate individuals in the descendents than in the populations of parents with a dumb-bell distribution. In severe isolation the opposite effect is possible, when the population acquires a form of assortativeness where the distribution of descendents and parents will coincide and, instead of disruptive and stabilizing selections, only a frequency-dependent selection will remain. As a result, an "evolution stable" dumb-bell structure will emerge. These processes are traced and explained in mathematical and computer models by A.S. Kondrashov and M.V. Mina [110, 319].

Sympatric groupings of Chukotka chars are apparently an example of a similar type of situation in nature. Of course, it is possible to assume that dumb-bell structures in Chukotka chars arose as a result of secondary intergradation. However, in this case they should have diverged in many features, since they had previously evolved in different locations. In this case, stable differences are noted in some features (pyloric caeca, spots, length of maxillary bone, smallest body depth, length of anal fin) which are apparently determined by a few genes, which most likely speaks for a sympatric emergence of forms. This is evidenced by the divergent values in the plastic and meristic features studied and by the similarity dendrograms (Figure 23) from which it follows that sympatric groupings of forms A and B are closer to one another than phenones of the same name living separately. Data on molecular hybridization [146] also speak for the sympatric emeregence of forms in the Kukekkuyum River basin.

In Lake Varapilen, which has an inconstant link with the Khatyrka River (Koryakskoe Plateau), lives a lake char which is phenotypically similar to the lake chars of the Kamchatka Peninsula [198, 206] and to the neiva of the Sea of Okhotsk [49]. All of these lake populations are similar to the Taranets char; moreover, the char population from Lake Varapilen (Figure 24) is closest of all to the Taranets char. K.A. Savvaitova, V.V. Volobuev et al attribute the Taranets char to the high arctic morphotype, which is predominantly represented by lake forms, and they consider that the anadromous way of life of these chars was acquired subsequently as a result of their leaving the lakes, where living conditions became unfavourable, for the sea [53, 218]. The migration of these anadromous chars is restricted by the areas around river mouths and they should probably be considered semi-anadromous fish.

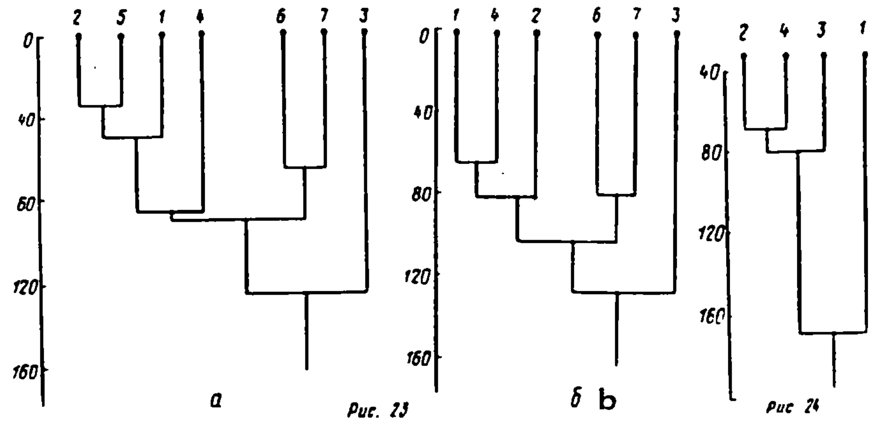

Рис. 23. Дендрограммы сходства гольцов Чукотки по пластическим и меристическим признакам:

а — без *ll, P, vt, P_c*; б — без *ll, P, vt*; 1 — голец Таранца (Уэлен); 2 — мальма (Уэлен); 3 — озерный голец (оз. Горное о-в Аракамчечен); 4 — озерный голец (оз. Варапилен); 5 — проходной голец (р. Курупкан); 6 — голец Таранца (р. Кукеккуюм); 7 — мальма (р. Кукеккуюм)

Рис. 24. Дендрограмма сходства чукотского гольца Таранца, озерных форм гольцов Камчатки и Охотоморского побережья:

1 — голец Таранца (Уэлен); 2 — озерный голец (оз. Дальнее); 3 — нейва (оз. Уегинское); 4 — озерный голец (оз. Начикинское)

Figure 23. Similarity dendrograms of Chukotka chars according to plastic and meristic features:

a - without *ll, P, vt, P_c*; b - without *ll, P, vt*; 1 - Taranets char (Uelen); 2 - Dolly varden (Uelen); 3 - lake char (Lake Gornoe, Arakamchechen Island); 4 - lake char (Lake Varapilen); 5 - anadromous char (Kurupkan River); 6 - Taranets char (Kukekkuyum River); 7 - Dolly varden (Kukekkuyum River)

Figure 24. Similarity dendrograms of Chukotka Taranets char, lake forms of Kamchatka chars and Sea of Okhotsk chars:

1 - Taranets char (Uelen); 2 - lake char (Lake Dal'nee); 3 - neiva (Lake Ueginskoe); 4 - lake char (Lake Nachikinskoe)

The existence of only lake groupings of this phenone in the south of its natural habitat (lakes of the Southern Kamchatka Peninsula and the Uegi River basin on the coast of the Sea of Okhotsk) is apparently related to their relatively stable living conditions in deep alpine lakes with corresponding niches. Farther north, on the Chukotka Peninsula, there are few such bodies of water, but then the coast of the peninsula abounds with brackish lagoons and lakes which are open to the sea and where there is good forage. Chars feed in them and reproduce more often in rivers where there are spawning-grounds. Purely lake populations of this phenone are rare on the Chukotka Peninsula due to the small number of suitable lakes.

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Of course, the current distribution of lake populations can be viewed as the result of the penetration of an anadromous char into the lakes of the Kamchatka Peninsula and the coast of the Sea of Okhotsk during a period of a drop in temperature. With warming, this char died out, being a form that preferred colder temperatures, and only its lake ecotypes remained. The Taranets char is phenotypically closer to chars of the arctic group, although its phyletic proximity to them cannot be considered proven.

The Chukotka Peninsula region has a complex hydrographic network. The majority of the rivers are of an alpine or semi-alpine nature. Their flow is characterized by a sharp fluctuation in discharge during the year: alternating high freshets and periods of low water levels, the latter being differentiated by a low discharge in summer and a very low discharge (5-6% of the annual discharge) in winter [191]. The channels of most rivers are slightly cut into the valley floors; in places they are broken down into a large number of small branches, almost shallow gullies, which run along extensive areas of pebbles devoid of vegetative cover. They meander a great deal and form old beds and dead channels. For most of the year, the rivers are icebound and often freeze to the bottom.

The lakes of the Chukotka Peninsula are sufficiently divergent (alpine, thermokarst, morainal, levee) and in the seaside lowlands, in direct proximity with the lagoons and the sea, they are filled with salt water and are subjected to high and low tides. The great majority of these lakes are drainage lakes and they are interconnected [191].

There are a great number of lagoons on the lowland shore of the Chukotka Peninsula that are separated from the sea by sand spits and are joined with the sea by narrow entrances.

Thus, the hydrographic network on the Chukotka Peninsula is inconstant and unstable. Such conditions are not likely to be favourable for the development of strong endemism. In similar bodies of water, small numbers of highly eurybiontic species can exist that are often represented by different groupings, where the level of isolation is not the same under different conditions. However, under isolation, and particularly, under lengthy isolation, the existence of sharply isolated groupings is possible. An example of a similar species can be the chars from the lakes of the continental coast of the Chukotka Peninsula and sympatric chars from Lake El'gygytgyn (Anadyr' River basin) [55] and from Lake Gornoe on Arakamchechen Island (Senyavina Strait).

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A large and a small char form* live in Lake El'gygytgyn. The former is attributed to the species *S. boganidae*, and the latter is classified as a new species *S. elgyticus* and called a small-mouth lake char [55]. The gonads of all the females we studied in the collections were at maturity levels IV and V; the males, with one exception, were at levels IV and VI. In appearance, all individuals were similar and the females and males were not different. They were characterized by: a conical (in 96%of the cases), rarely rounded head; large eyes; a straight, short maxillary bone which extends to the middle of the eye. In 76% of the fishes, the jaws were of equal length, or the lower jaw projected slightly. The mouth was semi-upper or terminal. There was no hook or notch on the jaws, in spite of the fact that all individuals were ready to spawn. The caudal fin was highly emarginate. The colour of these chars was specific: above the lateral line on the body there was a small number (~10-16) of large (greater than the diameter of the pupil) spots which took on a marble-like colouring on the back. Below the lateral line, the spots were smaller (less than the diameter of the eye). In addition to the spots, parr marks appeared on the body of some individuals. According to body proportions, differences in fin length were observed between males and females (the males had longer dorsal, anal, thoracic and abdominal fins), but overall they were very long. Thus, *S. elgyticus* differs from previously known forms and species of chars as follows: numerous, frequent and long gill rakers; short upper jaw bone, specific body colouring and long fins. In pattern and colouring, they are similar to East Siberian char; in number and length of gill rakers, they are similar to the chars inhabiting the lakes of the Kuando-Charskii watershed in the Zabaikal'e area; in number of pyloric caeca, they are similar to Far Eastern Dolly varden.

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* According to a report by employees of the Institute for Northern Issues, Far Eastern Scientifc Centre, USSR Academy of Sciences, they discovered another species of char characterized by an set of sharply divergent features of colour, morphology and seismosensory system, allowing it to be viewed as the representative of a new species.

Small chars from Lake El'gygytgyn differ from large chars that are sympatric with them. They are classified as *S. boganidae* [55]. The latter are known only on the Taimyr Peninsula and have been considered endemic to it until now. According to a number of features, the large chars from Lake El'gygytgyn are closest of all to the neiva of the coast of the Sea of Okhotsk and not to the Boganida lake char. In this body of water, it is a predatory bottom-living form consuming small *S. elgyticus*; it can attain a length of more than 1 m and a weight of 12-15 kg; it matures at a length of 45-50 cm. There are probably slow- and fast-growing groupings. These deep-water chars from Lake El'gygytgyn undoubtedly represent one of the most divergent forms of chars. They have most likely achieved species status. Their strong divergence was brought about both by lengthy isolation (about 1-3.5 million years) and great water depths (about 169 m). In the opinion of certain researchers, the lake depression is of meteorite origin (the age of the meteorite crater dates from the late Pliocene); however, a younger age of the body of water is also possible as is the possibility of another origin, in particular as a result of a volcanic explosion that took place only a few thousand years ago [17].

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In a small alpine lake (0.75 km^2 area, up to 26 m deep) with limited forage and spawning-grounds covering a small area, we discovered a small char on Arakamchechen Island, and since this island apparently appeared during the Holocene [176], then the colonization of the lake by an ancestral population of this char took place comparatively recently. Modern conditions of existence of this form are reflected in the peculiarities of its biology and external morphology. The reproductive capability of the population is low. The food spectrum is narrow, although separate individuals are capable of ichthyophagy. Fast- and slow-growing individuals are encountered in the population; however, they do not form stable groupings. Overall, in their features (number of gill rakers and pyloric caeca) the chars from this lake are closest of all to the alpinoid morphotype *S. alpinus complex* [218] which has a circumpolar distribution from which stems, possibly, the given specific population. The combination in phenotype of features of Arctic and Dolly varden-like chars can be considered its characteristic feature.

THE CONTINENTAL COAST OF THE SEA OF OKHOTSK

Chars of the genus *Salvelinus* living in the waters of the continental coast of the Sea of Okhotsk were attributed to the species *S. malma*, *S. neiva* and *S. leucomaenis* [239]. Recently, there was a report about the existence of yet another species, *S. albus*, in the basin of the Ola River; the species had been previously described only for the Kamchatka River [60]. According to reports by employees of the Institute for Northern Issues, they discovered yet another species of anadromous char in the upper reaches of the Yama River. However, in spite of a wide distribution and large numbers, until recently almost no research was done on chars from this area. This gap was to a significant degree filled by the research of V.V. Volobuev, N.M. Gubanov and E.D. Vasil'eva [37, 47, 48, 49, 50, 51, 75]. They give a detailed description of chars of this area.

Anadromous chars in this area are the most numerous and widely distributed. River chars are found in large rivers where there is rich forage. Dwarf stream chars are rarer and lake chars are found mainly in the basin of the Okhota and Viliga Rivers.

The life span and growth rate of each form is different. Anadromous and lake chars grow more quickly and live longer; freshwater chars grow slowly and their life span is short. Times of maturity are also related to growth features: anadromous and lake chars mature in their fith year, whereas freshwater chars mature in their third or fourth year. The nature and times of spawning, as well as the duration of incubation of the eggs, are similar in the anadromous, river, stream and lake chars; however, these forms differ in value of absolute fecundity. Chars also differ in the nature of their food: anadromous chars consume mainly marine fishes and crustaceans; river chars consume large benthos and fish; dwarf males and stream chars consume small benthos and flying insects: large lake chars consume mollusks and fish; dwarf lake chars eat zooplankton [51].

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A comparison of the morphological properties of chars reveals certain differences between them. The anadromous char differs from the river and dwarf stream char as follows: smaller eye diameter, width of the upper jaw, depth of the dorsal and length of the thoracic fin and a lesser caudal position of the dorsal fin. However, these features are subject to size variation and depend on growth rate. Comparable forms of chars differ considerably in size and growth rate. The values of plastic and meristic features overlap and significant differences between them, according to most indicators, are not detected [52]. Differences are exhibited only in the different frequency of occurrence of certain combinations of features. The values of many meristic features are subject to geographic variation. Interpopulation differences within one form often turn out to be greater than the differences that exist between populations of different forms [52]. Lake chars (neiva) differ to a great degree. The differences are exhibited first of all in the way of life. The neiva has more gill rakers and pyloric caeca, different colouring and brighter breeding colours. Anadromous chars are considered an original form from which all other forms began [52, 182].

There is a different level of isolation between forms and separate groupings of chars. In different areas of the natural habitat, in bodies of water that are of a different nature, the degree of subdivision into groupings of different hierarchical levels is not the same. The nature of the links between them is also not the same. The closest link exists between anadromous chars and dwarf males. The latter are actually part of an anadromous flock and compensate for the shortage of anadromous males. A similar link is observed with river chars. Spawning of all forms can occur jointly and during the same periods. Apparently river chars and dwarf males split off from the descendents of the anadromous char [52]. As a whole they form a population system connected by a common gene pool and are probably taxonomically identical.

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The structure of lake char populations in a number of bodies of water can also become complicated. In Lake Korral', the structure is represented by large and small dwarf groupings. The females dominate among the former, and the males dominate among the latter. Both groupings complement one another and reproduce jointly. The differentiation of neiva into large and small dwarf groupings is probably due to insufficient food in this body of water, in connection with which the dwarf grouping assimilated a planktophage niche and the large grouping became a benthophage and predator [52]. Lake chars are noticeably different from anadromous, river and stream forms of chars of this region. Their separation into an independent species *S. neiva* was based on this fact [8, 239].

The results of osteological analysis of the neiva indicated that its differences from other chars in qualitative characteristics amount to a different frequency of occurrence of polymorphous features common to all chars of the genus *Salvelinus*, which usually characterizes different populations of one species. However, it is a form where specific features of skull structure appear at the early stages of individual development [37].

Molecular hybridization of the DNA of the neiva and the anadromous Dolly varden of the Pacific Ocean basin did not reveal sharp differences either [342]. The coefficient of genetic divergence between them is 24, and at the same time the coefficient between the East Siberian char and the same anadromous char is 128. In researching the genetic divergence from the benchmark *S. alpinus* from Finland and Scandinavia, it turned out that the neiva is very similar to the Dolly varden and is located on the same evolutionary line, but retains more ancestral features [56].

The origin of the neiva is unclear. There are two opinions on this account: the neiva is a derivative of the anadromous char of the Sea of Okhotsk and the difference between them is the result of the development of the neiva under conditions of isolation; the neiva is a relic of the Quaternary Period whose ancestor found its way from the basin of the Arctic Ocean and remained thanks to stable living conditions [49]. The viewpoints of M.K. Glubokovskii [57] are close to the latter point of view. Previously this author affirmed that the neiva was quite isolated from the majority of char species, although closest of all to the *S. alpinus*. The divergence of the neiva from the Arctic char occurred no later than the Mid-Pleistocene when the neiva found its way through the Aldan watershed to the Okhota River [57]. In later publications, M.K. Glubokovskii et al [188] at first combined the neiva into one group with the Cherskii char and started to write the group *S. czerskii-S.neiva*; then M.K. Glubokovskii [160] attributed the neiva from the waters of the coast of the Sea of Okhotsk to the species *S. czerskii*. There were no materials in favour of such a transformation. As we indicated above, the Cherskii char has almost not been researched at all and its natural habitat is unknown. The data at hand are evidence of its originality and the intermediate character (between the Far Eastern and Eurasian forms) of a combination of such important diagnostic features as the number of gill rakers and pyloric caeca. Without overlapping, it differs from the neiva in the number of gill rakers. The latter is attributed to one of the char forms having the most rakers, whereas the Cherskii char is one of those having few rakers. First and foremost it was the number of rakers that served as a basis for separating the neiva into an independent species [239].

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In our opinion, the question of the interrelationship between the Cherskii char and the neiva remains an open one. As concerns the species independence of the neiva, this question cannot be answered without comparing chars from other regions and the question will be examined in the appropriate sections of the book.

THE KAMCHATKA PENINSULA

In 1792, Walbaum described the species *Salmo malma Walbaum* which was discovered in the waters of the Kamchatka Peninsula [261]. In 1811, Pallas described another species of char of the Kamchatka Peninsula: the East Siberian char (*Salmo leucomenis*). Subsequently, Jordan and Evermann [315] attributed them to the genus *Salvelinus*. In 1909, based on the great similarity between the Dolly varden and the Arctic char, L.S. Berg proposed that the Dolly varden was only its Pacific subspecies *S. alpinus malma*. In 1932, he once again raised the Dolly varden to the rank of species, but his description of the species and subspecies do not differ from one another [21, 23]. Researchers turned their attention to the variety of forms of Dolly varden [24, 119], and A.Ya. Taranets [239] described *S. malma infrasp. kuznetzovi* from Lake Ushkovskoe in the basin of the Kamchatka River. In 1960, V.V. Barsukov proposed that in the Far East, as well as in the Kamchatka Peninsula, lived the Arctic char *S. alpinus* and that the name *S. malma* was a synonym for it. In 1961, we arrived at the same conclusion. In our opnion, two species of char live in the waters of the Kamchatka Peninsula: East Siberian char and Arctic char; moreover, the latter is represented by various intraspecific forms [198, 200].

In subsequent years, such strongly divergent forms as the following were studied: the stone char from the basin of the Kamchatka River, the mollusk eaters and predators from Lake Azabach'e and the lake-river char from Lake Nachikinskoe. Proposals were made concerning the possible species isolation of these forms [41, 203, 210, 211, 215]. However, for a number of reasons, it was suggested that they be viewed together with other forms of chars within the *S. alpinus complex* [56, 204, 206].

Recently, the list of taxa from the waters of the Kamchatka Peninsula has been supplemented. R.M. Viktorovskii [43] described a new species and subspecies of char from Lake Kronotskoe (*S. cronocius* and *S. malma schmidti*) and M.K. Glubokovskii [58] described a new species *S. albus* from the basin of the Kamchatka River. In the opinion of these authors, in addition to the species mentioned aboved, the *S. malma* and *S. alpinus* and two species of lake chars live on the Kamchatka Peninsula in Lakes Dal'nee and Nachikinskoe.

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Thus, there are currently two different points of view on the systematic position of the chars of the Kamchatka Peninsula. Different criteria are taken in differentiating species. L.S. Berg [23, 24] used the length of the upper jaw and the degree of its extension beyond the posterior margin of the eye. J. McPhail [337] and R. Behnke [267, 268] took the number of gill rakers as their basis; L. Nyman [358] used the rate of polymorphous esterase locus; R.M. Viktorovskii [43] used karyotypes; V.T. Omel'chenko [164] used monomorphous proteins; M.K. Glubokovskii [57] used certain ostelogical features; V. Morton, R. Miller [348], A.N. Andriyashev [10] and I.A. Chereshnev [244] used the number of pyloric caeca.

Naturally the following seriously hinder the definition of forms: different levels of research and a variety of features, as well as an attempt to assign the meaning of absolute species criterion to them; frequent contradictions in results obtained through different methods, their lack of correspondence with original descriptions where not one of the above-mentioned criteria is found, and poor research into the variability of separate features in populations according to the natural habitat of species. Therefore, in order to solve this problem, it is expedient to first examine the actual data currently at hand.

In the literature, several forms of chars from the waters of the Kamchatka Peninsula are described (anadromous, lake-river, lake, stream and stone char) which differ clearly in morphological, biochemical and karyological features (Figure 25) [34, 35, 38, 88, 141, 198, 204, 206, 209, 210, 215]. These forms may be distributed allopatrically or sympatrically.

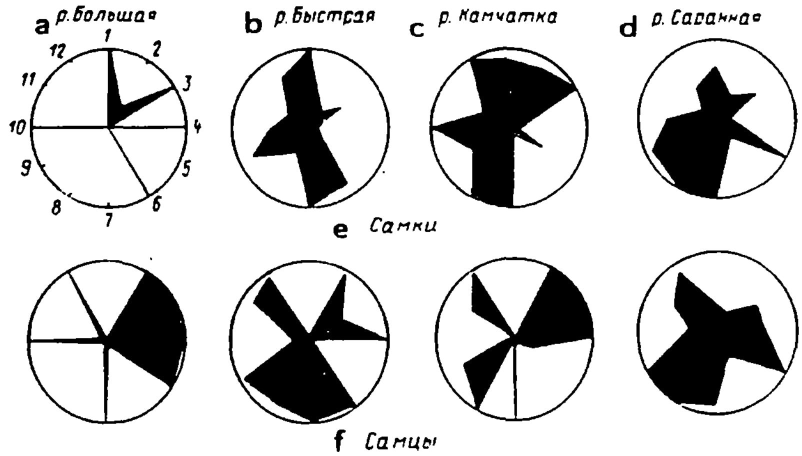

Рис. 25. Соотношение признаков у проходных гольцов из водоемов Камчатки. % встречаемости:

1 — голова закругленная; *2* — верхняя челюсть далеко заходит за задний край глаза; *3* — верхняя челюсть прямая; *4* — крюк и выемка есть; *5* — тело прогонистое; *6* — пятен много; *7* — челюсти равны; *8* — пятна красные; *9* — плавники красные; *10* — бока серые; *11* — брюхо оранжевое; *12* — губы оранжевые

Figure 25. Relationship of features in anadromous chars from the waters of the Kamchatka Peninsula, % occurrence:

1 - rounded head; 2 - upper jaw extends far beyond the posterior margin of the eye; 3 - upper jaw straight; 4 - hook and notch present; 5 - body elongate; 6 - numerous spots; 7 - jaws equal; 8 - red spots; 9 - red fins; 10 - grey sides; 11 - orange belly; 12 - orange lips. a - Bol'shaya River; b - Bystraya River; c - Kamchatka River; d - Sarannaya River; e - females; f - males.

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Characteristics of chars from the basin of the Bol'shaya River. In the basin of this river live anadromous, freshwater lake and lake-river chars. The two latter forms live in Lake Nachikinskoe [206, 215] and occupy completely different niches. Lake char lives exclusively in the lake and does not go beyond its boundaries, and the lake-river char prefers to stay in small rivers and the mouth areas of rivers flowing into a lake. Lake char is larger and lives longer (Table 11). The growth rate of the lake form is faster [215]. It is likely that this is related to the type of food. Lake char is euryphagous and the lake-river char feeds exclusively on benthos. Time of sexual maturity as well as frequency of spawning depend on the nature of the forage and the calorie content of the food consumed. Lake char matures later and does not reproduce annually, while the lake-river char matures earlier and spawns annually. The places for reproduction of these two groupings are different. Lake char reproduces in the lake itself in late autumn and lake-river char reproduces in rivers in August-September.

Sharp differences in ecology were reflected in the outer appearance of chars of both forms and in certain morphological features, mainly related to forage. They differ in size of the mouth and jaws, position of the upper jaw and degree to which the maxillary bone extends beyond the posterior margin of the eye (Figure 26).

In lake chars the maxillare extends far beyond the eye and is positioned at an angle towards the eye, while in the majority of lake-river chars, the maxillare ends at the level of the posterior margin of the eye and is positioned parallel to the eye. Their numbers of pyloric caeca and gill rakers are not identical: lake chars have many and lake-river chars have significantly fewer. The coefficient of difference is very high; for gill rakers it is 1.56 and for pyloric caeca it is 2.30.

11. Biological indicators of different forms of chars inhabiting the waters of the Bol'shaya River basin

Indicator	Bol'shaya River	Bystraya River	Lake Nachikinskoe	
	anadromous	anadromous	lake-river	lake
Body length (cm)	30-59	33-58	20-37	
Weight (gm)	300-2250	450-2000	70-320	230-1620
Maximum age (in years)	8	7	11	16
Time to mature (in years)	—	—	4+	6+
Spawning period	autumn	September	August-beginning of September	late autumn
Spawning frequency	not annually	not annually	annually	not annually
Ratio of the sexes (females to males)	—	1:1	1:1	1:1
Fecundity, number of eggs	—	1375-4800	—	—
Feeding	does not feed	does not feed	benthic	euryphagous, but fish predominate

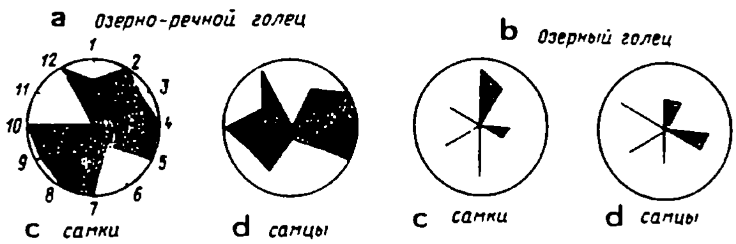


Рис. 26. Соотношение признаков у озерно-речных и озерных гольцов из оз. Начикинское. % встречаемости:

1 — бока серебристые; 2 — брюхо белое; 3 — пятна красные; 4 — плавники красные; 5 — губы ярко окрашены; 6 — спина мраморовидная; 7 — голова закругленная; 8 — верхняя челюсть на уровне или едва заходит за задний край глаза; 9 — верхняя челюсть прямая; 10 — верхняя челюсть узкая; 11 — крюк и выемка на челюстях имеются; 12 — пятна мелкие

Figure 26. Relationship of features in lake-river and lake chars from Lake Nachininskoe, % occurrence:

1 - sides silvery; 2 - belly white; 3 - red spots; 4 - fins red; 5 - lips bright orange; 6 - back marble-like; 7 - head rounded; 8 - upper jaw on same level as or extends slightly beyond the posterior margin of the eye; 9 - upper jaw straight; 10 - upper jaw narrow; 11 - hook and notch present on the jaws; 12 - small spots; a - lake-river char; b - lake char; c - females; d - males.

There is also a noticeable difference in colour. Moreover, there are features which can be considered to a certain degree alternative. Thus, for example, differences are observed in the quantity, dimensions and colour of spots on the sides of the body. In lake chars they are larger and can be white or pink, whereas in lake-river chars they can be orange-red.

The ecological and morphological differences between sympatric populations of lake and lake-river chars from the Lake Nachikinskoe basin are substantial. There are also some differences in karyotype. In lake-river char there are two subtilocentric chromosomes, but they were not found in lake char [215]. According to the data of molecular hybridization of DNA x DNA, lake-river char differs noticeably from sympatric lake chars and char forms from other regions [56].

The results obtained by different methods are evidence of reproductive isolation and strong divergence of sympatric groupings of chars in Lake Nachikinskoe.

Characteristics of chars from the basin of the Kamchatka River. This river is populated by varied forms of chars: anadromous, lake-river, lake, stream, etc. Each form in its turn breaks down into local populations characterized by specific features inherent in it alone.

Anadromous chars were caught in tributaries as well as in the Kamchatka River itself at different times of their migration to spawn, in a dissimilar physiological condition (see Figures 25, 27 and 28).

In addition to the usual anadromous chars, in many rivers of the peninsula, including in the Kamchatka River basin, live small chars, elongate and uniform in appearance, the so-called tysyachniks. They reach a length of 20-45 cm, a weight of 100-350 gm and an age of 4-6 years and they form very numerous concentrations when moving upriver. Their migration to the rivers occurs in early spring. Most likely it is possible to view this as a feeding migration, since they all have immature sexual products. They are younger than the anadromous chars who migrate first to spawn. The opinion exists that these are recruits of anadromous char. It is unknown what the clearly pronounced migrations of the tysyachniks are connected with. Unfortunately, these fish have barely been researched.

Lake-river chars living in the Kamchatka River basin are conventionally divided by preferred biotype into river chars that are found predominantly in large rivers and tributaries, into chars that live mainly in a lake, although they may leave the lake from time to time, and into chars populating equally a lake and a river and freely migrating back and forth.

River chars from the Kamchatka River reproduce in its tributaries and feed, depending on the season, either in the spawning areas or in the river itself, keeping to certain areas of the river without making significant migrations; they winter in the Kamchatka River. A few local populations of these chars are differentiated in the river basin. We studied char populations from the Urtsy and Nikolka Rivers and from Lake Ushkovskoe (Figures 29, 30, 31) [203].

Chars inhabiting Lake Azabach'e (below the flow of the Kamchatka River) apparently, on the whole, reproduce in the lake, as well as winter and feed there. However, it is possible that some of them spawn in the Bushuika River, which flows into the lake, and some of them leave to feed in the Azabach'ya River, etc. Among the Azabach'e chars, two groups of lake-river chars are distinguished which differ sharply in their forage: benthophages, feeding exclusively on mollusks; predators, feeding on fish [118, 203]. These chars are not identical in number. Predators predominate in catches (76%) and benthopages are encountered less frequently (22.4%); individuals with mixed forage make up 1.6 %; fish are very dominant in the food of these individuals and benthos organisms were likely caught by chance. Predator chars are infected by *Diphyllobothrium sp.*; this parasite is not present in the benthophages [111]. According to a number of indicators, the chars of both groups are ecologically clearly differentiated. A certain localization is observed in the distribution of benthophages; they keep mainly to the north-western part of the lake and in the region of the source of the Azabach'ya River, while the predators are found everywhere. The maximum body length of the predators is 75 cm (in the majority of cases 42-48 cm) and that of the benthophages is 55 cm (in the majority of cases 40 cm) [203, 211]; their weight is respectively 4015 gm (in the majority of cases 1000-1500 gm) and 2000 gm (in the majority of cases 800-1000 gm). Both of these chars reproduce predominantly in spring and autumn and possibly some reproduce in the spring. Spawning is quite prolonged and not annual; each time only a small portion of the population spawns [211]. The sexual ratio in the predators is 1:1, but the females predominate among the benthophages. The absolute fecundity of the benthophages is 900-1324 eggs (the average is 1180 eggs) and among the predators it is 1514-2782 eggs (the average is 2019 eggs). Sexual maturity is reached at the age of 5-6 years among the benthophages and, among the predators, the age is 3-4 years. Breeding colours appear during spawning. They are much brighter among the benthophages than among the predators. Predators grow more quickly than benthophages and their life span is longer (up to 15 years). Benthophages live up to 11 years. Among the predators, individuals aged 7+ - 8+ years dominate in the catches and among the benthphages the age is 6+ years. Some differences in karyotype are noted: among the predators, 2n 77-82, mode 80, M and SM 20, NF 100; among the benthophages, 2n 77-82, mode 80, M and SM 18, ST2, NF 98+2 (taking into consideration two smaller arms of subtilocentric chromosomes) [34].

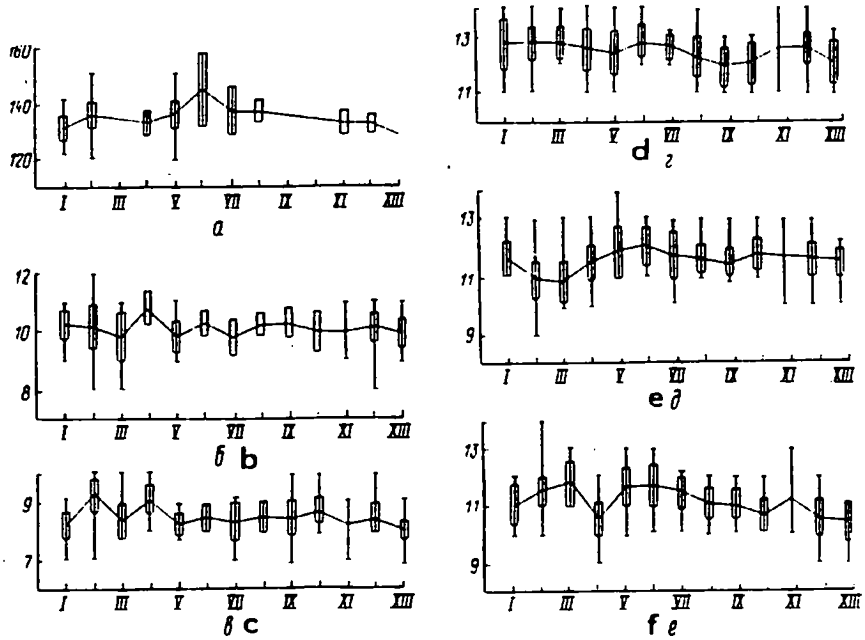
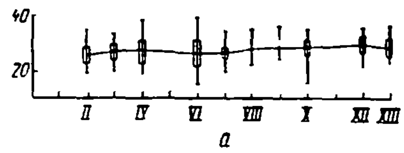


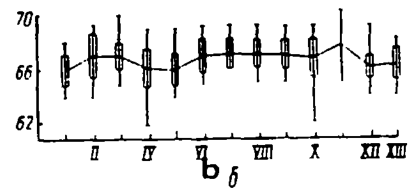
Рис. 27. Меристические признаки (числовые значения) проходных гольцов, обитающих на Камчатке:

а — чешуй в боковой линии; *б* — лучей в спинном плавнике; *в* — лучей в анальном плавнике; *г* — лучей в грудном плавнике; *д* — жаберных лучей справа; *е* — жаберных лучей слева; *I* — р. Квачина; *II* — р. Утхолок; *III* — р. Утхолок (карликовые самцы); *IV* — р. Утка; *V* — р. Большая; *VI* — р. Быстрая; *VII* — р. Быстрая (карликовые самцы); *VIII* — р. Николка; *IX* — р. Радуга; *X* — р. Камчатка; *XI* — р. Большая (тысячники); *XII* — р. Паратунка; *XIII* — р. Паратунка (карликовые самцы)

Figure 27. Meristic features (numerical values) of anadromous chars inhabiting the Kamchatka Peninsula:

a - scales on the lateral line; b - rays on the dorsal fin; c - rays on the anal fin; d - rays on the thoracic fin; e - branchiostegals on the right; f - branchiostegals on the left; I - Kvachina River; II - Utkholok River; III - Utkholok River (dwarf males); IV - Utka River; V - Bol'shaya River; VI - Bystraya River; VII - Bystraya River (dwarf males); VIII - Nikolka River; IX - Raduga River; X - Kamchatka River; XI - Bol'shaya River (tysyachniks); XII - Paratunka River; XIII - Paratunka River (dwarf males)





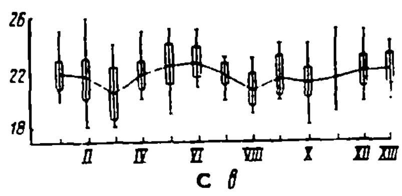


Рис. 28. Меристические признаки (численные значения) проходных гольцов, обитающих в р. Камчатке:

а — пилорических придатков; б — позвонков; в — жаберных тычинок; I — р. Квачина, II — р. Утхолок; III — р. Утхолок (карликовые самцы); IV — р. Утка; V — р. Большая; VI — р. Быстрая; VII — р. Быстрая (карликовые самцы); VIII — р. Николка; IX — р. Радуга, X — р. Камчатка; XI — р. Большая (тысячник); XII — р. Паратунка; XIII — р. Паратунка (карликовые самцы)

Figure 28. Meristic features (numerical values) of anadromous chars living in the Kamchatka Peninsula:

a - pyloric caeca; b - vertebrae; c - gill rakers; I - Kvachina River; II - Utkholok River; III - Utkholok River (dwarf males); IV - Utka River; V - Bol'shaya River; VI - Bystraya River; VII - Bystraya River (dwarf males); VIII - Nikolka River; IX - Raduga River; X - Kamchatka River; XI - Bol'shaya River (tysyachniks); XII - Paratunka River; XIII - Paratunka River (dwarf males)

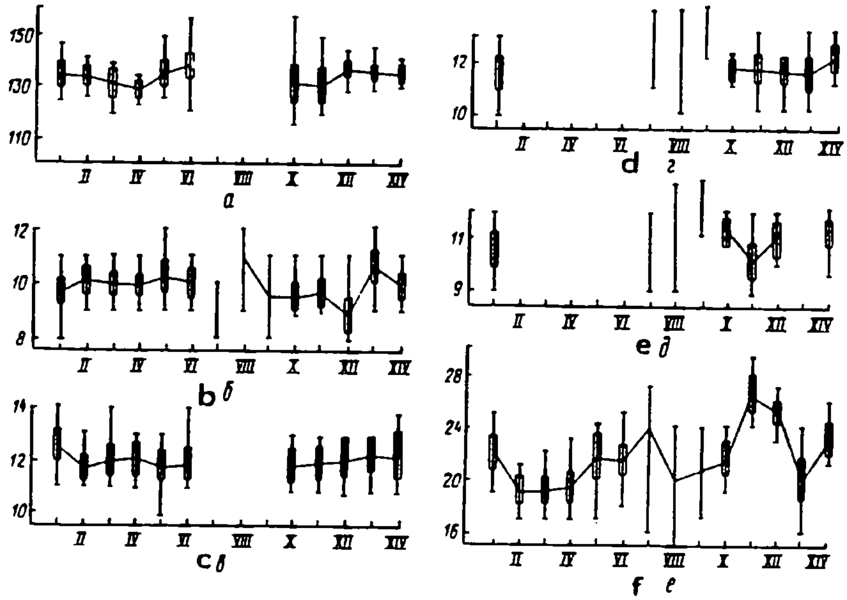


Рис. 29. Меристические признаки (числовые значения) пресноводных гольцов, обитающих на Камчатке.

а — лучей в боковой линии; *б* — лучей в спинном плавнике; *в* — лучей в грудном плавнике; *г* — жаберных лучей справа; *д* — жаберных лучей слева; *е* — жаберных тычинок; *I* — р. Дальняя; *II* — р. Урцы; *III* — р. Николка; *IV* — оз. Ушковское; *V* — оз. Азабачье (бентофаги); *VI* — оз. Азабачье (хищники); *VII* — оз. Начикинское (озерно-речной голец); *VIII* — оз. Кроноцкое (носатый голец); *IX* — оз. Кроноцкое (белый голец); *X* — оз. Кроноцкое (длинноголовый голец); *XI* — оз. Дальнее (озерный голец); *XII* — оз. Начикинское (озерный голец); *XIII* — р. Пономарка (ручьевой голец); *XIV* — р. Камчатка (каменный голец)

Figure 29. Meristic features (numerical values) of freshwater chars inhabiting the Kamchatka Peninsula:

a - rays on the lateral line; b - rays on the dorsal fin; c - rays on the thoracic fin; d - branchiostegals on the right; e - branchiostegals on the left; f - gill rakers; I - Dal'nyaya River; II - Urtsy River; III - Nikolka River; IV - Lake Ushkovskoe; V - Lake Azabach'e (benthophages); VI - Lake Azabach'e (predators); VII - Lake Nachikinskoe (lake-river char); VIII - Lake Kronotskoe (long-nosed char); IX - Lake Kronotskoe (white char); X - Lake Kronotskoe (long-headed char); XI - Lake Dal'nee (lake char); XII - Lake Nachikinskoe (lake char); XIII - Ponomarka River (stream char); XIV - Kamchatka River (stone char)

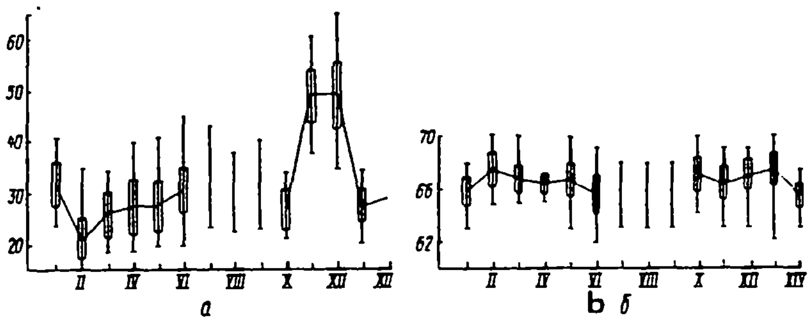


Рис. 30. Меристические признаки (числовые значения) пресноводных гольцов, обитающих на Камчатке:

а — пилорических придатков; *б* — позвонков; *I* — р. Дальняя; *II* — р. Урцы; *III* — р. Николка; *IV* — оз. Ушковское; *V* — оз. Азабачье (бентофаги); *VI* — оз. Азабачье (хищники); *VII* — оз. Начикинское (озерно-речной голец); *VIII* — оз. Кроноцкое (носатый голец); *IX* — оз. Кроноцкое (белый голец); *X* — оз. Кроноцкое (длинноголовый голец); *XI* — оз. Дальнее (озерный голец); *XII* — оз. Начикинское (озерный голец); *XIII* — р. Пономарка (ручьевой голец); *XIV* — р. Камчатка (каменный голец)

Figure 30. Meristic features (numerical values) of freshwater chars inhabiting the Kamchatka Peninsula:

a - pyloric caeca; b - vertebrae; I - Dal'nyaya River; II - Urtsy River; III - Nikolka River; IV - Lake Ushkovskoe; V - Lake Azabach'e (benthophages); VI - Lake Azabach'e (predators); VII - Lake Nachikinskoe (lake-river char); VIII - Lake Kronotskoe (long-nosed char); IX - Lake Kronotskoe (white char); X - Lake Kronotskoe (long-headed char); XI - Lake Dal'nee (lake char); XII - Lake Nachikinskoe (lake char); XIII - Ponomarka River (stream char); XIV - Kamchatka River (stone char)

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Рис. 31. Соотношение признаков у пресноводных гольцов из водоемов бассейна р. Камчатки, % встречаемости:

1 — голова закругленная; *2* — верхняя челюсть прямая; *3* — верхняя челюсть на уровне заднего края глаза или не доходит до глаза; *4* — челюсти равны; *5* — крюк и выемка имеются; *6* — тело прогонистое; *7* — бока серебристые; *8* — пятна округлые; *9* — пятен много (более 30); *10* — губы окрашены; *11* — брюхо белое; *12* — плавники окрашены

Figure 31. Relationship of features in freshwater chars from the waters of the Kamchatka River basin, % occurrence:

1 - rounded head; 2 - upper jaw straight; 3 - upper jaw at the level of the posterior margin of the eye or does not extend to the eye; 4 - jaws equal; 5 - hook and notch present; 6 - body elongate; 7 - sides silvery; 8 - roundish spots; 9 - many spots (more than 30); 10 - lips coloured; 11 - belly white; 12 - fins coloured; a - Urtsy River; b - Nikolka River; c - Lake Ushkovskoe; d - Lake Azabach'e (benthophage); e - Lake Azabach'e (predator); f - stream char; g - stone char.

No differences were discovered between Azabach'e chars in the antigen composition of the blood serum [88]. Both populations differ according to blood groups. In the great majority of benthophages, the erythrocytes adhere with normal pig's serum; among the predators, the percentage of individuals having erythrocytes that adhere is less [35]. Reliable differences between populations in a percentage of individuals with different blood groups is evidence of possible reproductive isolation.

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Sympatric populations of Azabach'e chars are very similar in phenotype [203]. According to morphological features studied with regular methods, differences were not revealed. For this purpose, S.Sh. Bagiryan [14] used computer classification methods. According to the entire set of 29 plastic and 8 merisitc features we used, according to the method of main components, an evaluation of general similarity revealed two strongly overlapping areas where only extreme variants were distinguishable. We were able to separate the sympatric chars only with the help of a regression equation, using only a few of the most informative features (l_{md}, io, r, HC_3, H, o, AV). As a result, one inaccurate definition was noted. However, the results obtained give no basis for conclusions concerning the taxonomic relationship of these chars.

Some differences between benthophages and predators are noted according to a conservative morphological feature such as the structure of the seismosensory system [243]. They also differ in certain osteological features [141]. These differences amount to a different frequency of occurrence of the structural types of three skull elements: the number of rows of teeth on the basibranchiale, the shape of the suboperculum and the shape of the upper edge of the hyomandibulare. As a whole, both groupings of chars represent a fairly uniform group; however, this does not exclude the possibility of reproductive isolation between sympatric forms in Lake Azabach'e [141].

Some differences are observed between groupings in the following features: colour (see Figure 31), shape of the body and head, growth rate, body length and peculiarities of fat metabolism [137]. A significant difference between them is displayed only in type of food. Such a differentiation is characteristic of chars. Clear differences in food are observed in different intraspecific forms [207], in different populations of the same form [24] and even practically in the same population [324]. However, as a rule, they are accompanied by morphological and physiological differences and most of all by differences in the number of gill rakers and pyloric caeca [24, 198, 324]. In this case, there was no reliable difference found in the number of rakers and caeca in populations with different feeding habits.

In Azabach'e populations of chars, morphological differences related to feeding habits are also not clearly expressed externally. The shape of the head, position of the mouth and structure of the jaw are similar overall. But still, individuals with a protruding upper jaw dominate in the benthophagous group and it is possible to view this as a certain tendency to form an inferior or semi-inferior mouth. The shape of the mouth and teeth in both forms are characteristic of 79
predators. It is possible that phylogenetically malacophagy is a secondary phenomenon. It is worth paying attention to the fact that benthophages differ from predatory chars with their smaller head and deeper body, which is in general characteristic of benthophagous salmons. Organs formed of soft tissues differ much more. Significant differences are exhibited in the structure of the digestive tract [41]. The length of the entire digestive tract differs greatly: from 133.5% in the benthophages to 86.7% in the predators. The shape of the stomach is also not uniform. The cardial branch of the stomach is better developed in predatory chars. In benthophages the pyloric section differs not only in greater relative length, but in significantly greater diameter and thicker walls. The mechanical function of the pyloric section is particularly important in these chars if one takes into account that their teeth are not specifically adapted for malacophagy. The digestive function of the pyloric section is secondary in these fish; more complex branching mucous pyloric glands protect the mucous membrance from damage by shells. There are major glands with a simple structure in the pyloric section of the predators. In mollusk eaters the intestine itself is

longer, which is in general characterisitic of fish where ballast in the form shells, cellulose, etc. dominates their food [41].

Thus, significant anatomical differences undoubtedly exist between the two sympatric groupings of chars in Lake Azabach'e. Nevertheless, many questions remain unclear and mainly the question of when the divergence in food occurs; does it occur within one population or are we dealing with two reproductively isolated groups of chars?

T. Kubo [324] reports a divergence in food in two groups of chars within a single population of one intraspecific form of *S. malma*. In his opinion, the young of char populating a river flowing into Lake Sikaribetsu give rise to a common anadromous form foraging in the sea, a lake form foraging in the open part of the lake and feeding on zooplankton and a lake form populating coastal shallow waters and consuming benthos organisms. But all of these groups differ in colour and certain physiological indicators. They emerge as a temporary phenomenon in some circumstances related to the young fishes' turning into smolts under certain illumination and they are viewed as part of a flock of a typical anadromous form.

It is possible that the predators and benthophages examined in this study belong to one population. But it is possible to suppose that these are two isolated populations and that their joint existence may be the result of one of the forms moving in. It is also valid to propose that these are two groups isolated in a joint habitat and occupying different ecological niches. 80

It is characteristic for each population that there be combinations of features specific to that population and that some of the features be dominant. Populations also differ from one another in the frequency of occurrence of these features. Differences in meristic features between populations are not uniformly expressed (see Figures 29, 30). The population of Azabach'e predators is different. Reliable differences in t_{st} are observed in this population with Urtsy chars (in all features except *ll*), with Nikolka chars (in all features), with Ushkovskoe chars (in all features except pyloric caeca). Only with the benthophages are reliable differences established in one feature alone: the number of vertebrae. Differences between the remaining populations are not so clearly pronounced and they involve a smaller number of features.

In spite of existing differences between populations, the extent of these differences is small. The coefficient of difference in all cases is less than 1.28 and its corresponding percentage of non-overlapping of partially overlapping curves does not exceed 87% [203].

According to plastic features, it is possible to compare only Azabach'e populations of chars, since in the other cases it is impossible to eliminate the influence of size variability. Azabach'e populations are noticeably different from one another ($t_{st} > 3$) in head proportions and sizes. However, $CD < 1.28$ and this is evidence of the external similarity of the populations studied [203].

Thus, the absolute and relative values of the features of all char populations overlap noticeably and significant differences between them cannot be established.

Characteristics of stream chars from the Kamchatka River basin. There is only sparse information on stream chars. There is fragmentary data on the systematics and biology of the stream form from southern regions of the habitat in A.Ya. Taranets [239], L.S. Berg [24] et al; only S.P. Krasheninnikov [119] mentions stream chars from the waters of the Kamchatka Peninsula. Their detailed characteristics are provided in the work of K.A. Savvaitova and N.S. Romanov [209]. According to their data, the stream char populates the entire length of rivers and streams flowing into Lake Azabach'e. It is distributed unevenly along the flow of small rivers and dominates in the upper flow, unlike the young lake-river form, and is particularly rare in the regions of river mouths. An analogous distribution in rivers is characteristic for dwarf forms of a number of salmons, particularly for dwarf males [24]. 81

The stream char is sympatric with the fry of the lake-river form and is externally very similar to it in form. Nevertheless, there is no doubt of the differences that exist between them. They are mainly exhibited in: the distribution habits of fish along the river, nonuniform gonad maturity coefficients, the different age composition of catches, a nonuniform growth rate (Table 12), and the varying condition of the pituitary [209].

12. Biological indicators of chars of different forms inhabiting the Lake Azabach'e basin

Indicator	stream char	young lake-river char
Body length (cm)	9-24	7-24
Weight (gm)	80	5-133
Maximum age (in years)	9	4+
Time to mature (in years)	2+ - 4+	—
Spawning period	July-September	—
Fecundity, number of eggs	165-346	—
Ratio of the sexes (females to males)	1:1	—
Feeding	benthophagous	benthophagous
Growth rate	high	lower than in dwarf char

With the stream char, an active secretion of gonadotropins begins during the reproductive period. In the young lake-river char, on the other hand, an intensive release of growth hormone is noticed. It is likely that the higher growth rate in the fry is related to the increased somatotropic function of the pituitary [209]. In comparison with the fry, the stream char has brighter and more pronounced colouring, longer upper jaw bone, fins and lower jaw, and a wider forehead. It sometimes has a developed growth on the lower jaw and a notch on the upper jaw. It is also different in the number of vertebrae and pyloric caeca (see Figures 29 and 30). However, as a whole, the differences are small between the stream char and the young of the lake-river form. Therefore, it is possible that a small number of immature stream chars could have appeared in the fry samples. The similarity of these chars with fry may be caused by their unity. Dwarf stream forms may form from some of the fry of the lake-river char under condition that they are detained in small rivers. Examples of similar links are well known among salmons [18, 24]. However, it is highly probable that these forms are well isolated from one another.

Stream char from the Azabach'e River basin is similar to the stream form living in more southern regions, *S. malma morpha curilus auct*, but they are significantly different in certain meristic features [24, 239]. The southern form has far fewer vertebrae and scales on the lateral line, which is probably a consequence of geographic variability [209]. 82

Characteristics of stone char from the Kamchatka River basin. Stone char is attributed to forms of char that are few in number, predominantly river forms, rarely found and scarcely researched. S.P. Krasheninnikov was the first to mention stone chars [119]. He writes: "...they are dark in colour; the belly is red; teeth are large; the lower half of the nose is bent with a bump and they appear to be a separate species". This description applies to large fish 70 cm in length. It is known that a few forms of chars live in the Anadyr' region and the average char among them, or the "stone Dolly varden" is 60 cm long [24]. This is the extent of the information on stone chars.

According to our data, this char is not numerous in the Kamchatka River basin. It rarely stays in one place and occurs everywhere from the upper reaches to the mouth of the river. It is more common in the average flow of the river and in the area of the tributaries of the Kozyrevka and Bystraya Rivers. It prefers different biotypes in different seasons. Body length of the males is 27.1-59.5 cm (48.6) and that of the females is 28.5-50.5 cm (46); weight is respectively 200-2150 gm (1260) and 230-1470 gm (1124). The age of the fishes caught was 5+ - 11+ years; males predominate in the 9-10+ age group and females in the 9+ age group. In growth rate, this form is close to anadromous chars [210]. These fish spawn at the end of summer and in the autumn, mainly in the Kamchatka River channel itself. In the majority of cases (males 83.4% and females 80%), in July-August the gonads are at the III-IV and IV stages of maturity. Judging by the state of the gonads, stone chars do not reproduce annually. Their fecundity consists of 1602-2624 eggs (2160 eggs on average). The eggs are large, pale yellow and up to 5 mm in diameter. It is a solitary predator and is reminiscent of the taimen in its way of life. The shape of the head and body, the large mouth, abundance of teeth and the short intestine are due to the nature of its food [210]. The skull structure is quite similar to that of the anadromous, lake and lake-river forms of chars [195, 210]. Karyotypes: 2n 80-86; mode 82-84; M and SM 16-18; NF 100 [34].

A.Ya. Taranets called the freshwater form of char from Lake Ushkovskoe *S. malma infr. kuznetzovi*. According to his data, these fish have the following features: *ll* 137-139; *r.b.* 11-12; *sp. br* 18-25; *vt* 62-66 (in the majority of cases 65); blunt and rounded snout; only the males have a growth on the lower jaw and a notch on the upper jaw during spawning and these are much less evident than in the typical form; characteristically noticeable increase in abdominal and thoracic fins; the body is more brightly coloured and covered in larger red spots. According to the description of A.Ya. Taranets [239], the form living in Lake Ushkovskoe is not similar to the 83

stone char that we studied. It is interesting that the author himself did not take it to be a stone char, since he considered that, on the Kamchatka Peninsula, in the Anadyr' region and in the Sea of Okhotsk basin, numerous forms of Dolly varden are differentiated, known under the name of "stone char", "osetinets", etc. However, the pattern on the body of the Kuznetsov Dolly varden is very similar to the pattern on stone chars. Therefore, we proposed that A.Ya. Taranets knew of the local name of the fish. Familiarity with the samples kept at the Zoological Institute of the USSR Academy of Sciences according to which he described this form confirmed our hypothesis that A.Ya. Taranets dealt with the stone char. One of two fish under No. 26888 did not differ in its features from those that we studied, but the second sample was of the ordinary lake-river form. It is possible that, in his description of *S. m. infr. kuznetzovi*, A.Ya. Taranets included the features of both samples, which are attributed to different forms. Therefore, his description does not coincide with ours. This is highly probable, since the stone char is very rare in Lake Ushkovskoe and the local residents are not familiar with it. In this connection, it is not likely possible to fully identify the Kuznetsov Dolly varden with the form that we described.

Characteristics of lake-stream chars from Lake Kronotskoe. R.M. Viktorovskii considers that the following chars exist in Lake Kronotskoe, separated from the Kronotskaya River by a waterfall: an endemic species of char, the long-headed char (*S. kronocius Viktorovsky*); an endemic subspecies, the long-nosed char (*S. malma schmidti Viktorovsky*) and a local population of Dolly varden, the white char [43]. In later studies, R.M. Viktorovskii, in the wake of M.K. Glubokovskii, attributes the white char to the species *S. albus* [43, 188].

Chars from Lake Kronotskoe are truly very interesting in finding a solution to the questions of taxonomy and the emergence of forms in this group of fishes and probably more than one generation of researchers will come back to these chars. Since there is no traditional ichthyological description of the forms he separated in R.M. Viktorovskii's work and since such a description is essential for comparison with chars from other regions, we were obliged to conduct a new study of external morphology according to his materials.

The long-headed and white chars are large fishes and similar in size. In comparison with them, the long-nosed char is much smaller (Table 13). Some differences in preferred biotype are noted [43]. The long-headed char occurs in the lake in very deep waters; the white char inhabits the entire lake and the long-nosed char is numerous in shallow waters, both in the lake and in streams. They all reproduce at the same times: during the second half of the summer and in the autumn. However, there is data indicating that the chars of Lake Kronotskoe also reproduce in the spring [120]. Only the spawning areas of the long-nosed char are known. It reproduces in large rivers (the Listvenichnaya, Unana and Uzon Rivers) that flow into the lake. The white char reproduces in the lake and in rivers. According to what S.I. Kurenkov observed, the white char also migrates to the Listvenichnaya River to spawn. The long-nosed char also swims up into this river to spawn, reproduces in the lake itself and possibly in the numerous streams [43]. 84

13. Biological indicators of different forms of chars inhabiting Lake Kronotskoe [43]

Indicator	long-headed char	white char	long-nosed char
Body length (cm)	50-60, up to 70	60-80, up to 86	30-40, up to 50
Maximum age (in years)	—	up to 16+*	—
Time to mature (in years)	—	6-8	—
Spawning period	end of August - middle of September	end of July - middle of December	middle of August until freezing-over
Feeding	specialized predator	benthophage up to 48-50 cm in length; larger individuals feed on fish	—

* According to the data of T.L. Vvedenskaya

Unfortunately, very little is known concerning the nature of spawning, its frequency, fecundity, age composition, growth rate and time of sexual maturity of the chars. Existing information involves only the white and long-nosed chars. The long-headed and white chars are similar in type of food; these are predators feeding on fish and insects. The long-losed char is benthophagous.

As a rule, the chars from the lake and the Kronotskoe River differ in external appearance. However, these differences are not expressed clearly enough in all cases. Familiar difficulties arise in differentiating the long-nosed and white chars. They may not be distinguishable according to their breeding colours, which can be well-pronounced in both forms. Therefore, it is better to compare these forms using materials that are uniform as concerns physiology and sizes. Unfortunately, there were no comparable samples of large individuals (>40 cm) in the materials available to us, since all long-nosed chars had gonads at the IV and II-VI stages of maturity, and among the white chars, only one male had fluid sexual products; the other fish had immature sexual products. In connection with this we made a comparison of small (20-40 cm) long-headed and white chars (Figure 32). Judging by the description of R.M. Viktorovskii [43] these chars also did not differ significantly in colour; only in the white chars does colour vary more widely. 85

In breaking down the material according to sizes, sex and condition of the sexual products, there was not enough material to calculate regular statistical characteristics. Therefore, we presented the data we obtained in scatter diagrams (Figures 33, 34, 35). Small chars do not differ in head length. Among the female long-headed and female white chars, relative head sizes do not change with an increase in body length. In the males of both forms, head length increases sharply and this is undoubtedly connected with the development of breeding colours. In this respect the name "long-headed" is justified for both forms. Both forms differ fairly noticeably in snout length (see Figure 33). There is a certain overlapping between the small chars, but almost none between the large chars. Moreover, among the white char females, snout length does not change with an increase in body size, whereas among the long-headed char females and males snout length increases significantly. The latter fact is possibly related to the development of breeding colours among sexually mature males and females. Unlike R.M. Viktorovskii [43], we propose that there are breeding changes among the long-headed char females and that these changes are exhibited in the lengthening of the ethmoidal section of the head and the growth of the cartilage at the end of the head, due to which the conical head is somewhat rounded. The males have a hook and notch on the jaws, but these are absent or barely discernible in the females, which creates the illusion that they have no breeding colours.

Рис. 32. Соотношение признаков гольцов, обитающих в оз. Кроноцкое. % встречаемости:

1 — голова коническая, закругленная на конце; 2 — верхняя челюсть на уровне заднего края глаза; 3 — верхняя челюсть прямая; 4 — челюсти равны

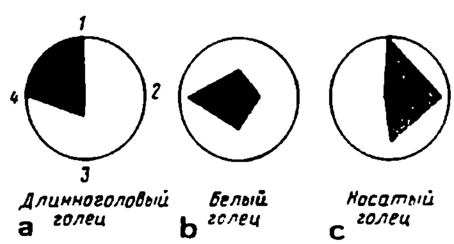

Figure 32. Relationship of the features of chars inhabiting Lake Kronotskoe, % occurrence:

1 - conical head, rounded at the end; 2 - upper jaw extends to the posterior margin of the eye; 3 - upper jaw straight; 4 - jaws equal; a - long-headed char; b - white char; c - long-nosed char

The long-headed and white chars do not differ in head depth. There are also no differences in the development of breeding colours. This does not correspond to the data of R.M. Viktorovskii [43] which indicates that there is a noticeable hiatus in this feature. We were not able to obtain such data. Our results coincide with his data on other features. There were no differences in head width or distance behind the eye. Small long-headed chars and white chars differed insignificantly on the length of the upper and lower jaws. The differences were greater between the large fish (see Figures 33 and 34). Moreover, in the white char females the length of the jaws does not change in proportion to an increase in body length; in both sexes of the long-headed chars and in the white char males, the length of the jaws increases. It is probable that this is connected with the development of breeding colours in sexually mature fish. 86

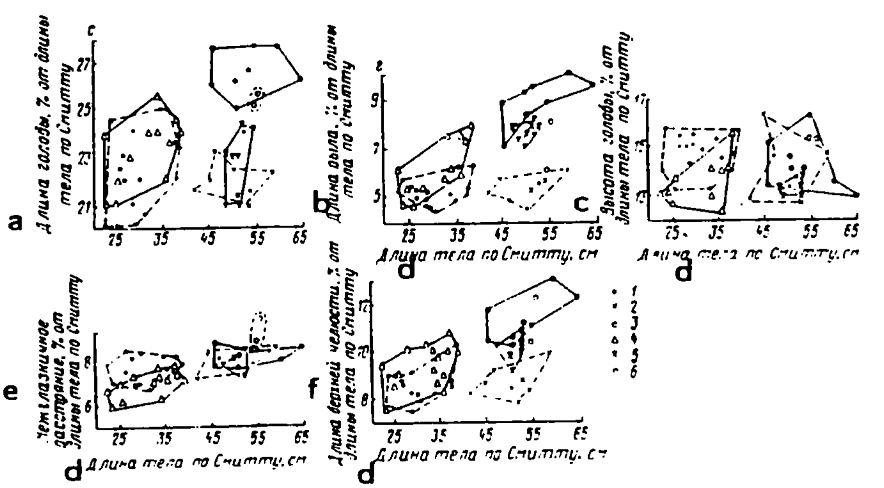

Рис. 33. Соотношение длины тела и некоторых признаков форм гольцов, обитающих в оз. Кроноцкое:
1 — белый, неполовозрелый; 2 — белый, самки; 3 — белый, самцы; 4 — длинноголовый, неполовозрелый; 5 — длинноголовый, самки; 6 — длинноголовый, самцы

Figure 33. Relationship of body length and some features of char forms inhabiting Lake Kronotskoe:

1 - white, sexually immature; 2 - white, females; 3 - white, males; 4 - long-headed, sexually immature; 5 - long-headed, females; 6 - long-headed, males

a - head length, % of body length (Smitt); b - snout length, % of body length (Smitt); c - head depth, % of body length (Smitt); d - body length in cm (Smitt); e - interorbital space, % of body length (Smitt); f - upper jaw length, % of body length (Smitt)

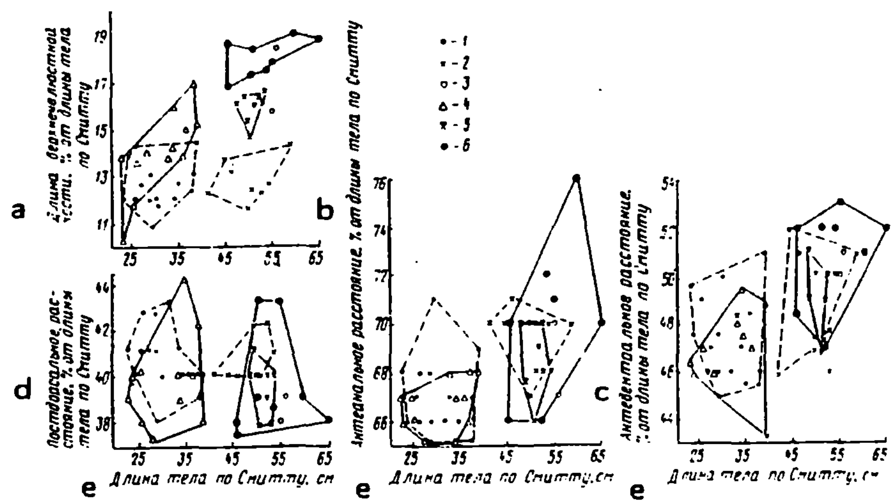

Рис. 34. Соотношение длины тела и некоторых признаков форм гольцов, обитающих в оз. Кроноцкое:

1 — белый, неполовозрелый, 2 — белый, самки; 3 — белый, самцы; 4 — длинноголовый, неполовозрелый; 5 — длинноголовый, самки; 6 — длинноголовый, самцы

Figure 34. Relationship of body length and some features of char forms inhabiting Lake Kronotskoe:

1 - white, sexually immature; 2 - white, females; 3 - white, males; 4 - long-headed, sexually immature; 5 - long-headed, females; 6 - long-headed, males

a - upper jaw length, % of body length (Smitt); b - anteanal distance, % of body length (Smitt); c - anteventral distance, % of body length (Smitt);. d - postdorsal distance, % of body length (Smitt); e - body length in cm (Smitt)

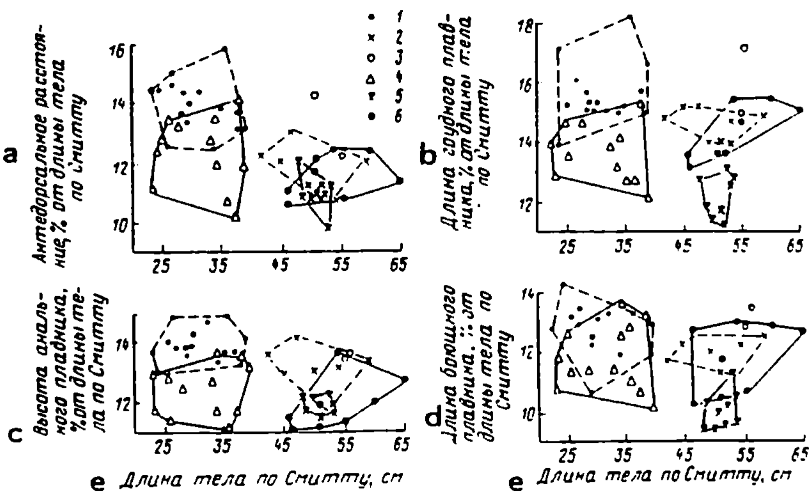

Рис. 35. Соотношение длины тела и некоторых признаков форм гольцов, обитающих в оз. Кроноцкое:

1 — белый, неполовозрелый; *2* — белый, самки; *3* — белый, самцы; *4* — длинноголовый, неполовозрелый; *5* — длинноголовый, самки; *6* — длинноголовый, самцы

Figure 35. Relationship of body length and some features of char forms inhabiting Lake Kronotskoe:

1 - white, sexually immature; 2 - white, females; 3 - white, males; 4 - long-headed, sexually immature; 5 - long-headed, females; 6 - long-headed, males

a - antedorsal distance, % of body length (Smitt); b - length of thoracic fin, % of body length (Smitt); c - depth of anal fin, % of body length (Smitt); d - length of abdominal fin, % of body length (Smitt); e - body length in cm (Smitt)

These two forms of chars differ only slightly in smallest body depth and postdorsal distance; there has been a great deal of overlapping (see Figure 34) There are very small differences between the small long-headed and white chars in anteventral and anteanal distances. However, in both forms there is a certain tendency for the abdominal and anal fins to be shifted towards the caudal (in larger chars) (see Figures 34 and 35). There are noticeable differences between the long-headed and white chars in the depth of the dorsal and anal fins and in the length of the thoracic fins. With an increase in body length, the relative length of these fins decreases in both forms (see Figure 35).

Thus, according to plastic features, differences between long-headed and white chars are exhibited in certain proportions of the head (length of the snout and jaws), which are mainly related to the development of breeding colours, and in the length of the dorsal, anal and thoracic fins. Differences in the latter may be determined by a nonuniform growth rate. No differences are noted in meristic features (see Figures 29 and 30) [43].

The long-nosed char differs from the two forms studied mainly with its small mouth. Its upper jaw bone is short (see Figure 32) and, in the majority of cases, it is level with the margin of the eye; when it is bent, then the protuberance is downward. The upper jaw often hangs over the lower jaw. In most cases, there is a cartilagineous outgrowth or "nose" on the upper jaw. The shape of the lower jaw varies from sharply angular to flat. There is a "hump" behind the head. Breeding colours are almost unevolved. Compared with the uniform in size long-headed and white chars, the long-nosed char has a shorter head and snout, a small distance behind the eye, shorter upper and lower jaws, a deeper caudal peduncle, a greater dorsal fin base, and longer, dorsal, anal and abdominal fins (Table 14). The long-nosed char does not differ from the other forms in merisitc features [43].

Our data indicate the strong proximity of the long-nosed char and the white char; it is difficult to differentiate certain examples that are similar in size. It differs to a great degree from the long-headed char (see Figures 33-35).

A limited amount of material and the fact that the available samples are not representative do not permit us to use the usual statistical techniques and obtain indicators characterizing the properties of the general population. This difficulty can be overcome to a certain extent by using multivariate statistical methods. S.SH. Mikhailova conducted the appropriate research at our request. Each sample char acts as a separate subject of comparison with its individual set of features; a comparison is made with all measured features at the same time. This removes the influence of the averaging of data that lowers informativeness as well as the subjective motifs determined by the experience, goals and viewpoints of the researcher. The results obtained permit an objective assessment of the degree of nonuniformity of the group being studied, in this case 90

of the relationship of the phenotypes of chars inhabiting Lake Kronotskoe. The method of main components gives a sufficiently clear representation of this; in using this method, we obtain miniumum distortion of the projection of relative arrangement of objects from a multivariate space to a space of decreased dimensions. The axes of the new space (the main components) are the actual vectors of the covariance matrix. The first component is the most informative; it represents the greatest part of the overall dispersion. The informativeness of the subsequent components decreases. The degree of morphological nonuniformity of chars from Lake Kronotskoe is evident in Figure 36 in the space of the first three main components that determine the linear combinations of twenty-two plastic and three meristic (number of branchiostegals on the right and the left and number of gill rakers) features. The first main component represents 33.17% of the overall dispersion; the second represents 13.46% and the third 7.64%. In analyzing the relative arrangement of chars on the plane of the first and second main components (see Figure 36a), the absence of clear differences between the char forms isolated by R.M. Viktorovskii [43] is noticed first. The existing differences are not so great that it would be possible to draw boundaries between the chars with fair certainty. The chars that differ most from one another are the long-headed and long-nosed chars. White chars occupy an intermediate position between these two forms and are closer to the latter form. If we turn out attention to the nature of the distribution of males, females and sexually immature individuals (among long-nosed chars, all individuals where the sex is unknown are attributed to the latter group; the sex was determined only in the samples dissected by R.M. Viktorovskii) in the overall set of subjects, then the following image appears: the fish that differ the most from all the others are male long-headed chars, which have clearly evident breeding changes. With respect to the long-headed char females and sexually immature individuals, it is quite difficult and, in some cases simply impossible, to distinguish them from analogous groups of white char. There were only two males with breeding colours in the white char group and they appeared fairly similar to the long-headed char males. The sexually immature white chars, being similar to the analogous group of long-headed chars, also appeared to be phenotypically very close to the long-nosed chars, which had no discernible differences between the males, females and sexually immature fish. In Figure 36b the arrangement of chars is apparent on the plane of the first and third main components. Here the first main component also has the major dividing influence and the image observed does not significantly differ from that represented in Figure 36a. In both cases, it is possible to note on the diagram such concentrations of points where all three forms of chars are mixed together. There is no separation at all in the projection on the plane of the second and third main components.

Thus, the comparison of char forms using different methods (univariate and multivariate) leads to identical results and does not provide any basis for the claim that there are clear differences of taxonomic rank between the chars from Lake Kronotskoe.

14. Plastic features of chars inhabiting Lake Kronotskoe

Feature	Form	Distribution series of feature values
Body length in cm (Smitt)		15—20—25—30—35—40—45
	long-headed char	— 3 2 3 4 —
	white char	— 2 6 3 5 —
	long-nosed char	1 4 7 10 9 5
Snout length, % of body length		3—4—5—6—7—8
	long-headed char	— 2 4 2 4
	white char	— 8 6 2 —
	long-nosed char	— 8 6 2 —
Head length, % of body length		18—19—20—21—22—23—24—25—26
	long-headed char	— — — 3 2 2 4 1
	white char	— — 3 3 3 3 2 2
	long-nosed char	3 3 12 11 7 — — —
Distance behind the eye, % of body length		10—11—12—13—14—15
	long-headed char	— 1 7 2 2
	white char	— 1 3 10 2
	long-nosed char	2 14 18 2 —
Maxillary bone length, % of body length		5—6—7—8—9—10—11
	long-headed char	— — 1 2 4 5
	white char	— — 3 9 3 1
	long-nosed char	3 9 18 5 1 —
Lower jaw length, % of body length		8—9—10—11—12—13—14—15—16—17
	long-headed char	— — 1 1 — 4 2 2 2
	white char	— — 1 2 7 4 2 — —
	long-nosed char	1 8 18 7 2 — — — —
Smallest body depth, % of body length		6—7—8—9—10
	long-headed char	4 8 — —
	white char	2 10 4 —
	long-nosed char	1 14 20 1
Length of dorsal fin base, % of body length		9—10—11—12—13—14
	long-headed char	2 4 4 2 —
	white char	— 3 7 5 1
	long-nosed char	— 3 15 17 1
Dorsal fin height, % of body length		11—12—13—14—15—16—17—18
	long-headed char	2 1 5 3 1 — —
	white char	— — 2 6 6 2 —
	long-nosed char	1 1 7 16 6 4 1
Anal fin height, % of body length		11—12—13—14—15—16
	long-headed char	6 2 5 — —
	white char	— — 10 6 —
	long-nosed char	— 4 9 18 4
Thoracic fin length, % of body length		11—12—13—14—15—16—17—18—19
	long-headed char	— 3 3 5 1 — — —
	white char	— — — 1 11 2 1 1
	long-nosed char	— 2 2 6 6 10 6 3
Abdominal fin length, % of body length		10—11—12—13—14—15
	long-headed char	3 5 2 2 —
	white char	1 2 7 5 1
	long-nosed char	— 5 12 13 6

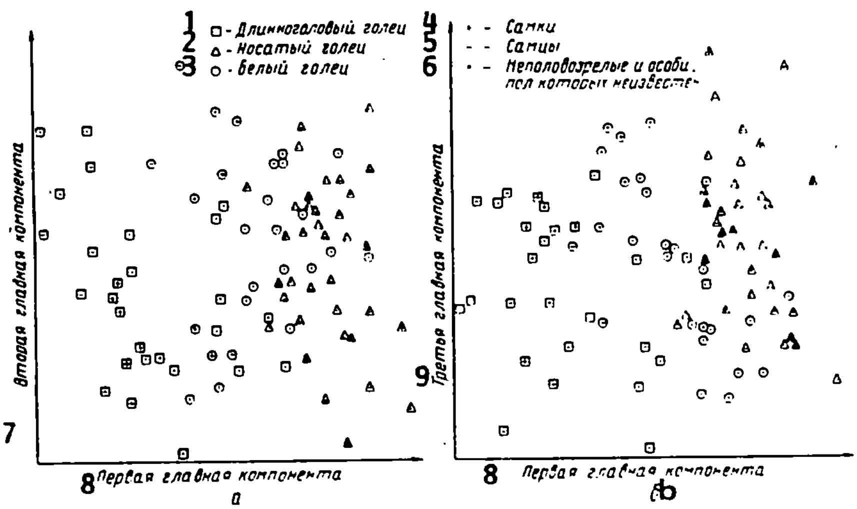

Рис. 36. Проекция расположения форм гольцов, обитающих в оз. Кроноцкое, на плоскость главных компонент:
а — первая и вторая компоненты; б — первая и третья компоненты

Figure 36. Projection of arrangement of char forms inhabiting Lake Kronotskoe on a plane of main components:

a - first and second components; b - first and third components

1 - long-headed char; 2 - long-nosed char; 3 - white char; 4 - females; 5 - males; 6 - sexually immature fish and individuals of unknown sex; 7 - second main component; 8 - first main component; 9 - third main component.

The karyological differences between forms established by R.M. Viktorovskii [43] fall within the scope of the intrapopulation chromosomal polymorphism known for salmons [34] and probably cannot ensure reproductive isolation. Osteological differences, which are at the basis of R.M. Viktorovskii's diagnosis, are mainly related to the sizes of fish, the degree of breeding colour development and the extent of migrations. As E.D. Vasil'eva [39] indicated, the osteological features used by R.M. Viktorovskii [43] cannot be used in the diagnostics of long-headed and long-nosed chars. The osteological materials, according to which diagnoses of "species and subspecies" of Kronotskoe chars were given, were an unfortunate choice; the relationship of fishes of different size, sex, age, physiological condition, way of life and patterns of ontogenesis of the char's skull were not taken into consideration. Certain differences in plastic features are likely the result of differences in growth rate and level of development of breeding colours. It should be emphasized that, in all cases without exception, strong overlapping is 92

observed. No differences in meristic features were established [43], which should not necessarily be viewed as a manifestation of the supposedly poor defining property of these features. Scanty morphoecological data also provide no basis for a categorical assessment of the reproductive isolation of these forms, rather the opposite. Places and times of reproduction apparently coincide in all forms, although very little is known about them. Food has been insufficiently studied. There is no detailed information on food, particularly that of the long-headed char. Therefore, where forage composition corresponds significantly in the long-headed and white chars, it is difficult to reach the final conclusion that the long-headed char is such a specialized predator. But even narrow food specialization in itself and a divergence in different food niches still cannot serve as proof of species isolation of forms.

The white char is designated in R.M. Viktorovskii's [43] book first as the species *S. malma*, later as a subspecies with respect to the Dolly varden, and in the same place as a local population of Dolly varden, whereas M.K. Glubokovskii [57] designates it as the species *S. albus*. The long-nosed char is described by R.M. Viktorovskii [43] as the subspecies *S. malma schmidti*. In his opinion, the long-nosed char is close to the white char, and is a subspecies precisely with respect to the white char. There are transitional forms between the long-nosed and the white chars and they are probably the result of hybridization [43].

However, independent of whether to call the white char the species *S. malma* or *S. albus*, the long-nosed char cannot be considered a subspecies of either one, since it does not have a geographical natural habitat separate from the main form. Its separation contradicts the rules of zoological nomenclature. In addition, this form cannot also be unambiguously defined. In a number of cases we were unable to differentiate the long-nosed char from the river Dolly varden from the Kronotskaya River, or in a number of cases - from the white char. The most characteristic feature of the long-nosed char is that the upper jaw overhangs the lower jaw and there is a cartilagineous or fatty outgrowth on the upper jaw ("nose"); not many chars have this feature; in many chars the upper jaw overhangs slightly and they do not differ from the ordinary Dolly varden. Small body dimensions and bright colouring cannot serve as proof of taxonomic isolation of this grouping. The relatively frequent occurrence, in comparison with the river Dolly varden population, of strictly long-nosed chars in Lake Kronotskoe may be the result of the propagation of a "long-nosed" mutation under conditions of isolation. This occurrence does not likely have an adaptive meaning and is related to the nature of the food of this form. In other bodies of water, the jaws of benthophagous chars have an ordinary structure.

Рис. 37. Схема формообразования у гольцов из оз. Кроноцкое:
а — по Р. М. Викторовскому [43]; б — наши данные: п — проходной голец; оз-р — озерно-речной голец; Д — длинноголовый; Н — носатый; Б — белый

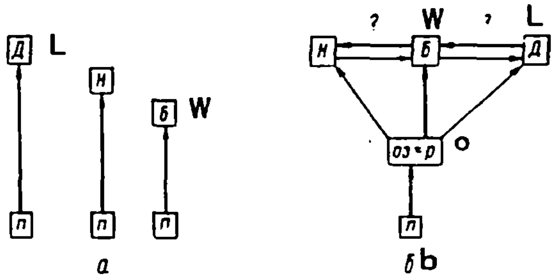

Figure 37. Diagram of the emergence of forms among chars from Lake Kronotskoe:

a - according to R.M. Viktorovskii [43]; b - our data; n - anadromous char; o - lake-river char; L - long-headed; H - long-nosed; W - white.

R.M. Viktorovskii [43], M.K. Glubokovskii and T.E. Butorina [61] consider that species isolation of Kronotskoe chars appeared as a result of successive invasions of anadromous chars separated by spatial isolation. We submit that a diagram of the emergence of forms of Lake Kronotskoe chars may look different (Figure 37). It follows from this diagram that the population of chars from Lake Kronotskoe as a whole represents a very dynamic system where the elements are interconnected. The degree of their isolation has not yet been studied; the information on hand is evidence in favour of their connection. Divergence of the groupings occurred earlier and is taking place now, most likely in the lake itself. It is probable that the anadromous char, having entered the lake, was the origin of the lake-river form. The white char is closest of all to such an ecotype. This is not a specialized, large, universally distributed and highly numerous char form [43]. It is similar to the long-headed char (it apparently does not differ in breeding colours), to the long-nosed char and to the common anadromous Dolly varden. Apparently, already in the lake, this form was the origin of more specialized, highly pronounced phenotypes of the long-headed and long-nosed chars. The latter are very different from one another and the white char is like a connecting link between them. It is possible that the long-headed char is a sexually mature char migrating into rivers with strongly pronounced breeding colours. The females also have pronounced breeding colours and their ethmoidal section is also very extended, but there is no hook or notch on the jaws; therefore, a comparison of the forms is done only according to the females [43]. Although this decreases the impact of the comparison, it does not eliminate it completely.

Undoubtedly the Kronotskoe chars require serious study. It is still premature to draw categorical conclusions with respect to the taxonomic status. One may only say that the lake-river ecotype in the lake is represented by two or three quite different phenotypes whose reproductive isolation from one another is not proven.

The lake-river char form inhabiting Lake Kronotskoe is the white char. It differs from the original anadromous form to the same degree that *morpha lacustris Salmo trutta* differs from the anadromous *S. trutta trutta*.

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Characteristics of chars from the Paratunka River basin. Anadromous, lake-river and lake chars inhabiting the Paratunka River basin occupy different ecological niches. They are noticeably different in maximum dimensions, age composition and growth rate (Table 15). Their differences are closely related to way of life and type of food [198, 200, 201, 207]. Large sizes of anadromous chars are apparently brought about by high, stable forage, mainly in the sea. The small sizes of lake-river char are connected with the absence of large food organisms in rivers and limited food resources. To a great degree, lake chars are predators and this allows them to grow more quickly.

The chars studied differ in the time they reach sexual maturity. The anadromous char matures earlier than all the others and the lake char matures later.

Spawning times and locations coincide to a certain degree in the anadromous and lake-river chars; lake chars have a very extended spawning period and reproduce in the lake itself, possibly in deep water.

All three forms also differ phenotypically, although difficulties may arise in identifying anadromous chars during the freshwater period of their life which are related to the fact that at this time they do not differ from lake-river chars in colouring. The differences of lake chars are more clearly pronounced [198]. The structure of both the skull and tail section of the skeleton is similar overall in char forms [195]. A significant variability which must be taken into consideration in taxonomic research is characteristic of certain features (shape and size of the maxillare, jugale, operculum, teeth, caudal plate, etc.).

15. Biological indicators of char forms inhabiting the Paratunka River basin

Indicator	Anadromous	Dwarf males	Lake-river form	Lake form
Body length (cm)	37-51	9-14	14-42	23-60
Weight (gm)	390-1230	9-58	29-470	2550, rarely up to 5000
Maximum age (in years)	9	3+	10	15
Time to mature (in years)	4+ - 5+	2+	4-6	6
Spawning period	September-October	September-October	September-October	July-March
Spawning frequency	not annually	_	not annually	possibly annually
Fecundity (number of eggs)	625-2800	_	470-1500	685-2400
Ratio of the sexes (males to females)	_	_	1:1	_
Feeding	benthos, flying insects	_	benthos, predominantly mollusks	plankton, benthos, fish
Growth rate	high	very low	average	high

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Lake chars from Lake Dal'nee are similar to the chars from Lake Nachikinskoe. They do not differ in colour, type of food, infection by Diphyllobothrium, age composition, growth rate or type of reproduction [206]. A great similarity of meristic features is observed between them and, although there are reliable differences in many cases, their extent is not great [see Figures 29 and 30] [206]. S.Sh. Mikhailova [154] obtained the results of a multivariate analysis on the aggregate of plastic and meristic features which also do not allow these two populations to be separated.

M.K. Glubokovskii views populations of chars from Lakes Dal'nee and Nachikinskoe as two separate independent endemic species [57, 188]. And he relies on data of osteological analysis and methods of numerical taxonomy. On the basis of electrophoretical research of hemoglobins and miogenes, V.T. Omel'chenko [164] came to a conclusion regarding species independence of char from Lake Dal'nee. The differences that he established are evidence only of the isolation of sympatric forms in Lake Dal'nee, but cannot serve as an absolute species criterion on their own.

In our opinion, there is no weighty basis to consider chars from Lake Dal'nee and Nachikinskoe as different species; taxonomically, they are uniform. Nevertheless, the proposal that lake char from these waters belongs to a species other than that of anadromous and lake-river chars deserves serious attention. As indicated above, significant differences between it and sympatric groupings of chars were discovered. At the same time, there is a clear similarity between Kamchatka Peninsula lake chars and lake neiva of the continental coast of the Sea of Okhotsk [49, 51].

The neiva is similar to the anadromous Taranets char in phenotype features and a set of osteological features [188]. Therefore, in order to solve the question of taxonomic status of all the chars mentioned, it is essential to study their interrelationship. The method of molecular hybridization of DNA many help in this area. But there is already a basis to suggest that the lake chars of the Kamchatka Peninsula and the coast of the Sea of Okhotsk, as well as the anadromous Taranets char may turn out to be very close in a taxonomic respect. In this case, their modern distribution may be viewed as the result of the penetration of the anadromous Taranets char into the lakes of the Kamchatka Peninsula and the waters of the coast of the Sea of Okhotsk during a period of cooling. With warming the anadromous Taranets char, being a more cold-loving form, 96
died out and only its lake ecotypes remained. The Taranets char is phenotypically closer to the chars of the Arctic group; however, its phyletic proximity to them cannot be considered proven. The molecular hybridization data of the Taranets char and the Dolly varden are evidence of their similarity and, possibly, of a sympatric divergence into phenotypically different forms [146]. Data on the karyotype structure obtained by G.V. Gorshkova and S.A. Gorshkov [64] are also evidence of the phyletic proximity of the Dolly varden and the lake char from Lake Dal'nee.

Emergence of forms, systematic position and structure of char groupings of the Kamchatka Peninsula. The anadromous char form is the most numerous and widely distributed in the waters of the Kamchatka Peninsula and a complex structure of populations is characteristic of this form.

Local populations of anadromous chars may be represented by seasonal races differentiated by migration times [85, 155, 184], by groupings differentiated by body dimensions and weight (tycyachniks and normal chars) and by groupings differentiated by how pronounced their breeding colours are (osetinets, dwarf males, etc.). These chars often form single population systems with river chars as well [43, 47, 213].

Dwarf males occur together with anadromous salmons only in bodies of water that are connected with the sea. There is a reverse correlation between the numbers of dwarf and anadromous males; dwarf males make up a shortage of anadromous males and are part of populations of an anadromous flock.

The structure of local populations is not uniform and all listed intrapopulation groupings are not often equally expressed. The simplest structure is characteristic for populations of chars from short rivers of the Western Kamchatka Peninsula (the Kvachina, Utkholok and Utka Rivers) where there are no large chars in the basin and the supplementary system is poorly developed. Shorter periods of anadromous migration are observed in the chars from these waters (July-beginning of September): there are no seasonal races that clearly differentiate the migrations of groupings of "tysyachniks" and "normal" chars by size. It is curious that in similar rivers there are no typical freshwater forms of chars; However, dwarf non-anadromous chars maturing in fresh water are very numerous.

A more complex structure of populations is noted in anadromous chars populating large bodies of water (the Kamchatka and Bol'shaya Rivers). The migration of fish into such rivers is exceptionally greatly protracted. In March-May tysyachniks come from the sea; then the individual "normal" chars appear; the peak of their migration is noted in July; the migration continues in August - beginning of September, but gradually declines in intensity. Towards the 97
end of the migration, individuals reminiscent of the "tysyachniks" are not rare; however, their numbers are not great. It is possible that seasonal groupings exist which are differentiated not only by migration periods, but by time of spawning. In any case, we discovered a few examples of spring-spawning anadromous chars in the Paratunka River basin. For local anadromous char populations of large rivers, dwarf males are just as characteristic, comprising an integral part of the anadromous flock and reproducing jointly with anadromous females. Their numbers usually increase sharply in the upper reaches of rivers. Freshwater river and lake-river char forms live in the basins of such bodies of water. Their level of isolation from the anadromous form may be distinct. In a number of cases they reproduce jointly with anadromous chars, constitute a common system and in this way complicate the structure of populations of the strictly anadromous form. Apparently the reproductive connection between anadromous and freshwater forms is closer in

small rivers [213]. Completely isolated river forms occur more frequently in the basins of large rivers. [204, 210]. The structure of anadromous char populations becomes significantly more complicated due to the fact that individuals not spawning in the given year migrate together with chars going to spawn. The number of such sexually immature fish increases noticeably towards the end of migration.

It is difficult to say what the cause is of the nonuniform structure of local anadromous char populations of the Kamchatka Peninsula. To explain to a certain degree, we have stated acceptable causes with regard to the population structure of the Kamchatka steelhead in different areas of its natural habitat [205, 214]. Food in fresh water and spawning grounds may play a familiar role in the formation of a structure of local populations. However, the complex structure of the migrations themselves apparently arose as a result of historical reasons. On the whole, anadromous chars of the Kamchatka Peninsula reveal a surprising similarity in features of biology, external structure and skull structure [36]. In this respect they are similar to anadromous chars of the continental coast of the Sea of Okhotsk. V.V. Volobuev [52] studied 9 populations of chars from rivers located in an area extending 2300 km which are also characterized by similar morphoecological indicators and population structure.

The population structure of freshwater chars apparently also depends on their natural habitat and the type of body of water. But the structure is simpler since separate forms are not so widely distributed as a rule. The ancestor of freshwater forms on the Kamchatka Peninsula is a char with an anadromous way of life (182). The degree of divergence of different forms and 98
populations of chars on the Kamchatka Peninsula from the ancestral form is not uniform (Figure 38). In comparing all forms with the anadromous char, it becomes clear that lake-river chars resemble it the most [198, 310]. However, among lake-river chars some populations are closer to the anadromous char in their features and others differ from it to a great extent. River chars from the Kamchatka River Basin (Kishimshina River) do not differ much from the anadromous char in ecology and type of food during the freshwater period of their life. They are morphologically close. Reliable differences are observed between them only in the blood groups.

Within populations of river chars of the Kamchatka River basin a differentiation in type of food is becoming evident between benthophages and predators, which are significantly more numerous. This is most likely a unified population or the isolation between benthophages and predators came about very recently and is not yet complete. Chars of this region do not differ in blood groups. Benthophages have a wide range of food and even fish is found in their food. But since a different type of food may lead to nonuniform growth and non-simultaneous maturity, conditions may gradually be created for the separation of one population into nonmixed or partially mixed populations.

The benthophages and predators from Lake Azabach'e are an example of a further stage of differentiation. Remaining morphologically similar to the anadromous char, they already differ from it significantly more in ecology. There are also differences between them in blood groups [35]. In turn a clearer divergence into different niches is observed between the predators and benthophages of this region. Food specialization is much narrower here. Substantial differences in the anatomical structure of the digestive tract are detected [41]. There is a difference in features connected with conditions of reproduction, spawning, blood groups and karyotype. This is all 99

evidence of a possibly genetic isolation between populations. At the same time, reliable differences have not been established according to the majority of morphological features. Many authors view similar forms as twin species [131]. It may be that an analogous scene is observed in Lake Kronotskoe, but additional research is needed to answer that question.

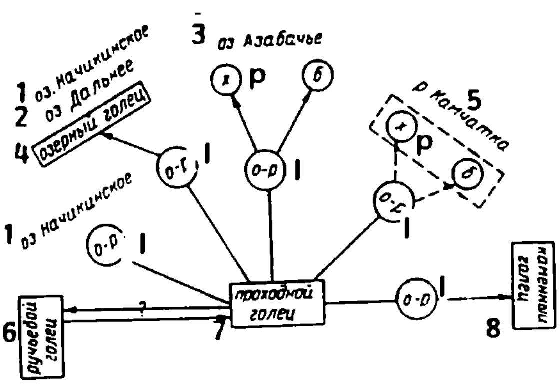

Рис. 38. Схема формообразования гольцов Камчатки:
о-р – озерно-речной голец; х – хищник; б – бентофаг

Figure 38. Diagram of the emergence of char forms of the Kamchatka Peninsula: l - lake-river char; p - predator; b - benthophage; 1 - Lake Nachikinskoe; 2 - Lake Dal'nee; 3 - Lake Azabach'e; 4 - lake char; 5 - Kamchatka River; 6 - stream char; 7 - anadromous char; 8 - stone char.

Lake chars from Lakes Dal'nee and Nachikinskoe differ to an even greater degree from the anadromous and lake-river chars. They are clearly separated in reproductive biology and morphological features.

The lake-river char from Lake Nachikinskoe and the stone char are also noticeably discernible in their morphobiological features. Moreover, there are also apparently differences in karyotype nature and antigenic composition of blood serum.

It is probable that the stream char is reproductively isolated from the remaining chars, although it does not differ in blood groups from the anadromous char or the Azabach'e lake-river predator. But since all of its distinctive features are similar to those of other neotenic fish we cannot say how extensive the divergence is, possibly that the changes are reversible.

The above statements can be illustrated by a diagram of the emergence of forms (see Figure 38). A. Kein [124] indicates similar examples; he writes that within closely related sympatric forms and species it is possible to observe morphological differences of varying degrees. There are no clear breaks in this series where it would be possible to draw a natural boundary. In the chars of the Kamchatka Peninsula it is possible to observe a few possible routes of the differentiation of forms. A divergence in food, in spawning locations and times and in mating behaviour are prerequisites for the emergence of forms [131, 143 et al].

The first route is the emergence of food specialization in the original panmixia population (river chars of the Kamchatka River, Azabach'e benthophages and predators). Food specialization leads to a divergence in times of maturity and originally the single, but extended spawning period breaks down. Thus, morphologically slightly different subpopulations may emerge which, under the appropriate conditions, turn into species whose only differences at first will be features connected with the divergence in food and nonuniform conditions in reproduction.

The second route is the emergence of behavior isolating mechanisms inhibiting crossing (lake char of Lake Dal'nee). Possibly the first and second routes are sometimes combined and then new forms can form. It is quite possible that the stone char emerged in this way, probably originating from a predatory form of lake-river char or directly from an anadromous form. 100

The third route is neoteny, i.e., sexual maturation of smolts in streams where large chars, as a rule, do not reproduce. The spawning grounds are divided and a known food specialization emerges immediately. Stream chars occupy a food niche similar to that of young fish of other forms. Apparently this route is widely distributed in salmonids since some families (*Retropinnidae Salan gidae*) are wholly characterized by a set of neotenic features.

A similar picture is obtained in studying genome structure by the DNA molecular hybridization method. An anadromous char from the Kamchatka River Basin was used in studying chars as a bench-mark form. The thermoelution profiles in local populations of anadromous char of the western and eastern coasts turned out to be almost identical. The DNA of freshwater fishes is characterized to a great degree by divergence; however, in no case does the coefficient of divergence reach that noted for East Siberian char. It may be proposed that there are forms which more or less diverged from the anadromous form. There is apparently no clear boundary between species and intraspecific groupings. The greatest values of the coefficient of divergence are noted for the melanistic form: the stone char and the lake-river dwelling char from Lake Nachikinskoe. It is possible that these species are in the making. Azabach'e benthophages and predators and the Nachikinskoe lake char do not differ substantially from the bench-mark form [342].

In a number of cases, differences in karyotypes were found in Kamchatka Peninsula chars [34, 43]. However, the information obtained does not provide a basis for classifying any form at all as a species. In those cases where differences are established (Azabach'e benthophages and predators, lake-river and river chars from Lake Nachikinskoe and chars from Lake Kronotskoe) they are apparently the result of one chromosomal rearrangement and are minimal from the point of view of cytogenetics. In case of secondary contact of populations they cannot be sufficient to maintain isolation [215].

All of the above proves that in this group of fish a different level of the divergence of forms is traced and intensive processes of the emergence of forms are currently being observed.

There is no doubt that char forms differing substantially from one another inhabit the Kamchatka Peninsula. However, in connection with the discovery of all sorts of transitions, a clear boundary cannot be drawn between species and intraspecific groupings in most cases. 101

M.K. Glubokovskii [57] suggested a different procedure for dividing the Kamchatka Peninsula chars. In his opinion, two species of char exist in the Kamchatka River basin and in some other regions; they are represented by anadromous and local forms: *S. albus* and *S. malma* [57, 58, 59, 61]. These species can be differentiated from one another only by a set of 60 craniological features; moreover, the deviation from the cited standard small number of any features cannot be considered a hindrance in the identification of a specific example with this species. The set of features itself is species specific and not a feature taken separately [58].

Based on an analysis of parasitic fauna, the authors have made the conclusion that these two species occupy different food niches: *S. albus* is a predator and *S. malma* is benthophagous [61]. However, according to the data of O.N. Pugachev, *S. albus* may feed on benthos [187].

Two forms of lake-river chars well-differentiated in type of food were studied in Lake Azabach'e. They are so-called benthophages and predators and it has been proposed that they are reproductively separate and that in Lake Azabach'e they behave towards one another like twin species. Forms of freshwater chars so clearly different in feeding habits were not found in other waters of the Kamchatka River basin, although a known food preference is seen.

The study of the food of strictly anadromous chars during anadromous migration is hindered since they do not feed at this time. It is also known that their food is not specialized either in fresh water or in the sea [52, 74, 207]. If anadromous chars were as strictly specialized in feeding habits as M.K. Glubokovskii and T.E. Butorina claim [57, 58, 61] then this specialization would likely also be retained in the sea, since chars migrate repeatedly to the sea. There would be the appropriate morphophysiological adaptations limiting food to which the species is not adapted. In reality this does not occur and the food of anadromous chars is very diverse [52]. We did not observe among these fish the clear differences in migration periods which T.E. Butorina indicates [32]. In May-June there are very few chars in the region of the Azabach'e channel and Lake Azabach'e and anadromous chars cannot be detected at all by external features. There is no mass migration in the Kamchatka River at this time either; the migration peak is noted there in July.

Anadromous and local chars of the Kamchatka Peninsula from the same regions where M.K. Glubokovskii worked were also studied using osteological methods by E.D. Vasil'eva [36, 37, 39]. She conducted a detailed analysis of her material according to the techniques of this author and assessed the taxonomic value of the features he used. The result was that, in the morphological standards of M.K. Glubokovskii, only 28.6% of the benthophages and 9.1% of the 102
predators from Lake Azabach'e more or less correspond (with deviations in 4-8 features out of 18). The position of 35.7% of the benthophages and 10.9% of the predators is unclear since they conform to each of the "standards" in 9 features, but in 9 features they do not conform. The remaining 37.5% of the benthophages do not conform to the "standard" of the morphological group of benthophages in more than 9 features and, as a result, should be included in the "morphological group" of predators. Accordingly, 80% of the predators should also be included in the "morphological group" of the benthophages. Thus, the results of the osteological analysis according to M.K. Glubokovskii's procedures did not coincide with the ecological differences of char groupings clearly different from one another.

With respect to the diagnostic value of individual features, E.D. Vasil'eva was unable to diagnose benthophages according to 9 features from the 20 indicated by M.K. Glubokovskii or predators according to 13 features. As a result, she concluded that, with the help of M.K. Glubokovskii's method, it was impossible to identify chars differing in food type or, possibly, reproductively isolated chars, and that this author's "morphological groups" were artificial, as was the separation, accepted on the basis of the "morphological groups", of anadromous chars into two groups combined with the benthophages and predators according to osteological features [35]. She considers that the diagnostic value of the majority of characteristics used is more than doubtful and that it is incompetent to separate one of the "morphological groups" (predatory anadromous and freshwater chars and part of the non-feeding anadromous chars) into a particular species *S. albus* based only on the osteological data of the author, data which do not permit an assessment of the relationships of predatory and benthophagous chars in the Kamchatka River basin.

The holotypes and paratypes of *S. albus* that we examined in the collections of the Zoological Institute of the USSR Academy of Sciences are local and do not differ from the usual lake-river char of the Kamchatka Peninsula either in number or size of spots; moreover, they are even closer to the benthophages than to the predators, i.e., closer to *S. malma* and not to *S. albus*. Thus the materials from our research of many years and the osteological data of E.D. Vasile'va [39] do not allow us to separate the species *S. albus* among the chars of the Kamchatka Peninsula.

The question of the status of the forms of Kamchatka chars cannot be decided without a discussion of the systematic position of chars as a whole and it will be examined in the following sections.

THE KOMANDORSKIE ISLANDS

The chars inhabiting the Komandorskie Islands are attributed to the most numerous and universal fishes. However, until recently in the literature there were no works dedicated to their 103
biology or systematics. It was only mentioned that chars occur in the waters of the Komandorskie Islands [24]. They were studied in more detail by K.A. Savvaitova, V.A. Maksimov and E.D. Medvedeva [138, 139, 140, 213].

The subject of our research was a small local population of an anadromous char form from the Sarannaya River. This local population of chars of a small 4-kilometre river turned out to be very heterogeneous. Three groupings were separated: strictly anadromous chars - relatively large chars of both sexes coming from the sea to spawn; small river males and females having first attained sexual maturity in fresh water; small dwarf males having matured in fresh water without going out to sea (Figure 39) [213].

These char groupings are characterized by a number of specific features. In outer appearance they differ somewhat from one another. In addition to dimensions, anadromous chars are typically separated either by a characteristic "marine" silvery colour or by bright breeding colours and the corresponding changes in body shape. River chars and dwarf males have freshwater colouring: a predominantly olive-coloured body, very bright spots and fins; many have an orange belly and lips. Lateral parr marks are retained on the sides of small fish. Such colouring is characteristic for river populations of char and not during spawning. Sexual dimorphism in colouring and head shape is less pronounced in the river grouping than in the typically anadromous grouping. However, not one of the char groupings has features that are absent in another; they differ from one another only by their degree of manifestation [213]. Directly connected to regular trips to the sea and a great availability of food is the relatively fast growth rate and high fecundity of typically anadromous chars. River chars and dwarf males, having first matured in fresh water, have a slow growth rate and river females have a low fecundity. Freshwater groupings attain sexual maturity earlier and their life span is apparently shorter. In contrast to anadromous chars, they feed during spawning and are infected with freshwater parasites (Table 16).

Spawning of the groupings studied occurs simultaneously in the same places, in the same spawning-grounds. River chars and dwarf males spawn together with anadromous chars; moreover, the role of freshwater, medium-sized and small dwarf males in producing a strictly anadromous grouping is apparently very large. There is no reproductive isolation between groupings. Data on meristic features are also evidence of this; there are no differences observed in them. Only the dwarf males have a few more vertebrae (Figure 40).

Differences in many ostelogical features (structure of the chondocranium, the jaw bones, the parasphenoideum, the glossohyale, the hyomandibulare vomer and the integumentary bones of the skull) are observed between intrapopulation char groupings. These features are subject to significant variability in individual size and sex and are mainly determined by the growth of the fish, mating changes and way of life (marine or freshwater) [138, 139, 140]. Here juvenile features gradually disappear in series: young fish - dwarf males - river chars - sexually immature anadromous - adult anadromous. The greatest differences from the original type of structure are attained by the adult anadromous chars.

Undoubtedly the intrapopulation groupings of anadromous char from the Sarannaya River are part of a single spawned flock and a single local population. They have a common gene pool and are not isolated from one another.

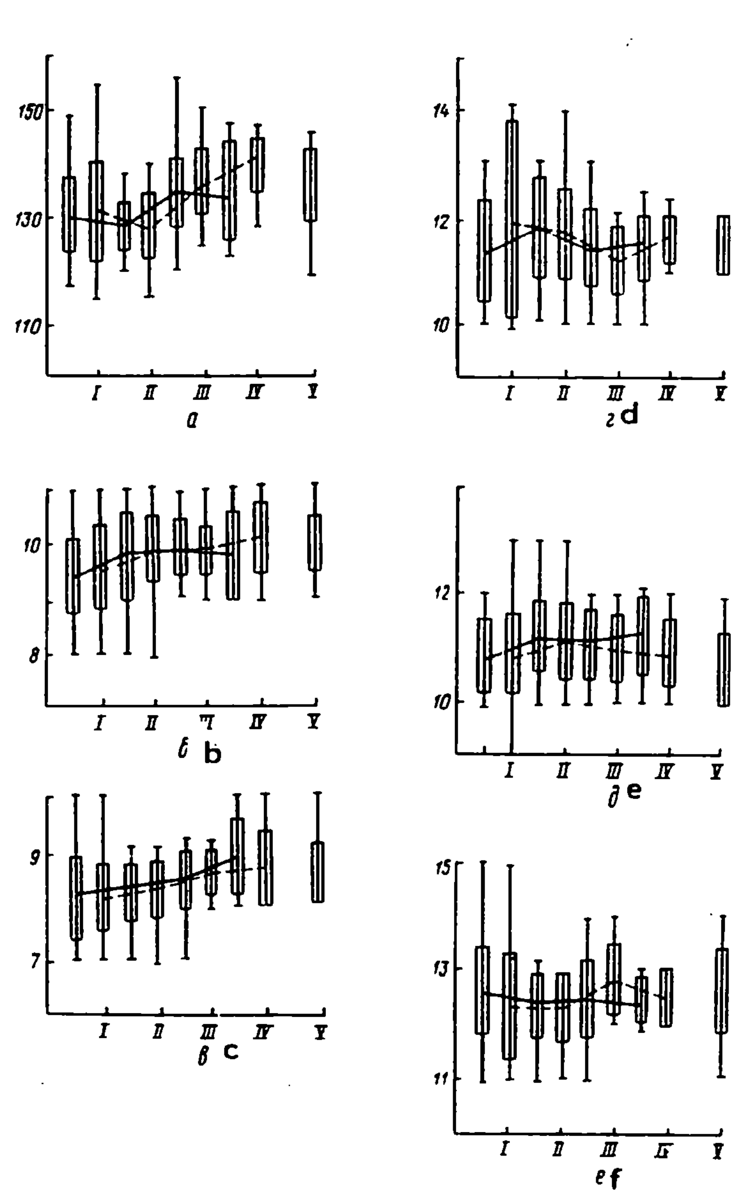

Рис. 39. Меристические признаки (числовые значения) гольцов, обитающих в водоемах Командорских о-вов и бассейна р. Амур:

а — чешуй в боковой линии; *б* — лучей в спинном плавнике; *в* — лучей в анальном плавнике; *г* — жаберных лучей справа; *д* — жаберных лучей слева; *е* — лучей в грудном плавнике; *I* — мальма из р. Мы; *II* — мальма из р. Иски; *III* — проходные гольцы; *IV* — речные гольцы; *V* — карликовые самцы. Сплошной линией обозначены самцы, а пунктирной — самки

Figure 39. Meristic features (numerical values) of chars inhabiting the waters of the Komandorskie Islands and the Amur River basin:

a - scales on the lateral line; b - rays in the dorsal fin; c - rays in the anal fin; d - branchiostegals on the right; e - branchiostegals on the left; f - rays in the thoracic fin; I - Dolly varden from the My River; II - Dolly varden from the Iska River; III - anadromous chars; IV - river chars; V - dwarf males. Males are indicated by the solid line and females by the dotted line.

16. Biological indicators of groupings of chars inhabiting the waters of the Komandorskie Islands

Indicator	Anadromous	Dwarf males	River form
Body length (cm)	26-54	12-21	16-26
Weight (gm)	180-1650	10-70	60-150
Maximum age (in years)	8	5	5
Time to mature (in years)	4-5	2-3	3
Spawning period	August-September	August-September	August-September
Spawning frequency	not annually	not annually	not annually
Fecundity (number of eggs)	537-4536	—	249-484
Ratio of the sexes (males to females)	1:1	—	3:1
Feeding	does not feed	benthos	benthos
Growth rate	high	low	delayed

The original maturing in fresh water of river male and female chars, as well as that of dwarf males does not mean that in the future, after the first spawning, they will not migrate to the sea and not return to a river typical with anadromous fish; therefore, the separation of all groupings examined is arbitrary to a certain extent.

The complex structure of a flock is apparently characteristic for the majority of populations of anadromous char from other rivers of the Komandorskie Islands as well. The structure is an adaptation to the specific living conditions in short rivers with a limited area for spawning-grounds and forage. Only thanks to extreme intrapopulation variety and an absence of strict isolation between groupings does the char attain such great numbers here and fill all 106

ecological niches accesible to it. In other natural habitat areas, in the regions where there are large bodies of water varied in nature, for example in the Kamchatka Peninsula, the intraspecific structure of chars is different. A species here is represented by significantly more differentiated intraspecific forms, each of which is capable of maintaining its existence independently [204]. Undoubtedly a genetic exchange between forms takes place, but it is of a more limited nature. In anadromous char populations of the Kamchatka Peninsula there are also dwarf males; however, their numbers and role in reproduction are significantly less.

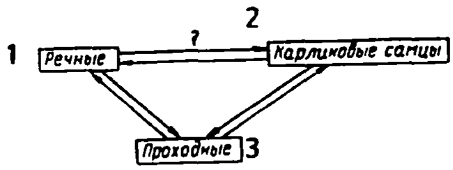

Рис. 40. Схема формообразования у гольцов, обитающих в водоемах Командорских о-вов

Figure 40. Diagram of emergence of forms in chars inhabiting the waters of the Komadorskie Islands.

1 - lake forms; 2 - dwarf males; 3 - anadromous forms

The intrapopulation groupings of chars described have analogous forms in other regions, for example the anadromous chars of the Kamchatka Peninsula [213]. However, there are also certain differences. Thus the Komandorskie chars differ from populations that are situtated at the same latitude and are part of a continuous series of clinal variability according to the number of vertebrae (Okhotsk and Kamchatka populations). The variability of this feature is apparently determined by temperature conditions during reproduction. Komandorskie chars spawn at a temperature of 12.5°C and Kamchatka chars spawn at 6°C.

Komandorskie chars are isolated to a significant degree from chars from other regions, although the areas where they feed in the sea are unknown. It is possible to propose that they do not go far from the shores [77]. Therefore, there is a formal basis for the separation of a new subspecies. However, the following objections to this are possible. The number of vertebrae in chars is a highly variable feature, reacting strongly to a change in surrounding conditions. It is possible that in average values of the number of vertebrae different generations of Komandorskie chars will diverge. The number of vertebrae in Komandorsie chars varies within the same limits as in Kamchatka chars. Dwarf males of the population of anadromous chars of the Sarannaya River do not differ in the number of vertebrae from the dwarf males of the Kamchatka Peninsula. The value of the coefficient of difference does not attain the subspecies level of 1.28 in any single case. The number of scales on the lateral line in Komandorskie chars does not differ from that in Kamchatka chars, i.e., it falls into the general character of clinal variability of this feature from south to north. The largest number of scales is apparently connected with the fact that they appear later than the formation of vertebrae and at lower temperatures. Considering the reasons cited, the separation of Komandorskie chars into an independent subspecies would probably not be justified. 107

THE KURIL'SK ISLANDS

Very little is known of the chars of the Kuril'sk Islands. This is a stream form of fish populating short, small streams [156], up to 20 cm in length, characterized by delayed growth [24]. In the waters of the Shikotan and Kunashir Islands they feed on insects [156].

Chars of Shikotan Island are characterized by the following features: *ll* - 103-135 (121, 1); *D* - 9-12 (10,8); *A* - 7-10 (8,6); *P* - 11-14 (13); *sp. br.* - 15-21 (17,1); P_c - 16-28 (21, 8); *vt* - 57-64 (59,8). Chars of Kunashir Island have the following features: *ll* - 105-128 (118,7); *D* - 10-11 (10,5); *A* - 8-10 (8,5); *r, b.* - 12-14 (13,1); *sp. br.* - 16-20 (17,5); P_c - 17-31 (22,8); *vt* - 55-63 (58,9).

There are reliable but insignificant differences in meristic features between the chars from the waters of these islands [212]. In comparison with the chars of Kunashir Island, the chars of Shikotan Island are longer; their dorsal, anal and abdominal fins are slightly shifted towards the caudal section; the caudal peduncle is shorter and the dorsal and thoracic fins are longer. The head is more elongate and shallower; the eye diameter and jaw dimensions are greater. It is likely that these differences should be attributed to a different allometric growth [212]. There are numerous bright, small red spots on the sides of the body.

V.L. Andreev, V.N. Ivankov and A.M. Bronevskii [9] separate the south Kuril'sk chars into the subspecies *S. malma curilus* (Pallas). L.S. Berg [24] attributes them to the *S. malma morpha curilus* or the *S. malma kraschenimnikovi morpha curilus* (Pallas).

SAKHALIN ISLAND

The chars of Sakhalin Island have been studied in fair detail [66, 67, 72, 73, 74]. Therefore, it is possible to compare their forms and discuss the problems of the emergence of forms and systematic position.

The anadromous char of Sakhalin Island, in comparison with river and stream forms, is characterized by greater dimensions and body weight, a faster growth rate, longer life and greater fecundity [71]. All chars are similar in food type, but crustaceans predominate in the food of the anadromous chars. River chars mainly consume eggs and salmon larvae; moreover, eggs are almost their only food during most of the year. The type of food of the stream char depends on

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whether or not it visits the waters of the Far Eastern salmons. If the salmons enter the streams, the chars do not differ from anadromous or river forms in food type. It should be noted that chars consume eggs washed out of the nests that are infertile and destined to die and that they perform the function of unusual cleaners [52, 66, 67, 117, 207].

The chars of Sakhalin Island exhibit certain differences in meristic features, but all distributions greatly overlap [72]. In colouring, the anadromous, river and stream chars do not differ. The colour of the fins, back, belly and spots is the same. Only the intensity of the colouring differs: the brightest colouring is a property of the stream form [72].

All chars are attributed to a single group of fish in the taxonomic sense: *S. malma kraschenimnikovi* or *S. alpinus kraschenimnikovi* [72, 239].

In the opinion of O.F. Gritsenko [67], the river char is possibly part of an anadromous flock. It matures in fresh water. There is reproductive isolation between the anadromous and stream forms. The stream form reproduces in small springs and rivers which the anadromous form never enters; the places and times of spawning of the anadromous and stream chars are different [67, 72]. Hypothetically the relationships between char groupings may be represented in the following manner: anadromous chars $\leftrightarrow$ river chars ?$\leftrightarrow$ stream chars, or river chars $\leftrightarrow$ anadromous chars $\leftrightarrow$ stream chars. It is possible that the level of isolation of the stream form may be different in various bodies of water.

THE AMUR BASIN

In comparison with chars from the Iska River, chars from the My River are larger, mature earlier and grow more quickly (Table 17). It is likely that they live longer. The difference in growth rate is related to feeding conditions in the river and in the estuary. According to 109

B.B. Bronskii's report, forage in the My River is rich, which lowers or completely excludes food competition in the river. In both rivers the chars do not spawn annually; in the My River spawning is extended over the entire summer; in the Iska River it occurs over shorter periods.

The results of comparing populations according to meristic features did not exhibit any substantial differences (see Figure 39). Noticeable differences in osteological features have also not been established [178]. The following may be viewed as specific features of morphology of the skull of chars of the My and Iska Rivers: a narrow operculum and the presence of two fontanelles on the olfactory pons in the great majority of individuals.

17. Biological indicators of chars from the Amur River basin

Indicator	My River	Iska River
Body length (cm)	20-56	15-38
Weight (gm)	120-1650	80-550
Maximum age (in years)	9	6
Time to mature (in years)	3-4	4-5
Spawning period	spring-autumn	August-September
Spawning frequency	not annually	not annually
Ratio of the sexes (males to females)	1:2	1:1
Feeding	predominantly fish and salmon roe	benthos, flying insects, fish
Growth rate	high	delayed

The following are characteristic of the females of the Iska River: rounded head, maxillary usually does not extend far beyond the posterior margin of the eye, there is either no hook or notch on the jaws or they are slightly developed. In the females of the My River, the head is conical; maxillary extends far beyond the posterior margin of the eye; the hook and notch on the jaws are more pronounced. The males of the two populations differ less from one another. The colouring of representatives of both populations is similar; however, the chars from the Iska River have dark lateral lines on the sides of the body (even in fish up to a length of 35 cm) and a more pronounced marble-like pattern on the back.

According to a set of features as a whole, interpopulation differences are close to intrapopulation differences (between the males and the females). There are data in the literature that two char forms inhabit the Amur River basin: the anadromous and river forms [24, 117, 136, 161, 239]. The interrelationships between them have not been studied. According to observances in other regions, the anadromous and river chars spawn in different areas of the rivers and are reproductively isolated [72, 239]. Apparently in the My and Iska Rivers the isolation is not as clearly pronounced or is completely absent since the differentiation of these forms is hindered.

According to the morphometric indicators, colouring and qualitative features that we studied, we were unable to reveal the anadromous and freshwater chars. The distribution curves of plastic and meristic features are usually unimodal. An analysis of the osteological features of the chars of these populations also did not permit their separation into ecotypes [178]. According to L.V. Kokhmenko's data [117], the food of the river and anadromous forms is similar, although large forms consume benthos less than the small forms do. According to the results of a parasitological survey, the chars of the My and Iska Rivers are slightly infected with marine parasites (5.2 and 14.3%); their infection with estuary species is significantly greater (53.5 and 43.8%) [136].

It is probable that the char populations of these rivers do not make significant migrations but feed in the estuaries of the Amur and Iska Rivers. There is a great deal of food available in 110
these waters and this is possibly the reason for the coincidence of chars of this region with desalinated waters. Forage in the rivers is also abundant and apparently sufficient for some portion of the chars to mature in fresh water without migrating to the estuary. Most likely the difficulties in separating chars into anadromous and river forms in the My River are connected with the fact that they are part of a single population system and reproduce jointly. It is possible that intrapopulation groupings, differing in their way of life, emerge in the ontogenesis of one generation [205].

The extended spawning period of chars in the My River gives rise to the formation of groups of fish differing in body length, growth rate, nutritional state and periods of sexual maturity. And this, in its turn, has an effect on the extent of migration routes. The char of the Iska River is less varied and is mainly represented by a river form, a fact which is indicated by the presence of dark stripes on the sides of the body. However, the occurrence of marine and estuary parisites, although in an insignificant quantity [136], allows us to propose that the char population from this river is characterized by the same structure as the chars from the My River.

The results of a comparison of both populations indicate that they are not taxonomically different. The determination of their status is interesting in connection with the problems of geographical variability (formation of clines and geographical isolats) and with the separation into subspecies on this basis.

Chars living south of the Shantarskie Islands to the Petr Velikii Gulf, including Sakhalin Island and the South Kuril'sk Islands, are attributed to the subspecies *S. malma kraschenínnikovi* [239] or *S. alpinus kraschenínnikovi* [72]. Until recently this subspecies was one of the least studied char groupings.

With the exception of some fragmentary information on the Sea of Okhotsk chars contained the the works of A.Ya. Taranets [239] and the circumstantial research of O.F. Gritsenko and A.A. Churikov [67, 68, 71, 72, 73, 74], data on the chars of Sakhalin Island is very sparse. Small river and stream forms of this subspecies *S. malma kraschenínnikovi m. curilus*, *S. malma m. curilus* [24, 239] or *S. alpinus kraschenínnikova m. curilus* [72] are widely distributed from Anadyr' to Korea; they are in Alaska, the Aleutian, Kuril'sk and Shantarskie Islands, on Sakhalin Island, in the lower reaches of the Amur River, in the Primor'ye territory and in Japan [24, 136, 239].

The southern char subspecies differs from the northern in a smaller number of scales on the lateral line (<130) and vertebrae (<64) [239]. It has more chromosomes (2 n=84), NF=96 [248].

It is known that the number of vertebrae and scales on the lateral line changes in accordance with a geographical variability having a clinal character. Temperature also affects the 111
formation of the number of vertebrae in fish where development was at early stages [240]. Under natural conditions a negative correlation is noted between the number of vertebrae and temperature [142]. Experimental studies have shown the presence of both a positive and a negative correlation [240].

An analysis of a series of meristic features of chars in a direction from north to south, and first and foremost according to features characterizing the southern subspecies, indicates that variability has a clinal nature. Char populations from the My and Iska Rivers occupy an intermediate position between Kamchatka and Sakhalin populations, which corresponds to their latitudinal position, at the same time as the char populations of the Kamchatka Peninsula and Shikotan Island, located at opposite ends of the cline, on the contrary, have high coefficients of difference (3,15 and 3,0 for the vertebrae and number of scales on the lateral line) [212].

In the literature different points of view are stated with respect to the status of these populations. They propose that South Kuril'sk chars may be separated into the subspecies *S. malma kraschenínnikovi* [72] or S. *malma curilus* [9]; others consider such a separation to have no basis [212].

Data on chars inhabiting the Amur River basin confirm the latest opinion and force agreement with E. Mair, who considers that, if geographical variability of a certain species is of a clinal nature, it is usually not expedient to differentiate subspecies, with the exception of forms found at two opposite ends of the cline, if they are very different or separable by a clearly pronounced ledge [131]. However, there are no such ledges in the cline that we examined. Therefore, we should consider that, at the present time, there are no weighty proofs exhibited of the existence of char subspecies along the Asiatic coast of the Pacific Ocean. The question of the species membership of chars from the Amur River basin may only be decided by examining the situation in the group as a whole.

Chapter 5

THE STRUCTURE OF POPULATION SYSTEMS AND THE SYSTEMATIC POSITION OF ARCTIC CHARS

The taxonomic position of chars is the subject of constant discussion. In order to solve the problem, it is important to first analyse the variability of at least the most frequently used diagnostic features in populations throughout the entire natural habitat of chars. The number of 112
gill rakers and pyloric caeca are such features and there is the fullest information on these features in the literature. In studying the variability of these features in populations from different areas of the natural habitat, a rather mixed picture is obtained [206, 207]. A certain correlation is observed between the number of gill rakers and pyloric caeca; to a certain extent they are functionally related [192].

Together with V.V. Volobuev [218], we attempted to trace the distribution of the average values of these two features throughout the entire natural habitat of Arctic chars. The values of these features were examined in anadromous and freshwater forms attributed by the authors to *S. alpinus* and *S. malma*, and some provisionally separated species.

DIFFERENTIATION ACCORDING TO NUMBER OF PYLORIC CAECA AND GILL RAKERS

It is apparent from the distribution analysis throughout the natural habitat that it is possible to isolate three char groups according to the average values of the number of pyloric caeca and only two according to the number of gill rakers (figures 41-43). There is no hiatus in any of the cases.

The distribution of the average values of these features according to regions (Europe, Siberia, Far East, America and Greenland) reveals the following trends.

1. The average number of pyloric caeca in various European populations of chars varies from 20 to 48, but populations with 36-39 caeca are predominant.

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* The figures in the right-hand margin indicate page numbers of the original (Tr.).

2. In Siberian populations one group is characterized by the values of the feature predominant in European chars and another has significantly more caeca. Even populations with a small number of caeca [220] were recently discovered; although rare, such populations occur in Europe.

3. In char populations of the Far East, a picture opposite to that in Europe is observed.

4. The greatest variety is noted in North America and Greenland.

The distribution of average values of the number of gill rakers have the following pattern.

1. The histogram in European populations is single-peak.

2. In Siberia it is possible to isolate two groups of populations with different feature values.

3. The distribution histogram of Far Eastern populations, as with European populations, is single-peak.

4. The distribution histogram of gill rakers in American and Greenland populations is multi-peak.

There is a certain correlation (see Figures 43 and 44) between the average values of the number of pyloric caeca and gill rakers in populations from different regions.

On the basis of the data presented, it is possible to conclude that the swing of the series fluctuations is approximately the same in all regions: from the lowest to the highest values, and, therefore, it is possible to speak only of the prevalence of groupings with some or other feature values in different geographic areas. 113

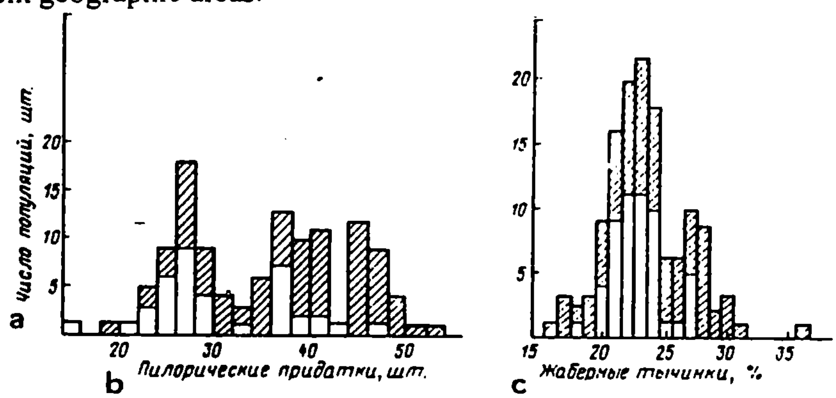

Рис. 41. Распределение средних значений числа пилорических придатков и жаберных тычинок в популяциях гольцов по ареалу (заштрихованы пресноводные популяции)

Figure 41. Distribution of average values of the number of pyloric caeca and gill rakers in char populations throughout the natural habitat (freshwater populations are marked with dashes)
a - number of populations; b - number of pyloric caeca; c - gill rakers, %

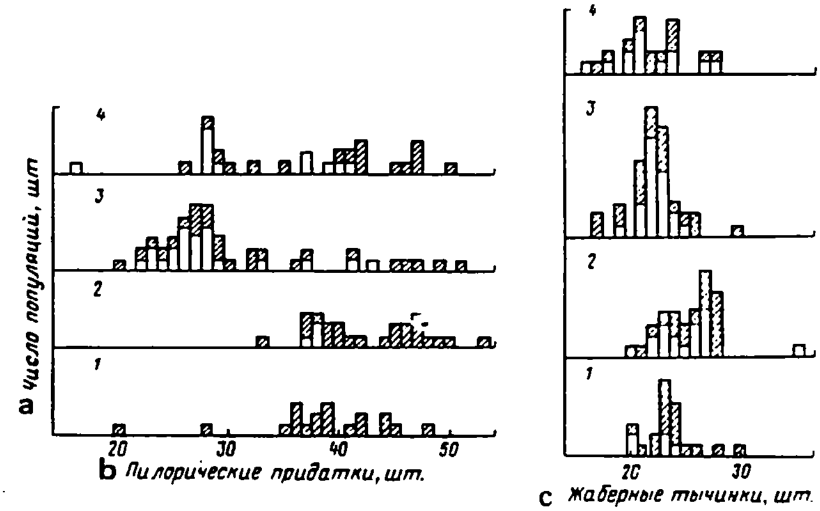

Рис. 42. Распределение средних значений числа пилорических придатков и жаберных тычинок в популяциях гольцов по регионам:
1 — Европа; 2 — Сибирь; 3 — Дальний Восток; 4 — Северная Америка и Гренландия (заштрихованы пресноводные популяции)

Figure 42. Distribution of average values of the number of pyloric caeca and gill rakers in char populations according to regions:
1 - Europe; 2 - Siberia; 3 - Far East; 4 - North America and Greenland (freshwater populations are marked with dashes)
a - number of populations; b - number of pyloric caeca; c - number of gill rakers 114

A group with an intermediate average number of caeca and rakers dominates in Europe, has a circumpolar distribution and is noted in all regions, including Siberia. This group is highly eurybiontic and includes anadromous, as well as various lake and river forms. The distribution of chars with a small number of pyloric caeca and rakers coincides mainly with the basin of the Pacific Ocean - from the Chukotka Peninsula to Korea and from Alaska to California. This group of chars is predominantly represented by anadromous and small stream forms; purely lake populations are rare. Chars with a large number of caeca and rakers are distributed in the Arctic regions of Siberia and North America; they occur in mountain lakes in Europe, in the basin of Lake Baikal (Lake Frolikh), the upper reaches of the Vitim River, certain lakes of the Anadyr' Plateau, the lakes of the continental coast of the Sea of Okhotsk and the Kamchatka Peninsula. As a rule, these are lake chars and, much less frequently, anadromous chars. Moreover, it is possible that an anadromous way of life was acquired in this case as the result of a departure to the sea from lakes where living conditions became unfavourable due to hydrogeological changes. Apparently there are chars from this very group on certain islands of the Arctic, in rivers of the Arctic coast of Siberia, the Chukotka Peninsula, North America and Canada.

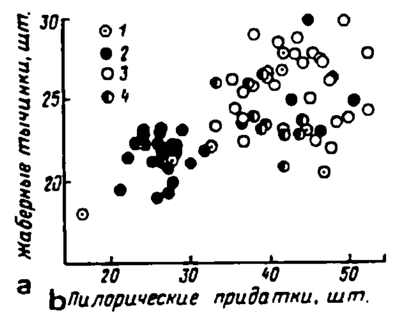

Рис. 43. Соотношение среднего числа пилорических придатков и среднего числа жаберных тычинок в популяциях гольцов из разных регионов:

1 — Америка; 2 — Дальний Восток; 3 — Сибирь; 4 — Европа

Figure 43. Relationship of the average number of pyloric caeca and the average number of gill rakers in char populations from different regions:

1 - America; 2 - Far East; 3 - Siberia; 4 - Europe

a - number of gill rakers; b - number of pyloric caeca

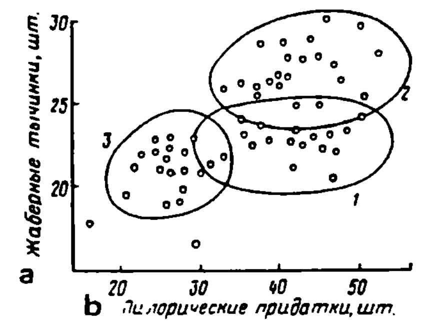

Рис. 44. Соотношение среднего числа пилорических придатков и среднего числа жаберных тычинок в популяциях гольцов по ареалу:

1 — альпиноидный; 2 — высокоарктический; 3 — мальмоидный

Figure 44. Relationship of the average number of pyloric caeca and the average number of gill rakers in char populations throughout the natural habitat:

1 - alpine-like; 2 - high-arctic; 3 - Dolly varden-like

a - number of gill rakers; b - number of pyloric caeca.

Therefore, in analysing distributions of average values of the number of pyloric caeca and gill rakers in chars throughout the natural habitat, it is possible to distinguish three char morphotypes (Figure 44) that we have tentatively called alpine-like, Dolly varden-like and high-arctic [218].

DIFFERENTIATION ACCORDING TO RATE OF OCCURRENCE OF VALUES OF MERISTIC FEATURES IN POPULATIONS FROM DIFFERENT PARTS OF THE NATURAL HABITAT

An analysis of the distribution of average quantities of gill rakers and pyloric caeca is related to the fact that, in the literature, usually only average values of features are cited, as well as the fluctuation limits of the variation series. The series themselves and the occurrence in populations of different feature values are usually not analysed. At the same time, a comparison of populations according to average values is likely, in a number of cases, to give only an approximate picture of their relationships. In this connection we decided to analyse the rate of occurrence in percentages of different values of one feature in a population and to compare the distribution curves of these rates in the char populations that we had studied from different parts of the natural habitat.

In the systematization of chars, the greatest attention is paid to meristic features [19, 24, 49, 72, 149, 206, 239, 244, 260, 267, 268, 276, 277, 281, 314, 337, 338, 346, 347, 348, 366, 403]; although the taxonomic value of the majority of these features is highly relative [206, 403], they undoubtedly play an important role in the differentiation of various forms of chars. Particular importance is given to the number of gill rakers and pyloric caeca. In a number of cases, particular importance is also given to the number of vertebrae [267, 268].

We are examining the nature of the curves of the distribution rates of meristic features usually cited in taxonomic descriptions of chars.

The rate of occurrence of the values of the number of gill rakers in char populations from different parts of the natural habitat. With char forms differing in lifestyle, in analysing the rate of occurrence of values of gill rakers in populations from different areas of the natural habitat, it is possible to tentatively separate few- (average ≤ 24) and many-raker (>25) groupings. We emphasize that the groupings may be roughly separated since, in all cases, significant overlapping is observed (Tables 18-20).

Populations of anadromous few-raker chars occur in the following areas: Greenland (mode 21; average 21.6; 20-23), the Kamchatka Peninsula (the Utkholok River: mode 21; average 21.3; 18-26. the Kamchatka River: mode 22; average 22.1; 18-25. the Bystraya River: mode 23; average 22.8; 21-25), the Komandorskie Islands (the Sarannaya River: mode 22; average 21.8; 20-24), the Chukotka Peninsula (the Kukekkuyum River: mode 22 and 24; average 22.8; 18-28), Chaunskaya Bay (mode 24; average 23.5; 21-26), the Varzina River (mode 23; average 23.8; 22-26). There were a few more rakers in the chars from the populations we studied from the Indiga River (the Cheshskaya Gulf of the Barents Sea: modal number 25; average 23.9; 21-28). The series of feature values in chars from this region extends from 17 to 28. The collection char samples that we studied from the Kanin Peninsula had 17-19 rakers. A.N. Suvorov [236] and A.N. Probatov [183] also indicate a small number of rakers in chars of the Cheshskaya Gulf. Therefore, there is some basis for attributing these chars to the few-raker form. At the same time, it is known that anadromous chars of the eastern part of the Barents Sea (Krestovaya Gulf, Novaya Zemlya) have an average of 25.9 rakers, whereas chars from the Karskoe Sea (Brandt Gulf, Novaya Zemlya) have 26.4 [86]. It is possible that the sampling from the Indiga River was not uniform.

Anadromous chars of the Taimyr Peninsula belong to the many-raker form (mode 26, 27; average 26.8; 23-30). Judging by the data in the literature, many-raker chars of this form occur in the north of the Chukotka Peninsula and further south [244]; they are also found to the east of the Mackenzie River [337], 343].

It is also possible to isolate few- and many-raker forms among the freshwater chars. However, as a rule, the number of gill rakers in few-raker lake chars is greater than in anadromous chars. The few-raker chars inhabit the lakes of the Kola Peninsula (Lake Noskovoe: mode 23; average 23.2; 19-26), the waters of the delta of the Lena River (Lake Zolotye Chiry: 117
mode 23; average 23; 17-28; Lake Dal'nee: mode 24; average 23.5; 19-27; Lake Perekhodnoe: mode 25; average 25; 21-28; Lake Forelevoe: mode 24; average 24.2; 22-26), in the lakes of the Chaunskaya Gulf (mode 22 and 23; average 22.5 and 23.4; 21-25 and 20-25). These chars also inhabit some lakes in Alaska [281, 346]. The many-raker lake chars of the Kamchatka Peninsula follow in number of gill rakers. The char populations from Lakes Nachikinskoe and Dal'nee have respectively a modal number of 25, an average of 25, 23-27 and 26 and an average of 26.5, 24-29. The many-raker lake chars populate the waters of the Taimyr Peninsula. In the char populations that we studied from the Norilo-Pyasinskie Lakes, the number of gill rakers varies from 25 to 32; the mode is within the limits of 26 to 28 and the average is from 26 to 28 (see Table 19).

18. Частота встречаемости значений числа жаберных тычинок в популяциях проходных гольцов, %

	1 Район	2 Число жаберных тычинок														
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	n
3	Гренландия				12	38	25									16
4	р. Варзина						5	36	19	6	2					72
5	р. Индига					2	15	15	23	36	6		4			47
6	Зал. Минина							1	7	22	29	29	6	2	4	100
7	Чаунская губа					12	12	23	29	18	6					17
8	р. Кукеккуюм		1		2	18	27	18	20	6	5	2	1			89
9	р. Анадырь*					15	37	22	22	4						27
10	р. Квачина				28	22	43	4	3							49
11	р. Утхолок	1	3	6	16	30	25	11	5	2	3					251
12	р. Утка				9	27	40	16	6	2						100
13	р. Большая			3	3	14	30	30	10	10						30
14	р. Быстрая					14	26	32	26	2						50
15	р. Камчатка		2	4	12	24	40	14	2			2				49
16	р. Радуга				25	21	33	16	5							24
17	р. Камчатка (тысячник)		1	5	21	30	22	17	4							81
18	р. Большакова (тысячник)			7	15	30	29	14	4	1						100
19	р. Николка			21	25	14	35	5								28
20	Тарьинская бухта				5	19	31	37	6	2						91
21	оз. Тополовое			4	9	32	33	18	4							54
22	о-в Беринга				12	24	34	38	2							65
23	р. Мы (Амур)		2	9	23	25	22	14	5							100

* Данные Ю. С. Решетникова.

Table 18. Rate of occurrence of numbers of gill rakers in anadromous char populations, %

1 - region; 2 - number of gill rakers; 3 - Greenland; 4 - Varzina River; 5 - Indiga River; 6 - Gulf of Minin; 7 - Chaunskaya Bay; 8 - Kukekkuyum River; 9 - Anadyr' River; 10 - Kvachina River; 11 - Utkholok River; 12 - Utka River; 13 - Bol'shaya River; 14 - Bystraya River; 15 - Kamchatka River; 16 - Raduga River; 17 - Kamchatka River (tysyachnik); 18 - Bol'shakova River (tysyachnik); 19 - Nikolka River; 20 - Tar'inskaya Bay; 21 - Lake Topolovoe; 22 - Bering Island; 23 - My River (Amur)

* Yu.S. Reshitnikov's data

The many-raker chars are not uniform and a group with high feature values is noted among them. Char populations from Lake Ueginskoe (Okhota River basin) differ in their large number of gill rakers: mode 30, average 30.2, 25-35 (39). We obtained these numbers from materials provided by V.V. Volobuev. In Lake Frolikh the number of rakers in chars fluctuates between 27 and 31; the mode is equal to 29 and the average is 29.2. A large number of rakers is noted in various groupings of chars from the lakes of the Kuando-Charskii watershed. As a whole, in all the populations from this region, the number fluctuates between 30 and 46; the mode in different bodies of water equals 34, 36, 37 and 38; the average is 36.4; 38.2; 37.3 and 34.7. The number of rakers is even greater in the *S. elgyticus* from Lake El'gygytgyn (30-55); the mode is 38 and the average is 40.

With the exception of the neiva from Lake Ueginskoe, the series of feature values in chars from these regions almost do not overlap with other populations (see Table 19). Lake-river and river chars of the Kamchatka Peninsula are attributed to the Dolly varden-like form (see Table 20).

It is difficult to distinguish clear trends in the geographical distribution of many- and few-raker forms of chars. At the same time, a certain connection is seen with specific habitat conditions. The few-raker chars of the Kola Peninsula and the delta of the Lena River populate small lakes covering a small area and feed mainly on benthos [40, 149, 220].

Many-raker chars occur in large and deep lakes. This is apparently connected the large biomass of plankton in these bodies of water. The chars in the waters are not planktophages by necessity, but the limits of their euryphagy expand due to the large number of rakers. During the short vegetation period on the Taimyr Peninsula, for example, they may consume various foods, including plankton. Chars consume plankton more in the ultraoligotrophic lakes of the Northern Zabaikal'e area, where there are two peaks in plankton development [186]. 121

The number of gill rakers is closely related to type of food [192] and, to a considerable degree, is determined by the density of the plankton in the fishes' food. The smaller number of rakers in the many-raker char populations of the Kamchatka Peninsula is apparently related to the smaller role of plankton in their diet, which includes the large consumption of fish and other food [206, 207].

Anadromous chars with a large number of rakers are apparently a derivative of lake many-raker chars. The young of these anadromous chars live a long time in fresh water, feeding on plankton [218].

19. Частота встречаемости значений числа жаберных тычинок в популяциях озерных гольцов, %

	1 Район	2 Число жаберных тычинок																		*n*
		17	—19	—21	—23	—25	—27	—29	—31	—33	—35	—37	—39	—41	—43	—45	—47	—49	—51	
3	оз. Еловое				11	64	25													50
4	Енозеро				11	59	26	4												27
5	оз. Лама (глубоководный)						16	56	26	4										53
6	оз. Капчук (глубоководный)					2	43	43	12											58
7	оз. Леприндо										66	25	19							16
8	оз. Гольцовое (мелкие)									9	4	38	43	5	1					80
9	оз. Гольцовое (крупные)										16	27	42	15	2					34
10	оз. Леприндокан (мелкие)									2	7	15	34	22	10	10				41
11	оз. Леприндокан (крупные)										21	35	30	7	4	3				43
12	оз. Даватчан (мелкие)										12	21	29	21	17					47
13	оз. Даватчан (крупные)										10	24	42	22		2				50
14	оз. Золотых чиров		6	11	25	31	21	6												156
				3	25	43	25	4												87
15	оз. Переходное				10	23	48	19												78
16	оз. Форелевое (мелкие)			5	18	67	10													22
17	оз. Форелевое (крупные)				7	56	37													48
18	озеро на п-ове Карчик				16	66	18													12
19	озеро на о-ве Айон				50	50														18
20	оз. Эльгыгытгын											4	15	43		4	15	11	44	18
21	оз. Уегинское							7	17	36	26	11	4							61
22	оз. Начикинское						34	62	4											50
23	оз. Дальнее (Камчатка)						6	46	43	5										96

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Table 19. Frequency of occurrence of values of the number of gill rakers in populations of lake chars, %

1 - region; 2 - number of gill rakers; 3 - Lake Elovoe; 4 - Lake Enozero; 5 - Lake Lama (deepwater); 6 - Lake Kapchuk (deepwater); 7 - Lake Leprindo; 8 - Lake Gol'tsovoe (small); 9 - Lake Gol'tsovoe (large); 10 - Lake Leprindokan (small); 11 - Lake Leprindokan (large); 12 - Lake Davatchan (small); 13 - Lake Davatchan (large); 14 - Lake Zolotye Chiry; 15 - Lake Perekhodnoe; 16 - Lake Forelovoe (small); 17 - Lake Forelevoe (large); 18 - Lake on Karchik Peninsula; 19 - Lake on Ayon Island; 20 - Lake El'gygytgyn; 21 - Lake Ueginskoe; 22 - Lake Nachikinskoe; 23 - Lake Dal'nee (Kamchatka Peninsula)

It is more correct to attribute many-raker anadromous chars to the semi-anadromous form. Judging by many features, they do not perform significant migrations and do not travel beyond the desalinated zone of the sea.

On the other hand, the few-raker lake and river chars probably originate from the anadromous few-raker form, feeding in fresh water on benthos and performing greater feeding migrations to the sea. The predominance in individual areas of few- and many-raker chars is related to the existence of corresponding niches. Sometimes the corresponding niche exists, but it appears to be occupied by different species. For example, in Lake Kronotskoe, where the planktophage niche is occupied by the sockeye-kokani, chars are obliged to feed on larger forage and selection leads to the secure position of few-raker chars. It is possible to draw a certain analogy with the few- and many-raker forms of whitefish *Coregonus Lavaretus L.* Their distribution is related to the state of the forage and feeding habits [193 et al]. Many-raker forms of whitefish are characteristic of the basin of the Baltic Sea and Scandinavia, whereas few-raker forms are more typical of the waters of Siberia. However, there are exceptions. Thus, the whitefishes inhabiting the Bauntovskie Lakes in the Zabaikal'e area, like the chars of the Kuando-Charskii Lakes, differ in their large number of rakers [185, 193].

20. Частота встречаемости значений жаберных тычинок в популяциях озерно-речных гольцов. %

	1 Район	2 Число жаберных тычинок																	
		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	n
3	оз. Носковое	—	—	—	2	3	12	14	26	23	14	6							65
4	оз. Кета (боганидская палия)										1.5	20	24	27	18	4	4	1.5	71
5	оз. Капчук (боганидская палия)									4	20	21	24	8	20				25
6	оз. Лама (боганидская палия)									3	7	14	21	11	18	16	5	5	43
7	голец Дрягина										6	11	20	26	16	14	5	2	64
8	оз. Фролиха												8	15	40	28	9		32
9	оз. Начикинское				8	20	25	25	13	9									44
10	оз. Азабачье																		
11	хищник			4	6	16	28	26	14	4	2								196
12	моллюскоед		2		9	13	14	25	26	11									89
13	р. Кишимшина																		
14	бентофаг					7	30	26	30	7									27
15	хищник			1	4	12	22	49	8	4									51
16	оз. Ушковское		2	19	41	25	11		2										53
17	р. Николка		6	25	41	18	8	2											96
18	р. Урцы		8	15	28	34	15												53
19	р. Камчатка (каменный голец)					1	6	8	22	26	2	2							67
20	оз. Кроноцкое																		
21	длинноголовый	3		3	7	7	3	26	19	23	3	3	3						28
22	белый				22	17	35	13	8	5									23
23	носатый		9	12	24	21	21	3	7	3									33
24	оз. Дальнее					2	10	15	33	34	5	1							100
25	оз. Ближнее			3			10	29	45	10	3								29
26	р. Иски		1	6	5	16	35	21	10	5			1						94

Table 20. Frequency of occurrence of values of gill rakers in populations of lake-river chars, %

1 - region; 2 - number of gill rakers; 3 - Lake Noskovoe; 4 - Lake Keta (Boganida lake char); 5 - Lake Kapchuk (Boganida lake char); 6 - Lake Lama (Boganida lake char); 7 - Dryagin's char 8 - Lake Frolikh; 9 - Lake Nachikinskoe; 10 - Lake Azabach'e; 11 - predator; 12 - mollusk eater; 13 - Kishinshina River; 14 - benthphage; 15 - predator; 16 - Lake Ushkovskoe; 17 - Nikolka River; 18 - Urtsy River; 19 - Kamchatka River (stone char); 20 - Lake Kronotskoe; 21 - long-headed char; 22 - white char; 23 - long-nosed char; 24 - Lake Dal'nee; 25 - Lake Blizhnee; 26 - Iska River

The number of gill rakers in whitefishes is genetically determined [397]. Features of the parent pairs are always displayed in the descendants. There are no known cases of the quick transformation of many-raker whitefishes into few-raker whitefishes or the other way around; however, during a relatively lengthy existence under new conditions, the number of rakers may change. It is likely that the patterns known for whitefishes are also characteristic for chars. The features of modern populations did not arise recently. The populations now living inherit the features of the ancestral forms to a certain degree. However, the similarity in quantities of a feature in geographically separated populations may more likely be a manifestation of parallel variability than evidence of a common origin. From the positions of the law of homologous variability [33], it is simpler to explain, for example, the existence of the many-raker lake chars of the Urals, the Taimyr Peninsula, the Zabaikal'e area, the Chukotka Peninsula, 122
the continental coast of the Sea of Okhotsk and the Kamchatka Peninsula. The age of these bodies of water is approximately the same. It is possible that the chars of these lakes had a common ancestor, but at a specified point in time their evolution went its own way. Similar conditions gave rise to the formation of similar features. It is possible to suppose that the similarity in the number of rakers is the result of the separation of forms and the exchange of fauna [43]. However, this appears less likely to us.

The frequency of occurrence of different values of the number of pyloric caeca in char populations from different parts of the natural habitat. Three groups of chars are distinguished according to number of pyloric caeca: small number (18-35, mode 25 and up), average number (25-50, mode 35 and up) and large number (30-60, mode 45 and up).

A small number of pyloric caeca is characteristic for certain populations of anadromous chars of the Chukotka Peninsula [53, 244], the continental coast of the Sea of Okhotsk [46, 47, 51], the Kamchatka Peninsula, the Komandorskie and Kuril'sk Islands [212], Sakhalin Island [72], Alaska and the Pacific coast of North America [267, 337, 343].

According to our data, the nature of the distribution of the frequency of occurrence of the values of this feature in few-raker anadromous chars is similar (Table 21).

Populations with average values of this feature occur in Cheshskaya Gulf, on Novaya Zemlya [86], in Chaunskaya Bay; those with a large number of pyloric caeca occur on the Taimyr Peninsula, the Chukotka Peninsula and in North America to the east of the Mackenzie River [343].

21. Частота встречаемости значений числа пилорических придатков в популяциях проходных гольцов, %

	1 Район	2 Число пилорических придатков						
		10	—20	—30	—40	—50	—60	n
3	р. Варзина				40	54	6	72
4	р. Индига				72	28		47
5	зал. Минина				21	69	10	100
6	Чаунская губа			36	43	21		14
7	р. Кукеккуюм			64	16	20		95
8	р. Анадырь			88	12			27
9	р. Утхолок		4	76	18	2		239
10	р. Утка		1	82	17			89
11	р. Быстрая		7	73	20			29
12	р. Камчатка		2	79	19			47
13	р. Радуга			63	37			11
14	р. Николка			70	30			19
15	Тарьинская бухта			69	31			71
16	оз. Тополовое			67	33			58
17	о-в Беринга		2	73	25			59
18	р. Мы (бассейн Амура)		18	65	6			87

21. Frequency of occurrence of values of the number of pyloric caeca in anadromous char populations, %

1 - region; 2 - number of pyloric caeca; 3 - Varzina River; 4 - Indiga River; 5 - Gulf of Minin; 6 - Chaunskaya Bay; 7 - Kukekkuyum River; 8 - Anadyr' River; 9 - Utkholok River; 10 - Utka River; 11 - Bystraya River; 12 - Kamchatka River; 13 - Raduga River; 14 - Nikolka River; 15 - Tar'inskaya Bay; 16 - Lake Topolovoe; 17 - Bering Island; 18 - My River (Amur basin)

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The same groups are also distinguished in populations of freshwater chars: populations with a small number of caeca are noted in Lake Azabach'e (Kamchatka Peninsula) and Lake Forelevoe (the Lena River delta). An average number of pyloric caeca is discovered in populations of deepwater chars of the Taimyr Peninsula, as well as in lake-river chars from Lakes Azabach'e, Dal'nee, Nachikinskoe and Kronotskoe (Table 22). Chars having many pyloric caeca are from the following locations: the Kola Peninsula, Chaunskaya Bay, the basin of the upper and lower currents of the Lena River, the lakes of the Kuando-Charskii watershed, the Kamchatka Peninsula - in Lakes Dal'nee and Nachikinskoe (Table 23), the continental coast of the Sea of Okhotsk [49, 51] and the lakes of the Amguema River basin.

22. Частота встречаемости значений числа пилорических придатков в популяциях озерных гольцов, %

	1 Район	2 Число пилорических придатков						
		20	—30	—40	—50	—60	—70	n
3	оз. Еловое			32	65	3		51
4	Енозеро			37	55	8		27
5	оз. Лама (глубоководный)			49	44	7		45
6	оз. Капчук (глубоководный)		9	52	37	2		56
7	оз. Леприндо			7	86	7		15
8	оз. Гольцовое							
9	мелкие		6	44	44	6		32
10	крупные			8	54	38		26
11	оз. Леприндокан							
9	мелкие		2	35	57	6		63
10	крупные		5	5	61	27	2	41
12	оз. Даватчан							
9	мелкие		3	22	63	13		46
10	крупные			20	55	25		47
13	оз. Золотых Чиров		1	40	49	10		152
14	оз. Дальнее (Лена)			6	70	24		82
15	оз. Переходное			13	65	22		78
16	оз. Форелевое							
9	мелкие		11	78	11			19
10	крупные		22	70	8			46
17	оз. на п-ове Карчик		20	20	50	10		10
18	оз. на о-ве Айон			41	53	6		17
19	оз. Угинское			8	67	22	3	60
20	оз. Начикинское		4	50	41	5		34
21	оз. Дальнее (Камчатка)		4	62	32	2		44

22. Frequency of occurrence of values of the number of pyloric caeca in populations of lake chars, %

1 - region; 2 - number of pyloric caeca; 3 - Lake Elovoe; 4 - Lake Enozero; 5 - Lake Lama (deepwater); 6 - Lake Kapchuk (deepwater); 7 - Lake Leprindo; 8 - Lake Gol'tsovoe; 9 - small; 10 - large; 11 - Lake Leprindokan; 12 - Lake Davatchan; 13 - Lake Zolotye Chiry; 14 - Lake Dal'nee (Lena River); 15 - Lake Perekhodnoe; 16 - Lake Forelevoe; 17 - lake on Karchik Island; 18 - lake on Aion Island; 19 - Lake Ueginskoe; 20 - Lake Nachikinskoe; 21 - Lake Dal'nee (Kamchatka Peninsula)

However, it should be noted that in all cases the distributions overlap; a significant variability is observed within individual populations. In the distribution of chars with a different number of caeca, there is also a certain tendency related to place of habitat and way of life. The number of pyloric caeca is higher in purely lake or semi-anadromous forms; it is also greater in more cold-water forms. Chars that perform more extended migrations, lake-river chars, river chars and more warm-water forms have fewer pyloric caeca.

23. Частота встречаемости значений числа пилорических придатков в популяциях озерно-речных гольцов, %

	1 Район	2 Число пилорических придатков							
		10	−20	−30	−40	−50	−60	−70	n
3	оз. Носковое				18	69	13		55
4	оз. Кета (боганидская палия)				23	35	35	7	42
5	оз. Капчук (боганидская палия)			4	16	68	3		25
6	оз. Лама								
7	боганидская палия				17	70	13		36
8	голец Дрягина				12	65	23		57
9	оз. Фролиха				69	31			32
10	оз Начикинское			72	28				22
11	оз. Азабачье								
12	хищник			44	54	2			86
13	моллюскоед			63	36	1			56
14	оз. Ушковское		4	65	28	3			49
15	р. Николка		4	65	31				54
16	р. Урцы		28	64	8				36
17	р. Камчатка (каменный голец)			21	12				33
18	оз. Дальнее (Камчатка)			30	67	3			100
19	р. Иски (Амур)		4	84	12				90

23. Frequency of occurrence of the values of the number of pyloric caeca in populations of lake-river chars, %

1 - region; 2 - number of gill rakers; 3 - Lake Noskovoe; 4 - Lake Keta (Boganida lake char); 5 - Lake Kapchuk (Boganida lake char); 6 - Lake Lama; 7- Boganida lake char; 8 - Dryagin's char; 9 - Lake Frolikh; 10 - Lake Nachikinskoe; 11 - Lake Azabach'e; 12 - predator; 13 - mollusk eater; 14 - Lake Ushkovskoe; 15 - Nikolka River; 16 - Urtsy River; 17 - Kamchatka River (stone char); 18 - Lake Dal'nee; 19 - Iska River (Amur)

Frequency of occurrence of different values of the number of vertebrae in char populations from different parts of the natural habitat. Chars may temporarily be subdivided according to the number of vertebrae into few-vertebrae (58-65, mode 62 and 63) and many-vertebrae chars (65-71, mode 66, 67 and above). The distribution overlaps strongly (Tables 24-26). Nevertheless, one is able to show sufficiently clear tendencies in the geographic distribution of populations with a different number of vertebrae.

24. Частота встречаемости значений числа позвонков в популяциях проходных гольцов, %

	1 Район	2 Число позвонков															
		58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	n
3	р. Варзина				4	34	46	14		2							72
4	р. Индига				9	22	33	29	7								47
5	Зал. Минина						4	21	38	17	13	5	2				100
6	Чаунская губа									12	12	26	31	19			16
7	р. Кукеккуюм									4	36	42	17	1			91
8	р. Анадырь								18	48	26	8					27
9	р. Квачина							14	33	23	23	7					48
10	р. Утхолок							2	4	26	35	23	6	3		1	251
11	р. Утка					1	2	7	17	38	26	8	1				89
12	р. Большая							7	30	40	17	3	3				30
13	р. Быстрая							2	22	32	22	8	14				50
14	р. Камчатка					2			8	26	46	14	4				50
15	р. Радуга								8	33	29	17	13				24
16	р. Камчатка (тысячники)								5	18	22	30	25				77
17	р. Большакова (тысячники)								2	7	45	36	9	1			100
18	р. Николка							5	21	38	31	5					19
19	Тарьинская бухта						3	23	32	34	8						87
20	оз. Тополовое					2	15	39	37	7							54
21	о-в Беринга					31	25	23	11	6	4						64
22	р. Мы (бассейн Амура)	9	10	10	27	17	27										28

24. Frequency of occurrence of the values of number of vertebrae in anadromous char populations, %

1 - region; 2 - number of vertebrae; 3 - Varzina River; 4 - Indiga River; 5 - Gulf of Minin; 6 - Chaunskaya Bay; 7 - Kukekkuyum River; 8 - Anadyr' River; 9 - Kvachina River; 10 - Utkholok River; 11 - Utka River; 12 - Bol'shaya River; 13 - Bystraya River; 14 - Kamchatka River; 15 - Raduga River; 16 - Kamchatka River (tysyachniks); 17 - Bol'shakova River (tysyachniks); 18 - Nikolka River; 19 - Tar'inskaya Bay; 20 - Lake Topolovoe; 21 - Bering Island; 22 - My River (Amur basin)

25. Частота встречаемости значений числа позвонков в популяциях озерных гольцов, %

	1 Район	2 Число позвонков														
		59	60	61	62	63	64	65	66	67	68	69	70	71	72	n
3	оз. Еловое		3	5	25	40	27									51
4	Енозеро			13	37	37	13									27
5	оз. Лама (глубоководный)					12	30	22	10	7	3,5	3,5	7		5	40
6	оз. Капчук (глубоководный)					11	30	28	21	10						56
7	оз. Леприндо		7				7	40	13	33						15
8	оз. Гольцовое															
9	мелкие				2	24	62	12								34
10	крупные						64	24	12							25
11	оз. Леприндокан															
9	мелкие			2	3	10	44	18	18	3	2					70
10	крупные		3	3	5	17	38	15	12	7						40
12	оз. Даватчан															
9	мелкие				5	20	33	22	15	5						45
10	крупные				1	15	30	41	13							47
13	оз. Золотых Чиров					1	3	10	38	40	5	1	2			142
14	оз. Дальнее (бассейн р. Лены)		1		1	4	6	12	32	25	1	3				85
15	оз. Форелевое															
9	мелкие						13	18	27	32	10					22
10	крупные						6	9	18	29	16	13	9			45
16	оз. Переходное							13	25	40	14	8				72
17	оз. на п-ове Карчик (Чукотка)										9		55	36		11
18	оз. на о-ве Айон									16	12	50	22			18
19	оз. Уегинское					2	13	45	23	12	5					60
20	оз. Начикинское						3	3	7	14	53	10	10			29
21	оз. Дальнее (Камчатка)						3	3	17	25	40	10	2			60

25. Frequency of occurrence of the values of the number of vertebrae in lake char populations, %

1 - region; 2 - number of vertebrae; 3 - Lake Elovoe; 4 - Lake Enozero; 5 - Lake Lama (deepwater); 6 - Lake Kapchuk (deepwater); 7 - Lake Leprindo; 8 - Lake Gol'tsovoe; 9 - small; 10 - large; 11 - Lake Leprindokan; 12 - Lake Davatchan; 13 - Lake Zolotye Chiry; 14 - Lake Dal'nee (Lena River basin); 15 - Lake Forelevoe; 16 - Lake Perekhodnoe; 17 - lake on Karchik Island (Chukotka Peninsula); 18 - lake on Aion Island; 19 - Lake Ueginskoe; 20 - Lake Nachikinskoe; 21 - Lake Dal'nee (Kamchatka Peninsula)

26. Частота встречаемости значений числа позвонков в популяциях озерно-речных гольцов, %

	1 Район	2 Число позвонков												
		59	60	61	62	63	64	65	66	67	68	69	70	n
3	оз. Носковое	4	14	18	23	12	23	4	2					56
4	оз. Кета (боганидская палия)					2	27	28	27	12	4			39
5	оз. Капчук (боганидская палия)					4		4	40	32	12	4	4	25
6	оз. Лама боганидская палия					3	22	17	28	17	10	3		41
7	голец Дрягина					5	8	28	26	18	11	2	2	61
8	оз. Фролиха					3	15	22	32	12	12	4		41
9	оз. Начикинское						3	8	18	37	21	10	3	38
10	оз. Азабачье													
11	хищники				1	3	13	25	26	23	7	2		198
12	бентофаги					2	4	18	24	16	24	10	2	88
13	р. Кишимшина													
12	бентофаги							23	19	38	15	5		26
11	хищники						4	18	31	37	8		2	51
14	оз. Ушковское							17	40	43				47
15	р. Николка							11	21	39	25	2	2	87
16	р. Урцы							6	22	22	29	14	7	55
17	оз. Дальнее (Камчатка)					3	5	27	37	26	2			100
18	оз. Ближнее									9		55	36	11
19	р. Камчатка (каменный голец)					2	4	19	15	11	6		1	58

26. Frequency of occurrence of the values of number of vertebrae in lake-river char populations, %

1 - region; 2 - number of vertebrae; 3 - Lake Noskovoe; 4 - Lake Keta (Boganida lake char); 5 - Lake Kapchuk (Boganida lake char); 6 - Lake Lama (Boganida lake char); 7 - Dryagin's char; 8 - Lake Frolikh; 9 - Lake Nachikinskoe; 10 - Lake Azabach'e; 11 - predator; 12 - benthophage; 13 - Kishimshina River; 14 - Lake Ushkovskoe; 15 - Nikolka River; 16 - Urtsy River; 17 - Lake Dal'nee (Kamchatka Peninsula); 18 - Lake Blizhnee; 19 - Kamchatka River (stone char)

Anadromous chars with a small number of vertebrae inhabit the waters of the Kola Peninsula (61-66, mode 63, average 62.7), Cheshskaya Bay (61-65, mode 63, average 62.8). Travelling east, the number of vertebrae in populations increases: in chars from the Gulf of Minin (Taimyr Peninsula) 63-69 vertebrae (mode 65, average 65.1), in Chaunskaya Bay 66-71 (mode 69, average 68.3). The number also increases travelling north. An anadromous char population from the basin of the Amur River has 58-64 vertebrae (mode 62, average 62.3); on the Kamchatka Peninsula in the Utkholok River, the number is 62-72 (mode 67, average 67.1); on the Chukotka Peninsula in the Kukekkuyum River, it is 66-70 (mode 68, average 67.7); in the Anadyr' River 65-67 and in the Amguema River 66-69. Therefore, a sufficiently clear clinal variability of this feature is traced. Similar tendencies are observed in comparing modal and average values of the number of vertebrae in freshwater populations.

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Few-vertebrae populations of freshwater chars are known on the Kola Peninsula: Lake Elovoe (60-64, mode 63, average 62.8), Lake Enozero (61-64), mode 62, 63, average 62.5), Lake Noskovoe (59-66, mode 62 and 64, average 62.1). In populations from the lakes of the Taimyr Peninsula, the waters of the lower current of the Lena River and Chaunskaya Bay, the distribution curves shift towards high values. The same thing occurs in comparing southern and northern populations from the basin of the Pacific Ocean.

The direction of clinal variability is brought about by climatic and temperature conditions in individual regions during spawning. For example, it is probable that the Gulf Stream influences the low number of vertebrae in chars of the Kola Peninsula. The living conditions of chars in Cheshskaya Bay are also characterized by higher temperatures [89]. The small number of vertebrae in the chars of Novaya Zemlya [86] and the Komandorskie Islands is apparently related to the milder climate on the islands and to the fact that spawning occurs at higher temperatures [213]. The small number of vertebrae in the char population of the Taimyr Peninsula and certain indirect data provide a basis for proposing the possibility of spring spawning at higher temperatures. The char populations from the lakes of the Northern Zabaikal'e area also have a small number of vertebrae. It is probable that this is related to greater exposure to sunlight and good warming of the bodies of water in the autumn-winter and spring months, i.e., when the embryos are developing.

The examples studied are evidence of the insignificant taxonomic value of this feature in chars. The number of vertebrae fluctuates within a single population, even within the limits of one generation and is subject to the influence of clinal variability. Therefore, this feature is given unjustified significant weight in determining taxonomic categories [72, 239, 267, 268].

Frequency of occurrence of various values of the number of scales on the lateral line in char populations from different parts of the natural habitat. Chars may be divided according to modal values into many- (145 and up), average- (~135) and few-scale (~125). It is difficult to establish a clear pattern in the distribution of populations with these feature values. Populations with the maximum number of scales on the lateral line are found on the Taimyr Peninsula, in the Zabaikal'e area and on the Chukotka Peninsula. However, in these same regions, populations with a small number of scales are known. Populations of many-scale chars do not occur in the western and eastern regions of the USSR.

Frequency of occurrence of different values of the number of branchiostegals in char populations from different parts of the natural habitat. The number of branchiostegals is a feature which varies little. As a rule, variations in this feature within a population are small.

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The number of branchiostegals also varies insignificantly throughout the natural habitat of chars in the USSR. Nevertheless, according to the nature of distribution of the frequency of the values of this feature, it is possible to differentiate populations with a small (9-11, mode 9 and 10), average (10-13, mode 11 and 12) and large (11-15, mode 13) number of branchiostegals.

A small number of branchiostegals is characteristic of the char population of the Indiga River and a large number is characteristic of the chars from the waters of the Zabaikal'e area.

Chars from the waters of the North, Siberia, the Chukotka and the Kamchatka Peninsulas are characterized by average feature values and are similar to one another.

The number of branchiostegals is rarely used in distinguising char forms. T. Cavender [276, 277] proposed this feature as one of the most important in describing the new species *S. confluentus (Suckley)*. In this species he noted the highest number of branchiostegals (r, b_I 12-16, mode 14, average 13.9 and r, b_{II} 12-15, mode 14, average 13.5). The differences in t_{st} from populations from other regions are reliable.

It is difficult to determine why chars from different parts of the natural habitat have a different number of branchiostegals. Their function is unclear. T. Cavender [276] considers that the large number of branchiostegals in *S. confluentus* and *S. namaycush* is the result of feeding on fish and various small animals that enter the water. However, among the populations that we studied, the chars of the Kuando-Charskii Lakes exhibit the largest feature values; plankton plays an important role in the food of these chars. Therefore, we find it difficult to answer this question definitively.

Frequency of occurrence of different values of the number of rays in the dorsal, anal and thoracic fins in char populations from different parts of their natural habitat. The distribution of the number of rays in the fins is similar in chars from different populations. It varies very little, both within individual populations and in comparison with different populations. Therefore, the taxonomic value of these features is insignificant.

According to the results of an analysis of the distribution of frequencies of the values of gill rakers and pyloric caeca, the same three morphotypes may be isolated within *S. alpinus complex*. The number of vertebrae is subject to clinal variability; the taxonomic value of the number of scales on the lateral line and of the number of rays on the fin is, on the whole, doubtful.

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DIFFERENTIATION ACCORDING TO PLASTIC AND MERISTIC FEATURES USING METHODS OF MULTIVARIATE STATISTICAL ANALYSIS

The alpine-like, high-arctic and Dolly varden-like morphotypes of chars may be revealed according to a set of 29 plastic and 8 meristic features, using the methods of multivariate analysis [154]. The characteristic property of such an approach lies in the fact that the intrapopulation variability of the features is taken into account. A comparison only according to average selective values of the features distorts the results, masks the presence of intermediate phenotypes and increases the phenetic distance between samples.

An assessment of similarity was conducted using the method of main components, according to the plastic features of 7 populations of anadromous chars from different parts of the natural habitat as follows: the Varzina River, the Indiga River, the Gulf of Minin, the Kukekkuyum River (Chukotka Peninsula), the Sarannaya River (Komandorskie Islands), the Utka River (Western Kamchatka Peninsula) and the Kamchatka River (Eastern Kamchatka Peninsula). The greatest dispersion of subjects is reflected on the plane defined by the first and second main components (Figures 45, 46). Each group of subjects, representing an individual population, occupies a particular place on the plane. However, a significant dispersion is observed within the groups, as a result of which there are no clear boundaries between them and a mutual overlapping is observed that is expressed to a different degree. The greatest scatter of points is among the chars of the Kola Peninsula and there is a lesser scatter among the chars of Cheshskaya Gulf and the Taimyr and Chukotka Peninsulas. The least dispersion is among the chars of the Pacific Ocean basin. The chars of the Kamchatka Peninsula and the Komandorskie Islands form a single area of subjects.

The influence of the geographical factor and living conditions is traced in the location of populations and reflected in growth rate and, consequently, body proportions. The upper part of the components plane (Figure 47) is occupied by northern populations (Taimyr and Chukotka populations) living in the harshest conditions of the Arctic zone. Then the chars of the Kola Peninsula and Cheshskaya Bay are positioned; they live at higher temperatures [89]. The lower left corner of the plane of main components is occupied by pacific chars living under the milder conditions of the boreal zone. The placement of chars on the main components plane may also be related to the extent of migrations of different populations, since the diametrically opposed positions in the overall area of subjects are occupied by semi-anadromous Taimyr chars and chars of the Kamchatka Peninsula that go relatively far out into the sea [154].

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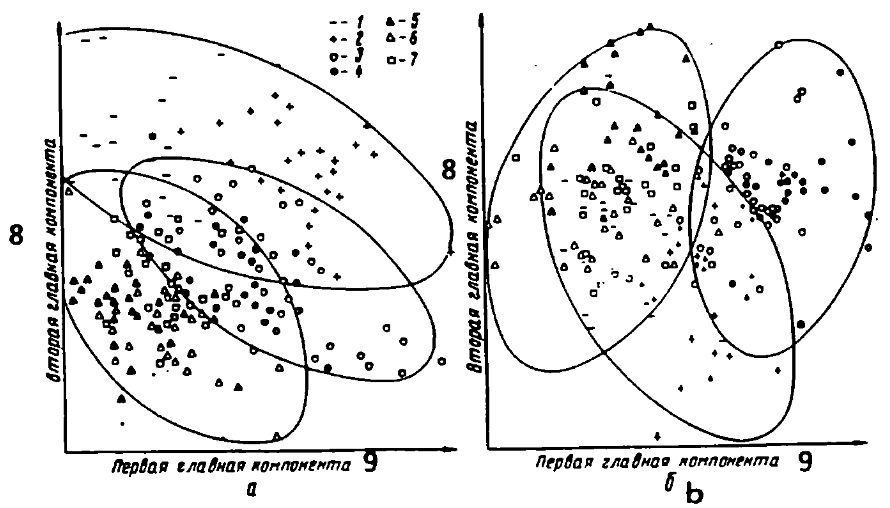

Рис. 45. Расположение проходных гольцов на плоскости главных компонент по пластическим (а) и меристическим (б) признакам:

1 — Чукотка; 2 — Таймыр; 3 — Кольский п-ов; 4 — Чешская губа; 5 — Камчатка (р. Утка); 6 — Командорские о-ва; 7 — р. Камчатка

Figure 45. Placement of anadromous chars on the plane of main components according to plastic (a) and meristic (b) features:

1 - Chukotka Peninsula; 2 - Taimyr Peninsula; 3 - Kola Peninsula; 4 - Cheshskaya Bay; 5 - Kamchatka Peninsula (Utka River); 6 - Komandorskie Islands; 7 - Kamchatka River; 8 - second main component; 9 - first main component

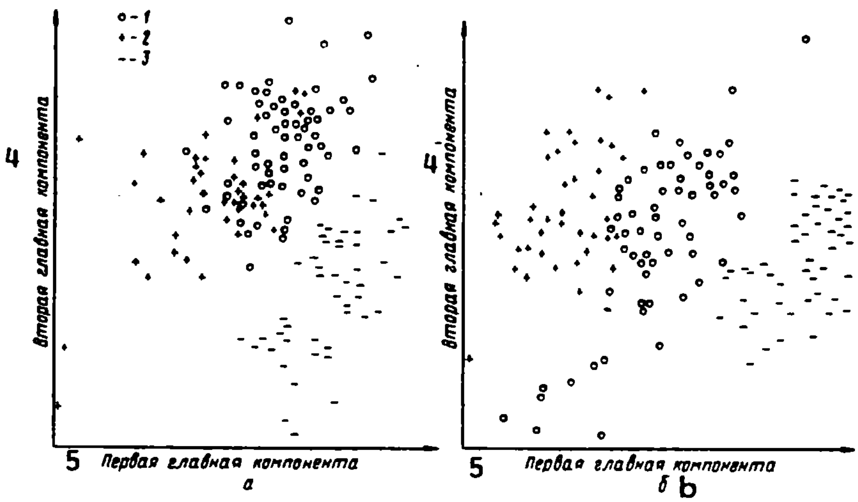

Рис. 46. Расположение проходных гольцов трех морфотипов на плоскости главных компонент по меристическим (а) и пластическим (б) признакам:
1 — альпиноидный; 2 — высокоарктический; 3 — мальмоидный

Figure 46. Placement of the three morphotypes of anadromous chars on the plane of main components according to meristic (a) and plastic (b) features:
1 - alpine-like; 2 - high-arctic; 3 - Dolly varden-like; 4 - second main component; 5 - first main component

A similar picture is also obtained in evaluating similarity according to meristic features. There are no clear boundaries between neighbouring groups of subjects on the plane of the first and second main components (see Figures 45-47). The opposite edges of the common set are occupied by Taimyr and Kamchatka chars. The greatest scattering of points is noticed within the Taimyr population. The remaining chars occupy an intermediate position. Chukotka chars, according to meristic features, display a significant similarity to chars inhabiting the Kamchatka River and the waters of the Komandorskie Islands. The chars of the two Barents Sea populations are very similar to one another. In this case a clinal variability is also revealed. The results of the research of S.Sh. Mikhailōva [154] did not allow her to isolate the two phenotypes which could have been identified with *S. alpinus* and *S. malma.* Although it is possible to delineate each population, even though there are no clear gaps between neighbouring populations, a gradual movement from one set of subjects to another is observed. In accordance with the data of K.A. Savvaitova and V.V. Volobuev [218] the alpine-like, Dolly varden-like and high-arctic morphotypes were delineated. As a result, three sets of subjects were obtained that overlapped substantially between one another, a fact which is evidence of the existence of anadromous phenotypes that cannot be completely identified with any of the morphotypes.

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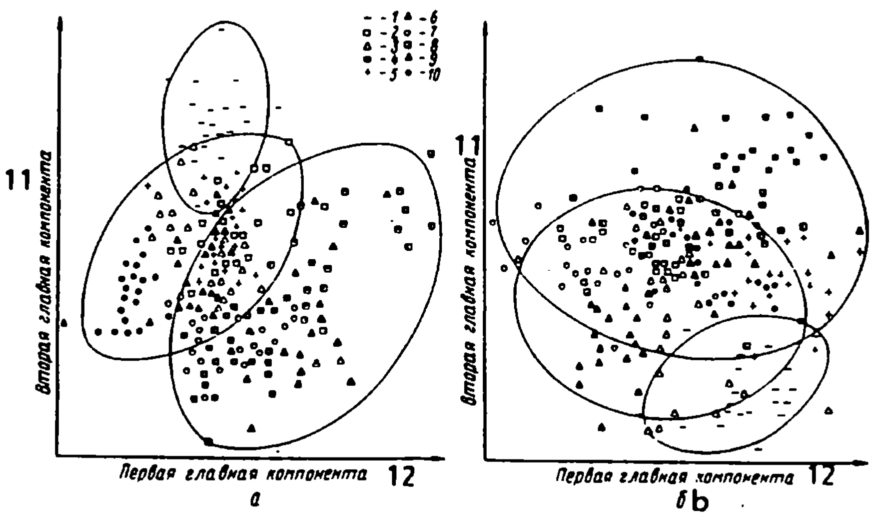

Рис. 47. Расположение озерных гольцов на плоскости главных компонент по пластическим (а) и меристическим (б) признакам:
1 — оз. Азабачье; 2 — оз. Дальнее; 3 — оз. Начикинское; 4 — оз. Корраль; 5 — оз. Фролиха; 6 — оз. Форелевое; 7 — оз. Переходное; 8 — оз. Лама (голец Дрягина); 9 — оз. Кета (боганидская палия); 10 — оз. Носковое

Figure 47. Placement of lake chars on the plane of main components according to plastic (a) and meristic (b) features:
1 - Lake Azabach'e; 2 - Lake Dal'nee; 3 - Lake Nachikinskoe; 4 - Lake Korral'; 5 - Lake Frolikh; 6 - Lake Forelevoe; 7 - Lake Perekhodnoe; 8 - Lake Lama (Dryagin's char); 9 - Lake Keta (Boganida lake char); 10 - Lake Noskovoe; 11 - second main component; 12 - first main component.

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The chars of the Chukotka Peninsula (Kukekkuyum River) occupy an unusual position: according to the set of plastic features, they can be attributed to the high-arctic morphotype and, according to the set of meristic features, to the Dolly varden-like morphotype. In those cases where those individuals having the most clearly defined characteristic features of the morphotypes (Kola chars - alpine-like; Taimyr chars - high-arctic; Kamchatka chars - Dolly varden-like) were used as model populations, it turned out that a change in the number of populations led to a certain change in the informativeness and composition of the components, although the nature of the relative position of the populations remained as before.

Therefore, the morphotypes that we isolated according to certain meristic features are distinguishable. The Dolly varden-like morphotype is the most isolated; the high-arctic and the alpine-like morphotypes are not clearly separated from one another and they overlap according to the set of meristic features.

An analysis of the features of 10 populations of lake chars from different parts of the natural habitat (Lake Noskovoe - Kola Peninsula, Lake Keta, Lake Lama - Taimyr Peninsula, Lake Perekhodnoe, Lake Forelevoe - Lena River Delta, Lake Frolikh - Zabaikal'e area, Lake Korral' - continental coast of the Sea of Okhotsk, Lake Azabach'e, Lake Dal'nee, Lake Nachikinskoe - Kamchatka Peninsula), using the method of main components, also revealed a different level of isolation of individual populations. Some sets of subjects strongly overlap; others are isolated. However, there are no clear gaps demonstrating the morphological originality of populations that are described by some authors as independent species, although such species as Dryagin's char, Boganida lake char and neiva are described precisely according to these morphological features. On the whole, the subjects form a single set that may be subdivided, to our understanding, into three morphotypes (see Figure 47). The set of subjects representing the high-arctic and alpine-like morphotypes overlap to a considerable degree with the lake chars; only the outer populations are differentiated.

The results of a study of the phenetic similarity of chars using methods of multivariate analysis are also evidence of the absence of a clear division of phenones. All of their variety may be tentatively reduced to three morphotypes with the boundaries between them blurred due to populations having intermediate feature values or, according to one set of features, attributable to one morphotype, and, according to another set of features, attributable to another morphotype.

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DIFFERENTIATION ACCORDING TO OSTEOLOGICAL FEATURES

Using the data of E.D. Vasil'eva [36, 37, 38, 39, 138, 139, 140 et al] and M.Yu. Pichugin [178], who studied the char populations researched using osteological methods, we attempted to differentiate the char morphotypes according to these features. It proved to be difficult to isolate clear osteological features characterizing char morphotypes to our understanding since the significant variability inherent in ostelogical features is determined by many factors. It is known that a change in skull structure takes place during ontogenesis in salmons [38, 140]. In chars, the structure of the skull is also related to ecology. Thus in anadromous chars the mandible arch is narrow; it is a bit wider in lake-river benthophages and even wider in predatory lake-river chars [38, 195, 250]. The bend on the suboperculum is well defined in anadromous and river chars; in lake chars this bend is rounded [195]. In anadromous chars the operculum is rounder and in lake chars it is elongated [250].

A number of researchers point to great ontogenetic changes in the fish's skull in connection with the marine period of life [140]. In certain works on Pacific salmons (genus *Oncorhynchus*) a suggestion is made concerning the connection between skull proportions and the growth rate of individuals.

Therefore, the successful use of the osteological method is possible only following a preliminary evaluation of the variability of each feature. As was shown by E.D. Vasil'eva [138, 139, 140] the following influence skull morphology in chars first and foremost: growth, sexual maturity, the distinctness of migrations in the life cycle, and diet. We conducted a comparison of char populations taking these factors into consideration.

E.D. Vasil'eva examined the anadromous chars that we attribute to the high-arctic (the populations of Novaya Zemlya, the Gulf of Minin and the Chukotka Peninsula - form I) and the Dolly varden-like (the populations of Western and Eastern Kamchatka Peninsula and Komandorskie Islands) morphotypes.

In analysing the skull morphology of anadromous chars from different parts of the natural habitat, E.D. Vasil'eva [36] did not discover a single ostelogical feature that would be peculiar to any specific population as opposed to all the others. Individual populations were distinguised by a different frequency of occurrence of similar phenotypes and, insignificantly, by certain skull proportions. According to plastic skull features, the differences between populations proved to be small and reached 1.28 [131] only in rare cases. One level of overlapping or another was even observed between the populations that were most remonte geographically.

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On the whole, chars from the populations of the Dolly varden-like morphotype (Komandorskie Islands, Kamchatka Peninsula, Chukotka Peninsula - form II) are more similar in skull proportions. The high-arctic Novaya Zemlya chars differ the most, on the one hand, and the chars of the Dolly varden-like morphotype on the other. Significant differences are also observed between the sympatric anadromous chars of the Chukotka Peninsula, which are attributed to different morphotypes [53].

Obviously not only hereditary factors influence the scope of the differences, but biological features as well (extent of migration routes, definition of breeding colours, etc.) [36].

The Dolly varden-like chars from the Bystraya River, and, to a lesser degree, the chars from the waters of the Komandorskie Islands [36], differ the most in qualitative features from the high-arctic Novaya Zemlya chars.

E.D. Vasil'eva [36] studied freshwater char populations. K.A. Savvaitova and V.V. Volobuev [218] consider that these may be attributed to the alpine-like (Kola chars), high-arctic (Taimyr chars and davatchan from Lake Frolikh, Zabaikal'e area) and Dolly varden-like (Kamchatka chars) morphotypes. We were unable to reveal principal differences in skull morphology in freshwater chars [36]. Some degree of overlapping was found in the plastic features. On the whole, according to these features, the alpine-like chars of the Kola Peninsula and the high-arctic chars of the Zabaikal'e area were closest to one another. The Dolly varden-like Kamchatka chars differ from the others to a greater degree. However, according to various skull proportions, the nature and magnitude of the differences of individual forms are not identical. For example, in the Dolly varden-like Kamchatka chars, the mandible arch and rostrum are significantly wider; the slope of the suboperculum, the depth of the dentale opening and the distance to the articulare opening are somewhat greater, and the dentale extension is positioned closer to the anterior end of the bone. According to some of these features, the alpine-like Kola and high-arctic Taimyr chars differ slightly; according to other features, the Taimyr chars are closer to the Dolly varden-like Kamchatka chars. The high-arctic davatchan is characterised by the widest base of the ethmoid section and an extended parasphenoid in the anterior part. According to the first feature, the alpine-like Kola chars are closer to the high-arctic davatchan, but, according to the second feature, the high-arctic Taimyr and Dolly varden-like Kamchatka chars are closer [36].

According to qualitative features, the differences between populations of chars attributed to different morphotypes amount to a nonuniform frequency of occurrence of similar phenotypes. The alpine-like Kola chars differ the most from the others. They retain juvenile features of morphology the most, the latter to a lesser degree, but also peculiar to populations of the high-arctic morphotype.

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Therefore, if Dolly varden-like chars were in contrast to all other forms according to plastic features, then they are closer to high-arctic chars than the alpine-like chars are, according to qualitative features.

Alpine-like and Dolly varden-like chars differ more strongly in skull structure. The high-arctic char populations of the Taimyr Peninsula and the Zabaikal'e area are closer to one another. According to many osteological features, the latter occupy an intermediate position and differ least of all from all the other forms studied.

In comparison with the alpine-like and the high-arctic populations, the Dolly varden-like chars have very pronounced ontogenic transformations in the structure of the chondrocranium, the supraethmoid, the jaw and frontal bones and the glossohyale. This may possibly be the result of a different lifestyle. The Kamchatka chars studied by E.D. Vasil'eva are lake-river chars and close to the anadromous form in lifestyle. The incomplete ontogenetic transformations in the skull of Kola chars are to a significant degree due to their slowed growth and small dimensions [36].

As the result of an ostelogical analysis of freshwater chars from different areas of the natural habitat that are attributed to different morphotypes, not one specific feature in the skull structure was found either. Forms differ only in the frequency of occurrence of similar phenotypes and certain skull measurements, the values of which always overlap [36]. Therefore, even when using this method, one is not able to reveal clearly separated phenones. The boundaries are blurred between alpine-like, high-arctic and Dolly varden-like morphotypes, which are separated according to osteological features. As E.D. Vasil'eva correctly points out [39], the nature of osteological differences is not always in accordance with the presence or absence of reproductive isolation and with the level of divergence according to other features (plastic and meristic features, blood groups, etc.). The process of divergence may involve different structures in each specific case. Therefore, various species may not differ osteologically, i.e. be twin species from the point of view of osteological analysis or, as a result of the strong ontogenetic variability of certain skull elements of the grouping within a single population, (for example, dwart males and anadromous males and females) they may differ greatly, right up to the existence of a hiatus between the distribution of the values of skull proportions changing in ontogenesis [138, 139, 140].

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In this respect, it is not likely possible to consider it justified to attach significant weight to osteological features [57, 58, 61]. The osteological method should be examined equally with other methods. It is essential to established the boundaries of its use and to confirm the conclusions made with data obtained by other methods. The above is in contrast to the conclusions of M.K. Glubokovskii [57] and other authors concerning the fact that species specific combinations of skull structure features in chars are highly stable and that there are no intermediate phenotypes at all. These authors, although in words they even recognise the existence of the intraspecific variability of osteological features [59], in deed they practically deny this existence. They isolate 15 phenones of species rank. However, the diagrams they present of skeletal elements characterizing these species fall within the framework of variability of individual populations.

THE STATUS OF ALPINE-LIKE, DOLLY VARDEN-LIKE AND HIGH-ARCTIC CHAR MORPHOTYPES

Determining the taxonomic status of char morphotypes is difficult for a number of reasons, mainly due to the connection between the quantities of the features examined and the living conditions at different latitudes. However, it is possible to find differences in northern and southern char populations. Thus, the function of pyloric caeca is mainly secretory. At low temperatures the essential fermentative activity is apparently ensured by a large number of caeca. At high temperatures, the ferments work actively and the secretion may be brought to the necessary level when there is a small number of pyloric caeca. Differences in the number of gill rakers are probably the result of the effect of temperature on forage. Thus, in certain lakes, where the size of food items varies greatly from small plankton organisms to large fish and the vegetation period is short, euryphagy in chars is more sharply pronounced and, accordingly, the number of gill rakers increases.

One should bear in mind that the scope of individual variability in certain populations is so great that it is possible to find individuals with feature values of all detected groups. For example, the number of pyloric caeca in anadromous char populations fluctuates: from the Utkholok River (Western Kamchatka Peninsula) - from 17 to 42 (average 24.2); from the Karluk River (Alaska) - from 21 to 39 (average 30); in freshwater char populations from the lakes of the Polyarnye Urals - from 25 to 43 (39.6); from the Pyasina River basin - from 20 to 55 (39); from Lake Azabach'e (Kamchatka Peninsula) - from 20 to 45 (30.6) and from 21 to 41 (28.2). The

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number of gill rakers also varies noticeably: in anadromous char populations from the Sagavanirktok River (Alaska) - from 19 to 27 (23); in freshwater char populations from the lakes of Sweden - from 19 to 27 (23); in the lakes of the Pyasina River basin - from 18 to 32 (27). Usually, even in those cases where obvious differences are observed, there is no hiatus between populations and overlapping is noted.

A large individual variability in the number of pyloric caeca and gill rakers makes it difficult to determine the species of both individual samples and populations. There is far from always a correlation between the number of gill rakers and pyloric caeca. This is particularly apparent in brook char populations that can be attributed to one species according to the number of rakers, but to another species according to the number of pyloric caeca [218].

Similar difficulties also arise in determining, according to these features, the status of chars from Lake Blizhnee (Lena River delta) and Cherskii chars, which, according to the number of gill rakers (18-28, 22.6 and 17-24), may be attributed to the Dolly varden-like chars, but, according to the number of pyloric caeca (31-62, 46.1 and 47), may be attributed to the high-arctic chars [24, 149]. The situation is even more complicated when such features are being examined as the colouring and shape of the body, the location of the upper jaw and fins, breeding changes, osteological features, etc. There is no complete conformity between them and the data obtained are often conflicting. This is evidence of the insufficient differentiation of chars into three groups. In this respect it appears expedient to examine the separate morphotypes within *S. alpinus complex*, without allocating them a taxonomic rank, the more so since the issue of their reproductive isolation is unclear. Apparently in some areas of the natural habitat they may act as species with regard to one another, but in other areas they act as intraspecific groupings of a different level [204, 218].

The char populations of one morphotype may apparently have different origins and ages. In some cases their ancestors are chars of the same morphotype to which they belong themselves and, in other cases, they are chars of another morphotype. Irrespective of origin, the final phenotype may be similar. In regions where one morphotype clearly dominates, sympatric populations of another morphotype are likely its derivatives and not relic forms. Thus, the predominant alpine-like morphotype in Europe is the source for individual populations of Dolly varden-like and high-arctic chars, and the Dolly varden-like morphotype in the Far East is the source for the chars of the Chukotka Peninsula, the Okhotsk coast, the Kamchatka Peninsula (Lakes Dal'nee and Nachikinskoe) etc. The following may be evidence of this: data on the molecular hybridization of DNA, the similarity of a number of osteological features (number of 138
fontanelles in the ethmoid area and on the olfactory cerebral pons and the degree of definition of the rostral fossa) in sympatric anadromous high-arctic and Dolly varden-like chars of the Chukotka Peninsula, the difference of both forms according to these features from the Novaya Zemlya high-arctic chars, as well as the presence of brightly-coloured lips and jaws, the hook and notch on the jaws of the sympatric high-arctic and Dolly varden-like chars in Lake Nachikinskoe on the Kamchatka Peninsula and the difference between both groups and the high-arctic forms of the Taimyr chars in which these features are not pronounced [53]. It is possible that, however, in certain situations rare in this region, a char morphotype may give rise to populations that are similar in phenotype to the dominant form.

Therefore, in different areas of the natural habitat, under similar conditions, as a result of the manifestation of a homologous [33] parallel variability, char phenotypes are formed that are similar according to individual features, but not identical.

THE ECOLOGICAL STRUCTURE OF CHAR GROUPINGS REPRESENTED BY DIFFERENT MORPHOTYPES

Ecological groupings in chars are not uniform. Anadromous, lake-river, river, lake, dwarf lake, dwarf stream and other ecological forms are distinguished. More specialized groupings in their turn may be in any of the forms. These groupings are differentiated by biotypes, spawning periods, type of diet, colouring, etc. Between the groupings there is a different level of isolation and of morphological as well as genetic differentiation.

Different groupings are the carriers of the high-arctic morphotype. The anadromous form with features of this morphotype, often designated as *S. alpinus*, lives on Novaya Zemlya [86], on the Taimyr Peninsula [155], in certain rivers of Asia and America that flow into the Arctic Ocean [183, 244, 337, 343, 344], in the Pacific Ocean basin - in rivers of the southern part of the Chukotka Peninsula [244]. This form is small in numbers; it occurs sporadically throughout the natural habitat and, apparently, it is a secondary-anadromous form originating from lake populations [218]. In some rivers this form is represented by spring and winter races, for example, in the Kara River on the Taimyr Peninsula [155, 184].

The lake form of the high-arctic char morphotype occurs more frequently. It lives mainly in the arctic, subarctic and boreal zones of Eurasia and North America. Apparently the following may be attributed to this form: some populations from the mountain lakes of Switzerland, Austria, Scandinavia and Karelia. These populations are attributed to *S. alpinus* and *S. alpinus lepechini* [108, 267, 268], davatchan *S. alpinus erythrinus* from Lake Frolikh [159, 216] and 139
chars from the lakes of the Kuando-Charskii watershed [185, 186, 221], *S. alpinus*, *S. drjagina*, *S. boganidae*, *S. taimyricus*, deepwater char, black lake char from the water of the Taimyr Peninsula [24, 127, 155, 217, 218, 222], chars from Lake El'gygytgyn (Anadyr' River basin) [55], *S. alpinus* from certain rivers of the Lena River delta [126], *S. neiva* from the lakes of the continental coast of the Sea of Okhotsk [49, 239], chars from Lakes Nachikinskoe and Dal'nee on the Kamchatka Peninsula [198, 206], chars from the lakes of America [337 et al], resident char from Lake Sikaribetsu (Hokkaido) known under the name of *S. malma miyabei* [332].

The lake form may be differentiated by growth rate, diet, spawning periods, habitat locations and colouring. Together with the regular form, a slow-growing dwarf form occurs, for example, in Lake Ayan on the Taimyr Peninsula [225], in Lake Korral' (basin of the Sea of Okhotsk) [50], in lake Gol'tsovoe (Zabaikal'e area) and in Lake El'gygytgyn (Chukotka Peninsula). In addition to the char euryphages, there are also highly specialized planktophages, for example, the dwarf neiva in Lake Korral' [50]. Chars may generate deepwater forms with the appropriate adaptations. Such forms are known in Lake Shchuch'e in the Polyarnye Urals [6], in Lake Labynkyr in Yakutia [102], in the Norilo-Pyasinskie lakes and in Lake El'gygytgyn. An isolated melanistic form inhabits the Norilo-Pyasinskie lakes.

The alpine-like char morphotype is represented by the same forms as the high-arctic morphotype. The anadromous form of this morphotype is known in Iceland [395], Scandinavia [313, 335], on Spitsbergen Island [301], on the Kanin Peninsula and in Cheshskaya Bay, on the Murmansk coast [183], in Chaunskaya Bay [199], in the waters of Canada [258, 297, 391] and in Greenland [354]. The lake form is more widely distributed. It populates the lakes of Iceland, Ireland, Great Britain [293], Sweden, Norway, Finland, Karelia, the Kola Peninsula, the mountain lakes of France, Switzerland and Austria [108, 285, 286, 287, 364, 356, 380], the lakes of the Lena River basin [126, 149, 220], Indigirka [102], Chaunskaya Bay [199, 253] and North America [267, 281, 337, 381]. These chars may be represented by groupings that are differentiated by growth rate and diet [285, 356 et al], spawning periods [293], colouring [285], etc.

Chars of the Dolly varden-type morphotype are mainly distributed in the Pacific Ocean basin along the Asiatic and North American coasts. The anadromous form of this morphotype occurs practically everywhere in this region, but its numbers decrease noticeably towards the south. It is particularly numerous on the Chukotka Peninsula [19, 244], the Kamchatka Peninsula and the Komandorskie Islands [204, 206 et al], the continental coast of the Sea of Okhotsk [46, 140
47], Sakhalin Island [72] and Alaska [259, 337, 338 et al]. Dwarf males are a component of local flocks of anadromous chars. These dwarf males mature in fresh water without going out to sea and reproduce together with the anadromous chars [46, 47, 51, 213].

In certain regions (the Kamchatka River basin, the Okhota River, etc.) one observes the differentation of the anadromous char by periods of movement to the river: the numerous tysyachniks and the small, sexually immature chars ascend the river in early spring. In summer the movement of ordinary chars begins; some of them go to spawn. It is possible that the structure of similar char flocks is to some extent similar to the structure of noble salmon flocks, particularly Atlantic salmon *S. salar L.* [24]. In the Kamchatka River basin, based on an analysis of ostelogical features, M.K. Glubokovskii [57] distinguishes two phenones that he attributes to different species: *S. malma* and *S. albus*. The first species, in his opinion, is represented by anadromous chars and char-benthophages from these waters; the second species is represented by anadromous chars and predators from these waters.

In the Kamchatka River basin and other bodies of water of the peninsula, on Sakhalin Island and in the rivers of the Okhotsk coast, anadromous chars are euryphagous; moreover, fish is not the main component of their diet [46, 72, 204, 207]. The morphobiological groups isolated by M.K. Glubokovskii [57] in the Kamchatka River basin do not have to be viewed within the confines of two species, even more so since, as he claims, chars less than 25 cm in length may not be attributed by osteological features to any of the species he described. The conflicting data in the literature on anadromous chars is evidence of the complex, but little-studied structure of individual local flocks.

The river form of the Dolly varden-like char morphotype is very numerous and occurs on the Kamchatka Peninsula, the Komandorskie and Kuril'sk Islands, on Sakhalin Island, the continental coast of the Sea of Okhotsk, the lower riches of the Amur River, in Primor'ye, in Japan and from Alaska to California [8, 24, 72, 204, 213, 239, 260, 267, 268, 337 et al]. In most regions, the river form exists sympatrically with the anadromous form and often represents a common population system with it. The river form exists independently in the south of the natural habitat. A melanistic river form, the stone char, is known in the Kamchatka River basin [210]. River form chars in certain bodies of water may be differentiated into predators and benthophages by type of food. However, there is apparently no strict isolation between them [204]. River forms are known that are differentiated according to growth rate. Dwarf chars live in small streams. They are found in Alaska, in the Mackenzie River basin [340], in the tributaries of Lake Azabach'e on the Kamchatka Peninsula [209], on Sakhalin Island [72] and on the Asiatic coast of the Sea of Okhotsk [51]. 141

Lake and lake-river char forms occur among the chars of the Dolly varden-like morphotype. Moreover, the pure lake form rarely occurs. They exist in some lakes in France [390]. These forms inhabit Lake Azabach'e where predators and benthophages exist sympatrically [118].

Long-headed, long-nosed and white chars are distinguised in Lake Kronotskoe [43]. These chars are also not uniform in type of food or in reproduction periods and locations. Two char groups occur in Lake Sikaribetsu (Japan). One of these groups lives in open waters and in other in coastal waters. These groupings differ in diet and colouring [317, 324]. The lake form, close to the Dolly varden-like morphotype, occurs in the waters of Alaska [260, 337].

SYMPATRIC MORPHOECOLOGICAL GROUPINGS AND THE EMERGENCE OF FORMS IN THE CHARS OF GENUS *SALVELINUS*

Throughout the natural habitat of the genus, sympatric groupings of individuals occur in chars; these individuals differ in ecology and morphology. Great difficulties arise in determining their status and origin. The level of their isolation from one another varies.

Within *S. alpinus complex* it is apparently possible to find all the types of isolation mechanisms isolated by E. Mair [132]. Initially any forms of isolation may arise that occur due to the action of precopulation mechanisms, which in future may lead to the appearance of postcopulation mechanisms. The appearance of a different type of isolation and its preservation are determined to a considerable degree by the action of ecological factors. Therefore, relying upon the data of an ecologico-morphological analysis of populations, it is often possible to assess the level of isolation.

Groupings of Arctic char are closely bound together in rivers. For example, in anadromous char flocks of the Kamchatka Peninsula dwarf freshwater males occur that reproduce together with anadromous fishes. These males retain throughout their life the morphology and colouring of young fish and their breeding colours develop only during the spawning period. According to the nature of their diet, they are benthophages and occupy a niche similar to that of young fish. In certain situations (the rivers of the Komandorskie Islands) a river grouping is part of the spawning flock of the anadromous form, as well as of the dwarf males. This river grouping is represented both by males and females. These intrapopulation groupings differ from one another according to a set of features: colouring, morphology, growth rate, fecundity and period of sexual maturation. Individuals of all groupings feed on benthos, but, as opposed to typically anadromous fish, the freshwater individuals consume insects vigorously. 142

On the whole, intrapopulation char groupings occupy similar, but different food niches. All of these groupings reproduce at the same time, at the very same spawning grounds. Membership in any particular grouping is not likely the result of heredity and the groupings represent a common gene pool [213]. In similar cases there is no basis for speaking of reproductive isolative of sympatric groupings. However, more isolated char groupings occur in certain river basins. The dwarf stream chars from the Lake Azabach'e basin on the Kamchatka Peninsula, represented by females and males, may serve as an example [209]. These chars live mainly in the upper reaches of small rivers that flow into a lake. For them a slow growth rate, early maturity, low fecundity and a short life cycle are characteristic. The gonadotropic activity of the pituitary is high in these chars, but somatotropic activity is suppressed [209]. In addition to the dwarf char form, the young of lake-river large chars live in these waters. Adult anadromous and lake-river individuals do not occur here, at least not during spawning. Dwarf chars are phenotypically similar to the young of other forms. It is possible that some examples of the young lake-river form may turn into dwarf individuals. This would be similar to how this takes place in other salmons [18, 24, 209, 249]. However, it is most likely that these forms are separated from one another. They differ in colouring and in a number of plastic and meristic features. Distribution in rivers speaks of their isolation. The young of lake-river chars stay lower in the current and there are fewer young in the upper reaches [209].

Although in type of diet the dwarf chars and the young of the lake-river forms are benthophagous, they do not compete, since they occupy different parts of the river. Apparently the dwarf chars of some rivers of Sakhalin Island [72] and the Okhotsk coast [52] are isolated from other forms. River chars coinciding with certain tributaries populate the Kamchatka River basin. Groupings differing in type of food, benthophages and predators, are part of the flock of each tributary. In external appearance they are similar in morphology and blood groups. They spawn at the same time and probably in the very same rivers [204]. River chars go out to feed in the Kamchatka River, but they do not perform significant migrations. Their local flocks are probably isolated from one another. In ecology and diet, they differ little from the anadromous char during the freshwater period of its life. It is possible that anadromous and lake-river chars may cross.

Yet another river form is known in the Kamchatka River basin: the stone char. This is a melanistic and probably reproductively isolated form. It is characterized by a number of specific features of morphology and ecology [210]. 143

Another example of sympatry among chars in rivers may be the anadromous groupings that differ according to the time they go to spawn. In the Kara River (Karskoe Sea basin) two mass movements are clearly pronounced: the spring-summer and the autumn movements. Chars in the first movement begin to ascend the river still under ice and end their migration at the beginning of July. Chars in the second movement go at the beginning of August and end in October. These groupings differ in ecology and apparently do not cross over from one grouping to another [184]. However, their spawning takes place at the same time: at the beginning of September to October. Possibly some of the chars from the spring and autumn movement reproduce jointly.

Therefore, reproductive isolation between sympatric char groupings in rivers is manifested in different ways. In the majority of cases this isolation is not absolute: individuals from different groupings cross and provide viable descendants. Similar interrelationships between groupings may be viewed as the result of unstable living conditions in river systems. Sharp changes first and foremost in flood and temperature patterns, flow rates, type of channel, etc. have an effect on the condition of forage and spawning grounds. The lack of strict isolation between char groupings in rivers allows for survival under changing conditions and the retention of large numbers.

The level of isolation of sympatric groupings also varies in lakes. For example, in Lake Nordlaguna on Jan Mayen [386] there exist groupings of a small dwarfish lake char-benthophage and a fast-growing large cannibal that are not reproductively isolated from one another. The first grouping clearly predominates in numbers. The char fry feed on benthos and the adult fish consume detritus. The majority of dwarfish chars die after 10 years, but some of them shift to cannibalism, reach large proportions and reproduce once again at the age of 12-16 years. This is observed in bodies of water with very poor forage. The division of chars into niches occurs in this case in the process of ontogenesis. Some small chars in Lake Nordlaguna have a genotype that determines the possibility of their shifting to cannibalism [386, 387]. An example of even more isolated sympatric char populations in lakes may be the slow-growing dwarf and fast-growing neiva from Lake Korral' [52]. These forms differ in proportions and growth rate, age of first maturity, diet and nutritional state. It is assumed that one of the factors determining differentiation is an unsufficient supply of large food items for the neiva. Apparently the 144
separation of the population into two ecological forms was facilitated by intraspecific food competition, as a result of which the dwarf population occupied the plantophage niche and the large population occupied the benthophage and predator niches. The clear predominance in the population of dwarf neiva males (93%), the simultaneous maturation of dwarf and fast-growing forms and their occurrence in the same spawning grounds provide a basis to propose that these forms are a single population.

However, a number of examples of reproductively isolated sympatric char populations are known in lakes. Populations of spring- and autumn-spawning chars exist in Lake Windermere (Great Britain) [293]. They differ not only in ecology of reproduction, but in growth rate in the first year of life and in number of gill rakers. Four forms of char live in Lake Tingvellir (Iceland). They differ in type of diet and growth, time of maturation, spawning periods and locations, upper jaw shape and number of vertebrae [293]. In the lakes of Norway, Sweden and Finland, there are sympatric populations of chars that differ mainly in diet, growth rate, time of sexual maturation, colouring, etc. [304, 309, 318, 355, 367, 357, 360]. The fast-growing (predators) and slow-growing (benthophages) are usually differentiated. Different food niches are also occupied by chars from the mountain lakes of Austria. Here at least 3 forms are distinguished in the same body of water. One of them is a predator and characterized by faster growth [293].

The sympatric chars from the lakes of mid-Europe are divided into 4 groups: the normal char (Normalsaibling), the melanistic form (schwarzreiter), the predatory char (wildfangsaibling) and the deepwater char (tiefseesaibling) [283]. The normal char is the most widely distributed and the most numerous. It is a euryphage that feeds on plankton, small fish and partly on benthos. The melanistic form of the normal char occurs in high mountain lakes. The predatory char is large (up to 10 kg), few in numbers, keeps to fairly deep waters and has an extended spawning period. The deepwater char is small in size and has large eyes and a light-coloured body, usually without spots. All features of these groupings overlap and their interrelationship is unclear [273, 275, 285, 303, 325, 353, 370, 374, 378, 379, 380]. Two sympatric char groupings inhabit the Bodensee. There is a noticeable difference between them in colouring, head and body shape, jaw placement, number of gill rakers, scale structure, age and growth, feeding and reproduction [285]. The niches that they occupy are clearly different. It is most likely that they are also isolated in places of reproduction. 145

Sympatric char groupings are also known in the lakes of Karelia. Two forms of lake char are distinguished in Lakes Ladoga and Onega and other lakes: the "flat stone" form and "high bank" or "hole" form. The first is darker, has a large head, lays eggs in the autumn in shallow water and attains a weight of 5-7 kg. The "hole" lake char is lighter in colour; its head is shorter; it lives at great depths; it may also reproduce in spring and it weighs approximately 0.8-2 kg [24, 228]. A.I. Kolyushev describes char forms from the lakes of Karelia that live together, but are isolated [108]. He writes that there is a light-grey char, which is darker during spawning, and with large spots, living in Lake Umbozero, as is a char that acquires bright breeding colours. These chars differ according to a number of biological features.

In Lake Taimyr, 3 char populations live together that are attributed to different species: *S. alpinus*, *S. taimyricus* and *S. drjagini* [155]. The arctic char is an anadromous form; the taimyr char is a lake form and Dryagin's char is a lake-river form. They differ in lifestyle, colouring and certain morphological features. They occupy different niches. The lake char is represented by small fish (up to 50 cm). Spawning takes place in the lake, close to shore. This char grows very slowly. The lake-river char is large (up to 1 m); it spawns in rivers, feeds on fish and grows quickly. There are individuals in this grouping that undertake irregular migrations to Taimyr Bay. The anadromous char is not homogeneous: a large-headed and small-headed char are distinguished. It is possible that they belong to winter and spring races [155].

Sympatric and probably reproductively isolated populations of benthophages and predators populate Lake Azabach'e [118, 203]. These chars differ in preferred biotypes, growth rate, life span, degree of development of breeding colours, parasite infestation, etc. [211]. There are differences between them in number of vertebrae, structure of the digestive tract [41], blood groups [35] and karyotype [34]. This is all evidence of the possible reproductive isolation between these groupings. It is possible that they are twin species [41]. However, it is difficult to assess the level of irreversibility of their differences, the more so since chars feeding on mollusks are also known in other regions of the Kamchatka Peninsula [207].

It is likely that, in the majority of lakes on the Kamchatka Peninsula, there exist sympatric char populations that are isolated from one another to a significant degree. A lake char lives in Lake Dal'nee (Paratunka River basin) that does not go beyond the bounds of the lake; lake-river and anadromous chars also live there [200]. They are differentiated by type of diet [207] and occupy different ecological niches.

Their differences are also manifested in growth rate, in nature of reproduction and morphological features related to diet, as well as in number of gill rakers and pyloric caeca [204]. 146
Similar sympatric forms are known in Lake Nachikinskoe (Kamchatka Peninsula) where isolation between groupings is apparently great. Lake chars are mainly pelagic and lake-river chars are littoral, occurring at the mouth of small rivers and in the lower reaches of the rivers themselves. The lake char is euryphagous according to type of diet, but fish is its predominant food; the lake-river char is benthophagous. The growth rate and times of sexual maturation of both forms depend on diet. Differences are observed in the number of gill rakers and pyloric caeca. Both forms differ in colouring and spawning locations and times. There are also differences in karytype [206, 215].

Cohabiting char populations also live in Lake Kronotskoe [43]. Here the long-head, long-nosed and white chars are distinguished. The first char occupies the niche of predator; the second is a coastal benthophage and the third is a euryphage that has a widely varied diet. Based on certain differences, the long-headed char is viewed as an independent species, the long-nosed char as a special subspecies *S. malma schmidti* and the white char as a local population of Dolly varden. There are no anadromous Dolly varden in the lake, as a waterfall barrs the way to the lake [43].

Cases are also known in North America where chars differing in preferred biotypes and food, biology of reproduction and morphology inhabit the same body of water. Sympatric char populations that differ in ecology and number of gill rakers inhabit Lakes Karluk and Frazer. They are attributed to the species *S. alpinus* and *S. malma*. Apparently there is reproductive isolation between them and hybrids are rare [281, 337]. Two populations of Arctic chars inhabit Lake Matamek. Individuals from these populations differ in proportions, colouring and morphology [376]. Sympatric Arctic char groupings are also found in lakes in northwestern Canada [314].

Examples of sympatric populations are rare in the species *S. fontinalis*, *S. namaycush* and *S. leucomaenis* [267].

There are more stable and varied living conditions in lake biocenoses. This allows for the fact that chars may occupy different ecological niches here, as a result of which groupings arise that differ in preferred biotypes, type of food, growth rate, times of sexual maturation, spawning times and locations, colouring, and morphological and biochemical features. The extent of these differences is not uniform in different lakes. There are different opinions on the origin of these groupings. The majority of researchers have no doubt that freshwater chars are derivatives of the anadromous form [43, 182, 199, 267, 275, 285, 293, 337, 355, 370, 378, 379, 380]. Some suggest that the ancestral populations of modern sympatric groupings were different and that numerous 147
invasions took place in the past, which were divided by periods of geographic isolation. A new grouping occupied an open ecological niche during an invasion. The morphological differences of today's sympatric groupings are influenced by the differences of ancestral populations [395]. This was stated with reference to sympatric populations of whitefishes of the genus *Coregonus* from the lakes of Sweden, and later with respect to chars. It is considered that sympatric populations are twin species that entered areas of the modern habitat from Lake Antsilovyi. G. Svardson [398] cites a list of 17 Scandinavian lakes where 2 or 3 char populations live and concludes that 3 species are apparently united under the name *S. alpinus*. Moreover, it is not clear which of them is a true Arctic char and what the other two should be called [398]. These views were accepted by many researchers to explain the origin of sympatric groupings [43, 318, 337, 356, 360]. Other authors propose that geographic isolation is not necessary in order for sympatric groupings to come about. Ecological factors may play a leading role here, particularly differentiation according to food niches, growth rate, and times and locations of reproduction.

There is yet another path to the emergence of sympatric forms: neoteny, the sexual maturation of young fish in streams, where large chars, as a rule, do not reproduce. An unlikely proposal is made suggesting that a species, in populating a new body of water, would assimilate only one niche, leaving the others unoccupied for subsequent invasions. The simultaneous assimilation by a single population of different niches is much more likely, leading to a reduction in food competition and allowing for complete utilization of the ecosystem's resources.

Following S. Gould [296], E. Balon [263] approached the problem of the emergence of sympatric forms in chars from the other side, analysing the patterns of ontogenetic development. He considers that, as a result of irregular development of embryos (heterochronia) in populations, groupings of dwarf chars may emerge, retaining juvenile features due to late ossification. This is usually related to a low level of morphophysiological processes in cold water and insufficient food. Such a process may lead to the emergence of sympatric forms; it is characteristic for extreme living conditions and the development of salmons. Dwarf forms are characteristic of fluctuating, unstable systems. Under the stabilization of ecosystems, accelerated development occurs and groupings of the so-called "normal" or fast-growing chars emerge. E. Balon calls his theory sympatric pedomorphosis. 148

There are many examples of sympatric forms among the representatives of the order *Salmoniformes*. The following arose sympatrically: races of Sevan trout *Salmo ischchan Kessler* and races of trout *Salmo trutta L.* in alpine bodies of water [76, 83], species of the genera *Salmothymus* and *Salmo* in Lake Ohridsko [392], forms of whitefishes of the alpine lakes of Europe [394], sympatric twin species among smelts [326], and sympatric subspecies of ciscos (genus *Coregonus*) from the Laurentian Great Lakes.

In the order *Cypriniformes*, sympatric forms are also known in different species. These forms occupy various food niches and differ in growth rate and in periods of maturation and reproduction. An endemic mountain-asiatic fauna that we studied provides a very clear example of such a species. It lives in the waters of Pamir: the false osman *Schizopygopsis stolickai Steind*, which produces plant-, plankton-, mollusk- and fish-eating forms. The extreme variants probably do not cross and there is some degree of reproductive isolation between trophic groupings. The existence of reproductive isolation is also confirmed by fairly well-pronounced differences in mouth structure and intestine length among groupings with different diets. In this case, the emergence of various false osman trophotypes from a common ancestral form, a river phytophage, probably occured under conditions of sympatry.

Examples of a similar emergence of forms are characteristic of Altai osmans of the genus *Oreoleuciscus* [78] from the waters of Mongolia.

Trophic polymorphism, which is manifested in the existence of plant-eating, predatory and other forms with varying numbers of teeth, is known among perch-like fishes of the genus *Cichlasoma* [375]. Moreover, in this case these groupings are part of one gene pool. Polymorphism in *Cichlasoma mikleyi* is interpreted as a stage of speciation [329]. However, the very fact of its existence does not lead directly to assortative crossing [322]. The initial stages of stable polymorphism, which is not connected with the assortativeness of crossing, lead to incomplete isolation. Complete assortative crossing arises under the influence of interior behavioural mechanisms and is a factor for sympatric isolation [284, 341].

Endemics from the genus *Ilyodon* (the order cyprinodontoids - Cyprinidontiformes) from the waters of the Central Mexican Plateau were subjected to adaptive radiation [401]. Sympatric wide-mouth and small-mouth morphs are known that differ in the colouring of the sexually mature males and in morphological features (shape and length of the jaws, number of teeth and gill rakers), which are connected with trophic adaptations. B. Turner and others [400, 401] discovered different stages of sympatric divergence of these forms in the populations. 149

In laboratory experiments on the crossing of descendants of both wide-mouth and small mouth morphs, individuals of all phenotypes and the intermediate variants between them were obtained. Thus, it was indicated that the latter are not interspecies hybrids, but fall into a common polymorphous species, together with both morphs [300].

The evolution of various trophic adaptations, including morphological features connected with food, is an inseparable part of the adaptive radiation of fish in general. In spite of their obvious importance, they have been insufficiently researched. It is most likely that trophic divergence is the result of changes, not in a large number of genes, but in a few genetic elements. If trophic differences have an oligogenic basis, then an ecologically significant differentiation may take place rather quickly [294, 298, 350, 401].

Trophic polymorphism, in the opinion of a number of authors, is the basis for sympatric speciation [388, 399]. It apparently played a decisive role in the evolution of a "bouquet of species" in rift-valley lakes.

The existence of ecological forms in fish does not necessarily lead to speciation. As per A.S. Kondrashov [110], at the early stages of the process of speciation, a population is close to panmixia; at subsequent stages, there are more extreme individuals in the population than average ones. Such a dumb-bell shaped structure may change in the direction of a break-up into species, but, under the appropriate conditions, it may remain evolution-stable for an indefinitely long time. Such structures come about when there is sufficiently pronounced disruptive selection.

To all appearances, dumb-bell structures consisting of more than two components occur fairly often in fish populations. Moreover, the impression is created that they are most often observed in populations of fish living under extreme, unstable conditions, for example, in arctic or subarctic regions, in high-mountain bodies of water or in the ephemeral lakes of a desert zone, where there are closely joined associations and unoccupied ecological niches. In similar ecosystems, the processes of the emergence of forms are not completed as a rule. On the contrary, under the stable conditions of some tropical bodies of water with an abundance of different niches, "bouquets" of true sympatric species of fish are found [298, 350], although even here it is possible that cases of incomplete speciation take place under conditions of sympatry. Some authors assume that many forms that are considered species are conspecific and belong to polymorphous species [322, 407]. 150

It is apparently incorrect to contrast the emergence of a "bouquet" of species in tropical lakes with the processes of the emergence of forms and speciation in temperate latitudes. Different stages of the process are observed at different latitudes and under different conditions. It is likely that polymorphous species are the smallest "bouquet of species" at the beginning [265, 329].

Thus, in examining different situations of the interrelations of sympatric ecological groupings of fish in nature, one is able to discover different levels of the process of the emergence of forms, which is evidence of the reality of sympatric speciation itself.

Until recently, even the very possibility of sympatric speciation was categorically denied. The followers of the synthetic theory of evolution, headed by E. Mair [132], were particularly intransigent. They accepted as an evolutionary unit the so-called Mendel panmixia population, where crossing is not assortative and its likelihood between any members of the population is identical. In such populations sympatric isolation is truly impossible, since any genetic complex that arises will break down as it comes into being. However, recently accumulated material is evidence of the fact that the likelihood of crossing varies greatly in natural populations representing complicated hierarchical systems [110, 116, 150, 284].

There are a number of causes limiting panmixia in self-reproducing groupings. With the emergence of mechanisms that increase the assortativeness of crossing (insignificant shifts in times and locations of reproduction, growth rate, maturation, behaviour etc.) sympatric groupings may become potential sources of new species, i.e., the main role in sympatric speciation is played by reproductive isolation in ecologically significant features affected by disruptive selection [87, 110].

Disruptive selection may create polymorphism in a population, with a predominance of individuals that are extreme in certain features [388]. The assortativeness of crossing should secure the function of selection, but even assortative crossing itself may be a push towards divergence and speciation. It increases the genotypical dispersion of a population, which may also be a step on the path towards speciation. However, this does not often come about.

Nevertheless, a definitive explanation of examples of sympatry observed in nature is not likely possible and does not conform to the true situation. The differentiation of the same populations may occur over a wide range of biological and physico-geographical conditions

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(from allopatry to sympatry and vice versa). The processes of allopatric and sympatric divergence complement one another. The boundaries between them are often arbitrary and it is sometimes impossible to demarcate sympatric and allopatric differentiation [265, 372]. In Greenwood's opinion [298], a discussion on this subject is more semantic than biological in nature and is reduced to the boundaries of usage of the prefixes sym and allo.

Supporters of the allopatric concept use as a null hypothesis an immigration and invasion model, in accordance with which the properties of modern species are determined by the properties of ancestral forms that moved in sequentially. In a number of cases they are also attracted to the fluctuation model, according to which modern sympatric species of fish in lakes achieved reproductive isolation at a still low water level when individual areas of the lakes were separated by barriers. The hypothesis of so-called intra-lake speciation proposes that the reproductive isolation and ecological differentiation of species originates in the lake itself and includes strictly allopatric, sympatric and parapatric divergence. Moreover, supporters of the concept of geographical speciation reduce "intra-lake" speciation to microallopatric speciation [132, 294, 341]. However, supporters of sympatric speciation, apart from the use of the concept of strict sympatry, use the terms "paraptry", "stasipatry" and "marginal sympatry", referring to the differentiation of populations within the natural habitat, not separated by immovable barriers, but where the exchange of genes between certain individuals is difficult, regardless of their genetic differences. Actually in both cases the very same reasons are what is had in mind.

However, in our opinion, the problem remains. Hasty taxonomic conclusions are often made from the theory of allopatric speciation, including conclusions concerning the absence of intermediate forms, spasmodic speciation, etc. Unfortunately, researchers quite often ignore numerous examples of various forms of sympatric isolation. Nevertheless, more and more works have appeared recently where different aspects of precisely sympatric speciation are discussed with arguments, not only in fish, but in other groups of animals [110, 116, 401].

The ecological model of sympatric intra-lake speciation proposes that divergence according to ecological features occurs simultaneously with a reduced flow of genes. In allopatric speciation, reproductive isolation occurs first, and then the corresponding differences. The concept of a biological species reduces the problem to the restrictions of reproduction. 152

However, for speciation under sympatry, not only the beginning of uncrossability is necessary, but the beginning of the ability to co-exist, dispersing among different niches. The principle of competitive exclusion has no less important a meaning for speciation than the Hardy-Weinberg law. Phenotypical differences are manifested in fish forms more in features that are connected with diet. The model of competitive speciation, at the basis of which are variations in the adaptation of population members to feeding on different forage, may explain the original divergence of populations [372].

It follows from the material examined above that there are a great many examples of ecological differentiation of fish. However, the interpretation of their origin may be varied. Sometimes even the same authors state opposing opinions [33]. One should remember that the actual evolutionary situation may be different in different groups of fish. One may agree with Mayr [336] in that evolutionary processses are highly varied and that what is characteristic for one group may not necessarily be applied to another.

The question, of course, arises each time that researchers come across sympatric populations of chars: how to interpret the differences observed and how to assess the taxonomic rank of these groupings? There are two main approaches. One proposes that the establishment of differences according to any sort of features and the absence of hybrids between sympatric groupings are sufficient for the description of char species [57, 244, 281, 337]. Most often with such an approach, some specific case is studied without analysing similar phenomena in other regions. Others abstain from separating new species [41, 72, 103, 285, 293, 356, 380]. The problem is truly complex. Groupings that are similar in ecology, colouring and morphology exist in many areas of the natural habitat. At the same time, there no absolutely identical populations. They may certainly differ from one another and are often reproductively isolated from neighbouring groupings. In this situation, the description of new species is fraught with the creation of a classification of chars that it will be impossible to use. This will be a return to those days when a new species was described from each body of water. Such an approach to the solution of the char problem is incompatible with the population concept of a species. Apparently, in those cases where sympatric and reproductively isolated char populations are studied, the main focus should be not on the very fact of isolation at a given moment, but on how reversible that isolation is. Convincing data are evidence in favour of the reversibility of isolation [293, 328], data which showed that populations of spring- and autumn-spawning chars, isolated 153
according to spawning periods in nature, may transfer from one to another in an experiment. It is also known that, in chars, intraspecific groupings of different levels emerge quickly, sometimes within a single generation in ontogenesis [386]. A period measured by the life of only a few generations is required in some cases for the emergence of isolation in spawning locations and times. However, isolation barriers often break down as a result of a change in the surrounding conditions and the plasticity of the chars themselves.

Extended arguments may be decided with the help of experiments in the area of experimental systematics and connected with the acclimatization of forms and the study of the reactions of those acclimatized to new conditions. Similar experiments have an already sufficiently long history. In the end, it was precisely such experiments that indicated species unity of the stream trout and the anadromous brown trout, the steelhead trout and the rainbow trout. Chars are not an exception here. From the chronicles of the Middle Ages it is known that in the 13th century a small dwarfish form from the alpine lakes of Liebizkogel and Falkertsee was introduced to the artificial city moats of Friesacher. Beginning in the year 1600, people started to catch large fish, up to 45 kg, with the phenotype of a predator. In 1890 small chars (length 22 cm, weight 90 gm) were transferred from the Zugersee to the Luganersee. After a time, people started to catch larger chars in this body of water (length 30 cm, weight 200 gm). Quite large predators up to 5 kg started to be found in the same place [370]. There are also reverse examples when, as a result of moving a normal form and a predator due to insufficient food, dwarfish chars emerged under the new conditions [275]. This is what happened with chars transferred to Grundlsee in 1753-1763 and Offensee in the 18th century.

Apparently a genetic-hybridological analysis may assist in solving the question of the taxonomic rank of sympatric char populations. However, even in this case, it will not be possible to rely completely on the results obtained. With all of its merits, the biological determination of species also has faults. In particular, the criterion for crossability and reproductive isolation is not comprehensive. There are a number of known cases where crossing and obtaining viable descendants between good species of fish is possible [70, 269]. This situation, together with objective difficulties that arise in identifying chars, points to a lack of clear species criteria. The boundaries between species and forms prove to be blurred in a number of cases and this reflects the true state of things in nature. Arctic char is a complicated complex of forms at different levels of isolation, beginning with groupings that appear each time in the ontogenesis of a single generation and ending with twin species or common well-distinguished phenotypical species. 154

One should agree with Mair [132] in that many populations may be found in nature that travelled only part of the path leading to species status. It can be difficult to apply a biological concept to them. An objective definition of species boundaries is impossible in a multivariate system. Natural populations in contact zones often behave with respect to one another as true species, until their biotypes break down. Isolating mechanisms in nascent species are not yet completely formed. Species level is reached after the speciation process becomes irreversible. However, it is often impossible to determine whether a species has reached the irreversible stage. Refinement of isolating mechanisms in different populations may occur at varying rates. Therefore, when their natural habitats overlap, species may be isolated in some regions, but cross easily in others. Species are populations divided by gaps, but not every gap gives the right to raise an isolated population to the rank of species. In the case examined, we have an analogue of circular natural habitats. Cases are known where extreme populations reach the species level. They do not cross upon meeting, but by all indications they are connected by uninterrupted transfers. *S. alpinus sensu stricto* - *S. malma* could be an example of such a distribution if one could prove species isolation of the extreme members of the series. In the case of sympatry of morphobiological groupings, the situation becomes even more complicated. The separation of species, as a rule, becomes impossible and not even necessary, more so since the varied forms of adaptive polymorphism cannot always be viewed as the initial stages of sympatric divergence. Most often these are forms of species existence that allow the possibilities of biocenosis to be realized to the optimum [163].

DIVERGENCE LEVELS IN THE GENUS *SALVELINUS* AND THE STRUCTURE OF ENDEMIC SPECIES

A group of char species exists in the genus *Salvelinus* where a different stage of subdivision is observed. The following are included in this group: East Siberian char (*S. leucomaenis*), a predominantly anadromous form whose natural habitat is limited by the continental seas of the western part of the Pacific Ocean; American anadromous, river and lake-river chars (*S. fontinalis*) distributed in the eastern part of North America from Hudson Bay and Labrador to the southern part of the Appalachian Mountains and towards the west, including the regions of the Great lakes and the upper reaches of the Mississippi River; lake char (*S. namaycush*) which occurs in the glacial lakes of North America and Canada [267, 268]. 155

It is probable that the species of this group originate from one common ancestor distributed around the northern and northeastern coasts of America. The subsequent isolation of Asiatic and American populations and the extinction of the original form living in the waters of the Pacific coast of North America led to the formation of these species. R. Behnke [267, 268] considers that the separation of the ancestor of brook chars from the others in Salvelinus occurred no later than the Pliocene. Evidence of the antiquity of *S. leucomaenis*, *S. fontinalis* and *S. namaycush* is also provided by the number of chromosomes, the maximum for chars (84-86) [34], and the level of morphological divergence. No one doubts their species isolation and the definition of separate individuals is not difficult. Divergence took the same directions in this group of chars as in *S. alpinus complex*.

For the reasons already examined above, selection acted towards the reduction of pyloric caeca (11-33) and gill rakers (12-20) in anadromous and more southern East Siberian char [202] and a sharp increase in the number of caeca in northern *S. namaycush* (95-210) [333]. The small number of gill rakers (17-27) in this char is apparently related to the fact that it did not occupy a plankotphagous niche and, in comparison with a high-arctic morphotype, *S. alpinus complex* occupies the narrow food niche of a predator [267, 268]. The isolation of *S. namaycush*, *S. fontinalis* and *S. leucomaenis* is also confirmed by data of the molecular hybridization of DNA [56].

The structure of endemic species is much simpler. In the largest part of its natural habitat, East Siberian char is monomorphous and represented by an anadromous form. Towards the south of the natural habitat, the occurrence of dwarf freshwater males increases in populations of anadromous East Siberian char. They are noted on Sakhalin Island and in the Southern Kuril'sk Islands [7, 67, 68, 91]. In some bodies of water of the Kuril'sk Islands, the differentiation of anadromous East Siberian char into two seasonal groups is seen. These groups differ in growth rate and spawning periods. A freshwater form of East Siberian char lives in the south of the natural habitat, in Japan and, apparently, in the lower reachers of the Amur River and in Primor'ye [136, 362]. *S. fontinalis* has freshwater and anadromous forms that are characterized by a significant variability of morphoecological indicators [365, 403, 404]. S. namaycush is predominantly a lake form [334].

A deepwater lake grouping occurs rarely. Some researchers divide it into a separate subspecies *S. namaycush siscowet*. Lake-river populations are also known [330]. Cases have been noted where *S. namaycush* goes out into the sea [271].

DIFFERENTIATION OF CHARS OF THE GENUS *SALVELINUS* ACCORDING TO DATA ON THE MOLECULAR HYBRIDIZATION OF DNA

According to the results of hybridization of thermostable fraction of DNA, using as a bench-mark DNAxDNA of anadromous *S. malma**, it was established that populations of anadromous chars from the Kola Peninsula to the Kamchatka Peninsula differ in a low degree of genetic divergence. Freshwater resident populations diverged significantly more, but only a few forms (stone char, lake-river Nachikinskoe char) attained substantial differences according to this indicator (Figures 48 and 49). However, the divergence level still proved to be less than in East Siberian char, whose species status is not in doubt [342].

An analysis of the genetic divergence of chars from the waters of Eurasia and America, according to a somewhat varied procedure, using as a bench-mark totally fragmented DNA of *S. alpinus* from the waters of Finland, i.e., a region close to Swedish Lapland where this species was described, showed the level of their divergence to be different from standard Arctic char [56]. In order to evaluate the difference of thermostability curves and the calculation of the coefficient of divergence *CD*, only those values of elution at the corresponding temperature spots were used that were reliably (P=0.95) different in homo- and heterological reactions.

The North American *S. (Cristivomer) namaycush* diverged most from the bench-mark species (Figure 50). Its coefficient of divergence *CD* was equal to 59. The shape of the curve is also noticeably different. Apparently, divergence in this case took the route of accumulating nucleotide substitutions. A high level of genetic divergence, contrary to V. Morton and R. Miller [348], confirms the opinion concerning the genus or subgenus isolation [268] of this group of chars.

A much lower level of genetic divergence is found in another endemic North American species *S. fontinalis*, attributed to the subgenus *Baione* (see Figure 50). The coefficient of divergence in this case does not exceed 7.4. However, hyperhybridization is found in the most thermostable zone (90-95^{o}C), which rarely occurs.

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* For the designation of phenones studied, in order to show which morphological description fits those populations that served as a source of DNA; the latin names accepted by L.S. Berg are used.

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Рис. 48. Генетическая дивергенция гольцов от реперной формы (камчатский проходной голец). Расстояния соответствуют *CD*:

1 — кунджа; *2* — кольский голец; *3* — черная палия; *4* — боганидская палия; *5* — голец Дрягина; *6* — глубоководный голец; *7* — каменный голец; *8* — азабачинский хищник; *9* — азабачинский бентофаг; *10* — командорский голец; *11* — камчатский проходной голец (реперная форма); *12* — большерецкий голец (проходной); *13* — озерный начикинский голец; *14* — озерно-речной начикинский голец; *15* — нейва; *16* — даватчан

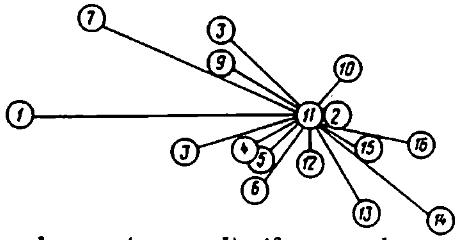

Figure 48. Genetic divergence of chars from the bench-mark form (Kamchatka anadromous char). The distances correspond to the *CD*:

1 - East Siberian char; 2 - Kola char; 3 - black lake char; 4 - Boganida lake char; 5 - Dryagin's char; 6 - deepwater char; 7 - stone char; 8 - Azabach'e predator; 9 - Azabach'e benthophage; 10 - Komandorskii char; 11 - Kamchatka anadromous char (bench-mark form); 12 - Bol'shaya River char (anadromous); 13 - lake Nachikinskoe char; 14 - lake-river Nachikinskoe char; 15 - neiva; 16 - davatchan.

A significantly high level of divergence is found in the endemic Far East species *S. leucomaenis* (*CD*=21.3). Reliable differences have been established in the area of high temperatures (80-95°C). On the other hand, the proportion of unstable duplexes increases. An analysis of the thermostable chars of the Far East, attributed to the species *S. malma* [24], indicates a relatively low level of divergence. Here we observed only one reliably different point of elution (at 80°C). Although *CD*=8.6, the differences in the high-temperature zone are not reliable.

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According to thermostable fraction of DNA there are almost no differences between anadromous Dolly varden and anadromous char of the Kola Peninsula [342]. Higher values of *CD* in this series of experiements should probably be attributed to a comparison of anadromous Dolly varden with a lake form of Finnish Lapland. It is possible that it would be more expedient to use as a bench-mark the DNA of anadromous Kola char, but not the resident form, although it is closest to the first one described by Linnaeus.

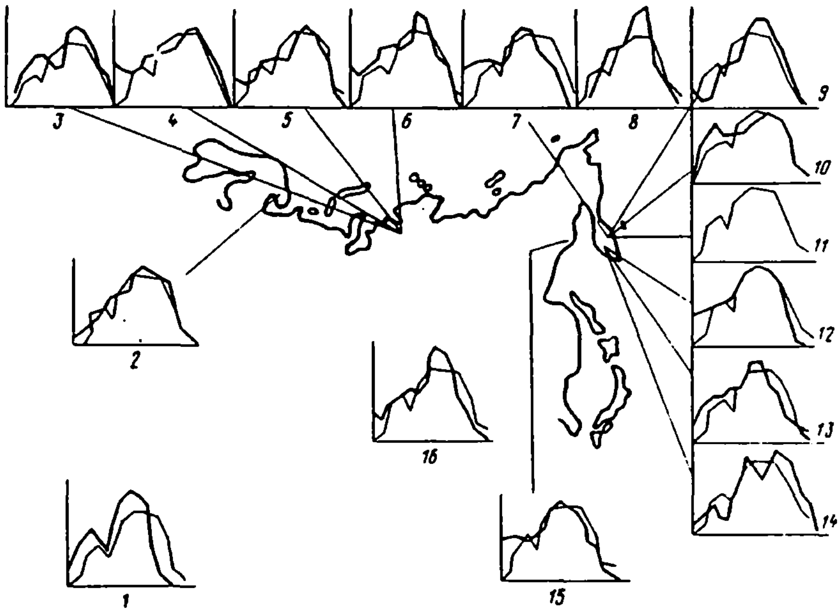

Рис. 49. Профили термостабильности гибридных дуплексов ДНК реперной (тонкая линия) и исследуемое (толстая линия) форм:

1 — кунджа; *2* — кольский голец; *3* — черная палия; *4* — боганидская палия; *5* — голец Дрягина; *6* — глубоководный голец; *7* — каменный голец; *8* — азабачинский хищник; *9* — азабачинский бентофаг; *10* — командорский голец; *11* — камчатский проходной голец (реперная форма); *12* — большерецкий голец (проходной); *13* — озерный начикинский голец; *14* — озерно-речной начикинский голец; *15* — нейва; *16* — даватчан

Figure 49. Profiles of thermostable hybrid duplexes of DNA of the bench-mark (thin line) form and the form being studied (thick line):

1 - East Siberian char; 2 - Kola char; 3 - black lake char; 4 - Boganida lake char; 5 - Dryagin's char; 6 - deepwater char; 7 - stone char; 8 - Azabach'e predator; 9 - Azabach'e benthophage; 10 - Komandorskii char; 11 - Kamchatka anadromous char (bench-mark form); 12 - Bol'shaya River char (anadromous); 13 - lake Nachikinskoe char; 14 - lake-river Nachikinskoe char; 15 - neiva; 16 - davatchan.

Another species of char of the Far East, *S. neiva*, shows a surprising similarity to *S. malma* according to the thermostability curve. Reliable differences are noted at the same point of elution, but the *CD* from the bench-mark *S. alpinus* is significantly less: 4.4. It is probable that the neiva is located on the same evolution line as the Dolly varden, although it has retained more ancestral features.

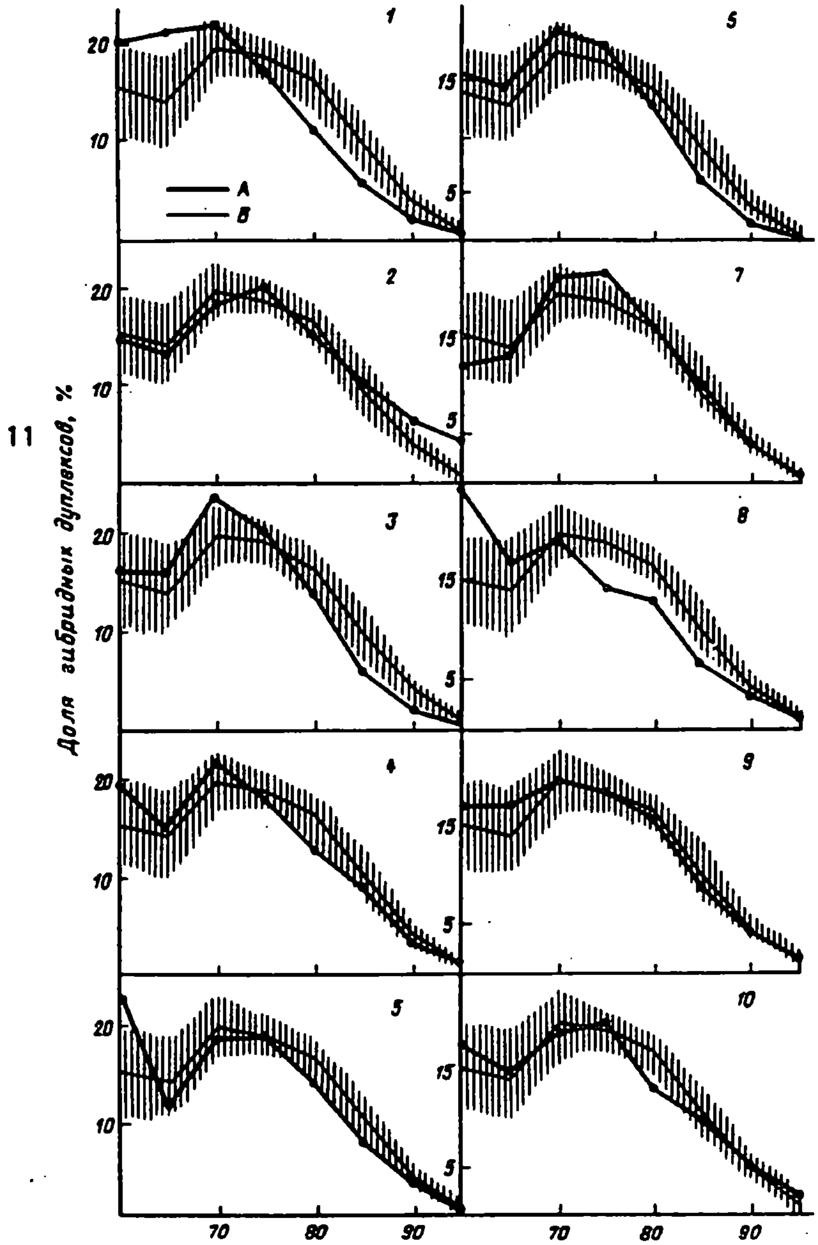

Рис. 50. Термостабильность гибридных дуплексов ДНК:

А — кривая гетерологичной реакции; Б — кривая гомологичной реакции S. alpinus× ×S. alpinus (заштрихована зона доверительного интервала 0,95); *1* — S. alpinus (Финская Лапландия, реперная форма)×S. namaycush (Канада); *2* — S. fontinalis× ×S. alpinus; *3* — S. alpinus×S. leucomaenis; *4* — S. alpinus×S. malma; *5* — S. alpinus×S. neiva; *6* — S. alpinus (каменный голец, Камчатка); *7* — S. alpinus×S. taranetzi auct; *8* — S. alpinus×начикинский озерно-речной голец; *9* — S. alpinus×S. drjagini auct; *10* — S. alpinus×голец озера М. Леприндо (Забайкалье)

Figure 50. Thermostable hybrid duplexes of DNA:

A - heterological reaction curve; B - homological reaction curve of *S. alpinus x S. alpinus* (dashed area of the confidence interval 0.95); 1 - *S. alpinus* (Finnish Lapland, bench-mark form) x *S. namaycush* (Canada); 2 - *S. fontinalis x S. alpinus*; 3 - *S. alpinus x S.leucomaenis*; 4 - *S. alpinus x S. malma*; 5 - *S. alpinus x S. neiva*; 6 - *S. alpinus* (stone char, Kamchatka Peninsula); 7 - *S. alpinus x S. taranetzi auct*; 8 - *S. alpinus* x Nachikinskoe lake-river char; 9 - *S. alpinus x S. drjagini auct*; 10 - *S. alpinus* x char of Lake Leprindo (Zabaikal'e);

11 - proportion of hybrid duplexes, %

The degree of genetic divergence of the stone char is much higher than in the neiva or the malma. This, as well as substantial differences in morphology, way of life [210], antigen composition of blood serum [88] and, possibly, karyotype [34] allow us to suppose that this form may more likely be considered an independent species with respect to *S. alpinus s. str.*, but not with respect to Dolly varden, although, according to the thermostable fraction of DNA, this form differs noticeably from the Dolly varden [342]. The stone char is the last form in the series; standard Arctic char (*CD*=0), neiva (4.4), Dolly varden (8.6) and stone char (14.4). Naturally it does not follow from this series that the neiva is an ancestor of the Dolly varden. This is a form that has retained more features of the common ancestor in genome structure. The initial and final forms of the series behave like species, although there is no gap between them: it is filled by intermediate forms, the neiva and the Dolly varden.

Similar series and rings of species and forms are known [132, 224 et al] in the higher vertebrates. They have not yet been sufficiently studied among fish.

Another line of evolution of the Far Eastern chars apparently led to the emergence of the secondary-anadromous form *S. taranetzi* from the waters of the Chukotka Peninsula. According to the data of B.M. Mednikov and V.A. Maksimov [146], the genetic divergence of the Taranets char from the Dolly varden is quite insignificant, since profiles of the thermoelution of hybrid duplexes of DNA of Taranets char and Dolly varden from the Kukekkuyum River basin are practically identical (see Figure 50). In addition, they differ substantially for DNA from such 160
chars of the Kola and Taimyr Peninsulas. This allowed the assumption that the phenetic similarity of *S. taranetzi* with chars of the Arctic basin was due to homological or parallel variability [33], since similarity in a DNA series cannot come about convergently.

The results of the DNA hybridization of Taranets char with the DNA of *S. alpinus s. str.* confirm this. The forms may be arranged in a series according to degree of divergence: *S. alpinus* (*CD*=0), Dolly varden (*CD*=8.6), Taranets char (*CD*=9.6). The latter differs the most from *S. alpinus s. str.*, although the claim of its species isolation requires further justification. A gradual transfer of one species to another without a gap is observed; the same Dolly varden fills the gap.

The greatest degree of genetic divergence is found in lake-river char from Lake Nachikinskoe (Kamchatka Peninsula) (see Figure 50). This form differs both from the sympatric lake char and from the anadromous Dolly varden in a number of features of morphology, ecology and karyotype [215]. Apparently, like the stone char, the Nachikinskoe char is the outer link in the chain of yet another direction of divergence of the Far Eastern chars. It is possible that the stone char is not endemic of Lake Nachikinskoe and will be found in other waters of the Kamchatka Peninsula. The high degree of its genetic divergence is apparently explained, not only by an accumulation of mutations, but by serious restructurings of the genome.

Another evolution line is revealed in experiments on the molecular hybridization of DNA. It unites the chars of Siberia that are attributed to the high-arctic morphotype [218]. Groupings are found in the evolution line with a different degree of genetic divergence. All the chars of the Taimyr Peninsula that we studied, including *S. drjagini* and *S. boganidae*, previously described as independent species, differ unreliably from *S. alpinus s. str.* on the curve of fusion of hybrid DNA duplexes (see Figure 50). Only the deepwater char [217] differs according to this feature, but quite insignificantly (CD<5). The greatest degree of divergence (compared with such in the Dolly varden) is observed in the many-raker chars of the alpine lakes of Zabaikal'e [221]: for the Lake Leprindo char *CD*=8.6. Zabaikal'e chars, an extreme morphological expression of the high-arctic morphotype *S. alpinus complex*, happen to be the most genetically divergent on this line (see Figure 50).

The results of studies on molecular hybridization of char DNA may be summed up as follows. The anadromous form *S. alpinus* from the Kola Peninsula to the Kamchatka Peninsula is genetically unified. Populations of resident chars may reveal a different degree of genetic divergence; moreover, some of them apparently attain semi-species or species isolation. In degree of divergence, these forms may be arranged in series [56]. The initial and final forms of 161
the series may differ significantly in degree of DNA homology, but they are joined by an uninterrupted series of intermediate groupings: *S. alpinus* (*CD*=0), *S. drjagini*, *S. boganidae*, deepwater Taimyr char (*CD*=5), neiva (*CD*=4.4), Lake Leprindo char (*CD*=8.6), Dolly varden (*CD*=8.6), Taranets char (*CD*=9.6), stone char (*CD*=14.4), and Nachikinskoe lake-river char (*CD*=29). Naturally, such series do not have a phylogenetic character and each sequential link in them is not derived from the previous one. They may be likened to comparative morphological and comparative anatomical series, where currently resident forms that are not sequentially ancestors are arranged according to the degree of development of some feature. In certain cases we can still trace the direction of the evolutionary process with fair certainty. It is possible to extract strongly divergent forms from the anadromous Dolly varden-like chars of the Far East: the secondary anadromous Taranets char, the lake-river Nachikinskoe char and the Kamchatka River kamenets.

Рис. 51. Генетическая дивергенция гольцов Евразии, % от *CD* кунджи: *1* — кунджа; *2* — каменный голец; *3* — озерно-речной голец оз. Начикинское; *4* — голец Беринга; *5* — голец Таранца; *6* — глубоководный голец Таймыра; *7* — нейва; *8* — боганидская палия; *9* — голец Дрягина; *10* — проходной голец

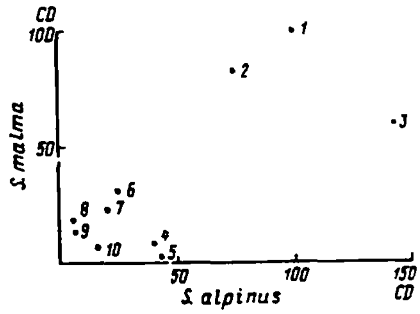

Figure 51. Genetic divergence of the chars of Eurasia, % from the CD of East Siberian char: 1 --East Siberian char; 2 - stone char; 3 - Lake Nachikinskoe lake-river char; 4 - Bering char; 5 - Taranets char; 6 - deepwater Taimyr char; 7 - neiva; 8 - Boganida lake char; 9 - Dryagin's char; 10 - anadramous char

Since experiments with different bench-marks (Dolly varden-like and Finnoscandia alpine-like chars) were done according to different procedures, the absolute values of *CD* are not comparable. Therefore, we juxtaposed them in relative quantities: percentage of divergence in comparison with the divergence of East Siberian char, whose *CD* was accepted as 100% (Figure 51). It follows from this that alpine-like Finnoscandia chars, the high-arctic Taimyr chars and the Kamchatka Dolly varden are characterized by a very slight degree of divergence, not exceeding 50% of the said East Siberian char, whose species status is not in doubt. Three forms reveal significant differences according to a set of average recurring nucleotide sequences of DNA: the East Siberian char itself, the stone char and the lake-river char from Lake Nachikinskoe. They have a high degree of genetic divergence and apparently a semi-species or species rank. On the other hand, all other forms studied reveal a rather compact generality in this respect, even 162

including those which were described as species in their time (Taimyr chars, Dolly varden, neiva, etc.). It is theoretically possible to assume the existence of young species whose primary DNA structure diverged so slightly that differences are not manifested using the molecular hybridization method. However, in our case this method only confirms the conclusions reached based on other procedures. Therefore, it is possible to consider that research into the genetic divergence of chars confirms our point of view on the Arctic char as a complicated complex of forms at different stages of isolation, but genetically unified in the majority of cases.

APPLYING CONCEPTS OF BIOLOGICAL AND TAXONOMIC SPECIES IN EVALUATING THE SYSTEMATIC POSITION OF CHARS OF THE GENUS *SALVELINUS*

The issue of species status is the most complex and insufficiently dealt with issue. Conclusions involving the fact of the existence of the main subdivisions of a species are amazingly contradictory. Representatives of different schools of traditional and experimental systematics, ecology and biocenology, researchers of microevolution and the genetics of populations approach and resolve the central issues of species structure differently. As V.L. Komarov [109] considers, it is difficult to establish a set formula of the eternally changing essence of a species. It is precisely for this reason that not one system of nomenclature and not one hierarchy of systematic categories is able to adequately represent the complex set of internal links and divergence that occur in nature [132].

In the treatment of the problem of species structure, misunderstandings of its scale emerge, as a rule, due to the fact that researchers start from different concepts of the species and, in the end, pursue different objectives: narrow classification tasks, the allocation of rank and latin name or the study of phenetic variety and the assessment of the microevolution situation in the group.

A biological species is the most complex population system in nature and in evolutionary biology. In taxonomy, a species is also a unit. Since taxonomy is concerned with formal classification, a species is viewed here mainly as a classification unit, and convenience and the possibility of practical use of features serve as the main criterion in its separation. A taxonomic species proves to be a symonym of a biological species only in those cases where the gaps in 163
variability that restrict biological species are sufficiently well-pronounced. However, most often the taxonomic species criterion does not coincide with the species criterion in population biology. This is usually observed in those cases where a population system cannot be divided into only two categories: races (subspecies) and species, since there are intermediate semi-species in them. There is no place in the formal taxonomic hierarchy for intermediate groups and, in order to satisfy the requirements of binomial and trinomial nomenclature, it is necessary to view the population system that is at a semi-species level of divergence either as an independent species or as a subspecies of some species. Twin species also cause difficulties since, being

reproductively isolated, they do not differ in external morphological features and do not satisfy the criteria of taxonomic species.

Therefore, contradictions arise between the taxonomic and population biological approaches to classification that may be eliminated, in the opinion of V. Grant [65], if each division of science remains true to its goals. Both concepts of species are legitimate and confusion may be avoided by calling one species taxonomic and the other biological.

E. Mair's [132] concept of biological species obtained wide distribution. In accordance with this concept, biological species are groups of crossing natural populations, reproductively isolated from other such groups [132]. The terminology of population subdivisions is very involved and different authors often attribute different meanings to them. The population structure of a species is quite fully characterized by F. Dobzhansky [282]. He considers that the Mendel population is an association of individuals of a species that is reproducing sexually and within which mating takes place. There is a hierarchy of Mendel populations. A Mendel population that is the largest in size is a species. A panmixia unit (a grouping) is found at the lowest level of the hierarchy. Mating occurs at random within this unit. In a completely populated territory, panmixia units have no clear boundaries and merge with one another. A local population, including one or several panmixia units, is a dem. A race is a set of local populations differing from other sets in the frequency of certain alleles or chromsome structures. V. Grant [65] considers that a biological species represents a population system consisting of local populations, between which a certain amount of crossing occurs. The members of a given local population have a common gene pool. A regional group of local populations - a race (subspecies) 164
- also has a common gene pool, but it is more extensive. A species has an even more extensive and varied gene pool. The boundaries of a biological species correspond to limits within which crossing between populations occurs. The visible result of crossing between populations and between races is the integration of phenotypical features that are subjected to regional variability. The variability that exists in nature is divided into: continuous clinal geographical; interrupted geographical (geographical isolats); ecological (differentiation of ecological races) [65]. These types of variability are often mixed together in nature, but their character within the same species may not be the same in different parts of the natural habitat.

In nature it is not unusual to find population systems representing intermediate stages of differentiation between isolated geographical races and allopatric species or between ecological races and sympatric races that cannot be attributed either to species or subspecies (races). Population systems of this type are connected to one another by different levels of gene flow that are intermediate between levels typical for races and species. As a result, the nature of variability in these systems also proves to be intermediate between intergradation and discontinuity.

A mixture of features is found in the same set of population systems. These features are similar to race and species features. Population systems may intergrade in one part of the natural habitat and exist sympatrically in another, without intermating, or they may be sympatric and isolated in the majority of locations, but cross in one or several locations [65, 116, 132, 151]. In order to designate population systems that are intermediate between races and species, the term "semispecies" is used. This is due to the fact that, to characterize various situations occurring in nature, the traditional categories of "subspecies" (or race) and "species" are clearly insufficient [65, 87, 132].

Most semispecies are more extensive population systems than species. A set of allopatric semispecies is called a supraspecies. A set of sympatric or, at least, marginally sympatric semispecies is called a syngameone [65].

Thus, a biological species is not an extensive crossing group in all cases. This is the most extensive group subject to normal crossing. However, in a number of cases, a supraspecies and a syngameone are a comprehensive population system. This all requires a more complex plan than a simple division into races (subspecies) and species. V. Grant proposed such a plan [65]:
1 - local races; 2 - continuous and isolated geographic races (allopatric); ecological races 165
(adjacent-sympatric); 3 - allopatric and sympatric semispecies; 4 - allopatric and sympatric species; 5 - supraspecies (group of allopatric semispecies) and syngameones (group of sympatric semispecies).

Although the biological concept of species has been widely disseminated recently, it is impossible to accept it universally. Its use in practice may cause difficulties. The concept is totally inapplicable to allopatric groupings. It is difficult to use it in cases where ecological isolation has a non-genetic nature and in cases of seasonal isolation of forms, etc. The morphological concept of species proposed by V.V. Gritsenko [116] defines species as groups of individuals within which the variability of quantitative features (determined polygenically) has a continuous character. They are separated from other such groups by a hiatus. The presence of a gap in allocating quantitative features, not morphological similarity, is the main feature of a species within the given morphological concept. Therefore, the step-type behaviour of boundaries of feature allocation serves as a species criterion. Morphological step-type behaviour and post-copulatory mechanisms of isolation are considered a consequence of the impossibility of the existence of intermediate development routes. The features used here may be highly varied and not only morphological. However, recognition of the morphological concept of species does not signify at all a rejection of the use of the reproductive isolation criterion. It requires only the recognition of the productivity of both criteria, their use only where, when and to what extent they are evidence of the genetic incompatibility of divergent races. The conclusion reached does not reject at all the ability of the biological concept to reflect objective patterns of the variety of the organic world. The existence in nature of ecologically or biologically isolated groupings is not in doubt at all. The question only consists in whether similar groupings should be accorded taxonomic status if they have not attained genetic incompatibility [116].

The structure of a taxonomic species, to V. Grant's understanding [65], is much simpler; it is represented by subspecies (races). In this case, it is not likely correct to refer to a taxonomic concept. This is more likely a certain approach, reflecting the overall level of research on the subjects, that is a stage in the development of knowledge concerning species structure.

M.V. Mina [151] provides another concept of taxonomic species. In his definition, a taxonomic species is a set of immense species (reproductively and phenetically isolated complexes of crossing local phenones, i.e., Mendel populations), separated from other similar 166
sets by a hiatus according to individual features. Like the biological species, it is a set of populations, but not necessarily crossing populations. In some cases the taxonomic species corresponds to the biological species, but most often this correspondence is impossible to determine due to the inapplicability of the criterion of reproductive isolation to allopatric populations. The taxonomic species as such is characterized by the method of its formation and the set of methods and features used. It has no immanent biological specific character. The separation of taxonomic species should be viewed as a procedure permitting orientation in the phenetic variety of organisms. M.V. Mina suggests the idea of a comprehensive species as a set, some subdivisions of which differ between themselves like good species, but cannot be separated as such, since they are connected by a number of transitions formed by other subdivisions of the same comprehensive species. He uses the term "comprehensive taxonomic species" to denote situations where the components making up the set are not equivalent and one of them is sympatric, whereas the other is allopatric. This is the so-called fully comprehensive species. In addition, it distinguishes the geographically comprehensive species and the locally comprehensive species, the phenetic variety of which is created due to the differences of geographically isolated groupings or the differences between sympatric subdivisions. In his opinion, these species should not be called morphological, since the assessment of reproductive relationships of sympatric phenones is an important point in the process of their separation.

Until now, to the understanding of V. Grant [65], in the problem of species in ichthyology the taxonomical approach has prevailed. However, the logical use of the reproductive criterion often leads to the absurb, to the recognition of any isolated population as an independent species. It is truly very difficult to combine these two approaches in the study of certain groups, and the known lack of clarity of the original positions and goals of different authors may be a source of discussion. The chars of the genus *Salvelinus* are an example of a similar situation. In this connection, it is expedient to attempt to present two plans of char classification in accordance with generally accepted taxonomic and biological concepts of species.

From the positions of traditional taxonomy, one layout of the species structure of *S. alpinus* may appear as follows: species *S. alpinus*; subspecies *S. a. alpinus (L)*, *S. a. lepechini (Gmelin)*, *S. a. erythrinus (Georgi)*, *S. a. malma (Walbaum)*, *S. a. kraschenninnikovi (Taranetz)*, *S. a. schmidti (Viktorovsky)*, *S. a. ssp. (Kirillov)*, *S. a. orientalis (Kirillov)*, *S. a. oquassa (Girard)* *S. a. marstoni (Garman)*, *S. a. aureolus (Girard)* and *S. a. spectabilis (Girard)*. The list of subspecies may be longer or some may be viewed as subspecies of other species. However, the 167
majority of them are artificially separated. The main feature of subspecies as taxonomic units is often ignored - the presence of an isolated geographical natural habitat, and they are described with a nominative subspecies [43, 102, 347]. Therefore, many researchers find a way out in raising subspecies to the rank of species and in describing new species [43, 57, 58, 59, 60, 61, 62, 164, 188, 244, 245, 247]. They divide chars into two groups: Arctic and Pacific. They attribute to the Arctic group as independent species: *S. alpinus*, *S. fontinalis*, *S. boganidae*, *S. namaycush*, *S. ezerskii*, *S. taranetzi*, *S. neiva*, lake char from Lake Nacikinskoe and lake char from Lake Dal'nee (Kamchatka Peninsula). The Pacific group includes: *S. malma*, long-nosed char from Lake Kronotskoe, *S. albus*, *S. leucomaenis*, *S. cronocius* and *S. andriaschevi*. Five of the 15 species that they isolate are anadromous [62, 188]. According to their claims, these authors find no intermediate phenotypes. According to a set of 60 craniological and traditional ichthyological features, the differences between species are supposedly highly stable.

These types of conclusions are contradictory to the representations of most researchers concerning the extraordinary plasticity and variability of char features. Intermediate phenotypes are also known. Many different char populations remained beyond the field of vision of these authors that, according to their logic, could also have been separated into independent species. The list of forms which some authors currently view as species may be divided in the following manner: *S. alpinus*, *S. lepechini (Gmelin)*, *S. willughbii (Gunther)*, *S. profundus (Schindler)*, *S. salvelinus (L)*, *S. stagnalis (Fabricius)*, *S. drjagini Logaschov*, *S. boganidae Berg*, *S. taimyricus Michin*, *S. jacuticus Borisov*, *S. czerskii Drjagini*, *S. elgyticus Viktorovsky et*

Glubokovsky, S. taranetzi Kaganovsky, S. andriaschevi Berg, S. malma (Walbaum), s. neiva Taranetz, S. albus Glubokovsky, S. cronocius Viktorovsky, S. sp. lake (Lake Nachikinskoe) (Viktorovsky), S. sp. (Blubokovsky), S. leucomaenis (Pallas), S. miyabei Oschima, S. oquassa (Girard), S. marstoni (Garman), S. aureolus (Girard), S. fontinalis (Mitchill), S. namaycush (Walbaum), S. confluentus Cavander, and *S. anaktuvukensis, Morrow.*

The great majority of these species is separated in violation of taxonomic procedures, i.e., only in evaluating the regional situation, without considering the position according to the natural habitat as a whole. The fishes that we studied could have been added to a list of similar species: deepwater Taimyr char, black Taimyr lake char, large and small chars of the Zabaikal'e, lake-river char from Lake Nachikinskoe, Azabach'e benthophages and predators, and the stone 168
char from the Kamchatka River basin. Therefore, a practically unlimited number of groupings may be attributed to the species category, since the majority of allopatric and sympatric forms differs significantly from one another according to a set of the most varied features and may be reproductively isolated. The process of separating taxonomic species in this group is practically without limit. C. Regan [369] considers that, if one begins to give species names to lake forms of char, then one will never know where to stop.

It is true that the number of species currently described and recognized by some researchers tends to come close to what was before the distribution of E. Mair's concept. The unsuitability of such classification and the impossibility of using it are apparent.

The materials of our research and the data of the literature may be presented in accordance with E. Mair's population-biological concept of species [132] and M.V. Mina's concept of taxonomic species [151]. The traditional analysis of morphological features that we conducted, the experience of using multivariate methods of statistical analysis of plastic and meristic features of different char populations, the study of osteological features and their variability in this very populations [36], the results obtained by using methods of molecular DNA hybridization [56] allow the complicated structure of the Arctic char complex to be revealed and the position of individual populations in this system to be determined (Figure 52). In constructing a design we used data obtained by different methods. As it is impossible to summarize them in order to obtain to obtain uniform indicators of similarities and differences, the distances between forms are tentative. However, these distances reflect the degree of divergence of groupings. The placement of char populations within the scope of morphotypes is arbitrary.

Local char populations whose features are subject to clinal, discontinuous and ecological variability are joined in three morphotypes of *Salvelinus alpinus complex*: alpine-like, Dolly varden-like and high-arctic [218]. A morphotype is a set of individuals characterized by a certain set of adaptive features and emerging on the basis of parallel variability in similar environmental conditions. Morphotype is not a taxonomic category, since the carriers of its features are groupings found at different stages of the population hierarchy (subspecies, semispecies and species). Morphotypes are unusual adaptational types. They coincide with certain biotypes and occur in different parts of the natural habitat, everywhere where there are suitable conditions. They are phenomena of ecological variability.

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Рис. 52. Структура S. alpinus complex и рода Salvelinus:

I — альпиноидный морфотип; *II* — высокоарктический морфотип; *III* — мальмоидный морфотип. Популяции: *1* — Кольского п-ва; *2* — оз. Дальнее (дельта р. Лены); *3* — озер Чаунской губы; *4* — р. Индиги (Чешская губа); *5* — оз. Дальнее (Камчатка); *6* — оз. Начикинское (Камчатка); *7* — оз. Переходное (дельта р. Лены); *8* — озер Таймыра; *9* — глубоководного гольца Таймыра; *10* — нейва оз. Уегинское; *11* — даватчана оз. Фролиха; *12* — куандо-чарских гольцов Забайкалья; *13* — оз. Эльгыгытгын; *14* — якутского гольца (дельта р. Лены); *15* — оз. Азабачье (хищник); *16* — оз. Азабачье (бентофаг); *17* — озерно-речного гольца оз. Начикинское; *18* — каменного гольца (Камчатка); *19* — рек Камчатки, Анадырь, оз. Кроноцкое, Командорских и Курильских о-вов, бассейна Амура; *20* — гольца Таранца; *21* — кунджи; *22* — S. fontinalis; *23* — S. (Cristivomer) namaycush.

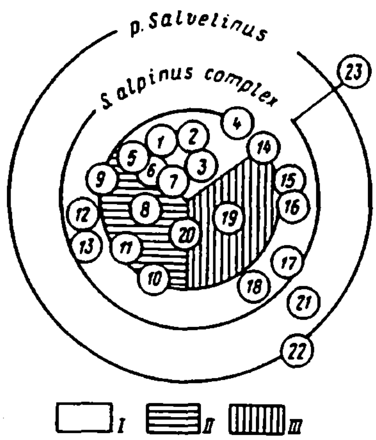

Figure 52. Structure of S. *alpinus complex* and genus *Salvelinus*:

I - alpine-like morphotype; II - high-arctic morphotype; III - Dolly varden-like morphotype. Populations: 1 - Kola Peninsula; 2 - Lake Dal'nee (Lena River delta); 3 - lakes of Chaunskaya Bay; 4 - Indiga River (Cheshskaya Bay); 5 - Lake Dal'nee (Kamchatka Peninsula); 6 - Lake Nachikinskoe (Kamchatka Peninsula); 7 - Lake Perekhodnoe (Lena River delta); 8 - lakes of the Taimyr Peninsula; 9 - deepwater Taimyr char; 10 - neiva of Lake Ueginskoe; 11 - davatchan of Lake Frolikh; 12 - Kuando-Charskii chars of Zabaikal'e; 13 - Lake El'gygytgyn; 14 - Yakutsk char (Lena River delta); 15 - Lake Azabach'e (predator); 16 - Lake Azabach'e (benthophage); 17 - lake-river char of Lake Nachikinskoe; 18 - stone char (Kamchatka Peninsula); 19 - rivers of the Kamchatka Peninsula, Anadyr', Lake Kronotskoe, Komandorskie and Kuril'sk islands, Amur River basin; 20 - Taranets char; 21 - East Siberian char; 22 - *S. fontinalis*; 23 - *S. (Cristivomer) namaycush*.

To the understanding of L.S. Berg [24] or M.V. Mina [151], morphotypes may be compared with races, but they cannot be considered races-subspecies since their natural habitat overlaps to a significant degree, although even a certain coincidence with geographical regions is observed. If desired, they may even be given latin names: *infraspecies alpinoides morpha lacustris* (1), *m. fluviatilis* (2), *m. profundus* (3), *m. migratorius* (4); *infraspecies arctoides* (1, 2, 3, 4); *infraspecies malmoides* (1, 2, 3, 4).

In its turn each morph may be divided into groupings differing in type of diet, growth rate and reproduction periods.

S. alpinus complex as a whole is a population system of the highest hierarchical level. Moreover, it may be viewed simultaneously both as a supraspecies and as a syngameone since it unites allopatric and sympatric semispecies and species. Intermediate groupings of any rank find a place in this system, groupings standing at an intraspecific level within a certain morphotype or occupying an intermediate position between morphotypes (lake Kamchatka chars from Lakes Dal'nee and Nachikinskoe; chars from Lake Perekhodnoe (Lena River delta); semi-anadromous Chukotka chars attributed to *S. taranetzi** by some authors; on a semispecies level (deepwater char from the waters of the Taimyr Peninsula and neiva from Lake Ueginskoe, isolated from a certain morphotype, located at the juncture of two morphotypes - *S. jacuticus* and, to a certain 170
extent, populations of anadromous char from the Indiga River); on a species level (twin species - Azabach'e chars, slightly isolated morphologically and more isolated satellite species - stone char, lake-river Nachikinskoe char; more distant are *S. elgyticus*, living in the waters of the Chukotka Peninsula and Kuando-Charskii chars of Zabaikal'e). Beyond its boundaries are *S. leucomaenis, S. fontinalis* and *S. (Cristivomer) namaycush*.

This configuration of the population structure of *S. alpinus complex* allows refinement. Newly studied char groupings of any level may be added to it. This configuration does not negate the reality of species at all, but proceeds from representations concerning their unequal value. Species are not uniform according to their historic age. They are at different stages of evolutionary development and differ in scope and structure. In this respect, the boundaries between them may be easily established in some cases, and in others they prove to be blurred. When there are series and circles of forms, it proves to be impossible to draw boundaries between them [132]. In an actual structured population where the processes of assortative

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* According to recent data, the position of these chars needs to be clarified. It is possible that they deserve a semispecies or species rank.

crossing and disruptive selection are widely distributed, groupings may exist that are at the most varied stages of genetic isolation. A situation is possible where in one part of the natural habitat sympatric populations remain isolated, and in another part they cross freely. Apparently one should not mix the concept of species reality with a representation of its boundaries.

M.V. Mina's view on a fully comprehensive taxonomic species is to a certain extent close to the knowledge we are developing concerning the structure of the Arctic char complex; it is a view that includes allopatric and sympatric components. From this positon *S. alpinus complex* may be viewed as a fully comprehensive species; alpine-like, high-arctic and Dolly varden-like morphotypes may be viewed as non-geographic units, without emphasizing the ecologically specific nature of a taxon. M.V. Mina allows for the possibility of the existence of sympatric subspecies of one species. However, for example, subspecies of lake, lake-river and anadromous chars in Lake Dal'nee on the Kamchatka Peninsula are attributed to different morphotypes. Even within non-geographic morphotypes it is possible to separate geographic units - breeds of alpine-like, high-arctic and Dolly varden-like chars that coincide with certain bodies of water.

This configuration allows a more careful assessment of the nature of interrelationships of groupings in the complex, even more so since nearly always in classifying phenones it is impossible to be sure that a few reproductively isolated populations are not part of the composition of one phenone [151]. However, in this case the accent on the final result is 171
displaced and the process of divergence of forms itself is concealed; intermediate groupings drop out. Therefore, although it is truly most often necessary to assess the level of gene exchange between groupings according to gaps or intergradation in phenotypical features, we prefer a configuration based on knowledge of the biological concept of species with all the completely justified critical considerations concerning it. Since the classification reflecting genetic relationships of individuals has the greatest prediction value, one should try if possible to reveal and analyse them by any acceptable methods, while being aware of their ability to resolve.

Chapter 6

EXAMPLES OF THE EMERGENCE OF FORMS AND THE STRUCTURE OF POPULATION SYSTEMS IN KAMCHATKA NOBLE SALMONS AND ICHTHYOIDS

The species *S. mykiss* is mainy distributed in the waters of the Kamchatka Peninsula. However, there is evidence that it occurs singly in the waters of the Sea of Okhotsk basin [24] and in the Amur estuary to the south of the mouth of the Amur River [94], as well as in the waters of Bol'shoi Shantar Island [2]. An anadromous form, the Kamchatka salmon, occurs in the rivers of the west coast of the Kamchatka Peninsula in small numbers. It apparently also occurs in the rivers of the east coast [24]. The freshwater form, judging by the literature data, lives in many of the peninsula's bodies of water [24, 132]. However, the maximum number is reached in the waters of the east coast of the Kamchatka Peninsula. Until recently these fish had been little studied. The Kamchatka steelhead was described as *Salmo mykiss B Petri Artedi Genera Riscium* [261]. The Kamchatka salmon was described as *Salmo purpuratus* by P. Pallas [363]. Later, the status of these species changed more than once. The salmon was viewed either as a synonym of the Kamchatka steelhead [22] or as an independent species [23, 24, 79]. However, at the base of all of this research was a small amount of fragmentary factual material.

Research that we conducted together with a group of colleagues from the Department of Ichthyology of the University of Moscow indicated that one species of the genus *Salmo* exists on the Kamchatka Peninsula. It is represented by anadromous and resident forms and, according to the rule of priority, it should be called *Salmo mykiss Walbaum* [97, 205, 208, 214]. R. Behnke came to a similar conclusion concerning the existence of one species of salmons of the genus *Salmo* on the Kamchatka Peninsula [266]. 172

The results of a multivariate analysis of morphometric features also confirmed the validity of the point of view in accordance with which Kamchatka noble salmons should be viewed as one species [15, 154]. The colouring of the anadromous and resident forms is evidence of their common gene pool. The nature of polymorphism in colouring in similar; there are identical polymorphous features in all variants. The differences between groupings are evident in how pronounced these features are. Peculiarities of colouring depend on coincidence with freshwater: freshwater individuals are more brightly coloured. The occurrence of freshwater colouring in anadromous fish depends on how much time they spend in the river and on how close the reproduction period is. Towards spawning time they are most similar to the freshwater fish, especially the males.

The findings of the analysis of morphometry were also confirmed by the results of processing the ostelogical material. A detailed examination of the variability of a series of ostelogical features showed that there were no significant differences between the anadromous Kamchatka salmon and the resident Kamchatka steelhead in the shape of the skull and in the structure of individual bones [133]. A significant stability and species character of the qualitative composition of serum proteins in salmons of the genus *Salmo* allowed G.G. Novikov to use this indicator in explaining the relationships between Kamchatka salmon and Kamchatka steelhead. It turned out that, as in cases where comparisons are made between various ecological forms of other species (anadromous and resident brown trout *S. trutta* and four races of *S. ishchan*) or geographically isolated populations of brown trout and noble salmon from the basins of the Sea of Okhotsk, the White Sea and the Baltic Sea, there were no differences between the Kamchatka Salmon and the Kamchatka steelhead in the protein pattern of blood [97]. A comparative analysis of the ecologico-morphological features of development of Kamchatka salmon and Kamchatka steelhead made by D.A. Pavlov and S.G. Soin showed that a considerable similarity between them is observed in the majority of indicators. An analysis of the karyotypes of Kamchatka salmon and Kamchatka steelhead revealed noticeable differences. However, in connection with the fact that interpopulation variability of karyotypes in salmons may be great, V.P. Vasil'ev [34] did not consider them sufficient to raise these groups to the rank of independent species. G.V. Gorshkova and S.A. Gorshkov [64] did not find differences in the karyotypes of Kamchatka salmon and Kamchatka steelhead.

According to data on the molecular hybridization of DNA, Kamchatka salmon and Kamchatka steelhead display a high degree of genetic kinship [12] and they should be viewed within one species: the Kamchatka steelhead.

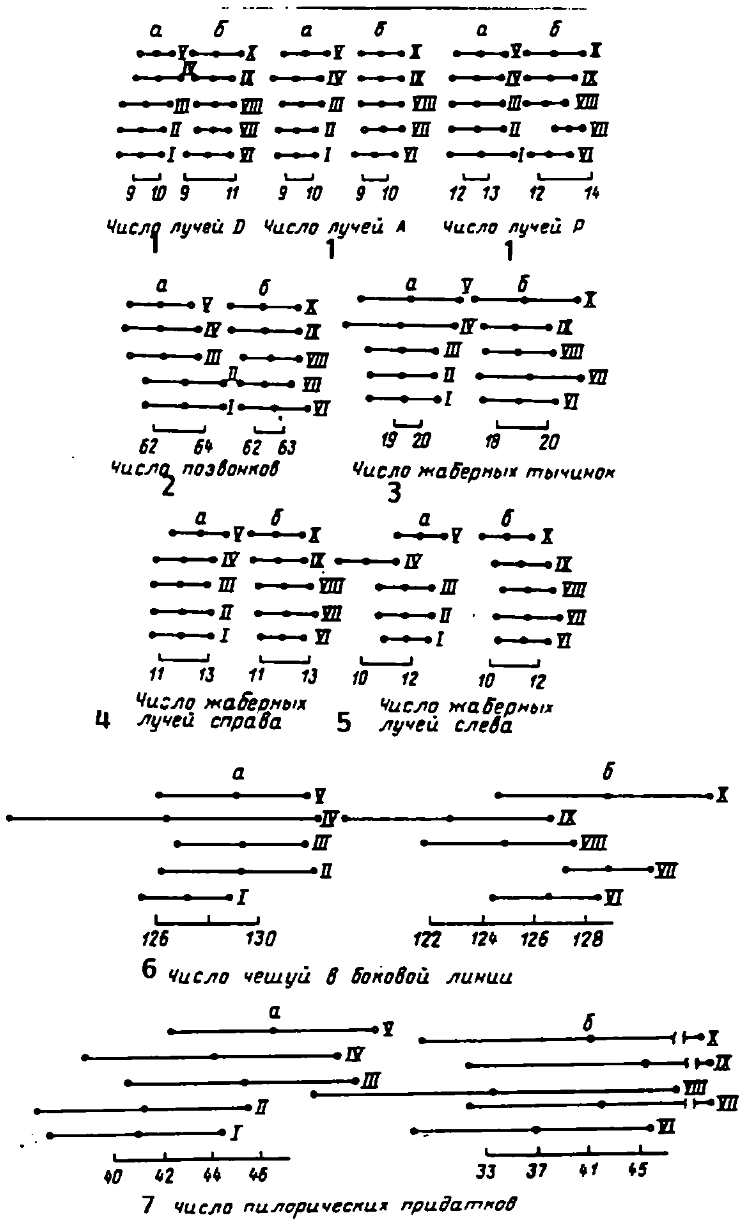
Kamchatka steelhead has a complex intraspecific structure. Local populations of the anadromous form consist of a number of intrapopulation groupings - typically anadromous 173
travelling out to sea to feed, anadromous - littoral, performing no significant migrations, river (predominantly males). The freshwater form is represented mainly by river populations [97].

The interrelationship of intraspecific forms and smaller groupings is not uniform in various parts of the species natural habitat. The Snatolvayam population of the anadromous form (Snatolvayam River, Kamchatka Peninsula) is represented by a typically anadromous grouping that travels far out into the sea to feed (95.5%). In the neighbouring Kvachina population

(Kvachina River), a grouping that migrates far out to sea also predominates (97.9%). It does not differ from the previous one in meristic features (Figure 53).

The lack of differences between these two populations is apparently caused by the following: similar conditions of reproduction in small rivers with a specific hydrological pattern, way of life, time spent in fresh water and in the sea, and type of diet [97]. It is possible that considerable exchange is observed between populations in this case, since both rivers have a common estuary. It is possible that the phenomenon of homing is not so clearly pronounced and that their genetic kinship is the reason for the strong similarity between populations.

The Utkholok population is somewhat different as the Utkholok River is further south. It has a large complex intrapopulation ecological structure: typically anadromous fish make up 85% of its total number of fish caught; The extent of this river and its total area are greater than those of the two previous rivers; its biotypes are more varied. However, in spite of this, ecological groupings of this local population do not differ from one another in merisitic features and, most likely, their reproduction and development occur under the very same conditions (Table 27). An analysis of meristic features provides a basis for the proposal that the emergence of groupings in the Utkholok River that differ in way of life occurs not at the time of reproduction and development, but later. The length of the freshwater period of life of the young fish is determined by its nonuniform physiological state [97], which is apparently connected to a considerable extent with the availability of food in the river; it is possible that it pre-determines the future lifestyle of the fish, the length and extent of their marine migrations and the ability of some of them to mature in fresh water, without going out to sea to feed. It is possible that the groupings discovered in the Utkholok population of the anadromous form can transfer from one to the other. Therefore, it is difficult to draw a boundary between typically anadromous and littoral fish in a case where the former, coming to spawn repeatedly, having run to sea, do not go far from the shore and have small growths in their scales during the marine period of life [97]. The fact of joint spawning of anadromous females and river males most likely speaks of the lack of genetic isolation between groupings in this population.



…. 53. Меристические признаки анадромной (а) и речной (б) форм микижи разных участков ареала популяций:

снатолваямской; II — квачинской; III — утхолокской; IV — уткинской; V — большекой; VI — урцовской; VII — никольской; VIII — крапивинской; IX — кишимшинской; азабачинской

Figure 53. Meristic features of the anadromous (a) and river (b) forms of Kamchatka steelhead from various parts of the populations' natural habitat:

I - Snatolvayam; II - Kvachina; III - Utkholok; IV - Utka; V - Bol'shaya River; VI - Urtsovskaya; VII - Nikol'sk; VIII - Krapivinskaya; IX - Kishimshinskaya; X - Azabach'e.

1 - number of rays; 2 - number of vertebrae; 3 - number of gill rakers; 4 - number of branchiostegals on the right; 5 - number of branchiostegals on the left; 6 - number of scales on the lateral line; 7 - number of pyloric caeca

27. Меристические признаки утхолокской популяции микижи

1 Признак	2 Проходная (n = 92)		3 Прибрежная (n = 15)		4 Речная (карликовые самцы), n = 4		5 Отношение проходной формы к прибрежной	
	lim	$\bar{x}$	lim	$\bar{x}$	lim	$\bar{x}$	T_d	CD
6 Число лучей в плавнике:								
7 спинном	8...11	9.5	9...10	9.5	9...10	9.5	0	0
8 анальном	9...11	9.6	9...10	9.3	9...10	9.6	0.3	2,1
9 грудном	11...14	12.6	12...14	12.7	12...13	12.3	0.07	0.5
10 Число чешуй в боковой линии	120...140	129.3	120...145	129.6	118...125	124	0,03	0.2
11 Позвонки	60...64	62,4	61...64	62.6	61...64	62.5	0.1	0,8
12 Жаберные лучи:								
13 справа	10...13	11.8	11...13	11.7	12...12	12.0	0.8	0.5
14 слева	10...13	11.6	11...12	11.5	11...12	11.2	0.9	0.6
15 Жаберные тычинки	17...21	19.2	17...21	19.0	19...20	19.4	0.1	0.6
16 Пилорические придатки	30...70	45.2	35...55	43.7	46...53	48.0	0.1	0.9

Table 27. Meristic features of the Utkholok population of Siberian steelhead

1 - feature; 2 - anadromous; 3 - littoral; 4 - river (dwarf males); 5 - ratio of the anadromous form to the littoral form; 6 - number of rays on the fin:; 7 - dorsal; 8 - anal; 9 - thoracic; 10 - number of scales on the lateral line; 11 - vertebrae; 12 - branchiostegals:; 13 - on the right; 14 - on the left; 15 - gill rakers; 16 - pyloric caeca

The Utka population (Utka River) is attributed to a group of southern populations of small rivers of the Western Kamchatka Peninsula. A typically anadromous grouping predominates here (72%), but the number of river males (28%) that mature in fresh water is higher here than in northern populations. Resident freshwater females occur rarely. There are no substantial differences in meristic features between the intrapopulation groupings (see Figure 53). The same arguments apparently apply to this population as to the Utka population, i.e., most likely there is no isolation between intrapopulation groupings and they are a single spawning flock similar to those described by G.P. Barach [18] for Black Sea salmon.

The Bol'shaya River population (Bol'shaya River, Western Kamchatka Peninsula) differs in ecological variety. There are 4 types of groupings here: typically anadromous; littoral; river groupings living permanently in the river; river-estuary groupings travelling out to the brackish estuary. Freshwater groupings, as opposed to other populations living in the rivers of the west coast, are represented by individuals of both sexes. The relationship of anadromous and freshwater forms in the Bol'shaya River levels out: there become fewer anadromous individuals 176

(typically anadromous 30%, littoral 20%) and the number of freshwater individuals in the population increases (50%). There are small differences in meristic features between typically anadromous and littoral groupings (Table 28). Typically river groupings and river groupings that travel out to the estuary are totally similar according to all indicators.

?8. **Меристические признаки большерецкой популяции микижи**

1 Признак	2 Проходная (n = 18)		3 Прибрежная (n = 10)		4 Речная (n = 29)		Речная-эстуарная (n = 18) 5	
	lim	$\bar{x}$	lim	$\bar{x}$	lim	$\bar{x}$	lim	$\bar{x}$
6 Іисло лучей . плавнике:								
7 спинном	9...10	9,8	10...11	10,3	9...10	9,6	9...11	9,8
8 анальном	9...10	9,7	9...10	9,7	9...10	9,5	8...10	9,5
9 грудном	12...14	12,8	12...14	12,9	11...14	12,8	12...14	12,8
10 Іисло чешуй в оковой линии	120...135	128,9	118...133	126,0	118...135	126,4	122...138	127,3
11 Іозвонки	61...64	62,3	62...64	63,2	62...64	62,9	62...64	62,7
12 Іисло лучей:								
13 справа	12...14	12,6	12...13	12,1	11...13	12,0	11...13	12,0
14 слева	11...13	12,2	—	12,0	11...13	11,8	11...13	11,8
15 Жаберные тычинки	18...22	19,6	17...21	19,5	18...22	19,2	18...21	19,3
16 Іилорические ридатки	40...60	46,5	32...53	45,0	35...65	50,0	44...63	51,2

28. Meristic features of Bol'shaya River populations of Kamchatka steelhead

1 - feature; 2 - anadromous; 3 - littoral; 4 - river; 5 - river-estuary; 6 - number of rays on the fin::; 7 - dorsal; 8 - anal; 9 - thoracic; 10 - number of scales on the lateral line; 11 - vertebrae; 12 - number of rays:; 13 - on the right; 14 - on the left; 15 - gill rakers; 16 - pyloric caeca

Differences in certain features are revealed when comparing anadromous and freshwater groupings. They exist in the number of vertebrae, branchiostegals and pyloric caeca. However, they are insignificant in all cases. As a rule, the nature of feature variability is similar in both forms. According to the majority of indicators, no difference is found in the average values either. It is logical to assume that conditions of reproduction in all groupings of the Bol'shaya River population are similar. It is highly likely that they reproduce in the same places, in the very same spawning grounds and the separation between them in lifestyle occurs later.

Representatives of all groupings are found in the same catches. Between groupings it is possible to find an entire range of transfers from one lifestype to the other. Often an individual that has a freshwater lifestyle until the first spawning, then goes out to feed in the sea and returns for repeat spawnings as an anadromous fish. However, judging by the data on hand, ecological differentiation in this population is more strongly pronounced. The noted weak tendency to differ 177
in the average number of vertebrae does not exclude isolation according to preferred biotypes and spawning locations. However, if such a tendency exists, it is very poorly pronounced.

The anadromous form of the species *S. mykiss* is rarely found to the south of the Bol'shaya River and on the east coast. The freshwater Kamchatka steelhead, represented by males and females and occurring everywhere along the east coast, is apparently greatest in number in the Kamchatka River basin. Here it reveals a known ecological variety and is mainly represented by relatively isolated river populations that coincide with small spawning tributaries. Judging by parasitological data, these populations are quite isolated [111]; they have parasitofauna specific to each population and do not move along the river very much. Differences between these river populations are not revealed in lifestyle as such, but in size-age structure, periods of maturation and ratio of the sexes.

The geographic variability of meristic features of the species *S. mykiss* is varied in different parts of the species natural habitat. Together with an undoubted similarity in nature of variability and average values, a barely noticeable trend is observed to increase the average number of branching rays on the dorsal, anal and thoracic fins of a typically anadromous grouping from the northern part of the natural habitat (Snatolvayam River) to the southern (Bol'shaya River). The number of rays on the fins of river populations increases slightly along the entire length of the Kamchatka River - from the upper reaches to the lower reaches. However, this trend is not always clearly manifested in neighbouring populations. The number of scales on the lateral line in the entire natural habitat is similar in all populations of anadromous and resident forms. One is not able to note any sort of trend. However, small differences in average values are frequent between the neighbouring populations. Changes in the number of vertebrae are more clearly pronounced: as we move from the northern parts of the natural habitat towards the southern ones their average values decrease. An insignificant decrease in the number of vertebrae is also observed in river populations in the Kamchatka River basin, from the upper reaches to the lower reaches.

The number of branchiostegals on the right and the left fluctuates throughout the entire natural habitat of the species, beyond an apparent connection with any geographic gradients. In comparison with the value of this feature in northern populations, it falls markedly. The

coefficient of differences in branchiostegals on the left is equal to 1.75 between the Snatolvayam and Utka populations, but it increases in the Bol'shaya River. Moreover, the value of the given feature here attains extreme values for the species. In the Kamchatka River basin, a certain trend towards decreasing the value of this feature towards the lower reaches is observed in river populations. The number of gill rakers throughout the entire natural habitat of the species 178
remains unchanged among all forms and populations. The number of pyloric caeca, on the other hand, changes more strongly. However, it is difficult to separate a certain geographic trend here. Their small increase in comparison with northern populations is observed in anadromous groupings in the Bol'shaya River. However, in this very river, the average number of pyloric caeca increases sharply in the freshwater form. Moreover, in this case it proves to be the largest known for the species as a whole. It is impossible to notice any pattern in the changes of this feature in the Kamchatka River basin. All neighbouring river populations, to some degree or another, differ from one another in number of pyloric caeca.

Thus, the nature of variability of meristic features is not uniform throughout the natural habitat of a species in populations of anadromous and resident forms or their intrapopulation ecological groupings. A trend towards clinal variability is observed in the number of branching rays and vertebrae, i.e., a certain link between the gradients of these features and climatic and other environmental factors. As these features are changed in a series of successive populations, it is impossible to see specific boundaries. However, the direction of clinal variability in these features is varied. The number of rays on the fins increases from north to south and from the upper reaches to the lower reachers of rivers, whereas the number of vertebrae decreases. The phenomenon of clinal variability according to these features in fish is well known. However, the nature of the change may be varied. It is accepted that changes in these features are connected mainly with temperature and period of development [240]. Other factors apparently influence their formation, for example, the density and viscosity of water, the content of CO_2, O_2 pH, etc. [142].

Throughout the natural habitat of a species, unconnected features do not change, such as the number of scales on the lateral line and the number of gill rakers. The first feature is characterized by strongly pronounced variability within individual populations. It is known that its value, to a significant extent, is determined by the influence of surrounding conditions, particularly water temperature during the period of embryogenesis. The second differs in its great stability.

Branchiostegals and pyloric caeca are an example of the independent change of features in populations. Here differences between neighbouring populations are almost always observed.

The number of branchiostegals is an extremely stable feature and, as a rule, it is characterized by little variability. The number of pyloric caeca, on the other hand, fluctuates greatly in each population and in a number of successive populations. 179

There are practically no significant differences in meristic features between populations that are close or remote in a geographic sense. All noticed trends are slightly pronounced: clinal variability, a lack of changes within the natural habitat of the species, independent variation. Thus the differences between populations located in different areas of the natural habitat of the species are predominantly reduced to the difference in their ecology and intrapopulation ecological structure. Moreover, in this case a certain geographic trend is appropriately revealed that is connected with a reaction to exterior influences.

As we noted, as we move towards the south of the natural habitat of the anadromous form, the number of groupings increases, which are to a great extent connected with life in fresh water. A similar phenomenon is characteristic for many species of fish from the salmon family. Towards the south the number of varied intrapopulation groupings within one population also increases. In the Kamchatka River basin, along the entire length of the river, river forms also have to a familiar degree a distinguishing ecological structure, a different ratio of the sexes, maturation periods and spawning.

We should also speak of the steelhead population of Bol'shoi Shantar Island, which was recently discovered far beyond the boundaries of its previously known natural habitat. It is apparently a derivative of the anadromous Kamchatka salmon, having shifted to a freshwater lifestyle later than the Kamchatka steelhead. This is confirmed by its intermediate position, according to ostelogical features, between both Kamchatka forms of the species, and its considerable proximity, according to morphometric features, to the Western Kamchatka steelhead, which exchanges genes with the anadromous form [2].

There is a great deal in common between the reproduction ecology of the anadromous and freshwater forms [214]. Both forms spawn in the spring in the upper and middle currents of small rivers and streams of the tundra-alpine type and, in essence, the spawning coincides with the same characteristic hydrological period - the period of the spring floods, immediately after the rivers break up. At this time, in the basins of Kamchatka rivers, the available area suitable for the spawning of Kamchatka noble salmons proves to be at its peak. Thanks to a short incubation period (30-60 days), the eggs are able to develop before the level of the rivers declines and the hydrological pattern becomes unfavourable at the spawning grounds. However, since the rivers break up earlier on the west coast of the Kamchatka Peninsula than in the east of the peninsula, spawning of Kamchatka salmon takes place earlier than the spawning of the resident steelhead

and the development of the salmon eggs occurs at lower temperatures. The freshwater Kamchatka steelhead most likely originated from the anadromous form and, having kept the 180
timing of its spawning to the period of the spring floods, it adapted to higher temperatures. Its preference for warmer temperatures is most likely a by-product.

A considerable similarity is found in the placement of the spawning mounds of the Kamchatka salmon and the freshwater steelhead. Both forms spawn in rivers where relatively deep holes and shoals alternate. The mounds are positioned mainly where a hole turns into a shoal or at some barrier where intensive water filtration takes place through the ground and aeration of the eggs is provided. In addition, the nature of the spawning grounds is different in many ways, and these differences are reflected in a number of features of the ecology of reproduction of both forms. In the rivers where the Kamchatka salmon spawns, the available areas suitable for spawning are very large. In the rivers where the resident steelhead reproduces there are few areas suitable for spawning. In the rivers where the salmon reproduces, large individuals (mainly the large females) capable of successfully withstanding the strong current of the water probably have a selective advantage. In small rivers, for example, in the Kishimshina River, the large sizes of fish not only do not give them an advantage, but can even play a negative role. In digging a nest they may simply destroy small accumulations of pebbles where the resident form deposits its eggs. It is interesting that the Kamchatka steelhead, living in Lake Azabach'e and travelling to spawn to the much rougher Bushuika River, differ in their large size. Therefore, there is the justified argument of a number of authors [273, 306] that there is a direct connection between the size of the spawning river and the speed of the current on the one hand, and the size of the individuals spawning in this river on the other hand.

Features of the reproduction areas also influence the behaviour of the Kamchatka steelhead during spawning. The female Kamchatka steelheads are slightly attached to the spawning mound and do not actively dig a nest [214]. The behavioural pattern common to all *Salmo* [351] appears blurred where the stage of preparing the nest is not clearly separated from the stage of depositing the eggs. It should be recognized that a characteristic feature of the males' behaviour is a small amount of aggression. In this case the situation described by G. Hartman [306] appears to be realized: when spawning occurs in isolated areas and large males cannot dominate in some spawning groups.

In an ecological sense and, possibly even in an evolutionary one, the freshwater Kamchatka steelhead of the Kishimshina River and the andromous Kamchata salmon of the Utkholok River are extreme variants within the species *S. mykiss*. The transfer from one type of ecology to another may have occurred gradually, through a series of intermediate stages. The

results of a multivariate analysis indicating the morphological isolation of extreme populations, related to one another by transitional forms, are not evidence of this [15, 154]. The initial stage of 181
this process is observed in the Utkholok, Snatolvayam and Kvachina Rivers. The resident form is represented here only by the few males spawning together with anadromous females. In the Kikhchik and Oblukovina Rivers, where the anadromous Kamchatka salmon lives, we also caught a small number of resident female Kamchatka steelheads. Already only the freshwater form of *S. mykiss* lives in the Kamchatka River, and it is represented by a number of populations isolated and differing from one another to varying degrees.

Thus, in the northern rivers the resident form is represented by the small number of males that spawn with the anadromous females. In more southerly rivers, a small number of females falls in with the freshwater males. Only freshwater males and females occur on the east coast (in the Kamchatka River). The proportion of groupings in populations is determined by specific living conditions. The lack of freshwater populations of *S. mykiss* in the basins of the small rivers of the west coast of the Kamchatka Peninsula is likely due to the insufficient forage in these rivers, and the absence of an anadromous form in the basin of the Kamchatka River is likely due to a lack of suitable spawning grounds. The freshwater form apparently originates from the anadromous form. Under conditions of shallow, small rivers, selection favoured small individuals. In this connection the proportions of the fish became smaller; food requirements decreased; migrations were reduced and the life cycle pattern of the anadromous form appeared on a reduced scale. The life cycle of both forms is basically the same. Spawning takes place in small rivers where the young fish spend the first years of their life. Then the young fish run to large bodies of water: the andromous form runs to sea, and the resident form runs to a large river or lake. After feeding, the fish return to their native river to spawn. The anadromous form enters rivers in autumn and reproduces in spring, i.e., it is a winter form. The freshwater form enters rivers just before spawning and it may be viewed as a spring form. The conversion of a winter form to a spring form was probably the result of a reduction in the length of the migration paths, due to the fact that the places for feeding and wintering are almost the same for the freshwater Kamchatka steelhead. By all appearances, the ecological and morphological divergence of the resident form occurs when there is no geographic isolation from the original anadromous form [214]. Apparently, under specific conditions, the external environment acts as a switch that determines the path of development according to one of several possible alternative routes [251].

Everything that has been said may be fully attributed to the American counterpart of the Kamchatka steelhead *S. gairdneri Richardson*. The formation of the resident form of this species - rainbow trout - probably occurred in the same way as the formation of the resident steelhead in

the waters of the Kamchatka Peninsula. Moreover, various stages of this process may currently be observed in different rivers. Thus, L. Shapovalov and A. Taft [385] indicate that some of the 182
steelhead trout individuals in Weddel Creek (California) reach sexual maturity and complete their life cycle without going out to sea. At the same time, J. Briggs [273], having conducted research on Prairie Creek, considers that the anadromous steelhead trout and the resident rainbow trout are reproductively isolated from one another here. It is difficult to say how far this divergence may go, at what stage it becomes irreversible and whether the resident population becomes an independent species in any cases at all. There is only no doubt that one should refuse the typological concept of defining "resident" and "anadromous" forms. It is necessary to remember that, in a number of cases, resident and anadromous populations from different bodies of water are not identical to one another, neither in an ecological, nor in an evolutionary sense. In this respect the taxonomic status of these populations may be different in different cases [214].

The group of fish species examined has extensive natural habitats where conditions for the anadromous form are more varied. These species perform long migrations and spend a few years at sea. It is possible that this determines the great ecological nonuniformity of the anadromous form.

Over the last 100 years, the question of the relationship of the Kamchatka steelhead with American salmons of the genus *Salmo* has come up more than once. However, their detailed comparison according to the main diagnostic features was first carried out by K.A. Savvaitova and V.D. Lebedev [208].

The Kamchatka steelhead is close to the steelhead salmon in its proportions, body and head shape, and colouring, but it is close to *S. clarkii* in the presence of basibranchial teeth in some examples. Some Kamchatka steelhead individuals have vague pink spots on the throat, which also brings it closer to *S. clarkii*. However, the differences in a number of features apparently cannot be accepted unconditionally, since some of them have a doubtful taxonomic value. This applies mainly to such features as a red stripe on the throat and basibranchial teeth. In spite of the fact that the first feature is considered the most characteristic for the red-throated trout, it is very vaguely pronounced in young fish and anadromous fish and may be completely absent in the latter. At the same time, some salmons from this group have a pink stripe on the sides. Old fish also do not always have basibranchial teeth. On the other hand, there are instances known where three hyoid teeth were discovered in the *S. gairdneri* [352]. R. Bulkley [274], who has studied the variability of these features, points to the relative value of colouring, location of spots, and the presence or absence, as well as the number of basibranchial teeth in the systematics of the Yellowstone trout *S. clarkii lewisi*.

A blood serum analysis of the anadromous and resident forms of Kamchatka steelhead and rainbow trout showed that their qualitative protein composition was similar [97]. The definition of common and specific components in the blood serums of Kamchatka steelhead and rainbow trout, with the help of immunological methods, also revealed the considerable proximity of these species to one another and a certain isolation of them from other species of the genus *Salmo*. Karyological data are also evidence in favour of the proximity of these species [34].

A great similiarity is observed between American and Kamchatka salmons of the species *Salmo* in species structure (anadromous and varied resident forms), nature of intraspecific variability, morphology and in lifestyle of intraspecific forms. Their main biological indicators are similar to those of the Kamchatka steelhead [97]. Thus, the close kinship of the Kamchatka steelhead with the American species of the genus may be considered to be in no doubt.

Previously we had difficulty in drawing a final conclusion concerning the degree of proximity of the Kamchatka steelhead to any other species.

A.D. Akhundov [12], having defined the genetic proximity of forms of the Kamchatka steelhead and the steelhead trout using methods of molecular hybridization of DNA, considers that all forms of the Kamchatka steelhead and the steelhead trout may be viewed as one polymorphous species *S. mykiss*. D.A. Pavlov [170, 171] and Yu.A. Biryukov [27] share this opinion, having studied the embryonic development of intraspecific forms of the Kamchatka steelhead and the steelhead trout. Experiments conducted in recent years on the basis of previously made recommendations [84, 97, 122, 214, 233] on breeding Kamchatka steelhead at a number of trout farms in the USSR, and the first results of its introduction to some natural bodies of water of the south-eastern Kamchatka Peninsula, also confirm that it is very close to, if not identical with, the American steelhead trout [27]. Results of laboratory experiments conducted at Rostock University (DDR) are evidence of the same thing [166].

The Kamchatka and American noble salmons form a single group in a taxonomic sense, which is divided by V. Vladykov [404] into an independent subgenus *Parasalmo* according to ostelogical indicators. However, the majority of his indicators proved to be unacceptable as taxtonomic tests [133]. Further research of blood serum proteins, karyotypes and osteological features indicated that not even two, but three groups of species could be distinguished in the genus *Salmo*: noble salmon, which includes *S. salar*; brown trout, which includes brown trout, Sevan trout and Mediterranean species; Kamchatka steelhead, which includes Kamchatka steelhead, steelhead trout, red-throated trout, etc. [82, 97, 133].

Therefore, if we follow the route of separating subgenera in the genus *Salmo*, then there are three of them. There is a monotypic subgenus, including *S. salar*, and two polytypic subgenera that correspond to the brown trout group and the Kamchatka steelhead group. Some authors go even further and propose the division of the latter group in the genus *Parasalmo* [63]. However, we consider that neutral names should be retained: the group *salar*, the group *trutta* and the group *mykiss*. The name is given according to species that were described first in the group. Currently it is impossible to separate equivalent subdivisions in a taxonomic and evolutionary sense, and the question may be only of obviously non-equivalent groups of forms (species) [97]. It is possible that these groups of forms, particularly the group *mykiss* or the subgenus *Parasalmo sensu Vladykov*, include not only species and subspecies, but, similar to chars, they include intermediate groupings of any level. Materials on the Kamchatka steelhead and data in the literature on West-American salmons make this premise highly likely.

One may see in the example of chars of the genus *Salvelinus* and Pacific noble salmons of the genus *Salmo* that the variability of features is almost always continuous; there are no clear gaps between phenotypes, particularly according to the set of features. Apparently, in all plastic groups of salmonid fish and possibly, not only salmonids, the lack of clear differences between populations in researching on the scale of the entire natural habitat is a real situation in nature that is supported by natural selection. Such systems are apparently characteristic for the genera *Coregonus* [151, 193], *Brachymystax* [1, 151], *Ogeoleuciscus* [78] and *Gasterosteus* [90].

A similar complex structure occurs apparently not only in fish, but in ichthyoids. In the waters of the Kamchatka Peninsula we observed the joint spawning of large and small lampreys attributed to the species *Lampetra japonica-Lethenteron japonicum*, *L. reissneri* and *L. kessleri* [24, 219, 405]. The joint spawning of the anadromous *L. fluviatilis* and the stream *L. planeri* was described by R. Lauterborn [327], V. Huggings and A. Thompson [310, 327]. However, the simultaneous spawning in the same nest and the subsequent copulation of representatives of two different species (*L. fluviatilis* and *L. planeri*; *L. japonica* and *L. reissneri*; *L. japonica* and *L. kessleri*) are doubtful. It remains unclear in this case how reproductive isolation occurs between them. M. Hardisty's [305] statement that the proportions of fish interfere with successful hybridization is not convincing. The following arguments are much more likely: the small lamprey is an anadromous form of *praecox* that matures at an earlier age or the small lamprey is a resident, freshwater part of the anadromous lamprey flock. Using these arguments, the small lamprey is taxonomically and biologically a single unit with the large anadromous form. Then an explanation is found for the complex spawning behaviour of both forms, i.e., synchronized reproduction.

One should also pay attention to the important feature of the ratio of the sexes in populations of stream lampreys [219]. It is known that males always predominate at their spawning grounds. This circumstance may also be indirect evidence in favour of the joint spawning of small and large forms under sympatric distribution.

In connection with the above, we would like to turn once more to the question of the surprising ecological parallelism between lampreys and salmons noted by L.S. Berg [26]. Both of these fishes have large anadromous and small stream and lake forms. As a rule, these forms are distributed sympatrically, although the freshwater forms may occur beyond the boundaries of the natural habitat of the anadromous forms. After hatching, both salmons and lampreys live for a few years in fresh water and then swim out to sea. They return to the river after a few years, but some individuals mature in that same year. Winter and spring races are known both among lampreys and salmons.

A Kamchatka steelhead with a complex structure lives in the rivers of the Kamchatka Peninsula where the lamprey lives. One may suppose that the species *L. japonica* has a similar structure. On the west coast, it is represented by an anadromous form with a complex structure (a large lamprey, a small early maturing *forma praecox* and, possibly, a freshwater form that is few in number). On the east coast, in the Kamchatka River basin, it is represented by a small freshwater form. A large lamprey is unknown there. On the whole, the species *L. japonica*, throughout the entire natural habitat from Alaska to the coast of Murmansk [24], is represented by anadromous and freshwater forms that differ in ecology. Moreover, in the outer areas of the natural habitat they are sympatric, whereas in Siberia, to all appearances, only freshwater forms occur, although cases have been noted of the capture of small lampreys attached to fishes in the littoral marine zone [24]. The anadromous form may consist of large lampreys and small early maturing *forma praecox*. These groupings may probably occur both jointly and separately. The suggested structure of the species *L. japonica* is reminiscent of the structure of *S. gairdneri*, *S. trutta*, etc. For example, *S. trutta* has a stream form - *morpha fario*, which was previously separated into an independent species *S. fario L*, and an early maturing anadromous form *whitling*.

Throughout the entire natural habitat of salmons, different intraspecific groupings are unequally distributed, as with the lampreys [24, 26]. It is difficult to say what this depends on. L.S. Berg [26] proposed that parallelism between lampreys and salmons was connected with the surrounding conditions. K.A. Savvaitova, M.V. Mina and V.A. Maksimov [214] explain the unequal distribution of the forms of Kamchatka steelhead on the Kamchatka Peninsula by the insufficient forage of the small rivers of the west coast, in connection with which there is no resident form there. On the contrary, the lack of an anadromous form in the Kamchatka River basin is apparently caused by insufficient areas suitable for spawning. The reduction in proportions and the reduction in migrations dependent on it when a resident form emerges from an anadromous form are probably determined mainly by the nature of the pressure of selection at the spawning areas. The resident and anadromous forms are tentative unions of versions of a continuous evolutionary ecological series.

To some extent these considerations are possibly applicable to lampreys as well, although the nature of their diet allows us to suppose that forage in this case is not such a restricting factor for the formation of a resident form.

Therefore, species structure in lampreys, as well as in salmons, is apparently rather complex. The simplest method of solving the problem, which is to separate the small resident forms into independent species, has prevailed in the literature until now. However, this matter is in reality apparently more complex. Stream species of lampreys are most likely freshwater forms of anadromous lampreys. Moreover, the relationships of the forms is similar to the relationships between trouts and anadromous salmons [24, 163].

Chapter 7

THE SIGNIFICANCE OF RESEARCH INTO THE ECOLOGICAL EMERGENCE OF FORMS AND THE POPULATION STRUCTURE OF ARCTIC CHARS TO CONSTRUCT A SCIENTIFIC BASIS FOR THEIR USE

Chars are valuable to commercial and sport fishing in many countries of the world. Thus, in Norway the anadromous char is caught in the sea, and in lakes and rivers. These catches make up more than 200 tonnes annually. Char catches in the inland waters of Norway make up 650-1000 tonnes annually [331].

In the USSR, on the Kola Peninsula, chars are caught in Lakes Imandra and Umbozero mainly with bottom gill nets. From 1950 to 1965, annual catches in Lake Imandra fluctuated from 8.5 to 13 tonnes; in Lake Umbozero, they were from 2 to 7.1 tonnes [107]. Anadromous 187
chars of Siberia and the Far East have a commercial value. A particularly large number of chars are caught on the Kamchatka Peninsula and in the rivers of the continental coast of the Sea of Okhotsk. On the Kamchatka Peninsula, chars caught out of the total catch of salmons is as follows: 3-41% on the east coast and 52-73% on the west coast. The role of chars in catches on the continental coast of the Sea of Okhotsk is also significant. In this region catches make up 12-29% [52]. With the exception of chars from the lakes of the Taimyr Peninsula and the Norilo-Pyasinskie Lakes, considerable stocks of these highly valuable fish do not become acclimatized at all in the number lakes in the north of our country. There is a huge number of lakes in this region. In the Lena River delta alone, ther are 58,700 lakes with a total area of 320,000 hectares. The area of the lakes in the Yano-Indigirskaya lowland is even greater: 850,000 hectares, and in the Kolymo-Indigirskaya lowland, it is almost 2 million hectares. Moreover, the average size of the lakes here is 23-26 hectares, whereas in the lower reaches of the Lena River, it is 5-7 hectares. In this respect, finding the lakes that are the most productive and convenient to use is a high-level problem.

Development of commercial fishing in the lakes currently comes up against considerable difficulties. These are mainly related to the distance from transportation routes and to limited fish stocks in these small bodies of water, which leads to scattered fishing.

Constant fishing for char is impossible without considering the specific nature of the structure of their populations, which are attributed to one and different intraspecific groupings. In this respect, it is expedient to compare the structures of Arctic char populations throughout the entire natural habitat of the species.

The population structure of the anadromous form of Arctic char. The population structure is not uniform in the anadromous form of the char. Two groups of populations may be separated that differ in their structure. The first is characterized by a long life cycle, a multi-age composition, a low growth rate, late sexual maturation, large-sized fish, body weight and absolute fecundity, non-annual spawning and a ratio of the sexes of 1:1. A similar population structure has been established in the anadromous chars of certain rivers of the coast of the Kola Peninsula, the Karskoe Sea, the Taimyr Peninsula (Table 29), Baffin Island, Northern Labrador and Greenland [258, 297]. For populations of this type, it is characteristic for the remainder to predominate over the replenishment; their periods of sexual maturation are extended. The structure of the remainder is highly complex since it consists of fish that skip the spawning season with an interval of one or more years and of a large percentage of old fish. The replenishment is also multi-age. Local populations may not be homogeneous. Winter and spring races are distinguished in certain rivers [155, 184]. The degree of the morphoecological varying quality of individuals in populations is also significant, which provides a wider adaptation to living conditions [162, 222].

The second group of populations differs by a shorter life cycle, a fast growth rate, earlier sexual maturation, smaller dimensions, body weight and fecundity. As a rule, females predominate in the populations, but there are also dwarf males that permanently live in fresh water [46, 71 et al].

Dwarf males are characterized by a slow growth rate, small dimensions and weight, short life and early sexual maturation. However, they should not be viewed separately, since they are part of an anadromous char population that increases its adaptive possibilities.

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Such a population structure is manifested in anadromous chars living in the Indiga River (Cheshskaya Bay of the Barents Sea), the Kukekkuyum River (south-eastern Chukotka Peninsula), in the rivers of the continental coast of the Sea of Okhotsk, the Komandorskie Islands, the Kamchatka Peninsula, Sakhalin Island and south-eastern Alaska [270]. These populations have a replenishment, i.e., the fish that mature first dominate the remainder.

The structure of the anadromous char populations of the islands of Spitsbergen and Novaya Zemlya has a somewhat intermediate character [85, 227].

Throughout the natural habitat of the species, the structure of anadromous char populations is not uniform. A certain trend is noted towards a change in the structure of anadromous char populations in a latitudinal direction - larger anadromous chars with the first type of structure of spawning populations predominate at high latitudes, and at lower latitudes, those with the second type of structure predominate. However, there are exceptions. These are the char populations from the Indiga River, from the waters of the south-western Chukotka Peninsula, and the islands of Spitsbergen and Novaya Zemlya [85]. The features of the structure of char populations from the Indiga River are determined by the feeding conditions in Cheshskaya Bay. The unusual temperature pattern, and specifically the strong warming of the depths of the water (up to $14^{0}C$ at a depth of 14-15 m) in summer months causes the existence of heat-loving relics here [89], a fast growth rate and earlier maturation of anadromous chars [160].

29. Структура популяций проходных гольцов в разных географических широтах

1 Район	2 Длина тела, см	3 Масса тела, кг	4 Максимальный возраст, годы	5 Возраст созревания, годы	6 Средняя плодовитость, тыс. шт.	7 Соотношение полов (самцы : самки)	8 Автор
9 Таймыр	70* / 91	4,0 / 6,6	14...16	7...12	—	1 : 1	[155, 222]
10 Кольский п-ов, 11 р. Варзина	48,8 / 60	1,2 / 2,4	16	8	—	—	Наши данные
12 Чешская губа, 13 р. Индига	47,5 / 58,3	1,2 / 2,5	7	3+...4+	3,2 / 5,2	1 : 1	[160]
14 р. Кара	41 / 88	0,9 / 9,0	15	4...7	4,0 / —	1 : 1	[184]
15 Чукотка (Залив Креста)	46 57 / 70 77	— — / 3,4 4,0	10+	4+	4,3 5,8* / 4,5 6,3	—	[53]
16 Материковое побережье Охотского моря	33...45	0,37...0,91	8+...10+	4+	3,2 / 8,2	—	[46]
17 Командорские о-ва	40 / 54	0,9 / 1,6	8+	4+	2,5 / 4,5	—	[213]
18 Камчатка	35 / 40	0,5 / 1,2	10+	4+	1,9 / 2,8	—	[201]
19 Сахалин	23 / 50		9+	3+	1,3...1,8 / 4,3	—	[71]
20 Командорские о-ва (карликовые самцы)	15 / 21	0,03 / 0,07	5	2...3	—	—	[213]
21 р. Паратунка, 22 Камчатка (карликовые самцы)	13,7 / 17,5	—	4+	2+	—	—	Наши данные

23 Примечание. В числителе даны средние значения, в знаменателе — максимальные.

* Два столбика характеризуют популяции, отличающиеся временем захода в реку.

29. The structure of anadromous char populations at different geographic latitudes

1 - region; 2 - body length, in cm; 3 - body weight, in kg; 4 - maximum age, in years; 5 - maturation age, in years; 6 - average fecundity, in 1000's; 7 - ratio of the sexes (males:females); 8 - author; 9 - Taimyr Peninsula; 10 - Kola Peninsula: 11 - Varzina River; 12 - Cheshskaya Bay; 13 - Indiga River; 14 - Kara River; 15 - Chukotka Peninsula (Krest Gulf); 16 - continental coast of the Sea of Okhotsk; 17 - Komandorskie Islands; 18 - Kamchatka Peninsula; 19 - Sakhalin Island; 20 - Komandorskie Islands (dwarf males); 21 - Paratunka River; 22 - Kamchatka Peninsula (dwarf males); 23 - NOTE: Average values are given in the numerator and maximum values in the denominator.

* Two columns characterize populations differing in the time they enter the river.

Apparently the connection noted between char population structure and the latitutude of the area where the chars live is a reflection of living conditions in the waters of different geographic zones - arctic and boreal. However, the char population structure is mainly related to the living conditions in each particular case.

The structure of lake form populations of Arctic char. The existence in one body of water of sympatric groupings that differ mainly in growth rate and type of food is a characteristic feature of lake chars. Their distribution mainly coincides with fairly deep alpine lakes (Tables 30-32). 190

30. Структура популяций озерных гольцов Севера

Район 1	2 Форма гольца	3 Длина тела, см	4 Масса тела, кг	5 Максимальный возраст, годы	6 Возраст созревания, годы	7 Средняя абсолютная плодовитость, тыс. шт.	8 Соотношение полов (самцы : самки)	9 Автор
10 оз. Лама, 11 оз. Таймыр	12 Крупная (голец Дрягина)	51,5 / 100	2,5 / 14	26	8...12	6309 / 9000	-	[155, 222]
13 оз. Капчук, оз. Лама (Таймыр)	Мелкая 14 (глубоководный голец)	33 / 45	0,25 / 0,30	18	10	540 / 637	1 : 1	[217, 222]
15 оз. Дальнее (дельта Лены)	16 Крупная	43,2 / 57	0,85 / 1,8	17	7	--	1 : 1	[220]
17 оз. Переходное (дельта Лены)	16 Крупная	43,5 / 53	0,93 / 2,2	23	9...10	2900 / 4280	1 : 1	[220]
18 Оз. Форелевое (залив Неелова)	16 Крупная	37,6 / 47	0,53 / 1,3	15	8...10	1276 / 1900	1 : 1	[220]
	19 Мелкая	29 / 33	0,17 / 0,30	15	6...8	—	2 : 1	[220]
20 Оз. Носковое (Кольский п-ов)	21 Крупная (палия)	37 / 41	—	12+	7+	1506	—	[40]
	22 Мелкая (голец)	33,6 / 38	—	11+	6+	942 / 1322	1 : 1	[40]

23 Примечание. В числителе даны средние значения, в знаменателе — максимальные.

30. The structure of lake char populations of the North

1 - region; 2 - char form; 3 - body length, in cm; 4 - body weight, in kg; 5 - maximum age, in years; 6 - maturation age, in years; 7 - average absolute fecundity, in 1000's; 8 - ratio of the sexes (males:females); 9 - author; 10 - Lake Lama; 11 - Lake Taimyr; 12 - large (Dryagin's char); 13 - Lake Kapchuk, Lake Lama (Taimyr Peninsula); 14 - small (deepwater); 15 - Lake Dal'nee (Lena River delta); 16 - large; 17 - Lake Perekhodnoe (Lena River delta); 18 - Lake Forelevoe (Neelov Gulf); 19 - small; 20 - Lake Noskovoe (Kola Peninsula); 21 - large (lake char); 22 - small (char); 23 - NOTE: Average values are given in the numerator and maximum values in the denominator.

31. Структура популяций озерных гольцов Забайкалья

Район 1	2 Форма гольца	3 Длина тела, см	4 Масса тела, кг	5 Максимальный возраст, годы	6 Возраст созревания, годы	7 Средняя абсолютная плодовитость, тыс. шт.	8 Соотношение полов (самцы : самки)	9 Автор
10 оз. Фролиха	11 Крупная	$\frac{38}{44}$	$\frac{0.5}{1.0}$	11	6...7	$\frac{536}{1300}$	1 : 1	[159, 216]
12 оз. Леприндокан	11 Крупная	$\frac{36}{46}$	$\frac{0.7}{1.3}$	13	7	—	1 : 1	[221]
	13 Мелкая	$\frac{24}{30}$	$\frac{0.13}{0.23}$	10	4...5	—	1 : 1	[221]
14 оз. Даватчан	11 Крупная	$\frac{44}{54}$	$\frac{0.75}{1.30}$	17	13	—	1 : 1	[221]
	13 Мелкая	$\frac{28.6}{32}$	$\frac{0.25}{0.30}$	13	8	170	1 : 3	[221]
15 оз. Гольцовое	11 Крупная	$\frac{27}{36}$	$\frac{0.24}{0.40}$	12	8	600	4 : 1	[221]
	13 Мелкая	$\frac{15.6}{19}$	$\frac{0.04}{0.06}$	12	9	58	1 : 2	[221]
16 оз. М. Леприндо	11 Крупная	$\frac{50}{63}$	$\frac{1.7}{2.7}$	12	9	$\frac{2935}{4200}$	—	[221]
17 оз. Б. Леприндо	11 Крупная	$\frac{—}{71}$	$\frac{—}{4.2}$	14	5...6	—	—	[185]

18 Примечание. В числителе даны средние значения, в знаменателе — максимальные.

31. The structure of lake char populations of the Zabaikal'e area

1 - region; 2 - char form; 3 - body length, in cm; 4 - body weight, in kg; 5 - maximum age, in years; 6 - maturation age, in years; 7 - average absolute fecundity, in 1000's; 8 - ratio of the sexes (males:females); 9 - author; 10 - Lake Frolikh; 11 - large; 12 - Lake Leprindokan; 13 - small; 14 - Lake Davatchan; 15 - Lake Gol'tsovoe; 16 - Lake Maloe Leprindo; 17 - Lake Bol'shoe Leprindo; 18 - NOTE: Average values are given in the numerator and maximum values in the denominator.

32. Структура популяций озерных гольцов бассейна Тихого океана

Район 1	2 Форма гольца	3 Длина тела, см	4 Масса тела, кг	5 Максимальный возраст, годы	6 Возраст созревания, годы	7 Средняя абсолютная плодовитость, тыс. шт.	8 Соотношение полов (самцы : самки)	9 Автор
10 оз. Угинское	11 Крупная	37/65	—/2,5	14	4...6	767/1840	1 : 1	[49]
12 оз. Корраль	11 Крупная	40,5/57	0,75/0,91	13	5+...6+	915/1530	2 : 1	[50]
	13 Мелкая	19,5/26	0,05/0,15	6+	3+	98/103	1 : 9	[50]
14 оз. Начикинское	11 Крупная	40/53	0,9/1,6	15	—	—	1 : 1	[206]
15 оз. Дальнее	11 Крупная	35/60	—	15	6	2150/2400	1 : 1	[198]
16 оз. Азабачье	17 Крупная (бентофаг)	40/55	—	11	5...6	1180/1324	—	[211]
16 оз. Азабачье	18 Крупная (хищник)	45/75	—	15	3...4	2019/2782	1 : 1	[211]

19 Примечание. В числителе даны средние значения, в знаменателе — максимальные.

32. The structure of lake char populations of the Pacific Ocean basin

1 - region; 2 - char form; 3 - body length, in cm; 4 - body weight, in kg; 5 - maximum age, in years; 6 - maturation age, in years; 7 - average absolute fecundity, in 1000's; 8 - ratio of the sexes (males:females); 9 - author; 10 - Lake Ueginskoe; 11 - large; 12 - Lake Korral'; 13 - small; 14 - Lake Nachikinskoe; 15 - Lake Dal'nee; 16 - Lake Azabach'e; 17 - large (benthophage); 18 - large (predator) 19 - NOTE: Average values are given in the numerator and maximum values in the denominator.

Some one grouping usually lives in thermokarst lakes (for example, certain lakes of the Lena River delta). Populations of large and small char groups are not uniform in population structure. For large chars, in comparison with small ones, the following are characteristic: long length, body weight and fecundity, long life cycle, later maturation, non-annual spawning and faster growth rate. Part of the energy of large individuals is spent on growth and, therefore, more time is required for gonad maturation. In this respect, the periods between spawnings are greater. Fish predominate in the food of these chars. Small plankton and benthos organisms predominate in the food of small chars. Their growth rate is very slow. They do not grow after sexual maturation and all of the energy acquired from food is apparently spent on gonad maturation.

The degree of isolation is not uniform in sympatric populations with a different population structure in different bodies of water. Groupings are known that emerge in the ontogenesis of one population, complementing one another, reproducing jointly, reproductively isolated and self-reproducing [206, 222, 386].

The structure of char populations should also be viewed depending on the degree of isolation. If isolation is not complete (which is indirectly evidenced by the differences in ratio of the sexes, and coincidence of places and times of spawning) and large and small chars reproduce jointly, they should be attributed to one population. For example, it is necessary to attribute the following to one population: chars from Lake Noskovoe (Kola Peninsula), Lake Forelevloe (Neelov Bay), Lakes Davatchan and Gol'tsovoe (Zabaikail'e), and lake Korral' (continental coast of the Sea of Okhotsk). The structure of char populations of a specific body of water becomes considerably complicated in this case; the rate of reproduction and the quality of descendants reproduced should change accordingly. Such a complicated population structure is observed in bodies of water with limited forage and size of spawning-grounds and allows the necessary number of fish to be supported under unfavourable conditions. It is sometimes impossible to attribute such a population structure to one of the above-described types, particularly if large and small chars within one population differ sharply in duration of life and periods of maturation [50].

In sympatric, isolated, self-reproducing large and small groupings of lake chars, the population structure should be viewed separately. Moreover, it may have a similar nature (chars of the Taimyr Peninsula) or it may be different (Lake Leprindokan, Zabaikal'e). In some lakes (Onega and Azabach'e) there are sympatric groupings of large chars with a similar population structure. A similarity in population structure in different char groupings is usually observed in large bodies of water (Norilo-Pyasinskie Lakes of the Taimyr Peninsula), Lake Onega and Lake Azabach'e). In small lakes the population structure of self-reproducing groupings is not uniform.

Thus, the population structure of sympatric char groupings depends on the level of isolation between them under specific living conditions. The population structure of chars represented in a body of water by one grouping is also determined by specific conditions in the bodies of water. For example, chars with a different population structure live in the thermokarst lakes of the Lena River delta [149].

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The structure of populations of lake-river and river forms of Arctic char. The structure of these populations is determined by river dimensions. In large rivers live large chars with a multi-age population structure, high fecundity, late sexual maturation and non-annual spawning. These populations are few in numbers. The river stone char from the Kamchatka River may serve as an example (Table 33). The following chars live in small rivers: smaller, multi-age in composition, relatively early maturing chars with a low fecundity, slow growth rate and an equal ratio of the sexes. These populations have a greater ability to reproduce and are greater in numbers. Very small chars live in streams; they have a rather simple age population structure and a slow growth rate. Their life is short; they mature early, have a low fecundity and an equal ratio of the sexes. They are also few in numbers. In certain cases they reproduce jointly with anadromous chars as, for example, in the Sarannaya River on Bering Island and in this way they complicate the population structure of the latter.

A comparison of population structures of different forms of Arctic char. We have not been able to reveal in chars a strong relationship between belonging to a certain ecological form 194
and the structure of their population. In all cases the structure of populations is to a much greater degree determined by the specific living conditions in bodies of water. Only the most general trends may be noted.

The most complex population structure is characteristic of lake chars and a simpler one is characteristic of river chars. Anadromous chars occupy an intermediate position. Only in the latter is there some connection between geographic distribution and the structure of their population. The population structure of freshwater forms is related to a familiar extent to the dimensions of a body of water and does not depend on its geographic location.

33. Структура популяций озерно-речных и речных гольцов

Район 1	2 Форма гольца	3 Длина тела, см	4 Масса тела, кг	5 Максимальный возраст, годы	6 Возраст созревания, годы	7 Средняя абсолютная плодовитость, тыс. шт.	8 Соотношение полов (самцы : самки)	9 Автор
10 Камчатка, протоки, впадающие в оз. Начикинское	Мелкая озерно-речная 11	28/37	0.15/0.45	11	6	..	1 : 1	[215]
12 р. Дальняя	Мелкая озерно-речная 11	30/35	--	9...10	4...6	870/1500	1 : 1	[198]
13 р. Камчатка	Крупная речная (каменец) 14	47/60	—	11+		2160/2624	..	[210]
15 р. Пономарка	16 Мелкая ручьевая	16.7/24	0.05/0.07	9	2+...4+	248/346	1 : 1	[209]
17 Командорские о-ва	18 Мелкая речная	20/26	0.10/0.15	5	3	353/484	-	[213]

19 Примечание. В числителе даны средние значения, в знаменателе — максимальные.

Table 33. The population structure of lake-river and river chars

1 - region; 2 - char form; 3 - body length, in cm; 4 - body weight, in kg; 5 - maximum age, in years; 6 - maturation age, in years; 7 - average absolute fecundity, in 1000's; 8 - ratio of the sexes (males:females); 9 - author; 10 - Kamchatka Peninsula, tributaries flowing into Lake Nachikinskoe; 11 - small lake-river; 12 - Dal'nyaya River; 13 - Kamchatka River; 14 - large river (kamenets); 15 - Ponomarka River; 16 - small stream; 17 - Komandorskie Islands; 18 - small river; 19 - NOTE: Average values are given in the numerator and maximum values in the denominator.

The second or third type of structure of spawning populations is characteristic of the chars of all intraspecific forms [158]. The multi-age structure of the flock in the first case provides a wide range of food, i.e., more stable forage under the severe conditions of high latitudes. The retarded and relatively slightly changeable rate of reproduction in such populations is related to the lack of enemies in adult chars and the low mortality of older age groups. Populations with a long life and a complex age structure maintain a low percentage of withdrawal from the adult flock. Populations attributed to the second type are capable of changing their numbers quickly, i.e., of high mortality.

Thus, among lake chars the populations' ability to reproduce is small and the numbers are limited. Their stocks may easily be undermined. Therefore, it is not likely possible to rely on the organization of extended fishing in any body of water: it will be necessary to change the locations for fishing and to periodically prohibit fishing. However, the latter must be done carefully. In a case where sympatric large and small char groupings live in a body of water and the large form is overfished, prohibition may not give the desired results; moreover, it will allow for the small form to capture the niche [147].

At the same time, an analysis of species structure and the structure of separate populations allows chars to be viewed as an object capable of withstanding considerable fishing demands in a case where bodies of water are not subjected to successive changes. This particularly relates to the anadromous form. The structure of the species and the features of the population structure determine the type of dynamics of numbers. The presence in populations of adult individuals of different sizes lowers the influence of selective fishing on the reproductive ability of populations. A large number of age groups in the flock and repeated spawning provide for more stable reproduction and lower the probability of undermining the numbers as a result of 195
overfishing. The existence of a majority of intraspecific intrapopulation groupings and the considerable varied quality of individuals in separate populations also reduces the negative effect of fishing. Overall, one should remember that each population is unique to a known extent in its ecological appearance. The population parameters were historically worked out as adaptations to exist under some conditions or others. In this respect one should assess all population features and their reactions to external influences.

Under rational use of northern lakes, subject to the overall use of ichthyofauna, 10-15 kg of high-quality fish may be obtained per hectare [80]. Considering the great number of lakes, this will provide a noticeable growth in fish production. It is also possible to intensify the fishing of anadromous chars in the Far East and in the North of our country.

Chars may be used both as subjects of fish breeding and acclimatization [11, 177, 183]. They are bred successfully on farms in Iceland, Norway, Sweden, Denmark, Switzerland, Austria, and the Federal Republic of Germany.

Prospective subjects of commercial farming are the hybrids *S. alpinus x S. fontinalis* and *Salmo salar x S. alpinus*, which have a fast growth rate.

It is possible to breed Arctic chars at cold-water farms, using factories that we already have for breeding salmons. Then the biotechnology of breeding will not differ substantially and will not require significant capital investment. However, attempts to farm Arctic char have been successful in far from all cases. Intensive fishing, eutrophication and pollution sharply lowered their stocks and led them to a catastrophic state. It is possible that an important cause of this was ignoring the systematic organization of chars and, to a great degree, the pronounced structuring, and the lack of suitable forecasts on the basis of this.

Species of fish that represent complex population systems live in a specific environment. At the present time, under the influence of various anthropogenic factors (fishing, acclimatization, artificial breeding, pollution, etc.), their balanced relationships with the environment are being destroyed more frequently.

The stability of populations, as Yu.P. Altukhov [4, 5] and S.M. Konovalov [113] point out, is determined by the systematic level of organization and the degree of subdivision into semi-isolated subpopulation units. The biological features of populations are products of their gene pools. They lend themselves to forecasting and are basically available for regulation. 196

However, local adaptations of populations that are formed by selection over thousands of generations in a specific environment are unique and conservative. Therefore, insufficient consideration of the structural organization of species of fish may have negative consequences. In marine fishing, which takes place in areas where there are the most fish, population systems are destroyed in sections - the percentage of fish removed from different subpopulations is not identical, which leads to the destruction of naturally established migratory connection channels between elements of the system, and a change in adaptive genetic structure. Nothing similar is observed in artificial reproduction and acclimatization.

However, although it is extremely desirable to prevent by all means a change in population structure, it is possible to achieve this merely by refusing exploitation. Under modern conditions, it is impossible to completely avoid the influence of human activities on the population structure of fish and, apparently, it is unnecessary. At the same time, fishing, on the one hand and fish breeding, on the other hand, influence population structure. In this respect, it is proposed that there be equal influence on populations and their components [5, 113].

It is also necessary to take into account the population structure of species when creating artificial populations [112]. For the emergence of population homeostatis, it is essential that founding individuals have the maximum number of genes from the species gene pool, in order to retain physiological and morphological variety and different age structure. The formation of sexual structure is also an important step in the creation of artificial populations. In nature, when a population transfers to a new state, the proportion of males and their hierarchical structure increases. This should be the goal in creating artificial populations. It is essential to take into account the trophic relationships of population groupings. It is also important to known the different ecological features of groupings used to create artificial systems. In the opinion of S.M.

Konovalov [112], artificial populations should be formed according to the similarity of their natural counterparts.

The features of fish population structure have a special meaning for environmental protection issues as well. A population's reaction to a harmful factor will not be uniform under any one age, sexual, spatial or genetic structure. The degree of resistance of natural populations to anthropogenic influence, to a significant degree, proves to be related specifically to the retention and maintenance of the population's structure [255].

However, the problem may also be viewed in another way. M.V. Mina [151] poses the question whether it makes sense, under the conditions of the influence of fishing, to strive to 197
maintain the population structure and genetic composition that is characteristic for a given flock under natural conditions where there is no fishing. He concludes that, in a case where populations disappear under the influence of fishing, their place in the ecosystem may be occupied by other populations of the same flock that are not genetically identical to the previous ones. However, this does not necessarily have a negative effect on the numbers or the reproductive capability of the flock as a whole. It is likely that in such an exchange even the genetic variety of the flock is not reduced.

In our opinion, M.V. Mina correctly suggests that similar substitutions, confluences and splits apparently took place in the history of each flock under natural conditions, when there was no fishing. He also analyses convincing examples indicating that high reparative capabilities of populations are also found under acclimatization when structured populations that are great in number emerge from small groups of founding individuals.

Data on the structure, distribution, level of variability, degree of isolation and transformation trends of population groupings of varying hierarchic rank in Arctic chars should make up an array of background information that is essential for ecological monitoring. At the present time, when anthropogenic influence on the biosphere is increasing every more noticeably, research involved with the issues of ecological monitoring have special meaning, i.e., tracking the condition and changes of the main functional blocks and elements of ecosystems with the highest indicating properties [181]. Such control has the goal of justifying and developing a scientific strategy for the rational use of nature.

Fish have high indicating properties and using them should lead to the following: carrying out, revealing, describing and mapping the modern spatial structure mainly of commercial species of fish and their individual populations, evaluating the level of interaction of population systems, evaluating the level of genetic homeostasis (balancing) of the populations studied, determining rates and trends of changes of these parameters, the appearance of connections and relationships between changes in the gene pool and substantial ecological parameters - the dynamics of numbers, size-age and sexual structures, growth rate, etc.

The study of the population structure of species should preferrably go in two directions: stock-taking and forecasting. Unfortunately, there are so far only a few species of fish that have been satisfactorily studied in this respect. Arctic chars may be named among them.

CONCLUSION

The results of comprehensive research into populations of salmons allow us to confirm that they are all polymorphs to some degree or another. Genetic polymorphism, together with the assortativeness of crossing may be a source of the emergence of forms and, in the end, lead to the emergence of sympatric ecological forms or independent species. The problem of the emergence of forms from genetic positions is reduced to the problem of polymorphism. What is meant by genetic polymorphism is the stable existence of two or more alleles with greater frequency than the probability of repeated mutations. This definition narrows the scope of the phenomenon somewhat. Polymorphism is usually defined by single phenes like electrophoretic forms of proteins. However, polymorphism is possible through genes that have an extremely high pleiotrophic effect. These genes determine hereditary factors that influence growth rate and rate of sexual maturation [103, 152]. If polymorphism is observed in a population according to these genes, then the emergence of groupings with highly varied phenotypes occupying different niches is realistic. When such groupings emerge, the direction of selection may change. If under ordinary polymorphism selection is in favour of heterozygotes or against both homozygotes, then in this case selection may have a reverse direction, i.e., in favour of homozygotes, to preserve the emerging ecotypes. In connection with this, various ecological forms of salmons may emerge in bodies of water, but the original form is apparently euryphagous. These may be benthophages, predators, or planktophages. A deepwater form emerges in a number of cases. It is possible to attribute almost the entire variety of chars to these main ecotypes. These ecological forms arise throughout the entire natural habitat, independently of one another. Under the appropriate conditions they may even reach species isolation.

Certain authors [43, 59] currently tend to deny any evolutionary importance of ecotypes and attach absolute importance to isolation, in connection with the fact that they contrast isolats with ecotypes. However, an isolat may exist only as an ecotype or several ecotypes, and each ecotype may be viewed only within the framework of some isolat. Isolation does not arise 199
immediately. It is established gradually under the influence of its worsening mechanisms. In addition, one should not consider the co-existence of several ecotypes to necessarily be a stage of speciation. More often ecotypes are only forms of existence of one species, which allow the fullest utilization of the resources of a body of water. Morphoecological structurization of a species allows intraspecific competition to be reduced to a minimum and the stability of the species as a system to be increased [33, 116]. Where an assortatively reproducing ecotype exists over many generations and under sufficiently stable conditions, its further genetic divergence is possible. In the end, this divergence may lead to the coming into being of a new species that is irreversibly isolated from the ancestral species. Such a situation occurs extremely rarely in ecosystems where conditions change sharply (high latitude bodies of water, high alpine lakes). G.V. Nikol'skii [163] pointed out that the faunistic complexes of these regions are poor in species. The freshwater ichthyofauna at high and moderate latitudes is highly conservative and from the Tertiary period [125, 163, 256]. Low rates of emergence of forms are characteristic for the flora and fauna of these regions. Temperature and lighting apparently have a powerful and limiting influence on the processes of speciation in fish, including chars [151]. Their seasonal fluctuations influence fish most often indirectly, rather than directly, sharply reducing the number of ecological niches and hindering any significant specialization. In connection with this, euryphagy is highly developed in fish, i.e., typical predators, benthophages and planktophages occur rarely, but only one type of food or another may predominate. The presence of semi-anadromous and anadromous forms, which are a connecting link between freshwater populations and the genes being exchanged between them, apparently hinders the geographic emergence of forms and speciation. They are probably not absolutely tied to their bodies of water.

The majority of mountain bodies of water where the groups of fish studied live are young: not more than 8,000 to 12,000 years old [135]. Thermokarst lakes are short-lived. Their young age in combination with the instability of the conditions in these lakes probably did not favour the processes of speciation. It is more likely that such processes may occur intensely in ancient bodies of water [55] or in the upper reaches of river systems that were untouched by overlapping and lay outside of the zone of continental icing. Stable conditions facilitating the emergence of forms and speciation could exist for a sufficient period of time only in such bodies of water. However, stability of ecosystems over an extended period, nevertheless, does not necessarily lead to speciation. It only increases the probability of this process. The chances for the emergence of a new species are not always realized by evolution. Therefore, these processes are reversible in the majority of cases.

In analysing the emergence of forms and speciation in the groups of fish studied, one should also bear in mind the formation patterns of fauna at different latitutdes. Ecosystems at low latitudes are often multi-component and represented by monomorphic, i.e., narrowly specialized species, although recently more and more facts have been emerging that are evidence of the fairly complex structure of many species of fish living in these regions [151, 194]. It is considered that the wealth of fauna species at low latitudes is the result of the stability of the conditions. Tropical fauna had more time for its development; seasonal fluctuations of the biomass and the number of food objects are not significant there. However, it is most likely that this is not so much the result of stable conditions as the result of the specific nature of variable factors, and most of all temperature [151].

The number of species is sharply reduced at high latitudes [162, 163, 193]. The majority of fish living in these regions are polymorphs. They are characterized by great plasticity, which allows them to exist under a wide range of conditions. However, monomorphic species also occur that have adapted to one niche. Both polymorphic and monomorphic species are found among the fish of the genus *Salvelinus* and among the Pacific noble salmons of the genus *Salmo*. These species are probably at different stages of their development. Monomorphism may be a property of both young and old species. The phase of polymodal homeostasis is more likely characteristic of historically formed population systems, which are represented by the majority of groupings providing the ecological plasticity and stability of the species as a whole.

The knowledge of spatial and biological structure, the detection of the conditions and factors of the stability of population systems in fish that are particularly important groups in the commercial sense have great significance due to increasing anthropogenic influence on natural ecosystems, the necessity to establish their original state and the expansion of artificial breeding of fish. The results of this study facilitate the solution of these problems and may be used as follows: to draw up recommendations on fishing for individual populations of chars and Kamchatka noble salmons; to assess and forecast the adaptive properties of populations of chars and Kamchatka noble salmons; to conduct studies on acclimatization and artificial fish breeding, hybridization and selection; for taxonomic research; in conducting stock-taking of modern ichthyofauna and studying the structure of ecosystems as a whole; to take measures in the

The knowledge of spatial and biological structure, the detection of the conditions and factors of the stability of population systems in fish that are particularly important groups in the commercial sense have great significance due to increasing anthropogenic influence on natural ecosystems, the necessity to establish their original state and the expansion of artificial breeding of fish. The results of this study facilitate the solution of these problems and may be used as follows: to draw up recommendations on fishing for individual populations of chars and Kamchatka noble salmons; to assess and forecast the adaptive properties of populations of chars and Kamchatka noble salmons; to conduct studies on acclimatization and artificial fish breeding, hybridization and selection; for taxonomic research; in conducting stock-taking of modern ichthyofauna and studying the structure of ecosystems as a whole; to take measures in the protection of nature directed at supporting the ecological balance and maintaining unique gene pools. 201

The research conducted indicated the prospects for using chars of the genus *Salvelinus* and Kamchatka steelhead as subjects of fish breeding and sport fishing.

The Kamchatka steelhead has all the biological properties that determined the success of the economic development of the steelhead trout. It matures early, grows quickly and is characterized by great ecological plasticity, which allows it to assimilate various niches. Its natural populations were not susceptible to inbreeding and are probably very resistant to the influence of unfavourable external factors, including illnesses [97].

Based on the materials of this work, where the proximity of the Kamchatka steelhead to the steelhead trout is proven, one may conclude that the standards for breeding the steelhead trout will also be suitable for the Kamchatka steelhead. Therefore, substantial economic expenditures will not be required in introducing the Kamchatka steelhead to the fisheries. The best prospects for fish farming development are the populations of Kamchatka steelhead living in the Kvachina, Unkholok, Utka and Bol'shaya Rivers. The bodies of water with the best prospects for collecting the eggs of this fish are: the rivers of the Western Kamchatka Peninsula - Utka, Mukhina, Khomutina, Kol', Oblukovina, Icha, Sopochnaya, Moroshechnaya, Utkholok and Kvachina; the rivers of the Eastern Kamchatka Peninsula - Kishimshina and Baran'ya [181].

The Kamchatka steelhead differs in being very tough; it is resistant to a lowering in the concentration of O_2 and to a worsening in the chemical composition of water [223, 323]. In breeding this fish in geothermal waters, it has been established that its growth rate under artificial conditions is considerably higher than under natural ones; sexual maturation begins sooner. The Kamchatka steelhead outstrips the rainbow trout in growth and reaches commercial weight sooner. The Kamchatka steelhead acclimatized well to the waters of the south-eastern Kamchatka Peninsula as well. There is almost no difference between it and fish from the same area [27, 166].

Chars from the genus *Salvelinus* live predominantly in bodies of water at high altitudes under extreme conditions. Therefore, they should be used as the subject of cold-water fish breeding and polar mariculture. It would be expedient to create seedstock flocks, to breed planting material and to set up commercial breeding. In doing this, it is necessary to consider the char morphotype and the possibility of its existing under given conditions.

Chars may also be recommended for acclimatization studies, since certain groupings of these fish grow quickly, mature early, are euryphagous and not susceptible to disease [32].

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