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by Yu.P. Altukhov

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By Yu.P. Altukhov

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Annotation

Original data obtained in the course of many years of investigations 2*
of the divergence of species of fishes are examined in the book according to the principles and by the methods of population and biochemical genetics. It is proven with comparative material that two qualitatively different levels of structure can be distinguished in the population organization of a species, regardless of its ecological characteristics: firstly, historically formed, genetically stable population systems corresponding to mathematical models of population subdivisions and, secondly, structural components of such systems -- more elementary, at times very variable, population units, formally corresponding to the model of a "Mendelian population."

The importance of such species organization is discussed in connection with problems of a rational fishing industry and in an evolutionary aspect.

Thirty-nine tables, 70 figures and a bibliography of 474 items.

*Numbers in the right-hand margin indicate the corresponding pages in the original.

Introduction

All bisexual species of plants and animals are represented by 3
more or less isolated groups reproducing in generations by populations groupings, the biological characteristics of which cannot be reduced to a simple sum of the properties of the organisms forming them. Now perceived as an axiom is the statement that a population is a basic unit of the evolutionary process. It must also be taken into account that it also is the basic object of the practical activity of man, especially in such spheres as the hunting, timber and fishing industries.

The economic importance of fish populations is rather great. Thus, whereas 16.4 million tons of fishes were caught in the entire world in 1938, by 1960 the catch had almost doubled and by 1969 had approximately tripled. Such a tendency of development of the fishing industry is dictated by the increasing need of mankind for protein food. However, the stocks of many fishes are already marginal now, and a catastrophic decrease of numbers is characteristic of individual species.

Why are apparently inexhaustible stocks decreasing? At first glance the answer is a simple one: the pressure of industry has increased excessively or the historically formed living conditions have changed. However, more and more data are being accumulated which testify that the reduction of the numbers of fishes can also be connected with a deficiency in the structural organization of industrial species -- their subdivision into isolated populations.

Consequently, to the degree to which the economically important properties of populations are derivatives of their gene pools, the corresponding approach to the recognition and identification of such communities,

and also to the explanation of factors of their stability and variability, can be of decisive importance in the creation of the scientific principles of a rational fishing industry. The same approach also has a general biological aspect, as the population genetic data themselves already require evaluations from the point of view of contemporary concepts of the problem of species and species formation.

Nevertheless, in spite of the great successes achieved by population genetics both in the development of mathematical apparatus and in investigations of natural and laboratory populations, questions of fish population genetics until recently were worked out only fragmentarily, being limited to two or three polymorphous non-industrial species. In recent years, thanks to the successes of immunological and biochemical genetics, substantial changes have occurred: genetically polymorphous systems of blood groups and various proteins have been discovered in practically all economically valuable fish species, which has made it possible to come to grips with many important questions of the population biology of fishes using the principles and methods of genetics. 4

The present investigation is devoted to a comparative genetic and biochemical analysis of the population structure of species.

In the organization and conducting of the investigation we strove:

1) to determine the hereditary variability of species different in ecology and on the path of a broad genogeographic analysis to use corresponding markers to solve a number of concrete problems in the recognition and identification of isolated populations, so-called local stocks or races;

2) to clarify distinctive features of the internal organization of such communities and on that basis to attempt to characterize a fish population as an object of genetic investigation and economic activity;

3) to estimate the importance of the genetic divergence of species in fish from the point of view of contemporary evolutionary theory.

Material has been obtained on the genetics and biology of populations of the redfish, anchovy and Pacific salmons.

The anchovy Engraulis encrasicholus L. was represented in our material by two geographic races: the Azov (E. e. maeoticus Pusanov) and the Black Sea anchovy (E. e. ponticus Alex.). Immunogenetic investigations were conducted on the expeditionary vessels of the Azov-Black Sea Scientific Research Institute of Sea Fisheries and Oceanography (AzcherNIRO). In January-March 1963 (Black Sea) and in July 1963 (Azov Sea) the author participated in the work. Blood groups were discovered in the anchovy during those expeditions. The remaining work amounted to to a series of detailed surveys of the space-time distribution of phenotypes mainly in the Azov Sea (1964-1966) and was done under our supervision by co-worker V.V. Limanskii of the AzcherNIRO.

Material reflecting the variability of antigenic properties of the red corpuscles of the redfish was gathered in the Newfoundland region during expeditions to the Northwest Atlantic (in July-October 1964 and 1965). 5

Investigations of distinctive features of the stocks of Pacific salmons in relation to various genetic markers -- electrophoretic variants of proteins and isoenzymes -- were conducted with the direct participation of the author during expeditions of the Laboratory of Genetics of the Institute of Biology of the Sea of the Far Eastern Scientific Center (FESC) of the USSR Academy of Sciences on Sakhalin, Kamchatka and the Kuril Islands (1968-1972). Work with the salmons is still far from completed, and so in the present investigation only a portion of the information on several

stocks of keta /chum/ and one stock of sockeye will be presented; this section of the work is complete, in accordance with the tasks assigned. tasks.

In the final chapter we examine the interspecies variability of proteins genetically monomorphous within a species. This line of analysis, which results logically from certain general corollaries from the population genetics section of the work, is based mainly on the author's own material and those of co-workers of the Genetics Laboratory of the Institute of Biology of the Sea, FESC of the USSR Academy of Sciences.

It is understandable that all this work could be accomplished only by a collective group of investigators, and the author sincerely thanks his closest co-workers and colleagues who made an important experimental contribution to the working out of the problem -- V.V. Limanskii, A.N. Payusova, G.N. Nefedov, E.A. Salmenkova, V.T. Omel'chenko, L.G. Volokhonskaya, G.D. Sachko and V.I. Slyn'ko.

In its various stages the present investigation enjoyed the constant support of the director of the All-Union Scientific Research Institute of Sea Fisheries and Oceanography (VNIRO), A.S. Bogdanov, and his deputy P.A. Moiseev, the director of the N.M. Kipovich Polar Scientific Research Institute of Sea Fisheries and Oceanography, A.P. Alekseev, and co-workers of the same institute K.G. Konstantinov and G.P. Zakharov. Much help was extended us in the organization and accomplishment of work on Pacific salmons by the chief of the Main Fish Breeding Administration I.V. Nikonorov, the head of the Fish Breeding Section of the Main Fish Breeding Administration L.V. Polikashin, the chief of the Sakhalin Fish Breeding Administration S.A. Ugryumov, the head of the Fish Breeding Section of the

Sakhalin Fish Breeding Administration I.M. Zolotarev and directors of Sakhalin fish hatcheries V.T. Petrenko and T.T. Kochetkov. The author takes this opportunity to express his sincere gratitude to all those persons.

I would also like to emphasize the great importance of my relations with Yu.G. Rychkov, both in the process of direct collaboration and in the discussion of general problems of population genetics, had in the formation of my ideas.

Chapter I. The Problem of Population Organization of Species in Fishes. The Necessity of Genetic Investigation

The concept of differentiation of widely distributed species of fishes into a large number of populations differing in numbers, distinctive features of biology and character of subordination seems at the present unquestionable. However, in ichthyology there still is no single concept of population, as is testified to by the variety of terms and notions usually encountered in works devoted to the structure of species. One can count up to ten names relating to various kinds of intraspecies groups below the subspecies: "race", "tribe", "morph", "stock", "population", "grouping", "seasonal race", "intraspecies biological grouping", etc.

Indefiniteness of this sort also exists in the latest works pursuing the goal of creating a universal classification of the population structure of species.

For example, according to N.V. Lebedev (1967) the population hierarchy of species in fishes is composed (from the top downward) of subspecies (= geographical races) -- ecological races -- stocks -- elementary populations.

G.V. Nikol'skii (1968, 1971) distinguishes four types of intraspecies groupings:

1) geographical races, or subspecies;

2) ecological groupings, or ecotypes;

3) seasonal forms;

4) temporary races or subfossil subspecies.

The author simultaneously expresses the hypothesis of the non-hereditary nature of most intraspecies groups in fishes, although he also stresses the importance of comprehensive study of the pupulation structure of species both for the further development of the theory of the dynamics of populations and for the organization of a rational fishing industry.

The practical aspects of the population biology of fishes were thoroughly discussed in the monograph of N.V. Lebedev (1967), but, in contrast with G.V. Nikol'skii, N.V. Lebedev considers only an elementary population to be a non-hereditary subdivision of a species.

Meanwhile, the answer to the question of the contribution of heredity and environment to the formation of the biological characteristics of populations is of fundamental importance for practical activity: if a species is subdivided into isolated population units, then without a clear idea of the specific features of their biology the organization of a rational fishing industry is unthinkable, as is the conducting of the corresponding fish breeding measures. 7

Estimation of the depth of the genetic divergence of a species must also be of interest for evolutionary theory, since from as far back as the time of M. Wagner isolation has been considered one of the important conditions of species formation.

In the new treatment of E. Mayer (1968) the problem of species formation is the problem of isolates.

It seems advisable to briefly review the history of the formation of this trend in ichthyology.

Some Traditional Approaches to Analysis of Intraspecies Differentiation of Fishes

The first work on this plane was that of the German ichthyologist F. Heincke (1898). In his monograph on divergence of the Atlantic herring Clupea harengus he emphasized adherence to the conception of Charles Darwin in the treatment of intraspecies variability. The author introduced the method of combined characters, which permitted distinguishing within the limits of the species up to 30 fine groupings which were called races by him and defined as groups of individuals "living in a single region, under identical conditions, having identical habits and being in a very close blood relationship; distinguishing characters of races are hereditary".

Since the time of Heincke investigations of races in ichthyology have been conducted mainly on the basis of analysis of morphological characters. We will not discuss here all the enormous literature on this subject, as there are several generalizing publications (Kirpichnikov, 1933, 1935, 1943; Altukhov, 1969a), but will only point out the extensive investigations of intraspecies divergence of the eelpout and the cod (Schmidt, 1917, 1930), the smelt (Kirpichnikov, 1935) and the sockeye (Gilbert, 1914-1925, according to Konovalov, 1972), which occupy a special place in this cycle of work and which led to the discovery of a large quantity of morphologically different local races. Thus, for example, the description and

mapping of the ranges of races of the cod are given on the basis of results of analysis of the variability of a number of vertebrae and fin rays of about 20,000 fishes from 114 stations which embrace the greater part of the range of the species in the Atlantic. Other species have also been studied in no less detail.

It should be acknowledged, however, that in spite of a considerable contribution to the problem this approach has encountered a number of serious difficulties in the interpretation of data. One of the most important limitations was establishment of a wide dependence of distinctive features of the external structure of a fish on changes of the environment, features reflected in both plastic and meristic characters (Schmidt, 1917, 1930; Hubbs, 1922, 1925, 1926; Kirpichnikov, 1933, 1935, 1943; Vladykov, 1934; Dannevig, 1932, 1933; Mottley, 1934, 1937; Hile, 1938; Wunder, 1939; Gabriell, 1944). All these widely known works, and also relatively new material obtained in the investigation of various species (Taning, 1952; Wilder, 1952; McHough, 1954; Lindsey, 1954, 1958, 1962; Hampell and Blaxter, 1961; Templeman and Pitt, 1961; Ben-Tuvia, 1963, etc.), clearly showed that the external expression of a given meristic character depends on a number of environmental factors (temperature, salinity, and the gas and light regimes) which exert the most substantial influence in the early periods of ontogeny (Fowler, 1970).

In studying such modification variability it is very difficult to decide with what the differentiation of morphologically or biologically different populations is connected: whether it is actually an indicator of their reproductive isolation or simply reflects the influence of external conditions on the eggs, embryos or larvae of fishes in geographically or ecologically separate sections of a range.

It is not surprising, therefore, that after a period of general enthusiasm for the description of new races a time came when races discovered earlier began to be "shut down". Thus, for example, T.F. Dement'eva et al. (1931) and E.V. Mesyatseva (1937), investigating the Barents Sea cod, described four to seven races of it which could not be found later (Dement'eva and Tanasiichuk, 1935). There was a similar situation with the Caspian roach (Petrov, 1930; Morozov, 1932; Zernov, 1938; Karavaev, 1939; Sergeeva, 1963). The number of examples could be increased greatly.

In the 1930's appeared a trend called "experimental systematics" (Schmidt, 1930; Huxley, 1942; Kirpichnikov, 1943), which regarded the problem of recognizing reproductively isolated races of fishes as primarily a genetic problem. In these studies the importance of a strict delimitation of the hereditary and modificatory variability of racial characters was emphasized and it was shown that many morphological features, in spite of the modifying influence of the environment on them, are hereditary. A classic example of investigations made from that point of view is the work of V.S. Kirpichnikov (1943) on the systematics of the carp (geographically remote races of that fish and their hybrids were analyzed in detail morphologically and biologically under practically identical conditions of habitation).

It is difficult to conduct such investigations on marine fishes, however, taking into account certain distinctive features of their ecology and the difficulties connected with keeping them in an aquarium. Similar difficulties often arise also in investigating many semi-anadromous or even freshwater fishes.

For these reasons the tagging of fishes and analysis of their parasites have obtained substantial development in ichthyology. Such investigations have given much that is new for understanding the patterns of fish migrations and differentiation of various intraspecies groups

(Dogel' and Bykhovskii, 1938; Shul'man and Shul'man, 1953; Templeman, 1953, 1962; Strelkov, 1956; Polyanskii, 1958; Shul'man, 1956, 1959; Hargis, 1958; Fleming, 1960; Sindermann, 1961a, Szidat, 1961; Templeman and Squirs, 1960; Yanulov, 1962b; Konovalov, 1963, 1971), but they also made known the limitedness of those methods of analysis. It has been made clear that tagging is costly, and for a number of deepsea and pelagic fishes* it is in general impossible.

For successful parasitological analysis it is necessary that the parasite be retained in the fish organism for at least a few years, not lead to its death and have a constant geographical localization (Sindermann, 1961a).

Consequently it becomes evident that neither of those two approaches can be considered universal in the analysis of the population structure of a species. In order not to make unsubstantiated statements, I will refer to all the generally known complications which are constantly encountered in studying the intraspecies differentiation of Pacific salmons, White Sea herring, cods, haddocks and redfish of the Northwest Atlantic and Barents Sea, etc. Similar problems also arise in the assimilation by industry of mackerel, sardines and tuna in the waters of the Atlantic and Indian oceans. In addition, even the question of differentiation of the stock of the Atlantic herring, studied almost a century, has not yet been solved and is the subject of unceasing discussions (Blaxter, 1958; Einarsson, 1958; de Ligny, 1969).

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*For example, mass tagging of herring and tuna gives tag returns of the order of 0.01-0.03 (Roedel, 1954; Dragesund, 1964).

It will not be an exaggeration to say that the problem of recognition and identification of reproductively isolated groupings within a species of fishes also in our day is, perhaps, no less acute than at the start of corresponding investigations in ichthyology. In the foreign literature now it often is called the problem of subpopulations (Marr, 1957); Soviet ichthyologists prefer to speak of local stocks or races, and in a number of works those concepts are treated as identical (Krykhtin, 1958; Yanulov, 1962a).

New Wording of the Old "Race" Problem. Hereditary Polymorphism as the Basis of Analysis of the Genetic Structure of Populations

According to Marr (1957a, p. 1) subpopulations are the smallest natural self-reproducing units, for which the term "dem", used by taxonomists, can serve as a synonym. Differences between subpopulations are slight, but they are hereditary. Members of subpopulations are segregated in the spawning period and, consequently, crossing within it proceeds in any possible directions, whereas gene exchange between different subpopulations is hindered to some degree. As a result of that each subpopulation is characterized by specific features of recruitment, growth, natural mortality, migrations, behavior, etc., which are to a greater or lesser degree independent of analogous biological indicators of other subpopulations within the same species. Thus a very high degree of genetic closeness of individuals within a subpopulation is a very important character which distinguishes it from a "stock" (Russian stado) and a "group" -- two additional non-taxonomic units distinguished by Marr. But, as the author

points out, these last-mentioned concepts are very indefinite; the closeness of members of the stock is not hereditary, but is caused by the conditions of existence, and the character of the difference between groups is not clear at all.

K.P. Yanulov interprets the term "stock"(stado) differently: "A 11
stock is a group of fishes sufficiently isolated in relation to region of habitation, and morphological anatomical and biological characteristics. The individuals forming the stock must have a more or less clearly expressed affinity which can be maintained, on the one hand, by exchange of hereditary characters between separate small biological units (populations) forming a part of it and, on the other, as a result of the absence of a considerable flow of hereditary characters from other genetic groupings. It is an essential feature of the stock that its abundance (numbers and biomass) are determined by environmental factors (biogenic and abiogenic) acting within the boundaries of the stock and, consequently, influencing the reinforcement of stocks and growth and mortality within it" (Yanulov, 1962a, pp 285-286). Thus the "stock" in the understanding of Yanulov absorbs in itself the "subpopulations" of Marr.

On the other hand, the definition of a subpopulation is similar to that of a race given long ago by Heincke, and almost identical to that which V.S. Kirpichnikov wrote in the 1930's on the matter, considering a race of fishes as a "freely multiplying, isolated (at least in the period of multiplication) community, representing a mixture of genotypes" (Kirpichnikov, 1933, p 618). "We consider races to be the smallest possible populations, in the main not mixing with other populations: completely free multiplication is possible in general only within each race, but if mixing

occurs on a considerable scale during multiplication, the differences of races from one another are not constant enough (Kirpichnikov, 1935, p 181, author's emphasis, Yu. A.).

Thus the just-discussed definitions of reproductively isolated groupings within the limits of species in fishes show that the old "race" problem faces us now, although in a form essentially unchanged, but already in a different edition: whereas in the 1930's and 1940's the races of fishes were the subject of investigations of experimental systematics, now features designating the problem as one of population genetics have been introduced into the definition of race.

In recent years this aspect has been especially emphasized in the cycle of studies stimulated by the Food and Agriculture Organization (FAO) (Division of the United Nations Organization for Questions of Food) and the International Council for the Exploration of the Sea (ICES) and directed toward the genetic and biochemical investigation of the population structure of economically valuable species of fishes.

Thus in 1964 Parrish formulated the concept of "the basic popu- 12
lation subdivision of fishes", distributed as a technical fishing industry document of the FAO. In that work a subpopulation (or separate stock -- "unit stock") is defined as "a relatively homogeneous and self-reproducing population, the losses of which as a result of emigration and acquisitions as a result of immigration, if there are such, can be ignored in estimating the rate of growth and mortality".

The author is aware of the relative character of such a definition, but for most species of fishes proposes a universal conception which distinguishes two types of populations:

1) geographically isolated groups which are protected from free mixing and interbreeding with members of neighboring groups by migration barriers;

2) reproductively isolated groups which constitute a general locality and are encountered and exploited together in the course of part (or all) of their life cycle.

It is considered that the first category of populations is well defined ecologically, for example, among bottom species whose stocks, inhabiting different banks, prove to be isolated from one another by deep trenches and (or) distinctive features of currents ("water type barriers"). The second category of populations, characteristic of pelagic species according to Parrish, is identified with difficulty, as the ranges of separate stocks overlap in the course of a large part of their lives, and the morphological differences between them are not amenable to unequivocal estimation. In connection with this Parrish emphasized the need to search for new, strictly genetically determined characters.

Running ahead a little, I will point out that already by 1969 the possibility of continuing this line of discussion in terms of population genetics had appeared. At a special seminar of the ICES on "Serological and Biochemical Identification of Fish Stocks", held in Dublin in 1969, it was proposed (Møller, 1971), in place of the term "unit stock", to use "population", defined by Dobzhansky (1951) as "a reproductive community of organisms with a common gene pool".

This is a very important circumstance, for only in population genetics has a quantitative theory been created and does it continue to be improved, a theory describing the laws of variability and stability

of populations in time and space and at the same time serving as a working tool of investigation of populations in nature by comparing them with theoretically postulated models. A systematic account of those principles, which were formulated in the works of J. Hardy, Weinberg, S.S. Chetverikov, N.P. Dubinin, D.D. Romashov, S. Wright, J. Haldane and R. Fisher, is given in the monograph of Li (1966), to which we will refer repeatedly in the future. 13

I will emphasize here, however, that to study the genotypical composition of populations one cannot limit oneself to external polygenic features with an unclear mechanism of gene control and with an at times inseparable paratypical component in their expression, and one should study qualitative characters with a simple hereditary basis, which correspond most, in our opinion, to the goals and methods of population genetics. Intraspecies variability of this type is the basis of genetic polymorphism -- the presence in a population of "...two or more well-designated forms capable of appearing in the offspring of a single female and encountered with a frequency high enough to exclude sustaining the rarest of them by repeated mutation" (Ford, 1940, p 493).

Such variability in fishes was investigated for the first time by M. Gordon (1947) on "platy" (Xiphophorus maculatus) living in rivers of Central America and Mexico. In those wild parents of our aquarium fishes there is a whole series of alternative states of one and the same gene (so-called multiple alleles) which are responsible for the synthesis of the pigment melanin, concentrated in special cells -- the melanophores on the tail; eight frequent and five rare types have been detected which differ sharply from one another by the character of the markings (Figure 1). Having

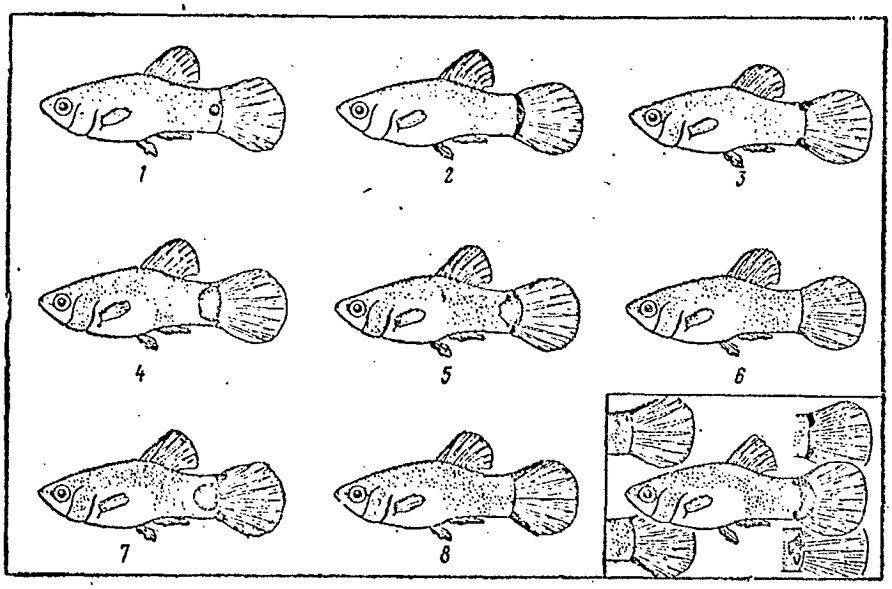

Рис. 1. Наследственный полиморфизм окраски хвоста у пецилий *Xiphophorus maculatus* (самцы), обусловленный серией аллельных генов:
1—8 — различные наследственные морфы пецилий. В правом нижнем углу — редкие типы (по Gordon, 1947; с изменением).

Figure 1. Hereditary polymorphism of tail coloration in the "platy" Xiphophorus maculatus (males), caused by a series of allele genes: 1 - 8: different hereditary morphs of "platy". In the right lower corner are rare types (acc. to Gorden, 1947, with modification).

demonstrated the hereditary nature of the polymorphism in the crossings of different "platy" with one another, M. Gordon then investigated more than 5000 fishes in four large rivers flowing into the Gulf of Mexico and showed that characteristic of each river is "its own" population which differs from the rest both in the frequency of encounter of general genes and in particular genes characteristic of it alone. It also was established that, besides large populations of "platy", small local populations form which dwell in brooks, tributaries or temporary lakes pinched from the main riverbed in the period of drought. The differences between small populations are less significant than between the large, but are reliable.

Gordon allowed for this circumstance and, when he created a "key" for the determination of large populations, pointed out that "a key of this type works only if samples taken at different points of the river system have been taken into account". 14

Since the spots did not lose their color in Formalin, the author was able to compare his own collections with those made during 70 years and show constancy of the frequencies of four out of seven genes responsible for the character of the markings on the tail. On the basis of these data M. Gordon established that "platy" imported into Europe in 1909-1911, which became a favorite of aquarists, derived from Honduran populations living in the Coatzacoalcos River. They could have been caught at one time only near the port of Puerto Mexico, since such types (1, 3, 5 and 7 on Figure 1) are no longer encountered at any other places.

Thus for the first time in ichthyological "race" investigations differentiation of isolated populations on the basis of gene frequency was demonstrated, that is, as this is usually done in works on population genetics. Later, in an example with stability of polymorphism, reproducibility was established in generations of populations in the absence of any sort of substantial genetic exchange between them. And, finally, the 15 dismemberment of large populations into second-order isolates -- local, at times temporary populations, was shown.

Such a direct genetic approach, based on the rapid and precise comparison of large samples, permits most completely analyzing the population structure of a species, but due to the striking external uniformity of many fishes (cod, the Pacific saury, and salmons) it has not been possible to carry out such a study. (Therefore the investigations of "platy"

and two or three other non-industrial species (Kosswig, 1964, 1966; Kirpichnikov, 1969) for a long time remained the only ones of their kind.

Only at the end of the 1950's, when the ideas and methods of immunological and biochemical genetics began to penetrate ichthyology, were the possibilities opened of population genetic investigations of any species on the basis of their variability with respect to blood groups and different proteins.

Chapter II. The Objects of Investigation

Striving to obtain sufficiently complete information about the population genetic organization of the species, we selected as objects of investigation representatives of bottom (redfish), pelagic (anchovy) and diadromous (salmons) fishes.

Our selection was also determined to a considerable degree by the fact that the most important biological characteristics of those species have been studied rather completely, including distinctive features of their internal subdivision into isolated communities, separated from each other by various natural boundaries and features of reproductive behavior. The unity of the range and the integrity of the morophological, biological and ecological properties of such stocks permit regarding them as historically formed groups of individuals amenable to the same study according to the principles of population genetics as they usually are investigated by ecologists.

Figure 2 gives a general concept of the regions of the work.

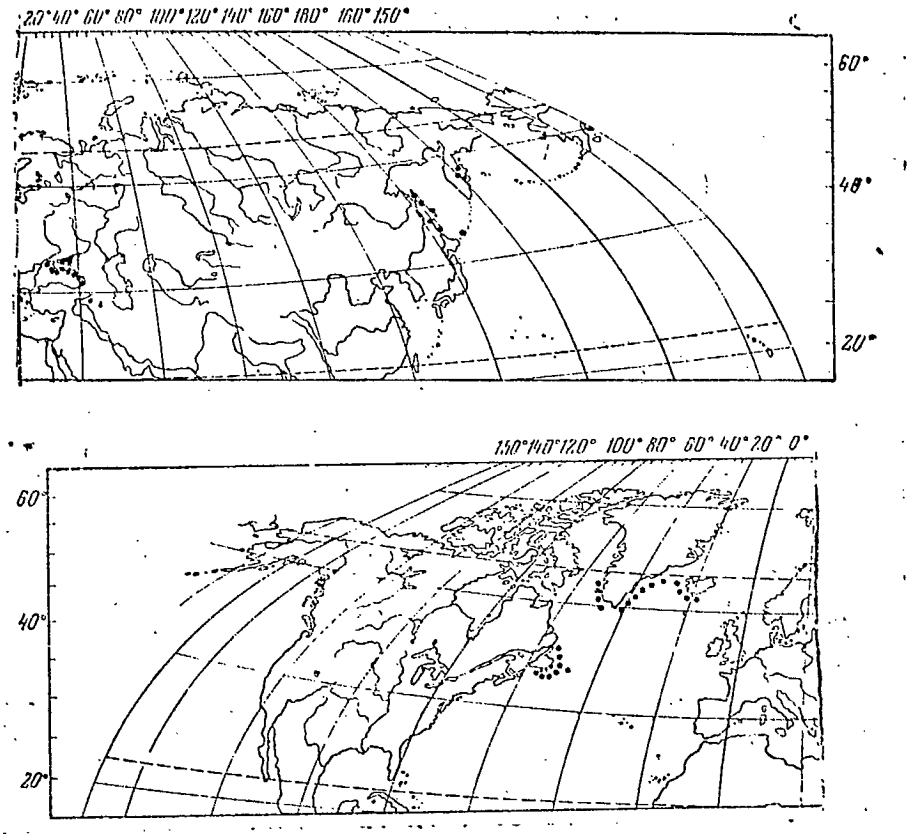

Figure 2. Regions of work on fish population genetics.

The Systematics and Biology of the Azov and Black Sea Races of the Anchovy 16

Systematics and phylogeny. The family of anchovies (Engraulidae) embraces 9 genera with 40 species, dwelling in the waters of the Atlantic and Pacific oceans. The anchovy is widely distributed in seas of the temperate zone, reaching 62° N. Lat. in the north with the Gulf Stream, and, in the south, to the west coast of Africa and in a limited quantity to the Canary Islands. At least four geographical races (subspecies) of the anchovy dwell in that extensive area. Their characteristics are known thanks to the work of Fage (1920), A.I. Aleksandrov (1927), I.I. Puzanov (1936), Demir (1968), and other authors.

Races of the anchovy differ from one another in their morphological characters and geographical distribution. The times of reproduction actually coincide, but this does not destroy reproductive isolation because, it is thought, each of the subspecies is strictly localized geographically.

The question of the phylogenetic relations of races of the anchovy also has been examined. According to Fage, the evolution of anchovies proceeded from ancestors which had emigrated from the tropics. There was an increase of the number of vertebrae and rays in the dorsal fin, and the latter also moved closer to the head. Of contemporary representatives of Engraulidae the largest number of primitive characters is inherent in tropical species, particularly the genus Stolephorus, which differs from the genus Engraulis in its smaller body dimensions, a smaller number of vertebrae, the position of the dorsal fin back of the center of the body, remains of serration on the belly and the presence of a narrow silver stripe on the sides of the body. 17

Referring to the description of the fossil E. evolans Agassiz, Fage considers the Mediterranean anchovy to be a tropical relict race and dates its appearance in the Mediterranean Sea to the Eocene-Miocene. Fage derives the group of anchovies of the eastern Mediterranean (including the Black Sea anchovy) from the group of the western Mediterranean, starting in the Quaternary, when Egenda sank and the Dardanelles formed.

The scheme of evolution of the anchovies proposed by A.I. Aleksandrov (1927) appears as follows. The anchovy E. evolans Agassiz, which penetrated the Mediterranean Sea of the Eocene from the ocean, at the same time or at the start of the Miocene settled the South Russian Sea and,

in particular, its southeastern part. This was an extensive water body, warm and salty, with similar external conditions in its western and eastern parts. In the Sarmatian time the eastern part of the water body proved to be cut off from the ocean for a long time and experienced a number of contractions and freshening. The western part of the Mediterranean Sea, except for a short period, communicated with the ocean the whole time. Thus formed two groups of anchovies which had evolved in dissimilar situations: the evolution of the eastern group proceeded at a slower rate than that of the western, and this also determined the preservation of a more primitive appearance by the Azov anchovy.

A.I. Aleksandrov concludes that since the Upper Miocene there have 18
been two centers of evolution of the species Engraulis encrasicholus: in the western part of the Mediterranean Sea and in the eastern part of the old Pontic basin. These isolated groups of anchovy also were the starting groups for the remaining European subspecies. The Atlantic anchovy derived from the Western Mediterranean group, and the Black Sea from the Eastern.

I.I. Puzanov (1936), accepting the general scheme of evolution of the anchovies presented by A.I. Aleksandrov, did not agree with him in relation to the phylogenetic connections of the Azov and Black Sea forms. He assumes that at the end of the glacial period, when the connection of the Pontic basin with the Mediterranean Sea was restored, that is, the contemporary Black Sea formed, the semi-freshwater organisms which had lived in it, including the anchovy, under the inrush of salty Mediterranean waters pouring through the Bosporus, were driven back into the freshened sections of the Black Sea basin -- into estuaries and into the Sea of Azov. Among the Mediterranean newcomers which settled the Black Sea was

the anchovy of the Mediterranean race. Under the influence of the freshened water, low temperature and, possibly, partial mixing with the Azov race, it formed the contemporary Black Sea race.

Thus the question of the phylogenetic relations of the Azov and Black Sea races of the anchovy, it seems to us, remains open. At the same time their taxonomic apartness gives rise to doubts in no one and subspecies independence is accepted by all ichthyologists. Their ecology has also been studied in sufficient detail. We will examine here the main data having a direct relation to the understanding of further material.

Ecological features of the Azov and Black Sea races of the anchovy.

The anchovy -- a pelagic fish living at a temperature of 6-29° C and a salinity of 5-41.5% -- belongs among fishes with a short life cycle. Its life is not more than three or four years long (Maiorova and Chugunova, 1954; Kornilova, 1960). The principal part of the stock of the Azov anchovy (60%) consists of yearlings (Kornilova, 1960; Taranenko, 1966). The anchovy matures and reproduces for the first time in the second summer of life; its spawning is very long and often continues for four or five summer months. Fertilization of the eggs is external, immediately after spawning. The incubation period lasts not more than three days. Hatched larvae are encountered in the same place in which the eggs were laid, and then are scattered over the area. The short length of life and early maturing lead to rapid renewal of the stock of anchovies, practically every other year. 19

A general characterization of the anchovy is given here. In the ecology of the Azov and Black Sea races, however, there are many fundamental differences.

N.V. Lebedev (1939, 1940) distinguished six periods in the life cycle of the Azov race: wintering, spring migration, pre-spawning feeding and growth, spawning, pre-migration feeding and growth and wintering migration.

After wintering in the Black Sea the Azov anchovy completes spring spawning and feeding migrations to the Sea of Azov. A general scheme of the migrations is presented in Figure 3. Moving away from its wintering places, the anchovy begins to feed intensively while still in the Black Sea, on the way to and in the Sea of Azov itself. On the way to the Sea of Azov the sex glands go from stage II of maturity into stage III. The spawning of the anchovy occurs on the entire area of the Sea of Azov except the very fresh Gulf of Taganrog. Immediately after spawning the pre-migration feeding and growth starts, during the time of which the anchovy remains dispersed, not forming dense accumulations. Upon conclusion of the feeding and growth, usually in September, the anchovy ceases feeding, assembles into large concentrations and starts advancing toward Kerch' 20
Strait.

Upon emerging from Kerch' Strait the anchovy accumulates in the northern part of the Black Sea near the strait and remains there for some time. The further direction of movement toward the shores of the Caucasus or the Crimea is determined by the predominance of one of the currents, the Black Sea or the Azov. The Black Sea current, warmer and constant, is directed toward the shores of the Caucasus; the Azov -- colder, superficial and less salty -- toward the Crimean. The entry of a fish into a given current depends on the time of its emergence from the Kerch' Strait, the distance from the shores, the depth of submergence and the spatial

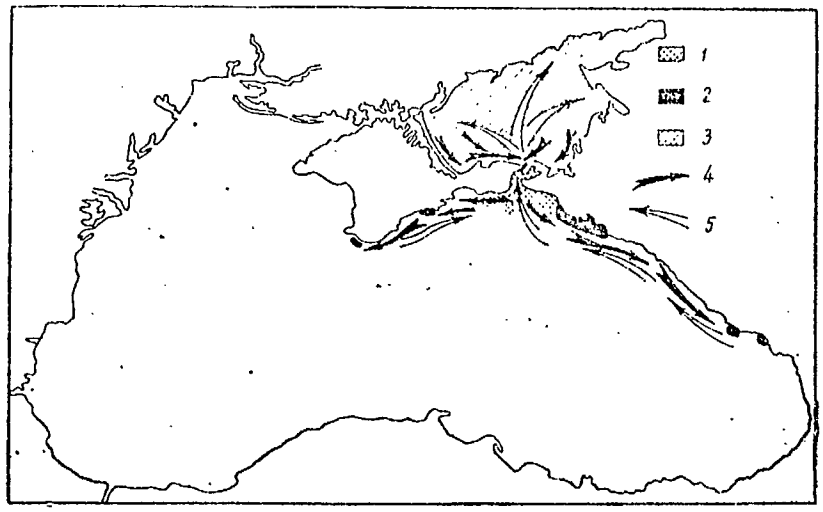

Рис. 3. Распространение и схема миграций азовского анчоуса (по Майоровой и Чугуновой, 1954):
1 — осенние скопления; *2* — зимние скопления; *3* — летнее распределение; *4* — пути осенних миграций; *5* — пути весенних миграций.

Figure 3. Distribution and schematic diagram of migrations of the Azov anchovy (acc. to Maiorova and Chugunova, 1954): 1 - autumn accumulations; 2 - winter accumulations; 3 - summer distribution; 4 - paths of autumn migrations; 5 - paths of spring migrations.

position of a given current. Therefore in different years the quantity of anchovies wintering off the coasts of the Caucasus and the Crimea is not the same. Most often the anchovy is directed toward the coast of the Caucasus, as the autumn cooling forces the fishes to submerge into the deep layers of the water where the Black Sea current runs, the temperature of which is 1 or 2° higher than that of the Azov. In some years the anchovy winters off the Crimean coast or the coasts of the Caucasus and the Crimea. Sometimes, after a long delay off the Crimean coasts the anchovy moves toward the coast of the Caucasus for wintering. Thus the wintering places of the Azov anchovy in the Black Sea do not remain strictly constant: in warmer years they are further north, and in colder years further south (to Sukhumi).

In the autumn and at the beginning of winter (November and December) the fishes complete daily vertical migrations, which usually cease towards January. At that time the anchovy descends deeper (in cold winters -- into so-called pits with a depth of up to 150 meters), where they winter without feeding. With warming (in March) it rises from the depths, but still remains for a long time at the wintering places. In April the anchovy approaches the coasts and, feeding intensively, migrates toward the Kerch' Strait.

Besides the above features of distribution and migrations, biological heterogeneity of accumulations of the Azov race of anchovy has been discovered in the periods of spawning and feeding and growth in the Sea of Azov, a fact of fundamental importance in further analysis. Investigating in detail the biological characters of the Azov anchovy, N.V. Lebedev (1946) pointed out that different groups of fishes do not complete the pre-migration feeding and growth in the Sea of Azov and start their winter migration simultaneously. Moreover, it has turned out that the migrating anchovy differs considerably in its biological state from the fishes remaining in the Sea of Azov. Thus, whereas in the migrating anchovy Fulton's condition factor is close to unity and the percentage of hemoglobin content in the blood is high, in the non-migrating the condition is smaller than unity and the hemoglobin content in the blood is much lower. Whereas the former does not feed and is distributed in the area of the sea before the strait in the form of a concentration, the latter at the same time feeds intensively and is dispersed.

As a result of analysis of the distribution of the anchovy it has been made clear that its biological state is considerably variegated at the same time and under conditions of uniformity of the environment over the entire range. In addition, it has turned out that the anchovy is not distributed disorderedly in the Sea of Azov, but in individual, clearly different groups. It also has been established that besides a similar biological state, individuals of one group are also similar with respect to linear dimensions (their variation is similar). Reflecting the rate of growth of individuals, the linear dimensions also are characters of physiological similarity.

In studying the internal structure of the discovered groups it turned out that the fishes in them are encountered in both dispersed and highly concentrated states. The scattering of groups can from day to day increase at one time and decrease at another, and the area occupied by the group also changes: the smaller the concentration of fishes in the group, the larger the area it occupies. However, even in the state of maximum dispersion a group preserves its spatial individuality and can be contoured and mapped side by side with other groups.

In giving a definition to the discovered communities, N.V. Lebedev compared them with schools, shoals, age-groups, stocks and races and concluded that they are not identical to any of those groups. Actually, the concept of shoal and school is always connected with the presence of a dense mass of fishes. Shoals and schools cease to be such if the individuals comprising them are scattered one by one. However, the discovered groups are characterized not by the size of the concentration of fishes but by their biological state; the fishes in them can be dispersed or in the form of

of schools and shoals. They also are not identical to stocks or races, as they are not represented by all age groups. At the same time these population units cannot be called age units (with the exception of groups of immature fishes) as they consist of fishes of different age, even if there is a predominance of one of them. Thus the author could not call the groups he detected by one of the names existing in ichthyology and, since they 22
differed from all known intraspecies communities primarily by physiological homogeneity, he gave them the name of elementary populations.

The annual life cycle of the Black Sea anchovy was subdivided by A.N. Maiorova and N.I. Chugunova (1954) into two periods, the summer and the winter. In the warm time of year (from May to September) the anchovy is widely distributed in the Black Sea, multiplying, feeding and growing, but in winter it leads a passive form of life. A general scheme of the distribution and migrations of the Black Sea anchovy is presented on Figure 4. Within the Black Sea race of anchovy the authors distinguished two stocks, the eastern and western*, with migration paths which do not coincide. The anchovy of the eastern stock, wintering in the Poti-Batumi region, migrates to the north along the coasts of the Caucasus and spawns near the Crimea and Kerch Strait The migrations of the anchovy of the western stock, which winters off the southern coast of the Crimea, are limited, as a rule, to the regions of the Crimean peninsula and the northwestern part of the Black Sea. The main part of anchovies of the western

*Anchovies of the eastern stock differ from the western in earlier times of the onset and conclusion of spawning; they are somewhat smaller than the western; they have a slower rate of growth, and this is expressed especially clearly in the first year of life.

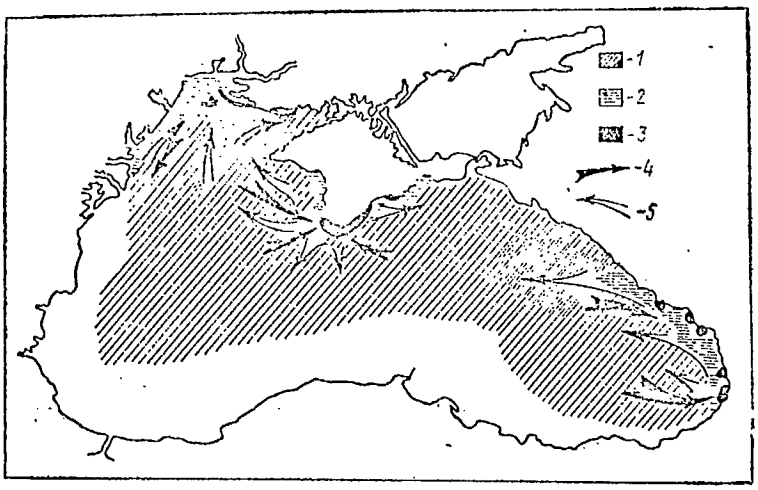

Рис. 4. Распространение и схема миграций черноморского анчоуса (по Майоровой и Чугуновой, 1954):
1 — летнее распределение; *2* — весенние и летние скопления. Позиции *3—5* те же, что и на рис. 3.

Figure 4. Distribution and schematic diagram of migrations of the Black Sea anchovy (acc. to Maiorova and Chugunova, 1954): 1 - summer distribution; 2 - spring and summer accumulations. Positions 3-5 are the same as in Figure 3.

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stock enters at that time the very shallow northwestern region of the sea, well-warmed and rich in plankton, where it spawns, and then it fattens in the region from Dnestrovskaya bank to Karkinit Bay. 23

The scheme of migrations of the Black Sea anchovy presented here is in fact, evidently, more complex. There is information that many Black Sea anchovies winter along the coasts of Bulgaria and especially of Turkey in the region of the Sinop peninsula. Completely from the Bulgarian coast and partially also from the Anatolian coast, the anchovy leaves in the spring for the northwestern region of the sea to reproduce, feed and grow. Another part of the accumulations which have wintered along the coast of Turkey migrates towards the coast of the Caucasus, and a third toward the Bosporus and the Sea of Marmara. In the autumn the anchovy returns (Puzanov,

1936; Danilevskii, 1960). According to the data of I.I. Puzanov (1936), the anchovy, wintering at Sinop and in the spring migrating along the western coast of the Black Sea, first arrives at the Crimea and then turns into both the northwestern part of the sea and the eastern part, toward Kerch' Strait. It also has been noted that the Black Sea anchovy of the eastern and western stocks does not always winter along the coasts of the Caucasus and the Crimea, but often all go out toward the Anatolian coast. Demir (1968) cites data on the spring migration into the Black Sea of anchovies which winter in the Sea of Marmara. In addition, there are indications that a considerable portion of the Black Sea race, especially the yearlings, enter the Sea of Azov to spawn, feed and grow (Danilevskii, 1958, 1960, 1964; Taranenko, 1966). There also is information about the entry of the Azov anchovy into the northwestern part of the Black Sea. At one time A.I. Aleksandrov (1927) pointed out that the shoals which are caught in February-April and October-November at Sevastopol' and Balaklava under the name of the "Azov anchovy" should be considered shoals of Black Sea yearlings, and not of the Azov anchovy, as at that age the two forms are difficult to distinguish on the basis of coloration and dimensions. However, later there again appeared statements about the migration of the portion of the Azov anchovy which winters along the Crimean coast, not toward Kerch' Strait, but into the northwest corner of the Black Sea, into which the Azov dolphins, which feed on them, move after them (Vinogradov, 1956).

The examined materials show that by now the ecological individuality of the Azov and Black Sea races of the anchovy has been argued in sufficient detail, but the central question of their genetic interrelations in the reproductive period, in essence, remains open. Especially the genetics of the so-called elementary populations has not been investigated.

The Systematics and Biology of the Redfish and Its Local Stocks 24

Redfishes of the genus Sebastes (family Scorpaenidae) are typical bottom species which dwell in extensive areas of the North Atlantic -- from the Barents Sea in the east to the coast of North America in the west. For a long time two species of redfishes were distinguished systematically, the small Sebastes viviparus Krøyer, 1845 and the large S. marinus Linne, 1758. In more detailed investigations it was discovered that large redfishes also can be subdivided into two forms (Lundbeck, 1940, according to Kotthaus, 1950); German fishermen have long distinguished them, calling them "goldbarsch" (golden redfish) and "schnabelbarsch" (deepwater redfish) (Kotthaus, 1950).

V.I. Travin (1951) investigated the two forms of redfish from the Barents Sea and concluded that they differ so much that the deepwater redfish can be separated into the independent species Sebastes mentella Travin sp. nov. Thus the deepwater redfish is characterized by considerable development of the "beak" -- a bony appendix on the lower jaw, the size of the eyes, larger dimensions of the head, and a higher and thicker body. Although the two forms are sympatric, their range is separate in depth: the golden redfish dwells in a zone of relatively small depths (to 300 meters), and the deepwater redfish to 700 meters, and possibly even deeper.

Similar evidence of differentiation has also been obtained for redfishes from the regions of Greenland, Labrador and Newfoundland (Borodatov and Travin, 1960; Travin and Pechenik, 1962). A recent morphological investigation of V.V. Barsukov (1968) testifies in favor of the species independence of the deepwater redfish. The genetic distinctiveness of the

two forms of the redfish has been also confirmed by some serological (O'Rourke, 1961), biochemical (Schaeffer, 1961) and parasitological (Sindermann, 1961a; Yanulov, 1962a) data.

Nevertheless the species independence of the deepwater redfish still gives rise to doubts in a number of authors, and this was very clearly formulated by A.P. Andriyashev (1954), who diagnosed it as the subspecies Sebastes marinus infraspecies mentella Travin. Some authors also prefer to speak of different subspecies or even "types", that is, as was done at the session of the International Commission for the Northwest Atlantic Fisheries (ICNAF), held in Biarritz in March 1959. The basis of that was above all the fact that in a number of regions of the North Atlantic, with the exception of Flemish Cap bank and the southern 25
slope of the Newfoundland Grand Bank, redfishes are encountered which on the basis of morphological characters occupy an intermediate position between the golden and deepwater redfishes ("intermediate type", according to Kotthaus, 1961b; Baranenkova, 1967; Kotthaus and Krefft, 1957; Travin and Pechenik, 1962; Borodatov and Travin, 1960). In addition, at great depths very large redfishes are encountered, with a length of 55-85 cm, which in external appearance remind one of golden redfish and have received the name of giants (Kotthaus, 1961b).

We have dwelt in such detail on disputed questions of the problem of taxonomic interrelations of the golden and deepwater redfish in order to show that our own investigations of the population structure of those fishes depended on unclear matters of that sort -- population genetics is in essence limited by the framework of species. Therefore, before the possibility appeared of giving the present section of the work a title

emphasizing the species independence of the deepwater redfish, we conducted taxonomic investigations.

The principal conclusions from that work can be summed up as follows.

1. The golden and deepwater redfishes differ in frequencies of the electrophoretic variants in the loci of albumin (Altukhov and Nefyodov, 1968) and haptoglobin (Nefyodov, 1971) of serum, that is, belong to genetically different populations.

2. In investigations of the variability of oligogenic and polygenic characters taxonomically important for fishes -- electrophoregrams of hemoglobin (Altukhov, 1969b) and the thermal tolerance of isolated cells (Ushakov, 1958, 1959a and b; Ushakov, 1964; Altukhov and Rat'kin, 1968) it was discovered that the golden and deepwater redfishes differ from each other as independent species within the limits of the genus (Altukhov et al., 1967, 1968a; Payusova and Nefedov, 1968).

3. Giant and intermediate forms of the redfish are characterized by a number of characters and properties which permit drawing a conclusion about their hybrid nature (Altukhov, 1970). The females of giants prove to be completely sterile, and this is very clearly demonstrated in immunochemical investigations of their ovovitellins (Altukhov et al., 1968b), and the males reveal only partial fertility (Zakharov, 1962; Altukhov et al., 1967) -- a picture very common for interspecies hybrids F_1 with female heterogamety. This testifies to the presence, between the golden and deepwater redfishes, of substantive reproductive isolation which evidently is disrupted only locally. As a result of this also appear the

so-called intermediate forms which in relation to variability of the character of thermal tolerance of the cells behave as typical backcrosses (Altukhov et al., 1967). 26

According to our observations, and also the literature data (Travin and Pechenik, 1962), intermediate redfishes are practically absent on the Flemish Cap bank and on the southern slopes of the Newfoundland Grand Bank. We did not encounter them even on its northeastern slope, at least south of 50° N. Lat. Thus, in those regions of the Northwest Atlantic there is practically no interspecies introgression of genes, and accumulations of redfish, the population structure of which has been investigated, are represented by only one species -- the deepwater redfish*.

Those accumulations, localized mainly in the ICNAF zones 3L, 3M, 3N, 3O and 3P, according to the data of morphological-biological and parasitological investigations of K.P. Yanulov (1962a and b), are subdivided into three local stocks (Figure 5), the isolation of which is assured by the hydrological conditions of the region, which has been studied in detail

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* When the present work was completed, an investigation of V.V. Barsukov and G.P. Zakharov was published (1972). They think that in this region an additional species of redfish lives, Sebastes fasciatus, which in their opinion, is a twin species in relation to S. mentella. This form, identical to the so-called rosefish of Canadian authors, has also been encountered by us, but we have not always separated it from S. mentella.

The conclusion of V.V. Barsukov and G.P. Zakharov on a number of facts and considerations appears questionable, but we still have re-examined our material and once more satisfied ourselves that almost all of it is represented by individuals of S. mentella. Only in 6 out of 72 samples investigated immunogenetically was rosefish encountered in the form of an admixture, and this could not have a substantial influence on the results of the analysis.

by Soviet and foreign authors (Buzdalin and Elizarov, 1962; Travin and Pechenik, 1962; see also Yanulov, 1962a). A briet characterization of the stocks according to K.P. Yanulov is given below.

1. The first stock includes populations dwelling in zones 2I, 3K and 3L. The principal isolating factor is the warm component of the Labrador Current, for the larvae drift from zones 2I and 3K along the outer edge of the Newfoundland shelf to the south, then along the northeastern slope of the Grand Bank almost to the east, and then, with the turn of the current, north into zones 2I and 3K.

2. The stock of the Flemish Cap bank (zone 3M) is the most isolated, as the larvae are drawn into the drift around the bank by a weak circular current, and the bank itself is separated from the Newfoundland region by oceanic depths.

3. The third stock dwells in the southern part of the Newfoundland region and on the banks of Nova Scotia and New England. The spread of the stock is limited by the Gulf Stream.

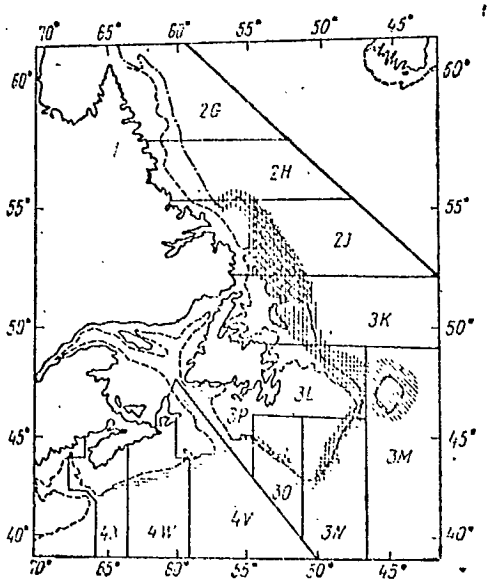

Рис. 5. Ареалы локальных стад окуня-клювача в Ньюфаундлендском районе Северо-Западной Атлантики (по Янулову, 1962а). Объяснения в тексте.

Figure 5. Ranges of local stocks of the deepwater redfish in the Newfoundland region of the Northwestern Atlantic (acc. to Yanulov, 1962a). Explanations are in the text.

Although on the figure borrowed by us there is no explanation of 27
the legend, the different hatching(shading)(see Figure 5) indicates heterogeneity of the stocks differentiated by K.P. Yanulov on the basis of morphological-biological and parasitological characters. In the text of the article such a division is argued only by mention of the dwelling of the following populations here: 1) the population of zones 2I and 3K; 2) the population of zone 3L; 3) the population localized in zone 3N; 4) the population of zone 30 and, finally, 5) the population of the Flemish Cap bank.

These populations are rather "felt" than studied by the author. In fact, the population of the Flemish Cap bank is equated with a stock, but the latter according to the definition of K.P. Yanulov (see page 13) represents a combination of populations. But the character of the hatching(shading)still indicates the presence in the Newfoundland region of a chain of populations smaller than a stock and changing into one another (or localized in a single place but at different depths); in such case it is not clear where the boundary should be drawn between stocks localized on the Newfoundland Grand Bank. Evidently, therefore the status of redfishes caught in zone 3N is in no way qualified, and only the mixed character of those accumulations is stressed. On the basis of the number of vertebrae they prove to be close to redfish of the Flemish Cap bank, and of parasitic marks (infestation by the copepod Shyrion lumpi) to the redfish of Southern Labrador. Their obvious similarity to redfishes from zone 30 is observed on the basis of some other characters.

The impression is created that, in general, there are no special grounds for distinguishing the two isolated stocks in that region, and it is necessary to speak of the existence of a single stock, represented by a

chain of populations which interchange with one another to some degree. 28
At the same time the advisability of separating the Flemish Cap redfish accumulations into an independent stock seems to be substantiated -- K.P. Yanulov has gathered and processed an enormous amount of material testifying to the sharp apartness of those fishes from all the accumulations of redfish localized on the Grand Bank.

Important biological features of redfish are the facts that they are viviparous, grow slowly and reach sexual maturity late -- in the 7-12th year of life at a length of about 30-40 cm.

Biological Characteristics of Pacific Salmons (the genus Onchorhynchus)

Salmons in general and Pacific salmons in particular belong to species of fishes best studied in all respects. Among the biological characteristics of Pacific salmons (according to the data of Neave, 1958; Foerster, 1968; Levanidov, 1969; Krogius et al., 1970; Konovalov, 1971; and Brannon, 1972) it is necessary to emphasize the following.

1. All Pacific species of the genus Onchorhynchus, which are distributed over an enormous range (Figure 6), are monocyclic. They reproduce once and die soon after spawning.

2. In their life cycle they combine sea and freshwater periods, changing the medium of habitation with ease. The sockeye Oncorhynchus nerka Walb., the masu O. masu Brevoort and, probably, the coho O. kisutsch W. have freshwater forms from the life of which the sea period has been completely excluded. Those populations, which have been cut off from the sea by one or another isolating factor, are smaller but have not lost their 29
reproductive capacity. In diadromous populations of these and other

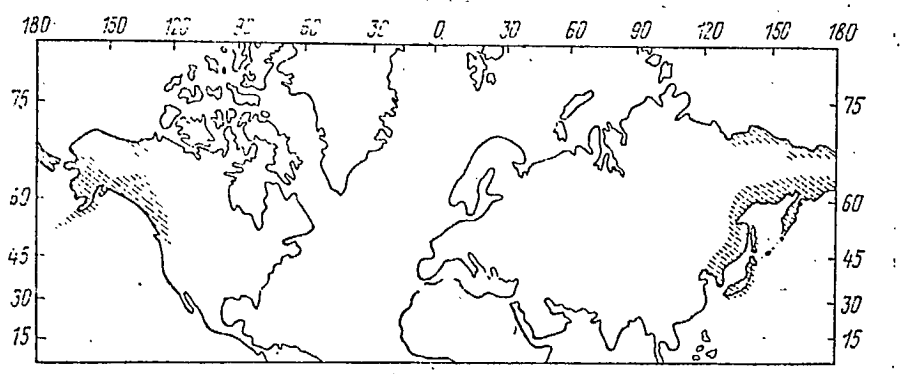

Рис. 6. Ареал тихоокеанских лососей р. *Oncorhynchus* (по Vladykov, 1963).

Figure 6. Range of Pacific salmons of the genus Oncorhynchus (acc. to Vladykov, 1963).

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species, the immature fishes born in redds and visiting in fresh water for from several weeks (keta Oncorhynchus keta Walb. and pink salmon O. gorbusha Walb.) to a year or more (sockeye, coho, etc.), then migrate to the sea.

3. Completing migrations of enormous extent from the spawning rivers to the sea and back and ascending the rivers for tens, hundreds and even thousands of kilometers, the spawning stocks confine themselves strictly to the same spawning water body and even individual spawning grounds.

A "homing instinct" of that kind creates obvious prerequisites for intraspecies divergence corresponding to the geographic features of the spawning area. This isolation, intensified still more by complex reproductive behavior, contributes to the formation in individual species, such as the sockeye, for example, of an innumerable quantity of reproductive communities scattered over an enormous species range. Among those populations there also are completely isolated ones.

4. Such surprising possibilities of adaptation of salmons to a broad spectrum of environmental factors in the presence of certain death of the brood stock which have spawned -- a biological puzzle unsolved to the present time -- find an unexpected parallel with their origin. Cyto-
genetic and genetic-biochemical investigations of recent years have shown 30
(in comparison with other families of the order Clupeiformes) tetraploidy of Salmonidae (Ohno, 1970a, 1970b; Ohno et al., 1968), and there are weighty bases for considering them amphidiploids* (Altukhov et al., 1972; Massaro and Markert, 1968; Wilkins, 1970). Evidently, the reason for the post-spawning death of some species will be in the final account understood, precisely with consideration of that circumstance.

A strongly expressed homing instinct was a prerequisite for maintenance and even increase of the numbers of stocks of salmons through the incubation of artificially fertilized eggs in hatcheries.

Among Pacific species the most suitable object for these purposes is the keta. Its stocks first began to be maintained by the Japanese on Honshu and Hokkaido in the second half of the 19th century.

For purposes of supplementing this brief characterization of Pacific salmons it is necessary to add concrete information about the objects of our own investigations.

Since we strove especially to have data of population genetics taken into consideration in fish-breeding activity, we will describe briefly the stocks of keta of the Kalininka and Naiba rivers on Sakhalin, maintained

*For all the polymorphous genes studied by us we have not once observed tetrasomy, which is inevitable for an autoploid in the process of diploidization.

exclusively (the former, always; the latter, for several recent year-classes) through the activity of fish hatcheries, and also the stock of sockeye of Lake Azabach'e, where there is a natural self-maintaining population.

Figure 7 shows the places where population genetics work has been done on salmons.

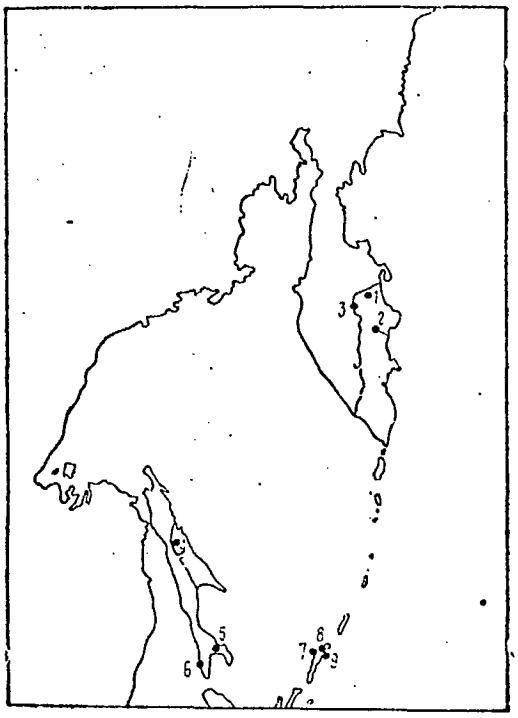


Рис. 7. Районы популяционно-генетических работ, проводившихся на тихоокеанских лососях:

1 — оз. Азабачье; *2* — оз. Кроноцкое; *3* — оз. Ушковское; *4* — р. Тымь; *5* — р. Найба; *6* — р. Калининка; *7—9* — реки о. Итуруп.

Figure 7. Regions of population genetics work on Pacific salmons: 1 - Lake Azabach'e; 2 - Lake Kronotskoe; 3 - Lake Ushkovskoe; 4 - Tym' River; 5 - Naiba River; 6 - Kalininka River; 7 - 9 - rivers of Iturup island

Basic Information about the Kalininka and Naiba Stocks of Keta

The Naiba stock of keta, which goes to spawn in the Bol'shaya River, a tributary of the Naiba, is maintained by two fish hatcheries -- the Bereznyakovsk, which went into operation in 1924, and the Sokolovsk, constructed in 1939. The sexual products are collected in a trap installed 80 kilometers from the Naiba mouth. The run of the brood stock is extensive: usually the first spawners of the keta appear in the trap on 15 August, the period of the mass run is from 15 September to 31 November, and the spawning migration ends in December or January.

The maximum number of the keta (from 1960 to 1971) of 659,000 was noted in 1968, and a sharp drop in the size of the spawning runs has 31
been observed in recent years. Thus, for example, 230,000 adult fishes (breed stock) were counted in 1970 and only 57,000 in 1971. Only in 1966 was the return just as low, but from 31 million released juveniles, whereas in 1967 and 1968, which assured the 1970 and 1971 returns, 89 and 46 million juveniles respectively were released.

Although the data on the number of adult fishes which returned to the Naiba can include some errors, still the differentiation of separate generations on the basis of the character "many fish -- few fish" creates no difficulty, and the drop of numbers in recent years is unquestionable. In accordance with that, when there is an insufficiency of "its own" fish the eggs are gathered from the spawners of other stocks and, above all, at the Kalininka hatchery. Thus, 65 million "alien" juveniles were released in 1966, 25 million in 1967, and 102 million in 1970.

On the other hand, in years of high numbers, after the production plans for the collection of eggs by the Sokolovsk and Bereznyakovsk hatcheries

have been fulfilled, eggs of the Naiba keta have been exported by air to the Amur fish hatchery, as in 1967-1969, for example, and then the rest of the adult fishes were taken commercially.

Among the possible reasons for reduction of the numbers of the stock, three can be named: overfishing of adult fishes in the sea, the influence of elemental factors, and imperfection of the biotechnique (for example, poor feeding of juveniles). It is not always easy to substantiate the last two statements, as the return of different generations proves to be different when the biotechnique is unchanged and the environment is relatively the same. As for the first reason, it gives rise to no doubts.

Substantial importance also has been acquired by analysis of the biology of the population itself in the period most critical for its reproduction.

The situation with the stock of keta going to the Kalininka to spawn -- a small river of the west coast of Sakhalin, about four kilometers long -- is diametrically opposite to that just considered. The Kalininka fish hatchery began to operate in 1951, when the stock numbered 5494, and in 1971 the numbers of that year-class, counted only in the river, amounted to over 240,000 adult fishes. On the whole the productive capacity of the hatchery has risen sharply, and a continuous growth of numbers with a reduction of variations in recent years has been characteristic of the stock (Figuare 8).

The high effectiveness of the activity of the plant finds reflection in a positive rectilinear correlation between the quantity of juveniles released and the size of the corresponding return of adult fishes (Figure 9). 32

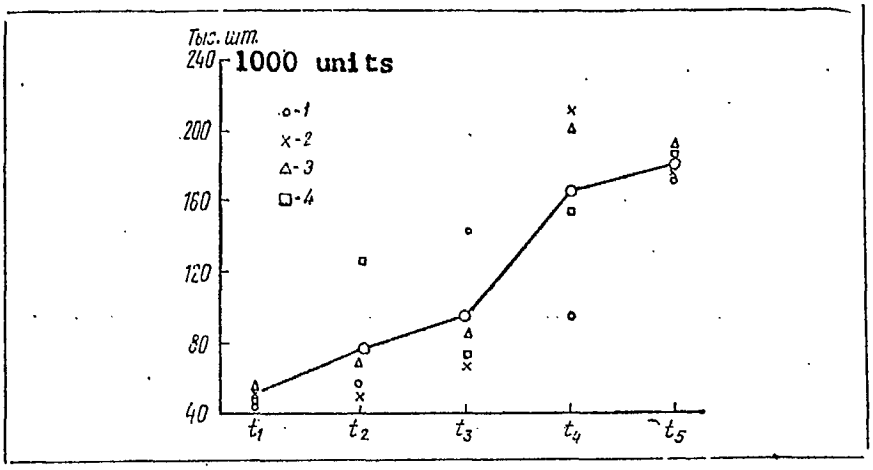


Рис. 8. Рост численности четырех смежных поколений, слагающих возрастную структуру калининского стада кеты:

1 — поколение 1947 г. рождения; *2* — поколение 1948 г. рождения; *3* — поколение 1949 г. рождения; *4* — поколение 1950 г. рождения. По оси абсцисс — последовательные четырехлетние интервалы; по оси ординат — численность производителей, учтенных в реке.

Figure 8. Growth of numbers of four adjacent year-classes forming the age structure of the Kalininka stock of keta: 1 - 1947 year-class; 2 - 1948 year-class; 3 - 1949 year-class; 4 - 1950 year-class. On axis of abscissas (X - axis) -- successive four-year intervals; on axis of ordinates (Y - axis) -- numbers of adult fishes counted in the river.

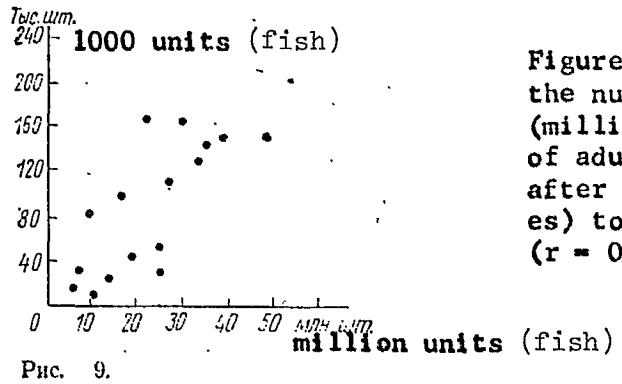


Рис. 9.

Figure 9. Correlation between the number of released juveniles (million fishes) and the number of adult fishes which returned after four years (thousand fishes) to the Kalininka River ($r = 0.799$; $P < 0.001$).

Besides the Kalininka and Naiba populations we investigated the Tym' stock (Northern Sakhalin), and also the stock of Kuril rivers, maintained by the Kuril and Reidovoi fish hatcheries on Iturup Island; a small sample was obtained from the stock of keta maintained by the Ushkovskii fish hatchery on Kamchatka.

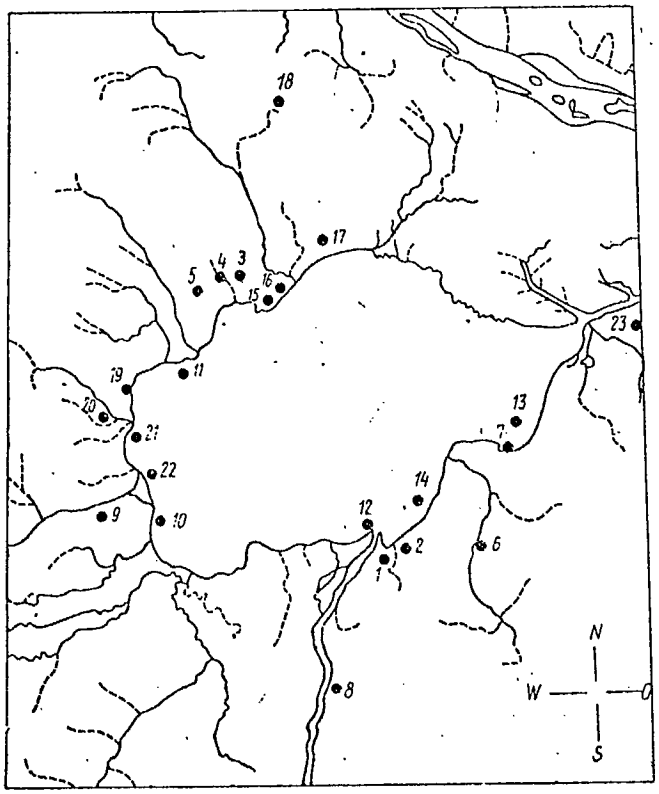
Considerable material regarding variability in the loci of malate dehydrogenase and serum lactate dehydrogenase has been gathered in pink salmon populations of the Lesnaya, Belaya and Lyutoga rivers (Southern Sakhalin), but those data, which fundamentally do not differ from other similar results, are almost not considered at all here. This occurs be- 34
cause, in the maintenance of the stocks of pink salmon the plant method is combined with the escapement of adult fishes to natural spawning areas and, consequently, the effectiveness of the fish-breeding process cannot be estimated. At the same time we cite facts relating to the electrophoretic properties of monomorphous proteins which distinguish that species from other species of Salmonidae. On the same comparative genetic plane investigations have been made of the masu O. masu, a species with low numbers limited in its distribution to the most southern part of the range, and the coho, O. kisutch Walb., a very cold-loving species.

Characteristics of the Azabach'e Stock of Sockeye

Local stocks of sockeye are practically untouched by the fish-breeding process, and the Azabach'e stock (basin of the Kamchatka River) is a typical self-maintaining community whose structure has not yet been destroyed by the marine and river fisheries.

That structure, according to data of ecological and morphological investigations (Konovalov, 1972), is represented by a combination of spawning populations grouped into two races, the "spring" and the "summer". It is thought that the spring race spawns in brooks and small rivers falling into the lake, and the summer in its coastal zone. According to a preliminary estimate about 30 elementary populations can reproduce in Lake Azabach'e; we have investigated genetic variability in 23 of them

(Figure 10). In addition, co-workers of the Laboratory of Population Ecology of the Institute of Marine Biology (S.M. Konovalov et al.) simultaneously gathered material on the ecology and morphology of the populations. With the kind permission of S.M. Konovalov we will make use of some of those data here.



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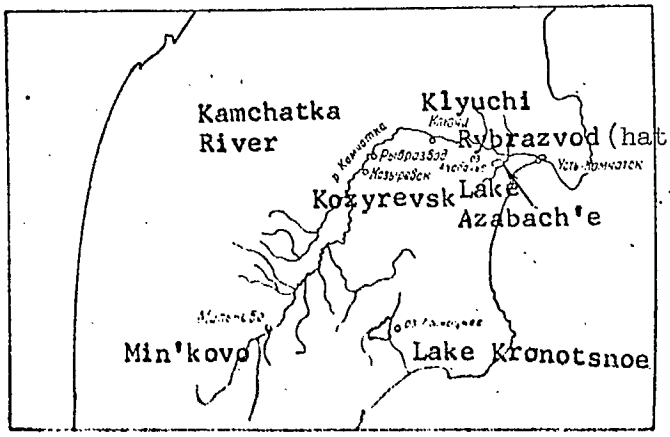

б

Figure 10. a - Spatial localization of spawning populations of sockeye (1-23) in Azabach'e Lake; b - position of the lake (marked with an arrow) in the system of the Kamchatka River

Рис. 10. Пространственная локализация нерестовых популяций нерки (*1—23*) в озере Азабачьем (*а*); местоположение озера (отмечено стрелкой) в системе реки Камчатки (*б*).

Chapter III. Methods of Determination and Principles of Interpretation of Biochemical Hereditary Variability

Used as genetic markers in the present work were blood groups and electrophoretic variants of proteins, determined by the methods of immunological and biochemical genetics respectively.

Polymorphism of such a kind fundametally does not differ in 35
principle at all from that examined using the example of the "platy", but to make our further account clear it is necessary to become acquainted with the general principles of determination of that variability and with the corresponding terminology.

Hereditary Variability of Antigenic Properties of Red Corpuscles

The hereditary variability of the antigenic properties of erythrocytes is observable thanks to immunogenetic methods, based most often on the specific agglutination of cells during interaction of their antigens or factors -- substances of a mucopolysaccharide nature -- with the corresponding antibodies -- agglutinins. If we mix on glass or in a test-tube erythrocytes and serum containing such antibodies, we can observe rapidly forming agglutinates which are clearly visible under a small magnifying glass or microscope or even with the naked eye (Figure 11).

Hemagglutinating antibodies are of both natural and immune origin. In the former case they are encountered in the norm, and in the second are produced by a test animal (recipient) in response to the introduction of erythrocytes of the donor into its bloodstream. The donor and recipient can be representatives of the same species (when one speaks of isoantibodies and isoagglutination) or belong to different species (in that case one speaks of heteroantibodies and heteroagglutination).

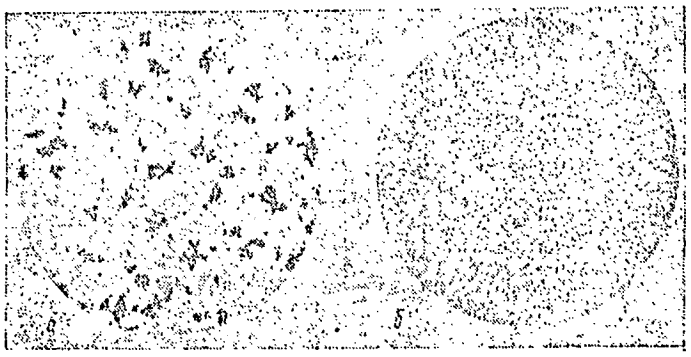

Рис. 11. Агглютинация эритроцитов черноморской ставриды нормальной сывороткой человека:
а — положительная реакция; *б* — отрицательная. Малое увеличение микроскопа (об. ×8 ок. ×10) (по Алтухову, Апекину и Лиманскому, 1964).

Figure 11. Agglutination of erythrocytes of Black Sea scad by normal human serum: a - positive reaction; b - negative. Small magnification of the microscope (obj. 8X, ocul. 10X (acc. to Altukhov, Apekin and Limanskii, 1964).

Moreover, it has been established (Boyd and Reguera, 1949; Bird, 1953) that some substances of plant origin, extracted mainly from seeds of legumes -- so-called phytagglutinins or lectins, have the ability to differentiate erythrocytes on the basis of their antigenic properties (Boyd, 1963). Their nature has not yet been thoroughly studied, although it is known that they are water-soluble proteins transporting into plants substances of a carbohydrate nature, similar in their chemical structure to the determinant groups of erythrocytic antigens. 36

Normal or immune isohemagglutinating serums are capable of detecting only one antigenic feature, of any kind, of erythrocytes. Serum of the A-group of man interacts only with erythrocytes of groups of B-blood and, consequently, is monospecific. Such serums are designated with the large Roman letter of the corresponding antigen, placing the word reagent after it or the prefix anti- before it. In the given case one can speak of anti-B or B-reagent.

Normal or immune heteroserums, as a rule, are polyspecific, and this causes definite difficulties in determining distinctive features of individual antigenic differentiation, but they can be overcome if the serum is specifically absorbed (exhausted) by the antigens, the antibodies for which one tries to exclude.

There are two equivalent empirical variants of determination of the individual antigenic differentiation of erythrocytes. One can, for example, start work with a search for a given kind of natural isoantibodies, then go over to investigation of its erythrocytes with different natural heteroantibodies and lectins, and in case of detection of individual variations, conduct the conclusive experiments with immune serums. But if the fact that the isoantibodies are not encountered so frequently is taken into account, a scheme is possible which is the reverse of that just considered: first strive to determine the known antigenic differences by means of immune hemagglutinating serums, and then, using natural antibodies or lectins, select the corresponding reagents. It turns out that where the immune serum reveals only a quantitative difference in the antigen composition of the erythrocytes of separate individuals, the normal serums of animals or lectins behave as reagents.

It has been rigorously proven that erythrocytic antigens are early established in ontogenesis, do not change in the postnatal period and are determined by heredity in such a way that a separate gene is responsible for the production of a separate antigen (Irwin, 1947, 1952; Cushing and Campbell, 1957, Wagner and Mitchell, 1958; Neal and Shell, 1958; Shtern, 1965; Race and Sanger, 1962; Efroimson, 1964; Tikhonov, 1966; Wiener, 1966). With consideration of the data of these and many other works a blood group

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can be defined as a more or less complex antigen consisting of one or several factors inherited as a single whole. Correspondingly the system of blood groups is an aggregate connected with a given mutually caused combination of antigens which are under the control of alleles of the same locus or in the case of coupling, several loci (Altukhov, 1969a).

In the analysis of blood groups, fairly often one encounters the phenomenon of multiple allelism, when the gene locus responsible for the synthesis of specific antigens is encountered in more than two alternative states. It should also be emphasized that in the inheritance of blood groups there occurs both dominance and co-dominance. In that case, when each of the antigens obtains complete expression in the heterozygotes, one can speak of close correspondence of the genotype to the phenotype.

In principle in the analysis of the relations of dominance and recessiveness with respect to blood groups the following dependences are discovered: firstly, complete dominance (one antigen is determined immunologically in hybrids); secondly, co-dominance; thirdly, neoplasm, when the heterozygotes give a phenotype not reducible to a simple inheritance of parental antigens. An example here is the discovery of the "substance of hybrids" in the erythrocytes and serums of animals (Sokolovskaya, 1936, 1938; Taliev, 1946; Irwin, 1947, 1952). This type of inheritance, evidently a result of interallele complementation, accompanies heterosis.

Recently such genetic phenomena as partial dominance and epistasis, expressed in incomplete suppression of the effect of one gene by another, have been discovered for blood groups of animals. Partial dominance, as an effect of the dose, occurs within the range of a given

allele pair; epistasis is caused by the presence of an allele from another allele pair of the same or a different system (Tikhonov, 1966). In series of multiple alleles both the first and the second types of inheritance and the effect of the dose can be combined.

These and some other discoveries were made on man and then confirmed on many zoological species, and they now form a solid foundation of immunogenetics. Immunogenetics became the principal methodical apparatus in the population genetics of man shortly after the military physicians K. and L. Hirszfeld discovered differences in the frequencies of blood 38
groups between representatives of different nationalities of Europe, Asia and Africa (1919). Subsequently that fact, in a different interpretation testifying to differences in the gene frequencies between reproductively isolated populations, acquired the rank of a universal law of population genetics; we observed differences of that kind earlier in the example with the "platys".

In the last 10-15 years considerable material has also been accumulated on the group variability of erythrocytic antigens of fishes. In about 30 species, including also such valuable ones as the flounder, tuna, and anchovy, genetic systems of blood groups have been found (Appendix 1), and in several tens of species more, not included in the present table, an entire series of individual antigenic factors (Altukhov, 1969a; de Ligny, 1969).

Figure 12 presents a schematic diagram of one of the investigations which led to the discovery in the spiny dogfish Squalus acanthias of a three-allele isohemagglutinational S-system of blood groups, similar to the ABO-system of man and represented by the four groups S_1, S_2, $S_{1,2}$ 39

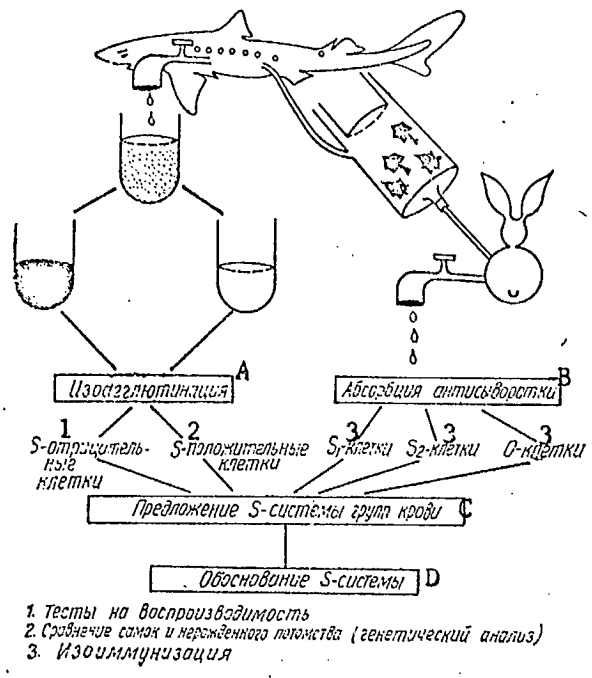

Рис. 12. Диаграмма, показывающая ход иммуногенетического исследования колючей акулы (по Sindermann, 1961).

Figure 12. Diagram showing the course of immunogenetic investigation of the spiny dogfish (acc. to Sindermann, 1961)

A - Isoagglutination
B - Absorption of antiserum
1 - S-negative cells
2 - S-positive cells
3 - cells (S_1, S_2 and 0)
C - Proposal of S-system of blood groups
D - Substantiation of S-system

1 - Tests for reproducibility
2 - Comparison of females in unborn offspring (genetic analysis)
3 - Isoimmunization

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and S_0. They are detected in isohemagglutinational tests with both immune and natural antibodies, and also during the use of heteroagglutinins produced on erythrocytes of the dogfish by the rabbit (Sindermann, 1961b).

Comparison of females and the unborn offspring (genetic analysis) testifies to the inheritance of the antigens S_1, S_2 and S_0 strictly in accordance with Mendel's laws (Figure 13): the offspring always proved to be identical with respect to the maternal antigen and in a number of cases a new antigen, inherited from the father, was discovered.

These data are especially interesting because they were obtained on a sea species; for most of them, however, the procedure of keeping them

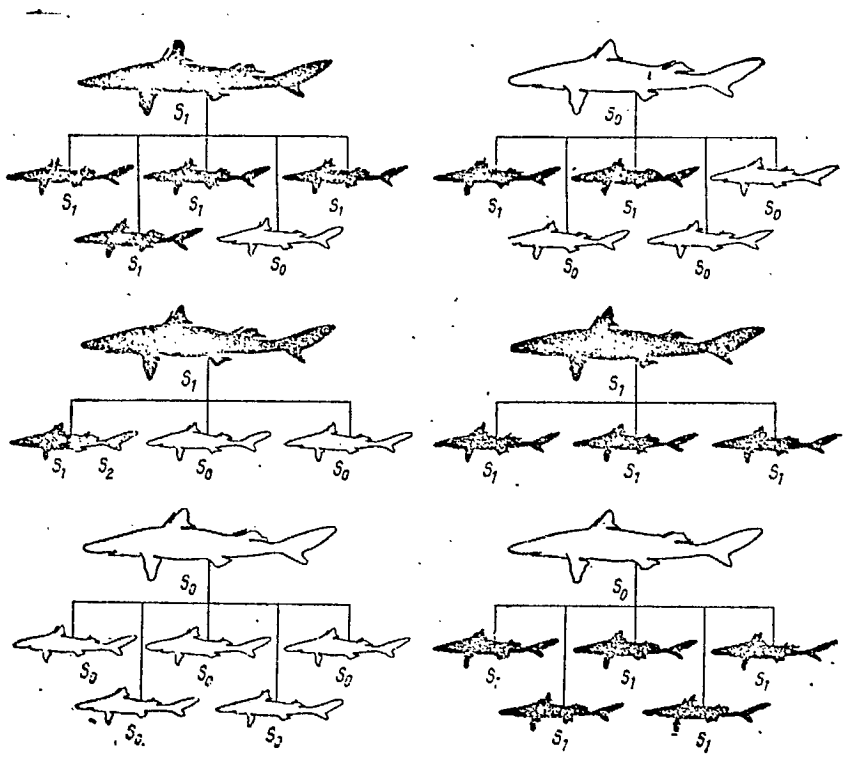

Рис. 13. Распределение групп крови *S*-системы среди самок и нерожденного потомства колючей акулы (по Sindermann, 1964).

Figure 13. Distribution of blood groups of the S-system among females and unborn offspring of the spiny dogfish (acc. to Sindermann, 1964).

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in aquariums a long time has not been worked out and therefore traditional genetic analysis is impossible. Such analysis can be accomplished on less 40
capricious freshwater fishes, as has been done by B. Sanders and J. Wright (1962) on rainbow trout Salmo gairdneri. By means of immune rabbit serum the two antigens R-1 and R-2 were found, which give the three blood groups R-1, R-2 and R-1-2, which also show Mendelian laws of sementation in the offspring of two co-dominant genes in the ratio 1:2:1 (Table 1).

There is one more way to verify the genetic hypotheses of inheritance of blood groups or any other alternative characters -- simple

Table 1. Inheritance of erythrocytic antigens in rainbow trout

Таблица 1. Наследование эритроцитарных антигенов у радужной форели

A Фенотипы родителей	B Фенотипы потомства, экз			C Тест ХИ-квадрат на гетерогенность	D Вероятность
	R-1	*R*-2	*R*-1-2		
R-1×*R*-1	99	0	0	—	—
R-1×*R*-2	0	0	90	—	—
R-1-2×*R*-1	91	0	115	1,1660	0,80—0,70
R-1-2×*R*-1-2	49	42	91	3,6389	0,80—0,70
R-2×*R*-1-2	0	66	58	1,4530	0,50—0,30
R-2×*R*-2	0	91	0	—	—

Key: A - Phenotypes of parents B - Phenotypes of offspring, examples
C - Test XI-quadrant for heterogeneity D - Probability

mathematical calculations directly on samples from natural populations, omitting analysis. This method takes into account the basic family principle of population genetics, the Hardy-Weinberg law: if in any large panmictic population the behavior of a pair of allele genes is observed, then already in the generation following free crossing it is possible to establish a definite dependence between the frequencies of those genes and the relative percentages of individuals homozygotic and heterozygotic with respect to them -- precisely in accordance with the expansion coefficients of a Newtonian binomial. In the absence of substantial pressure of selection or inflow of immigrants from neighboring populations these proportions will be transmitted stably from generation to generation, that is, the population will prove to be in a state of genotypic equilibrium, characterized by constancy of the gene frequencies.

In fact, if p and q are used to designate the frequencies of the corresponding allele genes, diverging randomly in meiosis over the sexual cells of males and females, then all the equiprobable crossings in the given generation can be written in the following manner:

41

Females Самки	Самцы Males	
	p	q
p	p^2	pq
q	pq	q^2

or $p^2 + 2pq + q^2 = 1$. And if it is taken into account that the crossings occur in a population of N individuals, then the percentages of homozygotes or heterozygotes can readily be found from the expression

$$p^2N + 2pqN + q^2N = N.$$

The correspondence of the empirical data of this very simple population genetics model has been established, with a slight exception, on all species of fishes investigated by genetic methods (de Ligny, 1969, etc.).

The fact that all the principles of genetics of mendelizing characters not coupled with sex are applicable to erythrocytic antigens of fishes has also been established by other investigations in both crossing experiments (family analysis) and in the comparison of actual frequencies with those expected from the Hardy-Weinberg equation. The following regularities have been detected (see also Appendix 1):

1. Complete dominance -- for example, the Tg-system of blood groups of tuna, the S-system of the spiny dogfish, and the A-system of the anchovy.

2. Co-dominance: the R-system of the rainbow trout, the Tg-system of tuna, and the S-system of the spiny dogfish.

3. The effect of the dose: the A-system of blood groups of the sockeye and the A-system of the anchovy.

Hereditary Variability of Serum and Intracellular Proteins

The genetic polymorphism of proteins dissolved in water or in water-salt solutions with a low ionic force is best detected by the method of zonal electrophoresis, and the hereditary nature of variability is readily interpreted on the basis both of the principles of that method and achievements in the region of theory of the gene and the mechanism of gene action (Henning and Janofski, 1963; Shaw and Barto, 1963; Shaw, 1965; Hubby and Lewontin, 1965; Lewontin and Hubby, 1966). In their main features the above-presented immunogenetic principles also preserve their force on this level of analysis. 42

Electrophoretic methods in various supporting media -- neutral fine-pored gels -- fractionate protein macromolecules on the basis of their differences in the summary electrostatic charge and (or) in molecular weight. The special coloration of the gels: nonspecific for protein in general or specific for a definite group of proteins (for example, a combination of electrophoresis with methods of histochemistry permits identifying many enzymes) makes it possible to obtain an electrophoregram -- a strip of gel with discrete dark-colored bands clearly noticeable on it, arranged at different distances from the beginning start. The bands correspond to individual, usually water-soluble proteins present before the experiment in the blood, cell extracts or any other biological liquids accessible for investigation. In an immunoelectrophoretic variant of the method the separate protein components are fixed at the places of "antigen-antibody" reaction in the form of turbid whitish arcs of insoluble precipitate.

In the investigation of such specimens from several representatives of a given species, individual variations are discovered in the mobility

and number of bands (all or separate ones) on the electrophoregram, determinable by the presence or absence of the corresponding structural gene or the existence of alleles in such a genetic locus which codes the individual polypeptide chain. Polypeptide chains (subunits) compose the structure of protein molecules, which can be monomers, that is, consist of single chains, or multimers, that is, be composed of two or more subunits, synthesized under the control of one, two or more loci, independent or coupled. The control of a single biochemical function by multiple genes leads to a corresponding multiplicity of the protein zones on the electrophoregram. And although cases are known in which a rather large number of protein fractions can be connected only with different degrees of polymerization of the same subunit, most often a picture of that type is determined by the presence of two or more genetic loci which control the corresponding link of the given biochemical cycle in the organism.

The problem of genetic and biochemical principles of multiple 43
molecular forms of proteins, on the level of enzymes which have been called isozymes, has been examined in detail in specialized works (Wilkinson, 1968; Yakovleva, 1968; Markert and Whitt, 1968; Massaro and Markert, 1968; 44
Vessel, 1968; Salmenkova, 1973, etc.). It has recently been found in higher organisms that the multiplicity of proteins of the same kind is adequate for the multiplicity of the corresponding structural genes. Consequently, in the organization of genetic material there is a duality: on the one hand, there are single loci; on the other, there are multiple genes, combined into systems and single in a functional respect.

A shortcoming of the electrophoretic method is that only five of the twenty amino acid residues composing the primary structure of protein

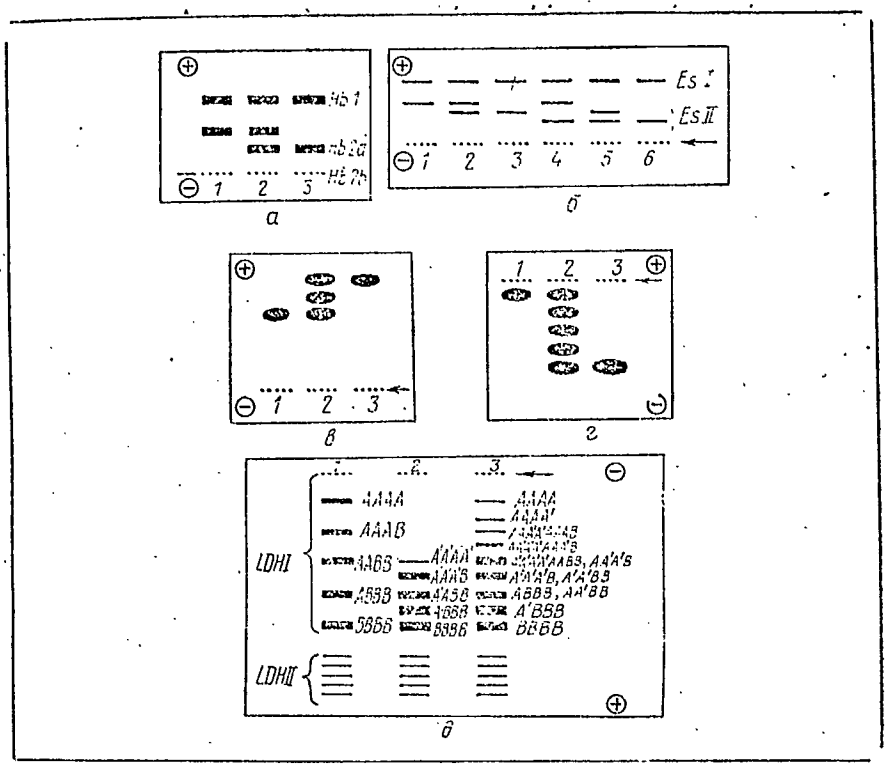

Рис. 14. Схематическое изображение наследственных электрофоретических вариантов белков у разных видов животных:

Figure 14. Schematic depiction of hereditary electrophoretic variants of proteins in different species of animals: a - hemoglobin of the whiting Odontogadus merlangus 1 and 3: homozygotic genotypes; 2 - heterozygote. Locus NZ1 is monomorphous. Electrophoresis in agar gel (acc. to Sick, 1961); b - esterase of the crustacean Mysis relicta 1, 3 and 6: homozygotes; 2, 4 and 5: heterozygotes. Locus Es1 is monomorphous. Electrophoresis in starch gel (acc. to Furst and Nyman, 1969); c - 6-phosphogluconate dehydrogenase of the quail Coturnix coturnix; 1 and 3 - homozygotes; 2 - heterozygote. The enzyme has a dimeric structure, and so three zones of activity are found in the heterozygote, that is, hybrid molecules are formed, represented by the middle band. Electrophoresis in starch gel (acc. to Manwell and Backer, 1970); d - malate dehydrogenase of the house mouse Mus musculus. This enzyme in the given species is a tetramer composed of two subunits, one each ("fast" or "slow") in the homozygotes (1 and 3). In the heterozygote (No. 2), both genes are active and free combination on four of the subunits synthesized under their control gives five isozymes. Electrophoresis in starch gel (acc. to Shows and Ruddle, 1968); e - isozymes of muscular lactate dehydrogenase of the keta Oncorhynchus keta. Two groups of isozymes,

shown by braces, are found. In each group the tetramer molecules of the enzyme are coded by pairs of independent genetic loci, one of which is invariant (L.DHII), whereas in the second, mutation on locus A is discovered. Since in that procedure the mobility of a number of enzymes overlaps (see the letter symbols), nine bands of activity are revealed in the heterozygote (3) instead of the 15 predicted by theory (Shaw and Barto, 1963). Electrophoresis in acrylamide gel (acc. to Altukhov et al., 1970, with modifications). The arrow indicates the starting position.

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molecules influence their total electric charge. Therefore one can discover only a portion of the nucleotide substitutions in the DNA which lead to amino acid substitutions. Nevertheless the world literature in general and the ichthyological in particular overflows with examples of the successful determination of individual electrophoretic variations of proteins (see Appendix 1) inherited strictly in accordance with Mendel's laws, and the inheritance, in contrast with erythrocytic antigens, is in most cases realized as a co-dominant type -- both genes are active in the heterozygote.

What has been said can be illustrated by several examples (Figure 14). The written material under the figure explains the reading of the electrophoregrams.

Methodical Procedures for Detection of Genetic Variability

Immunological Tests

The process of determination of blood groups of redfishes and anchovies amounted to testing in hemagglutination tests the blood corpuscles of those species with immune and natural antibodies and lectinins. Since the absence of natural isoantibodies had been established in preliminary tests, all the reactions were set up with heteroantibodies.

The variability of antigenic properties of the erythrocytes of redfishes was investigated with immune serums produced by rabbits on the erythrocytes of perch and the cod Gadus morhua [its erythrocytic antigens are very similar to antigens of redfishes (Sindermann, 1962)], as phytagglutinins of various origin and normal antibodies discovered in different species of animals did not give a clear and reproducible group differentiation of cells of redfishes.

The blood of fishes was taken with a sterile Pasteur pipette from 45
the aortic bulb and transferred into isotonic physiological solution containing anticoagulant [3% tri-substituted sodium citrate and 0.28% sodium chloride (Sick, 1961)]. To obtain a "working" suspension of erythrocytes, 2 drops of whole blood were added to 2 cc of physiological solution.

When the cells were stored for immunization, 3 parts of whole blood were added to 1 part of solution, and then the erythrocytes were washed off three times in ten times the volume of isotonic solution and a 50% suspension prepared.

Such a mixture of cells from several redfishes taken on the Flemish Cap bank, on the southern part of the Newfoundland Grand Bank and in the region of Southern Iceland was administered (1 cc intravenously) to rabbits living aboard the expeditionary vessel. Four rabbits were immunized in 1964 and four in 1965. At the conclusion of the immunization (3 or 4 injections) a blood sample was taken from the rabbit and the serum was tested for height of titer of agglutinins. Three antiserums were thus taken: one "anti-redfish" and two "anti-cod" (one was obtained in October 1964 and absorbed by the cells of a cod taken in Icelandic waters).

The antiserums preserved by merthiolate (1:10,000) were stored frozen in ampoules, and before a reaction was set up were warmed half an hour at 56°C to destroy the complement.

Two volumes of serum /drops from/ a loop of Nichrome wire 1mm in diameter were mixed with one volume of the working suspension of erythrocytes on slides. The reactions proceeded in moist chambers at room temperature, and the degree of agglutination was estimated at a small magnification of the microscope (obj. 8X, ocul. 10X). Different degrees of agglutination from complete adhesion of all cells to a complete absence of it, as was observed in a control (only the working suspension of erythrocytes), were reflected by the marks "++++", "+++", "++", "+" and "-". Preliminary observations showed that for the complete formation of agglutinate the incubation time must be not less than one hour.

To remove heterophilic antibodies from the serum, specific absorption was carried out: added to four parts of dilute (1:3) immune serum was one part of three-times washed concentrated erythrocytes from separate, previously selected fishes, and the mixture was incubated, while shaking it constantly, at room temperature for 1.5-2 hours. Then the cells were separated by centrifugation and the serum tested for completeness of absorption. If the serum preserved the ability to agglutinate cells used for absorption, the procedure was repeated but half the number of cells was added.

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In principle the same procedure (Altukhov, Apekin and Limanskii, 1964) was used in experiments with cells of the anchovy. The only difference was that the blood groups were determined first in tests with normal horse and hog serum, which gave very clear and reproducible results

regardless of which the serum belonged to, and then was confirmed by hemagglutination with immune antibodies produced on erythrocytes of the anchovy by rabbits (Limanskii, 1966; Altukhov et al., 1969).

Our attempts to detect blood groups in Pacific salmons (keta and pink salmon) proved unsuccessful. It should be noted that American authors (Ridgway, Cushing and Durall, 1958), although they observed some antigenic variations in those species, also could not adapt those markers for population genetics purposes; only in the sockeye in experiments with normal hog serum was a two-allele system of blood groups with partial dominance detected (Ridgway et al., 1958). Therefore the main efforts were directed toward the detection in salmons of genetic variability with respect to water-soluble proteins during their investigation by electrophoretic methods combined with specific coloration for enzymatic activity and total protein.

The following proteins were studied: serum albumins (Alb); lactate dehydrogenase (Ldh) of various tissues; cytoplasmic malate dehydrogenase (Mdh), serum esterase (Es), glucose-6-phosphate dehydrogenase (G-6-Pdh) of erythrocytes; alpha-glycerophosphate dehydrogenase (alpha-Gdh) of muscles; phosphoglucomutase (Pgm) of muscles; hemoglobins (Hb) and also crystallins and myogens -- water-soluble proteins of the crystalline lens of the eye and muscles respectively.

Electrophoresis of Proteins

1. Preparation of protein solutions for electrophoresis. To obtain serum the caudal fin of the fish was cut off and the blood freely flowing from the caudal artery was rapidly collected into carefully washed glass vessels. Several hours after retraction of the fibrin clot the serum was separated by centrifugation or suction.

Ground white skeletal muscles were homogenized in a glass homogenizer with a Teflon pestle (or in a porcelain mortar) with an equal volume of icy distilled water and centrifuged cold for one hour (10,000 or 16,000 rpm); in individual cases the centrifugation was repeated until a transparent supernatant was obtained. 47

The crystalline lenses of eyes were pulverized in a porcelain mortar with an equal volume of distilled water and centrifuged 20-30 minutes (5000 rpm). The erythrocytes were washed out four times with cooled isotonic Alsever's solution (Hodgins and Ridgway, 1964) and hemolyzed, an equal volume of icy distilled water was added, and the stroma was removed by 15-30 minute centrifugation (8000-10,000 rpm).

2. Electrophoresis in agar gel. Hand-made apparatus of Plexiglas was used, with platinum electrodes and a number of auxiliary devices intended for cutting trenches in the gel, for the application of fused gel on a glass plate (9 x 12 or 13 x 18 cm in size), for the drying of electrophoregrams and for their coloration for total protein or for enzymatic activity. The design of the apparatus permitted investigating at a single moment 10 or 16 specimens in barbital sodium-barbital buffer solution with a pH value of 8.6 and an ionic force (μ) of 0.25-0.05; the electric field intensity was $\sim$ 7 V/cm.

The procedure used was described in detail on the whole by Graybar and Burten (1963). Our co-workers V.I. Slyn'ko and G.N. Nefelov introduced a number of design improvements.

a) Buffer solutions. The buffer solutions for the gel contained 1.68 g of barbital, 10.6 g of barbital sodium, and distilled water to make 1 liter; μ = 0.1. The buffer solutions for the electrode vessels contained 1.38 g of barbital, 8.76 g of barbital sodium and distilled water to make 1 liter; μ = 0.05.

b) Agar gel. To 2% Difco bactoagar, prepared with distilled water, an equal volume of gel buffer was added, thus obtaining 1% gel with the same pH value and with an ionic force of 0.05. In some experiments, for example, to determine the isozymes of lactate dehydrogenase of muscles we used gel with μ = 0.025, prepared from 2% gel, washed in distilled water for several days in advance in order to remove low-molecular substances resembling pectin from it. This improved the differentiating properties of the gel.

One-percent fused gel was preserved with merthiolate (1:5000 to 1:10,000) and packed in 50-cc quantities in flat-bottomed flasks. Immediately before the experiment the gel was melted on a water bath and 40 cc were applied to a carefully washed, degreased photographic plate (13 x 18 cm in size) on a strictly horizontal plane.

Trenches 7 mm long and 1 mm wide were cut in the coagulated gel 48
with a special knife, the plate was placed in the apparatus and the gel on the plate was connected with the gel bridges of the apparatus by the melted gel. Then protein solutions were introduced into the trench separated in a field of direct current for two hours and 15 minutes in a combined regime: at first, before the molecules entered the gel, a voltage of 55 V was fed for 15 minutes, then it was increased to 90 V (on the ends of the plate) and the experiment was conducted for two hours in a refrigerator at a temperature of 4°C.

Upon conclusion of the experiment the plate was placed for 30 minutes in 10% solution of acetic acid to denature the protein molecules, after which the gel was covered with chromatographic paper and dried under a current of warm air. The protein fractions thus fixed were stained.

3. Electrophoresis in starch-agar gel. The procedure does not differ at all in principle from the above-described, except the composition of the gel, which contains 2% hydrolyzed starch and 0.8% Difco bactoagar in barbital sodium-barbital buffer solution with a pH value of 8.6 and an ionic force of 0.025.

4. Electrophoresis in starch gel. The procedure of horizontal electrophoresis in a Tsuyuki apparatus was used, with slight design changes introduced by our co-worker V.T. Omel'chenko. The apparatus permits analysis of 35-70 specimens simultaneously.

a) Buffer solutions. Two buffer systems were used: the Tsuyuki borate and the Poulick discontinuous (Poulick, 1957). In the former case, for the gel 0.023M H_3BO_3 and 0.25% Na_2-EDTA, titrated with NaOh solution to a pH value of 8.5; for the electrode sections, 0.3M H_3BO_3, titrated with NaOH solution to a pH value of 8.5. In the second case in the gel there are 0.076M tris-HCl and 0.005M citric acid; in the electrode sections, 0.3M H_3BO_3 and 0.06M NaOH, pH = 8.6.

b) Preparation of the gel. We used 13% gel, obtained after heating the suspension of hydrolyzed starch to about 80°C. The mixture thickened in 3 or 4 seconds and then liquefied after 15-20 seconds, after which we quickly decanted it into the cuvette and distributed it uniformly over the entire surface. The design of the cuvette permitted avoiding the use of paper bridges, used to connect the gel with the buffer solution in the sections; that contact was accomplished directly when both edges of the block of starch were submerged in the buffer solution.

The separation took 5 or 6 hours in a refrigerator at 2-4°C.

5. Electrophoresis in acrylamide gel. We used a variant of the method which permits separating proteins in a vertical block of gel constantly cooled by a mixture of ice and brine.

a) Buffer system: tris-EDTA-borate, pH 8.3 (Peacock et al., 1965).

b) Preparation of the gel. It is best to separate the isoenzymes in all cases in a 5.5% gel with use of TEMED /expansion not available/ and ammonium persulfate as catalysts. The methylene bisacrylamide concentration is 4%.

The gel polymerizes in the apparatus in 40 minutes, and the ammonium persulfate is removed from the gel for 20 minutes at 200 V. The design of the apparatus permits investigating 22-70 samples simultaneously.

6. Staining the gels for total protein. To determine the fractions of albumins, crystallins, hemoglobins and myogens, after electrophoresis the gels were stained with 0.1% solution of amide black 10B in 10% acetic acid (agar and starch-agar variant of the method) or 0.025% solution of coomassie blue GL in 12.5% trichloracetic acid (acrylamide variant of the method).

Staining for enzymes was accomplished in accordance with the principles of histochemistry (Berston, 1965) by incubating the gels at 37-40°C in special dyeing mixtures with the following compositions:

a) for Ldh of blood serum (development in agar gel): 6 ml of 1M Na lactate; 3.5 ml of 1% aqueous solution of nicotinamide adenine dinucleotide (NAD); 12 ml of 0.1M KCl; 6 ml of 0.005M $MgCl_2$; 1.5 ml of 0.1% aqueous solution of phenazine methyl sulfate (PMS); 2 ml of 1% aqueous solution of nitro blue tetrazolium (NBT); 90 ml of 0.1M phosphate buffer, pH 7.6; incubation for 1 to 2 hours;

b) for Ldh of blood serum and muscles in acrylamide gel: 15 ml of 1M Na lactate; 12 ml of 1% aqueous solution of NAD; 12 ml of 0.1M NaCl; 12 ml of 0.005M $MgCl_2$; 10 ml of 1% NBT; 30 ml of 0.5M phosphate buffer, pH 7.6; 2.5 ml of 1% aqueous solution of PMS; development proceeds about three hours.

c) for Mdh: 6 ml of 2M Na-L-malate; 6 ml of 1% NAD; 5 ml of 1% NBT; 0.3 ml of 1% PMS; 80 ml of 0.1M tris-HCl buffer solution, pH 8.4; incubation 2 or 3 hours;

d) for serum esterase: 10 ml of 0.2M tris-maleate buffer, pH 7.4 and 9.8 ml of 0.2M NaOH were made up with water to 40 ml, 1 ml of 1% solution of alpha-naphthyl acetate was added in a mixture of equal volumes of water and acetone and 40 ml of "fast blue PP" dye. Before being submerged in that mixture the gel immediately after electrophoresis was kept 30 minutes in 0.5M H_3BO_3 at 4^oC to reduce the pH value of the gel; incubation in the substrate mixture was 2 hours;

e) for alpha-Gdh: 100 mg of alpha-glycerophosphate Na in 100 ml of 0.1M tris-HCl buffer, pH 8.3; 3 ml of 1% NAD; 2 ml of 1% NBT; 2 ml of 0.1% PMS; incubation 3 or 4 hours;

f) for G-6-Pdh: 5 ml of 1% glucose-6-phosphate Na; 12 ml of 0.1% nicotinamide adenine dinucleotide phosphate (NADP); 5 ml of 1% NBT; 5 ml of 0.01M $MgCl_2$; 1 ml of 0.1M NaCl; 60 ml of 0.05M tris-HCl buffer, pH 8.5; 3 ml of 0.1% PMS were added 30 minutes after the start of incubation, which then continued 2 hours. The gel and electrode buffer solutions in those experiments contained 20 mg/liter of NADP;

g) for Pgm: 120 mg of glucose-1-phosphate K_2 in 100 ml of 0.05 tris-HCl buffer, pH 8.0; 3 ml of 1% solution of NADP; 2 ml of 1% NBT; 0.2 ml of suspension of glucose-6-phosphate dehydrogenase containing 0.1 g of enzyme in 25 ml; 1 ml of 0.01M $mgCl_2$; 2 ml of 0.1% PMS; incubation 2 hours.

The specificity of the bands of each enzyme on the electrophoregrams was established in preliminary experiments by incubating in parallel the gels in the staining mixtures with and without the substrate.

In concluding the chapter it is necessary to note those deviations from very simple genetic situations which were encountered recently in the analysis of polymorphism of blood groups and some proteins in fish populations. This, firstly, is ontogenetic regulations (Sanders and Wright, 1962; Vanstone et al., 1964; Wilkins, 1966; de Ligny, 1968), secondly, sex-limited inheritance (Utter and Ridgway, 1967a and b; Altukhov et al., 1968b), thirdly, lack of balance of the meiosis of some tetraploid species, which creates a false impression of coupling of genes (Morrison, 1970) and finally, fourthly, reduced adaptation or even lethalness of homozygotic genotypes (Fujino and Kang, 1968a and b).

Among all those examples only sex-limited differences in the synthesis of ovovitellins must be constantly taken into account in the investigation of polymorphism of serum proteins of fishes. The other cases affect only five or six species out of tens studied and, in addition, some situations allow the possibility of a different interpretation from that given by the authors.

For example, age differences in the frequencies of genes of blood groups of the flounder Pleuronectes platessa and transferrins of the tuna Katsuwonus pelamis can be completely explained by inadequacy of the compared samples, when the adult fishes were taken from one population and the juveniles from another. W. de Ligny (1969), after examining these cases in detail, could not herself exclude the indicated possibility.

It is probable that the same thing is indicated by an example 51
with sex differences in the frequencies of esterase types in the hake Merluccius productus from Puget Sound (Utter et al., 1970): in females and juveniles the actual distribution of genotypes corresponds to that

expectable according to Hardy-Weinberg, whereas in males aged two years or more a noticeable deficit of heterozygotes is observed.

On the other hand, the difference in the number of phenotypes of blood groups of the B-system among adult and juvenile rainbow trout can be estimated unequivocally.

In that case the absence of interaction of erythrocytes of mature fishes with one of the reagents effective for cells of juveniles actually is caused by the activation in ontogenesis of a factor covering the erythrocytic membrane and behaving as a Mendelian dominant (de Ligny, 1969).

When we started our investigations there were practically no data of that kind. However, such limitations were taken into account by us everywhere possible. In any case, all the experiments were set up on fishes which had reached reproductive age, and with consideration of their sex.

Chapter IV. Genetic Polymorphism

Antigenic Factors in Erythrocytes of the Redfish

Table 2 shows the character of reactions with rabbit hemagglutinating "anti-redfish" and "anti-cod" serums of the erythrocytes of six specimens of redfish taken 3 September 1965 on the southeastern slope of the Newfoundland Grand Bank.

In the examination of these data, unidirectional differences in the character of the reactions of cells of individual fishes with the two hemagglutinating serums are evident: agglutinins are contained in the highest titer only in relation to erythrocytes of redfish No. 4 (1:256-1:512); titers of all the other reactions are one or two orders of magnitude

lower (1:64 - 1:128). This difference is still more demonstrative in absorption experiments set up with anti-cod serum (Table 3).

Table 2. Agglutination of erythrocytes of the deepwater redfish by immune serums

Таблица 2. Агглютинация эритроцитов окуня-клювача иммунными сыворотками

A Номер рыбы	Разведения антисывороток B									C Контроль (физиологический раствор)
	«антиокунь» a				«антитреска» b					
	1:64	1:128	1:256	1:512	1:64	1:128	1:256	1:512	1:1024	
1	+	±	—	—	+	+	—	—	—	—
2	+	—	—	—	++	—	—	—	—	—
3	++	+	—	—	+	±	—	—	—	—
4	+++	++	+	—	++	++	+	±	—	—
5	++	—	—	—	+	—	—	—	—	—
6	++	—	—	—	++	±	—	—	—	—

Key: A - Number of fish B - Antiserum dilution a - "anti-redfish"
b - "anti-cod" C - Control (physiological solution)

Table 3. Agglutination of redfish erythrocytes by absorbed "anti-cod" rabbit serum

Таблица 3. Агглютинация эритроцитов окуня абсорбированной кроличьей сывороткой «антитреска»

Сыворотка «антитреска», абсорбированная клетками рыб, номер A	Номер рыбы B					
	1	2	3	4	5	6
1	—	—	—	+++	—	—
2	—	—	—	+++	—	—
3	—	—	—	+++	—	—
4	—	—	—	—	—	—

Key: A - "Anti-cod" serum absorbed by cells of fishes, number
B - Number of fish

Exhaustion of the immune serum by the erythrocytes of fish No. 4 removes the reaction in all cases, and the absorption by cells of fishes Nos. 1-3 eliminates homologous reactions and reactions with cells of fishes Nos. 5 and 6, whereas the erythrocytes of redfish No. 4 continue to adhere with the intensity +++. 52

Consequently, cross absorption tests also reveal two types of fishes different in the antigenic properties of their erythrocytes. The first type includes redfishes Nos. 1, 2, 3, 5 and 6, whose cells do not adhere in all variants of absorption; the second type is redfish No. 4, whose erythrocytes agglutinate in all cases. On the basis of these data one can distinguish two closely related antigens in a subgroup subordination: A_1 (cells of redfish No. 4) and A_2 (cells of remaining fishes)*, and evidently coded by a pair of alleles with dominance of A_1 over A_2 (Altukhov, 1969a). 53

Immune anti-redfish serum (see Table 2) differentiates cells of six investigated fishes unequivocally with the anti-cod serum; this is confirmed by absorption tests in which cells of redfish No. 3 were taken for exhaustion. Still another reagent of precisely the same specificity was obtained by us earlier in the Iceland region (Table 4).

It follows from the data of Table 4 that the three reagents can be regarded as identical in specificity, but the sample of six specimens is clearly insufficient to accept that statement as definitive. Therefore we investigated all the reagents simultaneously with two more samples

*Some variations of titers within this group reflect, possibly, quantitative variations in the content of the antigen or, more likely, errors in procedure.

Table 4. Interaction of three reagents with erythrocites of redfish

Таблица 4. Взаимодействие трех реагентов с эритроцитами окуней

	A Абсорбированные гемагглютинирующие сыворотки (реагенты)	Номер рыбы B						C Контроль (физиологический раствор)
		1	2	3	4	5	6	
1	«Антитреска» № 1, 1964 г.	—	—	—	++	—	—	—
2	«Антитреска» № 2, 1965 г.	—	—	—	+++	—	—	—
3	«Антинокунь»	—	—	—	+++	—	—	—

Key: A - Absorbed hemagglutinating serums (reagents) B - Number of fish C - Control (physiological solution)
1 - "Anti-cod" No. 1, 1964
2 - "Anti-cod" No. 2, 1965
3 - "Anti-redfish"

(30 and 26 specimens) of redfish (two trawl catches on the Flemish Cap bank) and satisfied ourselves of the unequivocality of the behavior of the reagents, which marked fishes in that region exclusively as carriers of the factor A_2, in contrast with the extremely heterogeneous fishes localized on the Newfoundland Grand Bank (see Chapter V). 54

Since we succeeded in obtaining reagents "anti-cod" No. 1 and "anti-cod" No. 2 in the largest volume, all surveys of the distribution of blood groups in space were made with those reagents. In concluding the discussion of distinctive features of individual antigenic variations of erythrocytes of redfish, we will point out that the revealed variability is not connected with sex: the uniform distribution of the factors among males and females ($\chi^2 = 0.33$; $p > 0.05$) is illustrated by Table 5.

Table 5. Distribution of antigenic factors A_1 and A_2 among males and females of the deepwater redfish caught on the Newfoundland Grand Bank on 2-4 October 1965

Таблица 5. Распределение антигенных факторов A_1 и A_2 среди самцов и самок клюворылого окуня, выловленного на Большой Ньюфаундлендской банке 2—4/X 1965 г.

	Пол рыбы A	Фенотип B		Итого C
		A_1	A_2	
a	Самцы	20	29	49
b	Самки	16	25	41
C	Всего . . .	36	54	90

Key: A - Sex of fish B - Phenotype C - Total
a - males b - females

Blood Groups of the Anchovy

We have already noted that the individual variability of antigenic properties of erythrocytes of the anchovy was discovered during their agglutination by normal serums of animals. The results of experiments set up in July 1963 in the Sea of Azov are presented in Table 6 and schematically on Figure 15.

Distinct differentiation of the investigated fishes into three groups was traced: the erythrocytes of the first of them are agglutinated by both serums (Nos. 1-4); the erythrocytes of the second only by the hog serums (Nos. 5-7); the cells of the third group do not give reactions at all. The discovered differences are just as distinct during the agglutination of cells of the same 12 fishes by absorbed hog serum (Table 7).

Table 6. Distinctive features of agglutination of erythrocytes of the anchovy by normal serums of animals (acc. to Altukhov et al., 1969a with supplement)

Таблица 6. Особенности агглютинации эритроцитов анчоуса нормальными сыворотками животных (по Алтухову и др., 1969а с дополнением)

	Сыворотка 1	Номер рыбы 2				
		1	2	3	4	5
a	Лошадиная	++++	++++	+++	+++	—
b	Свиная	++++	++++	++++	++++	++++
c	Контроль (физиологический раствор)	—	—	—	—	—

Table 6 (Continued)
Продолжение таол. 6

	Сыворотка 1	Номер рыбы 2						
		6	7	8	9	10	11	12
a	Лошадиная	—	—	—	—	—	—	—
b	Свиная	++++	++	—	—	—	—	—
c	Контроль (физиологический раствор)	—	—	—	—	—	—	—

Key: 1 - Serum 2 - Fish number a - Horse b - Hog
c - Control (physiological solution)

Exhaustion of the serum by erythrocytes of fish No. 2 (the first group) "removes" the reaction with all cells; the erythrocytes of fish No. 5 (second group) link the antibodies in relation to themselves and to the erythrocytes of the other two anchovies of the same group; absorption by negative erythrocytes (third group) gives no sort of effect at all. 56

Proof of the antigenic character of the detected variability are serological reactions set up simultaneously with normal serums and immune rabbit antibodies, which were examined in detail in the dissertation of

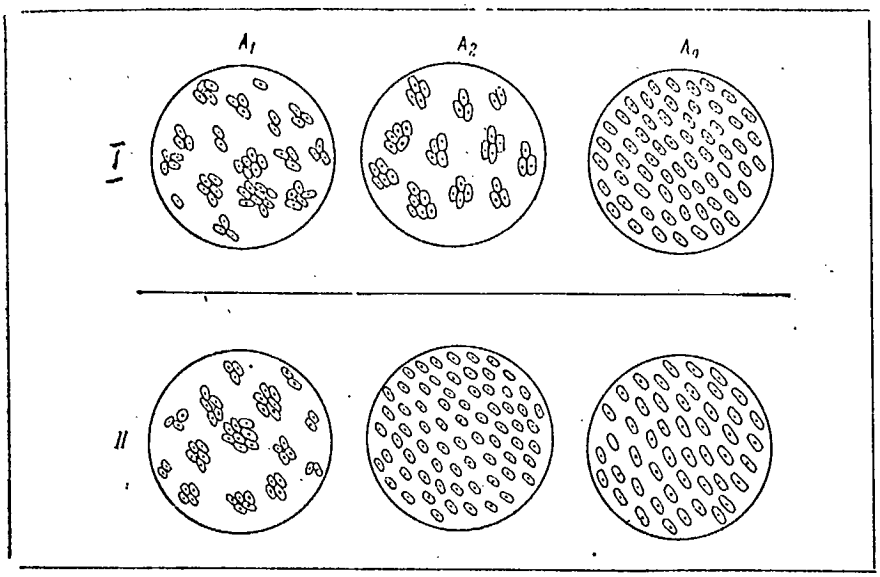

Рис. 15. Индивидуальная изменчивость антигенных свойств эритроцитов анчоуса в опытах гемагглютинации с нормальными сыворотками крови животных:
I — свиньи; *II* — лошади.

Figure 15. Individual variability of antigenic properties of erythrocytes of the anchovy in experiments of hemagglutination with normal animal blood serums: 1 - hog; 2-horse.

Table 7. Distinctive features of the agglutination of erythrocytes of the anchovy by absorbed hog serum (acc. to Altukhov et al., 1969a)

Таблица 7. Особенности агглютинации эритроцитов анчоуса абсорбированной свиной сывороткой (по Алтухову и др., 1969а)

Свиная сыворотка, абсорбированная клетками, номер A	Номер рыбы B											
	1	2	3	4	5	6	7	8	9	10	11	12
2	—	—	—	—	—	—	—	—	—	—	—	—
5	+++	+++	+++	+++	—	—	—	—	—	—	—	—
8	++++	+++	+++	++	+++	++	+++	—	—	—	—	—

Key: A - Hog serum absorbed by cells, number B - Fish number

V.V. Limanskii (1969). We will limit ourselves to a demonstration of only one table containing typical results (Table 8) and showing complete correspondence of the results of reactions of normal and immune agglutination. 57
Thus, if the erythrocytes of fishes of the first group (Nos. 1 and 2) are agglutinated by rabbit antiserum to its maximum dilution (1:128), then titers of reactions with cells of the second group (Nos. 3 and 4) are lower by three orders of magnitude. Negative cells (Nos. 5-7) do not react at all with immune serum in a number of the tested dilutions. The reaction of negative erythrocytes with other antiserums can take place only in titers of 1:8 - 1:16, and during agglutination of cells of the other two groups in titers of 1:32 - 1:64 and 1:64 - 1:128 respectively.

The results of absorption tests (Table 9) are just as evident.

It must be emphasized that such experiments were set up repeatedly, and in all cases the picture was identical -- only three groups of anchovies were discovered on the basis of the antigenic properties of their erythrocytes. During the entire period of investigations conducted both in the Azov-Black Sea basin and in the Atlantic Ocean off the coast of Africa (Limanskii, 1966), not once was a fourth group discovered whose erythrocytes would interact with horse serum and simultaneously not agglutinate with hog serum. The distinctive features of these reactions can be explained only by assuming that hog serum is polyspecific in relation to the complex antigen which can be designated as antigen A, and horse serum is a reagent toward factor A_1. Erythrocytes agglutinated only by hog serum contain the subgroup factor A_2, as a result of which the horse serum does not interact with such cells. Consequently combinatorial analysis of a pair of antigens must give three blood groups: A_1, A_2 and A_1A_2. However, in a qualitative 58

Table 8. Character of the reactions of three phenogroups of the anchovy found in experiments of normal agglutination with immune rabbit serum (acc. to Altukhov et al., 1969a)

Таблица 8. Характер реакций трех феногрупп анчоуса, выявленных в опытах нормальной агглютинации, с иммунной сывороткой кролика (по Алтухову и др. 1969а)

A Номер рыбы	B Нормальная сыворотка		C Иммунная кроличья сыворотка в разведениях		
	1 лошадиная	2 свиная	1:2	1:4	1:8
1	++++	++++	++++	++++	++++
2	++++	++++	++++	++++	++++
3	—	++	++++	+++	++
4	—	+++	++++	+++	+++
5	—	—	—	—	—
6	—	—	—	—	—
7	—	—	—	—	—

Продолжение табл. 8

A Номер рыбы	C Иммунная кроличья сыворотка в разведениях				
	1:16	1:32	1:64	1:128	1:256
1	++++	++++	+++	+++	—
2	++++	+++	+	+	—
3	±	—	—	—	—
4	++	—	—	—	—
5	—	—	—	—	—
6	—	—	—	—	—
7	—	—	—	—	—

Key: A - Number of fish B - Normal serum C - Immune rabbit serum in dilutions 1 - horse 2 - hog

estimate of the reactions we discovered only two phenotypes: A_1 (" ++ ") and A_2 (" + -"). However, attentive examination of the intensity of reactions within the limits of the phenotype of positive cells reveals its heterogeneity, as is evident in special experiments set up with normal serums (Tables 10-11).

Table 9. Agglutination of erythrocytes of the anchovy by immune rabbit serum after absorption (according to Altukhov et al., 1969a)

Таблица 9. Агглютинация эритроцитов анчоуса иммунной кроличьей сывороткой после абсорбции (по Алтухову и др., 1969а)

A Иммунная сыворотка, абсорбированная клетками, номер	Номер рыбы B						
	1	2	3	4	5	6	7
1	—	—	—	—	—	—	—
4	++	+++	—	—	—	—	—
5	+++	++++	++	+++	—	—	—

Key: A - Immune serum absorbed by cells, number B - Fish number

Table 10. Variability of reactions of erythrocytes of anchovy of the first group in experiments with normal antibodies (acc. to Altukhov et al., 1969a)

Таблица 10. Вариабельность реакций эритроцитов анчоуса первой группы в опытах с нормальными антителами (по Алтухову и др., 1969а)

A Сыворотка	Номер рыбы B					
	1	2	3	4	5	6
a Лошадиная	++++	+++	++++	++++	+++	+++
b Свиная	++++	++++	++++	++++	+++	++++

Table 10 (Continued)

Продолжение табл.10

A Сыворотка	Номер рыбы B								
	7	8	9	10	11	12	13	14	15
a Лошадиная	++++	++++	+++	++	++	++	++	++	++
b Свиная	+++	+++	++	+++	++	++	++	++	++

Key: A - Serum B - Number of fish a - Horse b - Hog

Table 11. Agglutination of erythrocytes of the anchovy by absorbed hog serum (acc. to Altukhov et al., 1969a)

Таблица 11. Агглютинация эритроцитов анчоуса абсорбированной свиной сывороткой (по Алтухову и др., 1969а)

Свиная сыворотка, абсорбированная клетками, номер (A)	Номер рыбы (B)						
	1	2	3	4	5	6	7
I	—	—	—	—	—	—	—
II	+++	+++	++	++	+	++	++

Table 11 (Continued)

Продолжение табл. 11

Свиная сыворотка, абсорбированная клетками, номер (A)	Номер рыбы (B)							
	8	9	10	11	12	13	14	15
I	—	—	—	—	—	—	—	—
II	+	—	—	—	—	—	—	—

Key: A - Hog serum absorbed by cells, number B - Number of fish

The data presented in Tables 10 and 11 show that erythrocytes of 59
the positive group of the anchovy differ from one another in intensity of reactions. Together with cells agglutinated on "+++" and "++++" (Nos. 1-8) there are cells exhibiting substantially weakened reactions (Nos. 11-15). These differences are also confirmed by absorption experiments which introduce certain refinements into the results of determinations with whole serums. Thus it turns out that the exhaustion by cells of type "++" (No. 11) disposes of the antibodies for erythrocytes /literally "eliminates the antibodies towards the erythrocytes"/ reacting somewhat more strongly with any single reagent at all (Nos. 9 and 10). At the same time

all the erythrocytes agglutinated by the two serums with an intensity of 3 and 4 points retain their reactions. Thus is explained the supplementary differentiation of a positive group, and together with cells agglutinated by hog serum alone, three phenotypes are found, as we assumed above. Running ahead a little, we will point out that the Black Sea race of the anchovy is represented by those blood groups, whereas in the Azov race negative fishes whose cells are not agglutinated either by horse or hog serum are encountered with considerable frequency (third group).

Serological data regarding the Black Sea anchovy suggest the idea of two-allele determination of its erythrocytic antigens; moreover weakened reactions within the limits of the group of "positive" cells, caused, very probably, by the effect of the dose, must correspond to the heterozygotes A_1A_2.

The assumed structure of this genetic locus could be proven precisely by family analysis but is not feasible in practice, as no procedure has been developed for keeping anchovies a long time in an aquarium. Therefore only one way remains -- verification of the hypothesis directly on samples from natural populations.

Regarding the assumed heterozygotes A_1A_2 of those positive fishes whose cells weakly agglutinated with horse and hog serums (erythrocytes of 60
types Nos. 9-15 in Table 11), we made corresponding calculations on five sufficiently representative samples of the Black Sea anchovy, taken at different times and at different places of its range, and satisfied ourselves of the absence of any sort of essential divergences between the gametic and zygotic frequencies expected according to Hardy-Weinberg. Just such an unequivocal answer, testifying to the validity of the hypothesis of

the pair of alleles, was obtained in processing the total Black Sea catch without samples with negative fishes ($\chi^2 < 3.84$; $df = 1$; $p > 0.05$; Table 12).

Table 12. Verification of hypothesis of two-allele control of blood groups of the Black Sea anchovy (acc. to Altukhov et al., 1969a)

Таблица 12. Проверка гипотезы о двуаллельном контроле групп крови черноморского анчоуса (по Алтухову и др., 1969а)

A Место и дата взятия проб	N	Частоты B фенотипические a A_1	A_1A_2	A_2
1 Сочи, 10—13/VI 1963 . .	80	0,5750	0,3625	0,0625
2 Батуми, 14—16/VI 1963 .	65	0,3539	0,4922	0,1539
3 Одесса, VIII 1963 . . .	168	0,8216	0,1666	0,0118
4 Кабулетти, 23/II 1964 .	40	0,7500	0,2250	0,0250
5 Тобечик, 12/V 1965 . . .	40	0,6250	0,3500	0,0250
6 Суммарная выборка по Черному морю за 1963—1966 гг.	633	0,6746	0,2859	0,0395

Table 12 (Continued)
Продолжение табл. 12

A Место и дата взятия проб	N	Частоты B генные b pA_1	qA_2	χ^2
1 Сочи, 10—13/VI 1963 . .	80	0,7500	0,2500	0,22
2 Батуми, 14—16/VI 1963 .	65	0,6077	0,3923	0,63
3 Одесса, VIII 1963 . . .	168	0,8909	0,1091	0,39
4 Кабулетти, 23/II 1964 .	40	0,8419	0,1581	0,90
5 Тобечик, 12/V 1965 . . .	40	0,8419	0,1581	1,13
6 Суммарная выборка по Черному морю за 1963—1966 гг.	633	0,8013	0,1987	3,14

Key: A - Sampling place and date
B - Frequencies
a - phenotypical
b - genic
1 - Sochi, 10-13 June 1963
2 - Batumi, 14-16 June 1963
3 - Odessa, August 1963
4 - Kabuletti, 23 February 1964
5 - Tobechik, 12 May 1965
6 - Total catch for the Black Sea in 1963-1966

In the Azov race, as has been pointed out, negative races are also frequently encountered (this phenotype can be designated as A_0) and, consequently, here we have a right to assume three-allele determination, known, for example, for the P-system of blood groups of man (Sanger, 1955) and the M-system of the blood groups of cattle (Rendel, 1958). In that case the interrelations between the assumed alleles and the genotypes and phenotypes of blood groups of the anchovy are laid out in an orderly system adequate for the distinctive features of serological reactions (Table 13).

Table 13. Blood groups of the anchovy

Таблица 13. Группы крови европейского анчоуса

A Аллель	B Генотип	C Фенотип	Характер реакций с реагентами D: анти-A (свиная сыворотка) a	анти-A_1 (лошадиная сыворотка) b
A_1	A_1A_1 A_1A_2 A_1a	A_1	+	+
A_2	A_2A_2 A_2a	A_2	+	—
a	aa	A_0	—	—

Key: A - Allele B - Genotype C - Phenotype D - Character of reactions with reagents a - anti-A (hog serum) b - anti-A_1 (horse serum)

If this scheme is valid, then in the Azov anchovy the A_1 group must in the intensity of serological reactions be more heterogeneous than in the Black Sea anchovy, as the allele A_0 is not present in the latter (see Table 12). The same should also be expected for the phenotype A_2. In fact, we have repeatedly observed heterogeneity similar to

that assumed, but in not all cases have we succeeded with the same ease as in the Black Sea anchovy in separating the assumed homozygotes from the heterozygotes A_1A_2, since the reactions of those cells possibly overlap in intensity. Nevertheless, in a sample numbering 1056 specimens (1964) good correspondence of the actual frequencies of phenotypes and those expected according to Hardy-Weinberg was observed (χ = 2.39; df = 1). In five other samples the actual frequency of the assumed heterozygotes A_1A_2 was much below the expected (fluctuations of χ^2 from 13.36 to 43.51) in the presence of a simultaneous sharp increase for the water body as a whole in the concentrations of phenotypes A_1 and A_2 and a drop in group A_0 (Altukhov et al., 1969a).

Possible reasons for such shifts will be discussed below. Here we will only emphasize the admissibility of the proposed genetic hypotheses, pointing out simultaneously the need to develop an experimental approach 63
to substantiation of the genetic structure of this locus in family analysis.

The inheritance of antigens of the A-system of blood groups of the anchovy is demonstrated rigorously enough in a comparison of three successive generations of the Azov race as a whole (see Chapter V).

We will also point out, taking into account all the enormous amount of material gathered by V.V. Limanskii in four years of field work, the autosomal type of this inheritance.

Electrophoretic Variants of Proteins of Pacific Salmons

1. Lactate dehydrogenase (KF 1.1.1.27) l-lactate: NAD-oxydo-reductase. Henceforth abbreviated Ldh.

The results of investigations are illustrated by the series of photographs (Figure 16).

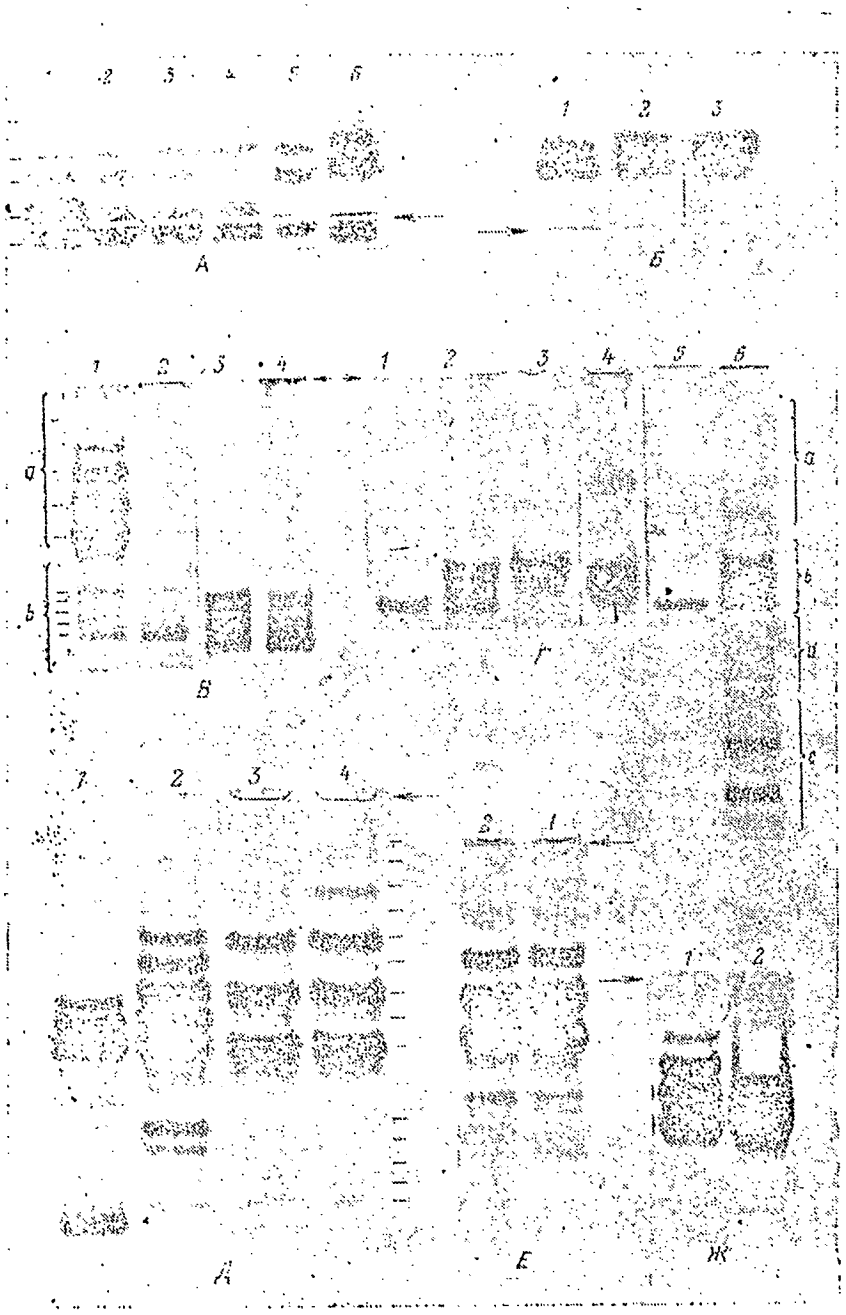

Figure 16. Isoenzyme spectra of lactate dehydrogenase of Pacific salmons. A - skeletal musculature of the keta: 1-5 - homozygotes AA; 6 - heterozygote A'A (electrophoresis in agar gel, 120 minutes, 6V/cm); B - keta blood serum: 1 and 3 - homozygotes FF and SS respectively; 2 - heterozygote FS (electrophoresis in agar gel, 75 minutes, 7 V/cm); C - skeletal musculature in blood serum from the same keta specimen (1 and 2 - electrophoresis in polyacrylamide gel, 180 minutes at 200 V); 3 and 4 - blood serum of "agar" types 2 and 1 respectively (electrophoresis in polyacrylamide gel 180 minutes at 200 V, 20 minutes at 250 V); D - various tissues

of keta: 1 - liver; 2 - intestines; 3 - heart; 4 - crystalline lens of eye; 5 - erythrocytes; 6 - eye (electrophoresis in polyacrylamide gel 140 minutes at 200 V and 10 minutes at 250 V); E - skeletal musculature of masu and keta: 1 - masu; 2 - heterozygote keta A'A; 3 and 4 - homozygote keta AA (electrophoresis in polyacrylamide gel, 200 minutes at 220 V); F - skeletal muscles of keta; homozygote (1) and heterozygote (2) individuals by genes of isozyme group b (electrophoresis in polyacrylamide gel, 165 minutes at 200 V and 15 minutes at 250 V); G - skeletal musculature of pink salmon (1) and coho (2) (electrophoresis in polyacrylamide gel, 165 minutes at 200 V). On all photographs the anode is from the bottom and the cathode from the top. Arrows indicate the starting positions. Remaining explanations are in the text.

On photographs A and B are "agar" zymograms for Ldg of muscles and blood serum of the keta respectively, and on subsequent ones, isozyme spectra developed by the method of acrylamide electrophoresis in different tissues of the keta, and also in some tissues of pink salmon, masu and coho. Since the "weak" bands of activity appearing as a result of difference in the quantity of synthesized subunits are unavoidably lost during photoreproduction or, on the other hand, due to the high activity of the enzyme the isozymes merge and we note their location in such cases with lines.

As is evident on the photographs, in extracts of the skeletal musculature of the keta agar electrophoresis reveals two groups of Ldg isozymes: one, negatively charged very little and consisting of four or five bands with diminishing intensity of coloration, and another, very negatively charged and represented maximally by two bands which remain at the start 64
(see Figure 16, A, 1-6). This second group of isozymes is also detected in blood serum, and under slightly different methodical conditions these proteins also move toward the cathode (see Figure 16, B, 1-3).

In a number of investigations (Massaro and Markert, 1968; Bouck and Ball, 1968) two groups of Ldg isozymes, consisting of five bands each,

have been detected by starch-gel electrophoresis in the skeletal muscles of some representatives of the family Salmonidae, in particular the rainbow trout Salmo gairdneri. They were designated as a and b by Massaro and Markert in order of decreasing cathode mobility. In addition, two more groups, d and e, have been found in the intestines and the eye (Figure 17). A very similar picture was also obtained by Bouck and Ball, who used electrophoresis in a block of acrylamide gel to investigate the isozyme composition of Ldg in different tissues of two species of chars: Salvelinus fontinalis and S. namaycush and the rainbow trout S. gairdneri. Still earlier, duplication of genes in loci A and B for the Ldg of Salmonidae was shown by Ohno and his co-workers (Klose et al., 1968).

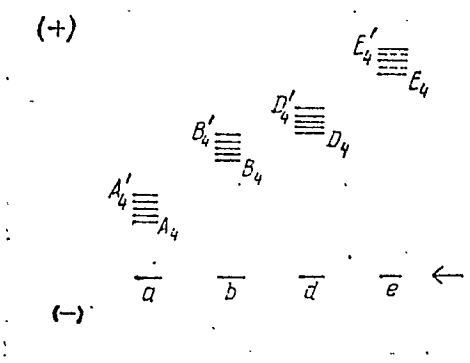

Рис. 17.

Figure 17. Schematic depiction of four izoenzymatic groups of lactate dehydrogenase, revealed by starch-gel electrophoresis in different tissues of rainbow trout. Group a - skeletal muscles; b - skeletal muscles and heart; d - intestines; e - isoenzymes specific for tissues of the eye; three other groups were also discovered in it (acc. to Massaro and Markert, 1968).

As for the keta, the results of electrophoresis in agar gel permit considering that we have found in the muscular tissue of that species the same isozyme groups as in other members of the family Salmonidae. This is confirmed in experiments with acrylamide electrophoresis. Thus, zymograms of the Ldg of blood serum and muscles from the same fish are shown in Figure 16, C, 1-2; the isozymes revealed in other investigated tissues

are in Figure 16, D, 1-6. It is clearly evident that for the tissues investigated by us and other authors (loc. cit.) the number of isozyme groups and their correlative mobilities coincide (see the legend under Figure 17). A difference is noted only in relation to the Ldg of the intestines: in the keta these isozymes belong to group b, and not to d 65
as in the trout.

In the pink salmon we have investigated in detail the isozyme spectra of Ldg of muscles, blood serum, erythrocytes and the crystalline lens of the eye, and in none of those tissues were differences from the keta found. In the coho (7 specimens from Sakhalin and 100 from Kamchatka) only the Ldg of muscles and blood serum was investigated. It turned out that the number and mobilities of serum isozymes in it are the same as in the two preceding species, whereas five isozymes of group a differ in mobility (see Figure 16, G, 1-2). The masu on the basis of the character of the Ldg of muscles -- the only tissue investigated so far in that species -- differs sharply from the keta, pink salmon and coho, but like them has two groups of isozymes. Thus, in all the species of the genus Onchorhynchus investigated by us, duplication of the genes of lactate dehydrogenase, reflecting their tetraploidy, is clearly traced.

With this fact taken into account there was a need for examination also of the individual variability of zymograms of the keta, pink salmon and sockeye. This variability was investigated in detail on muscular and serum groups of isozymes.

In Figure 16 A it is evident that keta No. 6 differs from the remaining fishes with respect to the muscular group of Ldg, but one cannot draw a conclusion about the number of bands because of their merging.

Acrylamide electrophoresis introduces clarity: agar type No. 6 proves to be represented by nine close bands (see Figure 16, E, 2), and in the extracts of fishes of agar types A, 1-5 only five bands are revealed which stand far apart (see Figure 16, E, 3-4). Variability of that sort, in accordance with theory (see Figure 14) and the data of family investigations (Shaw and Barto, 1963; Odense et al., 1966; Goldberg, 1966; Morrison and Wright, 1966), testifies to the presence of mutation at the locus A for Ldg. Consequently, individuals represented by five izozymes standing far apart must have the homozygotic genotype AA; fishes which have nine isozymes correspond to the heterozygotes A'A; homozygotes A'A', characterized by five close bands (see Figure 14) are extremely rare on Sakhalin but are encountered rather often on the Kuril Islands.

Verification of the hypothesis shows precise correspondence of the actual numbers of genotypes with that expected from the Hardy-Weinberg equation ($\chi^2 = 0.32$; $df = 1$; Table 14).

These data can now be supplemented by a family analysis made by us. Since the frequencies of the two phenotypes with respect to Ldg are low among stocks of keta and the crossing were accomplished blindly, in more than 50 random combinations of pairs we encountered only three 66
out of six possible genotypical combinations. Nevertheless these data (Table 15) quite definitely indicate, as was to be expected, the co-dominant type of inheritance.

A fish with nine isozymes on the basis of the serum group of Ldg has been discovered only once on Sakhalin, in a sample (N = 250) from the population of the Tym' River (see Figure 16, F, 2). As regards hundreds of other fishes from various Sakhalin, Kuril and Kamchatka rivers, in

Table 14. Distribution of electrophoretic variants of lactate dehydrogenase in the Naiba keta population

Таблица 14.

	A Сроки сбора материала	Постулированные генотипы B для мышечной группы изоферментов a			N	Частота гена C	
		BBAA	*BBA'A*	*BBA'A'*		Ldh^A	*F*
1	Октябрь, 1968 г.	130 (129,96)	14 (13,68)	0 (0,36)	144	0,95	0,87
2	Октябрь—ноябрь 1969 г.	455 (451,59)	35 (37,63)	0 (0,78)	490	0,96	0,85

Примечание. Здесь и в последующих аналогичных таблицах в скобках приводится ожидаемая численность.

для сывороточной группы изоферментов b			N
FF	*FS*	*SS*	
88 (87,04)	26 (26,02)	1 (1,94)	115
213 (210,25)	71 (74, 20)	7 (6, 55)	291

Key: A - Sampling dates
B - Postulated genotypes
a - for muscular group of isoenzymes
b - for serum group of isoenzymes
C - Gene frequency
1 - October 1968 2 - October-November 1969
Note. Here and in following similar tables the expected numbers are presented in parentheses.

them the Ldg of serum on acrylamide zymograms is represented by only five bands (see Figure 16, C, 2-4). In the agar variant of the method those phenotypes contain two bands of equal intensity (see Figure 16, B, 2) or can give weak coloration from the cathode and the anode sides of the zymogram (compare Figure 16, B, 1 and 3). At the same time, in the investigation of serum of such fishes in acrylamide gel, the five isozymes just spoken of are always revealed, and the weakening of coloration is parallel to that observed on agar zymograms (compare Figure 16, B, 1 and C,4; B, 2 and C, 3). It is clear that such variability is quantitative and not qualitative, but the observed variations are so discrete and always reproducible, that they can also be given a formal genetic interpretation (see Table 14). Calculations testify to the absence of contradictions between the really observed distribution and our genetic hypothesis, according to which the type showing two equally active bands (on agar) or five (on polyacrylamide) must be regarded as heterozygotic (we will conventionally designate it as FS) and the two others as the homozygotes FF and SS*.

Table 15. Inheritance of types of muscular Ldg in the keta

Таблица 15. Наследование типов мышечной ЛДГ у кеты

A Генотипы родителей	Генотипы потомства B			
	AABB	*A'ABB*	*A'A'BB*	*N*
AABB × *AABB*	80	—	—	80
AABB × *A'A'BB*	—	45	—	45
AABB × *A'ABB*	39	39	—	78

Key: A - Genotypes of parents B - Genotypes of offspring

*From the initial letters of the words "fast" and "slow".

Consequently, polymorphism is revealed with respect to both the muscular and serum groups of isozymes of Ldg of the keta. But if in the case with muscular Ldg its genetic nature is connected with the presence of a third subunit of the heterozygotes, for isozymes of blood serum, with the exception of one case (see Figure 16, F, 2) such a conclusion is unacceptable. At the same time, on the basis of population data (see Table 14) this variability also can be treated as hereditary, reflecting polymorphism of the corresponding regulator gene.

A similar variability of serum Ldg is observed also in the pink salmon (Altukhov et al., 1968) and the coho. However, polymorphism is not found with respect to the muscular group of isozymes of those species, 69
although over 500 specimens of pink salmon have been investigated from various rivers of Sakhalin, Kamchatka and the Kuril Islands, and over 100 coho.

Hereditary variability in the autosomal locus of serum Ldg in the sockeye has been discovered by American investigators (Hodgins and Utter, 1969), who used electrophoresis in starch gel. The polyacrylamide variant of the procedure adopted in our laboratory permits obtaining data agreeing completely with the results of Utter and Hodgins (Figure 18, A.) The only difference is that in our procedure still another invariant isoenzymatic group of Ldg is successfully found in the muscles of the sockeye, as well as of other Salmonidae.

2. Phosphoglucomutase (alpha-D-glucose-1,6-diphosphate: alpha-D-glucose-1-phosphate of phosphotransferase; KF 2.7.5.1; henceforth abbreviated Pgm).

Figure 18. Electrophoretic variants of proteins in Pacific salmons. A - serum lactate dehydrogenase of the sockeye: 1 - homozygote AAB'B'; 2,3,5,6 - homozygotes AABB; 4,7 - heterozygotes ABB'B (electrophoresis in polyacrylamide gel); B - phosphoglucomutase of muscles of the sockeye; 1,7 - heterozygotes AB; 6 - homozygote AA; 3-5 - homozygotes BB (electrophoresis in starch gel); C - phosphoglucomutase of muscles of the keta. Monomorphism (electrophoresis in starch gel); D - erythrocytic glucose-6-phosphate dehydrogenase of the keta. Monomorphism (electrophoresis in polyacrylamide gel); E - serum esterase of the keta. Monomorphism (electrophoresis in polyacrylamide gel); F - serum albumins of the keta: 1 and 6 - homozygotes CC and DD respectively; 2 and 3 - heterozygotes AC; 4 - heterozygotes CD; 5 - heterozygote BC (electrophoresis in starch-agar gel); G - malate dehydrogenase of muscles of the keta (electrophoresis in polyacrylamide gel). The anode is from the bottom and the cathode from the top on all photographs.

Two-allele polymorphism of the autosomal gene Pgm of muscles, described in the sockeye by Utter and Hodgins (1970), was discovered almost simultaneously also in our laboratory by E.A. Salmenkova under somewhat different methodical conditions (Figure 18, B).

In the keta the locus of Pgm in all the investigated populations is represented by two bands moving toward the anode. This corresponds to a constantly heterozygotic state, reflecting duplication of the corresponding alleles (Figure 18, C).

3. Glucose-6-phosphate dehydrogenase (D-glucose-6-phosphate: NAD-oxide reductase, KF 1.1.1.4º) has been investigated in the erythrocytes of the keta, pink salmon and sockeye (hundreds of individuals) from different populations. In all cases constant heterozygoticity is maintained, which permits speaking about a mechanism of duplication similar to that observed in relation to the locus of Pgm (Figure 18, D).

4. Esterase of blood serum and muscles (henceforth abbreviated Es) can be classed in the group of nonspecific enzymes, regarding the 70
molecular bases of the multiplicity of which almost nothing is known (Salmenkova, 1973), although in accordance with the general principles of biochemical genetics it is logical to treat each zone of activity on the electrophoregram as corresponding to a single locus.

Esterases investigated in the keta and sockeye proved to be monomorphous and represented by two or more fractions. A photograph of an electrophoregram of esterase of the keta (Figure 18, E) is presented as an example.

5. alpha-Glycerophosphate dehydrogenase of muscles (L-glycerol-3-phosphate: NAD-oxide reductase, KF 1.1.1.8), investigated in the keta,

gives on our electrophoregrams at least two groups of fractions of different intensity. If the same scheme "one gene -- one band on the zymogram" as in the preceding cases is adopted, which is most suitable for the given situation, it can be considered that the enzyme is coded, as a minimum, by two loci. In one of them a rare, probably allele, variation is observed (Altukhov et al., 1972). That locus is monomorphous in the sockeye.

6. Albumins of blood serum. Electrophoresis in starch-agar gel reveals in keta blood serum polymorphism of the fastest protein fraction, comparable in mobility with purified albumin preparations of different origin. The presence in that zone of five electrophoretic variants represented by one or two bands with different mobility and not revealing in their distribution a connection with sex, forces one to assume either a two-loci structure of that system (taking into account that the Pacific salmons are tetraploids) with several alleles in each locus, or single-locus with four alleles, as is represented in Figure 18 F. 71

It must be pointed out that the types designated here as AC and BC were encountered relatively rarely in the examined populations*, and the most frequent variants with a universal distribution were C, CD and D; the last-mentioned type always has a minor zone which almost coincides in mobility with zone C.

*In three field seasons the phenotype AC was encountered in 21 out of 1275 investigated individuals of the Naiba keta, in 1 out of 329 specimens of the Tym' keta, in 2 out of 346 specimens of the Kuril keta, and not once in the Kalininka stock (N = 526 specimens).

Table 16. Distribution of genotypes of albumin in the Naiba population of the keta upon the assumption of panmixia (F = 0) and with correction for subdivisibility (F = 0.114 ± 0.02)

Таблица 16

1 Номер пробы	2 Дата взятия проб	Alb^{CC}			Alb^{CD}		
		N_0	N_E		N_0	N_E	
			$F=0$	$F=0,11$		$F=0$	$F=0,11$
1	20/X	56	53,62	54,94	19	23,75	21,14
2	27/X	23	22,56	24,26	30	30,87	27,48
3	2/XI	20	20,25	21,98	32	31,50	28,03
4	9/XI	52	48,23	51,01	43	50,53	44,98
5	13/XI	32	32,40	34,78	44	43,20	38,45
6	23/XI	65	63,38	64,98	26	29,25	26,03
1—6	20/X—28/XI	248	235,22	247,18	194	219,55	193,79

Примечание. N_0 — фактическая численность генотипов; N_E — ожидаемая численность.

Alb^{DD}			N	χ^2		$qAlb^C$
N_0	N_E			$F=0$	$F=0,11$	
	$F=0$	$F=0,11$				
5	2,63	3,60	80	2,14	0,78	0,8187
11	10,57	12,26	64	0,05	0,42	0,5937
12	12,25	13,98	64	0,02	1,02	0,5625
17	13,24	16,02	112	2,45	0,17	0,6562
14	14,40	16,73	90	0,03	1,48	0,6000
5	3,37	4,98	96	1,17	0,01	0,8125
64	51,23	65,05	506	7,12	0,02	0,6818

Note. N_0 is the actual number of genotypes; N_E is the expected number.

Key: 1 - Number of sample 2 - Date sample was taken

Since a large enough volume of blood is necessary for electrophoretic analysis of albumin, it is impossible to explain the assumed mechanism of gene control of that variability in family analysis -- the

fingerlings of the keta grow at Sakhalin plants to several hundred milligrams and then migrate to the sea. If we assume, however, the probability of panmixia in the keta populations, our hypothesis can be verified on separate samples by comparison of the actual distribution of phenotypes with that expected from the Hardy-Weinberg binomial law. At this stage we deliberately simplify the scheme of analysis, taking into account only types D (slow homozygote), CD (heterozygote) and C (fast homozygote), that is, we assume a single-locus two-allele system* (Table 16). 72

As is evident from Table 16, in none of the investigated samples and no phenotypical class are there reliable differences between the theoretical and empirical distribution, and so the real picture does not contradict the genetic hypothesis adopted by us.

At the same time the individual samples differ in their phenotypical and gene frequencies, and characteristic of the stock as a whole is a statistically significant deficit of heterozygotes. These facts are discussed in detail in the following chapter.

7. Malate dehydrogenase (L-malate; NAD-octidoreductase; KF 1.1. 1.37; henceforth Mdh).

Polymorphism in the autosomal locus of the cytoplasmic form of malate dehydrogenase of the keta and pink salmon, discovered by V.I. Slyn'ko (1971), is represented by four electrophoretic variants (Figure 18 D). Two types of the four were described later by Numachi et al. (1972).

*In other calculations it turned out that the hypothesis of a two-loci structure of albumin polymorphism with two alleles in one locus, as discussed above, and with three in the other (zone C being considered common to both systems) is in accordance with empirical distributions.

Since in other Salmonidae Mdh is a dimer (Baailey et al., 1969), it can be considered that the observed variability in the keta is caused by two, probably uncoupled loci with a pair of alleles in each, some homodimers overlapping in electrophoretic mobility. In such an interpretation type 1 is the homozygote AA, type 2 the heterozygote AB, type 3 the heterozygote AC and type 4 the diheterozygote. The validity of the hypothesis for the corresponding pairs of alleles is confirmed by the results of crossing (Table 17).

Table 17. Inheritance of types of malate dehydrogenase in the keta

Таблица 17. Наследование типов малатдегидрогеназы у кеты

A Фенотипы родителей	B Фенотипы потомства			N
	A	*AB*	*AC*	
A × *A*	50	—	—	50
A × *AB*	57	57	—	114
A × *AC*	23	—	23	46

Key: A - Phenotypes of parents B - Phenotypes of offspring

Until the genetic structure of the loci of malate dehydrogenase is completely deciphered we will use as a basis the described scheme, assuming that at least the genetic nature of this polymorphism is unquestionable. We have not once encountered the homozygotes BB and CC among the investigated fishes, which probably indicates the lethality of the corresponding alleles, or their extremely rare occurrence in the studied

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populations. Type No. 4 also has a low frequency (1:1500). Therefore for population comparisons this system can be regarded as a two-allele one, finding the frequency of the one most frequent gene by extracting the square root of the relative number of the phenotype A and the frequency of the other gene by adding the found value up to unity.

In the investigations of Bailey and Wilson and ours in the sockeye the locus of Mdg proved to be monomorphous.

Such proteins, different in localization and function, as aspartate aminotransferase and tetrazolium oxidase also are monomorphous or extremely weakly variable in populations of different species of Salmonidae, water-soluble proteins of muscles are myogens, and water-soluble proteins of the crystalline lens of the eye and hemoglobins are crystallins. It is clear that invariant characters give nothing for the study of population genetics. On the contrary, analysis of that sort is accomplishable on the basis of those genetic systems which have proven to be polymorphous. On the basis of these data we can proceed to examine the variability of frequencies of corresponding phenotypes, genotypes and genes within the limits of and on the level of different local stocks (or races) which have been selected as the objects of the present investigation.

Chapter V. Local Stocks as Reproductively Isolated, Genetically Heterogeneous Populations

Of the morphological, biological and ecological characteristics of the populations selected for analysis it already is possible to speak of their spatial isolation. Especially essential is the circumstance that besides the isolation caused by obvious physical geographical barriers or

distinctive features of reproductive behavior, local differentiation has proven to be mathematically unavoidable for the simple reason that two individuals of opposite sex have far greater chances of meeting and leaving posterity when they are in each other's neighborhood than at a distance 74
exceeding the radius of their activity -- so-called isolation by distance (Wright, 1943).

Since a mathematical model reflects a certain general regularity, we have the right to expect some uniformity of the population genetic structure in the most differing species in nature. And, actually, in field investigations corresponding facts have been obtained, at least, with regard to the demonstration of the dispersion of gene frequencies over an entire range in the absence of any geographical barriers whatsoever.

A "range effect" of that sort (Cain and Curry, 1963a and b), corresponding to a great extent to the model in the analysis of any sort of relatively immobile species consisting of small colonies, such as the terrestrail mollusk Cepaea nemoralis, appears to be less probable for fishes whose species are at times extremely mobile and numerous and are characterized by external fertilization.

Nevertheless, in the first investigtion of spawning accumulations of anchovy scattered over the entire area of the Sea of Azov we encountered strong spatial variability of the frequencies of blood group factors. The discovery of such heterogeneity, at first glance, it would appear, of a panmictic population, gives rise to two consequences which predetermine the character of further work.

Firstly, it becomes evident that in order to characterize a stock (or race) as a whole it is impossible to limit oneself to the analysis of

random samples, and it is necessary to investigate a sufficiently large number of samples, more or less uniformly distributed in space or time.

Secondly, the genetic unity itself of the race or stock as a starting prerequisite for its selection as an object of a population genetics investigation can be put in doubt, requiring special argumentation.

We will present that argumentation mainly in the conclusion of the work, and in the present chapter present proofs of the reproductive isolation of stocks and show their genetic heterogeneity, revealed in a broad genogeographical investigation. It is clear that the simultaneous clarification according to the principles and by the methods of genetics of a number of features of the biology of those populations which were unclear earlier is a component part of such analysis.

Genetic Differences of Local Stocks of Redfish. Heterogeneity of a Separate Stock

Distinctive features of the spatial distribution of the blood group factor A_2 in redfish accumulations on the Flemish Cap bank and the Newfoundland Grand Bank are evident from Table 18 and the corresponding figures. The table was constructed so that it might be possible to form 75
a judgment about the time of catching the fishes, the number of fishes taken for analysis and the gene frequency in each sample. The spatial localization of the trawling stations is shown in Figure 19. The obtained data testify to substantial genetic differences of all Flemish Cap bank samples from the Grand Bank samples: in the first case the A_2 76
factor is close to fixation (fluctuations in individual samples from 0.91

Table 18. Frequency of blood group A_2 in samples from accumulations of redfish on the banks of the Newfoundland region of the Atlantic (1965)

Таблица 18. Частота группы крови A_2 в выборках из скоплений морского окуня на банках Ньюфаундлендского района Атлантики (1965 г.)

Номер проб (A)	Дата вылова (B)	N	qiA_2	Номер проб (A)	Дата вылова (B)	N	qiA_2
1	3/IX	40	0,97	37	21/IX	60	0,86
2	3/IX	38	0,51	38	22/IX	40	0,67
3	4/IX	40	1,00	39	23/IX	40	0,77
4	5/IX	20	1,00	40	24/IX	40	0,95
5	5/IX	60	1,00	41	25/IX	40	0,95
6	5/IX	40	0,97	42	25/IX	40	0,89
7	5/IX	20	1,00	43	26/IX	40	0,59
8	5/IX	40	0,92	44	27/IX	60	0,63
9	6/IX	40	1,00	45	27/IX	32	0,71
10	6/IX	80	1,00	46	28/IX	40	0,50
11	6/IX	60	1,00	47	28/IX	60	0,48
12	6/IX	60	1,00	48	28/IX	60	0,45
13	6/IX	60	1,00	49	2/X	60	0,88
14	7/IX	50	1,00	50	3/X	60	0,75
15	7/IX	80	1,00	51	4/X	60	0,71
16	7/IX	100	0,99	52	4/X	60	0,73
17	7/IX	58	1,00	53	5/X	60	0,61
18	7/IX	60	0,95	54	5/X	60	0,52
19	8/IX	78	0,99	55	6/X	60	0,68
20	8/IX	40	0,97	56	6/X	60	0,76
21	9/IX	40	1,00	57	6/X	60	0,77
22	12/IX	60	0,96	58	7/X	60	0,73
23	12/IX	60	0,91	59	7/X	60	0,63
24	13/IX	60	0,93	60	8/X	60	0,77
25	15/IX	40	0,81	61	10/X	60	0,73
26	15/IX	40	0,95	62	10/X	60	0,84
27	15/IX	40	0,87	63	10/X	60	0,85
28	16/IX	60	0,89	64	11/X	60	0,84
29	16/IX	60	0,85	65	11/X	60	0,84
30	16/IX	60	0,71	66	15/X	60	0,73
31	16/IX	60	0,83	67	15/X	60	0,89
32	19/IX	60	0,79	68	16/X	60	0,89
33	19/IX	60	0,79	69	17/X	60	0,35
34	20/IX	60	0,71	70	17/X	60	0,71
35	20/IX	40	0,63	71	17/X	60	0,68
36	20/IX	40	0,84	72	17/X	52	0,68

Key: A - Number of sample B - Date of catch

to 1.00; $\bar{q} = 0.95 \pm 0.02$); in the second a considerable dispersion of the gene frequencies is observed (from 0.35 to 0.95; $\bar{q} = 0.73 \pm 0.01$). If the genogeography of the A_2 factor on the Newfoundland bank is presented in rather rough and, consequently, reliable frequency intervals, then the

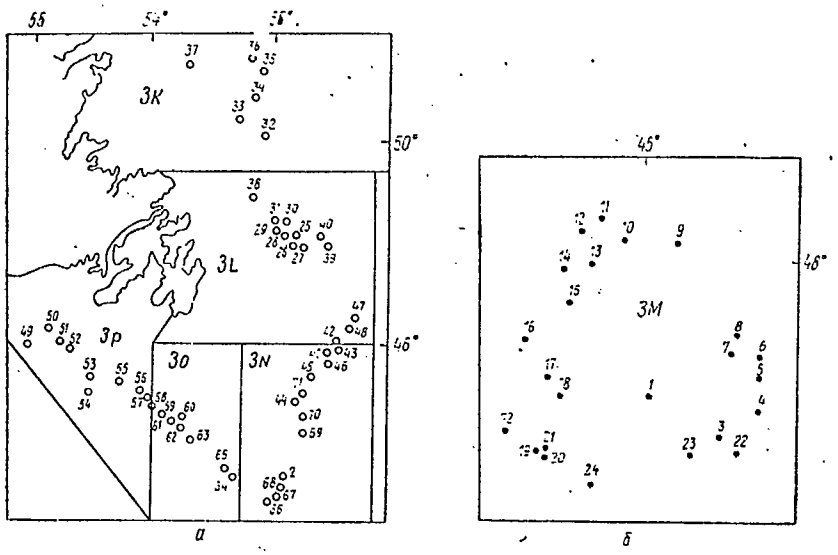

Рис. 19. Пространственная локализация траловых уловов окуня, исследованного иммуногенетически на Ньюфаундлендской банке (*а*) и на банке Флемиш-Кап (*б*). Нумерация станций соответствует принятой в табл. 18.

Figure 19. Spatial localization of trawler catches of redfish examined immunologically on the Newfoundland bank (a) and on the Flemish Cap bank (b). The numbering of the stations corresponds to that used in Table 18.

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mosaic character of its spatial distribution is evident (Figure 20). Reliable frequency differences are also registered on the level of separate hauls (Figure 21).

For the Flemish Cap bank it would have been necessary to paint 77
a similar map with only one color.

In a formal evaluation of the examined materials, conclusions should be drawn about the genetic homogeneity of the redfish of the Flemish Cap bank and the considerable heterogeneity of the population of the Grand Bank. Such an interpretation is unquestionable only in its latter part, as the absence of variations on a single locus cannot be considered proof of homogeneity of the investigated population; we will turn to this again, but here will point out the good agreement of the immunogenetic data with

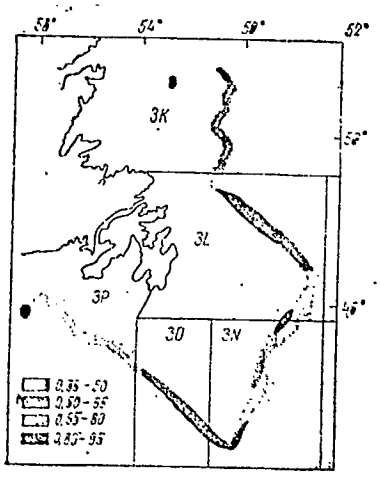

Figure 20. Spatial localization of A_2 blood group in accumulations of deepwater redfishes on the Grand Bank of Newfoundland. Hatching indicates frequency of occurrence of gene of blood group A_2 as %.

Рис. 20. Пространственная локализация группы крови A_2 в скоплениях кловорылого окуня на Ньюфаундлендской банке. Штриховка указывает частоту встречаемости гена группы крови A_2 в %.

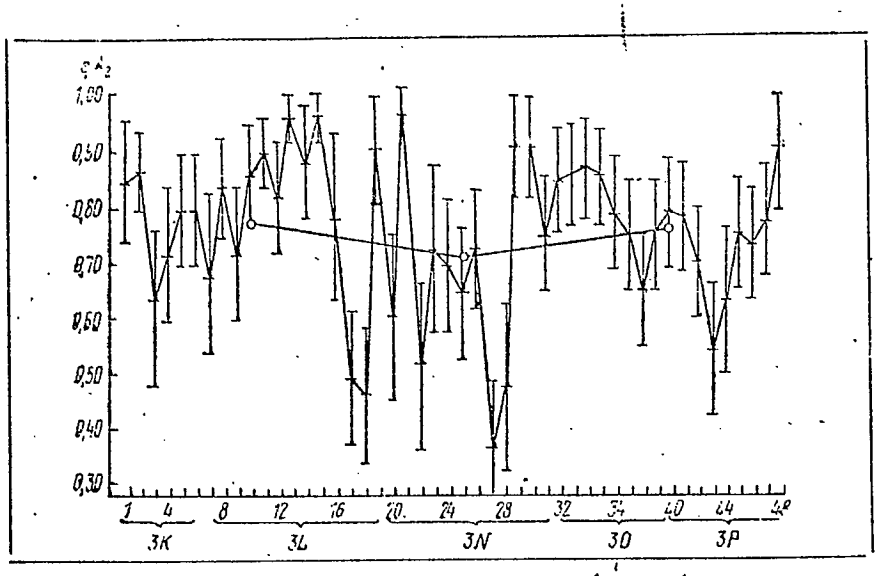

Рис. 21. Колеблемость частоты гена группы крови A_2 в выборках из скоплений окуня на Большой Ньюфаундлендской банке.

Figure 21. Fluctuation of the frequency of the gene of the A_2 blood group in hauls from accumulations of redfish on the Newfoundland Grand Bank. Lines with confidence intervals represent gene frequencies in individual hauls; light circles represent the gene frequency in the assumed stocks (zones 3K and 3L respectively on the one hand and 3O and 3P on the other) and in zone 3N. Numbers of samples are on the axis of abscissas (X-axis).

the results of morphological and biological investigations of K.P. Yanulov with respect to his conclusion about the sharp apartness of the Flemish Cap stock. As for the conclusion that several genetically separated stocks live on the Grand Bank, already in a hasty glance at the frequency distribution of the A_2 factor in hauls from redfish accumulations it is evident that that variability is irregular and comparable in different ranges. If one calculates the /numerical/ values of the character for the assumed stock localized in the northern part (samples Nos. 1-9; zones 3K and 3L) for the stock on its southwestern slope (samples Nos. 32-48, zones 3O and 3P) and simultaneously for redfish accumulations in zone 3N (samples Nos. 20-31), not investigated in detail and almost not discussed at all by K.P. Yanulov, then the irregularity of that variability becomes still more evident. On the basis of the given character (see Figure 21) there are no reliable differences between the stocks separated here; an accumulation is also weakly distinguished in zone 3N. 78

The same thing is indicated also by the variational statistical frequency distribution of the A_2 factor: when the samples taken on the Grand Bank are combined, a single series forms which satisfactorily follows the normal distribution law, whereas the addition of samples from the Flemish Cap bank sharply deforms it (Figure 22).

Moreover, as regards the number of vertebrae, regarded by K.P. Yanulov as the most important differentiating character, on the Grand Bank a clear wedge variability is observed from zones 2I and 3K through zones 3L, 3N, 3O and 3P toward zones 4V, 4W and 4X; a slight disruption of the wedge, probably caused by randomness of the haul, is noted only in zone 3N. However, the fish accumulations on the Flemish Cap bank differ sharply with respect to this character.

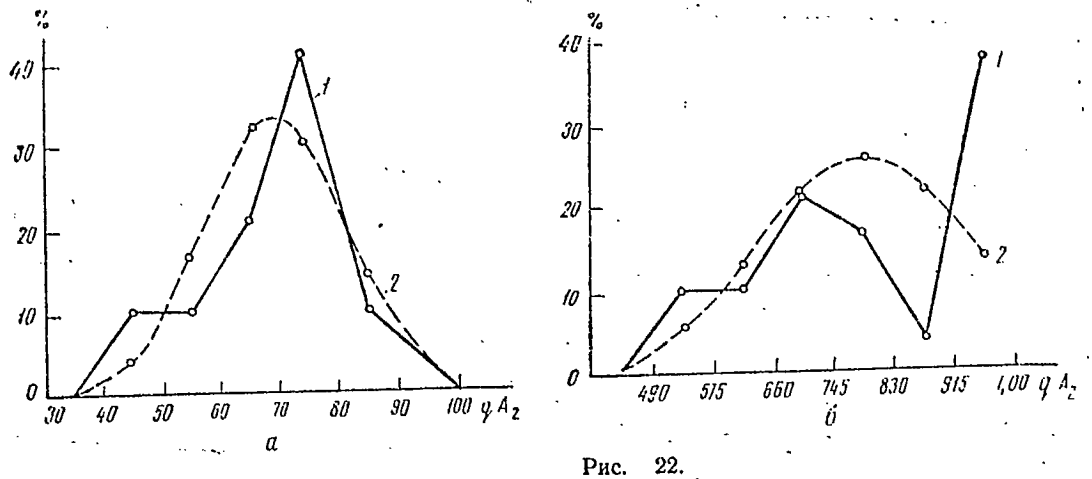

Рис. 22.

Figure 22. Spatial distribution of gene frequencies on the Grand Bank of Newfoundland (a) and on the entire investigated range (b): 1 - empirical series; 2 - theoretical curve of normal distribution law. For species a: n = 48, χ^2 = 5.73 and df = 3; for species b: n = 72, χ^2 = 22.38 and df = 3.

We present below the average number of vertebrae of fishes in the different ICNAF zones (according to Yanulov, 1962a). 79

Зоны ИКНАФ A	Среднее число позвонков B M ± m	Зоны ИКНАФ A	Среднее число позвонков B M ± m
2I	30,54±0,032	*3O*	30,17±0,015
3K	30,62±0,027	*3P*	30,17±0,034
3L	30,25±0,015	*4V*	30,16±0,010
3M	31,05±0,015	*4W*	30,11±0,031
3N	30,39±0,019	*4X*	30,04±0,019

Примечание. Значение, характерное для банки Флемиш-Кап, подчеркнуто.

Key: A - ICNAF zone B - Mean number of vertebrae, M ± m
Note: The value characteristic of the Flemish Cap bank is underlined.

Finally, besides blood group variability, we simultaneously investigated the polygenic character l/d -- the ratio of the length of the otolith to its width. The diagnostic importance of this character for fishes has been demonstrated in a number of investigations (Morovic, 1955;

Kotthaus, 1961a; Skazkina, 1965; Altukhov and Mikhalev, 1964*; Nefedov, 1969); the materials cited here testify to the same thing (Figure 23). It is evident from the figure that the genetically isolated Flemish Cap redfish stock differs sharply both in the mean value of the index and also in the range of its variations from redfish accumulations on the Newfoundland Grand Bank ($P < 0.001$), where differentiation of the assumed stocks is not detected. Simultaneously the variability of that character in separate hauls, in the same way as the corresponding data regarding blood groups, indicates heterogeneity of the studied fish accumulations not only in the Newfoundland region but also on the Flemish Cap bank.

Consequently the facts testify to a substantial genetic community of the Newfoundland redfish stock, which evidently represents (as has already been emphasized) an aggregate of more elementary populations which interchange to some degree. In fact, on the basis of parasite "tags" K.P. Yanulov has identified fishes which migrated from zones 2J and 3K to zone 3L. An admixture of fishes having common features with the redfishes of zone 30 and even with those of Southern Labrador also has been discovered in zone 3N; unfortunately, neither K.P. Yanulov nor we have investigated that region in sufficient detail.

At the same time the interchange between stocks seems far less 80
intensive than between populations within the stocks which have been

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*T.E. Saf'yanova and N.I. Revina (1965) dispute the conclusions of this work, but their criticism does not deal in any way with the facts published by us and therefore cannot be accepted. However, the authors' own material gives rise to legitimate perplexity, as they did not explain the method of differentiating "large" and "small" forms of the Black Sea scad in a mixed haul.

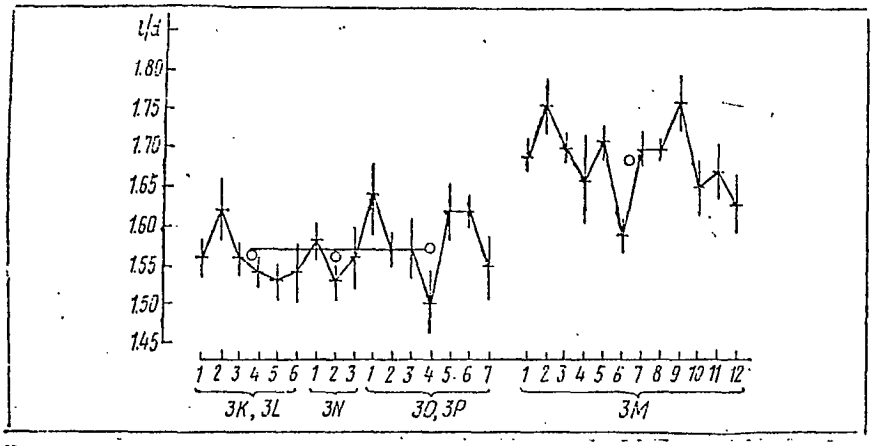

Рис. 23.

Figure 23. Variability of the index 1/d of otoliths of redfish on the level of local stocks as a whole (light circles) in comparison with variability within the stock (lines with confidence intervals).

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determined up to now indirectly. The sharp differences between stocks with respect to a number of characters testify above all to this.

Our own results establish an extremely limited admixture of Newfoundland fishes on the Flemish Cap bank (see Table 18, sample No. 72), which agrees well with the data of K.P. Yanulov. During his investigations, made 4-5 years before ours, on the same southern slope of the Flemish Cap bank redfish with 30 vertebrae also were caught from time to time and, what is especially important, the females there had stages III, IV and V of maturity of the sexual glands, whereas in the remaining parts of the Flemish Cap bank the gonads of all the females were in the post-spawning stages VI and VII. Thus reproductive isolation between the stocks is present also with regard to this basic character.

On the basis of what has been said we draw the following conclusions.

1. In accordance with the morphological and biological data, in the Newfoundland region of the Northwest Atlantic immunogenetic investigation reveals two reproductively isolated stocks of redfish -- the Flemish Cap and the Newfoundland. The A_2 blood group factor, which is near fixation on the Flemish Cap bank, is encountered more rarely on the Grand Bank.

2. The sharp and differently directed variability of frequency of the A_2 factor in the range of the redfish on the Grand Bank can be an indication that the stock is subdivided into smaller, genetically different population units. In the population localized on the Flemish Cap bank such subpopulations were not discovered in the investigation of that genetic locus. However, such a subdivision is detected on the basis of variability of a quantitative character -- the otolith length-width ratio. 81

3. The character of variability of the redfish with respect to an immunogenetic character and some polygenic morphological features with consideration of ecological data permits assuming that the subdivision of the stocks does not reflect the gathering together of any sort of heterogeneous populations but occurs within a single aggregate.

Genetic Differences of the Azov and Black Sea Races of the Anchovy. The Heterogeneity of the Azov Race

The space-time distribution of blood groups of the A-system in anchovy accumulations is reflected in Tables 19 and 20 and on the genographic maps (Figures 24-27).

Between the Azov and Black Sea races, when they are reproductively isolated and, consequently, correspond most to what has been described as

Table 19. Frequency of blood groups in hauls of anchovy from the Sea of Azov and the Black Sea

Таблица 19. Частота групп крови в выборках анчоуса из Азовского и Черного морей

A Море	B Номер выборок	C Место взятия проб и дата	n	Частоты D: фенотипические a A_1	A_2	A_0	генные[1] b p	q	r
Азовское of Azov	1	Июль, август 1963 г.	551	0,5699	0,1379	0,2922	0,3442	0,1152	0,5406
	2	Июль, сентябрь 1964 г.	1056	0,4384	0,0966	0,4650	0,2513	0,0678	0,6809
	3	Июнь 1965 г.	848	0,5993	0,1751	0,2256	0,3668	0,1582	0,4750
	4	Август 1965 г.	810	0,5234	0,2383	0,2383	0,3097	0,2021	0,4882
	5	Сентябрь 1965 г.	736	0,5636	0,2856	0,1508	0,3396	0,2721	0,3883
	6	Август 1966 г.	1932	0,7914	0,1775	0,0311	0,5432	0,2804	0,1764
Итого по Азовскому морю 1963—1966 гг.		Total for Sea of Azov 1963-1966	5936	0,6157	0,1808	0,2035	0,3240	0,2248	0,4512
Черное Black	7	Ялта, 18 марта 1963 г.	16	0,8750	0,1250	—	0,6465	0,3535	—
	8	Поти, 12 мая 1963 г.	20	0,9500	0,0500	—	0,7760	0,2240	—
	9	Ольгинка, 23, 25 мая 1963 г.	39	0,9500	0,0500	—	0,7760	0,2240	—
	10	Сочи, 10—13 июня 1963 г.	80	0,9375	0,0625	—	0,7500	0,2500	—
	11	Батуми, 14—16 июня 1963 г.	65	0,8461	0,1539	—	0,6077	0,3923	—
	12	Сулина, 26—28 июня 1963 г.	30	0,9000	0,1000	—	0,6840	0,3160	—
	13	Одесса, август 1963 г.	168	0,9882	0,0118	—	0,8909	0,1091	—
	14	Новороссийск, 27—29 февраля 1964 г.	90	0,7111	0,0111	0,2778	0,4620	0,0100	0,5280
	15	Кабулети, 23 февраля 1964 г.	40	0,9750	0,0250	—	0,8419	0,1581	—
	16	Балаклава, 6 августа 1964 г.	45	1,000	—	—	—	—	—
	17	Одесса, 21—27 июня 1964 г.	108	0,8148	0,0555	0,1297	0,5697	0,0701	0,3602
	18	Тобечик, 12 мая 1965 г.	40	0,9750	0,0250	—	0,8419	0,1581	—
	19	Новороссийск, 13 мая 1965 г.	20	1,000	—	—	—	—	—
	20	Новый Афон, 19 мая 1965 г.	40	1,000	—	—	—	—	—
	21	Сочи, 9 декабря 1965 г.	80	0,5625	0,3250	0,1125	0,3385	0,3261	0,3354
	22	Сочи, 8—16 октября 1966 г.	67	0,9552	0,0149	0,0299	0,7883	0,0388	0,1729
	23	Новороссийск, 17—18 октября 1966 г.	20	0,9092	0,0454	0,0454	0,6972	0,0895	0,2135
	24	Мыс Такиль, 20 октября 1966 г.	30	1,000	—	—	—	—	—
Итого по Черному морю 1963—1966 гг.		Total for Black Sea 1963-1966	998	0,8890	0,0600	0,0510	0,6668	0,1074	0,2258

Table 19 (Continued)

Key: A - Sea samples B - Number of haul C - Place and date of taking D - Frequencies a - phenotypical b - gene

1 - July and August 1963
2 - July and September 1964
3 - June 1965
4 - August 1965
5 - September 1965
6 - August 1966
7 - Yalta, 18 March 1963
8 - Poti, 12 May 1963
9 - Ol'ginka, 23, 25 May 1963
10 - Sochi, 10-13 June 1963
11 - Batumi, 14-16 June 1963
12 - Sulina, 26-28 June 1963
13 - Odessa, August 1963
14 - Novorossiisk, 27-29 February 1964
15 - Kabuleti, 23 February 1964
16 - Balaklava, 6 August 1964
17 - Odessa, 21-27 June 1964
18 - Tobechik, 12 May 1965
19 - Novorossiisk, 13 May 1965
20 - Novyi Afon, 19 May 1965
21 - Sochi, 9 December 1965
22 - Sochi, 8-16 October 1966
23 - Novorossiisk, 17-18 October 1966
24 - Cape Takil', 20 October 1966

[1]The gene frequency was determined from the formulas:

$$r = \sqrt{A_0};\ q = \sqrt{A_2 + A_0} - \sqrt{A_0};\ p = 1 - (q + r).$$

geographical races (= subspecies), there is a substantial difference (see Table 19). Especially important is the fact that besides purely quantitative differences in the frequencies of the same phenotypes, the two races also differ qualitatively. These data, which agree with the very first facts established only in a limited experiment (see Chapter IV) give weighty bases for considering a reality the complete absence in the Black Sea anchovy of the A_0 blood group, constantly encountered in the Sea of Azov. This phenotype is found in the Black Sea mainly in the winter (hauls

Table 20. Frequency of the gene of blood group A_0 in hauls from accumulations of the Azov anchovy (June 1965)

Таблица 20. Частота гена группы крови A_0 в выборках из скоплений азовского анчоуса (июнь, 1965 г.)

Sample number / Номер проб	Date / Дата	Fishing square / Промысловый квадрат	$2N$	qA_0
	June			
1	11 июня	26ц ts	56	0,707
2	11 июня	36ч ch	60	0,516
3	12 июня	33х kh	58	0,491
4	12 июня	34у u	40	0,224
5	12 июня	37т t	40	0,224
6	12 июня	38р r	40	0,316
7	12 июня	32р, 33о r o	100	0,245
8	13 июня	37о, 36н o n	80	0,274
9	13 июня	40н n	40	0,00
10	14 июня	39л l	56	0,00
11	14 июня	36к k	32	0,00
12	14 июня	33л, 34к l k	76	0,283
13	15 июня	31л l	82	0,412
14	15 июня	34е	34	0,245
15	19 июня	27к	58	0,454
16	19 июня	24н n	32	0,249
17	19 июня	27з z	42	0,219
18	19 июня	21к	52	0,332
19	20 июня	18о, 17н o n	46	0,548
20	20 июня	10л l	28	0,374
21	21 июня	8п p	80	0,612
22	21 июня	5р7у8ф r u f	160	0,742
23	21 июня	12х kh	36	0,574
24	21 июня	32р r	80	0,689
25	21 июня	11н n	80	0,224
26	21 июня	12р r	60	0,316
27	22 июня	8ц ts	80	0,725
28	22 июня	17у u	40	0,548
29	22 июня	23т	28	0,654

Nos. 14 and 21) or autumn (Nos. 22 and 23), and close to precisely those sections of the coast of the Caucasus which are known as the places of wintering of the anchovy of the Azov race. Only once, in the period of reproduction in the region of Odessa, were fishes taken which included all three phenotypes (haul No. 17). Comparison of that sample with samples of the anchovy caught during spawning and fattening in the Sea of Azov testifies to their considerable similarity, although the fairly high frequency of the first group (0.8648) can indicate a mixed composition of the

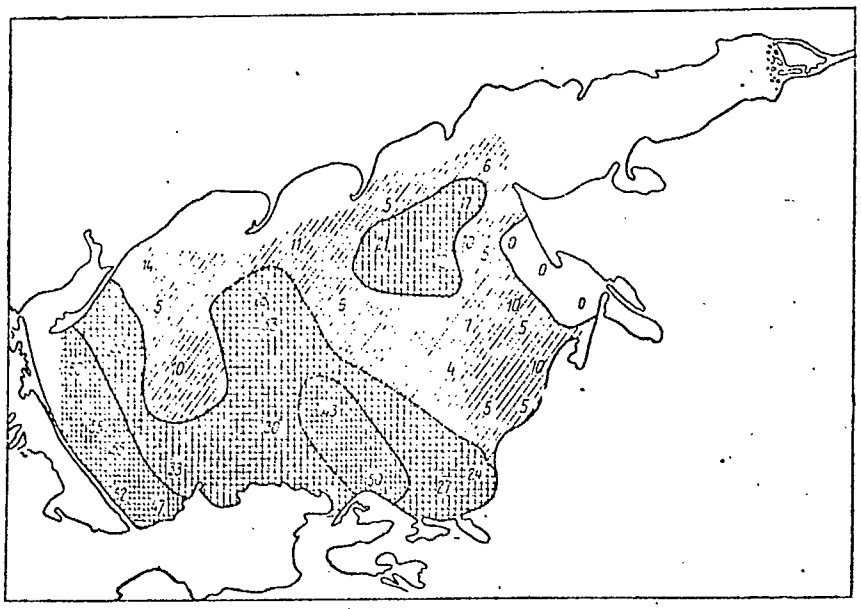

Рис. 24. Геногеография фактора группы крови A_0 анчоуса в Азовском море в июне 1965 г. (по В. В. Лиманскому). Оконтурены различные частоты группы крови A_0 в %.

Figure 24. Genogeography of the A_0 blood group factor of the anchovy in the Sea of Azov in June 1965 (acc. to V.V. Limanskii). Different frequencies of blood group A_0 as a % are outlined.

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population. Of the other Black Sea hauls of the same type, only Nos. 14 and 21 belong most probably to the Azov race; in hauls Nos. 22 and 23, gorup A_0 is contained as an insignificant admixture. Other samples taken in the Black Sea are represented by only two phenotypes: A_1 and A_2 with an average frequency of 0.96 and 0.04 respectively, although there also is an indication of subdivision of the Black Sea anchovy into two subgroups with the A_1 frequency close to 100% and with a frequency of about 85% (compare samples Nos. 7 and 11 with the rest). 84

Thus the difference of the two races of the anchovy established on the basis of analysis of morphological and biological features matches

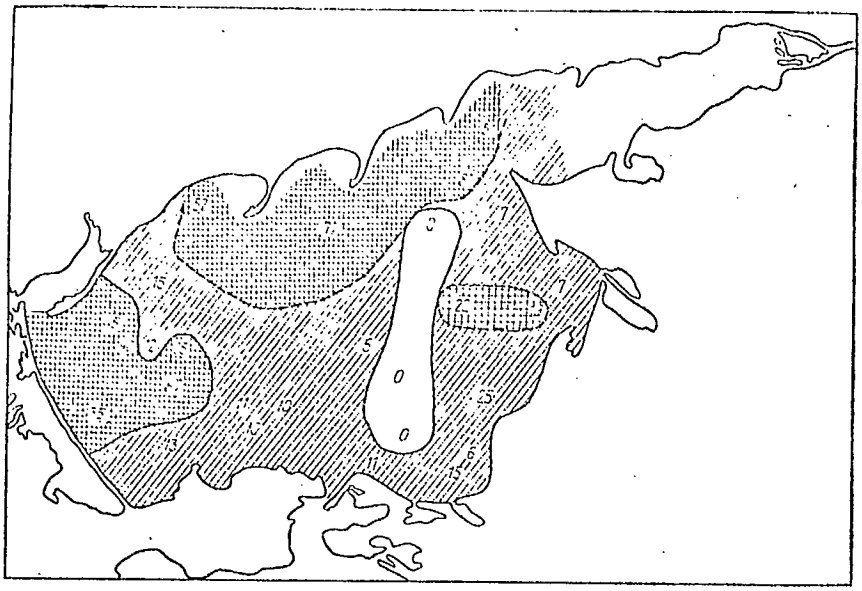

Рис. 25. Геногеография фактора группы крови A_0 анчоуса в Азовском море в августе 1965 г. (по данным В. В. Лиманского); условные обозначения те же, что и на рис. 24.

Figure 25. Genogeography of the A_0 blood group factor of the anchovy in the Sea of Azov in August 1965 (acc. to data of V.V. Limanskii); symbols as in Figure 24.

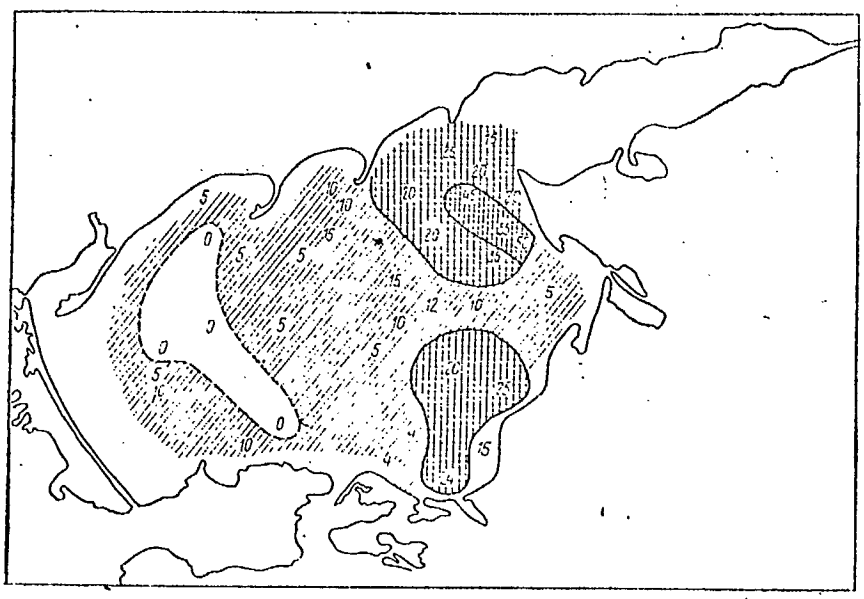

Рис. 26. Геногеография фактора группы крови A_0 анчоуса в Азовском море в сентябре 1965 г. (по данным В. В. Лиманского). Условные обозначения те же, что и на рис. 24.

Figure 26. Genogeography of the A_0 blood group factor of the anchovy in the Sea of Azov in September 1965 (acc. to data of V.V. Limanskii). Symbols as in Figure 24.

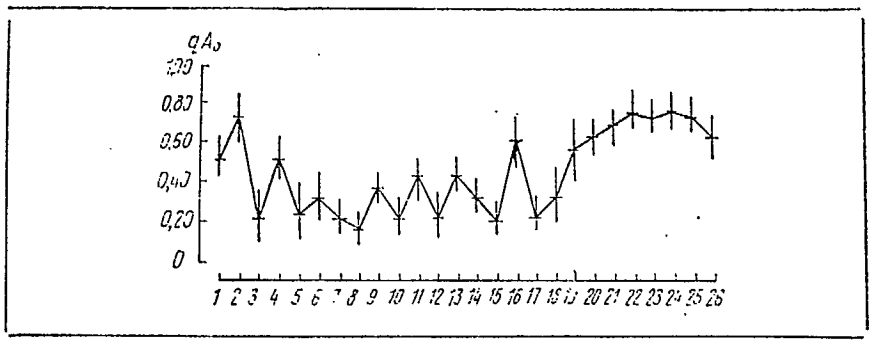

Рис. 27. Пространственная изменчивость частоты гена группы крови A_0 в выборках из скоплений азовского анчоуса в июне 1965 г.

Figure 27. Spatial variability of the frequency of the blood group gene A_0 in hauls from accumulations of the Azov anchovy in June 1965.

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their differentiation detected also in the immunogenetic approach. Moreover, the Azov race, phylogenetically older according to I.I. Puzanov, being represented by all three blood groups, proves also to be more heterogeneous. Its heterogeneity is also further expressed in strong variability of the phenotypical and gene frequecies by years, and the total hauls of 1964 and 1966 were especially anomalous in that respect. The fluctu- 85
ations of frequencies are less considerable in the Black Sea.

To explain the reasons for such shifts (random drift of genes, migration or natural selection) it is necessary to make a more detailed analysis of the spatial localization of blood groups in the Sea of Azov.

We will examine the same material as in Table 19, not in averaged form but for each separate sample, as was done with respect to the ocean perch. As an example we will examine the June 1965 survey, which includes the results of analysis of 36 trawling catches, more or less uniformly distributed over the area of the Sea of Azov.

Since it is not always easy to separate heterozygotic individuals on the basis of the dose effect, we will operate here with only three main blood groups, determined without error in a qualitative evaluation of reactions. Correspondingly the gene frequency is determined for the presumably recessive A_0 factor by extracting the square root of the relative numbers of that phenotype in the hauls. If we take into account the small volume of the samples investigated immunogenetically, it is advisable to 86
combine the series of trawling stations located in a given fishery square or in adjacent squares and made at practically the same time (see Table 20).

The materials presented in the table reflect the considerable heterogeneity of the trawling catches with respect to frequency of the gene A_0 down to its absence (samples Nos. 9-11). But such a feature is characteristic of the Black Sea race and, consequently, the question arises of whether those hauls reflect the presence of the Black Sea anchovy in the Sea of Azov.

To answer the posed question let us turn to the data of the most complete and uniform surveys of 1965, mapping the location of each separate haul (Figures 24-26). The spatial interlinking of the samples is evident: fishes without the A_0 blood group proved to be localized in June in the east in the zone of the sea near the coast (see Figure 24), in August they are already moving to the west (see Figure 25), and in September they prove to be still further west (see Figure 26). That we are dealing here with one and the same fish is proven by coincidence of the frequency of the phenotype A_1. In June it was 72% (N = 64), in August 75% (N = 83) and in September again 72% (N = 54).

On the remaining area accumulations of fishes of the Azov race were localized, represented by all three blood groups; the variegation of the spatial distribution of the gene A_0 in them is just as demonstrative (Figure 27) as on the area of the Newfoundland stock of the redfish.

In examining the dynamics of these fields of different gene concentrations we see their rapid shifts in time and space. Consequently, in the given case it also is necessary to investigate the question of the unity of the Azov population. The materials of surveys for a number of years which we have at our disposal permit examining the variability of the phenotypical and gene frequencies of blood groups in a number of successive generations. The discovery of genetic stability in such an examination could be more rigorous than the data of Table 19, an argument in favor of the belonging of those accumulations of the anchovy precisely to its Azov race as an integral community. The method of proving this requires explanations.

1. The anchovy is an extremely mobile pelagic fish. In making a survey in different periods of the same spawning-fattening season we have no guarantee that some genotypes will not prove to be more represented in our material than others -- anchovy accumulations are characterized at this time by an extremely diffuse distribution in space and different population density. Therefore the identity of the results of the June and August 1965 surveys (see Table 19) is not surprising.

2. If a two-year cycle of replacement of generations is adopted, and such an assumption can be made on the basis of the data on the biology of the anchovy, then, if we compare the materials of adjacent years we are not guaranteed either against artificial increase or decrease of the frequencies of individual phenotypes and genes.

If these considerations are taken into account, for a precise immunogenetic characterization of the Azov anchovy proper, one should use the data of the July 1963, June 1965 and September 1965 surveys, when V.V. Limanskii made an important investigation of the young fishes recently hatched there. If we exclude from the material samples without the A_0 group we actually obtain the possibility of comparing three successive generations which do not overlap in time. Their almost complete genetic similarity requires no additional argumentation (Table 21) and the corresponding values of frequencies must also be taken as a characteristic of the Azov race properly speaking*.

But already in August 1966 striking changes are revealed in the spatial localization of the anchovy of different groups in the Sea of Azov: 89 a considerable part of the range proves to be occupied by accumulations represented only by blood groups A_1 and A_2, and only on the periphery, in the west and in the east, are fishes with the A_0 blood group outlined (Figure 28). Characteristic of the sea as a whole is a sharp increase in the concentration of the phenotype A_1 and just as sharp a drop in the concentration of the phenotype A_0 (see Table 19).

It is improbable that such sharp changes in the genetic structure of the enormous population of the Azov race by 1966 (and it must be compared with the 1964 data) were a result of selection or the random drift of genes. There can be only one reason for such a reorganization -- a heavy migration of the Black Sea anchovy into the Sea of Azov not observed earlier.

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*This must also be taken into account in using data published earlier and, consequently, less rigorous (Altukhov et al., 1969a).

Table 21. Phenotypical and gene frequencies of the A-system of blood groups in three successive generations of the Azov race of the anchovy (according to data of V.V. Limanskii)

Таблица 21. Фенотипические и генные частоты *A*-системы групп крови в трех последовательных поколениях азовской расы анчоуса (по данным В. В. Лиманского)

A Поколения	N	Частоты B фенотипические a		
		A_1	A_2	A_0
1	357	0,60±0,05	0,17±0,04	0,23±0,05
2	784	0,65±0,03	0,15±0,02	0,20±0,03
3	604	0,63±0,04	0,16±0,03	0,21±0,03

Continuation of Table 21

Продолжение табл. 21

A Поколения	N	Частоты B генные b		
		p	q	r
1	357	0,43±0,04	0,09±0,02	0,48±0,04
2	784	0,47±0,03	0,08±0,01	0,45±0,03
3	604	0,45±0,03	0,09±0,02	0,46±0,03

Key: A - Generations B - Frequencies a - phenotypical b - gene

The frequency of the gene pA_1 for it is 0.8013 (see Table 12), and in the accumulation which occupied the central part of the Sea of Azov it is 0.72 (N = 980). For the water body as a whole pA_1 = 0.5432 (see Table 19). Consequently, if we take into account the corresponding mean frequency in the Azov race (pA_1 = 0.463, Table 21) we can determine the relative share of the Black Sea anchovy. Such a calculation (Neal and Shell, 1958) is made from the formula 90

$$\frac{c}{c+d} = \frac{q_n - q_d}{q_c - q_d},$$

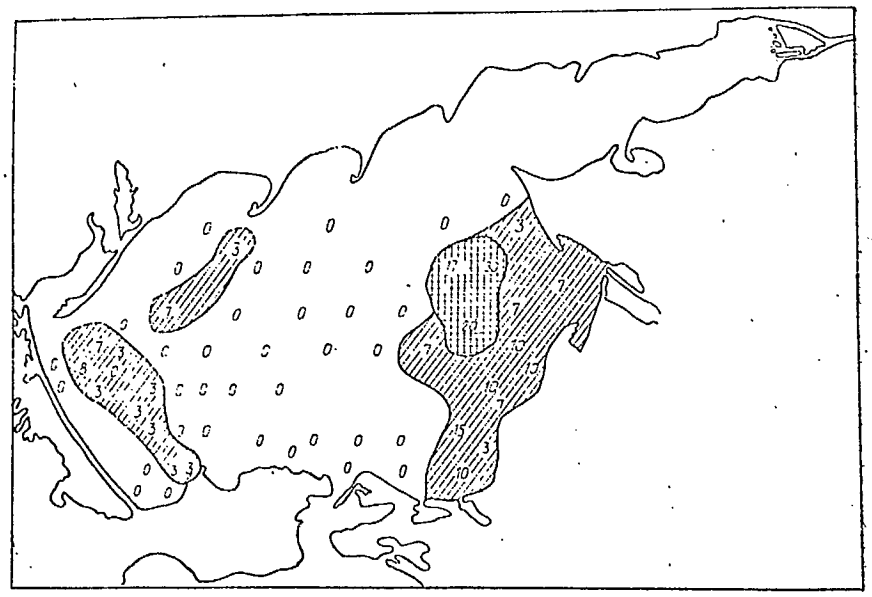

Рис. 28. Геногеография фактора группы крови A_0 анчоуса в Азовском море в августе 1966 г. (по данным В. В. Лиманского). Условные обозначения те же, что и на рис. 24.

Figure 28. Genogeography of the blood group factor A_0 of the anchovy in the Sea of Azov in August 1966 (acc. to data of V.V. Limanskii). Symbols as in Figure 24.

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where q_n is the definitive gene frequency in the mixed population;

q_c is the gene frequency in the Black Sea population;

q_d is the gene frequency in the Azov population;

c and d are the corresponding shares in the mixed population.

The result obtained is that in August 1966 up to 45% of Black Sea anchovy could be in the Sea of Azov. An estimate can also be given for the A_0 factor, not represented at all in the Black Sea race; the result proves to be similar (about 40%).

Of course the calculation made does not represent a final solution of the problem, but only designates a path to its further analysis. For fairly complete analysis of the question of the scales of penetration of the Black Sea race into the Sea of Azov, and also the periodicity of the phenomenon itself, it is necessary to work with facts obtained, not in four years, but in a longer time interval.

A corresponding attempt was undertaken by co-workers of the Azcher-NIRO (Azov-Black Sea Scientific Research Institute of Sea Fisheries and Oceanography) (L.M. Kokoz, V.V. Limanskii and N.F. Taranenko), who linked the immunogenetic data with the biological situation (increase in the numbers of fishes, their dimensions, and the percentage of yearlings in the catches) which accompanied that massive penetration of Black Sea anchovy into the Sea of Azov. The authors showed that similar migrations also occurred in past years, for example, in 1933, 1937, 1947, 1951 and 1958, but no regularity of such incursions was successfully established and, consequently, there are no conditions for forecasting them.

At the same time, the facts analyzed in the present section show that between the Azov and Black Sea races of the anchovy there are clearly expressed genetic differences. It is especially important that besides quantitative differences in the frequencies of common genes there also is a qualitative difference, expressed in the genetically closed state of the Black Sea race -- the absence of the gene A_0 in it. This fact, together with data on the qualitative antigenic differences between the races with respect to water-soluble proteins of muscles (Limanskii, 1964), usually

burdened with the property of species specificity (Altukhov and Rychkov, 1972), obviously forces us to acknowledge as erroneous our previous conclusion of gene exchange between races (Altukhov et al., 1969a), and after conducting supplementary investigations to describe the races themselves as twin species forming only mechanical mixtures in the zone of sympatry.

However that may be, detailed analysis of the blood group distribution in the Sea of Azov permits detecting without error the migration of the Black Sea anchovy and, moveover, revealing the hereditary heterogeneity of the Azov race properly speaking, which permits assuming its subdivision into smaller, genetically different population units. Thus, in spite of the extreme mobility of the anchovy, the same picture appears as with bottom redfish leading a clearly expressed settled form of life.

The heterogeneity of the Black Sea race of the anchovy is poorly detected on the basis of the studied markers, although reliable differences among some samples have been discovered. This agrees with the opinion of a number of authors (see Chapter II) who are inclined to subdivide the Black Sea race into several local stocks. However, here we will not discuss this question, which requires further investigations.

It is important to emphasize once more the fact of stable reproducibility in generations of the Azov race. This is an indicator of its genetic integrity, in spite of internal subdivision discovered in geno- 92
geographical analysis.

Reproductive Isolation and Genetic Heterogeneity of Local Stocks of Pacific Salmons

Due to difficulties in breeding heterozygotic individuals of the redfish and anchovy we have been able to make an immunological analysis of the variability of populations and their interactions only on the basis of comparison of phenotypical or, at best, gene frequencies. However, with the transition to the genetic and biochemical level of investigation, which permits detecting co-dominantly inherited electrophoretic variants of proteins, the possibilities of a more rigorous population genetics approach are opened up. These possibilities are also expanded because the genetic variability of populations can now be estimated at once on the basis of an aggregate of several independent gene loci.

On the basis of the frequencies of all the polymorphous gene markers a comparison was made of the keta populations of a number of rivers of Sakhalin, the Kuril Islands and Kamchatka (Tables 22-25). It is evident from the presented materials that in the genes of muscle Ldg the Kuril populations reliably differ from one another and at the same time are considerably different from all the Sakhalin populations, which are practically indistinguishable on the basis of that character.

In the presence of genotypical equilibrium in each separate case, in the total haul a heterozygote deficit, which is considerable on the third level is observed. With respect to the regulator gene of serum Ldg the Kamchatka and Tym' keta, investigated in September 1968, differ very strongly from all the others. In the remaining cases small differences

Table 22. Distribution of genotypes and genes of serum albumin in different keta populations

Таблица 22. Распределение генотипов и генов сывороточного альбумина в различных популяциях кеты

A Локализация проб (река)		B Время сбора материала	N	Постулированные генотипы C Alb^{CC}	Alb^{CD}	Alb^{DD}	χ^2	Частота гена D $pAlb^C$	$qAlb^D$
1 Найба	a	Октябрь — ноябрь 1969 г.	506	248 (235,22)	194 (219,55)	64 (51,23)	7,12	0,6818	0,3182
	b	Сентябрь — ноябрь 1970 г.	522	75 (55,38)	190 (229,26)	257 (237,36)	13,70	0,3257	0,6743
	c	Октябрь — ноябрь 1971 г.	257	44 (21,0)	59 (105,0)	154 (131,0)	49,23	0,2860	0,7140
2 Калининка	a	Сентябрь — октябрь 1970 г.	352	4 (5,75)	82 (78,47)	266 (267,78)	0,704	0,1280	0,8720
	b	Сентябрь — октябрь 1971 г.	176	9 (2,41)	24 (36,36)	143 (137,22)	22,471	0,1170	0,8830
3 Тымь	a	Сентябрь — октябрь 1970 г.	280	5 (9,11)	91 (82,80)	184 (188,09)	2,76	0,1804	0,8196
4 Сахалинские пробы, суммарно		1970 г.	1154	84 (61,79)	366 (410,49)	704 (681,72)	13,53	0,2314	0,7686
		1971 г.	433	53 (20,62)	83 (147,73)	297 (264,65)	83,16	0,2182	0,7818
5 Рейдовая (о-в Итуруп)	a	Октябрь 1970 г.	60	44 (45,07)	16 (13,86)	— (1,07)	1,425	0,8667	0,1333
	b	Октябрь 1971 г.	45	18 (14,4)	15 (22,1)	12 (8,4)	4,724	0,567	0,433
6 Курилка (о-в Итуруп)	a	Октябрь 1970 г.	95	14 (12,89)	42 (44,21)	39 (37,90)	0,238	0,3684	0,6316
	b	Октябрь — ноябрь 1971 г.	98	16 (9,80)	30 (42,39)	52 (45,81)	8,379	0,3163	0,6837
7 Курильские пробы, суммарно		1970 г.	155	58 (48,83)	58 (76,33)	39 (29,83)	8,94	0,5613	0,4387
		1971 г.	143	34 (22,32)	45 (68,36)	64 (52,32)	16,70	0,3951	0,6049
8 Все пробы, суммарно		1970 г.	1309	142 (95,71)	424 (516,49)	743 (696,80)	42,02	0,2704	0,7296
		1971 г.	576	87 (39,57)	128 (22,80)	361 (313,63)	102,67	0,2621	0,7379
9 Камчатка	a	10 октября 1970 г.	32	17 (18,00)	14 (12,00)	1 (2,00)	0,86	0,7500	0,2500
8 Все пробы, суммарно		1969 — 1971 гг.	2423	494 (314,02)	757 (1116,52)	1172 (992,460)	251,4	0,3601	0,6399

Примечание. Здесь и на последующих таблицах в скобках указана ожидаемая численность фенотипов (из уравнения Харди—Вейнберга).

Key:

A - Sampling place (river)
B - Sampling time
C - Postulated genotypes
D - Gene frequency

1 - Naiba
- a - October-November 1969
- b - September-November 1970
- c - October-November 1971

2 - Kalininka
- a - September-October 1970
- b - September-October 1971

3 - Tym'
- a - September-October 1970

4 - Sakhalin samples, total

5 - Reidovaya (island of Iturup
- a - October 1970
- b - October 1971

6 - Kurilka (island of Iturup)
- a - October 1970
- b - October-November 1971

7 - Kuril samples, total

Table 22 (Continued)

Key: 8 - All samples, total 9 - Kamchatka a - 10 October 1970
Note. Here and in the following tables the expected numbers of phenotypes (from the Hardy-Weinberg equation) are shown in parentheses.

Table 23. Distribution of genotypes and genes of serum lactate dehydrogenase in different keta populations

Таблица 23. Распределение генотипов и генов сывороточной лактатдегидрогеназы в различных популяциях кеты

	A Локализация проб (река)		B Время сбора материала	N	Постулированные генотипы: C Ldh^{FF}	Ldh^{FS}	Ldh^{SS}	χ^2	Частота гена D $pLdh^F$	$qLdh^S$
1	Найба	a	Октябрь 1968 г.	115	88 (87,04)	26 (26,02)	1 (1,94)	0,47	0,95	0,05
		b	Октябрь—ноябрь 1969 г.	291	213 (210,25)	71 (74,20)	7 (6,55)	0,285	0,96	0,04
		c	Сентябрь—ноябрь 1970 г.	528	400 (383,54)	100 (132,95)	28 (11,51)	32,49	0,8523	0,1477
		d	Октябрь—ноябрь 1971 г.	277	213 (204,87)	51 (66,70)	13 (5,43)	14,57	0,8600	0,1400
2	Калининка	a	Октябрь 1969 г.	80	65 (63,80)	13 (15,29)	2 (0,92)	1,63	0,893	0,107
		b	Сентябрь—октябрь 1970 г.	401	300 (293,83)	88 (94,48)	13 (8,09)	4,03	0,856	0,144
		c	Сентябрь—октябрь 1971 г.	145	116 (112,10)	24 (30,80)	5 (2,10)	5,57	0,884	0,116
3	Тымь	a	Сентябрь 1968 г.	67	33 (33,00)	33 (28,83)	1 (6,03)	4,78	0,7018	0,2982
		b	Октябрь 1970 г.	288	243 (242,18)	42 (43,84)	3 (1,98)	0,605	0,917	0,083
		c	Сентябрь 1971 г.	87	81 (80,18)	5 (6,68)	1 (0,14)	5,71	0,96	0,04
4	Сахалинские пробы, суммарно		1969 г.	371	278 (274,54)	84 (89,04)	9 (7,42)	0,67	0,8625	0,1375
			1970 г.	1217	943 (912,75)	230 (279,91)	44 (24,34)	25,9	0,8696	0,1304
4	Сахалинские пробы, суммарно		1971 г.	509	410 (397,02)	80 (101,80)	19 (10,18)	13,9	0,8841	0,1159
5	Рейдовка	a	Октябрь 1970 г.	78	62 (62,81)	16 (14,37)	0 (0,82)	1,02	0,8974	0,1026
		b	Октябрь 1971 г.	47	40 (39,26)	6 (7,39)	1 (0,35)	1,48	0,914	0,086
6	Курилка	a	Октябрь 1970 г.	100	85 (79,21)	7 (19,58)	8 (1,22)	46,18	0,89	0,11
		b	Октябрь 1971 г.	100	88 (87,42)	11 (12,15)	1 (0,42)	0,914	0,935	0,065
7	Глушь	a	Ноябрь 1971 г.	47	41 (41,0)	6 (5,8)	0 (0,3)	0,22	0,935	0,065
8	Курильские пробы, суммарно		1970 г.	178	147 (140,62)	23 (35,60)	8 (1,78)	26,3	0,8904	0,1096
			1971 г.	194	169 (166,84)	23 (25,22)	2 (1,94)	0,23	0,9304	0,0696
9	Сахалино-курильские пробы, суммарно		1970 г.	1395	1090 (1060,2)	253 (306,9)	52 (27,9)	31,11	0,8720	0,1280
			1971 г.	703	579 (569,43)	103 (126,54)	21 (7,03)	32,53	0,8969	0,1031
10	Камчатка (оз. Ушковское)	a	Октябрь 1970 г.	42	25 (24,38)	14 (15,42)	3 (2,28)	0,31	0,7619	0,2381
11	Все пробы, суммарно		1968—1971 гг.	2693	2093 (2046,68)	513 (592,46)	87 (53,86)	32,05	0,8724	0,1276

Key:

A - Sampling place (river)	B - Sampling time
C - Postulated genotypes	D - Gene frequency
1 - Naiba	a - October 1968
	b - October-November 1969
	c - September-November 1970
	d - October-November 1971
2 - Kalininka	a - October 1969
	b - September-October 1970
	c - September-October 1971
3 - Tym'	a - September 1968
	b - October 1970
	c - October 1971
4 - Sakhalin samples, total	
5 - Reidovka	a - October 1970
	b - October 1971
6 - Kurilka	a - October 1970
	b - October 1971
7 - Glush'	a - November 1971
8 - Kuril samples, total	
9 - Sakhalin-Kuril samples, total	
10 - Kamchatka (Lake Ushkovskoe)	a - October 1970
11 - All samples, total	

Table 24. Distributions of phenotypes of malate dehydrogenase in different keta populations

Таблица 24. Распределения фенотипов малатдегидрогеназы в различных популяциях кеты

	A Локализация проб (река)	B Дата сбора материала	N	Фенотипы Phenotypes 1	2	3	4	Частота генов D pA	qB
1	Найба	Oct. – Nov. 1969 г.	602	542	33	25	2	0,9188	0,0512
		Sept.–Nov. 1970 г.	466	396	21	49	—	0,9210	0,0790
		Oct. –Nov. 1971 г.	281	246	9	25	1	0,9354	0,0646
2	Калининка	Oct. 1969 г.	201	124	4	72	1	0,81	0,19
		Sept.–Oct. 1970 г.	349	238	1	110	—	0,8410	0,1590
		Sept.–Oct. 1971 г.	187	130	—	57	—	0,8476	0,1524
3	Тымь	Oct. 1969 г.	200	198	2	—	—	0,995	0,005
		Oct. 1970 г.	263	258	2	3	—	0,9905	0,0095
		Sept. 1971 г.	106	105	1	—	—	0,9953	0,0047
4	Сахалинские пробы, суммарно	1969 г.	1003	864	39	97	3	0,9281	0,0719
		1970 г.	1078	892	24	162	—	0,9097	0,0903
		1971 г.	574	481	10	82	2	0,9154	0,0846
5	Рейдовка	Oct. 1970 г.	97	92	5	—	—	0,9742	0,0258
		Oct. 1971 г.	50	44	6	—	—	0,9100	0,0600
6	Курилка	Oct. 1970 г.	95	87	8	—	—	0,9580	0,0420
		Oct.–Nov. 1971 г.	81	76	5	—	—	0,9691	0,0309
7	Глушь	Nov. 1971 г.	47	44	3	—	—	0,9681	0,0319
8	Курильские пробы, суммарно	1970 г.	192	179	13	—	—	0,9656	0,0344
		1971 г.	178	164	14	—	—	0,9598	0,0402
11	Все пробы, суммарно	1968—1971 гг.	3025	2580	100	341	4	0,9235	0,0765

Table 25. Distribution of genotypes and genes of muscle lactate dehydrogenase in different keta populations

Таблица 25. Распределения генотипов и генов мышечной лактатдегидрогеназы в различных популяциях кеты

	A Локализация проб (река)	B Дата сбора материала	N	Постулированные генотипы C			χ^2	Частота гена D	
				BBAA	*BBA'A*	*BBA'A'*		*pA*	*qA'*
1	Найба	Oct. Октябрь 1968 г.	144	130 (129,96)	14 (13,68)	0 (0,36)	0,36	0,95	0,05
		Nov. Октябрь—ноябрь 1969 г.	641	591 (591,48)	50 (48,05)	0 (0,97)	1,05	0,961	0,039
		Ноябрь 1970 г.	101	88 (87,49)	12 (13,03)	1 (0,48)	0,65	0,9307	0,0693
		Октябрь—ноябрь 1971 г.	276	256 (252,77)	19 (22,72)	1 (0,51)	1,12	0,957	0,043
2	Калинника	Октябрь 1969 г.	146	137 (137,14)	9 (8,72)	0 (0,14)	0,15	0,9682	0,0308
		Sept. Сентябрь—октябрь 1971 г.	161	156 (155,92)	5 (4,94)	0 (0,04)	0,04	0,984	0,016
3	Тымь	Октябрь 1969 г.	250	220 (220,90)	30 (28,20)	0 (0,90)	1,02	0,94	0,06
		Октябрь 1971 г.	64	58 (58,16)	6 (5,70)	0 (0,14)	0,15	0,957	0,043
4	Сахалинские пробы, суммарно	1969 г.	1037	948 (949,68)	89 (85,45)	0 (1,87)	2,02	0,957	0,043
		1971 г.	501	470 (469,48)	30 (31,01)	1 (0,51)	0,50	0,968	0,032
5	Рейдовка	Октябрь 1970 г.	96	53 (51,77)	35 (37,46)	8 (6,77)	0,41	0,7344	0,2656
5	Рейдовка	Октябрь 1971 г.	48	29 (27,0)	14 (18,0)	5 (3,0)	2,37	0,75	0,25
6	Курилка	Октябрь 1970 г.	100	73 (71,40)	23 (26,20)	4 (2,40)	1,49	0,845	0,155
		Октябрь—ноябрь 1971 г.	87	58 (57,0)	25 (26,85)	4 (3,15)	0,37	0,810	0,190
7	Глушь	Ноябрь 1971 г.	49	35 (35,20)	13 (12,70)	1 (1,14)	0,025	0,847	0,153
8	Курильские пробы, суммарно	1970 г.	196	126 (122,57)	58 (64,85)	12 (8,58)	2,18	0,7908	0,2092
		1971 г.	184	122 (119,03)	52 (57,92)	10 (7,05)	1,91	0,8043	0,1957
11	Все пробы, суммарно	1970 г.	297	214 (208,76)	70 (80,49)	13 (7,75)	4,93	0,8384	0,1616
		1971 г.	685	592 (584,96)	82 (96,09)	11 (3,95)	14,73	0,9241	0,0759
10	Камчатка, оз. Ушковское	a Октябрь 1970 г.	100	89 (88,36)	10 (11,28)	1 (0,36)	2,28	0,94	0,06
11	Все пробы, суммарно	1968—1971 гг.	2263	1973 (1958,90)	265 (293,15)	25 (10,95)	20,58	0,9304	0,0696

Key: Same as for Table 23, with exceptions as shown.

are observed between the rivers (compare Naiba in 1968 and 1969 with Tym' and Kalininka) or considerable uniformity of the gene frequencies. Also visible are changes in the genetic structure of separate populations: in 1968-1969 the Naiba stock was in equilibrium, but in 1970-1971 it had a severe shortage of heterozygotes. The same was characteristic of the Kalininka population, studied in detail in 1970-1971, and of one sample from the Kurilka River. On the other hand, for Tym' in 1968 and 1971 a shortage of S-gene homozygotes was observed. However, serious importance can hardly be attributed to that fact, as the deviations of the expected values from the actual fall in the rarest phenotypical class, which can be connected either with error of the sample or error in the classification of the electrophoretic variants. Let us also recall that 99
a rare mutation of one of the structural genes responsible for the synthesis of serum Ldg is encountered in the heterozygotic state in the Tym' population with a low frequency (1:250) (see Figure 16). A highly reliable deficit of heterozygotes is characteristic on the whole for the entire investigated Sakhalin-Kuril region, just as in the case with the muscle Ldg.

With respect to gene frequencies of serum albumin differences are observed both between stocks and between different year-classes of the Naiba keta, and also between the 1970 and 1971 hauls from the population of the Reidovka River on the island of Iturup. Only between the keta from the Kalininka and Tym' rivers is the difference unimportant, but those populations differ reliably in the gene frequencies of malate dehydrogenase. The same locus differentiates the Kalininka population from all the rest, which exhibit practically no interpopulation variability.

The deficit of heterozygotes in the albumin system, noted earlier when separate samples were combined which had been taken at different times of the spawning run in a single river (see Table 16), is still more clearly expressed in the total hauls of different years characterizing the Sakhalin-Kuril region as a whole.

If we use the graphic method of comparing populations (Serebrovskii, 1970) we show the interpopulation differences at once for all four polymorphous loci (Figure 29). The mutual position of those populations in the aggregate of the three systems -- albumin, lactate dehydrogenase of muscle and malate dehydrogenase -- can be estimated also by the method of "generalized distances" (Rychkov, 1969) in determining D as the mean difference between the populations with respect to alleles of each locus

$$D = \frac{\Sigma \mid p_i - p_j \mid \bar{p}}{S_{\bar{p}} f},$$

where p_i and p_j are the gene frequencies in the compared populations i and j;

S_p is the mean-square error of the gene frequency $\bar{p}$ in the total Sakhalin-Kuril aggregate of populations;

f is the number of genes, equal to the number of alleles in the system minus one.

A graphic interpretation of the results of calculations made relative to the Kalininka stock is given on Figure 30. The position of the population in relation to all the others is determined simultaneously by the three polymorphous systems representing the corresponding co-ordinates. The point of their intersection reflects the mean value of the differences between any one population and the rest with respect to the gene frequencies of each locus. The starting Kalininka population is located at the center

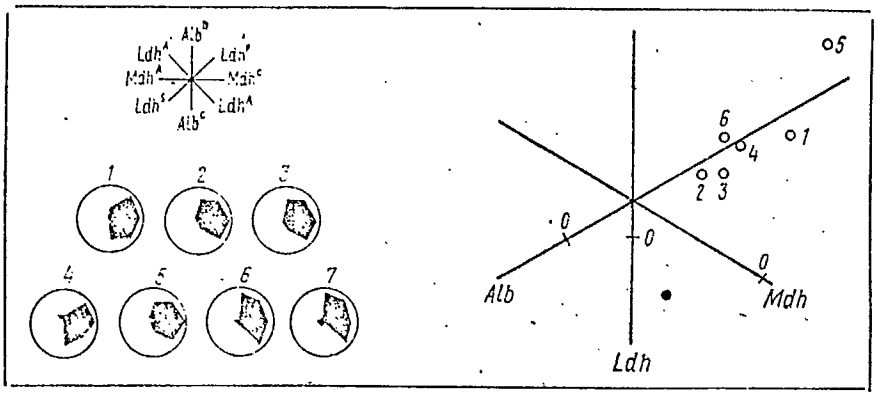

Figure 29. Graphic depiction of keta populations characterized by alleles of four genetic loci (see designations of vectors): 1 - Naiba stock, 1969; 2 and 3 - the same for 1970 and 1971; 4 - stock of Iturup island, maintained by the Reidovka fish hatchery, 1970 and 1971; 5 - stock of Tym' River, 1970; 6 - stock of Kalininka River, 1970; 7 - the same, 1971.

Figure 30. Generalized distances between stocks of keta in relation to the Kalininka stock (designated by black circles): 1, 2 and 3 - Naiba stock in 1969, 1970 and 1971 respectively; 4 - Tym' River stock; 5 - Reidovka River stock; 6 - Kurilka River stock.

of the equilateral triangle at the zero values of the co-ordinates; the positions for the other populations are found similarly. 100

Besides obvious interpopulation differences, it is especially important that the Kalininka population, investigated on all loci twice (1970 and 1971) and with respect to genes of malate dehydrogenase three times (1969-1971), is characterized by stability, whereas the Naiba population does not have such stability; in 1970 and 1971 it proves to be shifted, in the selected co-ordinate system in the direction of the Kalininka keta. This is readily explained by the fact that in 1966 and 1967 65 and 25 million eggs were transferred from the Kalininka to the Sokolovskii

fish hatchery respectively and 24 and 21 million eggs respectively "of their own" were also set out for incubation.

Consequently, it can be stated that the homing instinct of the keta has an epigenetic nature, although its acclimatization quickly succeeds beyond the limits of its natural range. However, we now obtain the possibility of giving a quantitative estimate of the success of such acclimatization when we have determined the percentage of the Kalininka keta in the Naiba population. A corresponding calcuation, based on data for 101
the allele Alb^C of the albumin locus* can be accomplished just as in the case of the anchovy: the percentage of the Kalininka fish in the Naiba River is about 39%.

To estimate the success of such transfers we will determine the coefficients of commercial return ($\eta = n_1/n_2$, where n_1 is the number of adult fishes which have returned and n_2 is the number of released juveniles) for the Kalininka and Naiba stocks (Figures 31 and 32).

It follows from the obtained data that:

1) whereas stabilization of the return coefficients grouped around the mean level characteristic of the stock as a whole has been noted for the Kalininka population in recent years, the population of the Naiba keta has no such stability; nevertheless the mean return still is higher in the 102
Naiba stock;

2) with transfers of the Kalininka keta to the Sokolovskii and Bereznyakovskii plants the coefficients of commercial return for the Naiba stock as a whole prove to be below the mean for the preceding years;

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*There are grounds for considering this locus as selectively neutral, which is essential for such calculations.

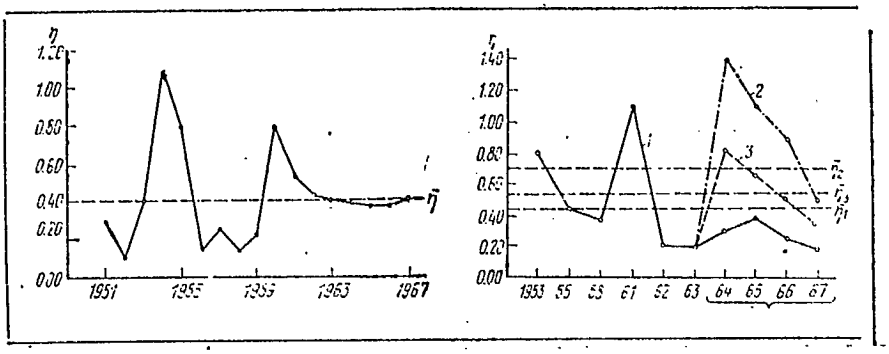

Figure 31. Fluctuation of the coefficient of commercial return (η_i as %) for non-overlapping year-classes of the Kalininka keta, maintained by the Kalininka fish hatchery, in relation to the mean level ($\bar{\eta}$) (broken line).

Figure 32. Fluctuation of the coefficients of commercial return (η_i as %) for a number of non-overlapping year classes of the Naiba keta, maintained by the Sokolovskii and Bereznyakovskii fish hatcheries. Transfers of eggs of the Kalininka keta are marked with a brace: 1 - total coefficients of return, calculated without reference to transfers of Kalininka keta; 2 - coefficients of return calculated on the assumption of lack of success of acclimatization of Kalininka keta in the Naiba river; 3 - coefficients of return calculated for Naiba keta after singling out on the basis of population genetics data of the percentage of actually acclimatized Kalininka keta; $\bar{\eta}_1$, $\bar{\eta}_2$ and $\bar{\eta}_3$ - mean coefficients of return for the three situations just indicated.

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3) If the corresponding coefficients have been calculated separately for the Naiba and Kalininka populations one can readily satisfy oneself of the low age of the Kalininka keta in the Naiba ($\bar{\eta}$ = 0.1% in 1970 and 0.05% in 1971), which is below the mean level characteristic of the Kalininka population in its own river ($\bar{\eta}$ = 0.4%). On the contrary, the return in those years of the portion which on the basis of population genetics data we classify as that of the Naiba properly speaking is fully commensurable with the return from the broods of the years when no transfers were made, although a reduction of the effectiveness of the work of the hatchery is observed.

Thus the return of adult fishes to a strange river proves to be much lower than to its own even in the first year-class. Probably in a number of cases the transfers bring no success at all. For example, in 1965 71 million eggs of the Kalininka keta were transported to the Bereznyakovskii plant, but 64 million of its own eggs were gathered and, evidently, corresponding to that the genetic characteristics of the year-class which returned in 1969 proved to be sharply different from the 1966 and 1967 broods, which were clearly mixed in composition. True, one cannot exclude the possibility that a small return of the Kalininka keta to the Naiba River in 1969 still took place but remained unnoticed, as we took the first sample from the spawning accumulations only on 20 October.

Nevertheless, all the above shows the relative success of the acclimatization of the keta even within the limits of the species range. This conclusion is also confirmed by still another important fact -- the stable reproducibility in the year-classes of genetic features characterizing the Kalininka stock as a whole and distinguishing it from the stocks maintained by the Ado-Tymovskii and Kuril fish hatcheries. Since there never was a transfer of eggs from the broods of those stocks to the Kalininka fish hatchery, the data obtained by us testify to an absence of any sort of noticeable natural exchange between the stocks of the different rivers. We can thus consider those stocks as genetically independent, reproductively isolated populations.

The same is also indicated by the above-noted deficit of heterozygotes in the total samples which, however, requires more careful examination in connection with genetic differences registered in a detailed investigation 103 of a separate stock at different times of the spawning run. One example

was presented earlier in relation to the frequencies of the allele Alb^C in samples from the Naiba population (see Table 16). The XI-square test for homogeneity shows highly reliable dispersion of the gene frequencies from haul to haul (χ = 41.5 at df = 5) and correspondingly a reliable shortage of heterozygotes is observed in the stock as a whole. The same thing is also characteristic of separate year-classes of the Kalininka population during investigations of gene frequencies in loci of albumin and serum Ldg (see Tables 22 and 23).

A shortage of heterozygotes can also be observed in a panmictic population, but then it must be assumed that either the selection was directed against the heterozygotes or there was a positive assortative crossing. However, the stability of polymorphisms in the year-classes refutes the first assumption, and the second does not agree with the fact that the biochemical variability investigated here is not expressed externally in any way. Consequently, also in explaining the genetic heterogeneity of a separate stock it is necessary to resort to the simplest and most natural reason -- its subdivision into isolated, genetically different populations. Such a treatment corresponds to a certain population genetics model according to which "the subdivision of a population into separate interbreeding groups is equivalent to the existence of inbreeding within the entire population" [the so-called Valund effect (Li, 1966)]. The corresponding coefficient of inbreeding, which actually reflects the correlation of gametes, can be found from the expression

$$F = \frac{H_e - H_o}{H_e},$$

where H_e is the heterozygotes frequency expected from the Hardy-Weinberg distribution; H_o is the actual proportion of heterozygotes. Calculation of the error of F is given by Rasmussen (1964).

With the introduction of the found correction ($F = 0.114 \pm 0.02$) the correspondence of the actual and expected distributions for a number of hauls shows a tendency toward improvement.

Thus on the basis of analysis of the gene and genotype frequency distributions in time and space it can be stated that the so-called local stocks of fishes represent reproductively isolated populations. At the same time, each separate stock in itself reveals hereditary heterogeneity -- 104
evidence of subdivision into smaller but also reproductively isolated population units.

With consideration of certain ichthyological data only the "elementary populations" discovered at one time by N.V. Lebedev can correspond to that level of organization. But in such case the conclusion that they are of a non-hereditary nature is erroneous.

The following chapter will in fact be devoted to the investigation of this question.

Chapter VI. Local Stocks as Aggregates of Genetically Different Elementary Populations

Elementary populations as biologically homogeneous groupings characterized by completeness of behavior have been discovered in other species of fishes besides the anchovy (Lebedev, 1967).

To what was said in Chapter II it must be added that in the reproductive period the isolation of these groupings is incomplete and exchange between them through marginal variants of physiological similarity at times reaches 30% (Lebedev, 1967). However, as special investigations have shown (Lebedev, 1946; Chubunova, 1951, etc.), including with the use of radioactive

tagging (Payusova, 1965; Lebedev, 1967), elementary populations do not decompose for a very long time. According to indirect data, the composition of an elementary population of the Caspian roach changed in five years (that is, in a generation) only by 24-29%. The regrouping of composition in elementary populations of the kilka does not exceed 10% per generation. Direct observations of populations of the same fishes were successfully accomplished up to two months and by the time the work was halted no sort of signs of their decomposition had been noted (Lebedev, 1967).

All that has been said applies to elementary populations of mature fishes. Such groups form, however, at the places of birth of the young fishes (Payusova, 1962, 1965, 1967).

Thus the ecological data suggest that the genetic role of elementary populations can be a dual one. Firstly, differentiation of the gene stocks of the larger populations (races or stocks), formed of elementary populations, must occur. Secondly, the genetic integrity of the races, which finds reflection in a higher level of their stability in both time and space, must be maintained, which has already been partially demonstrated in the preceding chapter. 105

However, until recently the genetics of elementary populations of fishes remained unstudied and in the view of their biological importance the evaluation of such groups as non-hereditary communities predominated, which themselves "do not reproduce but conclude their existence in ontogenesis... The following generation of each elementary population is of varying quality and therefore falls into very different, newly arising elementary populations" (Lebedev, 1967, p. 197; our emphasis, Yu.A.).

These two opposite treatments also have directly opposite consequences both for scientific work in the region of the population biology of fishes and for the working out of the very principles of a rational fishery. Therefore it is important not to limit oneself to indirect indications of the genetic nature of the differences between elementary populations, regarding which the material of the preceding chapter and the just-cited ecological observations testify, but to obtain direct information about this level of the population organization of a species.

Genetic Differences Between Elementary Populations of the Redfish

Data of analysis of trawling catches made on the Newfoundland Grand Bank and the Flemish Cap bank served as the basic material for the present section.

Elementary populations were divided on the basis of the results of the biological analysis of catches more or less uniformly distributed over the commercial fishing area along the continental slope of the depths.

The redfish does not make considerable horizontal migrations, but limits itself to vertical movements (Templeman, 1959; Poulsen, 1962; Travin and Pechenik, 1962). The catches were analyzed directly in the sea, and the analyses consisted of individual measurements of fishes and determinations of their sexual composition. Of all the characters used to determine elementary populations of fishes (Lebedev, 1946, 1967; Payusova, 1961) we were able to use only three: the character of the distribution curve of the length of body of the fish, the sex ratio and features of the interlinking of catches in the area. The average size of fishes in the catch and the 106
average depth of trawling also were taken into account.

Our experience shows that the average size of fishes, as a character to which importance is attributed in the identification of elementary populations, is not always reliable, as it varies when there is a considerable admixture of smaller or larger fishes from neighboring populations. At the same time that admixture is readily detected even during visual analysis of the distribution curves of body length, which, being very sensitive to any kind of changes in the composition of the catch, in relation to modal frequencies reveals high constancy if the samples have been taken mainly from the same population. Therefore in the recognition and identification of populations we gave more attention precisely to the form of the variational curves than to the average size, which served as a supplementary character.

No less importance was given also to the sex ratio in the sample, since it is known that it does not remain constant over the course of the life cycle of redfishes (Magnusson, 1959, 1961; Karasev and Sauskan, 1963; Sidorenko, 1967) and, as has been shown for many other species, is a character which fluctuates greatly in elementary populations of fishes in the spawning period (Lebedev, 1967). 107

At the same time the sex ratio in the sample haul does not correlate with the modal frequency of the variational series (Figure 33) and so the identity or great similarity in two independent characters of samples, which prove moreover to be spatially conjugated, permits detecting over a continuous range the boundaries between separate populations.

What has been said is illustrated by Figure 34, which depicts the distribution curves of the linear dimensions of fishes from different catches, and Table 26, in which some statistical parameters are tabulated.

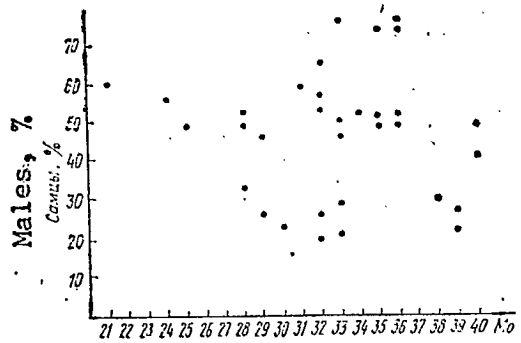

Рис. 33. Отсутствие корреляции между соотношением полов (% самцов) и модальной частотой длины тела рыбы (M_0) в выборках из элементарных популяций окуня, локализованных на Большой Ньюфаундлендской банке.

Figure 33. Absence of correlation between the sex ratio (% of males) and the modal frequency of the body length of the fish (M_0) in samples from elementary populations of the redfish located on the Newfoundland Grand Bank.

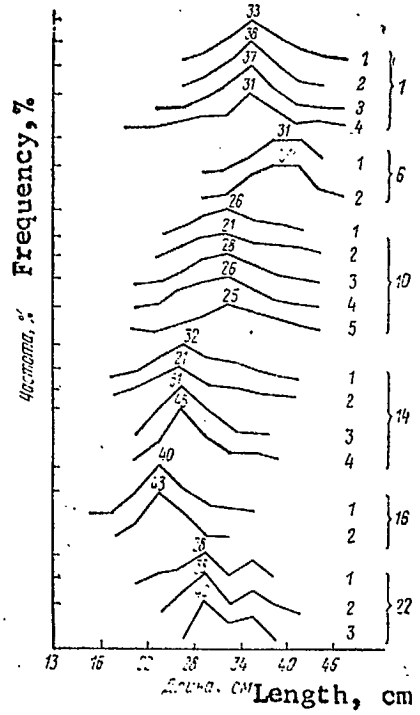

Рис. 34. Кривые распределения линейных размеров рыб в выборках из скоплений окуня, относимых к элементарным популяциям № 1, 6, 10, 14, 16 и 22 на Большой Ньюфаундлендской банке. Нумерация соответствует принятой в табл. 26. Здесь и на последующих аналогичных рисунках цифры над кривыми — частота модального класса.

Figure 34. Distribution curves of the linear dimensions of fishes in samples from accumulations of the redfish related to elementary populations Nos. 1, 6, 10, 14, 16 and 22 on the Newfoundland Grand Bank. The numbering corresponds to that in Table 26. Here and in subsequent similar illustrations the figures above the curves are the modal class frequency.

Table 26. Biological characteristics of redfish populations on the Newfoundland Grand Bank in 1965

Таблица 26. Биологические особенности популяций окуня на Большой Ньюфаундлендской банке в 1965 г.

A Номер популяции	B Номер выборки	C Дата	D Глубина, м	n	E Модальный класс, см	M±m	F Соотношение полов, % самцы 1	самки 2
1	1	19 сентября[b]	500	257	34	36,2	48	52
	2	19 сентября	300	149	34	35,3	54	46
	3	20 сентября	525	468	34	35,0	51	49
	4	20 сентября	305	88	34	35,2	53	47
Среднее[a]			424	962	34	35,3±0,08	51	49
6	6	28 сентября[b]	425	299	37—40	38,4	24	76
	2	28 сентября	420	188	37—40	39,2	19	81
Среднее[a]			422	487	37—40	38,7±0,16	22	78
10	1	22 июня[c]	300	341	31—34	34,3	23	77
	2	22 июня	335	442	31—34	32,9	32	68
	3	22 июня	270	249	31—34	33,3	23	77
	4	24 июня	262	359	31—34	32,1	23	77
	5	24 июня	265	609	31—34	33,7	26	74
Среднее[a]			293	2000	31—34	32,7	29	71
14	1	27 июня[c]	265	201	25	28,9	58	42
	2	15 октября[d]	285	209	25	27,8	43	57
	3	16 октября	285	123	25	27,2	55	45
	4	17 октября	250	282	25	27,6	44	56
Среднее[a]			271	815	25	27,9	49	51
16	1	10 октября[d]	122	191	22	24,0	60	40
	2	11 октября	255	180	22	23,7	51	49
Среднее[a]			188	371	22	24,0±0,16	56	44
22	1	2 октября[d]	340	233	28,34	31,1	62	38
	2	2 октября	280	30	28,34	32,0	63	37
	3	4 октября	375	199	28,34	30,1	72	28
Среднее[a]			331	462	28,34	31,8±0,27	65	35

Key: A - Number of population B - Number of haul C - Date
D - Depth, meters E - Modal class, cm F - Sex ratio, %
1 - males 2 - females
a - Mean b - September c - June d - October

All the investigated catches can be united, on the basis of the character of the variational curves, into the six groups designated on Figure 34 by different numbers. Within the limits of each group the curves are similar or identical in configuration, values of the modal class and range of fluctuations, but at the same time differ from other families of such curves. For example, in Table 26 it is evident that the sizes of fishes in different samples of aggregate No. 1 are very similar to each other, and the sex ratio is approximately identical, whereas in the group of samples united under No. 10 the fish is smaller and an excess of females is observed. Some fluctuations of the means are completely explained by the configuration of the distribution curves: the somewhat larger size of fishes in some samples from grouping No. 1 is caused by the obvious admixture of large individuals in them. The same thing is also characteristic of two samples (hauls) from the aggregates designated Nos. 10 and 14. At the same time, within the limits of each group the variability of even such an apparently unreliable character as the average fish size is incomparably less than on the level of the groups as a whole, which reliably differ from one another (Table 27).

But it is especially important that, besides the indicated similarity, all the biologically identical catches reveal a clear conjugation in space, forming a certain territorial whole -- an elementary population, not decomposing later.

On Figure 35 is a schematic map of such groups of redfish on the entire extent of the slope of the Newfoundland Grand Bank. Each of the populations is characterized by a definite range, but distinct boundaries are not successfully drawn everywhere between them. For example, in cases where fishes from neighboring catches differ in biological characters, the

Table 27. Values of the criterion t_d for differences in the average fish size between aggregates of biologically homogeneous samples

Таблица 27. Значения критерия t_d для различий по среднему размеру рыб между совокупностями биологически однородных проб

a Номер популяции	Номер популяции a				
	6	10	14	16	22
1	19,0	30,4	78,3	63,7	12,4
6		36,8	64,4	64,9	22,3
10			82,3	54,3	3,3
14				23,2	14,2
16					24,8

Key: a - Number of population

boundary drawn in the middle between those catches can be considered more precise than the boundaries turned in the direction of greater or smaller depths, where trawlings have not been made. The boundaries of populations in those directions can rather be considered provisional than strictly established, and so the contours are given as a broken line. But where trawlings have been made, even those not bringing catches, the boundary can be drawn more precisely, as, for example, on one of the sides of the southwestern slope of the Grand Bank.

Nevertheless the picture of the distribution of all the discovered populations appears very distinct, even in spite of the fact that the ranges of some of them overlap. The last-mentioned fact can be connected with the distribution of fishes at different depths. Thus, from summary Table 28, in which the entire set of elementary populations on the Newfoundland Grand Bank is presented, and Figure 35 it follows that, while in the same territory (1965 data) the populations occupy different horizons which differ in depth by 100

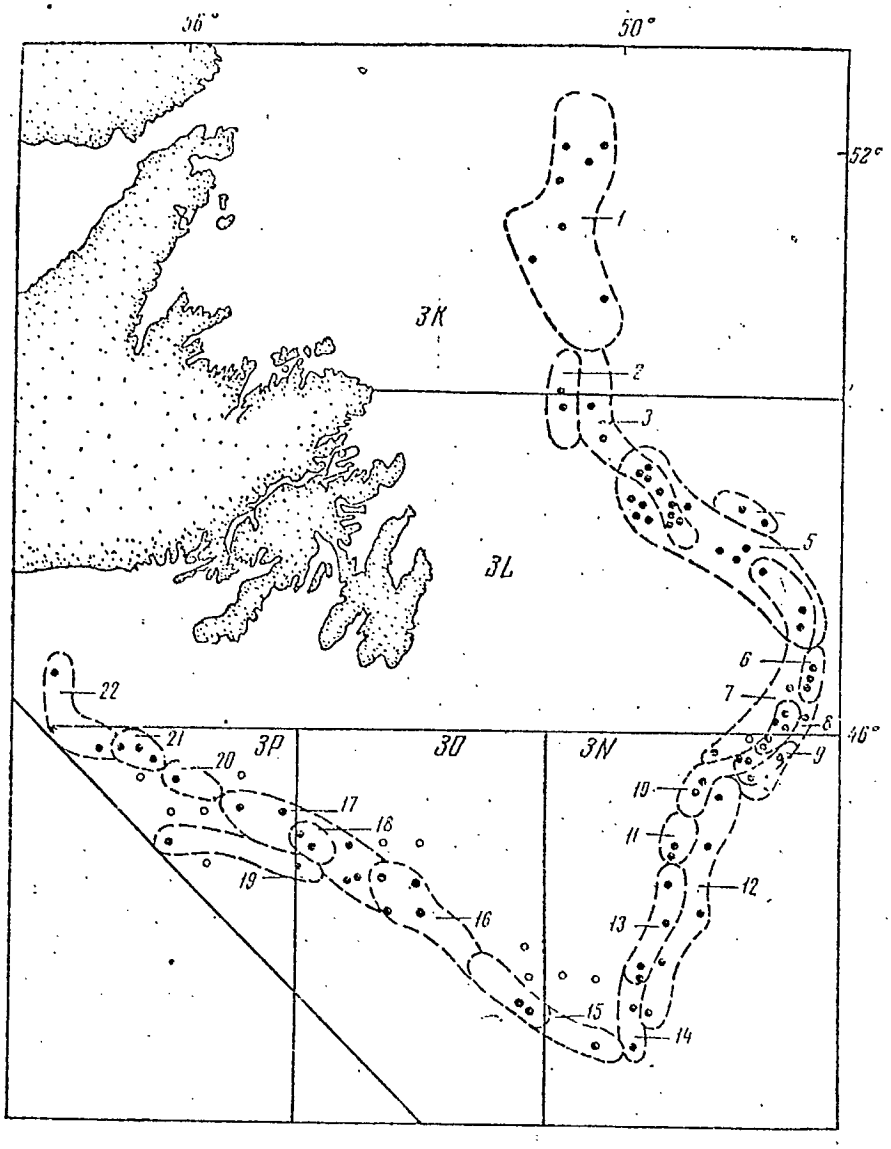

Рис. 35. Локализация элементарных популяций клюворылого окуня на Большой Ньюфаундлендской банке (1964—1965 гг.). Нумерация соответствует принятой в табл. 28. Светлые кружки — местоположение траловых станций, на которых рыба не облавливалась.

Здесь и на последующих аналогичных рисунках контуры отделяют совокупность проб, в которых рыба характеризуется максимальной биологической однородностью.

Figure 35. Location of elementary populations of deepwater redfish on the Newfoundland Grand Bank (1964-1965). The numbering corresponds to that adopted in Table 28. Light circles mark locations of trawling stations at which no fish were taken.

Here and in subsequent similar illustrations the contours separate an aggregate of samples in which the fish is characterized by maximum biological homogeneity.

Table 28. Elementary populations of redfish on the Newfoundland Grand Bank

Таблица 28. Элементарные популяции окуня на Большой Ньюфаундлендской банке

A Номер популяции	B Время сбора материала	C Глубина, м	n	D Модальный класс (длина тела), см	E Средняя длина M±m	Соотношение полов, % самцы a	самки b	G Изменчивость отолита l/d n	M±m	σ	H Частота антигена A_1 N	q_i
1	29 августа—21 октября 1964 г.	297	904	34	36±0,16	52	48	51	1,56±0,01	0,10	—	—
	19—20 сентября 1965 г.	424	962	34	35,3±0,08	51	49	—	—	—	320	0,78
2	28—31 августа 1964 г.	336	1695	31—34,40	34,7±0,26	49	51	73	1,543±0,01	0,11	—	—
	22 сентября 1965 г.	315	305	31—34,40	35,8±0,25	49	51				40	0,67
3	28 августа 1964 г.	345	716	31—34	33,4±0,15	46	54	20	1,57±0,02	0,11	180	
	15 июня—22 сентября 1965 г.	285	619	31—34	33,4±0,17	76	24	20	1,54±0,02	0,08		0,88
4	17—18 сентября 1964 г.	415	163	37	39,7±0,14	41	59	—	—	—		
	23 сентября 1965 г.	515	204	37	39,7±0,23	48	52				40	0,77
5	27 августа—17 сентября 1964 г.	355	1317	34	35,7±0,08	69	31	—	—	—	—	—
	15—16 сентября 1965 г.	237	831	34	36,2±0,11	76	24	30	1,62±0,02	0,12	180	0,83
6	28 сентября 1965 г.	422	487	34—38—40	38,7±0,16	22	78	45	1,53±0,01	0,10	120	0,50
7	13—22 апреля 1965 г.	326	873	25,31—34	32,9±0,07	50	50	—	—	—	60	0,71
8	6 июля—28 сентября 1965 г.	370	999	34,40	38,5±0,14	30	70	20	1,54±0,02	0,10	40	0,50
9	25—26 сентября 1965 г.	275	266	34	34,7±0,26	74	26	40	1,53±0,01	0,11	80	0,90
10	5—6 августа 1964 г.	371	705	31—34	34,2±0,15	52	48	20	1,55±0,02	0,10	—	—
	22—24 июня 1965 г.	293	2000	31—34	32,7±0,03	29	71	15	1,62±0,02	0,10	—	—
11	17 октября 1965 г.	330	333	19,25	25,2±0,49	49	51	—	—	—	60	0,68
12	27 июня, 1 сентября 1965 г.	308	1159	25—28	29,1±0,03	26	74	20	1,56±0,02	0,10	38	0,51
13	5 августа 1964 г.	405	300	31—34,40	38,8±0,26	27	73	—	—	—	60	0,63
	22 июня, 27 сентября 1965 г.	327	916	31—34	32,5±0,05	20	80	—	—	—	—	—
14	27 июня, 15—17 октября 1965 г.	271	815	25	27,9±0,05	49	51	—	—	—	240	0,74
15	6—29 августа 1964 г.	332	1091	28,34	32,2±0,11	26	74	37	1,64±0,02	0,12	—	—
	11—15 октября 1965 г.	402	335	28,34	32,4±0,21	57	43	—	—	—	120	0,79
16	10—11 октября 1965 г.	188	371	22	24,0±0,16	56	44	—	—	—	180	0,78

Table 28 (Continued)

Продолжение табл. 28

A Номер популяции	B Время сбора материала	C Глубина, м	n	D Модальный класс (длина тела), см	E Средняя длина M±m	F Соотношение полов, % самцы a	F самки b	G Изменчивость отолита l/d n	G M±m	G σ	H Частота антигена A_2 N	H q_i
17	8 августа, 17 октября 1964 г.	307	1367	25	28,8±0,09	46	54	29	1,57±0,01	0,06	—	—
	7—10 октября 1965 г.	346	489	25	28,4±0,03	52	48	—	—	—	420	0,73
18	9 августа 1964 г.	376	478	28—31,34	30,6±0,15	59	41	20	1,57±0,02	0,08	—	—
	4 октября 1965 г.	122	176	28—31,34	30,2±0,51	23	77	—	—	—	—	—
19	10 октября 1964 г.	362	797	31	28,1±0,11	33	67	20	1,55±0,02	0,11	—	—
20	5 октября 1965 г.	240	156	19	20,9±0,23	60	40	15	1,50±0,02	0,10	60	0,60
21	9 августа 1964 г.	356	342	31—34	33,4±0,18	21	79	60	1,68±0,01	0,13	—	—
	4 октября 1965 г.	280	30	31—34	32,4±0,61	53	47	19	1,565±0,02	0,08	60	0,73
22	2—4 октября 1965 г.	331	462	28,34	31,8±0,27	65	35	43	1,62±0,02	0,15	180	0,59
Total	1964 г.		10 242	—	32,57±0,05	48	52	597	1,57±0,005	0,11	—	—
Total	1965 г.		13 340	—	33,45±0,05	46	54	—	—	—	2478	0,73

Key: A - Number of population B - Sampling time C - Depth, meters D - Modal class (body length), cm E - Mean length, M±m F - Sex ratio, % G - Variability of otolith l/d H - Frequency of antigen A_2; a - males; b - females.

1 - 29 August-21 October 1964
19-20 September 1965
2 - 28-31 August 1964
22 September 1965
3 - 28 August 1964
15 June - 22 September 1965
4 - 17-18 September 1964
23 September 1965
5 - 27 August - 17 September 1964
15-16 September 1965
6 - 28 September 1965
7 - 15-22 April 1965
8 - 6 July - 28 September 1965
9 - 25-26 September 1965
10 - 5-6 August 1964
22-24 June 1965
11 - 17 October 1965
12 - 27 June, 1 September 1965
13 - 5 August 1964
22 June, 27 September 1965
14 - 27 June, 15-17 October 1965
15 - 6-29 August 1964
11-15 October 1965

Table 28. (Continued)

16 - 10-11 October 1965
17 - 8 August, 17 October 1964
7-10 October 1965
18 - 9 August 1964
4 October 1965
19 - 10 October 1964
20 - 5 October 1965
21 - 9 August 1964
4 October 1965
22 - 2-4 October 1965

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meters or more, for example, populations 5 and 7, 6 and 8, 3 and 14, 15 and 16, and 17 and 18. The distribution of redfish of different sizes by depths has also been pointed out by other authors (Travin and Pechenik, 1962; Hennemuth and Brown, 1964; Sidorenko, 1967).

It is evident from the data of Table 28 that there often are coincidences either in the modal class of the variational curve, the average size or the sex ratio. However, in this case the populations proved to be localized in different parts of the water area, for example, Nos. 1, 5 and 9; 3, 10, 13 and 21; 14 and 17, etc.

The important question arises of the stability of the discovered populations in time and space. An answer can be obtained by comparing 111
the results of repeated trawlings within the limits of the range of a given population. In Figure 36 and in Table 29 are presented the results of repeated trawlings on the range occupied by population No. 5 during 1964 and 1965. Three observations were made annually at different times.
In 1964 the first observation was made by us in August-September on the "Sevastopol'" expeditionary vessel, the second in October and the third by co-workers of the PINRO on the "Zapad", "Novorossiisk" and "Pobeda" in November. In June-July 1965 the first observation was also made by PINRO co-workers on the "Sever", and the second and third on different days of September by us on the "Sevastopol'".

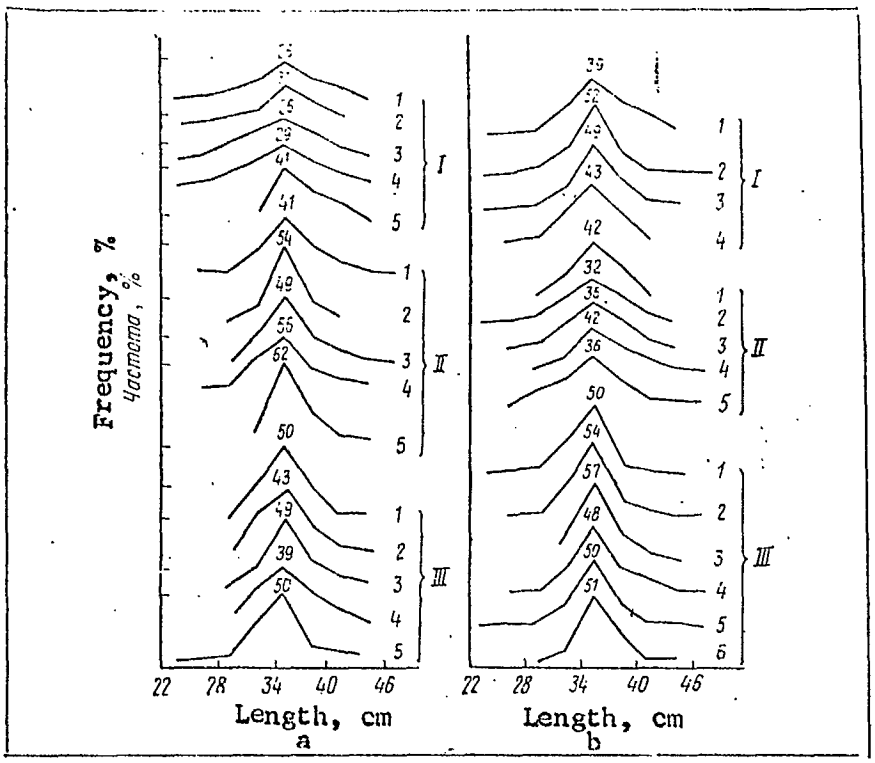

Рис. 36. Кривые распределения длины рыб в популяции № 5 на Большой Ньюфаундлендской банке:
а — выборки 1965 г.; *б* — выборки 1964 г. Нумерация соответствует принятой в табл. 29.

Figure 36. Distribution curves of the length of fishes in population No. 5 on the Newfoundland Grand Bank: a - 1965 samples (hauls); b - 1964 samples (hauls). Numeration corresponds to that adopted in Table 29.

The variational curves and average sizes of fishes in all the catches coincided both for separate periods of observations and for years. 112
Consequently, those data testify to stability of the size composition of fishes in a single population during a considerable time interval. The changes were connected only with the sex ratio, which was redistributed by seasons in the direction of predominance of males, as is well evident from the example of population No. 5, which remained all the time in the same northeastern section of the slope (see Figure 35).

Table 29. Stability of population No. 5 in time

Таблица 29. Устойчивость популяции № 5 во времени

1964 г.								1965 г.							
A наблюдения	B номер пробы	C дата	D глубина, м	n	M±m	E соотношение полов, % самцы a	самки b	A наблюдения	B номер пробы	C дата	D глубина, м	n	M±m	E соотношение полов, % самцы a	самки b
		August								June					
I	1	27 августа	296	300	36,6	62	38	I	1	30 июня	217	357	35,9	38	62
	2	28 августа	292	190	35,0	72	28		2	1 июля	300	200	36,3	39	61
	3	10 сентября	425	377	36,2	75	25		3	2 июля	270	394	36,4	37	63
	4	17 сентября	330	450	35,4	67	33		4	4 июля	—	328	35,4	49	51
		Sept.								July					
									5	8 июля	267	252	36,7	40	60
Среднее F.			336	1317	35,7±0,08	69	31	Среднее F . . .			263	1531	35,8±0,11	40	60
		October								September					
II	1	12 октября	315	158	35,6	59	41	II	1	5 сентября	238	252	36,6	75	25
	2	13 октября	270	502	35,7	54	46		2	15 сентября	238	159	35,7	81	19
	3	13 октября	377	358	35,4	48	52		3	15 сентября	230	201	36,5	73	27
	4	16 октября	330	155	36,7	48	52		4	16 сентября	238	143	35,1	75	25
	5	17 октября	345	91	35,3	42	58		5	16 сентября	238	76	35,5	79	21
Среднее F.			327	1264	35.6±0,10	47	53	Среднее F . . .			237	831	36,2±0,11	76	24
		November								September					
III	1	5 ноября	267	470	34,4	88	12	III	1	22 сентября	255	66	35,5	86	14
	2	5 ноября	262	299	35,1	91	9		2	22 сентября	250	63	35,3	83	17
	3	5 ноября	272	102	36,3	85	15		3	23 сентября	240	79	36,7	78	22
	4	7 ноября	292	334	36,2	64	36		4	23 сентября	233	147	36,1	72	28
	5	9 ноября	267	191	35,4	71	29		5	24 сентября	252	288	35,4	82	12
	6	9 ноября	245	110	36,6	75	25								
Среднее F.			267	1506	35,6±0,08	80	20	Среднее F . . .			245	643	35,7±0,12	80	20

Key: A - Observations B - Number of sample C - Date D - Depth, meters E - Sex ratio, % F - Mean; a- males; b- females.

The results of identification are still more demonstrative in different years in an examination of five populations of the Flemish Cap stock (Figures 37 and 38 and Table 30).

Comparison of samples(hauls) from catches made on the same water area and often at one and the same points permits comparing the character of the distribution curves, the values of the means, and if the trawlings were made in the same season, the sex ratios.

Table 30. Examples of identification of elementary populations on the Flemish Cap bank

Таблица 30. Примеры идентификации элементарных популяций на банке Флеминш-Кап

1961 г.								1965 г.							
A номер популяции	B номер пробы	C дата	D глубина, м	n	M	E соотношение полов, % самцы a	самки b	A номер популяции	B номер пробы	C дата	D глубина, м	n	M	E соотношение полов, % самцы a	самки b
24	1	June 15 июня	600	487	34,9	60	40	24	1	September 3 сентября	517	216	33,6	64	36
	2	August 3 августа	455	279	34,4	88	12		2	5 сентября	545	151	34,2	77	23
	3	December 2 декабря	392	543	34,3	74	26		3	5 сентября	525	315	33,5	62	38
	4	2 декабря	525	1127	34,5	62	38		4	7 сентября	502	353	33,8	66	34
									5	October 18 октября	360	130	33,7	74	26
		Среднее . F .	493	2436	34,2	67	33			Среднее .F. .	489	1165	33,7	67	33
25	1	August 21 августа	390	202	35,5	52	48	25	1	August 22 августа	392	306	35,2	46	54
	2	September 2 сентября	260	262	34,6	46	54		2	23 августа	685	298	36,2	49	51
	3	2 сентября	260	319	35,3	45	55		3	25 августа	320	244	34,9	52	48
	4	29 сентября	430	430	35,5	49	51		4	September 6 сентября	555	248	34,4	49	51
									5	16 сентября	305	216	34,8	46	54
		Среднее . F .	339	1213	35,0	48	52			Среднее .F. .	451	1265	35,1	49	51
28	1	August 3 августа	440	216	37,4	40	60	28	1	August 22 августа	635	234	37,3	43	57
	2	21 августа	350	70	36,2	36	64		2	25 августа	327	192	36,3	42	58
	3	31 декабря	490	423	36,1	48	52		3	27 августа	707	239	37,5	36	64
		Среднее . F .	426	709	36,1	45	55			Среднее .F. .	556	665	37,1	40	60
31	1	13 августа	420	530	32,5	54	46	31	1	September 7 сентября	510	425	32,1	58	42
	2	21 августа	432	437	33,0	43	57		2	8 сентября	387	208	32,2	63	37
	3	21 августа	570	315	33,3	51	49								
	4	September 1 сентября	305	101	33,9	54	46								
		Среднее . F .	432	1383	32,9	50	50			Среднее .F. .	449	633	32,2	60	40
34	1	December 1 декабря	342	570	30,1	59	41	34	1	9 сентября	317	406	29,0	51	49
	2	31 декабря	320	351	29,6	56	44								
	3	February 16 февраля	315	487	28,3	56	44								
		Среднее . F .	328	1408	29,3	57	43								

Table 30 (Continued)

Key: A - Population number B - Sample number C - Date D - Depth, meters E - Sex ratio, % F - Mean a - males b - females

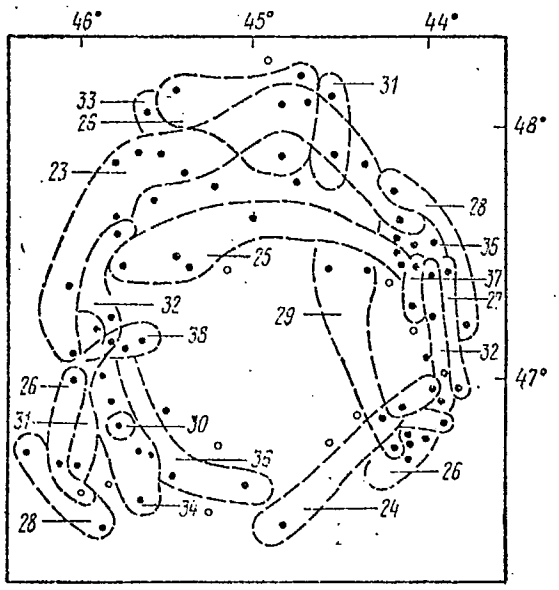

Рис. 37. Элементарные популяции окуня на банке Флемиш-Кап. Нумерация соответствует принятой в табл. 31.

Figure 37. Elementary populations of the redfish on the Flemish Cap bank. Numeration corresponds to that adopted in Table 31.

Data on other populations identified on the Flemish Cap bank are tabulated in Table 31.

Thus the presented material testifies to a considerable stability of the elementary populations of the deepwater redfish in both time* and 117

*This agrees well with the generally accepted concept of slow growth of the redfishes: where there are no distortions of the average sizes on account of admixture of fishes from neighboring populations, the increase of body length per year proves to be small, of the order of 0.5-1.4 cm (see corresponding samples from populations Nos. 23, 24, 26, 27, 28 and 29 in Table 31).

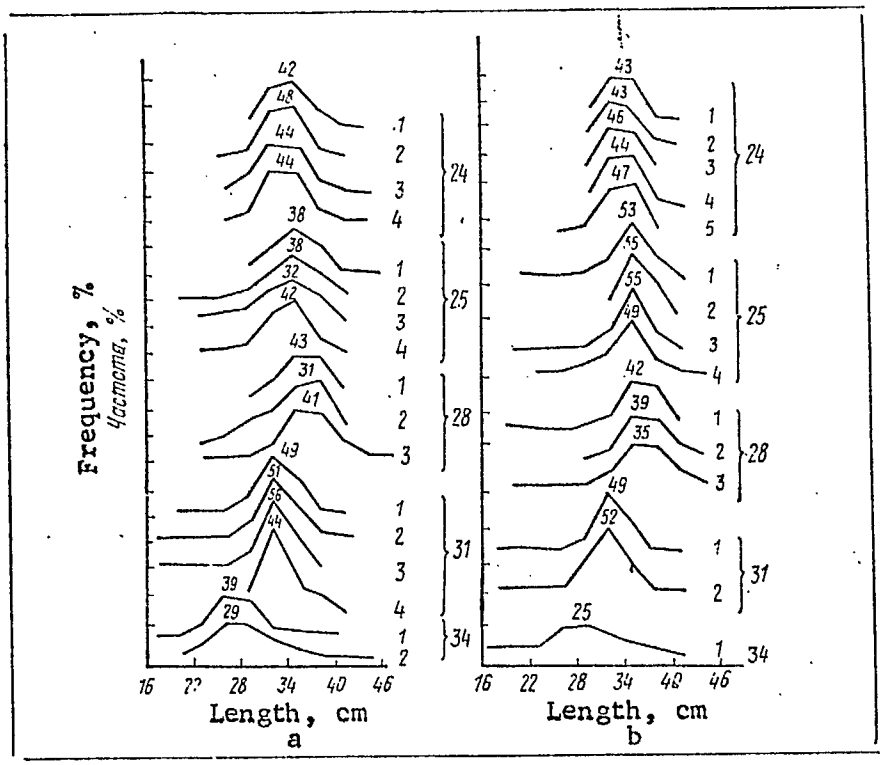

Рис. 38. Кривые распределения длины рыб в некоторых элементарных популяциях, идентифицированных на банке Флемиш-Кап в 1964 (*а*) и 1965 (*б*) гг. Нумерация соответствует принятой в табл. 30.

Figure 38. Distribution curves of fish length in some elementary populations identified on the Flemish Cap bank in 1964 (a) and 1965 (b). Numeration corresponds to that adopted in Table 30.

space. Since the corresponding ranges have been mapped we can characterize each population immunogenetically, "applying" the results of genogeographic analysis to that structure (see Tables 28 and 31). The same combination of separate samples permits comparing populations also with respect to the value of the 1/d index of the otolith.

As we see, the deepwater redfish populations on the Grand Bank differ reliably in the frequency of the A_2 factor and, consequently, one can

Table 31. Elementary populations of redfish on Flemish Cap bank

Таблица 31. Элементарные популяции окуня на банке Флемиш-Кап

Номер популяции A	Время сбора материала B	Глубина, м C	n	Модальный класс (длина тела), см D	Средняя длина, M ± m E	Соотношение полов, % F		Изменчивость индекса l/d G			Частота антигена A_2 H	
						самцы a	самки b	n	M±m	σ	N	q_l
23	21 августа — 6 сентября 1965 г.	415	1757	31—34	34,2±0,08	49	51	—	—	—	100	1,00
23	1 августа, 30 декабря 1964 г.	381	3480	31—34	33,9±0,05	47	53	57	1,686±0,01	0,11	—	—
24	3 сентября — 18 октября 1965 г.	489	1165	31—34	33,7±0,07	67	33	—	—	—	282	0,94
24	15 июня — 2 декабря 1964 г.	493	2436	31—34	33,2±0,05	67	33	18	1,755±0,02	0,08	—	—
25	22 августа — 16 сентября 1965 г.	451	1265	34	35,1±0,08	49	51	—	—	—	60	1,00
25	21 августа — 29 сентября 1964 г.	339	1213	34	35,0±0,09	48	52	58	1,703±0,01	0,105	—	—
26	26 августа — 13 сентября 1965 г.	521	2003	34	35,5±0,04	77	23	—	—	—	60	0,96
26	30 мая — 5 июня 1964 г.	465	2302	34	34,4±0,07	61	39	—	—	—	—	—
27	23 августа 1965 г.	670	441	34	36,5±0,11	38	62	—	—	—	—	—
27	28 мая — 2 августа 1964 г.	489	1384	34	35,1±0,08	39	61	10	1,659±0,03	0,010	—	—
28	22—27 августа 1965 г.	556	665	34—37	37,1±0,11	40	60	—	—	—	—	—
28	3 августа — 31 декабря 1964 г.	426	709	34—37	36,1±0,13	45	55	20	1,714±0,02	0,10	—	—
29	26 августа 1965 г.	715	198	37	39,2±0,19	66	34	—	—	—	—	—
29	10 июня — 2 декабря 1964 г.	318	954	37	37,8±0,12	38	62	20	1,584±0,01	0,07	—	—
30	9 сентября 1965 г.	305	274	37—40	39,3±0,25	78	22	—	—	—	100	0,98
31	7—8 сентября 1965 г.	449	633	31	32,2±0,12	60	40	—	—	—	100	0,99
31	13 августа — 1 сентября 1964 г.	432	1383	31	32,9±0,08	50	50	80	1,703±0,01	0,09	—	—
32	5—7 сентября 1965 г.	446	797	19,31—34	32,4±0,16	56	44	—	—	—	278	0,97
32	20 августа 1964 г.	450	332	19,31—34	32,6±0,33	57	43	20	1,697±0,01	0,08	—	—
33	6 сентября 1965 г.	477	351	19—22, 31—34	31,6±0,26	37	63	19	1,760±0,02	0,12	60	1,00

Table 31 (Continued)

A Номер популяции	B Время сбора материала	C Глубина, м	n	D Модальный класс (длина тела), см	E Средняя длина, $M \pm m$	F Соотношение полов, %		G Изменчивость индекса l/d			H Частота антигена A_2	
						самцы a	самки b	n	$M \pm m$	σ	N	q_l
34	9 сентября 1965 г.	317	406	25—28	29,0±0,27	51	49	—	—	—	—	—
34	1 декабря 1964 г. — 16 февраля	328	1408	25—28	29,3±0,11	57	43	30	1,653±0,02	0,12	—	—
35	23 августа — 5 сентября 1965 г.	385	987	19—22,34	26,4±0,22	53	47	29	1,670±0,02	0,14	60	0,97
36	7—13 сентября 1965 г.	315	414	22, 28, 34	29,3±0,29	60	40	21	1,626±0,02	0,10	120	0,94
37	9 сентября 1965 г.	330	526	28,34	32,6±0,20	46	54	—	—	—	—	—
38	7—26 сентября 1964 г.	303	1186	31,37	35,2±0,11	44	56	—	—	—	—	—
Total 1964 г.		—	11916	—	33,55±0,04	51	49	420	1,689±0,05	0,11	1220	0,975
Total 1965 г.		—	16788	—	34,09±0,03	56	44	—				

Key: A - Population number B- Sampling time C - Depth, meters
D - Modal class (body length), cm E - Mean length, $M \pm m$
F - Sex ratio, % G - Variability of index 1/d H - Frequency of antigen A_2 a - males b - females

23 - 21 August - 6 September 1965
23 - 1 August, 30 December 1964
24 - 3 September - 18 October 1965
24 - 15 June - 2 December 1964
25 - 22 August - 16 September 1965
25 - 21 August - 29 September 1964
26 - 26 August - 13 September 1965
26 - 30 May - 5 June 1964
27 - 23 August 1965
27 - 28 May - 2 August 1964
28 - 22-27 August 1965
28 - 3 August - 31 December 1964
29 - 26 August 1965
29 - 10 June - 2 December 1964
30 - 9 September 1965
31 - 7-8 September 1965
31 - 13 August - 1 September 1964
32 - 5-7 September 1965
32 - 20 August 1964
33 - 6 September 1965
34 - 9 September 1965
34 - 1 December 1964 - 16 February
35 - 23 August - 5 September 1965
36 - 7-13 September 1965
37 - 9 September 1965
29 - 7-26 September 1964

consider demonstrated the genetic nature of these groups, which actually reflect the not further decomposable, biologically elementary level of the population structure of the investigated local stock. 123

On the Flemish Cap bank the gene A_2 is near fixation, but there are no grounds for doubting that the further discovery of suitable systems of genetic polymorphism of the redfishes will make it possible to discover here also the same picture of variability as in the aggregate of isolated populations on the Grand Bank. In any case, in relation to a quantitative character such as the investigated index is, such a conclusion does not require additional argumentation.

Genetic Differences Between Elementary Populations of the Anchovy

A detailed account of the principles of recognition of elementary populations of the redfishes permits proceeding without additional explanations to an examination of the biological features of elementary populations of the anchovy, for which, just as for redfishes, it is possible to show the independence of the variability of differentiating characters -- the sex ratio in the sample(haul) and the modal frequency of the corresponding variational series (Figure 39).

The main part of the work was done on 1966 material. Data of 1963 and 1965 were partially included.

In Table 32 it is shown that the fish from different trawling catches can be united into groups of homogeneous samples. For example, all eight samples combined into aggregate No. 9 are practically identical with one another as regards average sizes, condition, the sex ratio and the type of variational curves of body length (Figure 40). A similar picture is observed also in the case of four samples from population No. 4

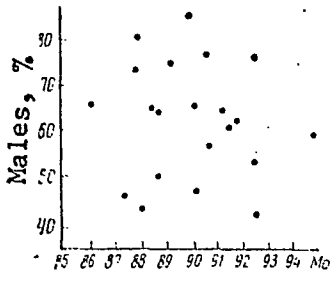

Рис. 39. Отсутствие корреляции между соотношением полов и модальной частотой соответствующего вариационного ряда для популяций азовского анчоуса. Обозначения те же, что и на рис. 33.

Figure 39. Absence of correlation between the sex ratio and modal frequency of the corresponding variational series for populations of the Azov anchovy. Designations the same as in Figure 33.

Figure 40. Distribution curves of body length of fishes of three anchovy populations. The numeration corresponds to that adopted in Table 22.

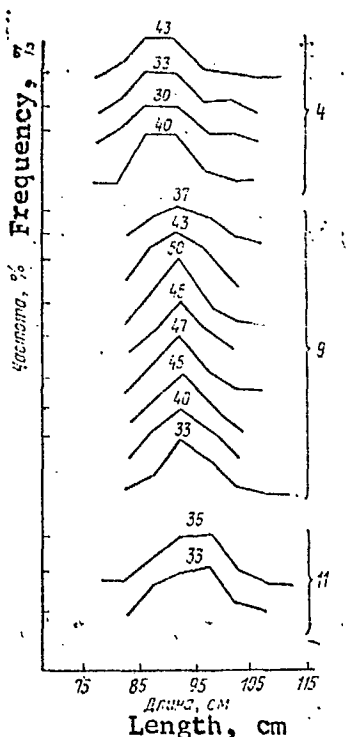

Рис. 40. Кривые распределения длины тела рыб трех популяций анчоуса. Нумерация соответствует принятой в табл. 32.

Table 32. Elementary anchovy populations in the Sea of Azov (August 1966)

Таблица 32. Элементарные популяции анчоуса в Азовском море (август 1966 г.)

A	B	C	Биологическая характеристика D							Частота групп крови, % E			
Номер выборки	Локализация проб (промысловый квадрат)	Дата	средний размер, мм a	средняя масса, г b	упитанность по Фультону c	Соотношение полов, d % самцы 1	самки 2	jun 3	n	A_1	A_2	A_0	n
1	14-ф	18	91,8	7,85	1,01	60	40	—	66	60	40	—	30
	20-х	18	91,7	7,87	1,02	59	41	—	51	59	41	—	27
	Средние Mean		91,75±0,65	7,86	1,02	60	40	—	117	60	40	—	57
2	10-ц	19	89,8	7,48	1,03	90	10	—	30	90	10	—	30
	11-ч	19	89,9	7,77	1,07	83	17	—	30	87	13	—	30
	Средние Mean		89,85±0,77	7,63	1,05	80	20	—	60	92	8	—	60
3	9-ч	19	87,5	7,29	1,09	83	7	10	68	87	13	—	30
	13-ц	22	87,9	6,62	0,97	57	43	—	87	83	13	4	30
	Средние Mean		87,75±0,53	6,96	1,03	70	25	5	155	85	13	2	60
4	9-у	23	90,8	8,35	1,12	73	27	—	91	67	30	3	30
	10-т	23	90,2	8,37	1,14	80	20	—	106	67	30	3	30
	10-ф	23	90,4	7,94	1,07	90	10	—	45	67	30	3	30
	12-т	23	90,8	8,89	1,19	60	40	—	89	67	33	—	30
5	Средние Mean		90,50±0,31	8,38	1,13	73	27	—	331	67	31	2	120
	7-с	23	87,9	7,51	1,11	90	10	—	51	80	20	—	30
	5-с	24	87,8	7,71	1,14	75	25	—	81	84	8	8	26
6	Средние Mean		87,85±0,77	7,61	1,12	76	24	—	132	82	14	4	56
	8-р	23	88,3	8,84	1,28	57	30	13	58	77	20	3	30
	6-р	24	88,9	7,98	1,14	63	30	7	38	77	16	7	30
7	Средние Mean		88,40±0,52	8,13	1,18	60	30	10	96	77	18	5	60
	3-с	24	92,6	7,92	1,00	75	25	—	92	53	47	—	30
	4-г	24	92,0	8,47	1,09	70	30	—	75	57	43	—	30
	Средние Mean		92,45±0,52	8,19	1,04	72	28	—	167	55	45	—	60
8	11-о	25	91,0	7,89	1,05	60	30	10	88	83	10	7	30
	11-р	25	91,2	7,86	1,04	60	40	—	198	80	20	—	30
	12-м	30	91,4	8,62	1,13	53	47	—	80	90	10	—	30
	17-м	30	91,2	8,50	1,12	63	33	4	59	83	17	—	30
	Средние Mean		91,45±0,23	8,11	1,13	59	37	4	425	84	14	2	120
9	14-р	25	92,2	7,96	1,01	43	57	—	97	87	13	—	30
	16-т	27	92,5	8,64	1,09	47	53	—	76	93	7	—	30
	18-р	28	92,6	—	—	57	43	—	45	93	7	—	30
	22-р	28	92,1	8,26	1,06	60	40	—	121	90	10	—	30
	16-о	30	92,8	8,13	1,02	53	47	—	91	87	13	—	30
	21-м	30	92,6	8,87	1,12	57	43	—	49	97	3	—	30
	24-о	30	92,5	8,21	1,04	57	43	—	86	100	—	—	30
	21-о	31	92,2	8,52	1,08	53	47	—	49	87	13	—	30
	Средние Mean		92,49±0,21	8,39	1,06	52	48	—	614	92	8	—	210
10	22-ф	27	90,6	8,01	1,07	60	30	10	82	93	7	—	30
	24-ф	27	90,8	8,00	1,07	57	37	6	33	97	3	—	30
	26-ф	27	90,4	7,52	1,02	50	30	20	72	97	3	—	30
	Средние Mean		90,60±0,45	7,84	1,05	55	32	13	187	96	4	—	90
11	20-т	28	94,7	8,98	1,06	58	42	—	117	90	10	—	30
	26-р	28	94,5	9,06	1,07	56	44	—	30	90	10	—	30
	Средние Mean		94,70±0,47	9,02	1,06	57	43	—	147	90	10	—	60

Примечание. Выделенные шрифтом цифры означают общее число рыб в каждой выборке.

Key: A - Sample number B - Sampling places (fishery square) C - Date
D - Biological characterization E - Blood group frequency, %
a - Average size, mm b - average mass, g c - Fulton's condition factor
d - Sex ratio, % 1 - males 2 - females 3 - juveniles

Note. The numbers in heavy print are the total number of fishes in each sample (haul).

and two samples taken from population No. 11. At the same time these three samples differ substantially from one another, if not as regards the entire complex of studied characters, then as regards some of them. Thus, samples Nos. 9 and 11 do not differ in the sex ratio and the coef- 124
ficient of condition, but the distribution curves are characterized by different modes and means (92.49±0.21 and 94.70±0.47 respectively; $P < 0.001$). Males predominate in sample No. 4, and it also differs in the average size of individuals (90.5±0.31) and the coefficient of condition.

All the biologically homogeneous samples were clearly conjugated in space (Figure 41). A similar differentiation is also traced in the analysis of other samples. Whereas in individual cases coincidence in the average sizes is observed (samples Nos. 1 and 8;4 and 10, 7 and 9), the sex ratio (Nos. 3 and 4; 6 and 8) or the coefficient of condition (Nos. 1 and 3; 4 and 5; 9 and 11), such groups proved to be localized in different sections of the range.

The examined materials testify that in the Sea of Azov in 1966, just as 20 years before that, differentiation of the anchovy into small homogeneous groups -- elementary populations -- was successfully detected. Due to the limitedness of the biological material at our disposal we succeeded in outlining their ranges only in the central and western regions of the sea. It is clear that the same structure given the corresponding data can also be detected in its eastern region, as was shown later by V.V. Limanskii and A.N. Payusova (1969).

Let us now turn to the part of Table 32 where the results of analysis of blood group frequencies within the limits of each of 11 elementary populations are presented. Already from the example of the same populations Nos. 4 and 9

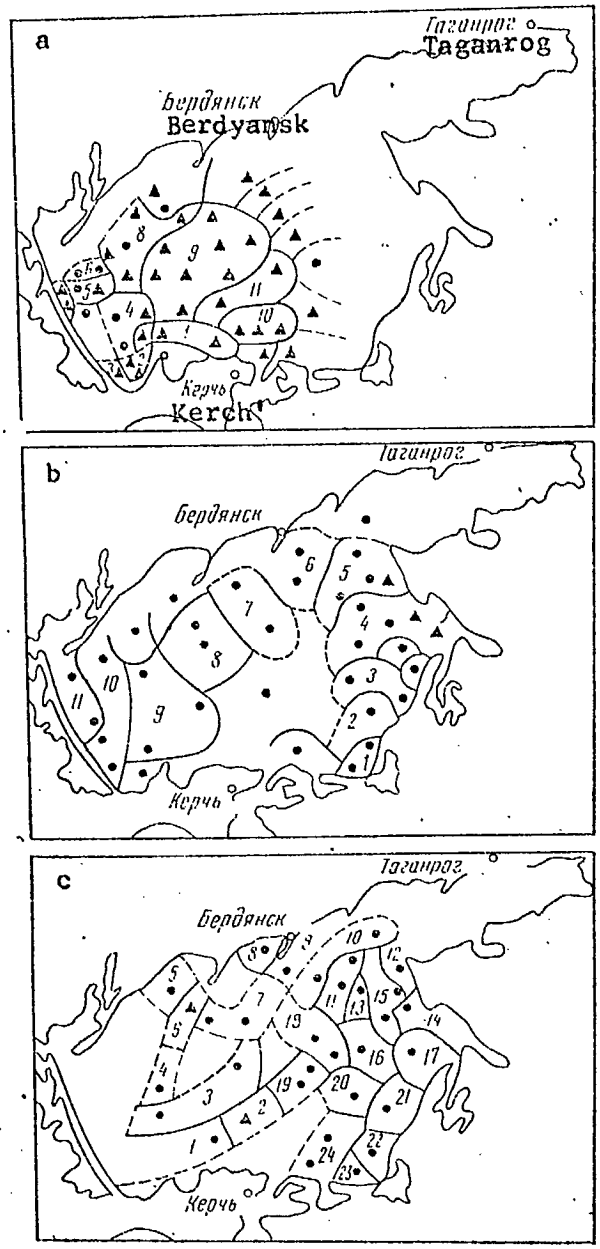

Рис. 41. Пространственная локализация элементарных популяций анчоуса в Азовском море:

а — август 1966 г.; *б* — июнь 1965 г.; *в* — сентябрь 1965 г. Треугольниками обозначен анчоус черноморской расы; кружками — азовской расы (по Алтухову и др., 1969б; Лиманскому и Паюсовой, 1969).

Figure 41. Spatial localization of elementary anchovy populations in the Sea of Azov: a - August 1966; b - June 1965; c - September 1965. Anchovies of the Black Sea race are designated by triangles and those of the Azov race by circles (acc. to Altukhov et al., 1969b; Limanskii and Payusova, 1969).

their serological differences are evident: whereas No. 9 is represented by phenotypes A_1 and A_2, No. 4 contains still more A_0 individuals and in addition differs reliably in the frequency of the A_1 and A_2 blood groups. It is clearly evident that the range of variation of the frequency characteristics of individual samples is just as insignificant as with respect to biological characters, and is not at all comparable with the interpopulation variability. 128

Table 33 has been compiled for all 11 populations and contains a statistical evaluation of their differentiation with respect to the frequency of phenotype A_1.

Table 33. Character of differentiation of elementary populations of the anchovy by frequency of phenotype A_1 (acc. to Altukhov et al., 1969)

Таблица 33. Характер дифференцировки элементарных популяций анчоуса по частоте фенотипа A_1 (по Алтухову и др., 1969)

Выборка A		Вероятность идентичности выборок B										C
a номер	b обозначение	0,500	0,400	0,200	0,100	0,050	0,020	0,010	0,005	0,002	0,001	Число исследованных рыб
1	А А	Ж	Г			Е		Д		В, З	Б, И, К, Л	57
2	Б В	И, Л	К	В	Д, З		Е				Г, Ж	60
3	В С	З	Е, Л	Д, И		К			Г		Ж	60
4	Г D			Е	Ж		Д			З	И, К, Л	120
5	Д Е			Д	И		К			Ж		56
6	Е F			З		Л		Ж, И		К		60
7	Ж G										З, И, К, Л	70
8	З Н		Л			И				К		120
9	И I			К								210
10	К J			Л								90
11	Л К											60

Key: A - Sample(haul) B - Probability of identity of samples(hauls)
C - Number of investigated fishes a - Number b - Symbol
See column b for English equivalent of Russian letters.

Table 34. Biological and immunogenetic characteristics of the anchovy migrating through Kerch' Strait (acc. to Altukhov et al., 1969)

Таблица 31. Биологическая и иммуногенетическая характеристики анчоуса, мигрирующего через Керченский пролив (по Алтухову и др., 1969)

A Номер пробы	B Промысловый квадрат	C Дата	D Биологическая характеристика: a средний размер, мм	b средняя масса, г	c упитанность по Фультону	d соотношение полов, %: 1 самцы	2 самки	3 ювен.	E Частота групп крови, %: A_1	A_2	A_0	n
1	23-ц	21 октября 1963 г.	81,3	5,28	0,98	26	74	—	68	25	7	40
2	22-ц	27 октября 1963 г.	87,5	6,42	0,96	20	80	—	25	17	58	40
3	22-ц	3 ноября 1963 г.	93,2	8,69	1,07	63	37	—	37	43	20	40
4	23-ч	12 ноября 1963 г.	76,5	3,55	0,79	62	38	—	13	47	40	50
5	23-ч	23 октября 1965 г.	66,1	2,40	0,83	50	48	2	50	16	34	50
6	23-ч	24 октября 1965 г.	79,4	4,74	0,95	52	44	4	66	22	12	50
7	23-ч	1 ноября 1965 г.	67,9	2,14	0,68	72	20	8	22	28	50	50
8	23-ч	2 ноября 1965 г.	69,9	2,12	0,62	71	25	4	25	29	46	24

Key: A - Sample number B - Fishery square C - Date D - Biological characteristics a - mean size, mm b - mean mass, g c - Fulton's condition factor d - sex ratio 1 - males 2 - females 3 - juveniles E - Blood group frequency, %

1 - 23-ts - 21 October 1963
2 - 22-ts - 27 October 1963
3 - 22-ts - 3 November 1963
4 - 23-ch - 12 November 1963
5 - 23-ch - 23 October 1965
6 - 23-ch - 24 October 1965
7 - 23-ch - 1 November 1965
8 - 23-ch - 2 November 1965

The results of analysis of the anchovy during the wintering migration through Kerch' Strait can be interpreted on the same plane (Table 34).

Each day fishes with a different blood group frequency were analyzed. For example, on 21 October 1963 individuals with blood group A_1 predominated (68%) in the sample, with comparatively rare occurrence of A_0(7%) but after six days the

the picture had changed to the reverse: the A_1 frequency had decreased to 25% and the A_0 frequency had risen to 58%. The same subdivision in principle, but expressed to a greater or lesser degree, was also found in other cases.

If each of the immunologically investigated samples is characterized according to biological characters (see Table 34 and Figure 42) it becomes evident that we are dealing with nothing other than elementary populations differing in their blood group frequency.

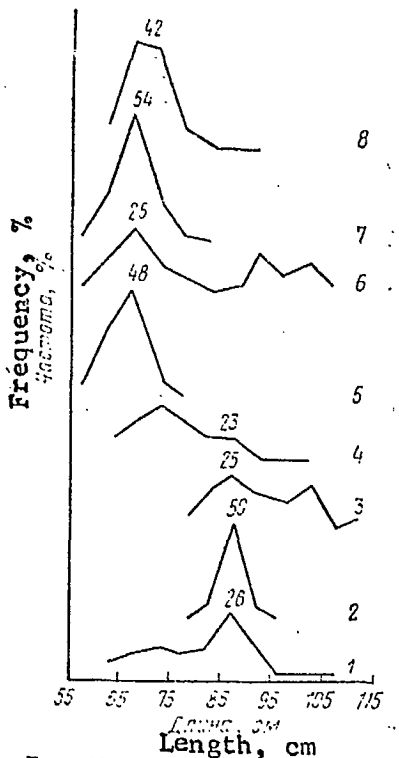

Figure 42. Distribution curves of linear dimensions of the anchovy migrating through Kerch' Strait from the Sea of Azov into the Black Sea. See table 34 for sample numbers.

Рис. 42. Кривые распределения линейных размеров анчоуса, мигрирующего через Керченский пролив из Азовского моря в Черное. Номера проб. см. табл. 34.

Now let us examine the ratio of elementary populations of the anchovy with its major subdivisions, the Azov and Black Sea races, which 129
in August 1966 were in the Sea of Azov and had been found there still earlier in a genogeographical analysis.

In such a comparison it is evident that within the limits of the range occupied by the Black Sea race (see Figure 41) (triangles) four populations disposed as neighbors are distinguished, three of which (Nos. 9, 10 and 11), as already noted, are very similar in blood group frequency, while the fourth(No.1) adjoining them on the soutwest, differs immunogenetically, revealing as regards this character identity with elementary population No. 7, localized at the Tongue of Arabat. The two populations represented only by phenotypes A_1 and A_2 are similar to the group(grouping) traced in a genogeographic investigation in June, August and September 1965.

Of the other populations only No. 6 can be classified in the Azov race, whereas Nos. 4, 5 and 8 represent mixtures of the Azov and Black Sea races.

These data are important in connection with the previously expressed 130
considerations of the role of elementary populations in the differentiation and integration of the gene pools of larger population communities. If one remains within the framework of the old concepts of the taxonomic interrelations of races, it becomes evident that the finding of genetically different populations within the Black Sea race (Nos. 1, 7 and 9) substantiates the former assumption, and the presence of mixed groups(groupings)(Nos. 4, 5 and 8), the second. But in any case the hereditary nature of the simplest population units, even in such a mobile species as the anchovy appears proven. The isolation mechanism also is clear. It is temporary isolation caused by the lengthiness of spawning of the anchovy in time.

Table 35. Distribution of phenotypes and genes of blood groups of the A-system in elementary populations of the Azov race of anchovy, June 1965

Таблица 35. Распределение фенотипов и генов групп крови A-системы в элементарных популяциях азовской расы анчоуса, июнь 1965 г.

A Номер популяции	B Численности фенотипов				n	χ^2	C Частота генов		
	A_1	A_1A_2	A_2	A_0			p^*	q^*	r^*
1	35 (36,57)	3 (4,05)	6 (4,85)	15 (13,83)	59	2,93	0,437	0,079	0,484
2	42 (40,04)	8 (8,85)	6 (5,66)	4 (5,42)	60	0,58	0,570	0,130	0,300
3	21 (20,50)	— (0,76)	1 (0,26)	1 (1,42)	23	2,82	0,729	0,023	0,248
4	56 (53,18)	11 (11,92)	13 (14,37)	7 (8,26)	87	0,58	0,533	0,154	0,313
5	54 (49,78)	11 (15,20)	20 (16,45)	10 (12,30)	95	1,88	0,453	0,186	0,361
6	39 (38,10)	1 (2,24)	3 (1,68)	7 (7,92)	50	1,76	0,561	0,041	0,398
7	45 (41,39)	4 (7,67)	12 (8,52)	10 (12,49)	71	3,96	0,456	0,127	0,417
8	4 (3,99)	4 (2,00)	8 (9,92)	7 (7,00)	23	2,00	0,142	0,309	0,549
10	34 (32,10)	5 (6,96)	23 (21,56)	36 (36,00)	98	0,28	0,229	0,162	0,609
11	16 (16,72)	3 (2,40)	10 (9,50)	31 (31,00)	60	0,23	0,172	0,115	0,713
Σ	346 (333,03)	50 (65,10)	102 (90,21)	128 (138,35)	626	6,32	0,395	0,132	0,473

* Частоты, рассчитанные с поправкой Бернштейна.

Key: A - Population number B - Numbers of phenotypes C - Gene frequency

* - Frequencies calculated with Bernstein correction.

The maximum biological homogeneity of elementary populations and at the same time their specific characteristics under conditions of surprising uniformity of the external environment over the entire course of the spawning range of the anchovy must, therefore, be regarded as derivatives of the population gene pools.

On the assumption of unlimited panmixia as the most probable state of each separate population sufficiently separated from all others, one can turn to the mechanism of inheritance of blood groups of the A-system in the Azov race and attempt to conduct the previous analysis with the new data taken into account.

Making use of material from the study of V.V. Limanskii and A.N. Payusova (1969), after preliminary separation of the assumed heterozygotes A_1A_2 by dose effect, we obtained a correspondence of the actual numbers of phenotypes expected from the Hardy-Weinberg equation in populations described immunogenetically rather completely (Table 35).

Thus the assumption of a three-allele structure of the A-locus of 132
blood groups in the Azov anchovy obtains confirmation on a different level of analysis, and the total deficit of heterozygotes noted earlier agrees completely with the population organization of the Azov race described here.

Genetic Differences Between Elementary Populations of Pacific Salmons

In contrast with the anchovy and especially the redfish, whose populations are concealed by the water columns pelagic zones of sea waters, the subdivision of local salmon stocks, caused by distinctive features of their ecology, is directly observable. However, as far as we know, this structure has been investigated and discussed mainly on the level of the so-called seasonal races (Berg, 1934; Abakumov, 1961; Levanidov, 1969, etc.), and never in the aspect of interest to us.

If we turn to the local stock of the sockeye of Lake Azabach'e, we see that the accumulations of fishes at separate spawning grounds correspond in their biological features precisely to the elementary populations of other species of fishes. The only differences are that, firstly, the numbers of those groups are measured not in tens or hundreds of thousands of individuals, as in the redfish or anchovy, but in only tens or hundreds; secondly, the ranges prove to be correspondingly very small -- of the order of hundreds of square meters, in contrast with the tens of square miles occupied by other species not so settled; thirdly, by virtue of distinctive features of the ecology intrinsic to them, the spawning accumulations of the sockeye are clearly isolated*, which frees the investigator from labor-consuming work on outlining them.

There are no fundamental differences in all the rest. The elementary sockeye populations are clearly disconnected in space (see Figure 10), differ in their linear dimensions (Figure 43) and sex ratios, and are characterized by specific gene pools (Table 36).

In this case the genetic description of individual populations is given for two loci, among which lactate dehydrogenase reveals the maximum interpopulation variability in relation to allele frequencies. On the other hand, for the locus of phosphoglucomutase the dispersion of gene frequencies proves to be small, and this will be examined in greater detail in the following chapter. However, in spite of such uniformity, reliable differences are still detected between some elementary populations: the corresponding tests for homogeneity give values of χ^2 of 87.23 and 33.08 (df = 22).

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*Probably, because of complex reproductive behavior, panmixia in spawning populations of sockeye may be expressed more weakly than in other species of fishes.

Table 36. Distribution of genotypes and frequency of genes of lactate dehydrogenase (Ldh) and phosphoglucomutase (Pgm) in the system of isolated populations of the sockeye of Lake Azabach'e

Таблица 36. Распределения генотипов и частоты генов лактатдегидрогеназы (*Ldh*) и фосфоглюкомутазы (*Pgm*) в системе изолированных популяций нерки озера Азабачьего

A	*Ldh*							*Pgm*						
Номер популяции	*BB*	*B'B*	*B'B'*	*N*	*qB*	*pB'*	χ^2	*AA*	*AB*	*BB*	*N*	*qA*	*pB*	χ^2
1	49 (50,1)	61 (58,7)	16 (17,2)	126	0,6309	0,3691	0,20	70 (70,1)	38 (37,8)	5 (5,1)	113	0,7876	0,2124	0,00
2	36 (35,0)	39 (41,0)	13 (12,0)	88	0,6306	0,3694	0,21	53 (51,2)	26 (29,5)	6 (4,3)	85	0,7765	0,2235	1,15
3	35 (34,2)	44 (45,6)	16 (15,2)	95	0,6000	0,4000	0,12	66 (65,8)	27 (27,4)	3 (2,8)	96	0,8281	0,1719	0,02
4	45 (41,3)	52 (59,4)	25 (21,3)	122	0,5819	0,4181	1,43	84 (85,2)	40 (37,6)	3 (4,2)	127	0,8189	0,1811	0,51
5	39 (34,4)	49 (58,1)	29 (24,5)	117	0,5427	0,4573	2,87	61 (63,3)	41 (36,4)	3 (5,3)	105	0,7762	0,2238	1,66
6	38 (34,2)	35 (42,6)	17 (13,2)	90	0,6166	0,3834	2,87	49 (52,3)	43 (36,4)	3 (6,3)	95	0,7421	0,2579	3,13
7	20 (19,0)	21 (23,0)	8 (7,0)	49	0,6224	0,3776	0,37	32 (32,8)	17 (15,4)	1 (1,8)	50	0,8100	0,1900	0,54
8	30 (31,2)	38 (35,6)	9 (10,2)	77	0,6363	0,3637	0,35	48 (49,3)	35 (32,4)	4 (5,3)	87	0,7529	0,2471	0,56
9	12 (12,2)	13 (12,6)	3 (3,2)	28	0,6607	0,3393	0,20	22 (23,2)	13 (10,6)	0 (1,2)	35	0,8143	0,1857	1,80
10	17 (15,8)	30 (32,5)	18 (16,7)	65	0,4924	0,5076	0,38	43 (43,2)	24 (23,6)	3 (3,2)	70	0,7857	0,2143	0,02
11	16 (15,2)	21 (22,5)	9 (8,3)	46	0,5760	0,4240	0,20	24 (25,1)	20 (17,7)	2 (3,1)	46	0,7391	0,2609	0,74
12	12 (13,8)	20 (16,4)	3 (4,8)	35	0,6285	0,3715	1,69	24 (24,4)	16 (15,2)	2 (2,4)	42	0,7619	0,2381	0,12
13	23 (21,1)	19 (22,8)	8 (6,1)	50	0,6500	0,3500	1,39	28 (29,6)	21 (17,7)	1 (2,6)	50	0,7700	0,2300	1,68
14	11 (11,0)	20 (20,0)	9 (9,0)	40	0,5250	0,4750	0,00	23 (22,3)	13 (14,4)	3 (2,3)	39	0,7564	0,2436	0,37
15	22 (23,4)	37 (34,2)	11 (12,4)	70	0,5785	0,4215	0,47	39 (38,4)	25 (26,2)	5 (4,4)	69	0,7463	0,2537	0,14
16	28 (28,1)	34 (33,8)	10 (10,1)	72	0,6250	0,3750	0,00	50 (49,3)	24 (25,4)	4 (3,3)	78	0,7948	0,2052	0,24
17	52 (51,4)	29 (30,2)	5 (4,4)	86	0,7732	0,2268	0,14	59 (60,8)	34 (30,4)	2 (3,8)	95	0,8000	0,2000	1,33
18	46 (45,6)	31 (31,8)	6 (5,6)	83	0,7410	0,2590	0,05	64 (63,2)	16 (17,6)	2 (1,2)	82	0,8780	0,1220	0,69
19	72 (73,0)	61 (59,0)	11 (12,0)	144	0,7118	0,2882	0,16	65 (65,4)	42 (41,1)	6 (6,5)	113	0,7611	0,2389	0,06
20	34 (34,5)	58 (57,0)	23 (23,5)	115	0,5478	0,4522	0,03	56 (57,5)	51 (48,5)	9 (10,2)	116	0,7026	0,2974	0,30
21	40 (41,0)	36 (34,0)	6 (7,0)	82	0,7073	0,2927	0,28	48 (49,7)	37 (33,6)	4 (5,7)	89	0,7471	0,2529	0,91
22	10 (9,2)	5 (6,6)	2 (1,2)	17	0,7353	0,2647	0,99	10 (9,9)	6 (6,2)	1 (0,9)	17	0,7647	0,2353	0,02
23	26 (29,1)	33 (26,7)	3 (6,2)	62	0,6855	0,3145	3,47	36 (37,3)	25 (22,3)	2 (3,4)	63	0,7698	0,2302	0,95
Total	713 (695,5)	786 (821,1)	260 (242,4)	1759	0,6288	0,3712	3,22	1054 (1066,8)	634 (608,4)	74 (86,8)	1762	0,7781	0,2219	3,12

A - Population number

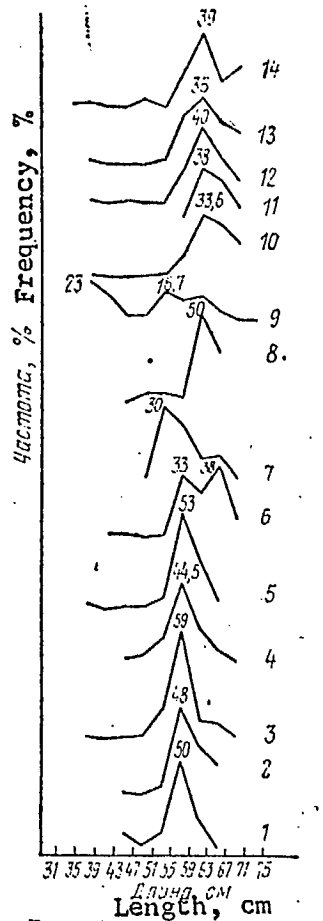

Рис. 43. Кривые распределения линейных размеров рыб из различных элементарных популяций локального стада нерки оз. Азабачьего в 1971 г.

Figure 43. Distribution curves of linear dimensions of fishes from various elementary populations of the local stock of sockeye of Lake Azabach'e in 1971.

Thus in accordance with the results of the preceding chapter it becomes evident that the elementary fish populations described at one time as non-hereditary groups(groupings) have different gene pools and, consequently,are **reproductively isolated just as are local stocks -- aggregates of those populations.** But the fact that separate stocks prove to be divided so much that **they can** be regarded as independent populations requires estimating the level of isolation of genetically different elementary populations

within the individual stock. For if their isolation is less complete, the grounds for which are already in the ecological data, then those groups (groupings) fall under the definition of combined populations. The population aggregate itself is transformed into a certain population system, within the framework of which each elementary population has independent value only to the extent that it makes its own special contribution to the general gene pool of the subdivided population as a whole.

The possibility of such an examination of the population structure of a species appears to be so essential for the entire problem that it requires a more complete analysis -- comparison of the natural picture with a mathematical model of the subdivided population. This analysis can be accomplished most reliably if we turn to the local sockeye stock of Lake Azabach'e.

Chapter VII. Local Stocks as Population Systems 136

Of the population structure models known to us the greatest interest is presented by the "insular model" of S. Wright (1951), which permits regarding the Azabach'e stock of sockeye as a single subdivided population (Figure 44). The following reasons can be cited in favor of such a selection.

1. The unity of the stock is clearly traced in the analysis of the sex ratio in populations. When there is an excess of males or females at different spawning grounds a ratio close to equilibrium is characteristic of the stock as a whole (Table 37).

2. The variability of the age structure is just as demonstrative. Whereas for the stock as a whole stability in relation to the average age of the multiplying brood stocks in adjacent year-classes is characteristic,

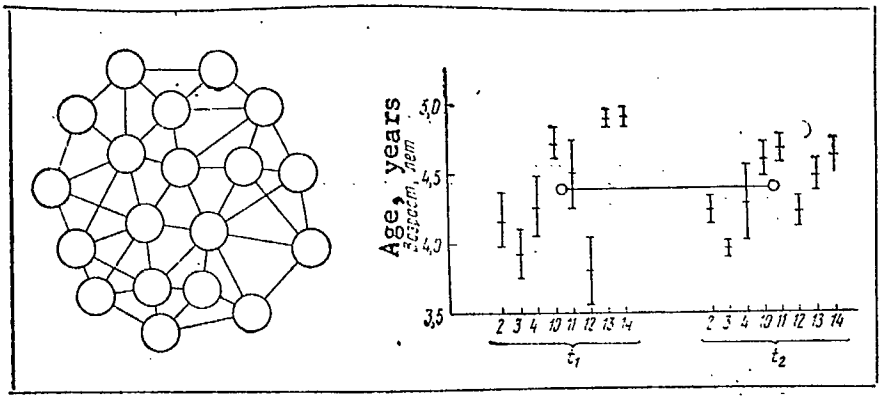

Figure 44. Island model of the structure represented by an aggregate of subpopulations (hierarchic level II) interacting with each other by gene exchange within the framework of the boundaries of isolate (hierarchic level I).

Figure 45. Average age of brood stock of sockeye in separate elementary populations (lines with confidence ranges) in 1971 and in the stock as a whole (light circles) for two year-classes.

in separate subpopulations a substantial variability of that character is observed (Figure 45). It should also be pointed out that in many subpopu- 137
lations there is no complete set of age groups characteristic of the stock.

3. Experiments for many years in the tagging and analysis of parasites as natural tags have shown the practically complete isolation of local stocks of sockeye from one another (Malyukina, 1969; Foerster, 1968; Konovalov, 1971). According to the estimates of S.M. Konovalov, exchange between stocks either is completely absent or, if it exists, its intensity does not exceed 1:10,000 for a year-class.

On the basis of the stratigraphy of Quaternary deposits of Kamchatka (Braitseva et al., 1968; Kuprina, 1970) it can be assumed that isolation of the stock took place at least 10,000 years ago.

Table 37. Numbers of brood stock (in thousands) and sex ratio in populations of local sockeye stock of Lake Azabach'e

Таблица 37. Численность производителей (в шт.) и соотношение полов в популяциях локального стада нерки оз. Азабачьего

A Номер популяции	1970 г. B абсолютная численность, шт.	C самки, %	D самцы, %	E генетически эффективный объем	1971 г. B абсолютная численность, шт.	C самки, %	D самцы, %	E генетически эффективный объем
1	200—250	—	—	225	200	58	42	195
2	200—250	—	—	225	300	53	47	299
3	200—250	—	—	225	250	72	28	201
4	200—250	70	30	189	300	60	40	288
5	250	—	—	250	200	62	38	188
6	—	—	—	—	—	41	59	—
7	—	—	—	—	300	70	30	252
8	—	—	—	—	—	12	88	—
9	—	—	—	—	—	31	69	—
10	250	46	54	212	500	50	50	500
11	100—150	47	53	124	400	53	47	399
12	—	—	—	—	—	55	45	—
13	—	70	30	—	—	60	40	—
14	—	—	—	—	400	61	39	334

Key: A - Population number B - Absolute numbers, fishes C - Females, % D - Males, % E - Genetically effective volume

Note. 1. Dashes indicate absence of precise data.
2 - At a certain sex ratio.
N_e = (4N males N females)/(N males + N females) (Li, 1966).
3. The genetically effective volume of population, found as the harmonic mean, is 226 individuals.
4. The sex ratio for the stock as a whole according to the most complete data for 1971 is 46% males and 54% females.

4. The subdivision of the stock into separate subpopulations is self-evident. Since the spawning accumulations of salmons are represented only adult fishes, the effective reproductive volumes (N_e) can be determined by direct counts of fishes at accessible spawning grounds. In a number of cases there are observations for two year-classes, and for such subpopulations N_e can be found as the harmonic mean. With a correction for the sex

ratio in the subisolates the mean value of N_e proves to be 226 individuals* (see Table 37).

5. Taking into account the uniformity of the population organization of the investigated communities and their stable reproducibility in year-classes, as was evident even from the example of the Azov race of anchovy and the Kalininka stock of the keta, one can by analogy postulate the same stability also for the subdivided sockeye population. Direct comparison of the data for two years confirms this statement (Figure 46).

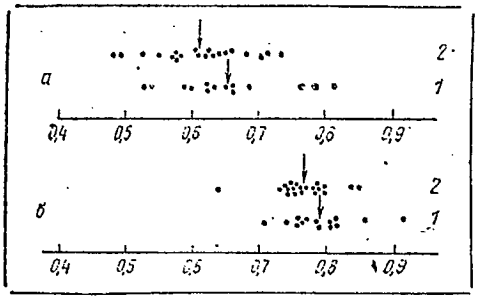

Рис. 46. Частоты генов фосфоглюкомутазы (*б*) и лактатдегидрогеназы (*а*) в субпопуляциях нерки, исследованных в 1971 (*1*) и 1972 (*2*) гг. Каждая точка — частота гена в отдельной субпопуляции; стрелки указывают средние частоты для стада в целом. Визуальные различия средних и дисперсий статистически несущественны.

Figure 46. Frequency of genes of phosphoglucomutase (b) and lactate dehydrogenase (a) in sockeye subpopulations investigated in 1971 (1) and 1972 (2). Each point is a gene frequency in a separate subpopulation: the arrows indicate the mean frequencies for the stock as a whole. Visual differences of the means and dispersions are statistically unimportant.

*The biological material for 1972 has not been taken into account here as there are data indicating that the structure of the corresponding year-classes was destroyed by the pressure of Japanese fishing.

Stability of the Spatial Distribution of Gene Frequencies in the Azabach'e Sockeye Stock. Random Drift of Genes, Migration and Selection as Factors of Stability

The fact that among most species of fishes spatial disconnection is especially characteristic of sockeye populations is of fundamental importance in our line of proofs of the genetic unity of a separate local stock: if such unity is traced in an aggregate of maximally isolated populations, it must be all the more obvious for species experiencing a stronger pressure 139
of isolation.

Under conditions of complete isolation the spatial distribution of the frequencies of neutral or almost neutral genes* has a U-shaped form, according to the models of S. Wright. However, this is not so in the cases under consideration -- the histograms are characterized by modal apices, in connection with which it is possible to assume some exchange of genes among the subpopulations and (or) pressure of selection (Figure 47).

In the investigation of a subdivided population we may estimate these regulatory factors when we compare empirical distributions of the gene frequencies with the steady theoretical /distributions/, representing for the variant of the "island" model beta-functions of the following type:

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*Genetic-biochemical investigations of recent years give a basis for considering biochemical polymorphism close to such a state in natural populations (Kimura, 1968), but there is no reason to extend that conclusion to all loci of the genome. As we will see later, the pressure of selection is detected in a corresponding approach.

**Here we neglect the pressure of mutations, as according to contemporary estimates the rate of mutation for genes coding protein synthesis does not exceed 1.5×10^{-5} (Kimura, 1968).

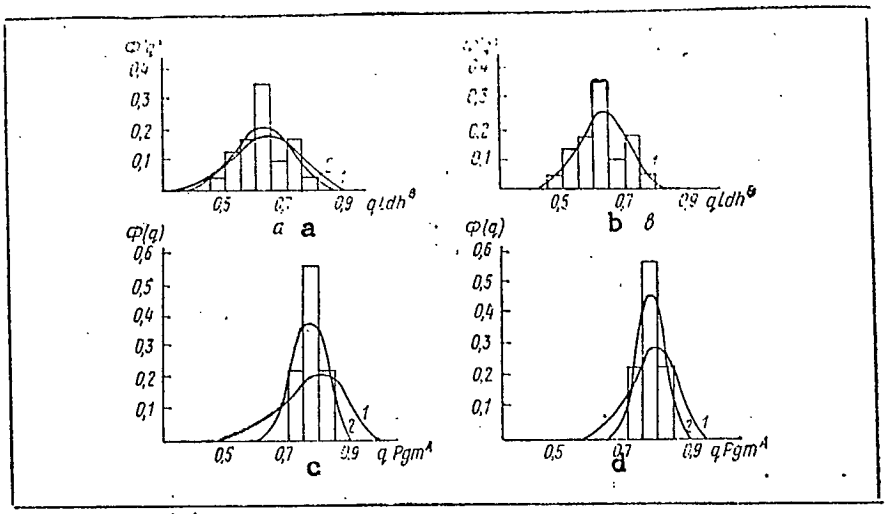

Рис. 47.

Figure 47. Distributions of frequencies of genes of lactate dehydrogenase (a and c) and phosphoglucomutase (b and d) in sockeye populations. Histograms -- empirical distributions; curves -- theoretical:

$1-\Phi(q)=Cq^{4Nm\bar{q}-1}(1-q)^{4Nm\bar{p}-1}$; $2-\Phi(q)=C(\overline{w})^{2N}q^{4Nm\bar{q}-1}(1-q)^{4Nm\bar{p}-1}$.

Remaining explanations in the text.

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1) on the assumption of equalization of isolation by the pressure of migrations 140

$$\Phi(q)=Cq^{4Nm\bar{q}-1}(1-q)^{4Nm\bar{p}-1}, \qquad (1)$$

where p and q are the frequencies of alleles in the subpopulations;

$\bar{p}$ and $\bar{q}$ are the mean frequencies of alleles in the system;

N is the genetically effective volume of the population;

m is the coefficient of migrations;

C is a normalizing factor, selected so that the area under the curve is equal to 1;

2) on the assumption of the combined effect of isolation, migration and selection

$$\Phi(q) = C(\overline{W})^{2N} q^{4Nm\overline{q}-1}(1-q)^{4Nm\overline{p}-1}, \qquad (2)$$

where all the symbols are the same as in the preceding case and $\overline{W}$ is the mean adaptation of the population within the locus

$$\overline{W} = W_{AA}p^2 + W_{Aa}2pq + W_{aa}q^2. \qquad (3)$$

For construction of theoretical curves of the gene frequency distribution it is necessary to have at our disposal values of N, $\overline{q}$ and m. On the basis of our material the first two parameters are estimated. The value of the coefficient of migrations m can be taken from the work of Hartmann and Raleigh (1964), who studied the intensity of the migration exchange between subisolates of the sockeye in nature and arrived at the conclusion that the exchange betwen them in the spawning period hardly exceeds 2-3%.

At m = 0.02 for the lactate dehydrogenase locus a correspondence of the empirical distributions of the allele frequencies with the expected steady distribution is established (see Figure 47a), but in the case of phosphoglucomutase there is no agreement ($\chi^2 = 26.33 > \chi^2_{0.01}$ (df = 3) = = 11.34; see Figure 47b). It is most logical to explain disagreement of this sort between the real picture of genetic variability and the mathematical model by the pressure of selective forces.

In fact, even in a rapid glance at the distribution of genotypes of the Pgm locus one can see a typical picture of balanced polymorphism: in spite of the small sizes of the populations and their great spatial disconnection, in many of them the same allele frequencies are observed, and a noticeable excess of heterozygotes is characteristic of the stock as a whole. The dispersion of gene frequencies expected on the assumption of

only drift and migration ($\sigma^2 = 0.0091$) proves to be much larger than the actual dispersion of 0.0014 $[6.5 > F_{0.01}(\infty, 22) = 2.31]$.

For such a stabilizing selection in favor of heterozygotes the equilibrium gene frequency according to Li (1967) can be found from the ratio of adaptations of the homozygotic and heterozygotic genotypes 141

$$\tilde{p}(A) = \frac{W_{BB} - W_{AB}}{(W_{BB} - W_{AB}) + (W_{AA} - W_{AB})}. \qquad (4)$$

If we solve equation of steadiness (2)* we can find the corresponding values of W, which for the genotypes of Pgm have the following absolute values:

$$W_{AA} = 0,9265;$$
$$W_{AB} = 1,0613;$$
$$W_{BB} = 0,8209.$$

If we assume the adaptation of the heterozygote to be 1, we get:

$$W_{AA} = 0,926;$$
$$W_{AB} = 1,000;$$
$$W_{BB} = 0,774.$$

If we substitute these values in expression (4) we get an equilibrium frequency of 0.755, which is very close to the actual frequency of 0.778 (see Table 36).

If the same coefficients are used in expressions (3) and (2), one can see the correspondence of the empirical distribution of frequencies of phosphoglucomutase genes with the theoretical, which presupposes steadiness as a result of mutual equalization of the processes of random drift of genes, migration and selection ($\chi^2 = 5.43 < \chi^2_{0.05}$ (df = 3) = 7.81; see Figure 47b).

The same can also be done with respect to data on lactate dehydrogenase genes and one can also satisfy oneself of improvement of the approximation

*Here, as in the preceding case, we omit all the intermediate stages of tedious calculations.

after introduction into the model of the selection factor (W_{BB} = 0.9832; $W_{BB'}$ = 1.0000 and $W_{B'B'}$ = 0.9739).

Also possible is a different way to estimate the generalized coefficients of adaptation of the genotypes of phosphoglucomutase which takes into account the fact that the actual distributions of allele frequencies in a different investigated locus -- the locus of lactate dehydrogenase -- in general is satisfactorily described by expression (1), which assumes selective neutrality of polymorphism*.

If one starts from the observed dispersion of frequencies of genes of lactate dehydrogenase in the subpopulations one can calculate the value of 4 Nm and, substituting it in formula (1), construct the corresponding 142
curve for the distribution of frequencies of the alleles of Pgm. Non-correspondence of the distributions in this case can be regarded as an indication of pressure of selection. The coefficients of adaptation obtained in that manner proved to be 0.916 (AA), 1.000 (AB) and 0.728 (BB), and the corresponding equilibrium frequency $\check{p}$ = 0.765, which is still closer to the actual 0.778 (see Figure 47d, 2).

And so the derived estimates, as was expected, indicate a considerably greater range of adaptation of genotypes precisely in the locus of phosglucomutase. In addition, in both cases greater adaptation of the heterozygotes is evident and, consequently, a certain condition of stable polymorphism is fulfilled here(Kimura, 1956), which we also expected. But this means that under the conditions of such superdominance the pressure of selection will oppose the random

*This approach was used recently in the work of Yu. G. Rychkov et al. (1973) on the population genetics of the aboriginal population of Siberia.

drift of genes, returning their frequencies in subsequent generations to the equilibrium state in each subpopulation.

Leaving to the future a more detailed study of the adaptations of genotypes of various loci, we draw only one conclusion which flows from the analysis made: the local stock of sockeye of Lake Azabach'e, in spite of the spatial disconnection of the populations composing it, represents a single system in a steady state. Consequently, the elementary populations can be regarded as independent units only to the degree to which each of them makes its own special contribution to the genetic unity of the stock as a whole.

The author is aware, of course, that the statistical analysis of only 23 variables where it is customary to deal with massive events can give rise to objections. However, beyond the framework of a formal approach this way seems justified if only because the 23 populations studied by us are at least two-thirds of their total number in the aggregate. In addition, the results of mathematical calculations fully agree with the real picture of genetic variability in the populations.

But if this is true, and the population structure itself in accordance with Wright's models represents a regular summing of successive transformations of the gene pool of the ancestral population in proportion to its assimilation of its range, then genetic stability in space and (or) time must be a property of such population systems in general. 143

Regardless of whether this structure is caused by "isolation by distance" or the "island model", with a large central population surrounded by semi-isolated small groups(groupings) assumed by it in a number of cases, proves to be more suitable, the result of such development proves to be the same --

the gene frequency which characterized the ancestral population or characterizes it now is stably preserved if it was preserved in the form of some nucleus in the zone of the ecological optimum. On the level of the subdivided population as a whole the mean gene frequency corresponds to it. It is known that one of the essential features of such a stationary random process can be the property of ergodicity, reflecting the equivalence of variability in time to variability in space. Consequently, in the genetic study of natural population systems representing a result of the development of those processes in a relatively uniform range, we must side by side with stability of the populations in generations note a drop in genetic dispersion in proportion to the turn toward higher hierarchical levels, including a certain number of very simple ones, and therefore also of variable population units.

This effect of averaging, if it can be so expressed, follows from analysis of genetic dispersion in a subdivided population, as was demonstrated at one time from the example of the annual Linanthus Parryae by S. Wright (1943) and by us (Altukhov and Rychkov, 1970) in a comparison of variability on the level of population systems and their structural components in a number of bisexual species.

The material of the present investigaion can be considered from the same point of view.

Genetic Stability of Population Systems in the Presence of Simultaneous Variability of the Components Forming Their Structure

The genetic stability of a subdivided population in time was partially discussed earlier, when we emphasized the stable reproducibility in generations of genetic features characterizing the Kalininka stock of the keta and the

Azov race of the anchovy. For spatially conjugated systems a similar effect could be observed from the example of the ocean perch. Here we will consider the same and some other material having especially mentioned methods of analyzing genetic variability on the level of population systems with supplements to previous argumentatio(Altukhov and Rychkov, 1970). 144

Actually, the formal estimation of the gene frequency in a subdivided population requires finding the mean, weighted by the numbers of the separate subpopulations. However, this often cannot be accomplished in practice: for most species direct data on numbers of populations cannot be obtained at all and, moreover, the volume of populations can undergo substantial fluctuations in successive generations -- the well-known "waves of life" of S.S. Chetverikov (Timofeev-Resovskii et al., 1969). For this reason it also is unjustified to calculate the mean weighted by volumes of samples, which very often prove to be random in relation to the sizes of subpopulations.

It is noteworthy, however, that in spite of such strong fluctuations of the absolute numbers of populations their genetically effective volumes remain contant both in time and in space, being limited by the environment, the history or distinctive features of reproductive behavior which prevent any sort of sharp growth of numbers of the reproducing part of an isolated population. Confirmation of this can be obtained from any sufficiently complete reports on the biology of populations (e.g., Lake, 1957; Timofeev-Resovskii et al., 1969) or from direct observations of the reproduction of species for which such observations are possible. An ideal object in this respect is the Pacific salmons, and among them especially the sockeye.

But also in other species the stability of genetically effective volumes of population is preserved even in years strongly different in numbers, and this finds reflection in an invariable density of redds on sections suitable for reproduction. Thus, for example, during the return of numerous year-classes of the pink salmon the brood stock which arrived later from the sea dug over again the spawning mounds containing the eggs of fishes which reached the spawning grounds earlier.

But if one also takes into account the gigantic range of biochemical hereditary variability recently discovered in natural populations, a considerable gap between the absolute numbers of populations and their genetically effective volumes (Kimura, 1968) becomes evident. Attention was turned to this at one time by N.P. Dubinin and D.D. Romashov (1932), who showed a situation of that sort by a very graphic scheme (Figure 48). From 145
that point of view the difference between the species investigated here, as can be concluded from the dispersion of gene frequencies in populations, is not so much in their effectively reproductive volumes as in their absolute numbers (Figure 49).

Only in such a sense can one explain the surprising heterogeneity in an enormous and apparently completely panmictic population of the anchovy. Purely theoretical predictions here completely correspond to the real natural situation, which can have only one cause -- a colossal natural mortality rate of the anchovy in the early ontogenetic stages. Such a mortality rate is generally known for fishes; it is the rule rather than a rare exception.

Finally, of fundamental importance is still another conclusion from the discoveries of recent years in biochemical genetics -- commensurability of the range of variability in the most diverse species (see Altukhov et al.,

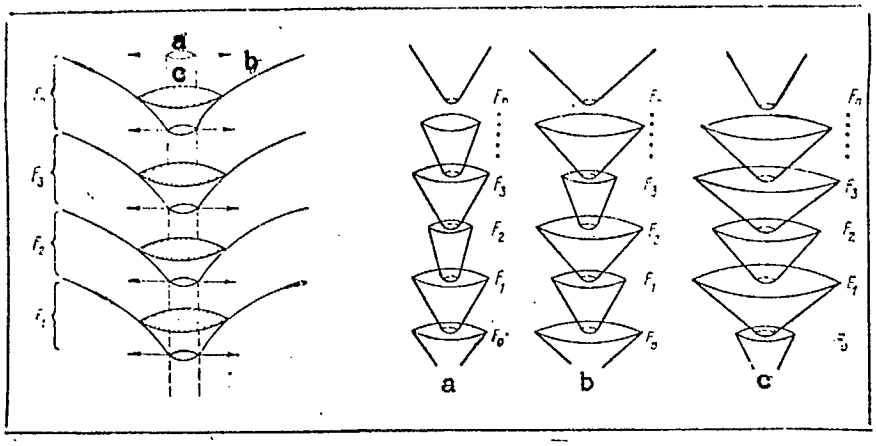

Figure 48. Correlation between quantity of coded /literally "produced"/ gametes (b), the absolute numbers of a population (c) and its reproductively effective volume (a) (acc. to Dubinin and Glembotskii, 1967).

Figure 49. Assumed correlations between absolute numbers and reproductively effective volumes of populations of different species similar in their biological characteristics to: (a) salmons, (b) redfish and (c) anchovy. In spite of sharp difference and fluctuation (dispersion) of the absolute numbers, similarity of the genetically effective volumes of the populations is postulated.

1972; Kirpichnikov, 1972) and, consequently, commensurability of the values of the effectively reproductive volumes of their populations*. 14

We have dwelt in such detail on these questions in order to show that the approach to analysis of a structured population in which preference is given precisely to the mean gene frequency ($\bar{q}$), calculated from frequency values in individual subpopulations (q_i), is not an arbitrary method dictated only by an absence in the theory of population genetics of adequate

*If one assumes a mutation rate similar for species with an identical DNA content and most of the allele variations of proteins and isoenzymes are classified as not significantly reducing viability, then the connection between the heterozygotic level of the individual according to its aggregate of polymorphous loci and the size of the effective reproductive part of the population is established by the formula (Kimura, 1968):

$$H_e = \frac{4N_e u}{4N_e u + 1},$$

where H is the mean heterozygosity of the individual, and
u is the mutation rate.

mathematical apparatus, but is based on a real concept of the biology of natural populations and on some new facts acquired during their study by the methods of immunological and biochemical genetics.

But even in cases where formally statistical requirements can be observed the essence of the matter does not change in the least. For example, the mean frequences of the genes of lactate dehydrogenase and phosphoglucomutase in the investigated sockeye stock are 0.63 and 0.79 respectively; the weighted means are 0.64 and 0.79.

Another statistical parameter which is important in estimating the stability of a subdivided population in time is the mean square deviation, which characterizes the variability in the isolate as the sum of the intra- and interpopulation variability; for steady distributions of gene frequencies the values of the mean and dispersion must remain unchanged in a number of generations.

The corresponding data for all the populations studied by us are summed up in Table 38. On Figures 50 and 51 is presented the spatial variability of the gene frequencies in elementary populations and on the level of the aggregate as a whole for the sockeye and redfish. Also presented here are the materials of G. Naevdal (1968), processed by us, which reflect the variability of the frequency of the allele of transferrin in hauls from the localities of sprat living along the coast of Norway. We see that the differences between the systems either prove to be insignificant or are absent, in spite of simultaneous variability on the level of elementary populations. Thus the localities of the sprat are practically identical with respect to the frequency of the allele Tf^A, and the redfish stock, with respect to the gene of the blood group A_2. The example with the

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Table 38. Statistical parameters of the frequency distribution of genes on the level of population systems in space and in time

Таблица 38. Статистические параметры распределения частот генов на уровне популяционных систем в пространстве и во времени

	Объект A	Популяционная система B	Исследованный локус, аллель C	n	$\overline{N}$	$\overline{q}$	$m_{\overline{q}}$	$\sigma_{\overline{q}}$	$m_{\sigma_{\overline{q}}}$
1	Морской окунь *Sebastes mentella* Ttavin	a Зоны НКНАФ *3K* + *3L*	b Группа крови A_2	7	134	0,730	0,014	0,427	0,01
		Зоны НКНАФ *3O* + *3P*	» » »	6	170	0,703	0,014	0,450	0,01
		Зоны НКНАФ *3N*	» » »	5	96	0,694	0,020	0,441	0,014
2	Нерка *Oncorhynchus nerka* Wald.	a «Весенняя раса» оз. Азабачьего, 1971 г.	Ldh^B	9	96	0,6203	0,017	0,484	0,012
			Pgm^A	9	98	0,7811	0,014	0,412	0,010
		b «Летняя раса» оз. Азабачьего, 1971 г.	Ldh^B	5	124	0,7161	0,018	0,439	0,012
			Pgm^A	5	122	0,8142	0,015	0,383	0,011
3	Европейский анчоус *Engraulis encrasicholus* Linne	a Азовская раса, июль 1963 г.	b Группа крови A_0	11	70	0,4703	0,0170	0,4712	0,0120
		c Азовская раса, июнь 1965 г.	» » »	26	62	0,4426	0,0114	0,4568	0,0081
		d Азовская раса, сентябрь 1965 г.	» » »	18	72	0,4508	0,0129	0,4667	0,0091
4	Кета *Oncorhynchus keta* Wald.	a Стадо р. Калининки, 1969 г.	Mdh^B	3	130	0,1669	0,0187	0,3677	0,0132
		Стадо р. Калининки, 1970 г.	Mdh^B	4	176	0,1718	0,0143	0,3771	0,0101
			Alb^C	4	152	0,1345	0,0118	0,3140	0,0081
			Ldh^F	4	200	0,0856	0,0119	0,3382	0,0084
		Стадо р. Калининки, 1971 г.	Mdh^A	4	92	0,8360	0,0189	0,3652	0,0133
			Mdh^B	4	92	0,1640	0,0189	0,3652	0,0133
			Alb^C	4	88	0,1397	0,0170	0,3197	0,0120
			Ldh^F	3	96	0,8850	0,0180	0,3059	0,0127
	b	Стадо р. Найбы, 1969 г.	Alb^C	6	170	0,6716	0,0144	0,4594	0,0102
			Mdh^B	7	186	0,0388	0,0052	0,1892	0,0037
			Ldh^F	5	92	0,9162	0,0128	0,2731	0,0091
		Стадо р. Найбы, 1970 г.	Alb^C	10	104	0,3500	0,0139	0,4199	0,0098
			Mdh^B	8	116	0,0510	0,0073	0,2240	0,0052
			Ldh^F	10	106	0,8502	0,0104	0,3393	0,0074
		Стадо р. Найбы, 1971 г.	Alb^C	5	104	0,2900	0,0196	0,4444	0,0139
			Mdh^B	5	112	0,0555	0,0095	0,2263	0,0095
			Ldh^F	5	110	0,8594	0,0144	0,3391	0,0102

Примечание. n — число исследованных выборок; $\overline{N}$ — среднее число генов в выборке; $\overline{q}$ — средняя частота гена; $m_{\overline{q}}$ — ошибка среднего; $\sigma_{\overline{q}}$ — среднее квадратическое отклонение; $m_{\sigma_{\overline{q}}}$ — ошибка среднего квадратического отклонения.

Table 38 (Key)

A - Item B - Population system C - Investigated locus and allele
1 - Deepwater redfish Sebastes mentella Travin
a - ICNAF zones b - Blood group A_2
2 - Sockeye Oncorhynchus nerka Wald.
a - "Spring race" of Lake Azabach'e, 1971
b - "Summer race" of Lake Azabach'e, 1971
3 - Anchovy Engraulis encrasicholus Linne
a - Azov race, July 1963; b - Blood group A_0; c - Azov race, June 1965; d - Azov race, September 1965
4 - Keta Oncorhynchus keta Wald.
a - Stock of Kalininka River b - Stock of Naiba River

Note: n - the number of investigated samples (hauls); $\bar{N}$ - the mean number of genes in a sample (haul); $\bar{q}$ - the mean gene frequency; $m_{\bar{q}}$ - error of the mean; $\sigma_{\bar{q}}$ - root-mean-square deviation; $m_{\sigma_{\bar{q}}}$ - error of the root-mean-square deviation.

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perch permits simultaneously accomplishing a "transition" to a practically independent population system localized on the Flemish Cap bank. However, no "effect of averaging" is obtained, for the direction of variability here is completely different -- the gene of the blood group is close to fixation. If it is taken into account that a drop in variability is a natural consequence of the pressure of isolation, this fact can indicate greater age of the population here as compared with the local stock of redfish on the Newfoundland Grand Bank.

Now let us examine the data regarding genetic variability in time, having turned to three successive generations of the Azov race of the anchovy. As was pointed out in Chapter IV, two generations are represented by adult 150
fishes, and the third by immature fishes (Figure 52). It is evident that in spite of considerable genetic variability with respect to separate components of structure the subdivided population as a whole remains unchanged in the investigated interval of generations. The same is also discovered

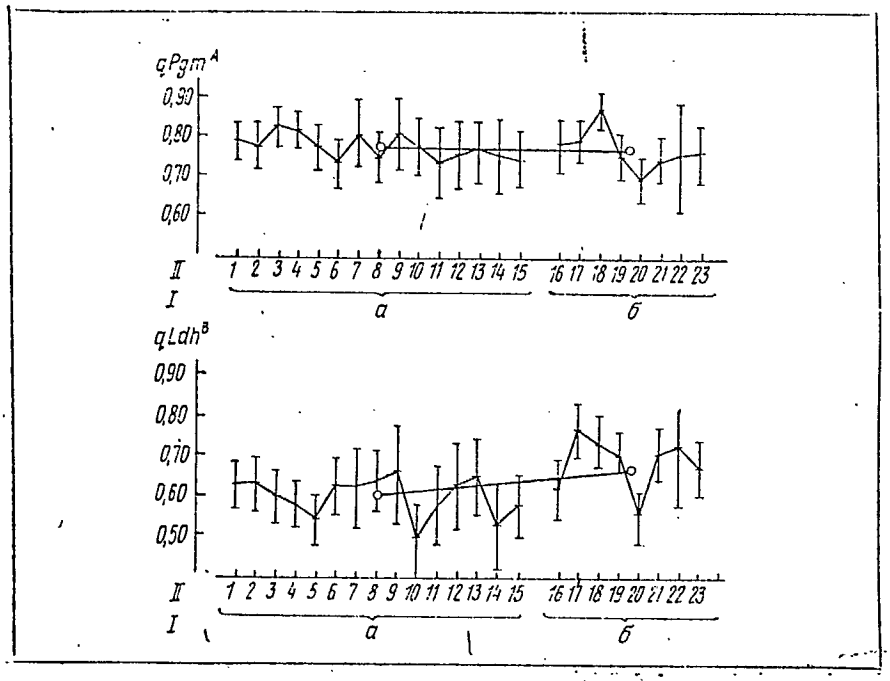

Figure 50. Spatial variability of gene frequencies on the level of the "spring" (a) and "summer" (b) races of sockeye as a whole (light circles) in comparison with variability by elementary populations (lines with confidence intervals). Here and in the following similar figures the qualitatively different levels of the population structure are designated with Roman numerals.

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for adjacent year-classes of the Kalininka stock of the keta, characterized in relation to the gene frequencies of several polymorphous loci separately (Figure 53) and together (Figure 54, see also Table 38).

Of course, two or three year-classes is not such a large time in- 151
terval, but in this case too the investigated locality behaves not as a collection of heterogeneous elements of some sort but as an integral system, an integral feature of which -- genetic stability in year-classes -- is obviously not derived from the properties of the variable components forming its structure. Examples of longer steady states of other populations with

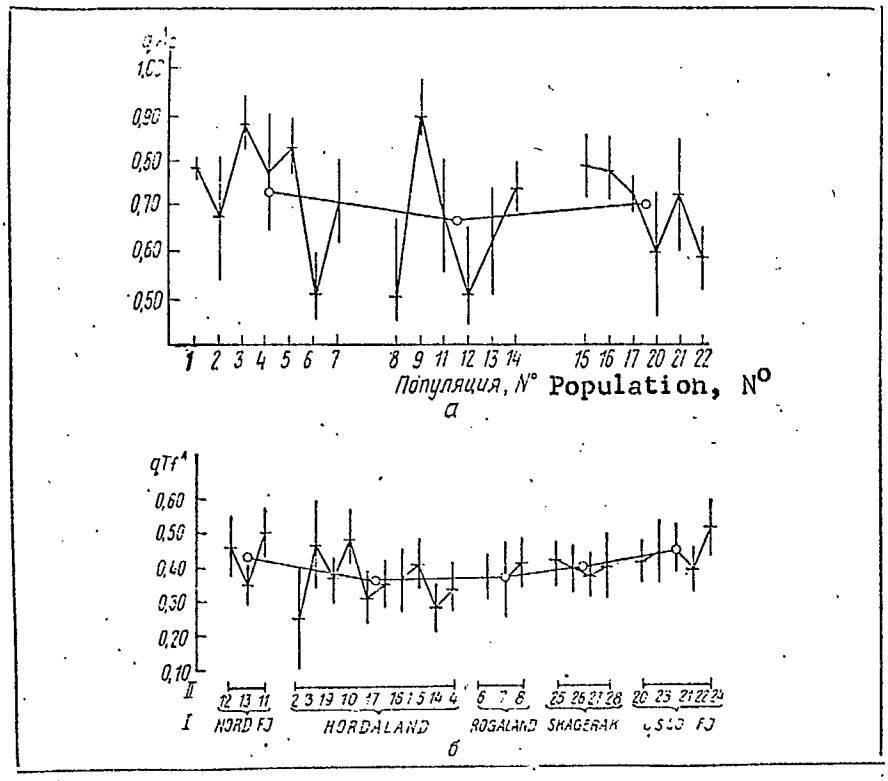

Рис. 51. Пространственная изменчивость частот генов в популяциях окуня и шпрота:

Figure 51. Spatial variability of gene frequencies in populations of **redfish** and sprat: a - spatial variability of frequency of the gene A_2 on the level of local stocks of **redfish** on the Newfoundland Grand Bank (light circles) in comparison with the variability in separate elementary populations comprising the structure of those stocks (lines with confidence intervals). Populations Nos. 1-7: stock of zones 3K and 3L; Nos. 15-17 and 20-22: stock of zones 3O and 3P; populations Nos. 8, 9 and 11-14: zone 3N (see Figures 5 and 34); b - spatial variability of the gene frequency of transferrin in localities of the sprat Sprattus sprattus (acc. to Naevdal, 1968).

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an internal structure were examined in the article of Altukhov and Rychkov (1970) and will be discussed later in Chapter VIII in connection with some general consequences from the fact of systemic organization of isolated populations. But here, while still remaining within the framework of the examination of ichthyological material properly speaking, we will direct attention to the functional aspect of such organization.

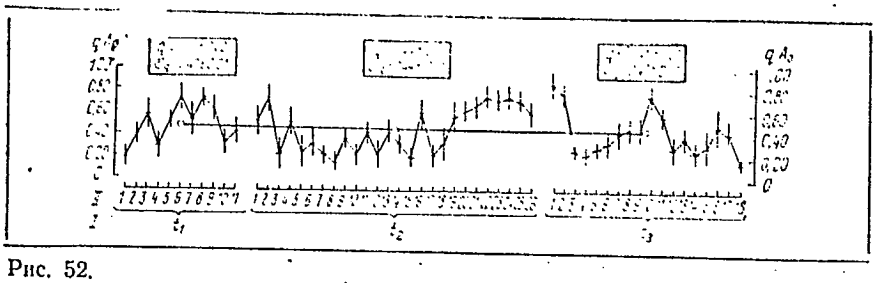


Рис. 52.

Figure 52. Genetic stability of three overlapping year-classes of the Azov race as a whole on the background of fluctuations of gene frequencies of the A_Q factor with respect to components: t_1 - provisional first year-class (1963); t_2 and t_3 - second (1965, spawning fishes) and third (1965, juveniles). Light circles represent mean values of the gene frequency for the system as a whole (separated by braces); lines with confidence intervals are gene frequencies in samples from separate populations.

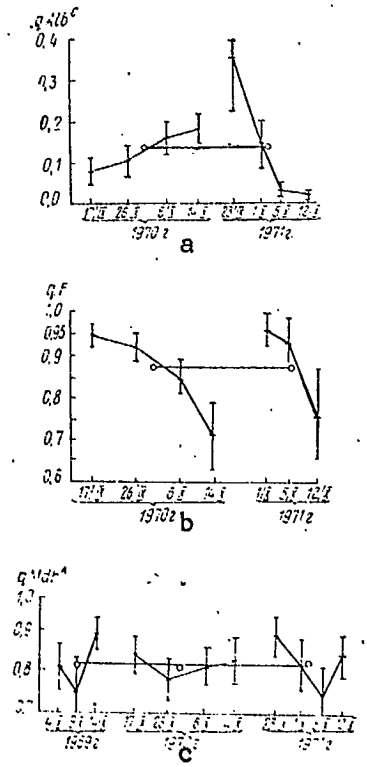


Рис. 53.

Figure 53. Genetic stability of adjacent year-classes of the Kalininka local stock as a whole (separated by braces) given simultaneous variability on the level of very simple population units (separate samples (hauls)): a - frequencies of allele Alb^C; b - the same, for serum lactate dehydrogenase; c - the same, for muscle malate dehydrogenase.

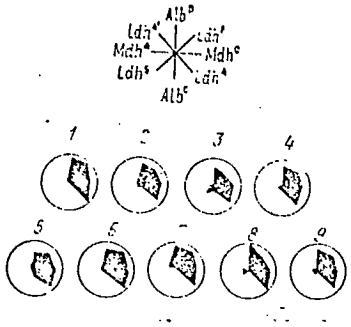


Рис. 54.

Figure 54. Genetic stability of two year-classes of the Kalininka keta stock as a whole (Nos. 4 & 9) given simultaneous variability on the level of separate samples. Nos. 1-3: 1970 samples of 23 September and 6 and 14 October respectively; Nos. 5-8: 1971 samples of 23 September, 1, 5 and 12 October respectively.

The article of S.S. Shvarts et al. (1972) was published when the present work was being put in final form. Accepting our treatment of the population organization of a species, the authors stress the functional unity of population systems which, from their point of view, is evident from the data of ecological observations. It should be emphasized, however, that such unity can be strictly proven only when there is a quantitative evaluation, and the advantages of a population genetics examination are unquestionable here. The same approach, which takes into account qualitative differences in genetic stability on different levels of a population hierarchy, permits designating a single principle of investigation of any biological features of populations, which, in our opinion, also is the main task of population biology in the broad sense.

In any case, the balanced sex ratio, the mean size of individuals 152
and the average numbers -- these are purely biological parameters, the stability of which in successive year-classes can be a no less clear proof of the preservation of integrity of the investigated population system than stability of gene frequencies. The stability of two such properties already has been demonstrated with our material.

Naturally, the question is asked, with what is such stabilization achieved? Only through mutual equalization of random processes of drift, selection and migrations, or do some autoregulatory mechanisms act in population systems? The discovery of such mechanisms could play a decisive role in the control of natural populations, but only the very first steps can be made now in that direction.

The Functional Unity of a Population System 153

We have already directed attention to the sharp fluctuations of the sex ratio in elementary populations.

Ecologists have accumulated numerous facts which permit regarding the sex ratio as a specific feature of isolated populations in general -- such populations, besides those of fishes, as those of insects (Novozhenov, 1971), crustaceans (Wenner, 1972) and even mammals (Naumov, 1967; Tarasevich, 1967; Kubantsev, 1972).

The number of such examples can be increased, but it should be pointed out that in none of the mentioned works was there discussion of the importance of these facts in connection with the existence in nature not of separate very simple populations, but of integral aggregates -- population systems, within the framework of which elementary populations also interact with one another.

It is precisely on this level of investigation that the above-mentioned important fact is discovered: in spite of fluctuations dispersion of the sex ratio in subpopulations, for the system as a whole the ratio remains balanced.

A regularity of this kind acquires biological meaning even if only because the sex ratio in a population directly affects the size of its effective reproductive portion which transfers the gene pool to the following generation.

But in such case the posing of the following question is appropriate: Is not the fluctuation of the sex ratio in elementary populations the unique ecological mechanism, based primarily on the preeminent migration of males*, by means of which the value of N_e is regulated, and through it, the "allowable" dispersion of biologically important characters and properties characterizing populations?

The reply to this question could be affirmative if correlation were discovered between the genetically effective volumes of the subpopulations (or deviations of the sex ratio in them from equilibrium) and deviations of their different characters and properties from the corresponding means characterizing the system as a whole.

Unfortunately, this line of analysis became evident only when the present work had been completed, and with its materials such correlations can be shown only for the Newfoundland stock of deepwater redfish** and 154
in relation to only two characters -- the A_2 blood group and the index "1/d" (Figure 55). It is evident that the elementary populations in which the sex ratio deviates maximally from equilibrium also differ greatly, as a rule, from the mean values with respect to the two characters.

The fact that this connection has a presumed biological meaning and is not a fortunate accident evidently is proven by the population genetics data analyzed above. They can be supplemented by still another argument: if one considers as a single aggregate all the populations localized on both the Grand Bank and the Flemish Cap bank, the discovered correlation collapses ($r = 0.19$; $P > 0.05$).

*The active role of males as the connecting link in a population system has been shown in many population-ecological investigations (Panov, 1970).
**Here a large enough number of populations forming the structure of the stock is of great importance.

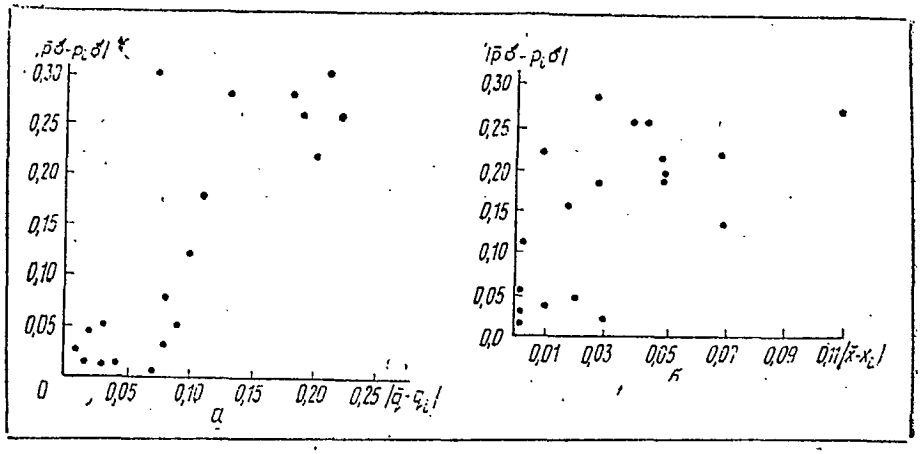


Figure 55. Correlation between deviations from a sex ratio in equilibrium (p males = p females = 0.5) and the mean values of the A_2 gene frequency (a) ($r = 0.715$; $p < 0.001$) and the index 1/d of the otolith (b) ($r = 0.591$; $p < 0.01$) in the system of elementary populations of the deepwater redfish on the Grand Bank.

The following aspect however, remains incomprehensible (see Table 28): in populations with an excess of males the frequency of the A_2 gene has a tendency to deviate from the mean in the direction of increase, whereas in populations with an excess of females the sign changes to the reverse. At the same time, it was noted earlier that the A_2 factor behaves as if it were autosomal! It is difficult to say what causes such a tendency. If the poor genetic determination of sex which is characteristic of many fish species (Yurovitskii, 1966; Kirpichnikov, 1969) is taken into account, one can 155 assume here an inheritance partially linked with sex and aligned toward the autosomal type of selection in early ontogenetic stages not investigated by us or, on the other hand, the type of inheritance is autosomal but the directions of selection are different for males and females. Moreover, the very fact

of autoregulation is evident, although it can be a matter of a genetic mechanism for maintaining a balanced sex ratio for the stock as a whole, as was assumed.

On the other hand, this must mean simultaneous regulation of other biological parameters of the system, regulation all the more evident the more strongly the hereditary sexual dimorphism is expressed in the species and the more intensive the exchange between subpopulations. In many species the numbers of an isolated population evidently are regulated in the same manner; in several cases, at least, a dependence has been proven between the sex ratio in the population and its density (Novozhenov, 1971).

Thus analysis of concrete genetic mechanisms of regulation of the sex ratio in fish populations represents an important task, one which, it seems to us, can be solved only beyond the framework of the formal Fisher theory (Fisher, 1930).

Among possible situations in the conditions of population systems with a clearly expressed internal structure a special place must belong to meiotic drift, when the sex ratio is controlled by only one gene, localized on a sex chromosome. Depending on the mechanism of sex determination (male or female heterogameticity or balance between a sex chromosome and genes localized on autosomes) the consequences of such drift can be different down to degradation or even complete extinction of the separate subpopulations if the historically formed connections between them are destroyed.

As a clear example one can cite the data of Owen (1970) for the butterfly Ecraea encedon from Equatorial Africa.

In populations of this species, characterized by a broad amplitude of variability of the sex ratio, the author discovered two types of females; one of them produces only females, and the other both females and males. The two sexes appeared in equal quantities only in crossings between sibs and in male x female combinations from mixed broods, whereas in male x female combinations from "female" broods females appeared in the progeny without exception. In Uganda one of those populations became extinct, and 156 the other was close to that but revived on account of an inflow of immigrants.

Owen assumes that here occurs drift of the Y chromosome which is compensated in a number of populations by the pressure of selection in favor of epistatic suppressors localized on other chromosomes. Migration of even one or a few females into a population in which the suppressor system has not been developed, rapidly leads to the birth of only females, as was observed in the case with the extinct population. As the author points out, this death is a result of hybridization of earlier isolated populations caused by the intervention of man.

Still another example. In the mosquito Aedes aegypti Y represents not a sex chromosome, but a gene. In families with Y mutants there can be several X alleles which only to a certain extent limit the aciton of Y mutation, and the hybrid males yield progeny with a sharp excess of the male sex; but sometimes the progeny consists of males without exception.

It is interesting that under the conditions of strict isolation of Lake Dal'nee on Kamchatka a small kokanee population consists of 90% males. (Personal communications of F.V. Krogius, S.M. Konovalov and E.V. Chernenko.)

In the summary of Hamilton (1967) examples are cited of extraordinary sex ratios in populations and a theory is given for that phenomenon with consideration of the possibilities of local competition to mate. Such an approach, if combined with the examined data on the systemic limitedness of isolated populations, appears very fruitful and, evidently, inevitable in investigations of fish population biology.

However, further consideration of the question goes beyond the framework of this study and requires additonal information. As for the limited data presented here, their analysis has meaning only to the degree to which it apparently permits designating the way to study the functional unity of a population on a quantitative genetic basis.

But if one returns precisely to these facts, one should acknowledge the possibility in principle of distinguishing in various species, regardless of their ecology, two levels of population organization. Firstly, population systems, to a considerable degree independent, subdivided populations and, secondly, connected, more elementary populations which are structural components of such systems and formally, and at times also in 157
essence, correspond to the "Mendelian populations" of Sewell Wright (Altukhov, 1969).

The inevitability of formation of such a structure is already built into the very process of the scattering of life over the face of the earth, but no lesser role belongs here to the natural discontinuity of the range in relation to habitats suitable for life, and also distinctive features of reproductive behavior, most often directed toward the prevention of unlimited hybridization. And although the degrees and mechanisms of isolation can be different in populations of different species, as types of structures, too, should differ, one important peculiarity si characteristic of all of them--higher genetic stability on the upper hierarchic levels.

Evidently, only on such a basis can a natural classification of intraspecies communities be constructed, but here we must not confuse the taxonomic and population-biological aspects. The determination of the real population structure of a species, as we have tried to show, is an independent region of investigation.

As for terminology, it has already been discussed in Chapter I, in a different context, it is true. If we exclude from the considered ideas the classification of Parrish as far from reality, then we see that closest of all to a population system is the stock in the understanding of K.P. Yanulov and, perhaps, the "large population" of M. Gordon. But the races of F. Heincke, J. Schmidt and V.S. Kirpichnikov and the "subpopulations" of J. Marr are structural components of a population system, elementary population units.

Probably, to put the terminology in order, henceforth to designate a system one should use such interchangeable terms as "stock", "race", "population" and "isolate"; to designate its structural components -- "elementary population", "subpopulation", "subisolate", etc. The question of such microraces has been analyzed in detail in connection with general aspects of the population structure of species in the monograph of N.P. Dubinin (1966, see also Altukhov et al., 1969b).

But in the line of analysis selected here questions of terminology do not seem to be so important for fruitful work. Something else is far more important: understanding that a population system is genetically stable and, consequently, endowed with the capacity for long existence, whereas subpopulations are parts of such systems, their structural, at times very variable components. 158

Such an organization of populations with its attendant picture of genetic variability and stability on different hierarchic levels must be a common property of widely scattered species, and if attention has not yet been directed to this, it is only because for the detection of this sort of pattern a special approach is necessary, one based on systematic

encompassment of the entire population heterogeneity of the species as a whole or its separate parts, the naturally formed isolates.

The aggregate of the above-examined materials also permits the assumption that the population structure of isolated stocks represents a natural result of the process of successive differentiation in time and space of the gene pool of one or several ancestral populations. This possibility, as far as we know, has never been discussed in ichthyology. However, in anthropology ideas of that sort are being developed by Yu.G. Rychkov (1964, 1968, 1969b), who has constructed a rigorous system of proofs of similarity of the natural history of such different isolates as the Pamirs and Siberia. The formation of an internal subpopulation structure emerges here as the main factor in the long stabilization of the gene pool of an isolated population.

Of course one can a priori consider population systems also as aggregates of populations not connected by kinship, only secondarily having become some functional unit /literally "unity"/ but such an interpretation is less probable in the light of the above-considered facts; a system of that type is rather an object of biocenology than of population genetics. But even if one has supported such a point of view one can satisfy oneself of the invariability of the essence of the matter if, following L. von Bertallanfi, we define a system as an isolated aggregate of interacting elements.

It is clear that in this case too one must encounter manifestations of stability as a new property of a system and, consequently, to the extent to which universality of the principles of population genetics is accepted it is possible to consider this phenomenon as a general biological law. It produces consequences requiring both revision of established approaches to

the economic use of natural populations and also correlation of new facts with the traditional interpretation of the biological importance of processes of intraspecies genetic divergence.

Chapter VIII. Practical and Theoretical Consequences of the Existence of Population Systems in Nature 159

Population Systems and a Rational Fishing Industry

To the extent to which biological characteristics of populations are derivatives of the historically formed gene pools the discovered differences in genetic stability on different levels of species population hierarchy have a direct relation to the development of an optimal strategy of a rational fishing industry.

In fact it is a far from indifferent matter with what sort of population we are dealing: is it with a variable elementary group(grouping) whose behavior it is difficult to predict on account of purely random circumstances or with an aggregate of such populations, characterized by stability in its generations and, consequently, amenable to long-term forecasting with respect to its important biological properties? If external effects which can be compared with catastrophes in nature are not taken into account, then to achieve long stability the need to approach the system as a whole with consideration of all its internal diversity becomes evident.

Let us consider the possibility of such an approach when the stock of keta is artificially maintained. Their subdivision into elementary populations is already evident from genogeographic observations, but the replacement of natural spawning by a fish-breeding process limits the possibilities of investigation. Moreover, at the Kalininka fish hatchery

there are careful ten-day records of the number of brood stock of both sexes used for fish-breeding purposes during the entire period of activity of the hatchery. Since the structure of this population has not been disrupted as is evident from the dispersion of gene frequencies in separate samples, we have the right to expect variability of the sex ratio in samples(hauls) of brood stock from different parts of the stock. In spite of the fact that the ten-day summaries must distort the expected dynamics of the character -- separate subpopulations cannot help but mix, even if only partially, in the zone of a weir -- our suggestion has proven to be valid (Figure 56).

The presented material, analyzable by year-classes predominant in the spawning part of the stock, reveals sharp changes in the percentage of males also in the process of the spawning run. In accordance with long- 161
known distinctive features of the biology of the keta, in most of the illustrations an excess of males is observed at the start of the spawning migration; in the middle the ratio is equalized, and at the end females predominate. Since thousands and tens of thousands of adult fishes are counted every ten days, the confidence intervals are negligibly small. They increase only at the very beginning or at the end of fish-breeding activity, when the fish are just starting to approach, or their run is already ending and the hauls are small. Figure 56a illustrates this; in other cases the differences in the frequency of males are no less reliable.

It is evident in Figure 56 that the Kalininka stock of keta can be subdivided into at least three components: with an excess of males, with an equal sex ratio, and with an excess of females.

Since the gene frequencies vary during the spawning run of the brood stock, it is possible to estimate the overall level of heterozygosity (H_e),

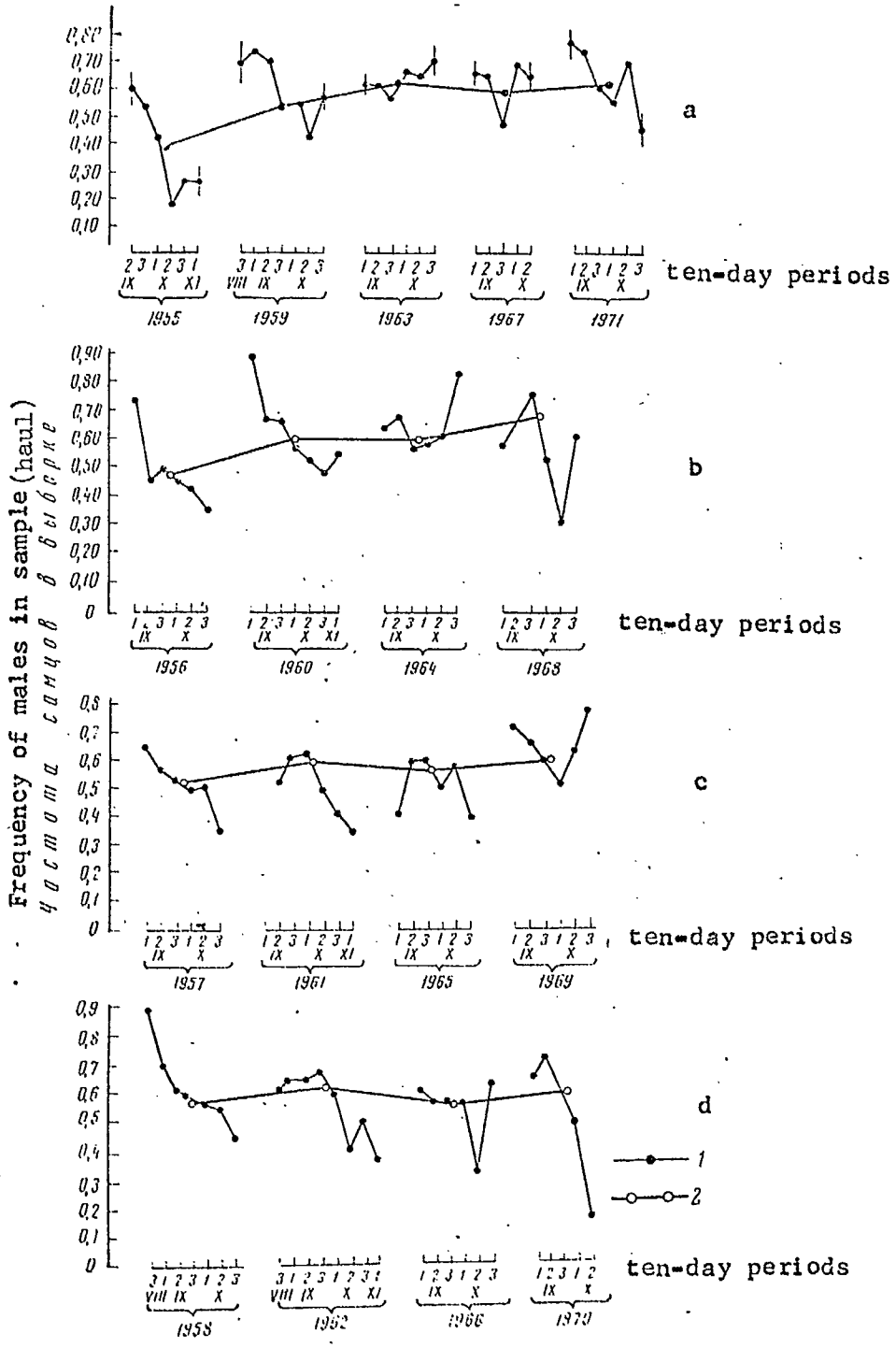


Figure 56. Changes in the sex ratio in time in four successive year-classes (a-d) of the Kalininka stock of keta. On the x-axis are times of fulfilment of the production plan for the given year by the fish hatchery: 1 - frequency of males by ten-day periods; 2 - frequency of males for stock as a whole.

considering it as a generalized indicator of the adaptation of the year-classes. Simple calculations for loci of albumin and lactate and malate dehydrogenases show a tendency of the value of H_e to increase together with equalization of the sex ratio.

For example, in 1970 the values of H_e were as follows: 0.19 (72% males) on 17 September, 0.28 (56% males) on 6 October and 0.35 (50% males) on 14 October. For the following season the biological data are more fragmentary, but the maximum level of heterozygosity (H_e = 0.24), registered at the end of September, also was observed in a population with a sex ratio close to equilibrium (57% males).

If further investigations confirm the discovered tendency it will be possible to pose the question of the presence in population systems of a population nucleus -- a group of maximally heterogeneous populations, a unique regulated part of the system. In any case, the data of Chapter VII testify in favor of such an interpretation.

Let us try to estimate quantitatively the contribution which each of those parts must make to the total volume of eggs collected for incubation. To do that let us examine the data regarding the year-classes which as a whole have equal sex ratios, but at the same time are characterized by fairly prominent variability of that character in time. This will make it 162
possible to determine the volumes of the gatherings of eggs in the first and second halves (September and October respectively) of the spawning run. The following picture emerges (Table 39). Undoubtedly it roughly reflects the natural situation, but the general tendency is still obvious: the more intensive gathering of eggs* occurs in the second half of the spawning run in accordance with the numbers of the approaching brood stock.

*In Table 39 are values reflecting the total gathering of eggs by both the Kalininka hatchery properly speaking and by hatcheries on other rivers.

Table 39

Таблица 39

A Месяц	Поколения (год рождения) B							
	1957 г.		1959 г.		1965 г.		1966 г.	
	a самцов, %	b собранной икры, млн. шт.	a самцов, %	b собранной икры, млн. шт.	a самцов, %	b собранной икры, млн. шт.	a самцов, %	b собранной икры, млн. шт.
1 Сентябрь .	62	4,9	58	24,3	59	60,5	57	57,1
2 Октябрь .	51	35,5	49	48,9	52	112,1	52	76,4

Key: A - Month B - Year-classes (year of birth)
a - males, % b - eggs gathered, millions
1 - September 2 - October

Thus, in gathering sexual products for hatchery purposes with simultaneous monitoring of the sex ratio in the samples(hauls), about 25% of the total volume should be gathered at the start of the spawning migration, 50% at its peak and 25% at the end of the spawning run. Such a plan ought to prove effective even if each of the three roughly divided parts of the stock has its own internal subpopulation structure, as evidently it actually does. This also is indicated by the data for the anchovy, in which among 11 separated elementary populations five had an approximately equal sex ratio (see Table 32), and also similar material obtained on the Azabach'e sockeye (6 populations out of 14, see Table 37) and the deepwater redfish (10 populations out of 21; see Tables 28 and 31).

The absence of scientific data on such organization of the local stock can lead to undesirable consequences during its artifical reproduction. To confirm what has been said, let us turn again to the illustrations showing the variability of the frequency of occurrence of males in the Kalininka population. On all the illustrations the dates of gathering the eggs

were noted by thickening the x-axis. It is clearly evident that, whereas in the early period of activity of the hatchery eggs are taken from all the fishes, later, in proportion to growth of the numbers 163
of the stock, it proves sufficient to gather eggs mainly from the leading subpopulations arriving first from the sea and characterized, as has been noted, by an excess of males, and only partially from populations with an equilibrium sex ratio. That is how it was, for example, in 1957, 1958, 1964, 1965-1967, 1968, 1970 and 1971. If one turns to the conclusion that the biological properties of elementary populations are derivatives of their gene pools, that is, inheritable, then a reliable correlation between the frequency of males (or females) in that part of the stock from which the hatchery gathers eggs in the given year and their frequency during the yield to the fishery after four years could serve as a good illustration of what has been said. Actually, the correlation coefficient calculated on the assumption of its rectilinearity proves to be +0.56 with reliability on the second level (Figure 57).

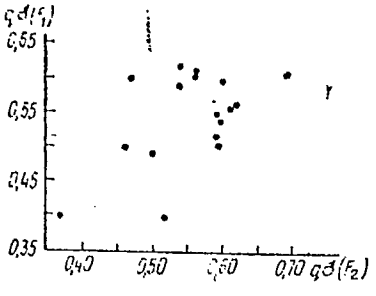


Рис. 57. Корреляция между частотами самцов среди производителей, чьи половые продукты были использованы для рыбоводных целей в данном году [$q\sigma^{\wedge}(F_1)$] и всего калининского стада спустя четыре года [$q\sigma^{\wedge}(F_2)$]; $r = 0{,}5625$; $p < 0{,}01$.

Figure 57. Correlation between the frequencies of males among the adult fishes whose sexual products were used for hatchery purposes in the given year $[q\,\sigma^{\wedge}(F_1)]$ and the entire Kalininka stock after four years $[q\,\sigma^{\wedge}(F_2)]$: $r = 0.5625$; $p < 0.01$.

The discovered connection is of moderate force, but it must be taken into account that it was obtained during a conscious simplification, due to the absence of data, of the age structure of the stock* and, what is no less important, it does not include the compensation mechanism of the birth of individuals of the sex opposite that found in excess, which is not amenable to calculation but is theoretically conceivable (Hamilton, 1967).

In accordance with the correlation for the Kalininka stock as a whole, which at the start of the hatchery's activity had an equal sex ratio or a shortage of males in separate year-classes, now an excess of them is observed which reaches 10% on the average for the last four year-classes (Figure 58). But an excess of one sex during a moderate growth of numbers leads directly to a reduction of the effectively reproductive part of the population. At a steady rate of decrease of females the stock must be represented exclusively by males already in the twentieth year-class. It is clear that the performed calculation is only hyperbole, and in fact 164 the negative consequences of this unconscious selection would certainly show up much sooner. However, the corresponding recommendations are already taken into account in maintaining the Kalininka population, and if in the future the pressure of the ocean fishery on its structure does not prove excessive, then the distribution of hatchery efforts over all subpopulation components will contribute to stabilization of the stock.

*Fourth-year fishes /age 3+/ constitute a predominant part (75-85%) of the spawning stock of the keta, but third- and fifth-year fishes are also represented in it.

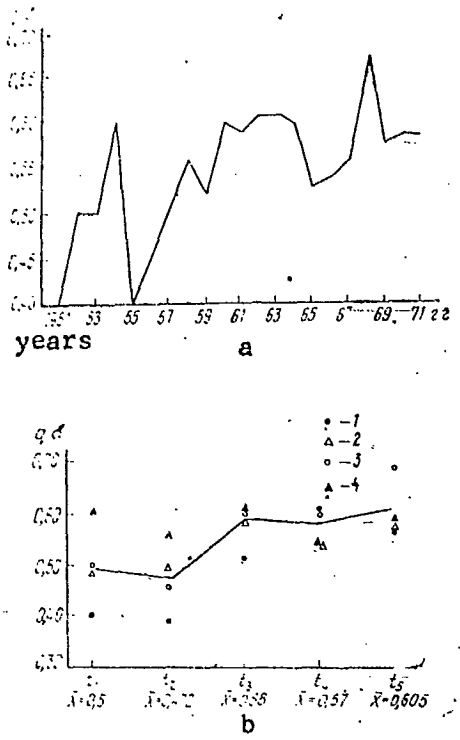


Figure 58. Changes of frequency of males by years (a) and in four adjacent year-classes (b) forming the return structure of the spawning part of the Kalininka keta stock before the start of the hatchery (1951, t_1) and after (t_2 - t_5): 1 - 1947 year-class; 2 - 1948 year-class; 3 - 1949 year-class; 4 - 1950 year-class.

Рис. 58.

The Naiba stock does not have such genetic stability nor, as a result, the necessary biological stability which is so important in the justification of the enormous efforts spent on the maintenance of the population naturally given to us. Destruction of the population structure of the Naiba keta was especially evident for the 1967 year-class, when only the rear-guard part of the stock, consisting two-thirds of females and 40% of fishes of the Kalininka stock, returned to spawn. Let us recall that the lowest level of numbers, 57,000 fishes, was also noted then. In this case the strong effect of the sea fishery is evident, and no matter how intensive the hatchery activity is it cannot recreate the whole on the basis of a separate part.

Destruction of the subpopulation structure of a subdivided population can on the basis of its genetic consequences be completely equated with the effect of selection on natural populations. The only difference is that in nature, as we have seen from the example of the sockeye, a certain optimum of heterozygosity is steadily maintained, and in commercial fishing, which does not take into account the genetic characteristics of populations, a reduction of their hereditary diversity occurs. 165

But this means nothing other than inbreeding, a decline of the level of heterozygosity of the year-classes and, consequently, a reduction of their adaptation. Simple loci ought primarily to react unequivocally to such pressure and, very probably, the uniformity of gene frequencies in the locus of muscle lactate dehydrogenase in the Sakhalin region already serves as an illustration of this phenomenon.

Meanwhile, as the experience of the Kalininka hatchery shows, the production possibilities of an isolated population are revealed most completely when natural spawning is replaced by the hatchery process, if it even unconsciously but unswervingly follows the genetic structure of the stock.

This confirms the validity of hypotheses suggestions based on population genetics data. On the basis of corresponding facts which evidently are of universal biological importance it is possible to recommend a single principle of management of a rational fishery: <u>distribute efforts over all the elementary population units making up the structure of the stocks to be maintained.</u> This principle, if the population gene pools prove to be distributed over even partially isolated subpopulations, must be effective in the fishing industry, fish management /or culture/ and attempts at acclimatization to

a greater degree than existing methods, which do not take into consideration at all the need to preserve all the historically formed genetic diversity of subdivided populations.

The author is aware that a different evaluation of the same population genetics data is possible, one which acknowledges the competence of the opposition of some populations, as better adapted, to others and, consequently, allows change of the biological habit of natural populations in a direction desirable for man -- so-called optimization from the human point of view (Larkin, 1972).

As is known, it is precisely on this principle that all our agricultural practice is based, but its transference to natural populations and species as a whole requires special substantiation by a long-term forecast: good things applied by such intervention to nature can prove 166
to be only short-term and turn into harm for future generations*.

Our opponents, however, ignore this fact. This evidently is caused not so much by an insufficiency of factual material as by the general structure of thinking, which directly connects reorganization of population gene pools with the evolutionary process; it is precisely within the framework of these ideas that the so-called biological or synthetic concept of species, widely accepted abroad, has been formulated. We will also discuss from the corresponding point of view the more general importance of the fact of genetic stability of population systems in nature, supplementing the above-considered data with comparative materials on other species.

*One should also approach with consideration of this fact the regulation of the numbers of salmon stocks during their artificial reproduction: unlimited increase of numbers may not correspond to the optimum of adaptation of a given population.

Population Systems and the Biological Concept of Species

The contemporary concept of species and species formation, which has been systematically discussed in many works, including widely known monographs (Mayer, 1947, 1962; Dobzhansky, 1951; Ehrlich and Holm, 1963; Cain, 1954; Sheppard, 1970; Timofeev-Resovskii et al., 1969), although it bears the name "synthetic" or "biological", in essence is genetic, as it is precisely within its framework that a synthesis of Darwin's theory of natural selection and the achievements of population genetics is accomplished.

Since all those works have become chrestomathic for biologists of our generation, it suffices to mention the main postulates.

1. Population is the basic unit of the evolutionary process.

2. Hereditary polymorphism is the material for the action of evolutionary forces.

3. The difference between a species and a variety is not in essence but in degree or, in other words, "All characters used for the delimitation of species have been subjected to geographic variability" (Mayer, 1968, p. 270).

Every sort of concept represents a system of interconnected views, and so contradiction of the facts in even one of the links of a logical chain can be a prerequisite for the construction of different hypotheses: However, the facts at our disposal permit investigating them from the point of view of all three main postulates.

As is known, the Hardy-Weinberg model reflects a stable state 167
without prospects for evolution, but evolutionary factors constantly active in nature (natural selection, the process of mutation, isolation and gene

recombination) shift those Mendelian populations from the zero point and, changing the gene frequencies in them, in their interaction cause the process of microevolution. One of the fundamental works of Sewell Wright (1931) is thus called, "Evolution in Mendelian Populations".

The further development of the mathematical direction in population genetics by the 1950's had introduced a number of corrections in that interpretation, but the essence of the matter remained unchanged. In that system of views the population remains the evolving unit, true, the most adapted to evolutionary transformation, and now it is not the large or small isolated group which is considered, but the population, which is broken down into a number of partially isolated subunits, scattered over all the adaptive and non-adaptive zones of the range (Wright, 1951). Only in such a population -- S. Wright equates it with a species -- are there the conditions for maintenance of maximum genetic heterogeneity and, thanks to that, during change of the adaptive landscape, at least some subdivisions prove to be better adapted to the new conditions, thereby assuring the possibility of phyletic evolution -- transformation of the species as a whole.

It is generally acknowledged that the same processes are also the basis of so-called "true species formation" -- segregation of the initial species into two or more as a result of spatial isolation.

The stated views can be graphically illustrated by a schematic diagram (Figure 59) borrowed from the work of Dobzhansky (1955). If we examine that diagram it is not difficult to understand that the groups of Mendelian populations diverging in it are also population systems in our understanding. But, as we are convinced, the various evolutionary factors causing reorganization of the gene pools of the simplest population units appear already in the role of stabilization factors on the level of a population system as a whole.

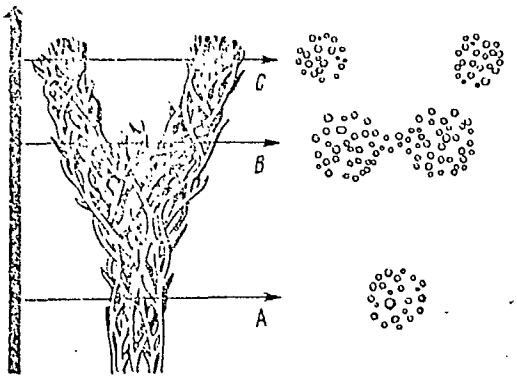


Figure 59. Schematic depiction of the segregation of the initial species (A) into two (B and C) in time (arrow). The separate, more or less interwoven branches are "Mendelian populations" (acc. to Dobzhansky, 1955).

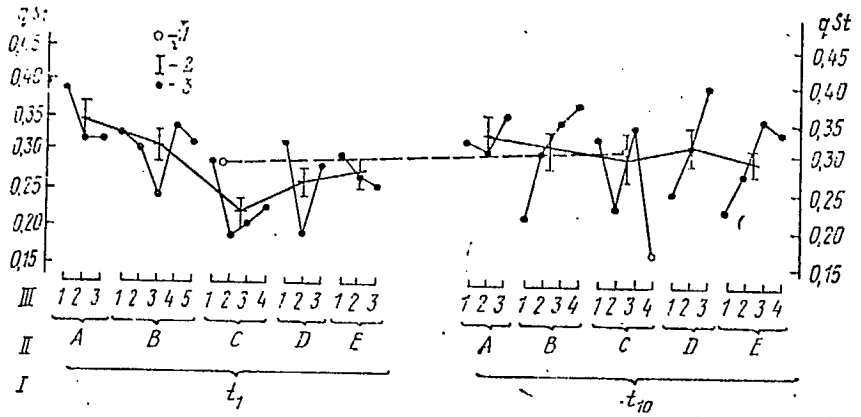
Рис. 59.

Such a result is postulated by the models of stationary distributions of gene frequencies themselves, and study of populations in nature does not contradict it. Moreover, ecological data indicate the possibility of existence also of special regulatory mechanisms in population systems.

Actually, population genetics data inevitably lead to the concept of stability, and we have only to move from the study of the simplest 168
populations to the analysis of higher levels of the population hierarchy.

If this circumstance is taken into account it is possible to use a corresponding approach to other bisexual species and in all cases show an absence of shifts of gene frequencies as a basic population genetics characteristic in any interval of generations accessible to direct comparison.

Let us examine examples of such long steady states, turning first to widely known works on the genetics of natural populations of Drosophila (Dobzhansky, 1943; Dobzhansky et al., 1964). The authors described the dynamics of the frequencies of various chromosomal inversions in Drosophila pseudoobscura and arrived at the conclusion of micro-evolutionary shifts in the gene pools of the studied populations. However, if that analysis



- Рис. 60.

Figure 60. Variability of the frequency of Standard chromosome inversion in provisional first (t_1, 1939) and approximately the tenth (t_{10}, 1940) generations of a population system of Drosophila pseudoobscura of the locality Kin Camp as a whole (1) in comparison with the variability by stations (2) and for generations within the limits of the stations (3). The remaining designations are the same as in Figure 50 (constructed on the basis of data of Dobzhansky, 1943).

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is supplemented by the concept of the dwelling in nature of naturally isolated population systems and the primary data are organized in a certain way, then a different conclusion can be drawn.

The first example (Figure 60) corresponds to ten successive generations of Drosophila studied at the end of the 1940's and beginning of the 1950's in the Sierra Nevada (California) at three localities separated by different height above sea level. Data are presented here for the Kin Camp locality (about 1500 meters above sea level), studied at five stations no more than 2.5 miles apart.

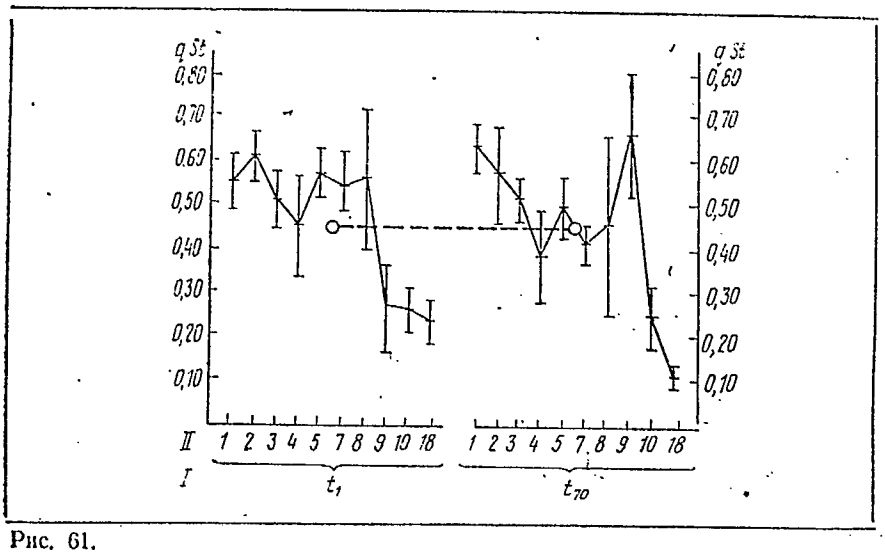

Рис. 61.

Figure 61. Variability of the frequency of Standard chromosome inversion in provisional first (t_1, 1957) and approximately the seventieth (t_{70}, 1963) generations of a population system of Drosophila pseudoobscura as a whol , localized on the territory of all of California, as compared with variability by stations (localities). (Constructed on the basis of data of Dobzhansky et al., 1964).

Since the frequency of the Standard inversion selected by us fluctuates cyclically by seasons, comparable characteristics of the May, June and July samples have been studied, and this is reflected in Figure 60 in the form of a third level of the hierarchy of that population structure, which has been subjected to maximal genetic variability. Smaller differences were successfully registered for stations within the limits of the locality (second hierarchic level), and for the Kin Camp locality as a population system (first level of the hierarchy) there was no reliable shift of the 169
gene frequency in the investigated interval of generations. The values of the root-mean-square deviation indicate also invariability of the frequency distribution.

The second example (Figure 61), corresponding to an interval of 70 generations of an aggregate of populations of Drosophila localized on the entire territory of California, is interesting because it makes it possible to investigate the resistance of the system to the pressure of a powerful factor of selection -- pesticides.

According to incomplete data (Dobzhansky et al., 1964) in 1951 and 1955 alone 17432 tons of various toxic chemicals were used on the territory of California, and during the entire investigated period one fifth of all the pesticides used in the United States were employed by California.

If we compare aggregates of the same stations for the time from 1957 to 1963 we see that for California as a whole, in spite of obvious fluctuations by localities (compare, for example, Nos. 7, 9 and 18 in Figure 61) there were no statistically significant changes of parameters of the frequency distribution of the Standard inversion.

These facts, which testify to the stability of a population system in a time measured in tens of generations, can be supplemented by the results of anthropological investigations of Yu. G. Rychkov (1965, 1968 and 1969), who showed an absence of substantial shifts in the summary gene pool of 170
the Northern Asiatic race of Mongoloids from the Neolithic to our day, that is, in a time interval of hundreds of generations.

Regarding the variety of contemporary physical types of aborigines of Siberia as a result of successive micro-evolutionary transformations of the original Neolithic gene pool, the author by averaging the frequencies of eight uncorrelated hereditary characters reconstructed that ancestral population nucleus, which proved to be identical to the corresponding summary characteristics of fossil material gathered in the Baikal region (Figure 62).

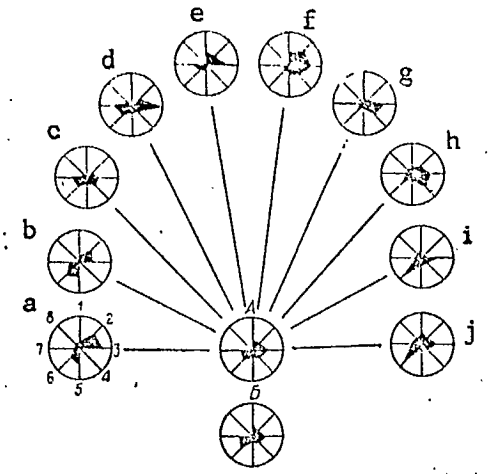

Figure 62. Graphic characterization by the method of Debets polygons of frequency distributions of some cranial anomalies (1-8) in contemporary and fossil populations of North Asiatic Mongoloids: A - contemporary Mongoloids (summarily); B - Neolithic of Pribaikal'e/the Baikal area/: a-j -- various presently living populations (acc. to Rychkov and Movseyan, 1972, with modification).

Рис. 62.

In conclusion we will examine the results of an analysis of contemporary and fossil populations of the gastropod Littorina squalida in the isolated Busse Lagoon on Southern Sakhalin which is being completed by B.A. Kalabushkin and us at the present time.

This species has a well-expressed polymorphism of the coloration of the shell, interpreted as a manifestation of a two-allele system with incomplete dominance (Figure 63). In this case, just as in the ground snail Cepaea nemoralis, differences of the genotypes are also preserved in the fossil forms and so the possibility is opened up of investigating 171
their distribution in samples from now living and old populations, divided by at least 2000 generations, which have replaced one another every three years for the 6000 years which have passed since the time the lagoon was formed. These data establish absence of shift of the gene frequency for the system as a whole in the investigated interval of generations (Figure 64).

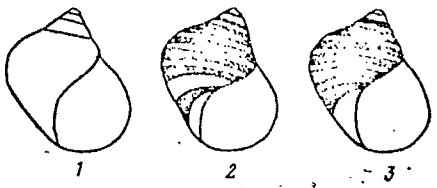

Рис. 63.

Figure 63. Polymorphism of coloration of the shell in Sakhalin populations of the gastropod Littorina squalida: 1 and 3 -- homozygotes; 2 - heterozygote.

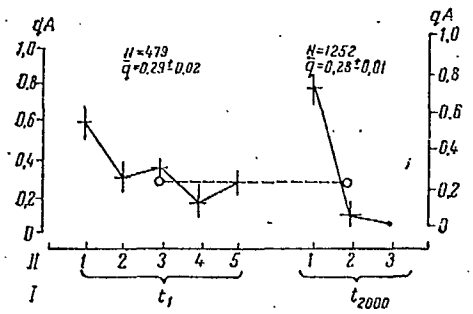

Figure 64. Variability of the frequency of the gene A (I) in provisional first (t_1; N = 479, $\bar{q}$ = 0.293±0.015) and approximately two-thousandth (t_{2000}; N = 1252 specimens; $\bar{q}$ = 0.28±0.01) generations of the population system of the gastropod Littorina squalida in Busse Lagoon on Southern Sakhalin as compared with the variability by separate stations (II).

It must be emphasized that the clearest example of long stability of polymorphism from the Pleistocene to our day, described at one time by Diver (1929) for Cepaea nemoralis and cited in many summaries, on evolution was detected by the author precisely thanks to a system of observations similar to that described above. Diver, of course, does not mention that fact at all and does not cite quantitative data, but the approach itself leaves no doubt. "In the now living colonies studied by me, various phenotypes are encountered with a very different frequency, and the frequencies of any of the phenotypes can differ greatly in specimens separated by only a few nuclei. But in the entire series of colonies the banded types, taken together, predominate over the bandless.

Bandedness is readily visible also in fossil forms; detailed data can be obtained on the frequency of different types and they will be very interesting for genetics and the theory of natural selection. Kennard 172
has provided me with drawings of three large samples, each of which contains two species (Cepaea nemoralis and C. hortensis -- Yu. A.) from strata near Goodwood... In all three samples the total number of banded types precominates over the unbanded shells and the frequencies of the different types are precisely such as can be found **even today**" (Diver, 1929; p. 183; emphasis ours -- Yu. A.).

We do not doubt that such a regularity must be traced in any bisexual species, no matter how complex or, on the other hand, simple, its internal structure is, but broad study of the genetics of natural populations of different species except man (Rychkov, 1965; 1968; 1969 a and b) has not introduced any corrections into the traditional generalizations: field investigations have proven to be linked with separate samples reflecting a very simple, very variable population level. Evidently therefore the important problem of genetic stability has been reduced only to investigation of the mechanisms of homeostasis and heterosis (Lerner, 1954; Kirpichnikov, 1967), and the main attention has proven to be concentrated on evolutionary aspects in general and, in particular, on the correlative contribution of the random drift of genes and natural selection in the reorganization of the gene **pools** of elementary populations. Variability on that level, as we have seen, actually is great, and this also contributes to the formation of concepts of unlimited interpopulation variety.

Meanwhile, the detection in nature of population systems as historically formed subdivided populations and the corresponding genetic analysis

testify to prevention of the consequences of non-adaptive divergence of the species by migrational connections and, as was evident from the example of loci of lactate dehydrogenase and phosphoglucomutase, the selective factor also plays the same stabilizing role. One can readily multiply the number of examples of a sharp predominance in nature of precisely the 173
stabilizing forms of selection, including that which is frequency-dependent(see Rychkov et al., 1973; survey in Kirpichnikov, 1972).

But the effects of stabilization must be especially strong on the edges of ranges, which together with the uniting effect of migrations (or even in its absence) will keep subpopulations within the framework of a population system regardless of distinctive features of its internal organization: isolation by distance does not differ in principle at all from the island type of structure, and stable wedges correspond to a "continuous model".

The adaptations of local populations thus formed are so conservative and unique that even forcible migrations within the framework of a species range lead to important consequences only in the sense of degradation, but not of evolution. This flows from the results of many unsuccessful attempts at acclimatization, usually not discussed; one example was examined in Chapter V (see also Rychkov and Sheremet'eva, 1972a, b and c).

Thus the genetic divergence of a species can be regarded as a process of systematic transformation of the gene pool of the ancestral population in proportion to its differentiation into subordinate subdivisions within generations and according to range. At least under the conditions of a normally fluctuating environment the mean gene frequency and upon achievement of a state of stability also the dispersion in the system remain

invariant in relation to all possible micro-evolutionary transformations, differently directed and mutually balancing one another. Figuratively speaking, the isolated population "unfolds into itself", congealing in the end in equilibrium with the environment (Altukhov and Rychkov, 1970).

The more complex the internal organization of the system and the greater its internal variety, the more resistant it is to various kinds of external effects. From this point of view, maximum stability in space and time must be characteristic of a widely settled species, for change of the level of adaptation achieved by it requires external effects such as it cannot endure. But if one remains within the framework of the geological theories deriving from C. Lyell and taken into account in the contemporary genetic concept of evolution, then it is difficult to perceive how the processes determining the maximum stabilization of the species as an integral population system simultaneously form the basis of the origin of new species.

Evidently, the traditional population genetics approach is inade- 174
quate for a reply to that question and it is necessary to make use of some sort of additional data.

For this purpose we will turn to the very last stage in the development of genetics, one directly connected with the molecular aspects of the organization of the genome in higher organisms. The corresponding facts have a direct relation to the second and third points of the synthetic conception of a species and were obtained in a comparative study of the phenomenology and biological importance of phenomena of biological polymorphism and monomorphism in populations of different species.

Biochemical Polymorphism and Monomorphism in Populations. Electrophoretically Invariant Proteins as Markers of Genes "Protecting" the Species Identity of the Individual

The hereditary polymorphism of proteins, examined and used earlier as the key to study of population structure, and more narrowly for the recognition and identification of populations, attracts the persistent attention of many biologists also for other reasons. Recently, we have already mentioned it casually, an incredible range of that sort of variability has been discovered in populations of the most different species,

Hubby and Lewontin (1966; Lewontin and Hubby, 1966) on Drosophila, Harris (1966, 1969a and b) on man, and Manwell and Baker on birds(Baker et al., 1966; Baker and Manwell, 1967; Manwell and Baker, 1968) have shown that in almost every one of natural populations polymorphism is revealed by up to 30% or more of the investigated genetic loci, and a certain average individual can be heterozygotic in relation to 12% of his genes. These discoveries were also confirmed later on other species (Petras et al., 1969; Selander at al., 1970; Manwell and Baker, 1970, etc.).

The number of works in this area is growing rapidly, generating a group of new genetic problems which are intensively discussed abroad and in our country in connection with aspects of the genetic load, the adaptation of genotypes and correlation of the random drift of genes and selection in the maintenance of such unprecedented molecular variety (Kirpichnikov, 1972).

At the same time it is impossible not to turn attention toward the important fact that in the genetic-biochemical approach, besides

polymorphous gene markers, monomorphous, invariant proteins are also always discovered in each of the examined populations under identical methodical conditions. 175

Probably because such characters do not permit studying the genetic divergence of populations they remain outside the field of vision of investigators. However, each protein in an organism carries a certain functional load, and even on the basis of this alone the fact of genetic invariance with respect to at least half and, more likely, an even larger number of proteins in a population requires careful analysis.

Let us turn to the corresponding data.

In the examples of biochemical polymorphism cited earlier (see Figure 14) we saw how variability in some loci is combined with an absence of variations in others. Thus the locus H_bI in the cod is polymorphous, whereas there is no variability in the locus H_bII; the same is characteristic of muscle lactate dehydrogenase (Ldh II) of the keta. But at times entire groups of electrophoretically invariant proteins are discovered, as was mentioned in one of the preceding chapters: these are multiple crystallins, hemoglobins and myogens.

Visible on Figure 65 is an absence of individual variations in the number and position of protein zones on the electrophoregrams, excepting only variability in the intensity of coloration, which can be connected with individual differences in the activity or in the quantity of product synthesized by the gene.

In a recently published work (Altukhov and Rychkov, 1972) it was shown on broad comparative material, including fishes, that such a surprising uniformity of protein electrophoregrams reflects a real natural

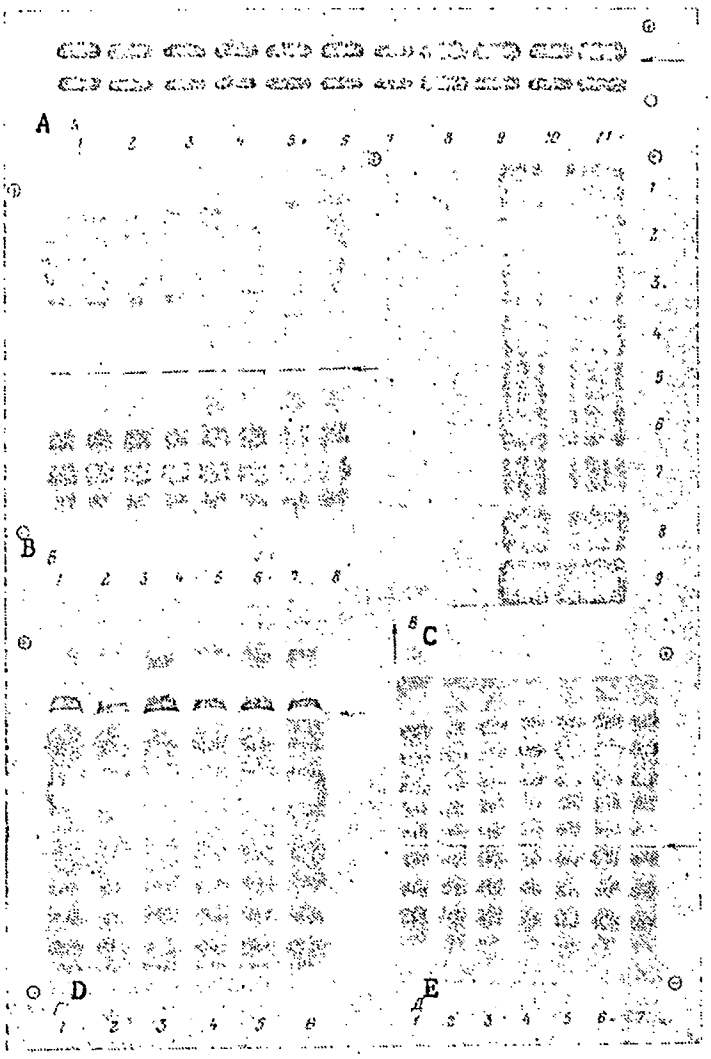

Рис. 65. Фотоснимки электрофоретически мономорфных белков тихоокеанских лососей, исследованных на одной и той же онтогенетической стадии:

Figure 65. Photographs of electrophoretically monomorphous proteins of Pacific Ocean salmons investigated in the same ontogenetic stage: A - hemoglobins of 11 specimens of the keta; electrophoresis in agar gel reveals two components; B - hemoglobins of 8 specimens of the keta. By starch-gel electrophoresis 18 components were revealed. Since in photoreproduction "weak" fractions are reproduced poorly, the positions of all the found protein zones have been marked with lines: C and D -- the same for several specimens of the pink salmon respectively. When the number of electrophoretic fractions is unchanged quantitative differences are visible in each specimen (see Nos. 1 and 6 of species C). Such multiplicity of hemoglobins of Salmonidae is caused by the presence of 7-8 different subunits in them (Wilkins, 1970; Tsuifuki and Roland, 1970); E - Water-soluble proteins of the crystalline lens of the eye in the keta. Electrophoresis in agar gel. A connection of this multiplicity with gene duplication has not yet proven, but can be postulated.

phenomenon characterizing the species as a whole. Consequently, genetic monomorphism can be defined as... "the absence of variability of a known hereditary character in the entire range of the species or the presence in it of qualitatively different variants with a frequency not exceeding the probability of recurrent mutation" (Altukhov and Rychkov, 1972, p. 288).

In fact, the Laboratory of Genetics of the Institute of Biology of the Sea of the Far Eastern Scientific Center of the USSR Academy of Sciences has investigated by various electrophoretic methods more than 1000 individual specimens of hemoglobin and several hundred specimens of crystallins from different keta populations of the rivers of Sakhalin, Kamchatka and the Kuril Islands, and only in 11 cases were variations observed in one single anode zone of the hemoglobin. The monomorphism of the close species Oncorhynchus gorbuscha is still more impressive: in about 1000 specimens from the same and other rivers we did not observe a single variation of the hemoglobin electrophoregrams, which could be interpreted as mutational 177
and not as a result of rare natural or artificial hybridization with the masu O. masu -- still another species of the same genus which also has monomorphous hemoglobins.

The structural genes responsible for the synthesis of isoenzymes of lactate dehydrogenase of group b are monomorphous in more than 3000 individuals of the keta and 1000 of the pink salmon caught in various rivers of the Pacific Ocean basin; the number of such examples can readily be multiplied, and the corresponding data for various species have been grouped in Appendix 2.

The genetic mechanisms maintaining polymorphism in at least a whole series of cases are well known to us, but the definition itself

(page 19) reflects the result of interaction on the population level of hereditary variability and natural selection. The difference in the relative adaptive importance of the genotypes of lactate dehydrogenase and phosphoglucomutase, discussed above, serves as still another illustration of this.

But what is the biological meaning of genetically invariant properties? The posed question can be answered only through investigation of their interspecies variability. For that purpose we will examine the results of electrophoretic analysis of the hemoglobins of Pacific Ocean Salmonidae (Figure 66) and also data on several groups of genetically monomorphous proteins in other species of animals (Figure 67). In all the investigated cases qualitative differences are traced -- according to those characters the species are as discrete and unique as individuals of different genotypes with respect to a given system of genetic polymorphism (compare Figure 14; also see Altukhov, 1969b). Moreover, when a comparison is successfuly made of rare interspecies hybrids or species of hybrid origin with parental species, an important law is discovered: species characters behave as integral genetic units, showing a simple summation of parental types, the formation of hybrid products or even dominance-recessiveness ratios (Figure 68; see Figure 66).

Consequently, in such cases even one individual carries species genetic information, and the problem of species identification is solved unequivocally, irrespective of which sort of species the investigator deals with -- bisexual or unisexual.

The biochemical systematics of fishes, which has developed strongly in recent years, is filled with data which establish the

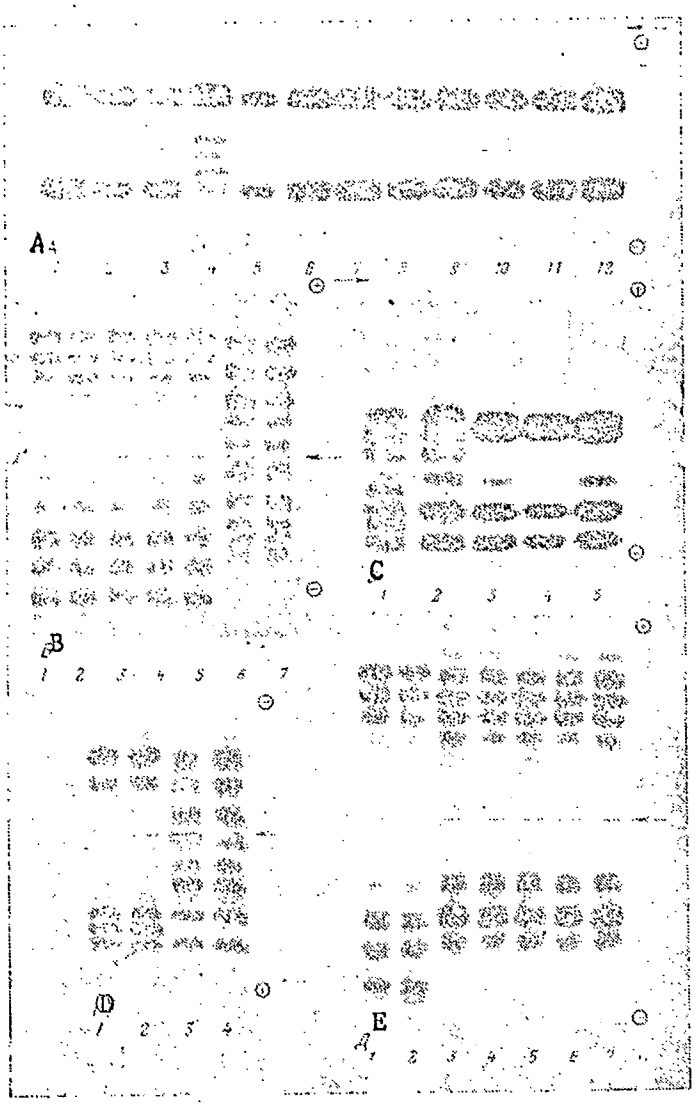

Рис. 66. Специфичность на видовом и родовом уровнях множественных гемоглобинов у рыб сем. Salmonidae:

Figure 66. Specificity on the species and generic levels of multiple hemoglobins of fishes of the family Salmonidae: A: 1-3 and 5-12 -- Oncorhynchus keta, 4 -- O. kisutch. (Electrophoresis in agar gel); B: 1-5 -- Salvelinus leucomaenis; 6 and 7 -- O. gorbuscha (Electrophoresis in starch gel; C: 1 - O. gorbuscha; 2 - hybrid (F_1?); 3-5 -- O. masu (Electrophoresis in agar gel); D: 1 and 2 -- O. keta; 3 and 4 -- O. gorbuscha; E: 1 and 2 -- Salvelinus leucomaenis; 3 - 7 -- O. keta (Electrophoresis in starch gel).

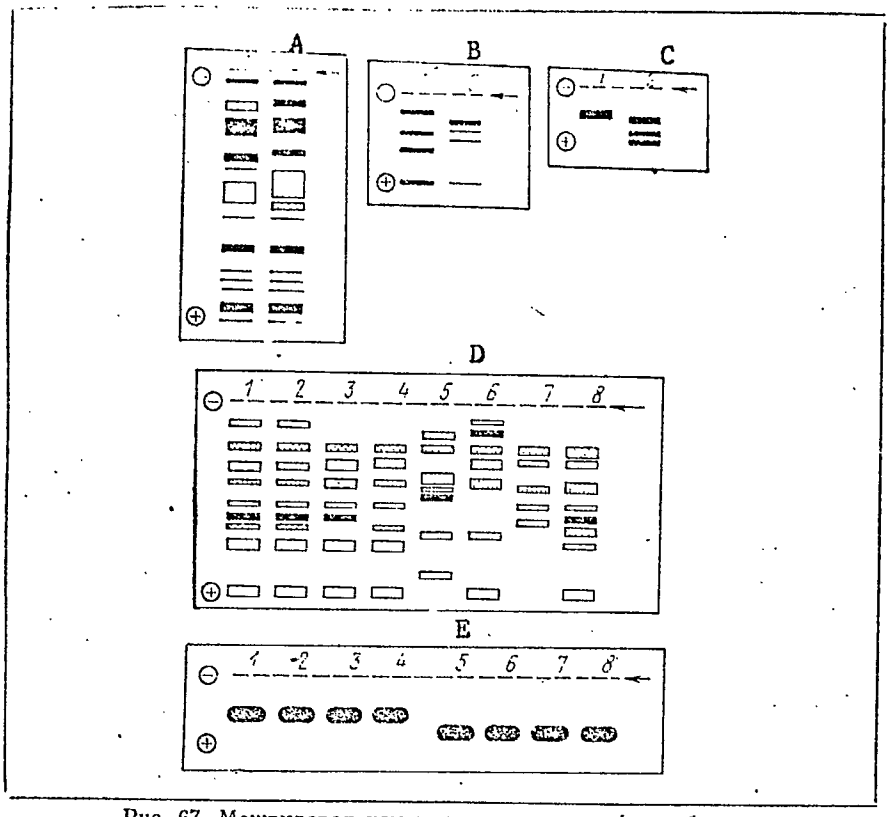

Рис. 67. Межвидовая изменчивость мономорфных белков:

Figure 67. Interspecies variability of monomorphous proteins: A - Myogens of two species of molluscs of the genus Unio: 1 - U. tumidus, 2 - U. pistorum (electrophoresis in starch gel); B - esterases of two species of gammarids: 1 - Gammarus duebeni; 2 - G. zaddachi (electrophoresis in starch gel); C - hemoglobins of salamanders: 1 - Desmognatus monticola; 2 - D. guadrimaculatus (Electrophoresis in starch gel); D - myogens of seven species of shrimps of the family Penaeidae: 1 & 2 -- Parapencopsis hungerfordi; 3 - P. hardwicki; 4 - Metapenaeus matatus; 5 - M. stridulans; 6 - M. barbata; 7 - Penaeus monodon; 8 - P. semiculatus; E - hemoglobins of lizards: 1-4 -- Anotis aeneus; 5-8 -- A. trinitatus (Electrophoresis in starch gel). The different hatching reflects variations in the intensity of the protein zones on the original electrophoregrams (acc. to Altukhov and Rychkov, 1972).

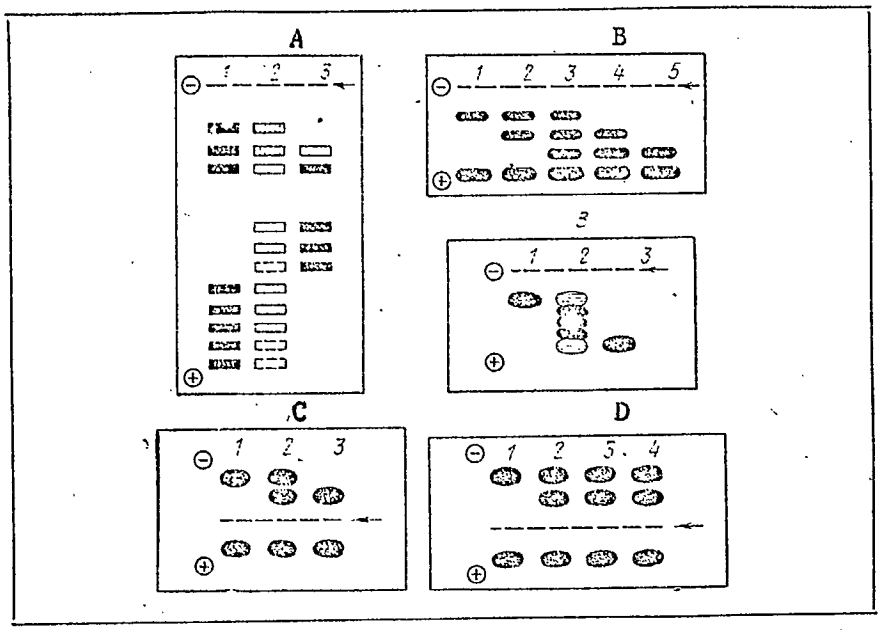

Рис. 68. Электрофореграммы видоспецифичных белков у межвидовых гибридов в сравнении с исходными видами:

Figure 68. Electrophoregrams of species-specific proteins of interspecies hybrids as compared with the starting species: A - anode zones of leaf peroxidase: 1 - Nicotiana sylvestris; 2 - N. tomentosiformis; 3 - Hybrid F_1 (electrophoresis in polyacrylamide gel); B - fish myogens: 1 - Richardsonius balteatus; 5 - Mylocheilus caurinum; 3 - hybrids F_1; 2 & 4 - corresponding backcrosses (electrophoresis in starch gel); C - lactate dehydrogenase of myocardium of lizards of the genus Cnemidophorus: 1 - C. gularis, a bisexual species; 2 - C. tesselatus, a parthenogenic species; 3 - C. tigris, a bisexual species (electrophoresis in starch gel); D - hemoglobins of birds: 1 - Coturnix coturnix; 3 - Gallus gallus; 2 - hybrid F_1 (electrophoresis in starch gel); E - globin chains of hemoglobin: 1 - ass; 2 - mule; 3 - hinny; 4 - horse (electrophoresis in starch gel). The different hatching reflects variations in intensity of fractions on original electrophoregrams (acc. to Altukhov and Rychkov, 1972).

the possibility of distinguishing monomorphous biochemical characters 179
of universal diagnostic importance not only on the level of the species but also on higher taxonomic levels distinguished still earlier in accordance with the principles of typological systematics. For example, among several tens of species belonging to 14-15 families of seven orders, only in 20% of the cases was genetic polymorphism of hemoglobins noted, whereas 80% of investigated species of fishes are characterized by multiple hemo-
globins, unique for a species (Altukhov, 1969b). This circumstance in fact 180
permits investigators to successfully solve complex questions of systematics where the population approach is impotent. A bright example is the recent cycle of genetic-biochemical and taxonomic works of Westrheim and Tsuyuki, 1967, 1971; Tsuyuki and Westrheim, 1970), who discovered several new species of redfish of the family Scorpaenidae in the Northeast Pacific.

The constancy and species specificity of myogens are still more clearly evident. Although the mechanisms of gene control of these proteins are still not clear, however, among the 100 or even somewhat more studied species polymorphism has been discovered in only three or four cases (Tsuyuki, 1966; Tsuyuki et al., 1965a and b, 1966, 1967, 1968, 1969; Uthe et al., 1966; Chen and Tsuyuki, 1970).

On the other hand, there is no such specificity in genetically poly- 181
morphous proteins; one and the same alleles are represented in known "good" species. Biochemical genetics literally overflows with examples of such homological hereditary variability (in the meaning of N.I. Vavilov), and we will limit ourselves here to only a few illustrations (Figure 69).

Consequently, on the basis of these characters independent species are differentiated just as populations are within a species, differing (or

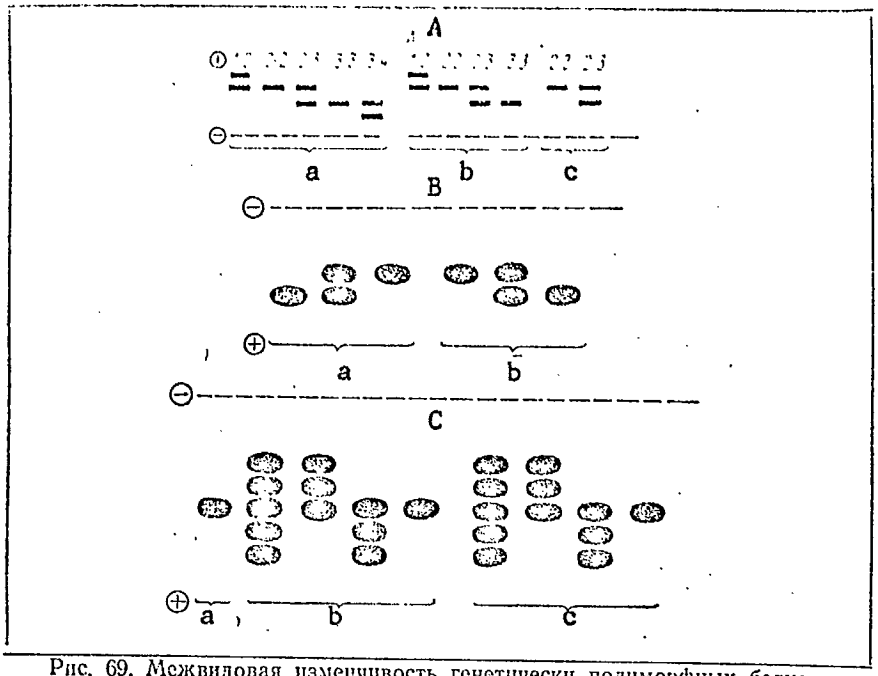

Рис. 69. Межвидовая изменчивость генетически полиморфных белков:

Figure 69. Interspecies variability of genetically polymorphous proteins: A - genotypes with respect to locus of serum esterase of three species of tuna: a - Thunnus maccoyii, b - T. obesus, c - T. albacares (electrophoresis in starch gel) (acc. to Sprague, 1967); B - genotypes of serum albumin of ocean perch of the genus Sebastes: a - S. marinus, b - S. mentella (electrophoresis in agar gel); C - genotypes of malate dehydrogenase of three species of salmons of the genus Onorhynchus: a - O. nerka, b - O. gorbuscha, c - O. keta (electrophoresis in polyacrylamide gel).

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not differing) both in the frequencies of common genes and also in particular genes characteristic to them alone. Thus redfishes and salmons have the same alleles in corresponding loci, whereas the tuna Thunnus massoyii has the allele Es_4, not found in two other species, T. obesus and T. albacares*.

*Situations in which a qualitative interspecies difference (for example, in the mobility of molecules) is noted with respect to a polymorphic protein system as a whole represent only a particular case in the interspecies variability of genetically monomorphous proteins.

It is not difficult to guess that from the point of view of the biological concept of species our example illustrates the previously cited scheme of species formation which treats micro-evolution as a continuous, gradual process, in the analysis of which all the successive stages of divergence of populations toward the status of new species are successfully revealed. Actually, in the light of the examined data the difference between a species and a variety on the basis of these characters is quantitative, for they are polymorphous, that is, geographically variable. 182

But how is it in such case with genetically monomorphous characters which have not been subjected to geographical variability and at the same time delimit close species? The synthetic theory of evolution gives no answer to this question, for from the very start only variability is acknowledged to be the sole source of information about species in nature, and invariant characters and properties of a species either are in general denied or, at best, treated as an abstruse phenomenon relating only to the sphere of systematics (Mayer, 1968).

Possibly, for its time such a concept was justified, as genetics itself as a science owes its origin precisely to the hereditary polymorphism of species. However, on the new level of investigation genetic facts are also discovered which testify that the content of species is not exhausted only by polymorphism, and that some part of the genome remains invariant on the level of such functionally important markers as proteins in all individuals.

But if genetic monomorphism is a real natural phenomenon, then the mere acknowledgment of this fact with consideration of distinctive features of interspecies variability of monomorphous properties gives the possibility

of treating species formation, not as a gradual probabilistic process proceeding on the population level, but as a consequence of qualitative genetic reorganizations marked by true species characters.

According to the same logic species characters and properties must be specialized for the performance of such vitally important functions, natural variability of which is not allowable.

Actually, in the latest works based on complete analysis of the amino acid sequence in proteins, the extremely conservative nature of natural selection, which cuts off all mutations affecting those sections of the protein molecule on which the main function of the gene product depends, has been discovered. For example, in various species of vertebrates lactate dehydrogenase has a different amino acid composition, but the active section of the enzyme, composed of 12 amino acid residues, is identical in all cases 183 (Kaplan, 1965; Ohno, 1970a and b; see also Baranov, 1972).

The mechanisms of maintenance of stability of the phenotype on the protein level can also be different (Altukhov and Rychkov, 1972), but testifying also in favor of the proposed treatment is the fact of principal importance that multiple proteins coded by multiple, duplicated genes prove, as a rule, to be the most monomorphous (Altukhov et al., 1972). But just as qualitative interspecies differences are traced precisely on these proteins, so the possible mechanisms of gene duplications also must coincide with the mechanisms of species formation in the rare cases where such genetic reorganization, which has proven to be compatible with ontogeny, after one or several steps leads the separate individual to reproductive isolation.

The duplications of genetic maerial which take place on the basis of local excessive self-copying of genes, on account of polyploidy or in the

process of unequal crossing over, unquestionably reflect qualitatively different **reorganizations** of the genome than the mutations which are the basis of polymorphism.

Among the large number of works devoted to these problems a special place belongs to the investigations of Suzum Ohno et al. (Ohno, 1970 a and b; Ohno et al., 1968) which presented numerous evidence that tetraploidization played an important integrating role in the evolution of vertebrates. With respect to at least two of the now known polyploid groups of animals -- three families of the order Clupeiformes and two genera of the Cyprinidae family -- it is possible to speak with confidence of their amphidiploid origin (Bender and Ohno, 1968; Wilkins, 1970; Altukhov et al., 1972), whereas the tetraploid and octaploid South American frogs of the family Ceratophrididae are autopolyploids (Becak, M., et al., 1966; W. Becak et al., 1967).

A hybrid nature has been demonstrated for parthenogenetic species of lizards of the genera Cnemidophorus (Neaves, 1969; Neaves and Gerald, 1968) and Lacerta (Darevskii and Kulikova, 1964; Darevskii and Danielyan, 1969) and for several gynogenetic species of fishes of the family Poeciliidae (Rasch et al., 1965, 1970; Rasch and Prehn, 1969; Prehn and Rasch, 1969; Abramoff et al., 1968; Schultz, 1961, 1966, 1967, 1969; Schultz and Kallman, 1968). It is assumed that in the evolution of animals hybridization, parthenogenesis (gynogenesis) and polyploidy are connected (Astaurov, 1969; Schultz, 1969). As for the evolutionary role of chromosome mutations not leading to intraspecies polyformism, but at the same time marking the level 184
of the species, it has been shown for the cytologically best studied Diptera (White, 1954, 1968).

A graphic concept of the range of variability of the dimensions of the genome of animals of different groups is given by the schematic diagram

borrowed by us from the work of Britten and Davidson (1971), who summarized a large amount of literature material (Figure 70). Although not all the taxons have been studied with the same completeness, in a whole series of cases the eye is struck by a surprising variability of the investigated character, one caused, as we now know thanks to the work of Ohno's school, by tandem duplications and polyploidy*.

Of course, all these new facts reflect only a little of the variety in the animal world, but we can unquestionably point out the existence in zoological species of evolutionary paths which quite recently seemed very problematical or even simply impossible (Mayer, 1968), in spite of their being widespread in the kingdom of plants. Evidently in the future still broader proofs of the role of genetic reorganizations of this sort in the evolution of zoological species will be obtained.

The most important biological meaning of these reorganizations is that they suddenly transfer all the genes in a genome or some of them into a constantly heterozygotic state and, consequently, provide individuals with the advantages of a qualitatively different adaptative level, freeing the future population of the load of less adapted genotypes; at the same time this means increase of the reliability of storage and transmission of information about vitally important functions, reflecting the uniqueness of the new species, to following generations.

Genome reorganizations of this kind constantly occur, probably with a low frequency, in the depths of different species, but they win the right

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*Obviously, polyteny gives a similar effect. A sharp interspecies variability of the DNA content in the absence of variability of the number of chromosomes is detected in a number of amphibians (W. Beçak et al., 1970).

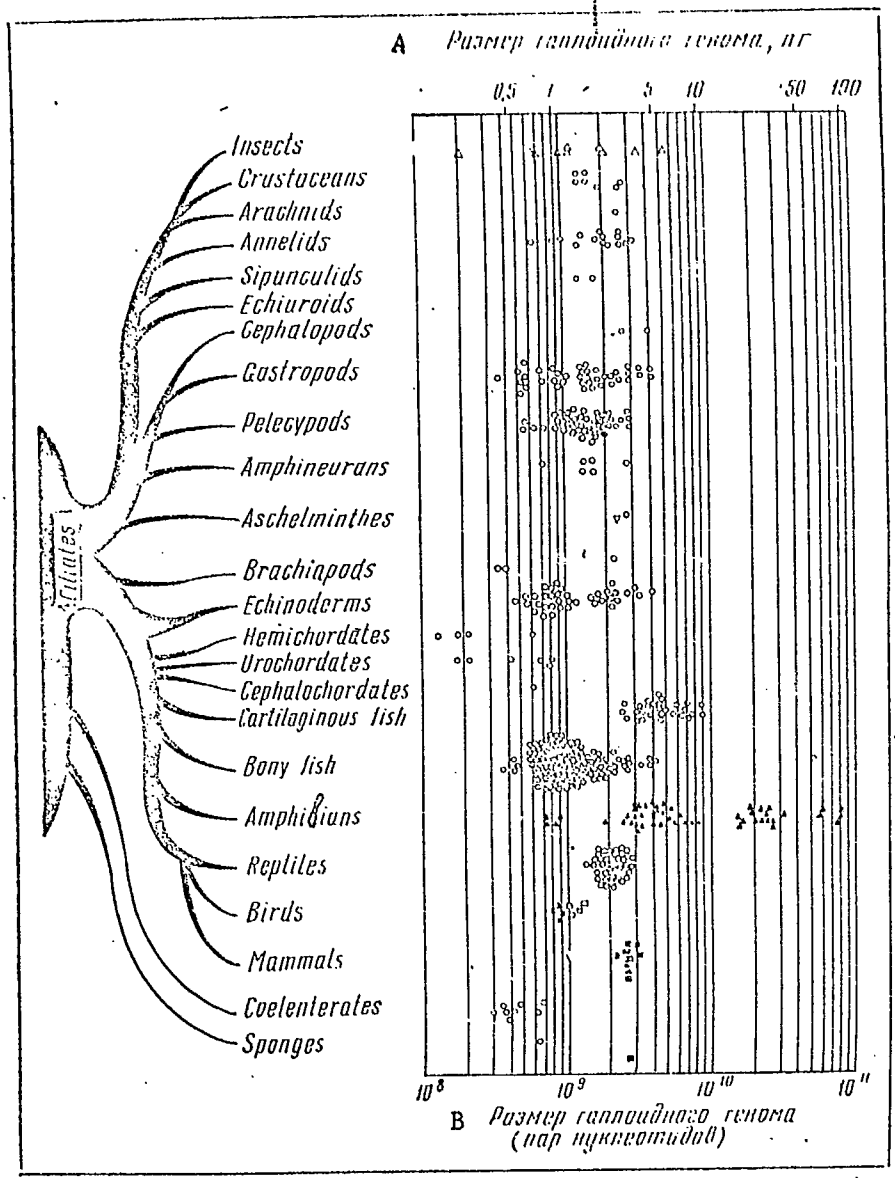

Рис. 70. Изменчивость величины генома у различных групп животных (по Britten a. Davidson, 1971).

Figure 70. Variability of size of the genome of different groups of animals (acc. to Britten and Davidson, 1971). A - Size of haploid genome, pg B - Size of haploid genome (pairs of nucleotides).

to life only when there are such shifts of the natural environment as when a breaking of the historically formed interpopulation and interspecies barriers sharply elevates the levels of genetic polymorphism of populations and the heterozygosity of the individuals forming them. "Polymorphism generates still greater polymorphism"(Ohno, 1970b; Watt, 1972) and in that case such combinations of genes can be accomplished as would have been considered "improbable" in the preceding stage of stable existence of the species.

Further work on the question ought to show the degree to which such 186
macromutations are random and to what extent they can be treated as caused by the preceding history of development of the group. At the same time the available facts already lead now to the conclusion of duality in the organization of the genome in higher organisms, as well as to the idea of the fundamentally different biological importance of genetically monomorphous and polymorphous properties. Whereas the former, preserving the identity of the species and the individual, thereby mark the existence of cardinal functions, the change of which can only lead to species formation, the latter, thanks to their broad variability, determine only the secondary adaptive possibilities of the species.

In such a treatment genetic polymorphism in populations is not material for the action of evolutionary forces but a universal strategy of nature, one assuring preservation of integrity of the species on the basis of continuous interaction of hereditary variability, random drift of genes and natural selection in normally fluctuating environmental conditions.

As we see, the conclusions from comparative genetic data interlock with the results of population genetics investigation. True, in the latter case it is fundamentally important that in the corresponding material

not the simplest population units but their integral aggregates -- genetically stable population systems, historically formed within the framework of the boundaries given by nature itself, be represented.

In concluding the chapter we will point out that the views on species formation presented here have something in common with the ideas of the geneticists G. de Fries (1904, 1912), R. Goldschmidt, 1940, 1948, 1952, 1955) and the physiologist B.P. Ushakov (1958, 1959a and b). In all these works there were discussions of the problem of duality (structural or functional) in the organization of the individual and, consequently, with a given degree of logical completeness, best expressed in Goldschmidt, a qualitative difference was postulated between the evolutionary process properly speaking and adaptive intraspecies divergence.

The author assumes that his own treatment has only an external similarity with those concepts, presenting a natural construction which flows from new experimental facts. In any case it must be emphasized once more that genetic monomorphism is just as real a phenomenon in nature as polymorphism, and that, if these phenomena are examined separately, evidently it is impossible to analyze the processes of evolutionary transformation and the adaptive stabilization of species.

Conclusion 187

We have striven as much as possible to systematically state and investigate from different points of view facts obtained in a comparative genetic approach to the problem of population organization of the species in fishes.

The proposed treatment does not agree with the traditional concepts of biologists. Thus, for foreign colleagues, in the foreground is

the differentiating role of the population structure, which emphasizes only the need for the recognition and identification of the simplest population units. With consideration of the results of the work done it becomes clear that both population systems and their structural components may actually be recognized on a genetic basis, but the problem of identification can be successfully solved only on higher hierarchic levels endowed with the integral property of stability and, consequently, having independent importance in nature.

Some Soviet ichthyologists consider elementary populations to be non-hereditary communities. This also is not true, for the heritability of racial characteristics does not at all mean their invariability in time and space: migrations, isolation and selection, acting separately or jointly, change the genetic appearance of populations. However, on the higher levels of intraspecies hierarchy variability of that sort is tranformed into stability, which also permits examining from another point of view the principles of rational exploitation of natural populations.

This circumstance, in our opinion, is not limited at all by the framework of particular problems of the fishing industry. On the contrary, it is directly linked with the very important general biological problem "Man and the biosphere" to the extent to which the preservation of nature depends not only on the inadmissibility of its direct destruction but also on the implementation of a scientifically substantiated approach which pursues the goal of rational exploitation of commercial species.

On the basis of clear ideas of distinctive features of the internal organization of a population system, uniformly and proportionally distributing

corresponding efforts over all components of its structure, we actually obtain the possibility of rational economic activity which pursues the goal not only of extracting the maximum economic gain but also of infinitely long 188 preservation of a natural population.

Wide realization that there is such a strategy evidently is inevitable, and then an independent scientific discipline, population biology, will be separated from the sphere of biology. This tendency is already perceptible but still predominant in it is the analytical stage, which finds reflection in attempts to substantiate the scientific independence of such sections as population ecology, population morphology, population etiology, etc. At the same time, remaining in the shadow is the important fact that population genetics, which has at its disposal mathematical theory and a large sum of facts acquired in the study of natural populations, has already been developing successfully for several decades. It is precisely here, perhaps unconsciously but in essence, that the above-indicated and other trends are being united. Nor is this surprising, as all the biological characteristics of populations are derived from the historically formed gene **pools**, and, consequently, broad possibilities are actually being opened up on a genetic basis for unification of the efforts of biologists of different specialties to work out a universal strategy of rational economic use of biological resources. Preservation of the genetic stability of still surviving population systems, restoration of those whose structure has already been destroyed and, finally, the creation of new systems -- these are the main tasks, the solution of which evidently is capable of eliminating the present conflict of mankind with the biosphere. True, on this path the role of the purely psychological factor, the very nature of man, remains not completely investigated, but that line of investigation is outside our competence.

The author will consider completed the task facing him if the present work, in spite of all its shortcomings, makes a contribution within its powers to the development of a corresponding approach to the analysis of the biology of natural populations and serves as a prologue to future, more basic research, which appears vitally necessary.

We can now sum up everything presented above, drawing the following conclusions.

1. The genetic approach to the problem of population organization of species in fishes on the level of local stocks has permitted discovering systems of biochemical polymorphism and on this basis making a broad geno-geographic analysis of different species. It has become clear that local stocks of fishes represent reproductively isolated communities with a characteristic 189
internal heterogeneity.

2. The heterogeneity of stocks, observable irrespective of the ecological characteristics of the studied species, finds reflection in their subdivision into more elementary population units. They differ in their gene frequencies and, consequently, also are reproductively isolated groups, formally corresponding to the model of a "Mendelian population".

3. In the genetic investigation of the stock as a whole a correspondence of the natural picture to a mathematical model of a subdivided population is discovered. It has been shown that such a community remains stable in both time and space, in spite of simultaneous variability of the elementary populations included in its composition.

4. This new quality of a population aggregate, obviously not deducible from the properties of the components forming its structure, permits regarding local stocks as genetically stable population systems, opposing

them to elementary populations -- variable structural components of such systems. Traditional biological investigations support this conclusion.

5. Since the biologically important properties of populations are derived from their historically formed gene **pools**, the obtained data on qualitative differences in the genetic stability of different levels of the population hierarchy permit formulating a single principle of management of a rational fishing industry, based on approach to the population system as a whole -- to distribute the corresponding efforts over all the components of its structure.

6. The existence of population systems in nature permits estimating in a new way the biological importance of the processes of intraspecies genetic divergence, regarding them as an adaptive strategy which permits the species to remain itself in normally fluctuating environmental conditions.

7. On the basis of the real existence in species not only of polymorphous but also genetically monomorphous properties, it is argued that it is possible to treat species formation, not as a continuous process proceeding on the population level, but as a result of qualitative reorganizations of the genome conjugated with the reproductive isolation of separate individuals.

Appendix 1. Systems of genetic polymorphism of erythrocytic antigens and various proteins of fishes

Приложение 1. Системы генетического полиморфизма эритроцитарных антигенов и различных белков у рыб

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Clupeiformes	Clupeidae	Clupea harengus	1 Лактатдегидрогеназа мышц, 2 локуса—*A* и *B*	2 в локусе *A*, + 4 в локусе *B* *	*AABB*, *AA'BB*, *AABB'*, *AAB'B'*, *AABB''*, *AABB''*	a Электрофорез (Э/ф) в крахмальном геле	Odense et al., 1966a, б; 1969
				2 в локусе *A* 3 в локусе *B*	*AABB*, *AA'BB*, *AAB'B* *AAB'B'*, *AABB''*	b Э/ф в крахмально-агаровом геле	Naevdal, 1969
			2 Аспартатаминотрансфераза печени, 2 локуса—*M* и *S*	3 в локусе *S*	*SS*, *SS'*, *S'S'*, *SS''* и S_x (отсутствие активности) **	a Э/ф в крахмальном геле	Odense et al., 1966a, б; 1969;
				2 в локусе *S*	*SS*, *SS'*	b Э/ф в крахмально-агаровом геле	Naevdal, 1969a;
				То же *	*SS*, *SS'*	a Э/ф в крахмальном геле	Schmidke a. Engel, 1972
			3 Эстераза сыворотки крови, 4 локуса	2 в локусе *m* 5 в локусе *F* и *S*	*mm*, *mm'*, *m' m'* F_1M, F_1F_1, *MM*, MS_1, MS_2, F_2F_2, F_2M, F_1F_2	b Э/ф в крахмально-агаровом геле	Naevdal, 1969a, в
				3	*fm*, *fs*, *mn*, *ms*, *ss*	a Э/ф в крахмальном геле	Ridgway et al., 1970
			4 Альбумины сыворотки крови	2	*Alb FF*, *Alb FS*, *Alb SS*	b Э/ф в крахмально-агаровом геле	Naevdal, 1969 в
			5 Трансферрины сыворотки крови	2	*Tf AA*, *Tf AB*, *Tf BB*	То же *	Он же *
			6 Фосфоглюкомутаза мышц, 2 локуса	in one locus 3 в одном локусе	*FF*, *FM*, *MM*, *MS*, *SS*, *FS*	b Э/ф в крахмально-агаровом геле	Lush, 1969
			7 *A*—система групп крови	3	A_1, A_2, A_0	c Гемагглютинация с нормальными и иммунными антителами	d Алтухов, Трувеллер и др., 1968
			8 Изоцитратдегидрогеназа, 2 локуса	2 в локусе *S* 2 в локусе *M*	*AA*, *AA'*, *A' A'* То же	a Э/ф в крахмальном геле То же *	Wolf et al., 1970
			9 Сорбитолдегидрогеназа	3	Фенотипы не обозначены ***	То же *	Engel et al., 1970
		Clupea pallasi	10 Глюкозо-6-фосфатдегидрогеназа эритроцитов, 3 локуса	2 в локусе *I* 3 в локусе *III*	*AA*, *AB*, *BB*, *AC*	e Э/ф в акриламидном геле	f Салменкова и Волохонская, 1973
			11 6-Фосфоглюконатдегидрогеназа	2	*FF*, *FS*, *SS*	То же *	То же *

\+ - in locus

** - absence of activity

*** - Phenotypes not designated

Appendix I (Page 2)

Продолжение прилож. 1

Отряд A	Семейство B	Вид C	Исследованный локус D	Число аллелей E	Фенотипы (генотипы), найденные в популяциях F	Метод G	Источник H
Clupeiformes	Clupeidae	Clupea pallasi	12 Миогены, ~10 локусов	По 2 в двух локусах	*AA, AB, BB* e	Э/ф в акриламидном геле f	Салменкова и Волохонская, 1973
			13 Эстераза, 2 локуса в сыворотке 3 локуса в мышцах 14	По 4 в каждом локусе По 4 в *I* и *III* локусах.	Фенотипы не обозначены *	** То же *	Те же *
		Sardinops caerulea	15 *C*-система групп крови	2	C_1, C_2 $C-$ g	Нормальная овечья сыворотка, иммунная сыворотка цыпленка	Sprague a. Vrooman, 1962
			16 *B*-система групп крови	3	*B, BI, I, Bi*, «——». h	Иммунные сыворотки крупного рогатого скота, утки и цыпленка	Vrooman, 1964
		Sprattus sprattus	Гемоглобин 17	3	*HbI*-1, *HbI*-2, *HbI*-3, *HbI*-1-2; *HbI*-2-3, *HbI*-1-3	i Э/ф в агаровом геле	Naevdal, 1967, 1968, 1970
			Трансферрин 18	2	*TfAA, TfAB, TfBB*	То же *	Те же *
			Сывороточная эстераза 19	2	EsS_1S_1, $Es\,S_1\,S_2$, EsS_2S_2	b Э/ф в крахмально-агаровом геле	Naevdal, 1967, 1969
	Salmonidae	Salvelinus alpinus	Сывороточная эстераза 19	2	*FF, FS, SS*	aЭ/ф в крахмальном геле	Nyman, 1967
		Salvelinus fontinalis	Лактатдегидрогеназа, 5 локусов 20	3 в локусе *B* 2 в локусе *A* 2 в локусе *C*	*BB, BB′, B′ B′, B″ B″, B′ B″, BB″* *AA, AA″* *CC, CC′*	j Э/ф в акриламидном и крахмальном геле	Goldberg, 1966; Morrison a. Wright, 1966; Wright a. Atherton, 1968, 1970; Wright a. Atherton, 1970
			Сывороточный трансферрин 21	3	*AA, AB, BB, CC, AC, BC* e	Э/ф в акриламидном геле	Wright a. Atherton, 1970
			Гексозо-6-фосфатдегидрогеназа 22	7	16 фенотипов phenotypes	То же *	Stegman a. Goldberg, 1971, 1972
		Salmo gairdnerii	Тетразолиевая оксидаза, 3 локуса 23	3 в локусе *I*, 2 в локусе *II*	*AA, AB, BB, AC ff, fs, ss*	a Э/ф в крахмальном геле	Utter, 1971 Utter a. Hodgins, 1972; Cederbaum a. Joshida, 1972
			Лактатдегидрогеназа 24	2 в локусе *C* (печень) (liver)	*CC, CC′, C′ C′*	То же *	Williscroft a. Tsuyuki, 1970; Northcote et al., 1970

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Clupeiformes	Salmonidae	Salmo gairdneri	25 Малатдегидрогеназа, 2 локуса	2 в локусе *B*	*AA, AB, BB, BB', AB', B', B'*	a Э/ф в крахмальном геле	Bailey et al., 1969; Utter a. Hodgins, 1972; Numachi, 1972
			26 Фосфоглюкомутаза, 3 локуса	2 в одном локусе in one locus	*CC, BC, BB*	То же *	Roberts et al., 1969; Utter a. Hodgins, 1972
			27 *R*-система групп крови	3	*R*-1, *R*-2, *R*-1-2, *R*-0	k Иммунные сыворотки кролика	Sanders a. Wright, 1962
			28 Трансферрин сыворотки крови	2	*AA, AB, BB*	a Э/ф в крахмальном геле	Utter a. Hodgins, 1972
			29 α-Глицерофосфатдегидрогеназа, 3 локуса	по 2 в локусах *A* и *C*	*AA, AB, BB* *AA, AA', CC, CC', C' C'*	То же * »	Те же * Engel et al., 1971a
			30 Креатинкиназа, 3 локуса	2 в локусе *S*	3 фенотипа 3 phenotypes	»	Perriard et al., 1972
			31 Изоцитратдегидрогеназа, 3 локуса	2 в локусе *M* 4 в локусе *S*	*AB, ABB', AB'* 9 фенотипов 9 phenotypes	» »	Wolf et al., 1970 Те же
			32 Сорбитолдегидрогеназа	2	*AAAA, AAAA', AA', A' A*	»	Engel et al., 1970
		Salmo trutta	33 Сорбитолдегидрогеназа, 2 локуса	2 в локусе *A*	*AB, AA' B, A' B*	»	Те же *
			29 α-Глицерофосфатдегидрогеназа, 3 локуса	2 в локусе *B*	*BB, BB', B' B'*	»	Engel et al., 1971a
			34 *B*-система групп крови	3	*B*-1; *B*-2; *B*-1, 2; *B*-0	k Иммунные сыворотки кролика	Sanders a. Wright, 1962
		Salmo salar	Трансферрин 18	2	*AA, AC, CC*	b Э/ф в крахмально-агаровом геле	Möller, 1970
		Salvelinus malma	Трансферрин 18	4	8 фенотипов 8 phenotypes	a Э/ф в крахмальном геле	Payne et al., 1971
			Сывороточные альбумины 35	2	*F, FS, SS*	i Э/ф в агаровом геле	f Салменкова и Волохонская, 1973
			23 Тетразолиевая оксидаза	2	*FF, FS, SS*	e Э/ф в акриламидном геле	Те же *

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Clupeiformes	Salmonidae	Salvelinus leucomaenis	35 Сывороточный альбумин	2	*C, CD, DD*	i Э/ф в агаровом геле	Payne et al., 1971 f Салменкова и Волохонская, 1973
			23 Тетразолиевая оксидаза	2	*FF, FS, SS*	e Э/ф в акриламидном геле	То же*
		Oncorhynchus nerka	24 Лактатдегидрогеназа	2 в локусе *B*	*BB, B′B′, BB′*	a Э/ф в крахмальном геле	Hodgins et al., 1969
			26 Фосфоглюкомутаза	2	*AA, AB, BB*	То же *	Utter a. Hodgins, 1970
			36 *A*-система групп крови	2	*AA, Aa, aa*	l Нормальная свиная сыворотка	Ridgway et al., 1959
		Oncorhynchus keta	24 Лактатдегидрогеназа, 8 локусов 8 loci	2 в локусе *A* 2 в регуляторном локусе для ЛДГ2 сыворотки	*AA, AA′, A′A′* *FF, FS, SS* in regulatory locus for serum Ldg	e Э/ф в акриламидном геле i Э/ф в агаровом геле	Алтухов и др. 1969, а,б; 1970 То же*
			25 Малатдегидрогеназа	3 в локусе *S*-МДГ3 in	*AA, AB, AC* locus of S-Mdg	e Э/ф в акриламидном геле	n Слынько, 1971 Numachi, 1972
			29 α-Глицерофосфатдегидрогеназа. 2 локуса	2 в одном локусе	*AA, AB, BB*	То же *	mАлтухов и др., 1972
		Oncorhynchus gorbuscha	37 Лактатдегидрогеназа сыворотки	2 в регуляторном локусе 2 in	*FF, FS, SS* regulatory locus	i Э/ф в агаровом геле	m Алтухов и др., 1969а, 1970
			25 Малатдегидрогеназа	3 в локусе *S*	*AA, AB, AC*	e Э/ф в акриламидном геле	n Слынько, 1971
			29 α-Глицерофосфатдегидрогеназа	2	*FF, FS, SS*	То же*	n Слынько, 1972
		Oncorhynchus kisutsch	18 Трансферрин, 1 локус	3	*AA, AB, BB, AC, BC, CC*	a Э/ф в крахмальном геле	Utter et al., 1970
			26 Фосфоглюкомутаза	2	*AA, AB, BB*	То же*	f Салменкова и Волохонская, 1973
		Oncorhynchus tschawytscha	25 Малатдегидрогеназа, 3 локуса	2 в локусе *S*-МДГ 2 in locus	*AA, AB, BB, B′B′ AB′, BB′* of S-Mdg		Bailey et al., 1969

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Clupeiformes	Coregonidae	Coregonus clupeaformis	24 Лактатдегидрогеназа, 4 локуса	2 в локусе *H*	*FF, FS, SS*	а Э/ф в крахмальном геле	Clayton a. Franzin, 1970
		Coregonus lavaretus	38 Глицерол-3-фосфатдегидрогеназа, 3 локуса	2 в локусе *A* и 3 в локусе *B*	14 фенотипов 14 phenotypes	То же *	Clayton et al., 1973
			39 Аспартатаминотрансфераза, 2 локуса	2 в одном локусе one	2 фенотипа 2 phenotypes	»	Schimdtke a. Engel, 1972
			40 Сорбитолдегидрогеназа	2	*AAAA, AAAA′, AAA′ A′*	»	Engel et al., 1970
	Osmeridae	Hypomesus olidus	41 Эстераза эритроцитов	4	5 фенотипов 5 phenotypes	е Э/ф в акриламидном геле	ƒ Салменкова и Волохонская, 1973
			42 Эстераза мышц, 3 локуса loci	4 в *I* локусе 2 в *III* локусе	6 6 фенотипов " 5 5 фенотипов "	То же* »	Те же* »
			26 Фосфоглюкомутаза	2	*AA, AB, BB*	»	»
			24 Лактатдегидрогеназа, 2 локуса	2 в локусе *B*	*BB, BB′, B′ B′*	»	»
			29 α-Глицерофосфатдегидрогеназа	3	*AA, AA′, A′ A′, AA″*	»	»
			25 Малатдегидрогеназа	2	*AA, AB, BB*	»	»
			11 6-фосфоглюконатдегидрогеназа	3	*FF, FM, MM, FS*	»	»
			23 Тетразолиевая оксидаза	2	*AA, AA′*	»	»
		Hypomesus pretiosus	43 Изоцитратдегидрогеназа, 2 локуса	2 в локусе *S ИДГ* 2 in locus of S-Idg	*FF,FS,SS*	а Э/ф в крахмальном геле	Quiroz—Guttierrez a. Ohno, 1970
		Osmerus eperlanus	29 α-Глицерофосфатдегидрогеназа, 3 локуса	По 2 в каждом локусе 2 in each locus	*AABC, AA′ BC, ABB′ C, ABCC′*	То же*	Engel et al., 1971, 6

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Clupeiformes	Engraulidae	Engraulis mordax	Лактатдегидрогеназа, 2 локуса *A* и *B* [24]	2 в локусе *A*	A^1A^1, A^1A^2, A^2A^2	а Э/ф в крахмальном геле	Klose et al., 1968; Ohno et al., 1968
		Engraulis encrasicholus	*A*-система групп крови [7]	3	A_1, $A_{1,2}$, A_2, A_0	о Нормальные лошадиная и свиная сыворотки, иммунная сыворотка кролика	р Алтухов, Лиманский и др., 1969 а
Cypriniformes	Catostomidae	Catostomus catostomus	Миогены [12]	2	*AA*, *AB*, *BB*	аЭ/ф в крахмальном геле	Tsuyuki et al., 1967
		Catostomus commersoni	Сывороточный трансферрин [21]	2	*AA*, *AB*, *BB*	То же *	Besmish a. Tsuyuki, 1971
		Catostomus clarkii	Сывороточная эстераза [19]	2	*Esl-a*, *Esl-b*, *Esl-ab*	»	Koehn a. Rasmussen, 1967
		Jctiobus cyprinellus	Сывороточный трансферрин [21]	2	*Tfa*, *Tfab*, *Tfb*	а Э/ф в крахмальном геле	Koehn a. Johnson, 1967
			Эстераза сыворотки [19]	2	*EsII-a*, *EsII-ab*, *EsII-b*	То же *	Те же *
	Cyprinidae	Alburnus lucidus	Сывороточная эстераза [19]	2	*FF*, *FS*, *SS*	»	Nyman, 1965, 1966
		Leuciscus rutilus (Rutilis rutilus)	То же same	2	*FF*, *FS*, *SS*	»	Тот же *
			6-Фосфоглюконатдегидрогеназа [11]	3	*A*, *A′*, *A″* *AA″*, *A′*, *A″*	»	Klose a. Wolf, 1970; Klose et al., 1969
			Аспартатминотрансфераза, 2 локуса *S* и *M* [39] and	3 в локусе *S*	*AA*, *AA′*, *A′A′*, *AA″*	»	Schmidtke a. Engel, 197
			R-система групп крови [27]	Нет данных	*R*+, *R*−	q Экстракт семян Vicia faba L.	r Балахнин и Потапов, 1963
			Сорбитолдегидрогеназа [40]	3	*AA*, *AA′*, *AA″*	а Э/ф в крахмальном геле	Engel et al., 1971б
			НАДФ-изоцитратдегидрогеназа, 4 локуса [44]	2 в локусе *S*	2 фенотипа 2 phenotypes	То же *	Те же *
		Tinca tinca	Сорбитолдегидрогеназа [40]	3	*AA*, *AA′*, *A′A′*, *AA″*	»	»

Продолжение прилож. I

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Cypriniformes	Cyprinidae	Tinca tinca	39 Аспартатаминотрансфераза, два локуса *S* и *M*	2 в локусе *S*	*AA*, *AA'*	а Э/ф в крахмальном геле	Schmidtke a. Engel, 1972
		Abramis blicca	19 Сывороточная эстераза	2	*SS*, *FS*	То же*	Nyman, 1969
		Barbus tetrazona	6-Фосфоглюконат-дегидрогеназа	3	*AA*, *BB*, *CC*, *AC*, *BC*	»	Bender a. Ohno, 1968
		Barbus barbus	11. 44 НАДФ-изоцитрат-дегидрогеназа, 4 локуса	2 в локусе *S*	2 фенотипа 2 phenotypes	»	Engel et al., 19716
		Carassius auratus	11 6-Фосфоглюконат-дегидрогеназа, 2 локуса—*A* и *B* loci and	3 в локусе *B*	AB^3/AB^3, AB^2/AB^2 AB^1/AB^2, AB^1/AB^3, AB^2/AB^3	»	Те же
			40 Сорбитолдегидрогеназа	2	S^A/S^A, S^A/S^B S^B/S^B	»	Chyi-chyang Lin et al., 1969
			44 НАДФ-изоцитрат-дегидрогеназа, 4 локуса	2 в локусе *S*-JDH-2	JDH-2 *aa*, JDH-2 *ab*, JDH-2-*bb*	»	Quiroz-Gutierrez a. Ohna, 1970
			45 Система групп крови	Нет данных No data	Шесть феногрупп, выявляемых путем абсорбции Six phenotypes determined by absorption	s Изоммунная сыворотка	Hildemann, 1956
		Cyprinus carpio	46 Сывороточные трансферрины	3	6 фенотипов 6 phenotypes	а Э/ф в крахмальном геле	Creyssel et al., 1964, 1966
			44 НАДФ-изоцитрат-дегидрогеназа, 4 локуса	3 в локусе *S*-JDH-I 2 в локусе *S*-JDH-II	Three phenotypes	То же*	Quiroz-Gutierrez a. Ohno, 1970
			39 Аспартатаминотрансфераза, 2 локуса *A* и *B* and	3 в локусе *A*	Три фенотипа *AB*, *AA'B*, *AA"B*	»	Schmidtke, Engel, 1972
		Rhinichthys cataractae	24 Лактатдегидрогеназа, 2 локуса *M* и *H* loci and	2 в локусе *M*	*MM*, *MM'*	»	Clayton a. Gee, 1969

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Cypriniformes	Cyprinidae	Pseudorasbora parva	Лактатдегидрогеназа, 2 локуса 24	2 в локусе *A*	*N*, *I*, *E* 3 ~~phenotypes.~~	a Э/ф в крахмальном геле	Numachi, 1972 б
	Amiuridae	Ictalurus nebulosus	Гемоглобин 17	2	3 фенотипа	То же*	Callegarini, 1966
			Система групп крови 45	3	1; 2; 1—2, «—»	t Изоагглютинация	Cushing a. Durall, 1957
Characiniformes	Characinidae	Astyanax mexicanus	α-Глицерофосфатдегидрогеназа 29	4	Не указаны Not indicated	a Э/ф в крахмальном геле	Avise a. Selander, 1972
			Пептидаза 47	2	»	То же*	Те же*
			6-Фосфоглюконатдегидрогеназа 48	2	»	»	»
			Фосфоглюкомутаза 26	6	»	»	»
			Фосфогексозоизомераза, 2 локуса 49	3 в локусе *I*	»	»	»
				6 в локусе *II*	»	»	»
			Аспартатаминотрансфераза 39	3 в локусе 1	»	»	»
				4 в локусе 2	»	»	»
			Эстераза, 3 локуса 13	2 в локусе 1	»	»	»
				4 в локусе 2		»	»
				7 в локусе 3	»	»	»
			Малатдегидрогеназа, 2 локуса 25	2 в локусе 1	»	»	»
			Изоцитратдегидрогеназа 31	3	»	»	»
			Лактатдегидрогеназа, 2 локуса 24	3 в локусе 1	»	»	»
				2 в локусе 2			
Anguilliformes	Anguillidae	Anguilla anguilla	Сывороточный трансферрин 46	3	*A*, *B*, *AB*, *AC*, *BC*	a Э/ф в крахмальном геле	Fine et al., 1964
				4	7 фенотипов	u Э/ф на бумаге и в крахмальном геле	Drilhon et al., 1966; Fine et al., 1966
			Эстераза 13	2	~~Phenotypes not~~ Фенотипы не обозначены designated	a Э/ф в крахмальном геле	Pantelouris a. Payne, 1968
		Anguilla rostrata	Гемоглобин 17	2	3 фенотипа 3 phenotypes	i Э/ф в агаровом геле	Sick et al., 1967
Gadiformes	Gadidae	Gadus morhua	Гемоглобин, 2 локуса 17	2 в локусе *I*	HbI-1, HbI-2, HbI-1-2	То же*	Sick, 1961
			Сывороточный трансферрин 46	5	*A*, *B*, *C*, *AB*, *BC*, *AC*, *AD*, *BD*, *CD*, C_1C	b Э/ф в крахмально-агаровом геле	Möller, 1966a, Möller a. Naevdal, 1967a, b
			Сывороточный альбумин 35	2	3 фенотипа, не обозначенные автором 3 phenotypes not designated by author	a Э/ф в крахмальном геле	Nyman, 1965/66
				2	То же*	i Э/ф в агаровом геле	Ulrich, 1968

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Gadiformes	Gadidae	Gadus morhua	Лактатдегидрогеназа, предполагается 5 локусов предполагается 3 локуса [50]	4 в локусе *B* 2 в локусе *H* (соответствует *B*)	*BB, B′ B′, BB′, BB″ BB‴* *FF, FS, SS* (corresponds to)	a Э/ф в крахмальном геле То же *	Odense et al., 1969 Lush, 1970
		Gadus pollachius	Сывороточный трансферрин [46] Гемоглобин 17	2 2	*AA, AB, BB* *HbI-1, HbI-1-2*	b Э/ф в крахмально-агаровом геле i Э/ф в агаровом геле	Möller et al., 1966; Möller a. Naevdal, 1968
		Gadus virens	Гемоглобин 17	2	*HbI-1, HbI-1-2*	То же *	Те же *
			Сывороточный трансферрин [46]	3	*AA, AB, AA′*	b Э/ф в крахмально-агаровом геле	Möller et al., 1966; Möller a. Naevdal, 1966 в
		Gadus merlangus	Сывороточный трансферрин [46] Гемоглобин 17	2 2	*A, B, AB* *HbI-1, HbI-1-2, HbI-2*	То же * i Э/ф в агаровом геле	Möller et al., 1966; Sick, 1961
		Gadus aeglefinus	Гемоглобин 17	2	*HbI-1, HbI-1-2*	То же *	Möller a. Naevdal, 1968
			Сывороточный трансферрин [46]	3	*IV, III, II, II—III, II—IV, III—IV*	b Э/ф в крахмально-агаровом геле	Möller et al., 1966
		Gadus potassou	Гемоглобин 17	2	*HbI-2, HbI-1-2*	i Э/ф в агаровом геле	Möller a. Naevdal, 1968
		Molva molva	»	2	*HbI-1, HbI-1-2, HbI-2*	То же *	Те же *
		Molva byrkelang	»	2	То же*	»	»
		Brosme brosme	»	2	»	»	»
		Merluccius bilinearis	Лактатдегидрогеназа [24]	2 в локусе *B*	*BB, BB′*	aЭ/ф а крахмальном геле	Markert a. Faulhaber, 1965
		Merluccius productus	То же	2 в локусе *A*	*AA, A′ A′, A′ A*	То же *	Utter a. Hodgins, 1969a
			same Сывороточный трансферрин [46]	4	*AA, BB, AB, AC, BC, AD*	»	Utter, 1969
			Многены 12	2	*AA, BB, AB*	»	Utter a. Hodgins, 1969

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Gadiformes	Gadidae	Merluccius productus	Эстераза, 3 локуса [13]	2 в *EsI* 2 в *EsIII* 5 в *EsII*	*EsI-b, EsI-d, EsI-bd* То же *bb, dd, cc, bd, bc, cd, ab, ad, ae, be, de*	a Э/ф в крахмальном геле » »	Utter et al., 1970 » »
Beloniformes	Scombere-socidae	Cololabis saira	Малатдегидрогеназа, 2 локуса—*A* и *B* [25]	2 в локусе *B*	*N, S, NS*	»	Numachi, 1970
Perciformes	Percidae	Acerina cernua	Сывороточная эстераза [19]	2	*FF, FS, SS*	»	Nyman, 1965, 1966, 1969
		Stizostedion vitreus	Миогены [12]	2	*A, B, AB*	»	Uthe et al., 1966
			Малатдегидрогеназа, 3 локуса [25]	3 в локусе *C*	C^1C^1, C^1C^2, C^1C^3, C^2C^2, C^2C^3, C^3C^3	»	Clayto et al., 1971
	Gobiidae	Gobius jozo	Гемоглобин [17]	3	6 фенотипов 6 phenotypes	»	Raunich et al., 1966a; Raunich et al., 1967
	Cybiidae	Sarda chiliensis	Трансферрин [18]	2	*FF, GG, FG*	»	Barret a. Williams, 1967
	Scorpaenidae	Sebastes mentella	Сывороточный альбумин [35]	2	*AA, AB, BB*	i Э/ф в агаровом геле	Altukhov a. Nefyodov, 1967
			Сывороточный гаптоглобин [51]	3	*A, AB, B, O*	a Э/ф в крахмальном геле	Nefyodov, 1971
			A-система групп крови [7]	2	A_1, A_2	k Иммунные сыворотки кролика	Sindermann, 1961a
		Sebastes marinus	Сывороточный альбумин [35]	2	*AA, AB, BB*	i Э/ф в агаровом геле	Altukhov a. Nefyodov, 1967
			Сывороточный гаптоглобин [51]	3	*A, AB, B, O*	a Э/ф в крахмальном геле	Nefyodov, 1971
		Sebastodes crameri	Гемоглобин [17]	2	*A, B, AB*	То же	Westrheim a. Tsuyuki, 1967
	Anoplopomi-dae	Anoplopoma fimbria	Миогены [12]	2	*A, B, AB*	»	Tsuyuki a. Roberts, 1969

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Perciformes	Cottidae	Myoxocephalus quadricornis	Пероксидаза [52]	2	*F, S, FS*	a Э/ф в крахмальном геле	Nyman a. Westin, 1968
	Scombridae	Scomber scomber	Сывороточная эстераза [19]	6	24 фенотипа 24 phenotypes	v Э/ф в крахмальном и крахмально-агаровом гелях	Jamieson et al., 1971
	Zoarcidae	Zoarces viviparus	Фосфоглюкомутаза, 3 локуса [26]	3 в *I* локусе	1^1, 1^{1+2}, 1^2 1^{1+3}, 1^{2+3}	a Э/ф в крахмальном геле	Hjorth, 1971
			Эстераза, 3 локуса [13]	2 (3) в *I* локусе, 2 во *II* локусе	Фенотипы не обозначены Phenotypes not designated 1—1, 1—2, 2—2	То же * »	Simonsen, Frydenberg, 1972
	Thunnidae	Thunnus obesus	Эстераза сыворотки [19]	3	E^b_{1-2}, E^b_{2-2}, E^b_{2-3}, E^b_{3-3}, E^b_0	»	Sprague, 1967
			То же	2	E_{bb} 1—1, E_{bb} 1—2	»	Fujino a Kang, 1968a
			АВО—система групп крови [53]	3	*A, B, AB, O*	w Нормальные сыворотки АВО—системы групп крови человека	Sprague et al., 1962
		Thunnus maccoyii	Эстераза сыворотки [19]	4	E^{bf}_0, E^{bf}_{1-2}, E^{bf}_{2-2}, E^{bf}_{2-3}, E^{bf}_{3-3}, E^{bf}_{3-4}	a Э/ф в крахмальном геле	Sprague, 1967
			Трансферрин [18]	2	2 фенотипа 2 phenotypes	То же *	Fujino a. Kang, 1968в
		Thunnus albacares	Эстераза сыворотки [19]	2	E^y_{2-2}, B^y_{2-3}	»	Sprague, 1967; Fujino a. Kang, 1968a
			Трансферрин [18]	2	*AA, BB, AB*	»	Barrett a. Tsuyuki, 1967
			То же	3	5 фенотипов 5 phenotypes	»	Fujino a. Kang, 1968a
			β-Глобулин [54]	2	3 фенотипа 3 phenotypes	»	Sprague a. Fujino, 1968
		Thunnus thynnus	Тетразолиевая оксидаза [23]	2	*FF, FS, SS*	»	Edmunds a. Simmons, 1971
		Thunnus alalunga	Трансферрин [18]	3	6 фенотипов, не обозначены 6 phenotypes, not designated	»	Barett a. Tsuyuki, 1967

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	Фенотипы (генотипы), F найденные в популяциях	G Метод	H Источник
Perciformes	Thunnidae	Thunnus alalunga	Эстераза сыворотки 19	2 in Pacific 2 в Пацифике 3 в Атлантике 3 in Atlantic	1—2, 2, 2—3	а Э/ф в крахмальном геле	Fujino a. Kang, 1968a
			Tg-система групп крови 55	3	*Tg*-1, *Tg*-2, *Tg*-1-2, *Tg*-0, *Tg*-1-3, *Tg*-1-2-3	x Иммунные сыворотки кролика, экстракты семян Lablab vulgaris, Virgiria divaricata, Gingko biloba, Glicine max Нормальные сыворотки рыб Eumakaria nigra, Marlina marlina	Suzuki, 1961, 1962, 1968, 1967 Suzuki et al., 1959
		Paratunnus mebachii	*Tg*-система групп крови 55	3	4 фенотипа 4 phenotypes	k Иммунная сыворотка кролика	Suzuki, 1961, 1962
			X-система групп крови 56	Полиалельная	Девять феногрупп 9 phenotypes	y Экстракты семян Lablab vulgaris, Venerupis semidecuscata Нормальные сыворотки Eumakaria nigra, Marlina marlina	Suzuki, 1961, 1962, 1967
		Katsuwonus pelamis	Эстераза сыворотки 19	3	E^1_{sy}, E^2_{sy}, E^3_{sy}, E^{1-2}_{sy}, E^{1-3}_{sy}, E^{2-3}_{sy}	а Э/ф в крахмальном геле	Fujino a. Kang, 1968b
			β-Глобулин 54	2	3 фенотипа 3 phenotypes	То же *	Sprague a. Fujino, 1965
			Трансферрин 18	3	*CC*, *DD*, *EE*, *CD*, *CE*, *DE*	»	Barrett a. Tsuyuki, 1967
			То же	3	T^1_{sf}, T^2_{sf}, T^3_{sf}, T^{1-2}_{sf}, T^{1-3}_{sf}, T^{2-3}_{sf}	»	Fujino a. Kang, 1968a
			Эстераза сыворотки, 19 3 локуса	7 (1 нулевой) в локусе *E*Ib 4 в локусе *E*III	Нет данных No data *E*III-1, *E*III-2, *E*III-3, *E*III-4	» »	Mc Cabe a. Dean, 1970
			6-Фосфоглюконат-дегидрогеназа 48	4	*AA*, *AB*, *AC*, *AD*	»	Mc Cabe et al., 1970
			α-Глицерофосфат-дегидрогеназа 29	3	*AA*, *AB*, *AC*	»	Те же*

Продолжение прилож. 1

A Отряд	B Семейство	C Вид	D Исследованный локус	E Число аллелей	F Фенотипы (генотипы), найденные в популяциях	G Метод	H Источник
Perciformes	Thunnidae	Katsuwonus pelamis	16 *B*-система групп крови	*E*, K_1, K_2	E^+, E^- K_1, K_2 «—»	z Экстракт семян Virgiria sp., иммунная сыворотка кролика	Sprague a. Holloway, 1962
			57 *y*-система групп крови	Полиаллельна Polyallele	15 фенотипов 15 phenotypes	То же*	Fujino a. Kazama, 1968
Cyprinodontiformes	Cyprinodontidae	Fundulus heteroclitus	24 Лактатдегидрогеназа, 3 локуса *A*, *B*, *E*	2 в локусе *E*, 2 в локусе *B*, 2 аллеля в локусе *A*	*E*, EE^1—два фенотипа, не обозначенные автором, *BB*, *BB′*, *B′ B′*, *AA*, *AA′*	aэ/ф в крахмальном геле 2 phenotypes not designated by author	Whitt, 1970a; Massaro a. Booke, 1972
			25 Малатдегидрогеназа	2 аллеля	3 фенотипа	То же *	Whitt, 1970в
			Эстераза 13	3 в локусе *Es2*	3 phenotypes То же *	»	Holmes a. Whitt, 1970
	Poeciliidae	Poeciliopsis monacha	24 Лактатдегидрогеназа, 3 локуса	2 в локусе *E*	*EE*, *EE′*, *E′ E′*	»	Vrijenhoek, 1972
		Poeciliopsis lucida	То же	То же	*EE*, *EE″*, *E″ E″*	»	То же
Pleuronectiformes	Pleuronectidae	Pleuronectes flesus	58 Плазменная эстераза	Полиаллельный локус Polyallele locus	*H*,*L*, *HL*, *LO*, *HO*, *GL*, *CL*, *CH*	»	de Ligny, 1968
		Pleuronectes platessa	То же*	То же *	*TN*, *TN*, *GL*	»	То же*
			21 Сывороточные трансферрины	»	*F*, *S*, *M*, *FS*, *FM*, *SM*	»	de Ligny, 1966
		Hypoglossus stenolepis	То же *	4	*AA*, *BB*, *CC*, *AB*, *AC* *BC*, *AD*, *BD*	»	Tsuyuki et al., 1969
Selachiiformes	Squalidae	Squalus acanthias	59 *S*-система групп крови	3	*S*-i, *S*-2, *S*-1-2, *S*-0	aa Изоагглютинация, иммунная сыворотка кролика	Sindermann a. Mairs, 1961
	Rajidae	Raja ocellata	60 *SK*-система групп крови	3	SK_a, SK_b, SK_o	bb Изоагглютинация	Sindermann a. Honey, 1964

Appendix 1. Key

A - Order B - Family C - Species D - Investigated locus E - Number of alleles F - Phenotypes (genotypes) found in populations G - Method H - Source * - The same

1 - Muscle lactate dehydrogenase, 2 loci -- A and B
2 - Liver aspartate aminotransferase, 2 loci -- M and S
3 - Blood serum esterase, 4 loci
4 - Blood serum albumins
5 - Blood serum transferrins
6 - Muscle phosphoglucomutase, 2 loci
7 - A system of blood groups
8 - Isocitrate dehydrogenase, 2 loci
9 - Sorbitol dehydrogenase
10 - Erythrocytic glucose-6-phosphate dehydrogenase, 3 loci
11 - 6-Phosphogluconate dehydrogenase
12 - Myogens, about 10 loci
13 - Esterase, (2 loci in serum)
14 - 3 loci in muscles
15 - C system of blood groups
16 - B system of blood groups
17 - Hemoglobin
18 - Transferrin
19 - Serum esterase
20 - Lactate dehydrogenase, 5 loci
21 - Serum transferrin
22 - Hexose-6-phosphate dehydrogenase
23 - Tetrazole oxidase, 3 loci
24 - Lactate dehydrogenase
25 - Malate dehydrogenase, 2 loci
26 - Phosphoglucomutase, 3 loci
27 - R system of blood groups
28 - Blood serum transferrin
29 - alpha-Glycerophosphate dehydrogenase, 3 loci
30 - Creatine kinase, 3 loci
31 - Isocitrate dehydrogenase, 3 loci
32 - Sorbitol dehydrogenase
33 - Sorbitol dehydrogenase, 2 loci
34 - B system of blood groups
35 - Serum albumin(s)
36 - A system of blood groups
37 - Serum lactate dehydrogenase
38 - Glycerol-3-phosphate dehydrogenase, 3 loci
39 - Aspartate aminotransferase, 2 loci
40 - Sorbitol dehydrogenase
41 - Erythrocytic esterase
42 - Muscle esterase
43 - Isocitrate dehydrogenase, 2 loci
44 - NADP-isocitrate dehydrogenase, 4 loci
45 - Blood group system

Appendix 1. Key (Continued)

46 - Serum transferrins
47 - Pentidase
48 - 6-Phosphogluconate dehydrogenase
49 - Phosphohexose isomerase, 2 loci
50 - Lactate dehydrogenase, 5 loci assumed, 3 loci assumed (corresponds to H)
51 - Serum haptoglobin
52 - Peroxidase
53 - ABO system of blood groups
54 - beta-Globulin
55 - Tg system of blood groups
56 - X system of blood groups
57 - y system of blood groups
58 - Plasma esterase
59 - S system of blood groups
60 - SK system of blood groups

a - Starch-gel electrophoresis
b - Starch-agar-gel "
c - Hemagglutination with normal and immune antibodies
d - Altukhov, Truveller et al., 1968
e - Acrylamide-gel electrophoresis
f - Salmenkova and Volokhonskaya
g - Normal sheep serum and immune chick serum
h - Immune serums of cattle, duck and chick
i - Agar-gel electrophoresis
j - Acrylamide-gel and starch-gel electrophoresis
k - Immune rabbit serums
l - Normal hog serum
m - Altukhov et al.,
n - Slynko,
o - Normal horse and hog serums, immune rabbit serum
p - Altukhov, Limanskii et al.,
q - Extract of seeds of Vicia faba L.
r - Balakhnin and Potapov,
s - Immune /literally "isommune"/ serum
t - Isoagglutination
u - Paper and starch-gel electrophoresis
v - Starch- and starch-agar gel electrophoresis
w - Normal serums of ABO system of blood groups of man
x - Immune rabbit serums, extracts of seeds of Lablab vulgaris, Virgiria divaricata, Gingko biloba and Glicine max. Normal serums of the fishes Eumakaria nigra and Marlina marlina
y - Extracts of seeds of Lablab vulgaris and Venerupis semidecuscata. Normal serums of Eumakaria nigra and Marlina marlina
z - Extract of seeds of Virgiria sp., immune rabbit serum
aa - Isoagglutination, immune rabbit serum
bb - Isoagglutination

Appendix 2. Genetic monomorphism in natural populations of different species

Приложение 2. Генетический мономорфизм в природных популяциях различных видов

	a Исследованные виды	b Исследованные белки	c Географическая локализация проб	d Число исследованных особей	e Метод	f Источник
1	Насекомые *Drosophila pseudoobscura*	Глюкозо-6-фосфатдегидрогеназа; α-глицерофосфатдегидроназа и др.	Флагстафф (Аризона); Мазер, Вилдроуз, Беркли (Калифорния); Кимаррон (Колорадо); Богота (Колумбия)	43 линии по 15—20 особей из каждой	Электрофорез в крахмальном геле	Hubby a. Lewontin, 1966; Lewontin a. Hubby, 1966
2	Моллюски *Anadara trapezia*	Гемоглобин[1]	Побережье Австралии; 7 популяций, удаленных друг от друга на сотни миль	1224	Электрофорез в целлюлозно-ацетатных мембранах	Nicol a. O'Gower, 1967; O'Gower a. Nicol, 1968
3	*Unio pictorum*	Миогены	Реки: Ока, Рожая, Истра, Каширка, Медведица, Днепр	217	Электрофорез в крахмальном и полиакриламидном гелях	Логвиненко и Кодолова, 1971 а, б
4	*Unio tumidus* *Anodonta piscinalis*	То же same »	То же »	232 265	То же »	Они же same »
5	Ракообразные *Mysis relicta*	Эстераза	Два озера в Швеции	430	Электрофорез в крахмальном геле	Fürst a. Nyman, 1969
6	Рыбы *Anguilla*	Гемоглобин[1]	Воды Дании, Швеции, Греции; разные локальности в Северной Америке	1514	Электрофорез в агаровом геле	Sick et al., 1962, 1967
7	*Oncorhynchus nerka*	Миогены, гемоглобины	Более 25 локальностей из разных рек Северной Америки и Азии, включая полностью изолированные популяции; практически весь ареал вида	>1000	Электрофорез в агаровом и крахмальном гелях	Ridgway, 1951; Tsuyuki a. Roberts, 1966, Tsuyuki et al., 1965a, в; 1966; Yamanaka et al. 1965a, в; 1967. Наши данные
8	*Oncorhynchus gorbuscha*	Гемоглобины	Популяции рек Сахалина, Камчатки, Курильских островов, Японии — практически весь ареал вида	>1000	Электрофорез в агаровом, крахмальном и акриламидном гелях	Наши данные Tsuyuki et al., 1965a, в; 1966; Tsuyuki a. Roberts, 1966; Yamanaka et al., 1965a, в; 1967.
		Лактатдегидрогеназа сыворотки крови[2]	Популяции рек Сахалина, Камчатки, Курильских островов	>900	Электрофорез в агаровом и акриламидном гелях	Алтухов и др., 1970
9	*Oncorhynchus keta*	Гемоглобин	Популяции рек Сахалина, Камчатки, Курильских островов, Японии, Северной Америки — практически весь ареал вида	>1000	Электрофорез в агаровом, крахмальном и акриламидном гелях	Наши данные, Tsuyuki et al., 1965a, в; 1966; Yamanaka et al., 1967
		Лактатдегидрогеназа сыворотки крови[2]	Популяции рек Сахалина Камчатки, Курильских островов	>3000	То же	Наши данные

Appendix 2. (Page 2)

Продолжение прилож. 2

	a Исследованные виды	b Исследованные белки	c Географическая локализация проб	d Число исследованных особей	e Метод	f Источник
10	*Gadus morhua*	Гемоглобины[1]	Десятки популяций в Северной Атлантике—практически весь ареал вида	>10 000	Электрофорез в агаровом геле	Sick, 1965a, в; Frydenberg et al., 1965; Möller, 1968; de Ligny, 1969
11	*Catostomus insignis, C. bernardini, C. latipinnis, C. tahoensis, C. macrocheilus; C. ardens*	Эстераза[3] сыворотки крови	11 локальностей в связанных и разобщенных притоках системы р. Колорадо	Несколько сотен	Электрофорез в крахмальном геле	Koehn a. Rasmussen, 1967
12	Амфибии *Acris crepitans*	Альбумин крови, гемоглобин, глобиновый полипептид № 4	27 локальностей в Северной Америке	392 299	То же	Dessauer a. Nevo, 1969
13	*Desmognatus*, четыре вида саламандр	Гемоглобин	15 локальностей в Северной Америке	190	»	Schontz, 1968
14	Рептилии Несколько видов сем. Iguanidae	Лактатдегидрогеназа эритроцитов, гемоглобин	9 островов в Карибском море, Антильские острова, южная часть Северной Америки, Южная Америка	281	»	Gorman a. Dessauer, 1965, 1966
15	Птицы. Представители разных отрядов	Кристаллины, миогены, гемоглобин, альбумины	Нет данных[4]	Нет данных	Электрофорез в агаровом и крахмальном гелях	Gysels, 1963; Manwell et al., 1963; Beckman, Nilson, 1965
16	Млекопитающие Mus musculus, 23 вида летучих мышей сем. Emballonuridae, Natalidae, Phyllostomatidae и др.	6-Фосфоглюконатдегидрогеназа Гемоглобин	Нет данных Более 60 точек ареала	>1000 >200	Электрофорез в крахмальном геле Электрофорез в крахмальном геле; фингерпринт	Ohno, 1970 Mitchill, 1970; Manwell a. Kerst, 1965
17	*Homo sapiens*	Карбоангидраза II эритроцитов	Разные популяции европеоидов и негроидов	Несколько сотен	Электрофорез в крахмальном геле	Taschian et al., 1968; Brewer a. Sing, 1969.
		Диафораза эритроцитов	То же	То же	То же	Brewer et al., 1967; Brewer a. Sing. 1969.
		Гексокиназа эритроцитов	»	»	»	Eaton et al., 1966; Brewer et al., 1967; Brewer a. Sing. 1969

[1] Второй локус полиморфен.

[2] Наблюдается полиморфизм по гену-регулятору (Алтухов и др., 1970).

[3] Константно поддерживается генотип, тождественный гетерозиготе в близкородственном полиморфном виде.

[4] В этих работах указания на отсутствие индивидуальных вариаций содержатся лишь в тексте.

Appendix 2. Key

a - Investigated species b - Investigated proteins c - Geographical localization of samples d - Number of investigated individuals e - Method f - Source

1a - Insects 1b - Glucose-6-phosphate dehydrogenase; alpha-glycerophosphate dehydrogenase, etc. 1c - Flagstaff, Arizona; Maser, Wildrose and Berkeley, California; Cimarron, Colorado; Bogota, Colombia 1d - 43 lines on 15-20 individuals from each 1e - Starch-gel electrophoresis

2a - Molluscs 2b - Hemoglobin (second locus is polymorphous) 2c - Coast of Australia, 7 populations hundreds of miles apart 2d - Cellulose-acetate membrane; electrophoresis

3b - Myogens 3c - Rivers: Oka, Rozhaya, Istra, Kashirka, Medveditsa and Dnepr 3e - Starch- and polyacrylamide-gel electrophoresis 3f - Logvinenko and Kodolova

5a - Crustacea 5b - Esterase 5c - Two lakes in Sweden 5e - Starch-gel electrophoresis

6a - Fishes 6b - Hemoglobin (second locus is polymorphous) 6c - Waters of Denmark, Sweden and Greece; various localities in North America 63 - Agar-gel electrophoresis

7b - Myogens and hemoglobins 7c - More than 25 localities from various rivers of North America and Asia, including completely isolated populations; practically all the range of the species 7e - Agar- and starch-gel electrophoresis 7f - Last line: our data

8b - Hemoglobins 8c - Populations of rivers of Sakhalin, Kamchatka, the Kuril Islands and Japan -- practically all the range of the species 8 e - Agar-, starch- and acrylamide-gel electrophoresis 8f - First line: our data

Second entry: 8b - Blood serum lactate dehydrogenase 8c - Populations of rivers of Sakhalin, Kamchatka and the Kuril Islands 8e - Agar- and acrylamide-gel electrophoresis 8f - Altukhov et al., 1970

9b - Hemoglobins 9c - Populations of rivers of Sakhalin, Kamchatka, the Kuril Islands, Japan and North America -- practically all the range of the species 9e - Agar-, starch- and acrylamide-gel electrophoresis 9f - First line: our data

Second entry: 9b - Blood serum lactate dehydrogenase(Polymorphism with respect to the regulator gene is observed -- Altukhov et al., 1970) 9c - Populations of rivers of Sakhalin, Kamchatka and the Kuril Islands 9e - Ditto 9f - Our data

Appendix 2. Key (Continued)

10b - Hemoglobin (second locus is polymorphous) 10c - Tens of populations in North America -- practically all the range of the species 10 e - Agar-gel electrophoresis

11b - Serum esterase (A genotype identical to the heterozygote in a closely related polymorphous species is constantly maintained) 11c - 11 localities in connected and disconnected tributaries of the Colorado River system 11d - Several hundred 11e - Starch-gel electrophoresis

12a - Amphibia 12b - Blood albumin, hemoglobin and globin polypeptide No. 4 12c - 27 localities in North America 12 e - Ditto

13a - Desmognatus, four species of salamander 13b - Hemoglobin 13C - 15 localities in North America

14a - Reptiles. Several species of the family Iguanidae 14b - Erythrocytic lactate dehydrogenase and hemoglobin 14c - 9 islands in the Carribean Sea, the Antilles, southern part of North America and South America

15a - Birds. Representatives of various orders 15b - Crystallins, myogens, hemoglobin and albumins 15c - No data (In these works indications of an absence of individual variations are contained only in the text) 15d - No data 15e - Agar- and starch-gel electrophoresis

16a - Mammals Mus musculus, 23 species of bats of the families Emballonuridae, Natalidae, Phyllostomatidae, etc. 16b - 6-Phosphogluconate dehydrogenase. 16c - No data 16e - Starch-gel electrophoresis Second entry: 16b - Hemoglobin 16c - More than 60 points of the range 16 e - Starch-gel electrophoresis; fingerprint

17b - Carbonic anhydrase of II erythrocyes 17 c - Various populations of Europeoids and Negroids 17d - Several hundred 17e - Starch-gel electrophoresis Second entry: 17b - Erythrocytic diaphorase 17c, 17d and 17e - Ditto Third entry: 17b - Erythrocytic hexosinase

Literature

1. Abakumov, V.A. "Seasonal races of diadromous fishes." Voprosy ikhtiologii, 1961, Vol. 17, pp. 179-190.
2. Aleksandrov, A.I. "Anchovies of the Azov-Black Sea basin, their origin and taxonomic designations." Trudy Kerchenskoi nauchnoi rybokhozyaistvennoi stantsii, 1927, Vol. 1, Nos. 2-3.
3. Altukhov, Yu.P. ""The immunogenetic approach to the problem of intraspecies differentiation in fishes." In the book: Successes of Modern Genetics, Moscow, 1969a, No. 2, pp. 161-195.
4. Idem. "The correlation of monomorphism and polymorphism of hemoglobins in the microevolution of fishes." DAN SSSR, 1969b, Vol. 189, No. 5, pp. 1115-1117.
5. Idem. "The genetics of fish populations." Priroda, 1971, No. 3, pp. 44-57.
6. Altukhov, Yu.P., and Mikhalev, Yu. A. "Difference in the size correlations of otoliths of 'large' and 'small' Black Sea scad, determined by the character of cell heat tolerance." In the book: Questions of the Physiology of Fishes of the Black Sea and Sea of Azov. Moscow, 1964, pp. 23-29.
7. Altukhov, Yu.P., and Rychkov, Yu.G. "Population systems and their structural components. Genetic stability and variability." Zhurnal obshchei biologii, 1970, Vol. 31, No. 5, pp. 507-526.
8. Altukhov, Yu. P., and Rat'kin, E.V. "Investigation of the genotypical conditionality of individual variability of heat tolerance of isolated cells." Tsitologiya, 1968, Vol. 10, No. 12, pp. 1546-1554.

9. Altukhov, Yu.P., Apekin, V.S., and Limanskii, V.V. "Basic principles of investigation of intra- and interspecies differentiation of fishes by serological methods." In the book: Questions of the Physiology of Fishes of the Black Sea and the Sea of Azov. Moscow, 1964, pp. 53-71.

10. Altukhov, Yu. P., Nefelov, G.N., and Payusova, A.N. "Cytophysiological analysis of the divergence of the golden and deepwater redfishes of the Northwest Atlantic." In the book: Variability of the Heat Tolerance of Cells of Animals in Ontogeny and Phylogeny. Leningrad, 1967, pp. 82-98.

11. Altukhov, Yu.P., and Rychkov, Yu.G. "Genetic monomorphism of species and its possible biological significance." Zhurnal obshchei biologii, 1972, Vol. 33, No. 3, pp. 281-300.

12. Altukhov, Yu.P., Salmenkova, E.A., and Sachko, G.D. "Duplication and polymorphism of genes of lactate dehydrogenase of Pacific salmons." DAN SSSR, 1970, Vol. 195, No. 3, pp. 711-714.

13. Andriyashev, A.P. Fishes of the Northern Seas of the USSR. Moscow-Leningrad, AN USSR Press, 1954, 567 pp.

14. Astaurov, B.L. "Experimental polyploidy and the hypothesis of indirect (by the intervention of parthenogenesis) origin of natural polyploidy." Genetika, 1969, Vol. 5, No. 7, pp. 129-148.

15. "The A system of blood groups of the Atlantic herring." Genetika, 1968, Vol. 4, No. 2, pp. 155-167. Authors: Yu.P. Altukhov, K.A. Truveller, V.S. Zenkin and N.S. Gladkova.

16. Balakhnin, I.A., and Potapov, M.I. "Determination of group differentiation of erythrocytes of the roach (Rutilis rutilis L.) by hemagglutinins." Zhurnal obshchei biologii, 1963, Vol. 24, No. 6, pp. 428-434.

17. Baranenkova, A.S. "Materials for the distribution of redfishes of the genus Sebastes." DAN SSSR, 1957, Vol. 113, No. 2, pp. 468-471.

18. Baranov, O.K. "Immunochemical analysis of the evolution of proteins." Uspekhi sovremennoi biologii, 1972, Vol. 74, No. 3, pp. 420-438.

19. Barsukov, V.V. "Systematic relations of redfishes of the genus Sebastes of the Northwestern part of the Atlantic Ocean." DAN SSSR, 1968, Vol. 183, No. 2, pp. 479-482.

20. Barsukov, V.V., and Zakharov, G.P. "Morphological and biological characteristics of the redfish." Trudy PINRO, 1972, No. 28, pp. 143-174.

21. Berg, L.S. "Vernal and hiemal races of diadromous fishes." Izvestiya AN SSSR, Otdel matematich. i estestv. nauk, 1934, No. 5, pp. 1115-1137.

22. Berston, M. The Histochemistry of Enzymes. Moscow, Mir Press, 1965, 464 pp.

23. Boyd W. Introduction to Immunochemical Specificity. Moscow, Foreign Literature Press, 1963, 186 pp.

24. Borodatov, V.A., and Travin, V.I. "Main stages of Soviet investigations of the redfish of the North Atlantic." In the book: Soviet Fishery Investigations in the Seas of the European North, Moscow, 1960, pp. 277-284.

25. Braitseva, O.A. The Stratigraphy of Quaternary Deposits and Glaciation of Kamchatka. Moscow, Nauka Press, 1968, 226 pp.

26. Buzdalin, Yu.I., and Elizarov, A.A. "Hydrological conditions in regions of the Newfoundland Grand Bank and Labrador." In the book: Soviet Fishery Investigations in the Northwestern Part of the Atlantic Ocean. Moscow, 1962, pp. 155-171.

27. Wagner, R., and G. Mitchell. Genetics and Metabolism. Moscow, Foreign Literature Press, 372 pp. (year not given).

28. Vinogradov, K.A. "The biology of the northwestern part of the Black Sea." Zoologicheskii zhurnal, 1956, Vol. 35, No. 4, pp. 492-500.

29. Grabar, P., and Burten, P. Immunoelectrophoretic Analysis. Moscow, Foreign Literature Press, 1963, 206 pp.

30. Danilevskii, N.N. "Migration of the Black Sea anchovy and factors causing it." Trudy AzcherNIRO, 1958, No. 17, pp. 51-74.

31. Idem. "Penetration of the Black Sea anchovy into the Sea of Azov and accompanying environmental conditions." Ibid., 1960, No. 18, pp. 118-129.

32. Idem. "The most important factors determining the times and regions of formation of commercial accumulations of the Black Sea anchovy." Ibid., No. 22, pp. 115-131.

33. Darevskii, I.S., and Kulikova, V.N. "Natural triploidy in the population group of the Caucasian rock lizards Lacerta saxicola Ewersmann as a result of hybridization between bisexual and parthenogenetic forms of that species." DAN SSSR, 1964, Vol. 158, No. 1, pp. 202-204.

34. Darevskii, I.S., and Danielyan, F.D. Diploid and triploid individuals in the offspring of parthenogenetic females of rock lizards naturally pairing with males of close bisexual species." DAN SSSR, 1969, Vol. 184, No. 3, pp. 727-730.

35. Dement'eva, T.F., and Tanasiichuk, V.S. "The question of races of the cod of the Barents Sea." Za rybnuyu industriyu Severa, 1935, No. 5, pp. 40-43.

36. Dogel', V.A., and Bykhovskii, B.E. "Parasites of fishes of the Caspian Sea." Trudy kompleksnogo izucheniya Kaspiiskogo morya, 1939, No. 7, pp. 118-120.

37. Dubinin, N.P. "Genetic automatic processes and their influence on the mechanisms of organic evolution." Zhurnal eksperimental'noi biologii, 1931, No. 7, pp. 463-470.

38. Idem. Evolution of Populations and Radiation. Moscow, Atomizdat, 1966, 743 pp.

39. Dubinin, N.P., and Glembotskii, Ya.L. Population Genetics and Selection. Moscow, Nauka Press, 1967, 591 pp.

40. Dubinin, N.P., and Romashov, D.D. "Genetic structure of the species and its evolution." Biologicheskii zhurnal, 1932, Vol. 1, Nos. 5-6, pp. 52-95.

41. Zakharov, G.P. "Biology of the redfish of Western Greenland." In the book: Soviet Fishery Investigations in the Northwestern Part of the Atlantic Ocean. Moscow, 1962, pp. 319-330.

42. Zernov, M.S. "Systematic and biological characteristics of the vobla of the region adjacent to Mertvyi Kultuk." In the book: Gulfs of the Caspian Sea. Astrakhan', 1938, No. 2, pp. 35-54.

43. "Immunogenetic analysis of the intraspecies differentiation of the anchovy living in the Black Sea and the Sea of Azov. Report No. 1." Genetika, 1969, Vol. 5, No. 4, pp. 50-64. Authors: Yu.P. Altukhov, V.V. Limanskii, A.N. Payusova and K.A. Truveller.

44. Idem. Report No. 2. Elementary populations and their place in the population genetics structure of the species. Genetika, 1969, Vol. 5, No. 5, pp. 81-94. Authors: Idem.

45. Karavaev, G.A. "Migration of the vobla (Rutilis rutilis caspicus Jak.) in the Northern Caspian." Trudy VNIRO, 1939, Vol. 10, pp. 33-80.

46. Karasev, B.E., and Sauskan, E.I. "Distribution of bottom fishes off Newfoundland and Labrador and possibilities of forecasting commercial concentrations." Trudy AtlantNIRO, 1963, No. 10, pp. 124-141.

47. Kirpichnikov, V.S. "The formation of races of fishes." Biologicheskii zhurnal, 1933, Vol. 2, No. 6, pp. 609-627.

48. Idem. "Systematic biological outline of the smelt of the White Sea, Chesha Bay and the Pechora River." Trudy VNIRO, Vol. 2, 1935, pp. 103-187.

49. Idem. "Experimental systematics of the carp (Cyprinus carpio L.)." Izvestiya AN SSSR. Ser. biol., 1943, No. 4, pp. 189-218.

50. Idem. "General theory of heterosis." Genetika, 1967, No. 10, pp. 48-64.

51. Idem. "The contemporary state of the genetics of fishes." In the book: Genetics, Selection and Hybridization of Fishes. Moscow, 1969, pp. 9-29.

52. Idem. "Biochemical polymorphism and the problem of so-called non-Darwinian evolution." Uspekhi sovremennoi biologii, 1972, Vol. 74, No. 2 (5), pp. 231-246.

53. Konovalov, S.M. "The possibility of using some parasites as indicators of local stocks of sockeye in the sea." Theses (Summaries) of Reports of Young Scientists of the VNIRO, 1963, pp. 13-14.

54. Idem. Differentiation of Local Sockeye Stocks. Leningrad, Nauka Press, 1971, 229 pp.

55. Idem. "The structure of the sockeye isolate of Lake Azabach'e." Zhurnal obshchei biologii, 1972, Vol. 33, No. 6, pp. 668-682.

56. Kornilova, V.P. "The biology and fishing industry of the Azov anchovy." Trudy AzcherNIRO, 1960, No. 18, pp. 50-67.

57. Krogius, F.V., Krokhin, E.M., and Menshutkin, V.V. The Community of Pelagic Fishes of Dal'noe Lake. Leningrad, Nauka Press, 1969, 85 pp.

58. Krykhtin, M.L. "Biologically homogeneous groups of Pacific salmons." Voprosy ikhtiologii, 1958, No. 10, pp. 3-11.

59. Kubantsev, B.S. "The sexual composition of populations in mammals." Zhurnal obshchei biologii, 1972, Vol. 33, No. 2, pp. 196-204.

60. Kuprina, N.P. The Stratigraphy and History of Sedimentation of Pleistocene Deposits of Central Kamchatka. Moscow, Nauka Press, 1970, 186 pp.

61. Lebedev, N.V. "The prediction of dates of migration of the Azov anchovy." Uchenye zapiski Moskovskogo gosudarstvennogo universita, 1939, Vol. 33, pp. 257-295.

62. Idem. "The possibility of predicting the dates of migration of the Azov anchovy." Zoologicheskii zhurnal, 1940, Vol. 19, No. 4, pp. 646-660.

63. Idem. "Elementary populations of fishes." Zoologicheskii zhurnal, 1946, Vol. 25, No. 2, pp. 121-135.

64. Idem. Elementary Populations of Fishes. Moscow, Food Industry Press, 1967, 211 pp.

65. Levanidov, V.Ya. "Reproduction of Amur salmons and the food supply of their juveniles in tributaries of the Amur." Izvestiya TINRO, 1969, Vol. 67, pp. 3-242.

66. Limanskii, V.V. "Analysis of the intraspecies differentiation of some fishes of the Black Sea and Sea of Azov using precipitation reaction". In the book: Questions of the Physiology of Fishes of the Black Sea and the Sea of Azov. Moscow, 1964, pp. 31-39.

67. Idem. "Serological analysis of the intraspecies differentiation of scads and anchovies of southern seas." In the book: Theses of the All-Union Conference on the Ecological Physiology of Fishes. Moscow, 1966, p. 3.

68. Limanskii, V.V., and Payusova, A.N. "Immunogenetic differences of elementary populations of the anchovy." Genetika, 1969, Vol. 5, No. 6, pp. 109-118.

69. Logvinenko, B.M., and Kodolova, O.P. "The possibility of differentiation of mollusc species by comparison of **electrophoregrams of** myogens." In the book: Ways, Methods and Results of Studying Molluscs. Leningrad, 1971a, pp. 18-19.

70. Idem. "The possibility of differentiation of species of bivalve molluscs by comparing electrophoregrams of muscle water-soluble proteins." Zoologicheskii zhurnal, 1971b, Vol. 50, No. 6, pp. 923-925.

71. Lake, D. The Numbers of Animals and Their Regulation in Nature. Moscow, Foreign Literature Press, 1957, 403 pp.

72. Maiorova, A.N. "The taxonomic position of the anchovy caught off the coasts of Georgia." Trudy nauchnoi rybokhoz. stantsii Gruzii, 1934, Vol. 1, No. 1, pp. 7-19.

73. Duplicate of No. 71.

74. Duplicate of No. 72.

75. Maiorova, A.N. The Biology and Fishing Industry of the Black Sea Anchovy. Simferopol', Crimean Press, 1951, 79 pp.

76. Maiorova, A.N., and Chugunova, N.I. "The biology, distribution and estimation of the stock of the Black Sea anchovy." Trudy VNIRO, 1954, Vol. 28, pp. 5-33.

77. Mayer, E. Systematics and the Origin of Species. Moscow, Foreign Literature Press, 1947, 334 pp.

78. Idem. Zoological Species and Evolution. Moscow, Mir Press, 1968, 598 pp.

79. Malyukina, G.A. The Sense of Smell and Its Role in the Behavior of Fishes. Results of Science. Biological Series. Moscow, 1969, pp. 32-78.

80. Mesyatseva, E.V. "The cod of the trawling fishery of the Barents Sea." Rybnoe khozyaistvo, 1937, No. 12, pp. 12-18.

81. Morozov, A.V. "Toward a procedure of racial investigations of fishes in general and the vobla in particular." Trudy Volgo-Kaspiiskoi rybkhozstantsii, 1932, 127 pp.

82. Naumov, N.P. "The structure of populations and abundance dynamics of land vertebrates." Zoologicheskii zhurnal, 1967, Vol. 46, No. 10, pp. 1470-1486.

83. Nefedov, G.N. "Serum haptoglobins of redfishes of the genus Sebastes." Vestnik Moskovskogo universita, 1969, No. 1, pp. 104-107.

84. Nikol'skii, G.V. "The relative stability of species and some questions of taxonomy." Zoologicheskii zhurnal, 1968, Vol. 47, No. 6, pp. 860-874.

85. Idem. "The structure of species and some questions in the study of the dynamics of a fish stock." In the book: Problems of Ecology. Tomsk, 1971, No. 2, pp. 19-24.

86. Neal, G., and Shell, W. Human Heredity. Moscow, Foreign Literature Press, 1958, 388 pp.

87. Novozhenov, Yu.I. "The sex ratio -- a specific parameter of an elementary population." Zhurnal obshchei biologii, 1971, Vol. 32, No. 1, pp. 37-44.

88. "The number of monomorphous and polymorphous loci in the population of the keta -- one of the tetraploid species of Pacific salmons." Genetika, 1972, Vol. 8, No. 2, pp. 251-259. Authors: Yu. P. Altukhov, E.A. Salmenkova, V.T. Omel'chenko, G.D. Sachko and V.I. Slyn'ko.

89. Panov, E.N. Association in the World of Animals (Evolutionary and Population Aspects of the Behavior of Animals). Moscow, Znanie Press, 1970, Series 8, No. 1, pp. 3-48.

90. Payusova, A.N. "Methods of observing immature vobla and bream in elementary populations." Trudy soveshchanii ikhtiologicheskoi komissii AN SSSR, 1961, No. 13, pp. 471-479.

91. Idem. "Experience in detailed observation of the downstream migration of immature vobla (Rutilis rutilis caspicus Jak.) from bayous into side channels of the Volga River Delta". Voprosy ikhtiologii, 1962, Vol. 2, No. 3 (24), pp. 467-472.

92. Idem. "The initial stages of formation of elementary populations of fishes." Zoologicheskii zhurnal, 1965, Vol. 64, No. 10, pp. 1560-1575.

93. Idem. "The importance of differentiation of larvae and aggregative behavior for the formation of elementary fish populations." In the book: The Behavior and Reception of Fishes. Moscow, 1967, pp 41-50.

94. Payusova, A.N., and Nefedov, G.N. "Analysis of the heat **tolerance** of isolated muscle tissue of redfishes of the genus Sebastes from the Barents Sea." Tsitologiya, 1968, Vol. 10, No. 1, pp. 133-137.

95. Petrov, V.V. Some Questions of the Procedure in the Delimitation of Fine Taxonomic Units. Press of Leningrad Scientific Research Institute of Ichthyology, 1930, Vol. II, No. 1, pp. 112-128.

96. "Polymorphism of isozymes of lactate dehydrogenase in the keta." Referaty nauch. rabot Instituta biol. morya, Vladivostok, 1968, No. 1, pp. 15-18. Authors: Yu. P. Altukhov, E.P. Altukhova, E.A. Salmenkova and G.D. Sachko.

97. Polyanskii, Yu.I. "Parasite fauna and the environment. Some questions of the ecology of parasites of ocean fishes." In the book: Principal Problems of the Parasitology of Fishes. Leningrad, 1958, pp. 55-89.

98. Puzanov, I.I. "The anchovy." Uchenye zapiski Gor'kovskogo gosudarstvennogo universiteta, 1936, No. 5, 101 pp.

99. "The racial composition of the cod of the Barents Sea." In the book: Reports of the First Session of the GOIN, 1931, No. 2, pp. 49-58. Authors: T.F. Dement'eva, E.K. Plechkova, M.I. Rozanova and V.S. Tanasiichuk.

100. Rychkov, Yu.G. "Distinctive features of the serological differentiation of the peoples of Siberia." Voprosy antropologii, 1965, No. 21, pp. 18-33.

101. Idem. "The reaction of populations to isolation." In the book: Problems of Evolution. Novosibirsk, 1968, Vol. 1, pp. 212-236.

102. Idem. "Some population genetics approaches to the anthropology of Siberia." Voprosy antropologii, 1969a, No. 33, pp. 16-33.

103. Idem. Anthropology and Genetics of Isolated Populations. Moscow State University Press, 1969b, 221 pp.

104. Idem. "Population genetics of the aboriginal population of Siberia." Voprosy antropologii, 1969, No. 31, pp. 3-32.

105. Rychkov, Yu.G., and Movsesyan, A.A. "Genetic-anthropological analysis of the distribution of cranial anomalies in Mongoloids of Siberia in connection with the problem of their origin." Trudy Moskovskogo obshchestva ispytatelei prirody, 1972, Vol. 43, pp. 114-132.

106. Rychkov, Yu.G., and Sheremet'eva, V.A. "Population genetics of the Aleuts of the Commander Islands. I." Voprosy antropologii, 1972a, No. 40, pp. 45-70.

107. Idem. "Population genetics of the Aleuts of the Commander Islands. II." Ibid., 1972b, No. 41, pp. 3-35.

108. Idem. "Population genetics of peoples of the northern part of the Pacific Ocean basin in connection with problems of the history and adaptation of the population." Ibid., 1972c, No. 42, pp. 3-30.

109. Salmenkova, E.A. "The genetics of isoenzymes of fishes." Uspekhi sovremennoi biologii, 1973, Vol. 75, No. 2, pp. 217-235.

110. Salmenkova, E.A., and Volokhonskaya, L.G. "Biochemical polymorphism in populations of diploid and tetraploid fishes." Proceedings of the All-Union Conference on the Biochemical Genetics of Fishes. Leningrad, 1973, pp. 54-61.

111. Saf'yanova, T.E., and Revina, N.I. "The delimitation of large and small scad on the basis of otoliths." Rybnoe khozyaistvo, 1965, No. 6, pp. 17-22

112. Sergeeva, A.I. "Qualitative characterization of the vobla Rutilis rutilis caspicus Jak. in the western and eastern parts of the Northern Caspian." Voprosy ikhtiologii, 1963, Vol. 3, No. 1 (26), pp. 29-38.

113. Serebrovskii, A.S. Genetic Analysis. Moscow, Nauka Press, 1970, 342 pp.

114. Sidorenko, I.N. "The distribution of the deepwater redfish (Sebastes mentella Travin) by depths in the northern region of the Grand Bank." In the book: Materials of the Session of the PINRO Scientific Council, Murmansk, 1967, pp. 166-177.

115. Skazkina, E.P. "Differentiation of the Azov and Black Sea anchovies on the basis of otoliths." Voprosy ikhtiologii, 1965, Vol. 5, No. 4 (37), pp. 600-605.

116. Slyn'ko, V.I. "Polymorphism of isoenzymes of malate dehydrogenase of Pacific salmons." Nauchnye soobshcheniya Instituta biologii morya, Vladivostok, 1971, No. 2, pp. 207-211.

117. Sokolovskaya, I.I. "Precipitin reaction in hybridization." Izvestiya AN SSSR. Ser. biol., 1936, Nos. 2-3, pp. 465-491.

118. Idem. "Serological investigations in distant hybridization." Izvestiya AN SSSR. Ser. biol., 1938, No. 4, pp. 947-957.

119. Strelkov, Yu.A. "Endoparasitic worms of ocean fishes of Eastern Kamchatka." Trudy ZIN AN SSSR, 1956, Vol. 28, pp. 147-196.

120. Taliev, D.N. "Serological analysis of some wild and domesticated forms of the carp (Cyprinus carpio L.)." Trudy Zoologicheskogo Instituta, 1946, Vol. 8, No. 1, pp. 43-88.

121. Taranenko, N.F. "The dynamics of the numbers of Azov anchovy." Trudy AzcherNIRO, 1966, No. 24, pp. 3-29.

122. Tarasevich, M.N. "The structure of groups of whales. II. The structure of groups of finback whales." Zoologicheskii zhurnal, 1967, Vol. 66, No. 3, pp. 420-426.

123. Timofeev-Resovskii, N.V., Vorontsov, N.N., and Yablokov, A.V. Short Outline of the Theory of Evolution. Moscow, Nauka Press, 1969, 407 pp.

124. Tikhonov, V.N. Genetic Systems of Animal Blood Groups. Novosibirsk, Nauka Press, 1966, 115 pp.

125. Tokarev, A.K. "Concentrations of the Caspian common kilka." DAN SSSR, 1955, Vol. 100, No. 6, pp. 1187-1189.

126. Travin, V.I. "A new species of deepwater redfish in the Barents Sea (Sebastes mentella Travin sp. nov.)." DAN SSSR, 1951, Vol. 77, pp. 741-744.

127. Travin, V.I., and Pechenik, L.N. "Soviet fishery investigations and fisheries in the Northwest Atlantic." In the book. Soviet Fishery Investigations in the Northwest Part of the Atlantic Ocean. Moscow, 1962, pp. 9-55.

128. Wilkinson, D. Isoenzymes. Moscow, Mir Press, 1968, 230 pp.

129. Ushakov, B.P. "The conservativeness of proteins of the species protoplasm in poikilothermal animals." Zoologicheskii zhurnal, 1958, Vol. 37, No. 5, pp. 693-706.

130. Idem. "Physiology of the cell and the problem of the species in zoology." Tsitoligiya, 1959a, Vol. 1, No. 5, pp. 541-545.

131. Idem. "The heat tolerance of tissues -- a species character of poikilothermal animals. Zoologicheskii zhurnal, 1959b, Vol. 38, No. 9, pp. 1292-1302.

132. "Factors of genetic differentiation of the population system of the aboriginal population of Northern Asia. I." Genetika, 1973, Vol. 9, No. 2, pp. 136-145. Authors: Yu.G. Rychkov, O.L. Rusakova, M.P. Rappoport and V.A. Sheremet'eva.

133. "The functional unity of populations." Zhurnal obshchei biologii, 1972, Vol. 33, No. 1, pp. 3-14. Authors: S.S. Shvarts, E.Ya. Gurvich, V.G. Ishchenko and V.F. Sosin.

134. Friz, G. de. "Theory of mutations. Mutation and mutation periods in the origin of species." In the book: Theory of Development. St. Petersburg, 1904, 237 pp.

135. Idem. Mutations and Periods of Mutations in the Origin of Species. St. Petersburg, 1912, 45 pp.

136. Idem. Selected Works. Moscow, Medgiz, 1932, 147 pp.

137. "Frequency of serum lactate dehydrogenase genes in the populations of keta and pink salmon of different rivers of the island of Sakhalin." Referaty nauchnykh rabot Instituta biologii morya, Vladivostok, 1968, No. 1, pp. 11-14. Authors: Yu.P. Altukhov, E.P. Altukhova, V.N. Ivankov, E.A. Salmenkova and G.D. Sachko.

138. Chugunova, N.I. "Growth and maturing of the vobla of the Northern Caspian as a function of the fattening conditions." Trudy VNIRO, 1951, Vol. 18, pp. 153-170.

139. Sheppard, F.M. Natural Selection and Heredity. Moscow, Prosveshchenie Press, 1970, 216 pp.

140. Shvarts, S.S. "Evolutionary ecology of animals." Trudy instituta ekologii rastenii i zhivotnykh, 1969, No. 65, pp. 175-198.

141. Stern, K. Principles of Human Genetics. Moscow, Mir Press, 1965, 627 pp.

142. Shul'man, S.S. "Parasite fauna of the White Sea herring, smelt and navaga." Trudy Karelo-Finsk. filiala AN SSSR, 1956, Vol. 4, pp. 50-67.

143. Idem. "Parasites of fishes of the eastern part of the Baltic Sea." Trudy soveshch. po boleznyam ryb, 1959, No. 9, pp. 184-187.

144. Shul'man, S.S., and Shul'man, R.S. Parasites of White Sea Fishes. Nauka Press, Moscow-Leningrad, 1953, 165 pp.

145. Efroimson, V.P. Introduction to Medical Genetics. Moscow, Meditsina Press, 1964, 490 pp.

146. Yurovitskii, Yu.G. "Determination of sex of fishes." Uspekhi sovremennoi bioligii, 1966, Vol. 62, No. 14, pp. 148-160.

147. Yakovleva, V.I. "Isoenzymes." Uspekhi biologicheskoi khimii, 1968, No. 9, pp. 55-94.

148. Yanulov, K.P. "Groups of the deepwater redfish (Sebastes mentella Travin) in the Labrador-Newfoundland region." In the book: Soviet fishery investigations in the Northwestern Part of the Atlantic Ocean. Moscow, 1962a, pp 285-296.

149. Idem. "Parasites as indicators of the locality of stocks of deepwater redfish." Ibid., 1962b, pp. 273-283.

150 Abramoff P., Darnell R. M., Balsano J. S. 1968. Electrophoretic demonstration of the hybrid origin of the gynogenetic teleost Poecilia formosa. Amer. Nat., 102; 555—558.

151 Altukhov Yu. P. a Nefejodov G. N. 1968. A study of blood serum protein composition by agar — gel electrophoresis in types of redfish (genus Sebastes). Internat. Comiss. N.W. Atl. Fish., Res. Bull., 5; 86—90.

152 Altukhov Yu. P., Nefyodov G. N., Payusova A. N. 1968a. Thermostability of isolated muscle in determining the taxonomic relationship of the marinus — and mentella — types of the redfish (Sebastes). Internat. Comiss. N.W., Atl. Fish., Res. Bull., 5; 130- 136.

153 Altukhov Yu. P, Artemyeva K. F., Borisova I. V. a. Nefyodov G. N. 1968b. Immunological analysis of serum proteins of redfish in connection with maturation. Internat. Commiss. N.W. Atl. Fish. Res. Bull., 5: 44—48.

154 Altukhov Yu P. Recent physiological, biochemical and immunological studies on the problem of intraspecific differentiation in marie fish. 1971 b, Cons. Internat. Expl. Mer. Rapp. Proc. Verb., 161: 103—108.

155 Altukhov Yu. P., 1970. Biochemical polymorphism in fishes and the problem of intraspecific differentiation. XIIth Internat. Conf. Anim. Blood Groups and Biochem. Polymorphisms, Yuly 6th—11th, Budapest.

156. Altukhov, Yu.P. "Genetic research concerning marine organisms" (in German). Poseidon, 1972, 122, 2, 60-61.

157 Aspinval N. and Tsuyuki H., 1968. Inheritance of muscle proteins in hybrids between the redside shiner (Richardsonitus balteatus) and the peamouth chub (Mylocheilus caurinum). J. Fish. Res. Bd. Canada, 25, 7: 1317—1322.

158 Avise J. C., Selander R. K. 1972. Evolutionary genetics of cavedwelling fishes of the genus Astyanax. Evolution, 26, 1: 1—19.

159 Baily G. S., Gocks C. T., Wilson A. C. 1969. Gene duplication in fishes: malate dehydrogenases of salmon and trout. Biochem. Biophys. Res. Commun., 34, 5: 605—612.

160 Bailey G. S., Wilson A C., Halver J. E. and Jonson C. L. 1970. Multiple forms of supernatant malate dehydrogenase in salmonoid fishes: biochemical, immunological and genetics studies. J. Biol. Chem., 245: 5927—5940.

161 Baker C. M. A., Manwell C., 1967. Molecular genetics of avian proteins. VIII. Comp. Biochem. Physiol., 23, 1: 21—42.

162 Baker C. M. A., Manwell C., Labisky R. F. and Harper J. A. 1966. Molecular genetics of avian proteins. V. Comp. Biochem. Physiol., 17: 467—499.

163 Barrett J. and Tsuyuki H. 1967. Serum transferrin polymorphism in some scombroid fishes. Copeia, 3: 551—557.

164 Barret J. and Williams A. A. 1967. Soluble lens proteins of some scombroid fishes. Copeia, 2: 468—471.

165 Beçak M. L., Beçak W. and Rabello M. N. 1966. Cytological evidence of constant tetraploidy in the bisexual South American frog Odontophrynus americanus. Chromosoma (Berl.), 19: 188—193.

166 Beçak W., Beçak M. L., Lavalle P. and Schreiber G. S. 1967. Further studies on polyploid amphibians (Ceratophrydidae). Chromosoma (Berl.), 23: 14—23.

167 Beçak W., Beçak M. L., Schreiber G., Lavalle D., Flavia A. O. 1970. Interspecific variability of DNA content in amphibia. Experientia, 26: 204—206.

168 Beckman L., Nilson L. R., 1965. Variation of serum enzymes in bird species and hybrids. Hereditas, 53, 1—2: 221—230.,

169 Bender K. and Ohno S. 1968. Duplication of the autosomally inherited 6-phosphogluconate dehydrogenase gene locus in tetraploid species of cyprinid fish. Biochem. Genet. 2: 101—107.

170 Ben-Tuvia A. 1963. Variation in vertebrae number of young Sardinella aurita in relation to temperature during spawning season.— «Rapp. proc.-verb reun. Cons. perm. inter. expl. mer., 17, 2: 313—318.

171 Bird G. W. C. 1953. Some interrelationships of the erythrocytes of various species with plant agglutinins.— «Nature», 172, 4374: 401—402.

172 Blaxter J. H. S. 1958. The racial problem in herring from viewpoint of recent physiological, evolutionary and genetical theory. Rapp. proc.-verb. reun. Cons. perm. intern. expl. mer., 143, 2: 10—19.

173 Bouck G. E. and Ball R. C. 1968. Comparative electrophoretic patterns of lactate dehydrogenase in three species of trout.— «J. Fish. Res. Bd. Canada», 25, 7: 1323—1331.

174 Boyd W. C. and Reguera H. M. 1949. Hemagglutinating substances for human cells in various plants.— «J. Immunol.», 62, 3: 333—339

175 Brannon E. L. 1972. Mechanisms controlling migration of sockey salmon fry. Internat. Pacific. Salmon Fish. Comm., 21: 1—86.

176 Brewer G. J., Eaton J. W., Knutsen C. A. and Beck C. C., 1967. A starch gel electrophoretic method for the study of diaphorase isozymes and preliminary results with sheep and human erythrocytes. Biochem. Biophys. Res. Commun 29: 198—204.

177 Brewer G. J. and Sing C. F., 1969. Survey of isozymes of human erythrocytes. In: Biochemical Methods in Red Cell Genetics, Ac. Press, N. Y.: 377—390.

178 Britten R. J. and Davidson E. H. 1971. Repetitive and non-repetitive DNA sequences and a speculation on the origins of evolutionary novelty. Quart. Rev. Biol., 46, 2: 111—133.

179 Cain A. T. 1954. Animal species and their evolution. London. Перевод: А. Кейн, 1958. Вид и его эволюция. ИЛ, М., 243 с.

180 Cain A. T., Currey T. D. 1963 a. «Area effects» in Cepea. Phill. Trans. Roy. Soc. Lond., 246: 1—81.

181 Cain A. T., Currey T. D. 1963 b. The causes of area effects. Heredity, 18: 467—471.

182. Callegarini, C. 1966. "The hemoglobins of some populations of Ictaluridae (Teleosts) of Northern Italy." Instituto Lombardo (Rend. Sc.), B 100, 31-35.

183 Callegarini C. and Cucchi C. 1967. Further contribution to the knowledge of hemoglobin polymorphism in «cat fish» (Ictalurus sp.) populations of the region of Ferrara. Riv. Biol., Univ. Perugia, 40: 39—47.

184 Cederbaum S. D., Yoshida A. 1972. Tetrazolium oxidase polymorphism in rainbow trout. Genetics, 72, 2: 363—367.

185 Chen F. J. and Tsuyuki H. 1970. Zone electrophoretic studies on the proteins of Tilapia mossambica and T. hornorum and their F_1 hybrides, T. zillii and T. melonopleura. J. Fish. Res. Bd. Canada, 27, 12: 2167—2177.

186 Clayton J. W. and Gee J. H. 1969. Lactate dehydrogenase isozymes in longnose and blacknose dace and their hybrid. J. Fish. Res. Bd. Canada, 26, 11: 3049—3053.

187 Clayton J. W. and Franzin W. G. 1970. Genetics of multiple lactate dehydrogenase isozymes in muscle tissue of lake whitefish. J. Fish. Res. Bd. Canada, 27, 6: 1115—1121.

188 Clayton J. W., Tretiak D. N., Kooyman A. H. 1971. Genetics of multiple malate dehydrogenase isozymes in skeletal muscle of walleye (Stizostedion vitreum vitreum). J. Fish. Res. Bd. Canada, 28, 7: 1005—1008.

189 Clayton J. W., Franzin W. C., Tretiak D. N. 1973. Genetics of glycerol — 3 — phosphate dehydrogenase isozymes in white muscle of lake whitefish Coregonus clupeaformis. J. Fish. Res. Board Canada, 30, 2: 187—193.

190. Creyssel, R., Silberzahn, F., Richard, G., and Manual, Y. 1961. "Study of carp serum by starch-gel electrophoresis" (in French). Bull. Soc. Chim. Biol., 46, 149-159.

191 Cushing J. E. 1964. The blood groups of marine animals. In: Adv. Mar. Biol., 2: 85—131.

192 Cushing J. E. and Durral G. L. 1957. Isoagglutination in fish. Amer. Naturalist, 91: 121—125.

193 Cushing J. E. and Campbell D. H. 1957. Principles of immunology. New York, Toronto, London.

194 Dannevig A. 1932. In the number of vertebrae in the cod influensed by light or high temperature during the early stages. J. Cons. Internat. Explor. Mer., 7 1: 60—62.

195 Dannevig A. 1933. The number of verterbrae in Gadus virens L. from the Norwegian Skagerak Coast. J. Cons. Internat. Explor. Mer, 8: 355—356.

196 Demir N. 1968. Analyses of local populations of the anchovy Engraulis encrasicholus L. in Turkish waters based on meristic characters. Rev. de la Faculte des Sci. de L'Univ. D'Istambul. Ser. B, 33 (1—2): 25—57.

197 Dessauer H. C. and Nevo E., 1969. Geographic variation of blood and liver proteins in cricket frogs. Biochem. Genet., 3: 171—188.

198 Diver C. 1929. Fossil records in Mendelian mutants. Nature, 124: 183.

199 Dobzhansky Th. 1943. Genetics of natural populations, IX. Temporal changes in the composition of populations of Drosophila pseudoobscura. Genetics, 28: 162—186.

200 Dobzhansky Th. 1951. Genetics and the origin of species. Columbia University Press. New York.

201 Dobzhansky Th. 1955. Evolution, Genetics and Man. J. Wiley, New York.

202 Dobzhansky Th., Anderson W. W., Pavlovsky O., Spassky B., Wills C. T. 1964. Genetics of natural populations, XXV. A progress report on genetic changes in populations of Drosophila pseudoobscura in the American south-west. Evolution, 18, 2: 164—176.

203 Dragesund O. 1964. Norwegian herring tagging experiments. Ann. Biol. Conseil Perman. Internat. Explor. Mer., 21: 119—120.

204 Drilhon, A., Fine, T.M., Boffa, G., Amouch, P., and Drouhet, T. 1966. "Transferrin groups in the eel" (in French). Comp. Rend. Acad. Sci., Paris, 262: 1315-1318.

205 Eaton G. W., Brewer G. J. and Tashian R. E., 1966. Hexokinase isozyme patterns of human erythrocytes and leucocytes. Nature, 212: 944—946.

206 Einarsson H. 1958. Icelandic herring and recial problems. Rapp. Proc.-Verb. Reun. Cons. Perm. Internat. Explor. Mer., 143, 2: 45—52.

207 Engel, W., Opt'Hof, J., and Wolf, U. 1970. "Gene duplication as a result of polyploidal evolution: The isoenzymes of sorbitol-dehydrogenase in herrings and salmonoid fish (Isospondyli)" (in German). Humangenetik, 9: 157-163.

208 Engel W., Schmidtke J., Wolf U. 1971 a. Genetic variation of α-glicerophosphate dehydrogenase isoenzymes in clupeoid and salmonoid. Experientia, 27, 2: 1489—1491.

209 Engel W., Faust J., Wolf U. 1971 b. Isoenzyme polymorphism of the sorbitoldehydrogenase and the NADP-dependent isocitrate dehydrogenase in the fish family Gyprinidae. Anim. Blood Croups a. Biochem. Genet., 2, 3: 127—133.

210 Erlich P. R., Holm R. W. 1963. The process of evolution. McGraw-Hill Book Company, N. — Y. — San-Francisco — Toronto — London.

211 Fage L., 1920. Engraulidae. Rep. Danish Ocean. Exped. 1908—1910. II, 6.

212 Fine, J.M., Drilhon, A., Amouch, P., and Boffa, G. 1964. "The existence of serum groups in Anguilla anguilla L. Determined by electrophoresis and autoradiography of several types of transferrins" (in French). Comp. Rend. Acad. Sci., 258, 2: 753-756.

213 Fisher R. A. 1930. The genetical theory of natural selections. Oxf. Univ. Press, Oxford.

214 Fleming A. M., 1960. Age, growth and sexual maturity of cod (Gadus morhua) in the Newfoundland area, 1947—1950. J. Fish. Res. Bd. Canada, 17, 18: 775—809.

215 Foerster R. E. 1968. The Seekeye Salmon. Bull. Fish. Res. Bd. Canada, 162, Ottawa.

216 Ford E. B., 1940. Polymorphism and taxonomy. The New Systematics. Clarendon Press, Oxford: 493 —513.

217 Fowler J. A. 1970. Control of vertebral number in teleosts — an embryological problem. Quart. Rev. Biol., 45, 2: 148—167.

218 Frydenberg O., Möller D., Naevdel G. and Sick K. 1965. Haemoglobin polymorphism in Norwegian cod populations. Hereditas, 53: 257—271.

219 Fujino K. 1970. Immunological and biochemical genetics of lunas. Trans. Am. Fish. Soc., 99, 1: 152—178.

220 Fujino K. & Kang T. 1968 a. Serum esterase groups of Pacific and Atlantic lunas. — «Copeia», 1: 56—63.

221 Fujino K. & Kang T. 1968 b. Transferrin groups of tunas. Genetics, 59: 79—91.
222 Fürst M. and Nyman L. 1969. Isoenzyme polymorphism in Mysis relicta Loven. Inst. Freshwat. Res., Drottningholm, 49: 44—48.
223 Gabriel M. L. 1944. Factors effecting the number and form of vertebrae in Fundulus heteroclitus. J. Exp. Zool., 95: 105—147.
224 Goldberg E. 1966. Lactate dehydrogenase of trout: hybridization in vivo and in vitro. Science, 151, 3714: 1091—1093.
225 Goldberg E., Cuerrier T. P., Ward T. C. 1967. Lactate dehydrogenase isozymes, vertebrae and caeca numbers in an isolated, interbreeding population of splake trout. Naturaliste Canad., 94, 3: 297—304.
226 Goldschmidt R. B. 1940. The material basis of evolution. Jale University Press, New Haven.
227 Goldschmidt R. B. 1948. Ecotype, ecospecies and macroevolution. Experientia, 4: 465—472.
228 Goldschmidt R. B. 1952. Evolution as viewed by one geneticist. Amer. Sci., 40: 84—98.
229 Goldschmidt R. B. 1955. Theoretical genetics. Univ. Calif. Press, Berkeley and Los Angeles.
230 Gordon M. 1947. Speciation in fishes. Advances in Genetics, 1: 95—132.
231 Gorman G. C. and Dessauer H. C. 1965. Hemoglobin and transferrin electrophoresis and relationships of island populations of Anolis lizards. Science, 150, 3702: 1454—1455.
232 Gorman G. C. and Dessauer H. C. 1966. The relationships of Anolis of the requet species group (Sauria: Iguanidae). Comp. Biochem. Physiol., 19, 4: 845—853.
233 Hamilton W. D., 1967. Extraordinary sex ratios. Science, 156, 3774: 477—488.
234 Hargis W. I. 1958. Parasites and fishery problems. J. Proc. Gulf, Caribbean Fish Inst., June: 70—75.
235 Harris H. 1966. Enzyme polymorphisms in man. Proc. Roy. Soc., Lond., B 164: 298—310.
236 Harris H. 1969 a. Genes and enzymes. Proc. Roy. Soc. Lond., B 174: 1—15.
237 Harris H. 1969 b. Enzymes and protein polymorphism in human populations. Brit. Med. Bull., 25: 5—13.
238 Hartman W. L. and Raleigh R. V. 1964. Tributary homing of sockeye salmon at Brooks and Karluk Lakes, Alaska. J. Fish. Res. Bd. Canada, 21: 3: 485—504.
239 Heincke, F. 1898. Biology of the Herring. Berlin.
240 Hempel G., Blaxter I. H. S. 1961. The experimental modification of meristic characters in herring (Clupea harengus L.). J. Cons. Perman. Internat. Explorat. Mer., 26, 3: 336—346.
241 Hennemuth R. C. and Brown B. W. 1964. Relationship of length distribution of redfish to depth catch. ICNAF, Ann. Meeting June 1964, Series, No 1383, Doc. No 87: 1—4.
242 Henning V. and Yanofsky C. 1963. An electrophoretic study of mutationally altered proteins of the tryptophan synthetase of Escherichia coli. J. Mol. Biol., 6: 16—21.
243 Hile R. 1938. Morphometry of the cito, Leycichthys artedi (Le Sueur), in the lakes of the Northeastern Highlands, Wisconsin. Internat. Rev. Ges. Hydrobiol. und Hydrog., 36: 57—130.
244 Hirszfeld L., Hirszfeld K. 1919. Serological differences between the blood of different races. Lancet, 2, 197: 675—679.
245 Hjorth J. P. 1971. Genetics of Zoarces populations. I. Three loci determining the phosphoglucomutase isoenzymes in brain tissue. Hereditas, 69, 2: 233—242.
246 Hodgins H. O., Ridgway C. J. 1964. Preservation of trout and salmon erythrocites for blood typing by freezing with dimethylsulphoxide. Nature, 201, 4926: 1336—1337.
247 Hodgins H. O., Utter F. R. 1969. Variants of lactate dehydrogenase isozymes in sera of sockeye salmon (Oncorhynchus nerka).— «J. Fish. Res. Bd. Canada», 26, 1: 15—19.

248 Holmes R. S. and Whitt G. A. 1970. Developmental genetics of the esterase isozymes of Fundulus heteroclitus. Biochem. Genet., 4: 471—480.
249 Hubbs C. L. 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of water during development. Amer. Nat., 56: 360—372.
250 Hubbs C. L. 1925. Racial and seasonal variation in the Pacific Herring, California Sardine and California Anchovy. California Fish Game Comm. Sacramento Fish. Bull., 8: 1—23.
251 Hubbs C. L. 1926. The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. Amer. Nat., 68: 57—61.
252 Hubby J. L. and Lewontin R. C. 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. The number of alleles at different loci in Drosophila pseudoobscura. Genetics, 54: 577—594.
253 Huxley J. 1942. Evolution: the modern synthesis. N. — Y.
254 Irwin M. R. 1947. Immunogenetics. Adv. Genet., I: 133—148.
255 Irwin M. R. 1952. Specificity of gene effects. N. — Y.
256 Jamieson A., de Ligny W., Naevdal G. 1971. Serum esterases in mackerel, Scomber scombrus L. Cons. Internat. L'expl. Mer., Rapp. Proc. Verb., 161: 109—117.
257 Johnson A. C., Utter F. M. and Hodgins H. O. 1971. Phosphoglucomutase polymorphism in Pacific Ocean perch, Sebastodes alutus. Comp. Biochem. Physiol., 39 B: 285—290.
258 Kaplan N. O. 1965. Evolution of dehydrogenases. In: Evolving genes and proteins. Ac. Press., N. — Y., 245—279.
259 Kimura M. 1956. Rules for testing stability of a selective polymorphism. Proc. Nat. Acad. Sci., 42: 336—340.
260 Kimura M. 1968. Evolutionary rate at the molecular level. Nature, 217: 624—626.
261 Klose J., Wolf U., Hitzeroth H., Ritter N., Atkin N. M., Ohno S. 1968. Duplication of the LDH gene loci by polyploidization in the fish order Clupeiformes. Humangenetik, 5: 190—196.
262 Koehn R. K. and Johnson D. W. 1967. Serum esterase and serum transferrin polymorphisms in an introduced population of the Ictiobus cyrinellus. Copeia, 4: 805—808.
263 Koehn R. K. and Rasmussen D. I. 1967. Polymorphic and monomorphic serum esterase geterogeneity in catostomid fish populations. Biochem. Genet., I, 2: 131—144.
264 Koehn R. K., Perez J. E., Merritt R. B. 1971. Esterase enzyme function and genetical structure of populations of the freshwater fish Notropis stramineus. Amer. Naturalist, 105: 54—69.
265 Kosswig K. 1964. Problems of polymorphism in fishes.— «Copeia», 1: 69—75.

266 Kosswig, K. 1966. "A report on 40 years of genetic investigations of fish." Abhandl. und Verhandl. Naturwiss. Vor. Hamburg, 10: 13-39.

267 Kotthaus, A. 1950. "Ecological and ichthyological investigations of the redfish. 3. Investigations of the races of the redfish. A. Redfish types of Norwegian coastal waters" (in German). Ber. Dtsch. Wiss. Komm. Meeresforsch., N.F., 12, 94-114.

268 Kotthaus A. 1958. German market investigations on redfish in 1956. Length composition of the Langing. Sex ratio. Ann. Biol., Copenhague, 13: 42—48.

269 Kotthaus A. 1961 a. Preliminary remarks about redfish ololiths. Rapp. Cons. Perm. Internat. Explor. Mer., 150: 45—51.

270 Kotthaus A. 1961 b. Contributions to the race problem in redfish. Rapp. Cons. Perm. Internat. Explor. Mer., 150: 42—44.

271 Kotthaus, A., and Krefft, G. 1957. List of the fish fauna obtained in the journeys of the F.F.S. 'Anton Dorn' to Iceland and Greenland (May-July and September)." Ber. Dtsch. Wiss. Komm. Meeresforsch. N.F., N.F. No. 14.

272 Larkin P. A., 1972. The stock concept and management of Pacific salmon. In: The Stock Concept in Pacific Salmon. Univ. British. Columbia, Vancouver: 11—15.

273 Lerner J. R. 1954. Genetic homeostasis. Oliver & Boyd, N. — Y.

274 Lewontin R. C., Hubby J. L. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of Drosophila pseudoobscura. Genetics, 54, 2: 595—609.

275 Li C. C. 1966. Population genetics. Univ. og Chicago Press., Chicago.

276 Li C. C., 1967. Genetic equilibrium under selection. Biometrics, 23: 397—484.

277 Li C. C. and Horwitz D. C. 1953. Some methods of estimating the in berec-ling coefficient. J. Human Genetics, 5: 107—117.

278 Ligny W. de. 1966. Polimorphism of serum transferrins in plaice. Polimorph. Biochem. Anim., Paris: 373—376.

279 Ligny W. de. 1968. Polimorphism of plasma esterases in flounder and place. Genet. Res., 11: 179—182.

280 Ligny W. de. 1969. Serological and biochemical studies on fish populations. Oceanogr. Mar. Biol. Ann. Rev., 7: 411—513.

281 Ligny W. de. 1971 Conclusion and recommendation. Spec. Meet. Biochem. Serol. Identification Fish. Stocks. Dublin, 1969. Cons. Internat. L'expl. Mer., Rapp. Proc. Verb., 161: 176—179.

282 Lindsey C. C. 1951. Temperature controlled meristic variation in the paradise fish Macropodus opercularis (L.). Canad. J. Zool., 52: 87—98.

283 Lindsey C. C. 1958. Modification of meristic characters by light duration in kokanee, Oncorhynchus nerka. Copeia, 2: 134—136.

284 Lindsey C. C. 1962. Observations on meristic variation in ninespine sticklebacks, Pungitius pungitius, reared at different temperatures. Canad. J. Zool., 40, 7: 1237—1247.

285 Lin Chyi-Chyong, Schipmann G., Kitrell W. A. and Ohno S. 1969. The predominance of heterozygotes found in wild goldfish of lake Erie at the gene locus for sorbitol dehydrogenase. Biochem. Genet., 3: 603—607.

286 Livingstone F. B. 1960. Natural selection, desease and ongoing human evolution, as illustrated by the ABO blood groups. Human Biology, 32, 1: 17—27.

287 Lundbeck, I. 1940. "Sebastes marinus (Rotbarsch), S. viviparus (Goldbarsch), S. mentella (Tiefenbarsch)." Dtsch. Fisch. - Rotsch., 63, 2: 32-33.

288 Lush I. E. 1969. Polymorphism of the phosphoglucomutase isoenzymes in the herring (Clupea harengus). Compar. Biochem. Physiol., 30: 391—395.
289 Lush I. E. 1970. Lactate dehydrogenase isoenzymes and their genetic variation in coalfish and cod. Comp. Biochem. Physiol., 32: 23—32.
290 Magnusson I. 1959. On the sex ratio of redfish in East Greenland and Icelandic waters in 1957. Ann. Biol., Copenhague, 14: 35—39.
291 Magnusson I. 1960. Icelandic research report, 1959. Intern. Comm. Northwest Atlantic Fish. Ann. Proc., 10: 61—64.
292 Magnusson I. 1961. Sex ratio of catches of redfish and migration. ICNAF Spec. Publ., 3: 251.
293 Manwell C. and Kerst K. V., 1966. Possibilities of biochemical taxonomy of bats using hemoglobin, lactate dehydrogenase, esterases and other proteins. Comp. Biochem. Physiol., 17, 3: 741—754.
294 Manwell C. and Baker C. M. A. 1968. Genetic variation of isocitrate, malate and 6-phosphogluconate dehydrogenases in snails of the genus Cepaea: introgressive hybridization, polymorphism and pollution. Comp. Biochem. Physiol., 26: 195—209.
295 Manwell C. and Baker A. 1970. Molecular biology and the origin of species: heterosis, protein polymorphism and animal breeding. London.
296 Manwell C., Baker C. M. A. and Childres W., 1963. The genetics of haemoglobin in hybrids. I. A molecular basis for hybrid vigor. Comp. Biochem. Physiol., 10: 103—129.
297 Markert C. L. and Faulhaber J. 1965. Lactate dehydrogenase isozyme patterns of fish. J. Exptl. Zool., 159: 319—332.
298 Markert C. L., Whitt G. S. 1968. Molecular varieties in isozymes. Experientia, 24: 977—991.
299 Marr J. C. 1957. The problem of defining and recognizing subpopulations of fishes. U. S. Fish and Wildlife Serv., Spec. Sci. Rept., Fish., 208: 1—6.
300 Massaro E. J. and Markert C. L. 1968. Isozyme patterns of salmonid fishes: evidence for multiple cistrons for lactate dehydrogenase polypeptides.— «J. Exptl. Zool.», 168: 223—238.
301 Massaro E. J., Booke H. E. 1972. A mutant A-type lactate dehydrogenase subunit in Fundulus heteroclitus (Pisces: Gyprinodontidae). Copeia, 2: 298—302.
302 McCabe M. M. and Dean D. M. 1970. Esterase polymorphisms in the skipjack tuna Katsuwonus pelamis. Comp. Biochem. Physiol., 34: 671—681.
303 McCabe M. M., Dean D. M. and Olson C. S., 1970. Multiple forms of 6-phosphogluconate dehydrogenase and alphaglycerophosphate dehydrogenase in the skipjack tuna Katsuwonus pelamis Linnaeus. 31: 753—757.
304 McBough I. I. 1954. The influence of light on the number of vertebrae in the grunion Leuresthes tenuis. Copeia, 1: 23—25.
305 Merritt R. B. 1972. Geographical distribution and enzymatic properties of lactate dehydrogenase allozymes in the fathead minnow, Pimephales promelas. The Amer. Naturalist, 106, 948: 173—184.
306 Mitchill G. C. 1970. An electrophoretic comparison of hemoglobin in bats. Comp. Biochem. Physiol., 35, 3: 667—677.
307 Möller D. 1966 a. Polymorphism of serum transferrin in cod. Fiskdir. Skr. Ser. Havünders., 14: 51—60.
308 Möller D. 1966 b. Genetic differences between cod groups in the Lofoten area. Nature, 212: 824.
309 Möller D. 1968. Genetic diversity in sprawning cod along the Norwegien coast. Hereditas, 60: 1—32.
310 Möller D. 1970. Transferrin polymorphism in Atlantic salmon (Salmo salar). J. Fish. Res. Bd. Canada, 27: 1617—1625.
311 Möller D. 1971. Concepts used in the biochemical and serological identidication of fish stocks. Cons. Internat. Expl. Mer. Rapp. Proc. Verb., 161: 7—9. Dublin, 1969.
312 Möller D. and Naevdal G. 1967. Transferrin polymorphism in fishes. In: Polymorph. Biochem. Anim., Paris: 367—372.
313 Möller D. and Naevdal G. 1969. Studies on hemoglobins of some gadoid fishes. Fisk Dir. Skr. Ser. Havünders, 15: 91—97.

314 Morovic, D. 1955. "Identifying Adriatic mugiloids by means of the shape of the sagitta." Glasnik Biol. Sek. Hrvatsko Prirodosl. Drustvo. Ser. 2B, 7. (Quoted in the Abstract Journal, Biologiya, No. 9, 1958).

315 Morrison W. J. 1970. Nonrandom segregation of two lactate dehydrogenase subunit loci in trout. Trans. Amer. Fish. Soc., 99, 1: 193—206.
316 Morrison W. J. and Wright J. E. 1966. Genetic analysis of three lactate dehydrogenase isozyme systems in trout: evidence for linkage of genes coding subunits A and B. J. Exptl. Zool., 163, 3: 259—270.
317 Mottley C. Mc. 1934. The effect of temperature during development on the number of scales in the Kamloopa Jordan. Contrib. Canad. Biol.Fish.,8, 18: 253—263.
318 Mottley C. Mc., 1937. The number of vertebrae in trout (Salmo). J. Biol. Sci. Canada, 3: 169—175.
319 Naevdal G. 1967. Serological studies on sprat from norwegian waters. Contrib. Symp. Life Hist. Sprat, Lysekil, Sweden: 1—7.
320 Naevdal G. 1968. Studies on hemoglobin and serum proteins in sprat from Norwegian waters. Fiskdir. Skr. Ser. Havünders, 14: 160—182.
321 Naevdal G. 1969 a. Studies on blood proteins in herring. Fiskdir. Skr. Ser. Havünders, 15: 128—135.
322 Naevdal G. 1969 b. Studies on serum esterase in herring and sprat. Fiskdir. Skr. Ser. Hevünders, 15: 83—90.
323 Naevdal G. 1971. Distributions of multiple forms of lactate dehydrogenase, aspartate aminotransferase and serum esterase in herring from Norwegian waters. Cons. Internat. Expl. Mer. Rapp. Proc. Ver., 161: 32.
324 Neave F. 1958. The origin and speciation of Oncorhynchus. Trans. Roy. Soc. Canada, 52, 5: 25—49.
325 Neaves W. B. 1969. Adenosine desaminase phenotypes among sexual and partenogenetic lizards in the genus Cnemidophorus (Teliidae). J. Exp. Zool., 171, 2: 175—183.
326 Neaves W. B. and Gerald P. S. 1968. Lactate dehydrogenase isozymes in partenogenetic teiid lizards. Science, 160: 1004—1005.
327 Nefvodov G. N. 1971. Serum haptoglobins in the marinus and mentella types of North Atlantic redfish. Cons. Internat. Expl. Mer. Rapp. Proc. Verb., 161: 126—129.
328 Nicol P. I. and O'Gower A. K. 1967 Haemoglobin variation in Anadara trapezia (Mollusca, Bivalvia). Nature, Lond., 216: 684.
329 Northcote T. G., Williscroft S. N. and Tsuyuki H. 1970. Meristic and lactate dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. J. Fish. Res. Bd. Canada, 27, 11: 1987—1995.
330 Numachi Ken-ichi. 1970. Polymorphism of malate dehydrogenase and genetic structure of juvenile population in sayry Cololabis saira. Bull. Jap. Soc. Sci. Fish., 36, 12: 1235—1241.
331 Numachi Ken-ichi. 1972 a. Genetic control and subunit composition of lactate dehydrogenase in Pseudorasbora parva. Japan. J. Genet., 47, 3: 193—201.
332 Numachi Ken-ichi. 1972 b. Genetic polymorphism of tetrazolium oxidase in black rockfish. Bull. Japan. Soc. Sci. Fish., 38, 7: 789.
333 Numachi Ken-ichi, Matsumiya Y. and Sato R., 1972. Duplicate genetic loci and variant forms of malate dehydrogenase in chum salmon and rainbow trout.—«Bull. Jap. Soc. Sci. Fish.», 38, 7: 699—706.
334 Nyman L. 1965. Inter- and intraspecific variations of proteins in fishes. Ann. Acad. Reg. Sci. Ups., 9: 1—18.
335 Nyman L. 1967. Protein variations in Salmonidae Rep. Inst. Freshwater Res., Drottningholm, 47: 6—38.
336 Nyman L. and Westin L. 1968. On the problem of sibling species and possible intraspecific variation in fourhorn sculpin, Myoxocephalus quadricornis (L.). Ibidem, 48: 57—66.
337 Odense P. H., Allen T. H. and Leung T. 1966. Multiple forms of lactate dehydrogenase and aspartate aminotransferase in herring (Clupea harengus harengus L). Canad. J. Biochem., 44: 1319—1326.
338 Odense P. H., Leung T. C., Allen T. H. and Parker E. 1969. Multiple forms of lactate dehydrogenase in the cod, Gadus morhua L. Biochem. Genet., 3: 317—334.
339 Ohno S. 1970a. The enormous diversity in genome sizes of fish as a reflection of nature's extensive experiments with gene duplication. Trans. Amer. Fish. Soc., 99, 1: 120—131.
340 Ohno S. 1970b. Evolution by gene duplication. Springer Verlag, Berl.
341 Ohno S., Wolf U., Atkin N. B. 1968. Evolution from fish to mammals by gene duplications. Hereditas, 59, 1: 169—187.
342 O'Gower A. K., Nicol P. J., 1968. A latitudinal cline of haemoglobins in a bivalve mollusc. Heredity, 23, 4: 485—491.
343 O'Rourke F. J. 1961. An immunological and chromatographic study of Sebastes marinus and Sebastes mentella. Internat. Comm. Northwest Atlantic Fish., Redfish Symp, Spec. Publ., 3: 100—103.

344 Owen D. F. 1970. Inheritance of sex ratio in the butterfly Acraea encedon. Nature, 225, 5233: 662—663.
345 Pantelouris B. M., Payne R. H. 1968. Genetic variation in the eel. I. The detection of haemoglobin and esterase polymorphisms. Genet. Res., II, 3: 319—325.
346 Parrish B. B. 1964. Notes on the identifications of subpopulation of fish by serological and biochemical methods. F.A.O. Fish. Biol. Techn. Pap., No 36: 1—9.
347 Payne R. H., Child A. R., Forrest A. 1971. Geographical variation in the atlantic salmon. Nature, Lond., 231: 250—252.
348 Peacock A. C., Bunting S. L., Queen K. G. 1965. Serum protein electrophoresis in acrylamide gel. Science 147, 1451.
349 Perriard J.-C., Scholl A., Eppenberger H. M. 1972. Comparative studies on creatine kinase isozymes from skeletal muscle and stomach of trout. J. Exper. Zool., 182, 1: 119—126.
350 Petras M. L., 1967. Studies of natural populations of Mus. I. Biochemical polymorphism and their bearing on breeding structure Evolution, 21, 2: 259—274.
351 Petras M. L., Reimer J. D., Biddi F. G., Martin J. E. and Linton R. S., 1969. Studies of natural populations of Mus. Y. A surwey of nine loci for polymorphisms. Canad. J. Genet. Cytol., 11, 3: 497—513.
352 Poulik M. D. 1957. Starch gel electrophoresis in a discontinuous system of buffers. Nature, 180: 1477.
353 Poulsen M. 1962. Length distribution and sex ratio of commercially caught redfish (Sebastes) from the ICNAF area based on sampling Year Book vol. I—4. ICNAF Ann. Meet. June 1962, Doc. No 2.
354 Prehn L. M. and Rasch R. M. 1969. Cytogenetic studies of Poecilia (Pisces). I. Canad. J. Gen. Cytol., II, 4: 880—895.
355 Race R. R. and Sanger R. 1962. Blood groups in man. Oxford.

356 Raunich, L., Battaglia, B., Callegarini, C, and Mozzi, C. 1966a. "Hemoglobin polymorphism of Gobius jozo of the Venice Lagoon." Ac. Naz. Lincei, Rend. Sci. Fish. Nat. Ser. VIII, 41, 6: 581-585.

357 Raunich, L., Callegarini, C., and Cavicchili, G. 1966b. "Hemoglobin polymorphism and systematic characteristics of the genus Ictalurus of Northern Italy." Arch. Zool. Ital., 51: 497-510.

358 Raunich, L., Battaglia, B., Callegarini, C., and Mozzi, C. 1967. "Hemoglobin polymorphism of the genus Gobius of the Venice Lagoon." Atti Ist. Veneti Sci., 125: 87-105.

359 Rasch E. M., Darnell R. M., Kallman K. D., Abramoff P. 1965. Cytophotometric evidence for triploidy in hybrids of the gynogenetic fish, Poecilia formosa. J. Exp. Zool., 160, 2: 155—169.
360 Rasch E. M., Prehn L. M., Rasch R. W. 1970. Cytogenetic studies of Poecilia (Pisces). II. Chromosoma (Berl.), 31: 18—40.
361 Rasch E. M., Prehn L. M. 1969. Cytogenetic studies of Poecilia. J. Cell. Biol., 43: 112.
362 Rasmussen D. I. 1964. Blood group polymorphism and inbreeding in natural populations of the deer mouse Peromyscus maniculatus. Evolution, 18, 2: 219—229.
363 Rendel T. 1958. Studies of cattle blood groups. Acta, Arg. Scand., 8.

364 Ridgway G. I., Cushing J. E. and Durall G. L. 1958. Serological differentiation of populations of sockeye salmon (O. nerka). U. S. Fish and Wildlife Sp. Sci. Rep. Fish., 257: 1—9.

365 Ridgway G. I. and Clontz G. W. 1961. Blood types in pacific salmon. Bull. Int. North. Pacific Fish. Comm., 5: 49—55.

366 Ridgway G. I., Sherburn S. W. and Lewins R. D. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Amer. Fish. Soc., 99, 1: 147—151.

367 Roberts F. L., Wohnus I. F. and Ohno S. 1969. Phosphoglucomutase polymorphism in the rainbow trout, Salmo gairdnerii. Experientia, 25, 10: 1109—1110.

368 Roedel Ph. M. 1954. California's tuna and yellowtail tagging programs. Trans. Nineteenth N. Am. Wild. Conf., March 8—10: 404—417.

369 Ronald A. P. and Tsuyuki H. 1971. The subunit structures and the molecular basis of the multiple hemoglobins of two species of trout, Salmo gairdneri and S. clarki clarki. Comp. Biochem. Physio., 39, B: 195—202.

370 Rychkov Yu. G. Studies on the process of isolation among some tribes in the Pamirs and the Caucasus VII in Congr Internat Sci. Anthropol. at Ethnol., 1964, 1: 275—282.

371 Sanders B. C. and Wright J. B. 1962. Immunogenetic studies in two trout species of the genus Salmo. Ann. N.—Y. Acad. Sci., 97, 1: 116—130.

372 Sanger R. 1955. An association between the P— and Gay systems of blood groups. Nature (Lond.), 176: 1163—1164.

373 Schaeffer H. 1961. A biochemical contribution to the redfish problem. Rapp. Proc. — Verb. Reun. Cons. Perm. Internal Expl. Mer., 156: 104—110.

374 Schmidt J. 1917. Zoarces viviparus and local races of the same. C. R. Trav. Lab. Carlsberg, Copenh., 13: 279—396.

375 Schmidt J. 1930. The Atlantic cod (Gadus calarias L.) and local races of the same. C. R. Trav. Lab. Carlsberg, Copenh., 18, 6: 1—72.

376 Schmidtke J., Engel W. 1972. Duplication of the gene loci coding for the supernatant aminotransferase by polyploidization in the fish family Cyprinidae. Experientia, 28, 8: 976—978.

377 Schultz R. J. 1961. Reproductive mechanism of unisexual and bisexual strains of the viviparous fish Poeciliopsis. Evolution, 15: 302—325.

378 Schultz R. J. 1966. Hybridization experiments with an all — female fish of the genus Poeciliopsis. Biol. Bull., 130: 415—429.

379 Schultz R. J. 1967. Gynogenesis and triploidy in the viviparous fish Poeciliopsis. Science, 157: 1564—1567.

380 Schultz R. J. 1969. Hybridization, unisexuality, and polyploidy in the teleost Poeciliopsis (Poeciliidae) and other vertebrates. Am. Naturalist, 103, 934: 605—619.

381 Schultz R. J. and Kallman K. D. 1968. Triploid hybrids between the all — female teleost Poecilia formosa and Poecilia sphenops. Nature, 219: 280—282.

382 Selander R. K., Yang S. Y., Lewontin R. C. and Johnson W. E. 1970. Genetic variation in the horseshoe crab (Limulus polyphemus), a phylogenetic «relic». Evolution, 24, 2: 402—414.

383 Shaw C. R. 1965. Electrophoretic variation in enzymes. Science, 149: 936—943.

384 Shaw Ch. R. and Barto E. 1963. Genetic evidence for the subunit structure of lactate dehydrogenase isozymes. Genetics, 50: 211—214.

385 Shows T. B. and Ruddle F. H. 1968. Malate dehydrogenase: Evidence for tetrameric structure in Mus musculus. Science, 160: 1356—1357.

386 Shontz N. N., 1968. Electrophoretic patterns of proteins of Salamanders of the genus Desmognathus (Family Pilethodontidae). Copeia, 4: 683—692.

387 Sick K. 1961. Haemoglobin polymorphism in fishes. Nature, 192, 4805: 894—896.

388 Sick K., 1965a. Haemoglobin polymorphism of cod in the Baltic and Danish Belt Sea. Hereditas, 54: 19—48.

389 Sick K., 1965b. Haemoglobin polymorphism of cod in the North Sea and the North Atlantic Ocean. Hereditas, 54: 49—73.

390 Sick K., Westergaard M. and Frydenberg O., 1962. Hemoglobin pattern and chromosome number of american, european and japanese eels (Anguilla). Nature, 192: 1001—1002.

391 Sick K., Frydenberg O., Nielsen J. T. 1963. Haemoglobin patterns of plaice, flounder and their natural and artificial hybrids. Nature, 198, 4878: 411—412.

392 Simonsen V., Frydenberg O. 1972. Genetics of Zoarces populations. II. Three loci determining esterase isozymes in eye and brain tissue. Heredi- [illegible] 70, 2: 243—247.

393 Sindermann C. J. 1961a. Parasitological tags for redfish of the western North Atlantic. Rapp. Proc. — Verb., 150: 111—117.

394 Sindermann C. J. 1961b. Serological techniques in fishery research. Trans. 26th N. Am. Wild. Natur. Resources Conf. Wash., D. C.: 298—309.

395 Sindermann C. J. 1962. Serological studies of Atlantic redfish. U. S. Fish. Wildl. Serv., Fish. Bull., 191: 351—354.

396 Sindermann C. J. 1964. Immunogenetic and biochemical approaches to the identification of marine subpopulations. Proc. Symp. Exp. Mar. Ecol., Occ. Publ. No. 2, Univ. Rhode Isl.: 33—38.

397 Sindermann C. J. 1966. Diseases of marine fishers. Adv. Mar. Biol., 4: 1—89.

398 Sindermann C. J. and Mairs D. F. 1961. A blood group system for spiny dogfish, Squalus acanthias L. Biol. Bull., 120, 3: 401—410.

399 Sindermann C. J., Honey K. A. 1964. Serum hemagglutinins of the winter skate Raja ocellata Mitchill, from the western North Atlantic ocean. Copeia, I: 139—144.

400 Sprague L. M. 1967. Multiple molecular forms of serum esterase in three tuna species from the Pacific ocean. Hereditas, 57: 198—204.

401 Sprague L. M. and Vrooman A. M. 1962. A racial analysis of the Pacific sardine (Sardinops caerulea) based on studies of erythrocyte antigens. Ann. N.—Y. Acad. Sci., 97: 131—138.

402 Sprague L. M. and Holloway J. R. 1962. Studies of the erythrocyte antigenes of the skipjack tuna (Katsuwonus pelamis). Amer. Natur., 96: 233—238.

403 Sprague L. M., Holloway J. R. and Nakashima L. I. 1963. Studies of the erythrocyte antigenes of albacore, bigeye, skipjack, and yellowfin tunas and their use in subpopulation identification,: 1381—1395. In H. Rose, Jr. (ed) Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species. La Jolla, Calif., 2—14 July 1962. FAO Fish. Rept. 6 (3).

404 Sprague L. M. and Nakashima L. I. 1962. Studies on the erythrocyte antigenes of the skipjack tuna (Katsuwonus pelamis), In J. C. Marr (ed.) Pacific Tuna Biology Conference, Honolulu, Hawaii, Aug. 14—19, 1961. U. S. Fish Wildl. Serv., Spec. Sci. Rept. Fish. 415 (Abstr.).

405 Sprague L. M. and Fujino K. 1965. Serum esterase polymorphisms of the skipjack and the yellowfin tunas. Genetics, 52: 467—477.

406 Stegeman J. J., Goldberg E. 1972. Inheritance of hexose—6—phosphate dehydrogenase polymorphism in brook trout. Biochem. Genet., 7: 279—288.

407 Suzuki A. 1961. Serological studies of the races of tuna. V. The blood groups of yellowfin tuna. Rep. Nankai Reg. Fish. Res. Lab., 13: 53—67.

408 Suzuki A. 1962a. Serological studies of the races of tuna. VI. Bigeye—3 antigene occurred in the albacore. Rep. Nankai Reg. Fish. Res. Lab., 16: 67—78.

409 Suzuki A. 1962b. On the blood types of yellowfin and bigeye tuna. Amer. Natur., 96, 889: 239—246.

410 Suzuki A. 1967. Blood type of fish. Bull. Jap. Soc. Sci. Fish., 33. 4: 372—381.

411 Suzuki A. 1968. Studies on the blood types of fish with radioactive antibodies. I. Bull. Tokai. Reg. Fish. Res. Lab., 56: 117—124.

412 Suzuki A. and Higasa S. 1962. Serological studies of the races of tuna VII. Preliminary investigation on the plant hemagglutinins. Rep. Nankai Reg. Fish. Res. Lab., 16: 71—82.

413 Suzuki A. and Morio T. 1959. Serological studies of the races of tuna. III. Preliminary investigation on the antigenes in tunas sera by the agar plate diffusion method. Rep. Nankai Reg. Fish. Res. Lab., II: 165—173.

414 Suzuki A. and Morio T. 1960. Serological studies of the races of tuna. IV. The blood groups of the bigeye tuna. Rep. Nankai Reg. Fish. Res. Lab., 12: 1—13.

415 Suzuki A., Morio T. and Mimoto K. 1959. Serological studies of the races of tuna. II. Blood groups frequencies of the albacore in Tg system. Part I. Comparison of the Indian and the northwestern Pacific Ocean. Rep. Nankai Reg. Fish. Res. Lab., II: 17—23.

416 Suzuki A., Shimizu Y. and Morio T. 1958. Serological studies of the races of tuna. I The fundamental investigations and the blood groups of albacore. Rep. Nankai Reg. Fish. Res. Lab., 8: 104—116.

417 Szidat, L. 1961. An Attempt to Establish a Zoogeography of the South Atlantic With the Aid of Indicator Parasites of Marine Fish (in German). Jena, Fischer.

418 Tåning A. V. 1952. Experimental study of meristric characters in fishes. Biol. Rev. Cambrige Philosoph. Soc., 27, 2: 169.

419 Tashian R. E., Shreffer D. C. and Shows T. B., 1968. Genetic and phylogenetic variation in the different molecular forms of mammalian erythrocyte carbonic anhydrases. Ann. N. Y. Acad. Sci., 151: 64—77.

420 Templeman W. 1953. Knowlege of division of stocks of cod, haddock, redfish and american plaice in subareas 3 and 2 of the Northwest Atlantic Convention Area. ICNAF Ann. Proceed., 3: 62—66.

421 Templeman W. 1959. Redfish distribution in the North Atlantic. Bull. Fish. Res. Board Canada, 120: 1—171.

422 Templeman W. 1962. Divisions in cod stocks of the Northwest Atlantic. Ann. Meeting ICNAF Redbook, part 3: 79—123.

423 Templeman W. and Squirs H. J. 1960. Incidence and distribution by Sphyrion lumpi (Krøyer) on the Redfish Sebastes marinus (L.) of the Western North Atlantic, 1949—1953, J. Fish. Res. Bd. Canada, 17, 1: 9—31.

424 Templeman W. and Pitt T. K. 1961. Vertebrae numbers of redfish, Sebastes marinus (L.) in the North — West Atlantic, 1947, 1954. Internat. Comiss. North — West Atlantic Fish. Spec. Publ., 3: 56—89.

425 Trujillo J. M., Walden B., O'Neill P. and Astall H. B. 1967. Inheritance and sub — unit composition of haemoglobin in the horse, donkey and their hybrids. Science, 213, 1: 88—90.

426 Tsuyuki H. 1966. Comparative electrophoregrams of hemoglobins and other proteins in fish. Proc. XI—th Pacific. Sci. Congr., Abstr. v. 7: 1.

427 Tsuyuki H., Roberts E., 1966. Inter — species relationships within the genus Oncorhynchus based on biochemical systematics. J. Fish. Res. Bd. Canada, 23, 1: 101—107.

428 Tsuyuki H., Roberts E., Vanstone W. E., Markert J. R. 1965a. The species specificity and constancy of muscle myogen and emhoglobin electrophoregrams of Oncorhynchus. J. Fish. Res. Bd. Canada, 22, 1: 215—217.

429 Tsuyuki H., Roberts E. and Vanstone W. E. 1965b. Comparative zone electrophoregrams of muscle myogens and blood hemoglobins of marine freshwater vertebrates and their application to biochemical systematics. J. Fish. Res. Bd. Canada. 22 1: 203—213.

430 Tsuyuki H., Uthe J. F., Roberts E. and Clarke L. W. 1966. Comparative electrophoregrams of Coregenus clupeaformis, Salvelinus namaycush, S. alpinus, S. malma and S. fontinalis from the family Salmonidae. J. Fish. Res. Bd. Canada, 23, 10: 1599—1606.

431 Tsuyuki H., Roberts E. and Kerr R. H. 1967. Comparative electrophoregrams of the family Catostomidae. J. Fish. Res. Bd. Canada, 24, 2: 299—301.

432 Tsuyuki H., Roberts E., Lowes R. H. and Hadaway W., and Westrheim S. J. 1968. Contribution of protein electrophoresis to rockfish (Scorpaenidae) systematic. J. Fish. Res. Bd. Canada, 25, II: 2477—2501,

433 Tsuyuki H. and Westrheim S. J. 1970. Analyses of the Sebastes aleutianus — S. melanostomus complex, and description of a new scorpaenid species, Sebastes caenaematicus, in the northeast Pacific Ocean. J. Fish. Res. Bd. Canada, 27, 12: 2233—2254.

434 Tsuyuki H., Ronald A. P. 1970. Existance in salmonid hemoglobins of molecular species with three and four different polypeptides. J. Fish. Res. Bd. Canada, 27: 1326—1328.

435 Tsuyuki H. and Ronald A. P. 1971. Molecular basis for multiplicity of Pacific salmon hemoglobins: evidence for in vivo existence of molecular species with up to four different polypeptides. Comp. Biochem. Physiol., 39 B: 503—522.

436 Ushakov B. P. Thermostability of cells and proteins of poikilotherms and its significance in speciation. 1964, — «Physiol. Revs», 44, 3, p. 518—560.

437 Uthe J. F., Roberts E., Clarke L. M. and Tsuyuki H. 1966. Comparative electrophoregrams of representatives of the families Petromyzonidae, Esocidae, Centrarchidae and Percidae. J. Fish. Res. Bd. Canada, 23, 11: 1663—1671.

438 Utter F. M. 1969. Transferrin variants in Pacific hake (Merluccius productus). J. Fish. Res. Bd. Canada, 26, 12: 3268—3271.

439 Utter F. M. and Ridgway G. J. 1967a. A serologically detected serum factor associated with maturity in English sole, Parophys vetulus and Pacific halibut, Hippoglossus stenolepis. Fish. Bull. U. S., 66: 47—58.

440 Utter F. M. and Ridgway G. J. 1967b. Cross — reactive properties of antisera preparated in rabbits by stimulations with teleost vitellins. Ibid., 66: 209—213.

441 Utter F. M. and Hodgins H. O. 1970. Phosphoglucomutase polymorphism in sockeye salmon. Comp. Biochem. Physiol., 36, 1: 195—199.

442 Utter F. M., Hodgins H. O. 1972. Biochemical genetic variation at six loci in four stocks of rainbow trout. Trans. Amer. Fish. Soc., 101, 3: 494—502.

443 Utter F. M., Ames W. E., Hodgins H. O. 1970. Transferrin polymorphism in coho salmon (Oncorhynchus kisutch). J. Fish. Res. Bd. Canada, 27: 2371—2373.

444 Utter F. M., Stormont C. J., Hodgins H. O. 1970. Esterase polymorphism in vitreous fluid of Pacific hake Merlluccius productus. Anim. Blood. Groups Biochem. Genet 1: 69—82.

445 Vanstone W. E., Roberts E. and Tsuyuki H. 1964. Changes in the multiple haemoglobin patterns of some Pacific salmon Genus Oncorhynchus, during the Parr — Smolt transformation. Canad. J. Physiol. Pharmacol., 42: 697—703.

446 Vessel E. S., Ed. 1968. Introduction multiple molecular forms of enzymes. Ann. N. Y. Acad. Sci., 1—689.

447 Vladykov V. D. 1934. Environment and taxonomic characters of fishes. Trans. Roy. Canad. Inst., 20: 99—140.

448 Vladykov V. D. 1963. A review of salmonid genera and their broad geographical distribution, Trans. Roy. Soc. Canada, I, Ser. 4, sect. 3: 459—504.

449 Vrijenhoek R. C. 1972. Genetic relationships of unisexual hybrid fishes to their progenitors using lactate dehydrogenase isozymes as gene marcers (Poeciliopsis, Poeciliidae). Amer. Naturalist, 106, № 952: 754—766.

450 Vrooman A. M. 1964. Serologically differentiated subpopulations. of the Pacific sardine, Sardinops caerulea. J. Fish. Res. Bd. Canada., 21, 4: 691—701.

451 Watt W. B. 1972. Intragenic recombination as a source of population genetic variability. Amer. Natiralist, 106, 952: 737—753.

452 Wenner A. M. 1972. Sex ratio as a function of size in marine crustacea. Amer. Nat., 106, 949: 321—350.

453 Westrheim S. J. and Tsuyuki H. 1967. Sebastodes reedi, a new scorpaenid fish in the Northeast Pacific Ocean. J. Fish. Res. Bd. Canada, 24, 9: 1945—1954.

454 Westrheim S. J. a. Tsuyuki H., 1971. Taxonomy, distribution, and biology of the northern rockfish, Sebastes polyspinis. J. Fish. Res. Bd. Canada, 28: 1621—1627.

455 White M. J. D. 1954. Animal cytology and evolution. Cambridge, 1954.

456 White M. J. D. 1968. Models of speciation. Science, 159, 3819: 1065—1070.

457 Whitt G. S. 1970a. Genetic variations of supernatant and mitochondrial malate dehydrogenase isozymes in the teleost, Fundulus heteroclitus. Experientia, 26: 734—736.

458 Whitt G. S. 1970b. Developmental genetics of lactate dehydrogenase isozymes of fish. J. Exp. Zool., 175: 1—36.

459 Wiener S. A. 1966. The blood groups. Three fundamental problems: serology, genetics and nomenclature. Blood, 27, 1: 110—126.

460 Wilder D. G. 1952. A comparative study of anadromus and freshwater populations of brook trout, Salvelinus fontinalis Mitchill. J. Fish. Res. Bd. Canada, 9, 4: 105—115.

461 Wilkins N. P. 1966. Haemoglobin polymorphism and ontogeny in herring and sprat. Comp. Biochem. Physiol., 17: 1141—1158.

462 Wilkins N. P. 1970. The sub-unit composition of the haemoglobins of the Atlantic salmon (Salmo salar L.). Biochem. Biophys. Acta, 214: 52—63.

463 William B., Neaves and Park S. Gerald, 1968. Lactate Dehydrogenase Isozymes in Parthenogenetic Teiid Lizards (Cnemidophorus). Science, 160, 3831: 1004—1005.

464 Williscroft S. N. and Tsuyuki H. 1970. Lactate dehydrogenase systems of rainbow trout. Evidence for polymorphism in liver and additional subunits in gills. J. Fish. Res. Bd. Canada, 27, 9: 1563—1567.

465 Wolf, U., Engel, W., and Faust, J. 1970. "On the mechanism of diploidization in the evolution of vertebrates: coexistence of tetrasomal and disomal gene loci of the isocitrate dehydrogenases in the rainbow trout (Salmo iridens). Humangenetik, 9: 150-156.

466 Wright J. E. and Atherton L. M. 1968. Genetic control of interallelic recombination at the LDH-B locus in brook trout. Genetics, 60: 240.

467 Wright J. E. and Atherton L. M. 1970. Polymorphisms for LDH and [illegible] loci in brook trout populations. Trans. Am. Fish. Soc., 99, 1: 179–182.

468 Wright S. 1931. Evolution in Mendelian populations. Genetics, 16, 2: 97—159.

469 Wright S. 1943. An analysis of local variability of flower color in Linanthus parryae. Genetics, 28, 2: 139—156.

470 Wright S. 1951. The genetical structure of populations. Ann. Eugen., 15: 323—354.

471 Wunder, W. 1939. "The 'starved' and 'fattened' types of the carp (Cyprinus carpio L.)." Zs. Morphol. Ökol. Tiere, 35, 4: 594-614.

472 Yamanaka H., Yamaguchi K. and Matsuura F., 1965. Starch gel electrophoresis of fish hemoglobins. II. Electrophoretic patterns of hemoglobin of various fishes. Bull. Jap. Soc. Sci. Fish., 31, 10: 833—839.

473 Yamanaka H., Yamaguchi K., Hashimoto K. and Matsuura F., 1967. Starch — gel electrophoresis of fish hemoglobins. III. Salmonoid Fishes. Bull. Jap. Soc. Sci. Fish., 33, 3: 195—203.

СПИСОК ИСПОЛЬЗОВАННОЙ ЛИТЕРАТУРЫ

1 Абакумов В. А. Сезонные расы проходных рыб.— «Вопросы ихтиологии», 1961, т. 17, с. 179—190.

2 Александров А. Н. Анчоусы Азово-Черноморского бассейна, их происхождение и таксономические обозначения.— «Труды Керченск. науч. рыбохоз. ст.», 1927, т. 1, вып. 2—3.

3 Алтухов Ю. П. Об иммуногенетическом подходе к проблеме внутривидовой дифференциации у рыб.— В кн.: Успехи современной генетики. М., 1969а, вып. 2, с. 161—195.

4 Алтухов Ю. П. О соотношении моно- и полиморфизма гемоглобинов в микроэволюции рыб. ДАН СССР, 1969б, т. 189, № 5, с. 1115—1117.

5 Алтухов Ю. П. Генетика популяций рыб.— «Природа», 1971, № 3, с. 44—57.

6 Алтухов Ю. П., Михалев Ю. А. Различие в размерных соотношениях отолитов «крупной» и «мелкой» черноморских ставрид, определенных по признаку клеточной теплоустойчивости. — В кн.: Вопросы физиологии рыб Черного и Азовского морей. М., 1964, с. 23—29.

7 Алтухов Ю. П., Рычков Ю. Г. Популяционные системы и их структурные компоненты. Генетическая стабильность и изменчивость. — «Журнал общей биологии», 1970, т. 31, № 5, с. 507—526.

8 Алтухов Ю. П., Ратькин Э. В. Исследование генотипической обусловленности индивидуальной изменчивости теплоустойчивости изолированных клеток.— «Цитология», 1968, т. 10, № 12, с. 1546—1554.

9 Алтухов Ю. П., Апекин В. С., Лямайский В. В. Основные принципы исследования внутри и межвидовой дифференциации рыб серологическими методами.— В кн.: Вопросы физиологии рыб Черного и Азовского морей. М., 1964, с. 53—71.

10 Алтухов Ю. П., Шефедов Г. Н., Паюсова А. Н. Цитофизиологический анализ дивергенции золотистого и кловорылого окуней Северо-Западной Атлантики.— В кн.: Изменчивость теплоустойчивости клеток животных в онто- и филогенезе, Л., 1967, с. 82—98.

11 Алтухов Ю. П., Рычков Ю. Г. Генетический мономорфизм видов и его возможное биологическое значение.—«Журнал общей биологии», 1972, т. 33, № 3, с. 281—300.

12 Алтухов Ю. П., Салменкова Е. А., Сачко Г. Д. Дупликация и полиморфизм генов лактатдегидрогеназы у тихоокеанских лососей. ДАН СССР, 1970, т. 195, № 3, с. 711—714.

13 Андриашев А. П. Рыбы северных морей СССР. М.—Л., Изд-во АН СССР, 1954. 567 с.

14 Астауров Б. Л. Экспериментальная полиплоидия и гипотеза непрямого (опосредованного партеногенезом) происхождения естественной полиплоидии.— «Генетика», 1969, т. 5, № 7, с. 129—148.

15 *А*-система групп крови атлантической сельди.— «Генетика», 1968, т. 4, № 2, с. 155—167. Авт.: Ю. П. Алтухов, К. А. Трувеллер, В. С. Зенкин, Н. С. Гладкова.

16 Балахнин И. А., Потапов М. И. Выявление групповой дифференциации эритроцитов плотвы (Rutilis rutilis L.) гемагглютининами.— «Журнал общей биологии», 1963, т. 24, № 6, с. 428—434.

17 Баранецкова А. С. Материалы к распределению морских окуней рода Sebastes. ДАН СССР, 1957, т. 113, № 2, с. 468—471.

18 Баранов О. К. Иммунохимический анализ эволюции белков.— «Успехи современной биологии», 1972, т. 74, № 3, с. 420—438.

19 Барсуков В. В. О систематических отношениях морских окуней рода Sebastes северо-западной части Атлантического океана. ДАН СССР, 1968, т. 183, № 2, с. 479—482.

20 Барсуков В. В., Захаров Г. П. Морфологические и биологические особенности американского морского окуня.— «Труды ПИНРО», 1972, № 28, с. 143—173.

21 Берг Л. С. Яровые и озимые расы у проходных рыб.— «Известия АН СССР. Отдел математич. и естеств. наук», 1931, № 5, с. 1115—1137.

22 Берстон М. Гистохимия ферментов. М., «Мир», 1965, 464 с.

23 Бойд В. Введение в иммунохимическую специфичность. М., ИЛ, 1963, 186 с.

24 Бородатов В. А., Травин В. И. Основные этапы советских исследований по морскому окуню Северной Атлантики.— В кн.: Сов. рыбохоз. исследования в морях европейского Севера, М., 1960, с. 277—284.

25 Брайцева О. А. Стратиграфия четвертичных отложений и оледенения Камчатки, М., «Наука», 196[illegible], 226 с.

26 Буздалин Ю. И., Елизаров А. А. Гидрологические условия в районах Ньюфаундлендских банок и Лабрадора.— В кн.: Сов. рыбохоз. исследования в северо-западной части Атлантического океана. М., 1962, с. 155—171.

27 Вагнер Р. Митчел Г. Генетика и обмен веществ. М., ИЛ, 372 с.

28 Виноградов К. А. К биологии северо-западной части Черного моря.— «Зоол. журн.», 1956, т. 35, вып. 4, с. 492—500.

29 Грабар П., Буртен П. Иммуноэлектрофоретический анализ. М., ИЛ., 1963, 206 с.

30 Данилевский Н. Н. Миграция черноморской хамсы и факторы ее обуславливающие.— «Труды АзчерНИРО», 1958, вып. 17, с. 51—74.

31 Данилевский Н. Н. О проникновении черноморской хамсы в Азовское море и сопутствующих условиях среды.— «Труды АзчерНИРО», 1960, вып. 18, с. 118—129.

32 Данилевский Н. Н. Важнейшие факторы, определяющие сроки и районы образования промысловых скоплений черноморской хамсы.— «Труды АзчерНИРО», 1964, вып. 22, с. 115—131.

33 Даревский И. С., Куликова В. Н. Естественная триплоидия в полиплоидной группе кавказских скальных ящериц Lacerta saxicola Ewersmann как следствие гибридизации между двуполыми и партеногенетическими формами этого вида. ДАН СССР, 1964, т. 158, № 1, с. 202—204.

34 Даревский И. С., Даниелян Ф. Д. Диплоидные и триплоидные особи в потомстве партеногенетических самок скальных ящериц, естественно спаривающихся с самцами близких бисексуальных видов. ДАН СССР, 1969, т. 184, № 3, с. 727—730.

35 Дементьева Т. Ф., Танасийчук В. С. К вопросу о расах трески в Баренцовом море.— «За рыбную индустрию Севера», 1935, № 5, с. 40—43.
36 Догель В. А., Быховский Б. Е. Паразиты рыб Каспийского моря.— «Труды комплексного изучения Каспийского моря», 1939, вып. 7, с. 118—120.
37 Дубинин Н. П. Генетико-автоматические процессы и их влияние на механизмы органической эволюции.— «Журнал экспериментальной биологии», 1931, № 7, с. 463—470.
38 Дубинин Н. П. Эволюция популяций и радиация. М., Атомиздат, 1966, 743 с.
39 Дубинин Н. П., Глембоцкий Я. Л. Генетика популяций и селекция. М., «Наука», 1967, 591 с.
40 Дубинин Н. П., Романов Д. Д. Генетическое строение вида и его эволюция.— «Биологический журнал», 1932, т. 1, вып. 5—6, с. 52—95.
41 Захаров Г. П. О биологии золотистого окуня Западной Гренландии.— В кн.: Сов. рыбохоз. исследования в северо-западной части Атлантического океана, М., 1962, с. 319—330.
42 Зернов М. С. Систематическая и биологическая характеристика воблы района, прилегающего к Мертвому Култуку.— В кн.: Заливы Каспийского моря. Астрахань, 1938, вып. 2, с. 35—54.
43 Иммуногенетический анализ внутривидовой дифференцировки европейского анчоуса, обитающего в Черном и Азовском морях. Сообщение I.— «Генетика», 1969, т. 5, № 4, с. 50—64. Авт.: Ю. П. Алтухов, В. В. Лиманский, А. Н. Паюсова, К. А. Трувеллер.
44 Иммуногенетический анализ внутривидовой дифференцировки европейского анчоуса, обитающего в Черном и Азовском морях. Сообщение II. Элементарные популяции и их место в генетико-популяционной структуре вида.— «Генетика», 1969, т. 5, № 5, с. 81—94 Авт.: Ю. П. Алтухов, В. В. Лиманский, А. Н. Паюсова, К. А. Трувеллер.
45 Караваев Г. А. Миграции воблы (Rutilis rutilis caspicus Jak.) в Северном Каспии.— «Труды ВНИРО», 1939, т. 10, с. 33—80.
46 Карасев Б. Е., Саускан Е. И. Распределение донных рыб у Ньюфаундленда и Лабрадора и возможности прогнозирования промысловых концентраций.— «Труды АтлантНИРО», 1963, вып. 10, с. 124—141.
47 Кирпичников В. С. К вопросу об образовании рас у рыб.— «Биол. журн.», 1933, т. 2, вып. 6, с. 609—627.
48 Кирпичников В. С. Биолого-систематический очерк корюшки Белого моря, Чешской губы и р. Печоры.— «Труды ВНИРО», т. 2, 1935, с. 103—187.
49 Кирпичников В. С. Экспериментальная систематика сазана (Cyprinus carpio L.) — «Изв. АН СССР. Сер. биол.», 1943, № 4, с. 189—218.
50 Кирпичников В. С. Общая теория гетерозиса.— «Генетика», 1967, № 10, с. 48—64.
51 Кирпичников В. С. Современное состояние генетики рыб.— В кн.: Генетика, селекция и гибридизация рыб. М., 1969, с. 9—29.
52 Кирпичников В. С. Биохимический полиморфизм и проблема так называемой недарвиновской эволюции.— «Успехи современной биологии», 1972, т. 74, вып. 2 (5), с. 231—246.
53 Коновалов С. М. О возможности использования некоторых паразитов индикаторами локальных стад красной в море. Тезисы докладов молодых ученых ВНИРО, 1963, с. 13—14.
54 Коновалов С. М. Дифференция локальных стад нерки. Л., «Наука», 1971, 229 с.
55 Коновалов С. М. Структура изолята нерки озера Азабачьего.— «Журнал общей биологии», 1972, т. 33, № 6, с. 668—682.
56 Корнилова В. П. Биология и промысел азовской хамсы.— «Труды АзчерНИРО», 1960, вып. 18, с. 50—67.
57 Крогиус Ф. В., Крохин Е. М., Меншуткин В. В. Сообщество пелагических рыб озера Дальнего. Л., «Наука», 1969, 85 с.
58 Крыхтин М. Л. О биологически однородных группах у дальневосточных лососей.— «Вопросы ихтиологии», 1958, вып. 10, с. 3—11.
59 Кубанцев Б. С. О половом составе популяций у млекопитающих.— «Журнал общей биологии», 1972, т. 33, № 2, с. 196—204.
60 Куприна Н. П. Стратиграфия и история осадконакопления плейстоценовых отложений Центральной Камчатки. М., «Наука», 1970, 186 с.
61 Лебедев Н. В. К вопросу предсказания сроков миграции азовской хамсы.— «Учен. зап. Моск. гос. ун-та», 1939, т. 33, с. 257—295.
62 Лебедев Н. В. Возможность предсказания сроков миграции азовской хамсы.— «Зоол. журнал», 1940, т. 19, вып. 4, с. 646—650.

63 Лебедев Н. В. Элементарные популяции рыб.— «Зоол. журнал», 1946, т. 25, вып. 2, с. 121—135.
64 Лебедев Н. В. Элементарные популяции рыб. М., «Пищевая промышленность», 1967, 211 с.
65 Левандидов В. Я. Воспроизводство амурских лососей и кормовая база их молоди в притоках Амура.— «Известия ТИНРО», 1969, т. 67, с. 3—242.
66 Лиманский В. В. Анализ внутривидовой дифференциации некоторых рыб Черного и Азовского морей при помощи реакции преципитации.— В кн.: Вопросы физиологии рыб Черного и Азовского морей. М., 1964, с. 31—39.
67 Лиманский В. В. Серологический анализ внутривидовой дифференцировки ставрид и анчоусов южных морей.— В кн.: Тезисы Всесоюзн. совещания по экологической физиологии рыб. М., 1966, с. 3.
68 Лиманский В. В., Паюсова А. Н. Об иммуногенетических отличиях элементарных популяций анчоуса.— «Генетика», 1969, т. 5, № 6, с. 109—118.
69 Логвиненко Б. М., Кодолова О. П. О возможности дифференцирования видов моллюсков путем сравнения электрофореграмм миогенов. В кн.: Моллюски, пути, методы и итоги их изучения. Л., 1971а, с. 18—19.
70 Логвиненко Б. М., Кодолова О. П. О возможности дифференцирования видов двустворчатых моллюсков путем сравнения электрофореграмм мышечных водорастворимых белков.— «Зоол. журнал», 1971б, т. 50, № 6, с. 923—925.
71 Лэк Д. Численность животных и ее регуляция в природе. М., ИЛ, 1957, 403 с.
72 Майорова А. Н. Таксономическое положение хамсы, ловимой у берегов Грузии.— «Труды научной рыбохоз. станции Грузии», 1934, т. I, вып. 1, с. 7—19.
73 Лэк Д. Численность животных и ее регуляция в природе. М., ИЛ, 1957. 403 с.
74 Майорова А. Н. Таксономическое положение хамсы, ловимой у берегов Грузии.— «Труды научной рыбохоз. станции Грузии», 1934, т. I, вып. 1, с. 7—19.
75 Майорова А. Н. Биология и промысел черноморской хамсы. Симферополь, Крымиздат, 1951. 79 с.
76 Майорова А. Н., Чугунова Н. И. Биология, распределение и оценка запаса черноморской хамсы.— «Труды ВНИРО», 1954, т. 28, с. 5—33.
77 Майр Э. Систематика и происхождение видов. М., ИЛ, 1947. 334 с.
78 Майр Э. Зоологический вид и эволюция. М., Мир, 1968. 598 с.
79 Малюкина Г. А. Обоняние и его роль в поведении рыб.— «Итоги науки. Сер. биологическ.» М., 1969, с. 32—78.
80 Месяцева Е. В Треска тралового промысла Баренцева моря.— «Рыбное хозяйство», 1937, № 12, с. 12—18.
81 Морозов А. В. К методике расовых исследований рыб вообще и воблы в частности.— «Труды Волго-Каспийской рыбхозстанции», 1932, 127 с.
82 Наумов Н. П. Структура популяций и динамика численности наземных позвоночных. — «Зоол. журнал», 1967, т. 46, вып. 10, с. 1470—1485.
83 Нефедов Г. Н. Сывороточные гаптоглобины морских окуней рода Sebastes.— «Вестник Моск. ун-та», 1969, вып. 1, с. 104—107.
84 Никольский Г. В. Об относительной стабильности вида и некоторых вопросах таксономии. — «Зоол. журнал», 1963, т. 47, вып. 6, с. 869—874.
85 Никольский Г. В. Структура вида и некоторые вопросы изучения динамики стада рыб.— В кн.: Проблемы экологии. Томск, 1971, вып. 2, с. 19—24.
86 Ниль Дж., Шелл. У. Наследственность человека. М., ИЛ, 1958. 388 с.
87 Новоженов Ю. И. Соотношение полов — специфический параметр элементарной популяции.— «Журнал общей биологии», 1971, т. 32, № 1, с. 37—44.
88 О числе мономорфных и полиморфных локусов в популяции кеты — одного из тетраплоидных видов тихоокеанских лососей.— «Генетика», 1972, т. 8, № 2, с. 251—259. Авт.: Ю. П. Алтухов, Е. А. Салменкова, В. Т. Омельченко, Г. Д. Сачко, В. И. Слынько.
89 Панов Е. Н. Общение в мире животных. (Эволюционные и популяционные аспекты поведения животных), М., «Знание», 1970, сер. 8, вып. 1, с. 3—48.
90 Паюсова А. Н. О методах наблюдения за молодью воблы и леща в элементарных популяциях. — «Труды совещаний ихтиологической комиссии АН СССР», 1961, вып. 13, с. 471—479.
91 Паюсова А. Н. Опыт детального наблюдения за скатом молоди воблы (Rutilis rutilis caspicus Jak.) из ильменей в протоки дельты Волги.— «Вопросы ихтиологии», 1962, т. 2, вып. 3 (24), с. 467—472.

92 Паюсова А. Н. О начальных этапах образования элементарных популяций у рыб.— «Зоол. журнал», 1965, т. 64, вып. 10, с. 1560—1575.
93 Паюсова А. Н. Значение дифференциации личинок и стайного поведения для формирования элементарных популяций рыб.— В кн.: Поведение и рецепция рыб». М., 1967, с. 41—50.
94 Паюсова А. Н., Нефедов Г. Н. Анализ теплоустойчивости изолированной мышечной ткани морских окуней рода Sebastes из Баренцева моря.— «Цитология», 1968, т. 10, № 1, с. 133—137.
95 Петров В. В. О некоторых вопросах методики разграничения мелких таксономических единиц. Изд-во Ленингр. н.-и. ихтиол. ин-та, 1930, т. II, вып. 1, с. 112—128.
96 Полиморфизм изозимов лактатдегидрогеназы у кеты.— «Рефераты науч. работ Института биол. моря», Владивосток, 1968, вып. 1, с. 15—18. Авт.: Ю. П. Алтухов, Е. П. Алтухова, Е. А. Салменкова, Г. Д. Сачко.
97 Полянский Ю. И. Паразитофауна и окружающая среда. Некоторые вопросы экологии паразитов морских рыб.— В кн.: Основные проблемы паразитологии рыб. Л., 1958, с. 55—89.
98 Пузанов И. И. Анчоус.— «Учен. зап. Горьковского гос. ун-та», 1936, вып. 5. 101 с.
99 Расовый состав трески Баренцева моря.— В кн.: Доклады 1-й сессии ГОИН. 1931, № 2, с. 49—58. Авт.: Т. Ф. Дементьева, Е. К. Плечкова, М. И. Розанова, В. С. Танасийчук.
100 Рычков Ю. Г. Особенности серологической дифференциации народов Сибири.— «Вопросы антропологии», 1965, № 21, с. 18—33.
101 Рычков Ю. Г. Реакция популяций на изоляцию.— В кн.: Проблемы эволюции. Новосибирск, 1968. т. 1, с. 212—236.
102 Рычков Ю. Г. Некоторые популяционно-генетические подходы к антропологии Сибири. — «Вопросы антропологии», 1969а, вып. 33, с. 16—33.
103 Рычков Ю. Г. Антропология и генетика изолированных популяций. Изд-во МГУ, 1969б, 221 с.
104 Рычков Ю. Г. К популяционной генетике коренного населения Сибири. — «Вопросы антропологии», 1969, № 31, с. 3—32.
105 Рычков Ю. Г., Мовсесян А. А. Генетико-антропологический анализ распределения аномалий черепа у монголоидов Сибири в связи с проблемой их происхождения.— «Труды Моск. о-ва испытателей природы», 1972, т. 43, с. 114—132.
106 Рычков Ю. Г., Шереметьева В. А. Популяционная генетика алеутов Командорских островов. Сообщение I. — «Вопросы антропологии», 1972 а, вып. 40, с. 45—70.
107 Рычков Ю. Г., Шереметьева В. А. Популяционная генетика алеутов Командорских островов. Сообщение II.— «Вопросы антропологии», 1972 б, вып. 41, с. 3—35.
108 Рычков Ю. Г., Шереметьева В. А. Популяционная генетика народов севера Тихоокеанского бассейна в связи с проблемами истории и адаптации населения.— «Вопросы антропологии», 1972 в, вып. 42, с. 3—30.
109 Салменкова Е. А. Генетика изоферментов рыб.— «Успехи совр. биологии», 1973, т. 75, № 2, с. 217—235.
110 Салменкова Е. А., Волохонская Л. Г. Биохимический полиморфизм в популяциях диплоидных и тетраплоидных рыб.— «Труды Всесоюзн. совещан. по биохим. генетике рыб.», Л., 1973, с. 54—61.
111 Сафьянова Т. Е., Ревина Н. Н. К вопросу о разграничении крупной и мелкой ставриды по отолитам.— «Рыбное хозяйство», 1965, № 6, с. 17—22.
112 Сергеева А. И. Качественная характеристика воблы Rutilis rutilis caspicus Jak. в западной и восточной частях Северного Каспия.— «Вопросы ихтиологии», 1963, т. 3, вып. 1 (26), с. 29—38.
113 Серебровский А. С. Генетический анализ. М., «Наука», 1970. 342 с.
114 Сидоренко И. Н. Распределение морского окуня-клювача (Sebastes mentella Travin) по глубинам в районе Северной Ньюфаундлендской банки.— В кн.: Материалы сессии Ученого Совета ПИНРО, Мурманск, 1967, с. 166—177.
115 Сказкина Е. П. Различение азовской и черноморской хамсы по отолитам.— «Вопросы ихтиологии», 1965, т. 5, вып. 4 (37), с. 600—605.
116 Слынько В. П. Полиморфизм изоферментов малатдегидрогеназы у тихоокеанских лососей.— «Научн. сообщ. Ин-та биол. моря», Владивосток, 1971, вып. 2, с. 207—211.
117 Соколовская Н. И. Преципитиновая реакция в гибридизации.— «Известия АН СССР. Сер. биол.», 1936, вып. 2—3, с. 465—491.
118 Соколовская Н. И. Серологические исследования при отдаленной гибридизации.— «Известия АН СССР. Сер. биол.», 1938, вып. 4, с. 947—957.

119 Стрелков Ю. А. Эндопаразитические черви морских рыб Восточной Камчатки.— «Труды ЗИН АН СССР», 1956, т. 28, с. 147—196.

120 Талиев Д. Н. Серологический анализ некоторых диких и одомашненных форм сазана (Cyprinus carpio L.).— «Труды Зоол. ин-та», 1946, т. 8, вып. 1, с. 43—88.

121 Тараненко П. Ф. К динамике численности азовской хамсы.— «Труды АзчерНИРО», 1966, вып. 24, с. 3—29.

122 Тарасевич М. Н. О структуре группировок китообразных. II. Структура группировок финвалов.— «Зоол. журнал», 1967, т. 66, вып. 3, с. 420—426.

123 Тимофеев-Ресовский Н. В., Воронцов Н. Н., Яблоков А. В. Краткий очерк теории эволюции. М., «Наука», 1969. 407 с.

124 Тихонов В. Н. Генетические системы групп крови животных. Новосибирск, «Наука», 1966. 115 с.

125 Токарев А. К. О стаях каспийской обыкновенной кильки. ДАН СССР, 1955, т. 100, № 6, с. 1187—1189.

126 Травин В. Н. Новый вид морского окуня в Баренцевом море (Sebastes mentella Travin sp. nov.). ДАН СССР, 1951, т. 77, с. 741—744.

127 Травин В. Н., Печенник Л. П. Советские рыбохозяйственные исследования и промысел в Северо-Западной Атлантике.— В кн.: Сов. рыбохоз. исследования в северо-западной части Атлантического океана. М., 1962, с. 0—55.

128 Уилкинсон Д. Изоферменты. М., «Мир», 1968, 220 с.

129 Ушаков Б. П. О консервативности белков протоплазмы вида у пойкилотермных животных.— «Зоол. журнал», 1958, т. 37, вып. 5, с. 693—706.

130 Ушаков Б. П. Физиология клетки и проблема вида в зоологии.— «Цитология», 1959а, т. 1, № 5, с. 541—545.

131 Ушаков Б. П. Теплоустойчивость тканей — видовой признак пойкилотермных животных.— «Зоол. журнал», 1959 б, т. 38, вып. 9, с. 1292—1302.

132 Факторы генетической дифференциации популяционной системы коренного населения Северной Азии. Сообщение I.— «Генетика», 1973, т. 9, № 2, с. 136—145. Авт.: Ю. Г. Рычков, О. Л. Русакова, М. П. Раппопорт, В. А. Шереметьева.

133 Функциональное единство популяций.— «Журнал общей биологии», 1972, т. 33, № 1, с. 3—14. Авт.: С. С. Шварц, Э. Я. Гурвич, В. Г. Ищенко, В. Ф. Сосин.

134 Фриз Г. де. Теория мутаций. Мутации и мутационные периоды в происхождении видов.— В кн.: Теория развития, Спб, 1904, 237 с.

135 Фриз Г. де. Мутации и периоды мутаций при происхождении видов. Спб, 1912. 45 с.

136 Фриз Г. де. Избранные произведения. М., Медгиз, 1932. 147 с.

137 Частота генов сывороточной лактатдегидрогеназы в популяциях кеты и горбуши разных рек острова Сахалина.— «Рефераты научн. работ Ин-та биологии моря», Владивосток, 1968, вып. 1, с. 11—14. Авт.: Ю. П. Алтухов, Е. П. Алтухова, В. Н. Иванков, Е. А. Салменкова, Г. Д. Сачко.

138 Чугунова Н. Н. Рост и созревание воблы Северного Каспия в зависимости от условий откорма.— «Труды ВНИРО», 1951, т. 18, с. 153—170.

139 Шеппард Ф. М. Естественный отбор и наследственность. М., «Просвещение», 1970. 216 с.

140 Шварц С. С. Эволюционная экология животных.— «Труды ин-та экологии растений и животных», 1969, вып. 65, с. 175—198.

141 Штерн К. Основы генетики человека. М., «Мир», 1965. 627 с.

142 Шульман С. С. Паразитофауна сельди, корюшки и наваги Белого моря.— «Труды Карело-Финск. филиала АН СССР», 1956, т. 4, с. 50—67.

143 Шульман С. С. Паразиты рыб восточной части Балтийского моря.— «Труды совещ. по болезням рыб», 1959, вып. 9, с. 184—187.

144 Шульман С. С., Шульман Р. С. Паразиты рыб Белого моря. «Наука», М.—Л., 1953. 165 с.

145 Эфроимсон В. П. Введение в медицинскую генетику. М., «Медицина», 1964. 490 с.

146 Юровицкий Ю. Г. Об определении пола у рыб.— «Успехи современной биологии», 1966, т. 62, № 14, с. 148—160.

147 Яковлева В. И. Изоферменты.— В кн.: Успехи биологической химии, 1968, вып. 9, с. 55—94.

148 Янулов К. П. О группировках окуня-клювача (Sebastes mentella Travin) в Лабрадорско-Ньюфаундлендском районе.— В кн.: Советские рыбохозяйственные исследования в северо-западной части Атлантического океана. М., 1962 а, с. 285—296.

149 Янулов К. П. Паразиты как индикаторы локальности стад морского окуня.— В кн.: Советские рыбохозяйственные исследования в северо-западной части Атлантического океана, 1962 б, с. 273—283.

Summary

1. Genetic approach to the problem of population organization of species in fishes at the level of local stocks or «races» has permitted to detect systems of biochemical polymorphism and on this basis to carry out a broad geno-geographical analysis of various species. It has been found that local stocks of fishes are reproductively isolated communities with a characteristic inner heterogeneity.
2. The heterogeneity of stocks observed irrespective of ecological features of the species under investigation manifests itself in their subdivision into more elementary population units. They are characterized by gene frequences and therefore are also reproductively isolated groupings, corresponding formally to the model of «Mendelian population».
3. During genetic investigation of the stock as a whole the correspondence of natural picture to mathematical model of subdivided population is detected. It is shown that such a community is stable both in time and in space despite the simultaneous variability of elementary populations composing it.
4. This new quality of population totality which cannot be deduced from properties of its structural components let us regard local stocks as genetically stable population systems in contrast to elementary populations — variable structural components of such systems. Traditional biological investigations support this conclusion.
5. Since biologically significant properties of populations are derivatives of their historically formed gene pools, the obtained data on qualitative differences of genetic stability of different levels of population hierarchy make it possible to formulate a uniform principle of management of rational fishing industry based on the approach to the population system as a whole — to distribute the appropriate efforts among all components of its structure.
6. The existence of population systems in nature makes it possible to estimate in a new fashion to biological significance of processes of intraspecific genetic divergence regarding them as an adaptive strategy enabling the species to remain as it is in normally varying environmental conditions.
7. But also on the basis of the real existence in species not only of polymorphic but also of genetically monomorphic properties the possibility is argued to treat the speciation not as a continious process on a population level but as a result of qualitative rearrangements of the genome correlated with the reproductive isolation of separate individuals.