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Reproduction of Amur salmon and the food supply of their juveniles in the tributaries of the Amur

by V. Ya. Levanidov

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REPRODUCTION OF AMUR SALMON AND THE FOOD SUPPLY OF THEIR JUVENILES IN THE TRIBUTARIES OF THE AMUR

By: V. Ya. Levanidov

(From: "Izvestiya Tikhookeanskogo nauchno-issledovatelskogo Instituta, rybnogo khozyaystva i okeanografii."
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INTRODUCTION

The Pacific salmons of the Oncorhynchus genus right from the beginning of the development of the Far Eastern Fisheries and to the end of the 1940's were one of the basic objects of the fisheries. Their yields in the years before the war reached four hundred thousand metric tons a year.

Today because of the development of a powerful ocean fishing industry, because of the cyclonic deterioration of the climatic conditions, and because of the intensification of salmon fisheries by the Japanese, the ratio of the Pacific salmon to the total Soviet fish industry has decreased considerably. Nevertheless the Pacific salmons continue to maintain their position as a high quality food resource in our country. It should be pointed out here that the diadromous salmons are fish of our inland waters since they reproduce in rivers. Therefore, assistance to their reproduction and a control of the numbers of their stock is a highly essential task.

The interest for the study of the reproduction of fish reserves originates, as a rule, at the exploitation stage when the depletion or at least the limitation of such reserves becomes evident. Exactly at that time the human thought turns towards the study of the conditions and the pattern according to which the species reproduces itself.

The very term "reproduction" (which very successfully reflects the basic property of live organisms to reproduce individuals of its kind) has acquired its acceptance comparatively recently. Indeed, this term already occurs in the first edition of A.N. Eleonsky's textbook (1936, page 5), but in this textbook it is basically the fishery in natural water bodies that is discussed.

In 1937 a popular scientific book by I.I. Kuznetsov "Chum and its reproduction" was published; in this book the author means by the term "reproduction" a complex of measures contributing to an increase in resources: the limitation of fisheries, improvement (including also the biological improvement), acclimatization and fishery operations.

A.I. Berezovsky (1938) considers the reproduction of fish resources in the Caspian sea from the same point of view, while B.G. Chalikov (1938) and others do this for the diadromous fish in Volga (Acipenseridae).

B.I. Cherfas (1940) discusses in his monograph the problems of natural reproduction, but he mentions only casually the term "reproduction" itself. In particular, he speaks of the weakening of the reproduction process in connection with a decrease in the numbers of the producers at the spawning grounds. In the second edition of this publication (Cherfas, 1950) the author calls a chapter "The place of fishery in the system of measures on the reproduction of the fish resources in natural water bodies".

During the recent two decades in the majority of piscicultural /4
institutes of the USSR fish reproduction laboratories were created, whose operation thematics usually concerns the problems of fish raising, acclimatization of fish, but mainly the study of the reproduction and of the first periods of ontogenesis. The adult individuals are considered here from the point of view of the importance their quantitative and qualitative indices have upon the progeny.

The term "reproduction of reserves" achieved an extensive application thanks to A.N. Derzhavin, who published two large compilations (1941, 1947).

The study of natural reproduction of fish may be briefly characterized as a complex study of the biological patterns determining the dynamics of the population from the reproduction to the beginning of "body ripening period" (Nikolsky, 1965) with the purpose of developing the system of measures contributing to the prosperity of the population.

Thus, "the natural reproduction" is a discipline studying the population ecology; from here its complexity originates: the attraction of the chemical, geochemical, physical and other methods of research for understanding of the mechanism of the biological processes and for the characteristics of the interrelation between the organism and the environment.

The reproduction process continues during the entire life cycle of the salmon, since each new generation at the stage of late larvae or of fingerling already carries the embryos of the future generation. It is however, expedient to delineate two phases of the life cycle:

Reproduction: multiplication and the first periods of ontogenesis with a frequent alternation of the development stages; a phase when the mortality processes dominate the growth processes and the biomass of the new salmon generation decreases from stage to stage. In the Pacific salmon this portion of life cycle takes place in fresh water.

The growth and maturation begin predominantly from the sub-stage of sexual maturation. These stages are prolonged; the growth processes dominate the natural mortality rate and, therefore, the biomass of the population increases. In chum and pink salmon this period of the life cycle takes place in the ocean water, in other Pacific salmons (sockeye, chinook salmon, coho salmon) it takes place partially in fresh water, but even in this case a sharp increase in the individual growth and in the biomass of a population takes place in the ocean waters.

The efficiency of the natural reproduction is primarily determined by the survival rate and by the food supply during the first periods of ontogenesis. The death rate is a directly affecting factor determined by abiotic causes and by the preying of predators, parasites and diseases.

The food supply indirectly affects the dynamics of the population, however, in the Pacific salmon it has no direct affect upon the numbers of the generation.

The indirect effect of the food supply can in a number of cases turn out to be the decisive factor in the population dynamics, because the Pacific salmons during their ontogenesis live in two media: in the fresh water and in the ocean. At transition from one medium to the other the preparation of the organism to the new conditions acquires a special importance.

The effect of insufficient food supply upon the numbers of salmons is realized through a directly acting biotic factor, namely the predators: an elimination of a part of the population takes place, however, it is basically the weak individuals and retarded who perish.

The reproduction problems are closely intertwined with the dynamics of fish population; the type of dynamics of one or another species to a considerable degree is characterized by such indices of natural reproduction as the fertility (of individuals and populations), the efficiency of spawning and the survivability of eggs and juveniles. T.F. Dementyeva, Yu.Yu. Marti, /5
P.A. Moiseyev and G.V. Nikolsky (1961) indicate in their work the importance of the enumerated factors.

At the end of 1940's G.N. Monastyrsky (1952) expressed certain hypotheses of the theory on the dynamics of fish. Later its foundations were developed by V.V. Vasnetsov (1947, 1953 a, b) and by G.V. Nikolsky (1958, b, 1952, 1953). The basic theory of these works is the dialectic unity of the organism and medium, at which the ecology of the species (or of population) is considered as a system of adaptations, i.e., as a series of adaptive interrelations between the organism and the medium. Here the term "medium" for the given organism includes all the other organisms connnected ecologically with it for which in each term this organism is the element of their medium.

Only after that the author had already written the present paper, a book of G.V. Nikolsky (1965) was published; this book expounds the theory of the dynamics of the fish population. Among the most important questions in this book the problems of food supply and of the food ratios of fish, of their natural mortality rate, of the dynamics of population numbers and of the biomass of the population are discussed, in other words, problems of ecology that constitute the basis for a research on the reproduction processes.

Very important is the fact that G.V. Nikolsky renounced the generally used term "dynamics of numbers" which stresses the quantitative side of the phenomenon and replaced it with a more accurate one, "the dynamics of population" considering inseparably the qualitative and the quantitative changes.

The term "reproduction" may be extended to all the species of aquatic creatures. In particular, we may speak about the reproduction of the food invertebrates. Important indices in the efficiency of the reproduction of aquatic invertebrates, as we know, are the ratios between the biomass and the production. The transfer of these concepts to the solution of the problems of the dynamics of fish population (the field of ichtyology) and the determination of production possibilities of one or another species of fish are highly prospective.

The history of the research of Pacific salmons in the basin of the Amur River begins with the works of V.K. Brazhnikov and particularly of V.K. Soldatov, whom I.F. Pravdin (1940) justly calls "the founder of the extensive scientific commercial studies of the Far Eastern salmons". The history of the salmon research in the Russian Far East from the 18th Century to 1937 is presented by I.F. Pravdin in his survey of the research on the Far Eastern salmon. This relieves us from the necessity to discuss the pre-War studies that were carried out by Dalryba and by TINRO (the Pacific Research Institute for Marine Fisheries and Oceanography) in the basin of the Amur River. However, we cannot but mention the studies on the reproduction biology of the Amur salmon carried out by I.I. Kuznetsov (1928, 1937), A.Ya. Tarants (1939b) and by A.G. Smirnov (1947), as well as the studies carried out by the Kamchatka branch of TINRO (Pacific Research Institute for Marine Fisheries and Oceanography), but first of all we must mention the classical works of F.V. Krogius and E.M. Krokhina (1937, 1954, 1956a and b) and by F.V. Krogius (1949, 1951) on the biology of sockeye.

In recent times, A.G. Smirnov (1947 to 1954) and I.B. Birman (1947 to 1957) were carrying out research on the Amur salmons. A.G. Smirnov (1947) published, unfortunately, only one paper in which he discussed the salmon yields, their periodicity, he described the results of his observations on the mortality of eggs and larvae of the Amur salmons during the period of their development in the ground and discussed the causes of their death.

A.G. Smirnov came to the following important conclusions: the fluctuations in the numbers of the Far Eastern salmons taken over periods of considerable length are caused by changes in climatic conditions (by the change in the water temperature in the northern part of the Pacific Ocean). The /6 fluctuations in the numbers of individual generations of salmon, other conditions being equal, take place basically owing to the freezing of the spawning grounds.

I.B. Birman wrote a number of papers (Birman, 1951b, 1952, 1954, 1955, 1957) on the fluctuation dynamics in the numbers of the Amur salmons, on the effect of the climatic fluctuations on the conditions of their resources and on the reproduction rate, on the pattern in the changes of qualitative indices and of the numbers of fall chum.

In 1949 A.G. Kaganovsky published a general work on the Far Eastern pink salmon (1949) in which he discusses the entire life cycle of this fish including the problems of natural reproduction and of fluctuation in their numbers. He uses extensively in his article the material of Amur researchers I.I. Kuznetsov and A.Ya. Tarantz. A.G. Kaganovsky also comes to the conclusion that the cooling and warming of the sea connected with the periodic disturbances in the Kurosio produce fluctuations in the numbers of pink salmon considered over long periods.

At the beginning of the 1950's mutual research is organized on the Amur salmon by the Department of Ichtyology of the Moscow University, by the Institute of the Evolutionary Morphology of the USSR Academy of Sciences and by the Amur branch of the TINRO (Pacific Research Institute for the Marine Fisheries and Oceanography). The research was conducted under G.V. Nikolsky, who published several papers (1952, 1954) in which he describes the basic pattern of the spawning character of pink salmon, spring chum and fall chum. G.V. Nikolsky accepts the opinion of A.G. Smirnov concerning the considerable effect of the freezing of the spawning grounds as a factor determining the mortality rate of eggs and indicates that the freezing must have different effects on the survival rate of eggs of the fish mentioned above. He agrees with A.G. Kaganovsky in the fact that the biannual cycle is characteristic of the pink salmon, taken as a species, and is characteristic of its type of the population dynamics; he also comes to the conclusion that the cause of the drop in the spring chum resources consists in the unfavourable climatic conditions within its spawning area during the period from 1911 to 1914.

A conference was held in 1953 in Khabarovsk where the probems of the salmon industry in the Far East were discussed. The results of the first stage of joint research were summed up in the papers of I.B. Birman, G.V. Nikolsky, V.V. Abramov and V.Ya. Levanidov. The conference projected the main tasks of the scientific research works in the field of the study of Far Eastern salmons.

Of considerable importance for the study of the natural reproduction, as well as for the solution of applied practical problems in the field of fishery, were the papers of N.N. Disler (1951, 1954, 1957) and of A.I.Smirnov (1954 a, 1955, 1958, 1963, 1965) on the development of salmons.

The content of the present monograph constitutes the results of 15 years of research by the author on the natural reproduction of the Amur salmons, particularly of the fall chum.

In the research on the natural reproduction of the Amur salmons scientists from the Laboratory for Fish Resources Reproduction of the Amur branch of TINRO (Pacific Research Institute for Marine Fisheries and Oceanography) participated. In the study of the ecology of the Amur salmons during the freshwater period of their lives, carried out by the author, participated young scientists: M.D. Zazhigina, L.A. Rostovtseva, Yu.S. Rosly, L.A. Slobodchikova, N.I. Kulikova, V.S. Tolchanov (Manager of the Observation Station at the Amgun' River). Feeding and food ratios of the ichtyofauna in tributaries of the Amur River were studied by L.V. Kokhmenko and by the author; the feeding of fingerlings of the Amur salmon were carried out by the author and by I.M. Levanidova. The study of the invertebrate fauna in tributaries of the Amur River were carried out by me and I.M. Levanidova jointly. The coverage by the hydrobiological research of extensive water territories and the detailed determination of the collected material was only possible because of the participation of colleagues and specialists from other institutes who are remembered with gratitude in the introduction to the chapter "Biological Productivity of /7
Tributaries of the Amur River and Food Resources of Fish".

We received considerable help in the organization of the experimental operations and observations at the Teplovskoye fish hatchery from its manager, late I.M. Vasilyev and from the pisciculturist M.I. Muratov.

The author expresses his special gratitude to A.P. Lavrova, Manager of the Georgiyevskaya piscicultural-meliorational station of the Glavamurrybvod who participated from 1949 to 1961 in the study of the natural reproduction of salmons in the Khor River. Without her assistance we could never have completed the long, often year-round observations.

In the presented paper materials are also used which have been collected during a ten to twelve year period by other stations of Glavamurrybvod.

A.L. Shidlovsky, head of the Glavamurrybvod, the initiator and organizer of the business cooperation of the fish reproduction laboratory of the Amur branch of TINRO (the Pacific Research Institute for Marine Fisheries and Oceanography) with the fish hatcheries and with the fishery-meliorational stations of the Gosamurrybvod, contributed considerably to a successful study of the natural reproduction of salmons.

The author is highly grateful to G.V. Nikolsky, E.V. Borutsky, and A.I. Smirnov for their valuable advice during the preparation of this monograph, as well as to I.A. Piskunov who was so kind as to undertake the scientific editing of the same.

Part I

NATURAL REPRODUCTION OF THE AMUR SALMONS

Brief Biological Characteristics of the Amur Salmons

In the basin of the Amur River, three species of the Pacific salmon multiply: chum Oncorhynchus keta (Walbaum), pink salmon Oncorhynchus gorbusha (Walbaum) and masu salmon Oncorhynchus masu (Brev.). The last species is very scant, it has no commercial importance and never had. Its natural reproduction is poorly studied, for this reason it will not be discussed in the present paper.

The chum and pink salmon are the two most numerous species of the Pacific salmon. Common ecological characteristic distinguishing these two species from the other species of this genus is the shortness of the freshwater period of their juveniles. The juveniles of pink salmon migrate seawards from the spawning river almost immediately after the emergence from the ground at the end of the larva stage of the development or at the beginning of the fingerling stage.

Chum migrates from the rivers predominantly during the fingerling stage of its development; first year chum contitutes a small percentage of all the migrating individuals.

The spawning populations of pink salmon consist of coeval two-year-old fish, therefore, their structure is less complicated than of the chum. Information concerning dimension, weight and fertility of the Amur pink salmon are presented in the papers of V.V. Abramov (1954), L.M. Kryuhtin and A.G. Smirnov (1962).

As we know, the chum is represented in the basin of the Amur River by two forms: the spring and fall forms (Berg, 1948). Its biological indices are better studied than those of any other Pacific salmon. Information concerning the growth rate, dimensions and weight, fertility, age and sex ratio in the spawning populations are shown in the papers of V.K. Soldatov (1912), I.I. Kuznetsov (1937), E.A. Lovetsky (1948), I.B. Birman (1951a, 1954), I.B. Birman and V.Ya. Levanidov (1953), M.L. Krykhtin and A.G. Smirnov (1962). Therefore, in the present paper we will limit ourselves only to a general comparative description.

The chum is represented at the Asiatic and the American coasts of the Pacific Ocean by two forms: the summer and fall chum which differ in the date of their spawning approach to the coast. The fall form, as a rule, is larger than the summer one. L.S. Berg (1948) classifies the summer chum of the Amur River, of the Okhotsk Sea coast north of the Tatarsky Strait, the chum of the Kamchatka Peninsula of the southern Sakhalin as well as the chum of the American coast as belonging to the summer variation. According to Berg the fall chum lives in addition to the Amur River on the islands of Sakhalin, Hokkaido and Hondo and, probably, in the rivers of the southern ocean coasts. During the recent decades, material is accumulated permitting us to complement the knowledge of L.S. Berg on the distribution of the fall form of chum. Thus, V.V. Abramov (1948) described the fall chum from the Bolshaya River (western coast of the Kamchatka).

At the American coast, in British Columbia, the fall chum multiplies, it enters the fresh water later than other salmons, even later than the coho salmon. According to the data of Hunter (1959) the major approach of the fall chum in the Hooknose Creek River (north of the British Columbia) continues from September 17th to October 15th. According to Wickett's data (1958) in the rivers of the Vancouver Island the chum enters from the middle of October to the beginning of December.

According to the data of the International Commission on Fisheries chum enters in the northern part of the Pacific Ocean (1962) the rivers of the Washington and Oregon (USA) basically during October. And finally, Wickett (1964) writes that in the Nanaimo River he observed spawning of chum in February, and the latest entrance of a chum male for spawning was recorded on April the 9th (!), 1962.

According to its dimensions, the chum in the British Columbia also is classified as belonging to the fall chums, thus, Godfrey (1959) presents the following data on the average chum weight for the period 1946 to 1958 for the individual regions of British Columbia. The minimum average weight was recorded in 1947 for chum from the Queen Charlotte Islands and was 3.4 kilograms. The maximum weight was observed in 1957 in respect to chum from the northern regions (6.75 kilograms!). The average weight of chum in Canada in coastal catches was 5.3 kilograms, according to the data of the Bulletin of the International Pacific Commission, the chum in Washington was 4.5 kilograms and in Oregon it was approximately 5 kilograms (Bulletin, 1962; 1963).

According to the data of Foerster and Pridchard (1936), of Wickett (1958) and of Hunter (1959) the Canadian fall chum differs from the typical Amur form in low fertility. The average fertility of the chum from the Hooknose Creek River during the period 1947-1956 according to the data of Hunter (1959) was 2,468, from the Nail-Creek River 2,726 (Neave, 1953) and from the Namu River (according to the data of Foerster and Pridchard) 2,760 eggs.

According to Rounsefell (1957) the fertility of fall chum from Hokkaido was 2,625 eggs, while the fertility at the Southern Kuriles was only 2,000 eggs.

Likewise the fall chum from Sakhalin Island has low fertility, which according to P.A. Dvinin (1952) is 2,600 eggs. Still lower is the fertility of the Kamchatka fall chum, which is 2,122 ± 36 eggs (Abramov, 1948).

The average fertility of the fall chum from the Amur River according to I.I. Kuznetsov (1937) is 3,456 eggs (for the period from 1925 to 1934), according to M.L. Krykhtin and A.G. Smirnov (1962) it is 3.430 eggs (for the period from 1951 to 1958).

The populations of fall chum reproducing in the tributaries of the Ussuri River and in the Middle Amur River are distinguished by particularly high fertility. The average fertility of chum from the Khor River (a tributary of Ussuri) taken over a period of several years, (1946 to 1953) was according to I.B. Birman (1956) 3,676 eggs, while the average fertility of the chum from the Bir River (Middle Amur) was 3,668 eggs. In individual years the average fertility of chum from the Khor River was 4,000 eggs.

Eggs of the Amur fall chum are relatively small; its diameter is 6.0 to 6.5 millimetres while in the fall chum from Sakhalin Island it is on the average 7.2 millimetres (Yastrelkov, 1965), while in the fall chum from America it is 7.4 millimetres (Rounsefell, 1957). According to weight (and size) the fall chum from Amur does not differ significantly from the chum of the American coast (Table 1).

To the north of the estuary of the Amur River, along the northwestern coast of the Sea of Okhotsk and along both coasts of the Kamchatka Peninsula, the summer form of the chum occurs extensively. The Amur River is the southern boundary on the continent for this form of chum (on the Sakhalin Island, in its southern part occurs the summer form of chum).

The Kamchatka and the Okhotsk chums begin to enter fresh water at the beginning of July, but the main movement takes place towards the end of the month and in August. The spawning movement of the summer chum ends towards September. R.S. Semko (1954) indicates the following arrival data for the chum in the Bolshaya River (southwestern coast of the Kamchatka Peninsula): the general period is from July 16th to August 21st, the main movement from July 24th to August the 10th. The movement data do not change much from year to year.

Thus, the summer chum (compared to the fall chum) is the northern form on the Arctic coast of the Pacific Ocean.

Identical phenomenon is observed at the American coast. The American chum enters for the multiplication purposes predominantly into

Table 1.

Length and weight of Amur fallchum taken over a period of several years (Amur liman)

Годы Years	Длина, см			Вес, кг			Источник Source
	самцы males	самки females	самцы и самки both	самцы males	самки females	самцы и самки both	
1	2	3	4	5	6	7	8
1907—08	75,0	72,0	73,5	4,92	4,14	4,53	В. К. Солдатов (1912) V.K. Soldatov
1929	71,0	66,3	68,7	5,00	4,02	4,51	Е. А. Ловецкая (1948) E.A. Lovetskaya
1932	69,0	64,9	67,0	3,98	3,40	3,69	Е. А. Ловецкая (1948)
1935	69,5	64,8	67,2	4,49	3,43	3,96	И. Б. Бирман (1951а) I.B. Birman
1936	70,7	66,3	68,5	4,62	3,78	4,20	Журналы измер. (архив ТИНРО) Mensuration journal (TINRO Archives)
1938	65,3	61,9	63,6	3,46	3,04	3,25	И. Б. Бирман (1951а) I.B. Birman
1939	62,4	60,8	61,6	3,45	3,13	3,29	И. Б. Бирман (1951а) "
1940	64,3	61,6	63,0				И. Б. Бирман (1951а) "
1941	66,6	62,9	64,8	3,42	2,95	3,14	И. Б. Бирман (1951а) "
1942	63,9	61,3	62,6				И. Б. Бирман (1951а) "
1943	65,4	63,3	64,4	4,23	3,67	3,95	И. Б. Бирман (Вес по данным журналов измерений) (Weight according to data in mensur. journals)
1944	65,6	62,8	64,2	—	—	—	И. Б. Бирман (1951а) "
1945	72,3	69,7	71,0	—	—	—	И. Б. Бирман (1951а) "
1946	66,0	63,9	65,0	4,10	3,60	3,85	И. Б. Бирман (1951а) "
1947	65,0	63,8	65,0	4,08	3,76	3,92	И. Б. Бирман (1951а)
1948	69,0	65,7	67,4	4,72	3,88	4,30	И. Б. Бирман (1951а) "
1949	67,0	65,2	66,1	5,03	4,01	4,52	И. Б. Бирман (1951а) "
1950	67,1	65,2	66,2	5,10	4,02	4,56	И. Б. Бирман (Вес по данным журналов измерений) ditto
1951	67,2	64,5	65,5	4,98	4,30	4,60	М. Л. Крыхтин и А. Г. Смирнов (1962) M.L. Krykhtin and A.G. Smirnov
1952	68,1	66,5	67,1	4,70	4,32	4,50	М. Л. Крыхтин и А. Г. Смирнов (1962) "
1953	67,5	65,1	66,5	5,29	4,43	4,86	М. Л. Крыхтин и А. Г. Смирнов (1962) —Вес самок по данным журналов измерений " (weight of females according to data in m. journals)
1954	67,3	64,5	65,8	4,32	3,93	4,10	М. Л. Крыхтин и А. Г. Смирнов (1962) "
1955	67,3	65,2	66,1	4,54	3,96	4,22	М. Л. Крыхтин и А. Г. Смирнов (1962) "
1956	66,6	65,2	65,8	4,59	4,10	4,40	М. Л. Крыхтин и А. Г. Смирнов (1962) "
1957	68,4	66,0	66,5	4,82	4,32	4,53	М. Л. Крыхтин и А. Г. Смирнов (1962) "
1958	65,8	64,3	65,1	4,44	4,09	4,20	М. Л. Крыхтин и А. Г. Смирнов (1962) "
1959	70,4	66,2	68,3	4,69	3,72	4,21	В. Я. Леванидов V.Ya. Levanidov
1960	65,5	63,9	64,7	4,14	3,43	3,79	В. Я. Леванидов "
1961	65,0	64,0	64,5	4,02	3,72	3,85	В. Я. Леванидов "
1962	68,2	66,1	67,1	4,82	4,20	4,51	В. Я. Леванидов "

the rivers of the Alaska Peninsula. The chum enters the rivers in the southeastern part of the Alaska between the 23rd June and 9th September; the average length of the chum taken over a period of several years is 62 cm (Thorsteinson, Noerenberg & Smith, 1963). According to the dimensions and the migration data this chum is, evidently, close to the Okhotsk and Kamchatka chums. The average size of the four year old Okhotsk chum measured over the years 1958 to 1964 is 62.3 cm, of the West-Kamchatka chums measured over the years 1951 to 1960, it is 62.1 cm, of the summer chum from the Sakhlain Island measured over the years 1946 to 1952, it is 62.5 cm (Dvinin, 1952).

The Amur summer chum is distinguished from the other forms by a relatively early migration to fresh waters: it begins to enter the Amur River at the end of June, and as a rule, its migration ends during the first half of the month of August. This chum is also characterized by its small size. Its average length measured over the years 1951 to 1958 was 55.7 cm (Krykhtin and Smirnov, 1962), and over the years 1958 to 1964, according to our data, was 56.5 cm.

The Amur forms of chum are particularly sharply distinguished according to their weight, they seem to form boundaries within which the other local chum population of the Soviet Far-East are enclosed (Fig. 1). Apparently the Amur chum, while distinguishing itself from all the other chum populations deserves a segregation into a separate form not less than the Amur fall chum deserves among the other fall populations.

As a rule, the four year old ones predominate among the chum generations, the five year olds are relatively numerous. However, in chum generations in the coastal zone of the Sea of Okhotsk, within the boundaries of the Okhotsk fishery region, and of the chum from the western coast of Kamchatka right to the present time the four year olds and the five year olds predominated alternatively (Semko, 1954; Birman, 1964). From 1958 on, at the western Kamchatka, the four year old ones begin to predominate persistantly (Birman, 1964).

In the spawning chum population in Alaska and British Columbia the four year old individuals also predominate.

The data in Table 2 indicate that on the average the length of the chum's life cycle is approximately 4 years and, all the conditions being equal, after a certain period of time the periodicity of the approaches of particularly strong or particularly weak spawning populations will also be on a four year cycle.

The ratio of sexes in the spawning population of chum at the Asiatic and the American coasts is usually 1:1 (Semko, 1954; Thorsteinson and others, 1963).

The sex ratio in the population of the Amur fall chum was studied initially by V.K. Soldatov (1912) in 1907 and 1908. In these years it was: 53.5% and 46.5%, i.e., was rather close to 1:1.2 ratio. According to the data of TINRO (Pacific Research Institute for Marine Fisheries and Oceanography) for the years 1935 and 1936 during the period of mass migration of the fall chum we observed a predominance of females in the Amur liman. The sex ratio was 1:1.5. In the years 1937, 1938 and 1940, according to A.G. Smirnov's data the sex ratio of fish in the estuary of the Amur river (460 km from the mouth of the river) was 1:1.4. The indicated ratios were observed in the years of high numbers in the spawning population of fall chum.

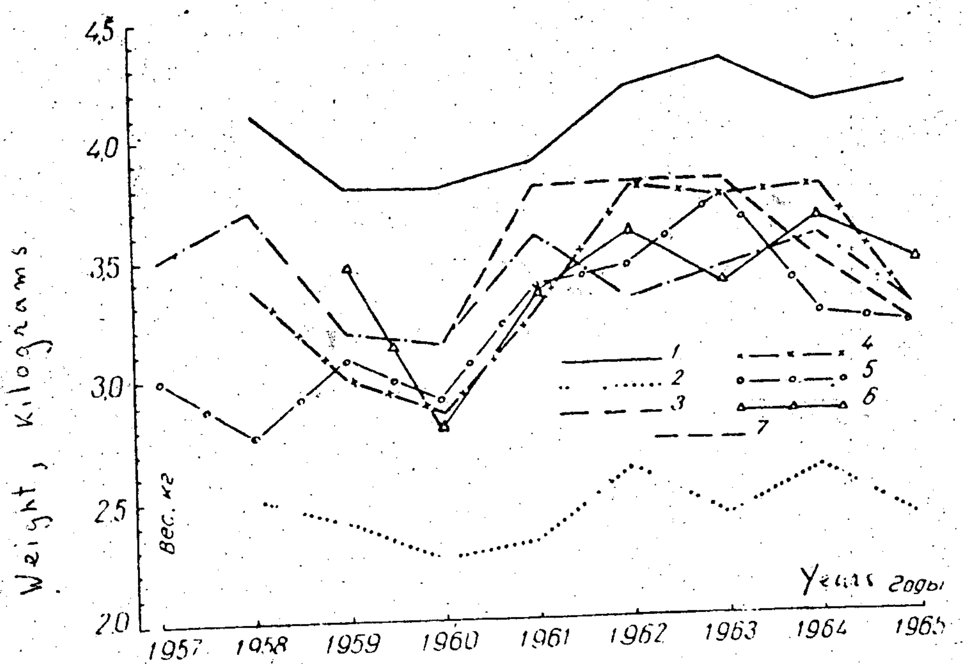

Fig. 1. The average weight of the four year old chums from various local population: 1 - fall chum from Amur; 2 - summer chum from Amur; 3 - chum from eastern Kamchatka; 4 - chum from the Okhotsk coast; 5 - chum from the northwestern Kamchatka; 6 - chum from the southwestern Kamchatka; 7 - chum from the Island of Sakhalin.

Table 2

Age structure of the chum population, in percent

	Локальные стада Local population	Годы Years	Возраст Age 2+	3+	4+	5+	6+
Fall p. Amur	Осенняя Амура	1943—56	6,9	73,9	18,9	0,3	
Summer Amur	Летняя Амура	1947—57*	2,4	79,6	17,9	0,1	
Sakhalin Fall	Сахалинская осенняя	1959—64	11,9	75,0	12,8	0,3	
Okhotsk region	Охотского района	1958—64	1,9	43,9	48,4	5,7	0,1
West Kamchatka (Bolshaya river)	Западнокамчатская (р. Большая)	1958—64	3,6	67,0	28,5	0,9	
East Kamchatka (Kamchatka r.)	Восточнокамчатская (р. Камчатка)	1958—64	2,7	68,9	26,8	1,6	
Alaska *	Аляскинская *	1951—58	10,0	75,0	15,0	—	

* Data on the Alaska chum taken from Thorsteinson, Noerenberg & Smith (1963).

In the years after the World War II, when the level of the resources was rather low, the ratio of sexes in the spawning population was in the Amur liman according to I.B. Birman's data: 1:1 in 1946, 1:1.1 in 1947, and 1:1 in 1948. In 1949, when a more numerous population than in the preceding three years returned for spawning the sex ratio was 1:1.3. In 1955, and in 1956 the sex ratios, according to R.I. Enyutina's data, were 1:1.1, and 1:1.5 in 1957.

According to our data the sex ratio was the following: 1:1 in 1959, 1:1.1 in 1961. /16

The presented data permit us to come to the conclusion that for the spawning population of the fall chum the constant predominance of females is characteristic, and in the years of high numbers there is a tendency towards an increase in the domination by females. The latter phenomenon may be considered as an adaptation ensuring high efficiency of the reproduction at high numbers of population. However, the mechanism of this phenomenon remains unclear: it is possible that the indicated ratio of sexes is already established during the fresh water, period of their life, during the fattening period at the spawning ground, since only then the high numbers may be an active factor.

The sex ratio in the summer chum populations was determined considerably less frequently then in the populations of the fall chum; it was almost always 1:1.

M.L. Krykhtin and A.G. Smirnov (1962) present data on the sex ratios in Amur pink salmon, indicating that in the spawning populations, in the years of high numbers, the males predominate; in 1958, when the highest migration in the latest thirty years was observed, the number of males was 55.5% of the spawning population, in 1948, when the migration was likewise very high, 33%.

The decrease in the relative number of females in multitudinous generations of pink salmon together with a decrease in the fertility and in the size of these generations may be considered as an adaptation to a weakening of the natural reproduction in the population, whose food supply is low because of its maximum numbers. In pink salmon, which has the shortest life cycle, the "mechanism of autoregulation" is pronounced very distinctly. This constitutes the cardinal difference between the fall chum and the pink salmon.

When the numbers of the fall chum are high owing to insufficient food supply the growth and maturation rates are slowed down (the spawning population "turns old"), but at the same time these shifts are to a certain degree compensated by changes in the sex ratios.

In pink salmon, who has practically coeval population, the inhibition in reproduction rates causes a decrease in the fertility and in the relative number of females.

As A.I. Smirnov (1963) has established, "the task of the maximum fertilization of eggs under complex ecological spawning conditions in Pacific salmons is solved in two mutually complementing ways: a) by the development by the males of the ability to produce an enormous amount of spermatozoids; b) by mass spawning and formation of special spawning groups consisting of one female and several males".

The first way is characteristic of the chum. It permits a numerical predominance of females and as a result of this we obtain economical utilization of food resources with reproduction rates unchanged.

The second way is characteristic of the pink salmon. It requires predominance of males or at least a numerical equality between males and females as a prerequisite to maintain the normal reproduction by means of a decrease in the relative potential of the population fertility.

LOCAL SALMON POPULATIONS.

In the pre-war research period, salmon in a single river basin or in a number of small adjoining river basins of a particular geographic region were considered as a single population. It is true, F.V. Krogius and E.M. Krokhin have already carried out a research on the sockeye from the Paratunka River which has shown the presence in the basin of this river of two populations: one, multiplying in the Dalneye Lake, another /17
in the Blizhneye Lake, but the results of the research were published only after the war (Krogius, 1954). However, in respect to the chum and pink salmon still the opinion predominated of the homogeneity of the spawning population. Thus E.A. Lovetskaya (1948) studying the dynamics taken over a number of years of the qualitative indices of the Amur chum uses equally the data collected in the Amur liman and in individual spawning grounds in the tributaries of Amur and Ussuri, taken at different years. A.G. Smirnov (1947) on the basis that the upstream migrations of the summer chum into one of the third rate spawning tributaries, namely Beshenaya River, and the catches of this chum in the Amur liman were in reverse relation in the years 1934 to 1938, concluded that the Amur salmon chum was generally overharvested. R.S. Semko (1954) in order to explain the fact that the fertility of pink salmon of Bolshaya-reka was in the estuary of this river 4% below the fertility of pink salmon that entered the Karamaysk springs, expresses such a doubtful hypothesis like that the fertility of pink salmon increases with the movement upstream. In this case the varying fertility may be explained much simpler by local conditions.

E.B. Birman (1952) was the first to express the opinion on the existence of local populations (and to use the term "local population" itself) of the Amur salmons and in particular of the fall chum. Later, I.B. Birman (1956) proved that three large local populations ("groupings") of the fall chum from Amur differ in morphological and biological characteristics. According to I.B. Birman the Amur salmon chum also has local populations.

A.A. Svetovidova (1961) has shown that the summer chums from various Amur tributaries differ from each other in a number of morphometrical characteristics and in biological indices. It is true, fish was analyzed with various stages of breeding colours and the material was taken from separate periods of the spawning migration and for similar years. However, in a number of cases the characteristics determining the given local population are absolutely indubitable.

Thus, in respect to the very concept "local population" at the present time there is a certain indefiniteness. Thus, for example, one calls "local population" the entire spawning population of the fall or spring Amur chum or of the pink salmon at the southwestern coast of the Kamchatka. But these populations as I.B. Birman has proved consist of local groupings restricted to individual regions of the spawning area. In their turn, these local groupings are subdivided into populations of individual spawning tributaries or even of individual spawning grounds.

The term "local population" itself is closely connected with "the theory of the native water basin", i.e. with the assumption that adult salmons return for reproduction to the same water basins from where they have left as fingerlings. Therefore, different degree of locality is characteristic of different species of salmon.

Among other salmons the quality of being bound to the native river is developed the strongest in sockeye which is generically connected with large lakes. The large lakes are spawning and breeding water bodies that are most stable in time and space.

We have already mentioned the studies of F.V. Krogius and E.M. Krokhin who established the difference between local populations of sockeye in two lakes closely located, but nevertheless different in water conditions. Later Vernon (1957) presented a morphometric characteristic of certain local populations of the land-locked form of sockeye. Hartman and Raleygh (1964) have proved experimentally that sockeye returns to a definite native tributary within the lake basin.

The attachment of coho salmon to the native river was experimentally checked by Wisby and Hasler (1964) by the methods of second return: the coho salmons which have already entered the spawning grounds were removed back to the river bed. Here the second return to the native water body was between 71 and 100% (among fish with severed olfactory nerve between /18
16 and 77% returned for the second time).

Evidently, the Amur fall chum also has a rather fractioned localization, whose embryogenesis, as we know, takes place always in ground waters, same as in the reproduction of sockeye and coho salmon. The phenomenon of rigid attachment to the native water body is also supported by data on extensive marking of fingerlings from 1947 to 1949 and in 1954 at the Teplovsky hatchery. Indisputably, the marked adult fish were detected exclusively in the Teplovsky channel in an amount of several hundred individual (in addition to two or three very doubtful cases of finding marked fish in the Bidzhan and Koor Rivers). Our experiments at the Teplovsky hatchery indicated 100% the second return for adult fish.

The following example indicates the existence of small local groupings. At the Georgiyevsky spawning grounds, in the Khor River, the fall chum establishes from year to year two spawning nests in a mound, the mounds themselves were relatively small. 90 kilometres higher upstream at the Ambansk spawning grounds, in the Khor River, in the spawning mounds, as a rule, were found three nests and the mound was 1.5 to 2 times greater than the one in the Georgiyevsky spawning grounds.

The eggs of pink salmon and of summer chum, as we know, develop in the channel below the river bed (the summer chum usually develops with an admixture of ground waters, a fact indicated by higher temperature in the spawning nests during the winter months).

Different viewpoints exist in respect to the degree of localization in the reproduction of these salmons. V.V. Abramov (1954) claims, however, without presenting any proof, the extreme point of view, namely, pink salmon's return to the native spawning grounds is compulsory. A.G. Kaganovsky (1949) writes that "under corresponding changes in the development conditions or in the conditions of fish habitat (of pink salmon - V.L.)

extensive deviations from the usual return to the native rivers may also be observed". A.P. Vedensky (1954) believes that pink salmon is not attached to its native river, but the distribution of the spawning population within the boundaries of the area are the results of environmental conditions. R.S. Semko (1954) considers it possible to speak of "an absence in the salmons, particularly in pink salmon, of a strict attachment to certain spawning grounds". Experiments which he carried out according to the method of second return gave the following results. When releasing below the estuary of the spawning spring the following portion of fish returned: pink salmon from 9.6 to 13.9%, chum - 21.2% and sockeye - 35%. When 30 pink salmons were released above the estuary of the spring, not a single fish returned to the spring. Further observations at the Karymaysk Spring (Bolshaya River, west coast of Kamchatka) indicated clearly the absence of any feeling for the native spawning grounds (but not for the native river) in pink salmon of the Bolshaya River. In 1950, only 18 pink salmons entered the Karymaysk Spring, in the spring of 1951 not a single fingerling descended from this spring (Semko, 1954), but in 1952, 95,000 pink salmons "returned" to the spring. This is the most striking example, but in 1956 to 1963, we observed several cases in which the number of returned adult individuals of sockeye and coho salmon was greater than the corresponding numbers of fingerlings who migrated downstream several years earlier.

Similar cases of incongruence between the number of downstream migrated chum and pink salmon fingerlings and the number of returned adult fishes was observed in the practice of censuring operations at the hatching and melioration stations of the Amurrybvod.

Observations of I.I. Kuznetsov and M. Bolbat (1939) support one of the possible causes for the disturbance in the feeling for the native tributary, they observed the spawning migrations of the summer chum in the Amur River in 1938, when owing to increased water temperature all the schools turned off into the very first large cold-water tributary, the Amgun', without trying to reach the native spawning grounds located further upstream from the estuary. All this indicates that the pink salmon, same as the summer form of chum, is attached not to the native spawning grounds, but to the native river system. In cases when we deal with adjoining small rivers we can, apparently, speak of an attachment to the spawning area.

However, we cannot agree with some of the scientists of the Sakhrybvod (I.K. Chernyavskaya and others) who deny the attachment of pink salmon to such large spawning areas as the western or eastern coast of the Sakhalin Island, on the ground of a methodologically imperfect marking of fingerlings by means of cutting one fin off. To what degree such a marking is capable of confusing the issue was well proven by A.P. Vedensky (1954) on the example of American studies.

Thus, the pink salmon has local groupings (Enyutina, 1954a and b) restricted to definite geographical regions (local populations of the first order). It is possible that the populations exist which are hereditarily connected to large river systems within such regions; for example, in the basin of the Amur River there may exist a local population of pink salmon in the Amgun' River (local population of second order), but most probably the pink salmon has no attachment to definite spawning grounds (it has no local populations of third order). Available data indicate a possibility of an exchange in pink salmon individuals between local populations of the second order.

The distribution of pink salmon within the spawning area is determined by the abundance of populations and by the conditions of the environment.

The matter with the summer chum is more complicated. As mentioned above, A.A. Svetovidova has established the presence of morphometrical differences in local populations in a number of large and small tributaries of the Amur River, in particular, of the Beshenaya River. However, a case is known which contradicts this conclusion. Thus, in the winter of 1953 to 1954, in the Beshenaya River the spawning grounds froze completely to the bottom. In 1957 when the main part of the offspring of the summer chum spawned in 1953 should have returned to the Amur River, 2.6 times as many fish entered the Beshenaya River than in 1953 (5,100 individuals). Here the age determination according to scales indicated that in 1957 the fish aged 3 constituted 73% of the spawning population of the Beshenaya River (scales of 100 fish were analyzed).

On the basis of this and other observations we may assume that a considerable exchange in individuals takes place between the local populations of third order, and in a number of cases affected by sharp changes in the environment, also between the local populations of second order. The relatively weak attachment of the local populations of summer chum to the native river is furthermore confirmed by the report of I.I. Kuznetsov (1937), which states that in 1934 the spawning schools of summer chum entered the Tunguska River (a tributary of the Amur River), which is located 350 kilometres above the area of its major occurrence. Here the migration was so abundant that the inhabitants of villages located along the lower reaches of the river, in spite of the unexpectedness of the summer chum appearance, succeeded in catching about 15,000 salmons.

A possibility of intermixture between various local populations complicates the morphological studies. In particular, the question remains unsolved concerning the stability over a period of many years of one or another morphometric feature. From this point of view the data on the relative maximum body height of the fall chum in the Teploye Lake are interesting. I.B. Birman (1956) indicates that this chum together with the chum from the Ussuri River forms a long body morph of the fall chum, the Amur chum proper is a different chum compared to the high body fall chum from the Amgun' River (a tributary of the Amur River). Table 3 indicates a fluctuation of this feature in the fall chum in the Amur liman and in the Teploye Lake.

Data in the Table indicate that the relative body height of the fall chum from the Teplovsky population was lower during the entire period of observation than the height of the fall chum in the Amur liman.

Table 3

The Maximum Body Height of Females of Fall Chum in Percentage to the Body Length

Place of data collection Место сбора материалов	1926	1940	1946	1951	1952	1956	1957	1958	1959	1960
Lake Teploye (Bira river) Оз. Теплое (р. Бира)	30,8	30,5	29,4	28,4	29,4	28,8	28,2	29,4	28,6	27,9
Amur liman Лиман Амура		31,6	31,5		31,6				31,6	31,9

We must remember, that the body height in the fall chum females in the /20
Teploye River is higher because of the development of mating colours. The difference would have been still greater if the fish was compared under similar biological conditions.

The leveling effect of the mating colour can be seen from the following example. The relative body height of fall chum females in the Ussuri River is 30.2% according to I.B. Birman's data of the body length, but after their entry to the spawning grounds in the tributaries of the Ussuri River, the height attains according to our data, 34.4%, in other words, it increases considerably.

It should be noted, that although the presence of morphological differences is a sufficiently reliable criterion for distinction between the local salmon populations, the absence of such morphological differences does not mean at all that the fishes in question belong to one local population. Apparently many local populations are distinguished only by a few ecological peculiarities. This is natural since in freshwater bodies they live under similar conditions, while they either mix in the sea, or live there under identical conditions. Thus, the salmons are almost not subjected to any sharply distinguishing factors of the environment, which may contribute to emergence of morphological differences. (We are speaking here of the local populations of the third order in the case of sockeye and fall chum, and of populations of the second order in the case of pink salmon).

Existence of local populations is very important in the reproduction of salmons: it ensures the most complete and uniform utilization of the spawning area and of the food base of the growth water bodies. The relative stability of the numbers of local populations of the third order (lake sockeye, Amur fall chum) is also connected with the divided localization.

The phenomenon of the localization of populations is much less pronounced in pink salmon, which is connected to the fresh waters to a lesser degree and which has enormous spawning resources; therefore, the pink salmon is the species with the strongest numerical fluctuations. If strictly local small populations were characteristic of pink salmon, then the practical homogeneity in age of the population and the development of eggs in the stream below the main channel of the river bed, which is subject to periodical freezings, would lead to depletion of a portion of its spawning area.

Since the Amur summer chum is connected with ground waters only to an insignificant degree, the freezing of individual rivers will not cause their total disappearance from the spawning stock, because they have a more complex age structure of the population.

The relatively poor localization of the spawning populations of summer chum is an adaptation to a faster repopulation of depleted sections of the spawning and growing areas.

Local populations of the fall chum are the most distinctly and fractionally pronounced among the Amur salmons. Since the reproduction of fall chum is connected with ground waters, the freezing never destroys the local population completely. This permits the fall chum, regardless of any general decreases in their numbers, to maintain the same dimensions of the spawning area covering the entire basin of the Amur River, as in years of high numbers.

The embryonic and larval development of fall chum in ground waters ensures, even in the most adverse years, survival of a portion of the /21
offspring at each of the spawning grounds. Therefore, the attachment of fall chum to the native river may be considered as adaptation to a dispersion within the spawning area. This dispersion contributes to the most efficient utilization of the spawning areas and of food resources.

PATTERN IN SALMON REPRODUCTION

The following peculiarities characterize the reproduction of the Pacific salmons: single-phase reproduction at the end of the life cycle, low fertility, large size of eggs, prolonged embryogenesis, embedment of eggs into the ground (protection of progeny from predators). All the above said peculiarities ensure a relatively higher individual survival rate of Pacific salmons during the period of embryogenesis, than in the case of fish, who reproduce repeatedly, who have a high fertility and who do not protect their progeny (herrings, carps, cods and others).

The protection of offspring only has biological importance in fish if the amount of fingerlings in the new generation, at the transition moment to active feeding, depends on the number of reproducing individuals. In fish who do not protect their progeny the mentioned relation may be upset by climatic and biological conditions of the environment, up to an including a complete absence of any correlation between the numbers of the reproducing individuals and their progeny.

In Pacific salmons the relation of the numbers of parent stock to the numbers of progeny has a curvilinear character during the fingerling period. When the spawning areas are insufficiently, optimally or slightly excessively filled, the numbers of the parent stock and of their progeny are correlatively connected; when the spawning grounds are overfilled, the efficiency of spawning decreases and the moment may arrive, when an increase in the numbers of spawning fish does not lead any more to an increase in progeny. The limiting moment in the case of pink salmon is the size of the spawning area, and in the case of chum also the size of food resources in the water body.

The existing belief that the absolute number of fingerlings drops sharply as a result of an increase in the number of spawning fish is not supported by actual data and must be considered erroneous (Levanidov, 1964b). Already the initial researchers of chum, sockeye and other Pacific salmons noticed the existence of high-yield generations yielding maximum harvests at time-intervals equal to the average length of the life cycle. As A.G. Smirnov (1947) wrote, fluctuations in the size of salmon approaches, considered over short periods of time, show a cyclic character; such fluctuations once started, repeat themselves over a long period of time. He used this hypothesis for prognostication of fall chum harvests in the Amur River. It should, however, be noted that for the hydrologically normal years these prognoses were rather accurate. These prognoses were based on the assumption that there is a relation between the quantity of spawning /23
salmons and the number of their progeny.

This problem attracted attention of Canadian and American scientists during the 1950-ies. After the theoretical study by Ricker (1954) a number of works appeared showing the relation of the numbers of the spawning salmon population to the numbers in the parental generation (Rounsefell, 1958).

Wickett (1958) expressed this relation for the chum of the Vancouver Island for the period from 1942 to 1947, by the following simple linear equation: resources = 3.31 + 0.885·x (number of spawned fish). The resources and the number of spawned fish are given in millions of individuals.

Apparently, this was a period when the climatic factors did not deviate from the average values taken over a period of several years. For the years 1926 to 1941 and for the years 1948 to 1952, when these factors were changing sharply, the ratio resources to number of spawned chum at the Vancouver Island cannot be expressed by the shown equation.

In principle, the relation between the resources and the numbers of spawned pink salmon in the Prince William Strait is expressed by a similar equation for the years 1940 to 1956, in the Bulletin of International North Pacific Fishery Commission (Bulletin INDFC No. 10, 1962), namely, $y = 1.1 + 0.76x$, where y symbolizes resources in millions of individuals, and x shows the numbers of spawned fish in millions of individuals.

Johnson (1956) found that the number of first-year sockeye at the end of the first year of life is proportional to the number of spawned fish.

In the Bulletin of the International Fishery Commission (sic!) (Bulletin INPFC, No. 10, 1962) the equations of direct proportionality between the numbers of the spawned chum females from the Minter River (state of Washington) and the numbers of downstream-migrating fingerlings are also shown as: $y = 0.03 + 0.0002x$, where y is the number of spawned fish in millions, x is the number of downstream-migrated fingerlings in millions. The occupation rate of the spawning grounds in Minter Creek was low during the entire period of observation. However, judging from the data in the table, the dispersion of the points is nevertheless very considerable and the equation is in poor correlation with the observed data.

Table 4 presents a picture of the relation between the number of spawned salmons and migrating fingerlings in the basin of the Amur River.

Table 4

Correlation coefficient between the number of spawned fish and the number of downstream-migrated fingerlings.

Rivers	Correlation Coefficient			
	Pink salmon	Number of years	Summer chum	Number of years
Iski	0.73 ± 0.22	11	0.74 ± 0.22	11
Beshenaya	0.71 ± 0.27	9	0.60 ± 0.27	11
My	0.59 ± 0.28	10	0.67 ± 0.28	11
Im	0.84 ± 0.33	5	-	-
Somnya	0.30 ± 0.55	5	0.59 ± 0.37	6
Ul	-	-	0.54 ± 0.29	10

The total correlation between the number of adult fish arrived for spawning and the number of fingerlings is $r = 0.35 \pm 0.24$ for Amur pink salmon, and $r = 0.46 \pm 0.36$ for summer chum. In the case of Amur fall chum the correlation is $r = 0.69 \pm 0.26$. However, in each more or less long chain of observations on the reproduction of pink salmon and summer chum, individual years occur, in which the mentioned correlation disappears (such are the particularly low-yield years: 1938 to 1939 and 1958 to 1959). But-accepting the correlation between the numbers of two generations, as well as between the number of spawned salmons and the number of their progeny, it is necessary also to accept as a logical conclusion the presence of correlation between the number of fingerlings migrated to the sea and the age of adult salmons. Nevertheless, some authors believe that the number of returned salmons (pink salmons) is independent of the number of fingerlings migrated to the sea (Vedensky, 1954). This delusion is based upon a comparison of the results of the downstream migration of pink salmon fingerlings from one small spawning spring with catches of salmons returned to the river basin. The non-correlation in the given case does not indicate that there is no relation, but indicates an incorrect solution of the problem. /24

If the censusing operations on the downstream-migrating fingerlings (for example in the basin of the Amur River) are conducted on a sufficiently large scale, then the relation between the downstream migration of fingerlings and the return of adult fish becomes indubitable.

In the case of pink salmon the total coefficient between the downstream migration of fingerlings and the age of adult fish into the Amur liman for the period ranging from 1952 to 1962 is 0.55 ± 0.19, for the summer chum it is 0.77 ± 0.13, for the fall chum it is 0.84 ± 0.22 (except for one reproduction season, namely 1950-1951, when heavy freezing of spawning nests was observed). If we include data from this low-yield year, then the correlation coefficient will decrease to 0.69 ± 0.26.

It is interesting to note that in individual separate rivers, to which local pink salmon populations are restricted, the correlation coefficient is very high between the downstream migration of fingerlings and the return of the adult fish. Thus, in the case of pink salmon in the Iski River, this coefficient was 0.75 ± 0.21 for a 12-year period of observations, while for pink salmon in the My River it was 0.81 ± 0.19 for the same period.

Presence of the relations discussed above indicates that a certain tendency is potentially intrinsic to the populations of the Pacific salmons towards the stability of resources, and not towards an origin of the sharp fluctuations characterizing the dynamics of their numbers. However, as G.V. Nikolsky (1958, 1963) determined the fluctuations in the numbers are specific to the species being a species-characteristic. Therefore, on the basis of concepts of the unity of organism and environment, one must look for causes for the changes in the environmental conditions, to which the fluctuations are the adaptive answer. Consequently, the immediate causes of fluctuations in the numbers of salmons and in the efficiency of their reproduction are found in the abiotic or biotic conditions of environment.

The abiotic factors of environment cause destruction of salmons predominantly during the period of embryogenesis. After the emergence of salmon fingerlings from the ground these factors are practically non-lethal to the salmons any more. A.G. Kaganovsky (1949) wrote about them concerning the pink salmon, but this factor is equally applicable to all the Pacific salmons.

The biotic factors, as protection against which the salmons bury their eggs in the ground, have, conversely, little effect during the embryogenesis and during the larval period (Levanidov, 1951c), but they determine the numbers of salmons at all the remaining stages of the life cycle.

Considering the entire species the death rate in the embryo-larval period is in conformity with the food supply of the salmon juveniles in the fresh waters. When the numbers in the generation are too high the food base of the water bodies will be insufficient. Pink salmon is the only exception, its juveniles almost never feed in fresh waters. However, this contradiction is apparent; A.G. Kaganovsky (1949) pointed out that "in the case of pink salmon, which feeds very intensively (and compared to other salmons is the most numerous salmon. V.L.), the amount of food in the sea is not that great, and even in ordinary years, this factor limits to a certain degree the productivity of the population". A.G. Kaganovsky supports his opinion by indicating the close reverse relation between the dimensions and the numbers of pink salmon.

Still another indirect proof of this assumption appeared during the latest decade. After a general decrease in the numbers of pink salmon in the northwestern part of the Pacific Ocean the growth rate in the sea /25
increased for the chum and sockeye in various local populations (Birman, 1959, 1964; Krogius, 1960; Petrova, 1964).

For the efficiency of reproduction of salmons and for the character of the dynamics of these numbers it is not the absolute measurement of the effect of the environment factors that is significant, but the amplitude of their fluctuations. The factors of environment, particularly the abiotic factors, change because of accidental or regular climatic fluctuations. Therefore, all the fluctuations in physical and chemical factors are climatic fluctuations. The biotic factors (predators, food base, parasites) are also indirectly connected to the climatic factors, but these conditions are very complicated and poorly studied.

The type of population dynamics is primarily a results of the adaptational relations formed in the biocoenosis on the background of regular fluctuations in climate, changing the strength of food relations within the biocoenosis.

SURVIVAL RATE OF PACIFIC SALMONS IN FRESH WATERS

As we know, the beginning and the end of the Pacific salmon's life cycle takes place in fresh water. The pink salmon spends 50% of its life (including the period of embryogenesis) in fresh waters, the sockeye spends 40 to 60%, and the coho salmon from 66 to 75%. Chum spends less time in fresh waters than the other salmons, on the average about 25% of its life. Natural mortality rate among adult fish on the way to spawn is relatively low and, only with few exceptions, it does not lower the efficiency of the natural reproduction to any significant degree. Conversely, at the beginning of the life cycle, the mortality rate is extremely high, like in most animals, and it eliminates an overwhelming portion of very new generation.

Quantitative indices of the survival rate in Pacific salmons at the present time, are only determined for a few periods of the life cycle, namely:

in the ground, soon after the spawning, the number of eggs deposited by the female is determined together with the mortality rate of the initial development stages of the embryo;

the mortality rate during the subsequent period of the embryogenesis;

the survival rate prior to the migration of fingerlings from the spawning grounds. In sockeye, coho and other salmons, whose juveniles stay in fresh waters for a long period of time, the survival rate prior to the fingerling stage is not always determined; more often the survival rate of juveniles is determined until the period of downstream migration;

The final total survival index is the number of salmons returning to the shores after the fattening period at sea; expressed in percents of the fertility potential this survival figure is called the "return coefficient".

The amount of eggs found in females arrived for spawning serves as the initial point to which all the indices of the survival rate are referred. This value may be called the "fertility potential"; in the future we are going to use this term. The mortality rate of eggs during the period of embryogenesis is expressed in the percents of this value.

The number of the downstream migrated fingerlings, considered in percents of the fertility potential, is called the "coefficient of downstream migration".

The study of natural mortality rate of salmons in the fresh waters is a problem of high methodological complexity. Furthermore, it should be noted that for various development stages the mortality rate is determined with very different degree of accuracy and reliability.

For determination of the survivability of the Pacific salmon eggs and larvae in the ground, we use extensively the method of opening spawning nests or mounds, or floor platforms at the spawning grounds.

I.I. Kuznetsov must be considered as the author of this method. Results of the first years of his studies are described (Kuznetsov, 1928), but, unfortunately, the entire extremely valuable material collected under his guidance during the years from 1927 to 1946 remains unpublished.

In the years 1938 to 1941, A.G. Smirnov (1947) and A.Ya. Taranets (1939b) were opening spawning nests; the latter of the two contributed a number of major improvements to the methodology of determining the survival rate from the results of such openings.

However, the method of opening spawning nests of Pacific salmons as a measure for determination of the survival rate of eggs and larvae in the ground period of life has some major shortcomings. First of all, its results are difficult to compare with the determination result of the fertility in females (initial value) and with the number of downstream-migrated fingerlings (final value). The fertility potential is found very accurately by determining fertility in a sufficiently high number of females. The coefficient of downstream migration may also be accurately determined by means of complete or selective censusing.

A similarly accurate determination of the survival rate of eggs in the ground presents considerable difficulties. The mortality rate in individual salmon spawning nests fluctuates, even at the same spawning grounds, from 0 to 100%. Because of such fluctuations in the mortality rate, it is necessary to perform a considerable number of observations to obtain statistically reliable results.

In the case of Amur fall chum, for example, when fluctuations of live eggs range in a spawning mound from 0 to 3600, at a permissible inaccuracy of ± 100 eggs, one hundred mounds have to be opened (on the basis of the equation $\frac{t^2}{k^2}$, where t is the index of probability and k is the accuracy (Plokhinsky, 1961), at an empirically derived ± 700). The area of one spawning mound of the fall chum is from 1.5 to 2 square metres. Consequently, to obtain reliable results of the survival rate, we must dig up from 150 to 200 square metres of pebble and rock ground to a depth of one half of a metre.

The following example shows how unreliable are the results when the number of openings is small. In the fall of 1953, at the Ambansk spawning grounds of the Khor River, ten spawning mounds with a total area of 25 square metres were dug up. The average number of eggs per mound was 2784 ± 200. Towards the end of January, 1954, another 10 mounds were dug up with identical area, in this case the average number of eggs per mound was 2271 ± 240. The reliability criterion (t_d) was $\frac{513}{312} = 1.6$, in other words, considerably below the first degree of probability (t_d at 95% probability is 2.1). Consequently, the authenticity of the obtained results is not statistically supported, regardless the difference between the two batches being 513 eggs.

Excavations in the ground may be carried out only at accessible shallow locations, therefore, they do not give any complete picture of the survival rate of eggs under various conditions. These circumstances and the extremely time-consuming excavations at a scale required for obtaining reliable results explain the low popularity of this method in the studies of survivability.

Canadian scientists (Neave, 1953; Hunter, 1959) were determining the numbers of chum and pink salmon larvae at their emergence from the ground by means of indirect method, namely, by summing up the downstream-migrated fingerlings together with the calculated amount of fingerlings eaten by predators prior to the downstream migration.

I.I.Kuznetsov (1928) accumulated considerable amount of data on the survival rate of eggs in the ground based on comparison of the amount of live and of dead eggs. This scientist evaluated the average survival rate of chum eggs in the ground to be 50% of the average fertility. A.Ya. Taranets (1939) indicated that this method gives too high results, because part of the eggs dead during the period of incubation disappear without trace. The results obtained by I.I. Kuznetsov are also too high because a number of excavations were carried out at the end of April (Kuznetsov, 1928), when the fingerlings have already left the ground. In cases, when during the excavations neither live, nor dead eggs were found, I.I. Kuznetsov took the survival rate as 96% (?).

Other researchers, A.G. Smirnov (1947), R.S. Semko (1954), and I.I. Strekalova (1963) opened too small a number of nests to obtain reliable indices of survivability.

A.Ya. Tarants carried out in the Iski River considerable studies on the survivability of chum and pink salmon during the period of embryogenesis, during the years 1938 and 1939. Unfortunately, his studies remained unpublished. At the end of 1938, he excavated 100 platforms of the river floor one square metre each. Here the average mortality rate of pink salmon eggs was 29%, and of chum eggs, 39%. In the spring of 1939 (towards the end the ground period of life) 72 platforms were excavated, which were of identical size; the mortality rate of eggs was already 89% in the case of chum, and 93% in the case of pink salmon. The winter 1938 - 1939 was catastrophic for the reproduction of the salmons along the entire basin of the Amur River, therefore, the indices of the survival rate obtained by A.Ya. Tarants cannot be considered as average values characteristic of the species.

In order to determine the average mortality rate of fall chum, I carried out for a period of years together with scientists of the fishery-meliorative stations excavations of the spawning mounds. We opened every year from 25 to 100 mounds; a total of 385 mounds was excavated. The results of the openings are shown on table 5.

Table 5

Survival rate of fall chum eggs during the period of development.

Years	Ambansk spawning grounds			Georgiyevsk spawning grounds		
	live eggs, individuals	in percents of laid eggs	in percents of fertility	live eggs, individuals	in percents of laid eggs	in percents of fertility
1948	1789±64			711±169	60	39
1949	1272±86	59	35	714±124	—	39
1950	1428±142	60	40	514±85	44	27
1951	1286±463	62	33	—	—	—
1952	1425±59	60	36	700±116	42	36
1953	1923±250	66	52	921±108	64	48
1954	951±370	40	26	636±152	45	33
Среднее Average		58	37±5		51	37±3

Remarks: Notwithstanding the fact that the Ambansk and the Georgiyevsk spawning grounds on the Khor River are located 90 kilometres from each other, the character of oviposition into ground is different at the two spawning grounds. At the first one, the fall chum makes one large mound with an area of 3 square metres, at the second spawning ground one female, as a rule, lays her eggs into two mounds each with an area of 1.6 square metres.

A considerable number of openings of the spawning mounds was carried out by the fishery-meliorative station of the Koor River (left-bank tributary of the Amur River). 180 mounds were opened during a period of eight years; the average survival rate during the period of embryogenesis was 28.6% of the fertility potential, or 40.6% of eggs laid in the ground.

Summing up the results for a number of years (from 1949 to 1954) of excavations of spawning mounds by six fishery-meliorative stations located at the tributaries of the Amur River (the Beshenaya and Ul Rivers), at the tributaries of the Amguni River (the Somnya and Im Rivers), in the liman of the Amur (My River) and in the Schastye Gulf (Iski River), we have determined the survivability of the summer chum eggs for the period of embryogenesis to be 24 $\pm$ 4% (according to openings of 150 spawning mounds), while the survival rate of pink salmon eggs was 22 $\pm$ 5% of the fertility /28
potential (according to the opening of 125 spawning mounds).

Since the mortality rate of free embyos and larvae of the salmons in the spawning nests is very small, the indicated values may with a certain approximation be considered as indices of the survival rate of the Amur salmons during the ground period of their life.

The subsequent stage at which the values of the natural mortality rate usually are determined is the migration of salmon fingerlings from the spawning and growing water body. The chum migrates downstream from the spawning grounds basically at the fingerling stage, although a small percentage of the migrants consists of late larvae. The main migration of the pink salmon takes place at the end of the larval stage.

The determination of the number of migrating fingerlings is carried out by a complete barrier across the estuary of the spawning water body or by means of the selective method using traps of various design.

During recent decades Soviet, Canadian and American scientists have accumulated a rather substantial material on the survivability of chum and pink salmon in the period prior to the beginning of the migration from the spawning grounds. Table 6 demonstrates the longest series of observations; the data presented in this table are taken from the following sources: on the MacClinton River (British Columbia, Queen Charlotte Islands) according to Pritchard (1948); on the Hooknose River (British Columbia, King's Island) according to Parker (1962b) and Hunter (1959); on the Sashin River (south-eastern Alaska) according to Merrel (1962) and Skud (1958); on Ulkhan River (northwestern coast of the Sea of Okhotsk) according to V.L. Kostarev (1964); on Karymaysk Spring for the years from 1942 to 1950 (basin of the Bolshaya River) according to R.S. Semko (1954). Indices characterizing the survival rate of chum and pink salmon in the Karymaysk

Table 6

Coefficient of downstream migration of the Pacific salmon fingerlings.

1 Год нерес-та	2 Горбуша				3 Кета			4 Красная	5 Кижуч
	6 р. Мак-Клинтон	7 р. Хук-ноуз	8 р. Сашин	9 Карымайский ключ	7 р. Хук-ноуз	9 Карымайский ключ	10 р. Улхан	9 Карымайский ключ	9 Карымайский ключ
1930	10,6		—						
1932	17,4		—						
1934	9,0		—						
1936	6,9		—						
1938	23,8		—						
1940	19,0		6,4						
1941			1,2						
1942			0,8	5,7					
1943			1,5	0,35				18,4	6,9
1944			2,7	0,02		2,7		16,8	1,6
1945			0,8	0,19		0,68		6,5	0,65
1946			0,2	—		0,87		8,2	4,8
1947		0,88	2,0	0,12	0,99	2,7		9,9	15,9
1948		8,17	1,7	—	7,35	1,5		18,7	0,35
1949		6,45	3,7	4,4	6,22	2,5		11,8	10,3
1950		15,12	0,1	—	15,09	4,2		10,7	13,1
1951		16,47	9,3		16,92				
1952		14,42			19,41				
1953		13,95	7,0		16,36				
1954		3,22	4,8	—	6,34				
1955		6,76	12,2	—	3,87				
1956		2,87	0,5	—	1,72		25,3		
1957		2,80	22,8	—	2,82		9,6		
1958		12,63	6,1	—	15,33		10,0		
1959		15,05	13,2	—	15,45		33,0		
1960		37,23			22,04		4,4		
1961							21,0		
1962							7,0		
1963							0,4		
1964							14,4		
Average	14,4	11,1	5,2	1,8	11,0	2,3	13,9	12,5	6,7

1. Year of spawning
2. Pink salmon
3. Chum
4. Sockeye
5. Coho
6. MacClinton river
7. Hooknose river
8. Sashin river
9. Kary-Maysky spring
10. Ulkhan river.

Spring are considerably lower than the data obtained for other water bodies. This low survival rate can, evidently, not ensure the maintenance of the salmon numbers and must lead to a catastrophic drop in resources. R.S. Semenko himself does not comment on his data, but these data have attracted attention of many ichtyologists. A.G. Kaganovsky (1949) expressed an opinion that Karymaysk Spring is a spawning ground uncharacteristic of pink salmon and "it has a number of negative qualities for the spawning of the mentioned fish, therefore, the emergence of fingerlings here may be low". B.I. Cherfas (1950) considers the data on the downstream migration of pink salmon for the first three years of observations and comes to a conclusion that these indices belong to years with a catastrophically low survival rate, as a result of the influence of some unfavourable factors. However, as indicated by the data in table 6, during the entire observation period at the Karymaysk Spring the coefficients of downstream migration remained at the same catastrophically low level. Furthermore, in retrorespect, we may say that the results of the censusing of salmons migrating downstream from the Karymaysk Spring in the years 1951 to 1964 turned out to be considerably lower than at the time of the published data.

Data shown in table 7 indicate that from 1952 on the yield of chum fingerlings, and particularly of sockeye and coho ones, dropped by many times and, as a rule, the coefficients of downstream migration are only fractions of one percent. Starting with 1954 the pink salmon is not appearing at all in the Karymaysk Spring. An almost complete disappearance of salmon in the spring, where only 20 years ago up to 120,000 fish used to come, is difficult to explain, a phenomenon which will be later discussed.

According to the data of Neave (1953) the coefficient of downstream migration of pink salmon from the Morrison River (Canada) was during two seasons 4.7% and 6.7% respectively. Hanavan (1954) when studying the reproduction efficiency in pink salmon above the tidal zone, obtained 9.2%, 11.2%, 13.9% and 20.9%. Wickett (1952) obtained the following coefficients of downstream migration in the Nail-Creek River: 1.4% for pink salmon in 1950, 7.2% for the same in 1952; 0.4% for chum in 1948, 6% in 1949, and 7% in 1952. Foerster (1955) records that the ground of this river's bottom is "bad" for natural reproduction (too shallow).

In salmon whose juveniles remain in fresh waters for a year or more, the freshwater survival rate indices are for the same period of development close to the indices of chum and pink salmon.

All the presented data are obtained by means of a complete permanent barrier across the spawning water body and by passage of all the fingerlings through a censusing trap-receiver. Only the Ulkhan River constitutes an exception, this river was periodically barred (only during the censusing). Thus, the natural living conditions of the chum fingerlings were not disturbed here, and this is probably the explanation why this river has the highest survival rate. I used a similar method at the Khor River (Georgiyevskiye Springs): barring of the estuary of the spawning channel, release at the beginning of the downstream migration from the spawning grounds of fall chum fingerlings, marking with vital dye and their repeated catching by means of (control) removals. By this method high indices of fingerling survival were obtained. In the years 1957 to 1959, this value was 17.9, 21.6 and 28.4% respectively (on the average 22.7%) of the fertility potential.

Foerster (1955) presents the following data on the survivability of Canadian sockeye from the fertility potential to the fingerling (in percents): in the Scally-Creek River it is 13.7%, 9.3%, 13.6%, 12.2% and 10.1%; in the Folly-Creek River, 25.2%, 1.8%, 5.1%, 8.9%, 5.0% and 13.4%; in the Six-Mile Creek River, 12.0% and 19.0% (on the average 11.5%).

The survival rate of the coho salmon from the fertility potential to fingerling is according to Foerster (1955), in the Kovichan River, taken over an observation period of twelve years, 22.8% (at fluctuations ranging from 11.8 to 40%.

Thus, the survival rate indices of the sockeye in the Canadian rivers and in the Karymaysk Spring (in the latter for the period preceding 1951) are very close. The mortality rate of the coho salmon in the Karymaysk Spring is, however, considerably higher than in the Canadian rivers.

It is interesting to note that the average coefficients of downstream migration are practically very close in salmons as different in their fertility, as pink salmon, on the one hand, and as chum, coho and sockeye, on the other. Only the chum and pink salmon from the Karymaysk Spring and pink salmon from the Sashin River constitute an exception. However, the value of the coefficients of downstream migration to the Sashin

Table 7

Number of migrating fingerlings (in individuals) per one female.

	2 Горбуша					3 Кета				4 Красная	5 Кижуч
1 Год нереста	6 р. Мак-Клинтон	7 р. Сашин	8 р. Хукноуз	9 Карымайский ключ	10 р. Улхан	8 р. Хукноуз	11 р. Минтер	9 Карымайский ключ	10 р. Улхан	9 Карымайский ключ	
1930	120										
1932	306										
1934	162										
1936	136										
1938	400										
1939							225				
1940	294	144					1640				
1941		25					286				
1942		17					200				
1943		30		70,0			689			824	299
1944		53		5,0				63		784	71
1945		17		0,3			263	32		297	31
1946		3		2,7			110	21		460	230
1947		40	12	0,0		21	444	65		470	760
1948		35	107	1,8		154	277	39		961	17
1949		73	90	66,6		126	73	50		568	450
1950			234	0,0		359	123	100		498	656
1951		187	270	1,3		384		260		216	175
1952			246	0,03		520	210	4		5	3
1953		136	250	0,05		447	384	—		8	3
1954		96	53	—		190	280	—		5	3
1955		238	123	—		30		4		220	57
1956		10	41	—	440	43		10	700	120	42
1957		453	50	—	84	85		12	225	16	8
1958		122	300	—	375	340		2	388	3	2
1959		268	240	—	136	385		56	830	3	2
1960			580	—	200	552		2	150	1	4
1961					413			40	600	9	33
1962					50			2	190	30	12
1963					50			3	20	25	129
1964								2	500		6
Average	236	103	184	14	218	260	329	40	400	263	136

1. Year of spawning
2. Pink salmon
3. Chum
4. Sockeye
5. Coho
6. MacClinton river
7. Sashin river
8. Hooknose river
9. Karymaysk spring
10. Ulkhan river
11. Minter river.

River cause a certain doubt; in the calculation of pink salmon's coefficient of fertility for the entire period of observations, it was accepted as constant and equal two thousand eggs (Skud, 1955, Merrel, 1962). Such a fertility is very high for pink salmon, especially if we take into consideration that in 1940-ies and in 1950-ies the resources of pink salmons in southeastern Alaska were at a high level. It is also difficult to assume that the pink salmon fertility was constant. As Skud's data show (1958), the average weight of pink salmon from the Sashin River fluctuated not less than by 1.5 times during the years 1935 to 1953.

In connection with the above-said, it is interesting to evaluate the efficiency of the reproduction of salmons not merely according to /31 the relative, but also according to the absolute coefficient of downstream migration, i.e. according to the average number of migrating fingerlings per one spawning female. Data in table 7 show that the average numbers of progeny per one chum female during the downstream migration is considerably higher than of a pink salmon female. This fact proves that the assumption about the higher survival rate of pink salmon in fresh waters is unfounded (Vedensky, 1954; Soin, 1954; Strekalova, 1963). The relative survival rate of chum and pink salmon in fresh waters is approximately identical, while the absolute survival rate is higher in the former than in the latter.

The survival rate of pink salmon fingerlings in the Sashin River is relatively low in absolute indices, but is expressed by a value of same order as the survival rate of pink salmon in Hooknose River.

The survival rate of Amur salmon fingerlings was initially studied by A.Ya. Taranets at the end of the 1930-ies. However, contrary to Pritchard, who at that time was censusing pink salmon in the Mac-Clinton Creek River, A.Ya. Taranets set as his goal to determine the coefficient of downstream migration of chum and pink salmon not from a single spawning ground, but from the entire basin of the river; the latter is visited for spawning purposes by 1.2 million salmons. A maximum of 0.15 million pink salmons entered the Mac-Clinton River, usually it was entered by merely 40,000 to 50,000 fish.

Naturally, under such conditions a complete censusing of the migrating fingerlings is almost impossible, therefore, A.Ya. Taranets used the selective method of censusing by means of traps (conic nets) suspended in the water mass. The harvest rate of the traps was determined by means of the release and recapture of marked fingerlings.

A.Ya. Taranets obtained for the pink salmon fingerlings a correction in the harvest rate of approximately 2.0 (according to Vedensky, 1954). For chum fingerlings, according to unpublished data of A.Ya. Taranets, during three years of observations the correction in the harvest rate was 3,3, 1.8 and 2.4, the average being 2.5. Larger and more mobile fingerlings of chum, apparently avoid the traps to a greater degree than the pink salmon.

A correction for trap avoidance is not a constant value; this value depends on the depth and width of the river, speed of the current, weather conditions and other factors. This correction varies not only from river to river, or from censusing profile to censusing profile in the same river, but it varies also within the same profile owing to fluctuations in the hydrological and meteorological conditions. Therefore, in practice one has to use an averaged correction determining the boundaries of accuracy in the method of the selective censusing by means of A.Ya. Taranets' traps*.

Starting with 1951, the Amur branch of the Pacific Research Institute for Marine Fisheries and Oceanography and the Glavamurrybvod /Amur Main Fishery Department/ organize censusing of migrating chum and pink salmon fingerlings in all the rivers at which the fishery-melioration stations are located. During the past fourteen years a considerable comparison material is accumulated on the numbers of the downstream-migrating fingerlings of summer and fall chum and pink salmon. However, it is far from always that one can determine the coefficients of downstream migration: the fingerling traps suspended in the water mass operate every year under conditions of any type of flood waters, but high waters often wash away the barriers for censusing adult salmons. Table 6 shows the coefficients of downstream migration calculated with application of corrections for avoidance of traps. Correction coefficients fluctuate for pink salmon from 1.5 to 2.0, and for summer chum from 1.0 to 2.5.

The average coefficient of downstream migration for pink salmon according to table 8 is 16.3 ± 3.5 (in these calculations the catastrophically poor harvest years 1958 and 1959 are excluded). The average coefficients /32
of downstream migration for summer chum are 16.7 ± 3.9.

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* In 1960 and 1961 I have tested zepelin-shaped nets of scarce plankton gauze or of congress-canvas, which were two to three times longer than the Taranets traps. At current speed of one metre per second the correction was 1.0.

Table 8

Coefficients of downstream migration of pink salmon and summer chum

Река River	Годы ската year of migration										
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961
						Горбуша Pink salmon					
My Мы	18,0	10,0	23,5	3,0	25,9	25,8	11,1	—	—	16,8	—
Ul Ул	—	—	—	—	—	—	—	—	—	—	2,6
Im Им	—	7,0	7,0	—	—	—	—	—	0,6	—	—
Somnya Сомня	—	—	9,8	28,2	17,9	—	33,2	—	1,1	—	—
Beshenaya Бешеная	—	5,5	—	—	—	—	21,0	—	—	—	7,6
Iski Иски	27,2	8,3	21,7	3,3	15,4	25,5	6,7	17,4	0,7	15,6	17,0
						Кета Chum					
My Мы	6,7	3,0	—	—	12,4	35,4	—	—	2,0	—	—
Ul Ул	—	—	25,2	27,6	22,7	28,0	20,5	14,0	3,4	—	11,0
Im Им	—	—	16,9	—	—	—	—	—	26,3	—	—
Somnya Сомня	—	8,7	10,5	12,5	—	34,5	7,0	21,0	—	—	9,0
Beshenaya Бешеная	—	9,2	17,0	—	25,2	—	22,1	—	22,4	20,2	21,0
Iski Иски	—	10,2	8,1	2,2	—	32,6	8,6	—	10,2	1,7	10,5

Coefficients of downstream migration are, possibly, too low, since the major part of the figures in the table refers to the period of the decrease in the level of Amur salmon resources. They are close in size to the coefficients of downstream migration obtain by V.L. Kostarev at the Ulkhan River and by Hunter at the Hooknose-Creek during the observation years 1958 to 1961.

Starting with 1956, in Canada, together with complete censusing in spawning streams and rivers, in large tributaries of the Skeena River, one began to introduce the selective censusing of migrating fingerlings of pink salmon by means of traps suspended in the water stream. Censusing operations were organized in three rivers: Lakeelse, Kispioks and Kitvanga. The following examples indicate the importance of these rivers in the reproduction of pink salmon: in 1961, 705,000 pink salmons entered these rivers (325,000, 280,000 and 100,000 in each river respectively), while in 1962, the first of the three rivers alone was entered by 635,000 pink salmons (Annual Report of the Fisheries Research Board of Canada, 1962, 1964).

The coefficient of downstream migration of fingerlings in 1960, in Lakeelse River, was 18%, in the Kispioks River, 23%, and in the Kitvanga River, 15%. In 1963, in the Lakeelse River, the coefficient of downstream migration was 13%, but it must be taken into consideration that in 1962 a very considerable ("surplus") number of pink salmon spawned there.

The average coefficient of downstream migration of pink salmon according to the data presented above is 22.5% for tributaries of the Skeena River. Assuming that the average fertility of pink salmon in British Columbia is, according to Hunter (1959), 1600 eggs, we obtain on the average 360 fingerlings of pink salmon migrating downstream from each female. The future will show, whether these figures are the most characteristic indices of pink salmon reproduction in the late 1950-ies and in the early 1960-ies. In any case, the survival rate to the stage of fingerling of 15 to 20% is very high and is explained by the care for offspring characteristic of Pacific salmons. Such fish like carps have a survival rate from the fertility potential to the four-month age under natural conditions of 0.042% and even under pond conditions, where predators are absent, this rate only reaches 4.7% (Cherfas, 1950).

SURVIVAL RATE AT SEA /33

We have considerably fewer data on the quantitative evaluation of the survival rate of salmons while at sea, than we have on the fresh-water period of their life. The numbers of chum and pink salmon fingerlings in a spawning spring are determined by complete censusing, but it is impossible to isolate adult fish of this water body in total coastal catches. Furthermore, many data are accumulated on pink salmon supporting the opinion of A.G. Kaganovsky (1949), A.P. Vedensky (1954), R.S. Semko (1954) and other authors concerning the relatively poor restriction of this salmon to its native spawning ground. R.S. Semko (1954) demonstrated experimentally that the attachment to the native spawning ground is very poor in the Kamchatka pink salmon and chum.

The first evaluations of the value of the mortality rate of salmons at sea were carried out on the basis of the results of complete census in small spawning rivers and on the basis of the return of adult fish to the same. Data of Pritchard on the Mac-Clinton River are well-known. According to these data the return of adult pink salmon from the sea to the native river (to the censusing barrier) fluctuates from 0.3 to 6.75% of the number of downstream migrated fingerlings at a geometrical mean value of 1.02%.

A.G. Kaganovsky (1949) while analyzing Pritchard's data came to the conclusion that fluctuations in the mortality rate in fresh waters are considerably smaller than in the sea, and that the relative mortality rate in the sea is higher than in fresh water. The logical consequence of this conclusion is the recognition of the considerable difficulty in prognostication of pink salmon numbers by means of the number of fingerlings migrated downstream.

Neave (1953) sums up the data on three rivers where for a number of years a complete censusing was conducted, and presents the following data (table 9).

Table 9

Survival rate of pink salmon at sea. Return of adult fish to the spawning water body in percents of the downstream-migrated fingerlings.

Rivers	Years	Number of years	Age fluctuation, in %	Geometric mean value, in %
Mac-Clinton	1930-1940	6	0.29-6.75	0.824
Morrison	1943	1	-	2.10
Hooknose	1947-1948	3	3.1-5.2	3.74
Sashin	1940-1945	6	0.6-3.5	1.61

Neave assumes on the basis of the data in this table, that the average return rate of adult fish in the spawning rivers is 2% of the number of fingerlings. Having determined the mortality rate of pink salmon caused by fishery under conditions of coastal fisheries to be 60% of the spawning population, Neave evaluates the total survival rate of pink salmon at sea to be 5% of the downstream-migrated fingerlings. By comparing the survival rate of pink salmon in the fresh water and at sea, Neave comes to the conclusion that the data on the Mac-Clinton River are not representative in this respect and that the mortality rate of pink salmon in fresh waters at the beginning of their life cycle fluctuates considerably more than at sea. He presents the following figures for pink salmon from the Sashin Creek: the survival rate in fresh waters fluctuates by 32 times, in the ocean, by 5.2 times; the survival rate of pink salmon from Hooknose-Creek in the fresh water fluctuates by 17 times, but in the ocean it fluctuates by only 1.7 times. In the case of chum from British Columbia Neave calculated the survival rate in the ocean to be 4% of the downstream-migrated fingerlings.

Foerster (1955) presents the following geometrical averages of survival rate in the ocean until the return to the spawning grounds: pink salmon from Mac-Clinton Creek, 1.016%, from Hooknose Creek, 2.67%, from Morrison Creek, 0.93%; chum from Hooknose Creek, 2.6%, from Nail Creek, 1.8%.

Hunter (1959), using data on the return of pink salmon to Hooknose Creek and on the fishing intensity, determined the average return rate of pink salmons (on the basis of fingerlings) to the region of coastal fishery as 6.7% with survival rate fluctuation of 10.8 times.

The average survival rate of chum from Hooknose Creek at the return to the spawning river is, according to his data, 0.85%. If we assume, as suggested by Neave, that approximately 50% of the spawning populations is harvested, then the return rate to the region of coastal fishery is evaluated as 1.7% for the British Columbia chum. All these figures are obtained by using data on complete censusing in one or two small spawning rivers.

During recent years Canadian and American scientists were convinced that the environmental factors, particularly the predators (Vernon, 1962), had different effects upon a small salmon population in a single spawning spring and upon the entire offspring of the spawning population in a river basin, switched to the selective censusing of the downstream migration of fingerlings in such large rivers as the Skeena River (Manzer and Shepard, 1962). According to their data, the survival rate of pink salmon in fresh waters fluctuated during the five years (1955 to 1959) approximately by three times, and the survival of pink salmon from the fertility potential of the spawning population of pink salmon in this river, calculated according to data from annual censuses of the Canadian Fishery Institute (Annual Report of the Fishery Research Board of Canada, 1961, 1962, 1963, 1964) was 0.4%. These data refer to populations of considerable size: in odd years up to 3.2 million fish and in even years from 0.5 to 1.7 million fish.

As mentioned earlier, the coefficient of downstream migration of pink salmon in the Skeena River has a value of an order of 20%, consequently, the return of adult fish is 2% of the number of downstream-migrated fingerlings, i.e. considerably lower than estimated by Neave and Hunter. At these survival rate indices the fishing industry can take 65% of the spawning population, in other words, exactly the value derived by Neave (1953).

Thus, in foreign literature we find few data on the size of the oceanic survival rate of pink salmon and individual figures on the survival rate of chum. Data on these two species are also scarce in Soviet literature.

On the basis of the marking of fall chum fingerlings at Teplov hatchery and of the determination of the intensity of the fishery, I have calculated the return rate of chum in the region of coastal fishery to be 1.5% of the downstream-migrated fingerlings (Levanidov, 1954a), and then (Levanidov, 1964a) I have presented data on the oceanic survival rate of the entire population of the Amur pink salmon and of the Amur summer chum. Here the geometrical mean value of the coefficients of the oceanic survival rate for Amur pink salmon, in even years, was 3.4% of the downstream-migrated fingerlings for the period from 1952 to 1960, while for pink salmon in odd years this survival rate was 2.2%. The geometrical mean value of the coefficient of the oceanic survival rate of the summer chum was 1.6% for the years 1955 to 1960.

The presented data represent only an evaluation of the mentioned values based on the censusing operations covering approximately 30% of the spawning stock of pink salmon and approximately 60% of the spawning stock of summer chum (Levanidov, 1962). One may assume generally that the natural mortality rate of pink salmon in the ocean is 97% of all the downstream-migrated fingerlings, of chum, 98 to 99% of the same. The survival rate equals, consequently, one to two percent of chum fingerlings and two to four percent of pink salmon fingerlings.

According to data of the Canadian and American scientists (Parker, 1962a; Ricker, 1964), the bulk of the pink salmon and chum mortality takes place in ocean during the coastal period of life, when fingerlings stay close to the shores. Mortality in open sea is low according to Parker: for pink salmon it constitutes 16% and for chum 44% of the entire population.

Insufficient information on the numbers of chum and pink salmon fingerlings migrating downstream from large river systems does not allow us to obtain reliable indices for various local populations. Therefore, for the total evaluation of reproduction rates we most often use total indices of reproduction shown above for the course of the entire life cycle without any division into a freshwater and a marine periods.

SURVIVAL INDICES FOR THE ENTIRE LIFE CYCLE

The terms "return coefficient" or "return in percents", "percent of return" (Cherfas, 1950) are the most extensively used ones. This index is determined by the ratio of the abundance of offspring at the moment when individuals reach commercial size to the fertility potential.

The return coefficient may also be calculated for the remainder of the commercial population that returned to the spawning ground. The determination of the average value of the return coefficient in relation to the remainder of population that participated in the reproduction may be relatively easily calculated for various populations of Pacific salmon on the basis of a certain average level of their numbers.

Neave (1953) was the first to carry out such a calculation for pink salmon. By using his data we may determine the average return coefficient for the British Columbia pink salmon as 0.008%. These calculations are obtained from a simple assumption that in order to maintain constant numbers two individuals must survive out of each female's offsprings, if the ratio between sexes is 1:1. In the case of Pacific salmons, at an average sex ratio of 1:1 in the spawning population and at a single reproduction the average return coefficient is $\frac{2 \times 100}{\text{average fertility}}$ (in percent).

Undoubtedly, this index is too general to be used directly, but a comparison with it of observed return coefficients permits us to speak of a decrease or an increase in the reproduction efficiency. In cases when we know the portion taken by the fishery we can determine the return coefficient of the spawning population in the fishing region.

Besides the return coefficient another index is used for the determination of the total survival value; when using this index it is not necessary to determine the fertility of salmons. This index is the ratio of the numbers of the commercial population to the numbers of the spawning salmons of the parent generation. M.P. Somov (1930) and later I.I. Kuznetsov (1937) called this index "survival coefficient". The same index, but referred to the generation instead of the spawning population, was called by V.V. Azbelev (1958) "coefficient of the return of generations". Wickett (1958) calls this relation "production index" and expresses it in percent. A number of authors use this index, but without giving it any special name. T.V. Yegorova, F.V. Krogius and others (1961) use the ratio of the numbers of parent stock (accepted as a unit) to the return. The International Commission on Fisheries in North Pacific uses extensively this index by determining the return per one spawned individual (Bulletin of INPFC, No. 9, 10, 1962). Finally R.S. Semko has used now for a number of years the term "kratnost" / "multipleness"/. Among the enumerated terms the term "survival coefficient" should not be used, because in the fishery literature (Cherfas, 1950, 1956) a different interpretation is given to this term.

The "production index" is very unspecific. The term of R.S. Semko seems to me to be best chosen, as it expresses well the very essence of the concept. /36

It is easy to see that the return coefficient and the "multipleness" are connected by the following simple relation:

$$\frac{\text{Return coefficient}}{100} \times \frac{\text{Average fertility}}{2} = \text{multipleness.}$$

The multipleness, as an index, has the advantage of having greater objectivity than the return coefficient, the latter normally is very low in the highly fertile fish and is many times greater in the low-fertile species.

In the case of the Amur pink salmon the return coefficient to the Amur liman, for the years 1952 to 1960, fluctuates between 0.02 and 1.01.

The indices of the reproduction of the Amur chum are better studied (table 10).

Table 10

Spawning years	Number of spawning females, in millions	Average fertility, number of eggs	Total number of eggs, in millions	Return of adult fish, in millions	Return coefficient, %	Multipleness index
1947	2,2	3400	7480	17,5	0,28	4,0
1948	0,4	3400	1360	2,8	0,21	3,5
1949	1,2	3400	4080	5,3	0,13	2,2
1950	0,8	3325	2660	2,3	0,09	1,4
1951	3,3	3353	11065	7,6	0,07	1,2
1952	0,5	3603	1802	7,0	0,38	7,8
1953	0,4	3500	1400	4,2	0,30	5,3
1954	0,3	3238	9710	4,1	0,42	6,8
1955	0,6	3616	2170	6,0	0,28	5,5
1956	0,9	3538	3184	5,2	0,16	2,9
1957	0,6	3300	1980	7,5	0,38	6,3
Arithmetical mean . . .					0,24	4,3
Geometrical mean					0,21	3,6

The average return coefficient of Amur fall chum to the spawning grounds is $\frac{2 \times 100}{3600} = 0.056\%$. Consequently, to preserve the resources at the same level 72 to 73% of the numbers of the spawning population may be taken. Here, in case of return coefficients like those in 1952, 1954 and 1957, the chum resources at a constant fishing rate will increase from generation to generation to the double. On the other hand, at the lowest of the observed return coefficients the fishing industry may take only 20% of the fall chum's spawning population without harming the resources.

The fertility of summer chum changed insignificantly during the years of our observations, therefore, fluctuations in the return coefficients and in the coefficients of multipleness have identical character (table 11).

It should be noted, that the indices of multipleness for summer chum, regardless of the fishing prohibition, in three instances were less than one (Levanidov, 1964a), a factor indicating anomolous reproduction conditions.

The index of multipleness or of return per one spawned individual is widely used in recent years for the determination of the efficiency in the natural reproduction of salmons. In table 12 we see some data characterizing the numerical value of this index according to data of different authors. /37

V.V. Azbelev (1958) points out that his results were obtained during a period of increase in the numbers of chum, therefore, the average value of multipleness is probably too high.

The main character of fluctuations in numbers also reflects upon the indices of other salmons. Thus, the low indices of the multipleness in pink salmon in Central Alaska may be explained by a progressive decrease in pink salmon resources in this region, a decrease which started in 1946 to 1947.

Table 11

Indices of the multipleness of Amur summer chum.

Spawning year	Number of spawned fish, in thousands	Number of progeny according to age, in thousands			Total, in thousands	Multipleness	Return coefficient	Fertility, number of eggs
		2+	3+	4+				
1947	900	—	3540	432	3972	4,4	0,42	2100
1948	600	—	300	46	346	0,6	0,06	2000
1949	1080	64	582	214	860	0,8	0,08	2000
1950	1470	34	1182	185	1401	1,0	0,10	2250
1951	1720	29	555	365	949	0,6	0,06	1991
1952	320	—	505	81	592*	1,8	0,17	2187
1953	250	—	729	93	824*	3,3	0,33	1938
1954	1400	—	1590	151	1741	1,2	0,11	2300
1955	640	167	1790	464	2421	3,8	0,34	2250
1956	800	40	721	189	950	1,2	0,11	2200
1957	450	26	1016	300	1342	3,0	0,24	2542
Geometrical mean.						1,54		

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*) In the total numbers are included chum aged 5+ (in 1952, 6000 fish, in 1953, 2000 fish).

On the whole, the data in table 12 show that the average value of pink salmon taken by the fishing industry at the American coast and of Alaska chum is approximately 60% of the entire population with the average index of multipleness of

$$2.5 : \frac{(2.5 - 1) \times 100}{2.5} = 60\%.$$

However, in years of the maximum reproduction efficiency the harvest percent may reach

$$90 : \frac{(9 - 1) \times 100}{9} = 90\%.$$

Table 12

Indices of multipleness in the reproduction of salmons

Fish species	Average multipleness	Fluctuation limits	Number of observation years	Reproduction region	Source
Atlantic salmon	4.20	1.67-7.34	9	Tuloma and Kolvitsa Rivers	Azbelev, 1958
Pink salmon	3.4	0.9-7.7	14	British Columbia	Neave, 1953
same	2.45	0.17-8.21	9	British Columbia	Wickett, 1958
same	1.9	0.6-4.6	22	Central Alaska	Bulletin of INPFC, No. 10, 1963
same	2.3	0.5-4.8	22	Kodiak Island	
same	2.7	0.2-12.9	28	Southeastern Alaska, Northern region	
same	2.3	0.4-6.0	29	Southeastern Alaska, Southern region	
same	2.80	1.28-7.24	18	Pudget Sound	
same	3.1	0.8-6.0	6	Skeena River	Annual report F.R. of Canada, 1961-62; 1962-63.
Sockeye	4.6	1.5-9.4	14	Kurile Lake	Yegorova, Krogius and others, 1961
same	2.2	0.76-4.55	32	Elegnik River, Alaska	Bulletin of INPFC, No. 10, 1963
same	3.7	0.8-7.0	31	Naknak & Kvichak Rivers, Alaska	
same	2.5	0.28-9.75	32	Ugashik River, Alaska	

All the discussed survival indices show fluctuations in the decrease of the numbers in the generation of Pacific salmon during the course of the life cycle.

The analysis of the biomass dynamics of the generation is doubtlessly also of great interest.

Pink salmon. The biomass of producers (parent stock) constitutes three weight units, when the sex ratio is one to one. The weight of laid eggs at a fertility of 1500 eggs constitutes 0.275 weight units (9% of the weight of the producers), when one egg weighs on the average 170 milligrams. The number of larvae migrating from a river is 250 individuals from one pair of producers; one larva weighing on the average 220 milligrams the biomass of the offspring of one pair of producers is 55 grams (1.8% of the weight of the producers). Actual observations on the natural mortality during the stay of pink salmons at sea are lacking, but if we assume, in accordance with Neave, that from each pair of spawned fish, on the average, five pink salmons return (with no marine fishery in operation), then the biomass of the generation during this period of life will be 7.5 weight units, or 250% of the biomass of producers, and it will exceed by 136 times the final biomass of the generation in fresh water.

Fall chum. Similar calculations in the case of Amur fall chum give the following values: the biomass of the producers is 9, when the sex ratio is one to one, the biomass of fertilized eggs is one, the biomass of migrating fingerlings is 0.18, the biomass of the population returned to the shores is 32 weight units. These examples show the exclusive predominance of the growth processes in salmon over natural mortality rate at sea.

The presented data show very considerable fluctuations in the indices of natural reproduction of Pacific salmons, both according to individual periods, and according to the life cycle taken as a whole.

Because of these fluctuations the correlation between the number of spawned salmons and the numbers of progeny may disappear; the same may happen to the correlation between the numbers of salmon in the fingerling period of life and the numbers of adult salmon during the last period of ontogenesis. Therefore, when studying reproduction of salmons, it is a problem of extreme importance to study the causes of fluctuations in efficiency and in the rates of natural reproduction.

ENVIRONMENTAL FACTORS DETERMINING THE EFFICIENCY OF THE NATURAL SALMON REPRODUCTION.

Effect of the Climatic Fluctuations upon the Efficiency of Natural Reproduction

L.S. Berg (1935) expressed his opinion that fluctuations in the numbers of Atlantic salmon must be connected with the fluctuations in climate, the effect of the latter fluctuations is reflected during their river period of life.

A.G. Smirnov (1947) confirmed this assumption in regards to the Amur salmons. He was the first to show that in the years of catastrophic freezing of the spawning rivers in the Amur basis an extensive destruction of the salmon eggs takes place. A.G. Smirnov's viewpoint upon the freezing of the spawning grounds, as being the main cause of the origin of the short-term fluctuations in the numbers of Pacific salmon achieved almost universal recognition.

I.B. Birman (1954), while developing a conception of the origin of low-yield chum and pink salmon generations under influence of the climatic fluctuations, presents a number of deliberations about how the abnormally high summer floods and water temperatures, as well as the abnormally low fall and winter water levels may "reflect in a most unfavourable way, primarily, upon the conditions of the efficiency in the reproduction of summer chum and of pink salmon." I.B. Birman was the first to point out that the fluctuations in the salmon numbers are regularly connected with the periodicity of the solar activity (Birman, 1957, 1959). According to this author, the particularly unfavourable life conditions of salmons in fresh water determine their future low numbers (poor yield) also for the marine period of their life.

G.V. Nikolsky (1954) takes a similar stand; he explains the sharp drop in the numbers of commercial population of the summer chum, in the years 1911 to 1914, by low winter air temperatures and by the small amount of precipitation in the mentioned years.

V.V. Abramov (1954) sees in the severeness of the winters 1911 to 1914 the cause of not only a sharp drop in the resources of Amur summer chum and of pink salmon in the odd-years, but also the cause of their significant depression right to the beginning of the 1950-ies, i.e. during a period of several generations.

Z.I. Petrova (1964) presents measurements of the decrease in the pink salmon resources at the western coast of Kamchatka affected by abnormally low winter temperatures. V.L. Kostarev (1964a) believes that there is a connection between the amount of precipitations in July of the spawning year of the Okhotsk pink salmon, and the yields of its progeny. He also believes that snowless winters with low air temperatures have a strong effect upon the reproduction results in the salmon resources.

M.N. Lishev and E.Ya. Rimsh (1961) have published an extensive work on the effect of climatic elements upon the dynamics of the numbers of Baltic salmon.

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I have reported in 1960 (Levanidov, 1964a) on the immediate effect of climatic fluctuations upon the survival rate of chum and pink salmon in fresh waters. V.L. Kostarev (1964b) has also established a correlation between the yield level in chum juveniles at the coast of the Sea of Okhotsk and the thickness of the snow cover. The correlation coefficient between these two values is 0.79 ± 0.25. Canadian and American scientists write about the existence of such a relation. Thus, Wickett (1951) found a negative correlation between the summer water temperatures in the rivers in British Columbia, and the survival rate of coho yearlings. Foerster (1955) points to the negative correlation between the run-off of the river in October (fall floodings) and the survival rate of pink salmon from eggs to migrating fingerlings.

Neave and Wickett (1949) found relation between the amount of precipitations in July and August during the spawning year and the return of pink salmon.

In the latest work of Wickett (1958) examples are shown demonstrating the relation between the efficiency of the natural reproduction and the elements of the climate. Thus, the November expenditure of waters in the rivers on Vancouver Island and the index of the chum reproduction are connected with a high coefficient of correlation (0.7356).

A definite relation also exists between the November expenditures of water in the Hookmose-Creek and the indices of chum and pink salmon reproduction in the central region of British Columbia.

Vernon (1958) found a corresponding inverse correlation ($r = -0.8595$) between the temperatures of waters in the Georgia Strait from April to August in the year preceding the fishery, and the yields of pink salmon in the Frazer River.

Hunter (1959) indicated a correlation between the survival percent from egg to fingerling, and the water expenditure in September and October for chum and pink salmon in Hooknose-Creek.

An article of Merrel (1962) shows an exception; in this article the author points out that climatic factors are not decisive in the survival of pink salmon in the Sashin River. According to the information presented by the author the winters in this region are exceptionally mild, the average January air temperature is only -0.5° to $-1^{\circ}C$, while both in December and February these temperatures are positive (TR: i.e. higher than $0^{\circ}C$.). Under such conditions we cannot expect any freezing of the ground in the spawning river.

On the other hand, Skud (1958) in his study of the same data finds that the fluctuations in the survival rate of pink salmon in the Sashin River are explained by climatic conditions, in particular by winter floods, during which the eggs and larvae are washed out of the ground.

The presented data permit us to maintain that there is a definite relation between the hydrological conditions in the river and the survival rate of eggs and fingerlings of salmons. Insofar as the numbers of the downstream-migrated fingerlings correlate with the numbers of return, there is also a relation between the numbers of two generations and the hydrological conditions in fresh water during the reproduction period of the parental population.

This correlation is relatively small. By using a qualitative "tetrachoritic" connection index and by comparison of winter fluctuations in the water level in the Amgun' River and the fluctuations in the pink salmon numbers for the period ranging from 1936 to 1962, we obtained a correlation coefficient of 0.27 ± 0.23. In the case of the Amur summer chum this coefficient is 0.30 ± 0.22, and in the case of fall chum it is 0.47 ± 0.21.

As indicated by the presented figures the relation is rather poor. At the same time direct observation on the survival of eggs and on the downstream-migration of fingerlings in the years with abnormal hydrological conditions show a very heavy effect of the latter upon the reproduction. Thus, A.Ya. Taranets observed in the Iski River and A.G. Smirnov in the Beshenaya River, in the winter of 1938/1939, a very heavy freezing of the spawning grounds, after which only a very small number of fingerlings migrated downstream from the rivers. In 1953, at the same Beshenaya River, a complete freezing of the spawning grounds was observed, and not a single fingerling was found in the spring. In 1958/1959, a very strong freezing hit the channels in the lower reaches of the Amgun' River. Regardless of the exceptionally high pink salmon population at the spawning grounds , in the spring of 1959, the downstream migration in the Somnya and the Im Rivers was poor: on the average five to ten fingerlings per female.

It should be noted, when analysing the connection between the fluctuations of the hydrometeorological conditions and the survival rate of salmon, that a high correlation coefficient is observed, when a number of observations occurs in a year with sharp deviation of the climate from normal. In ordinary non-catastrophic years the correlation between the elements of the climate and the survival rate is not significant (fig. 2, the central rectangle), and the numbers of fingerlings are determined by biotic factors, primarily by the numbers of spawned salmons.

The connection between the survival rate of salmon and the hydrometeorological conditions in the period of embryogenesis has parabolic character; the farther the latter deviate from the normal towards the unfavourable direction, the stronger is the negative correlation between them and the efficiency of reproduction (fig. 2, left branch of the curve). Conversely, even a considerable deviation in the favourable direction is not accompanied by any significant increase in the survival rate as compared to the normal for the species (fig. 2, the right branch of the curve).

The effect of the climatic factors upon the reproduction /p.42 of pink salmon and upon the summer forms of chum reproducing directly in rivers with the most changeable hydrological conditions. (floods, winter drop in water level etc. is particularly high). The fall chum, same as sockeye and coho, multiplies at the emergence points of the ground waters. The behaviour of ground waters is relatively independent from the hydrometeorological conditions.

Of this reason the sharp fluctuations in the numbers are more often observed in pink salmon and summer chum from the Amur River, than in the fall chum.

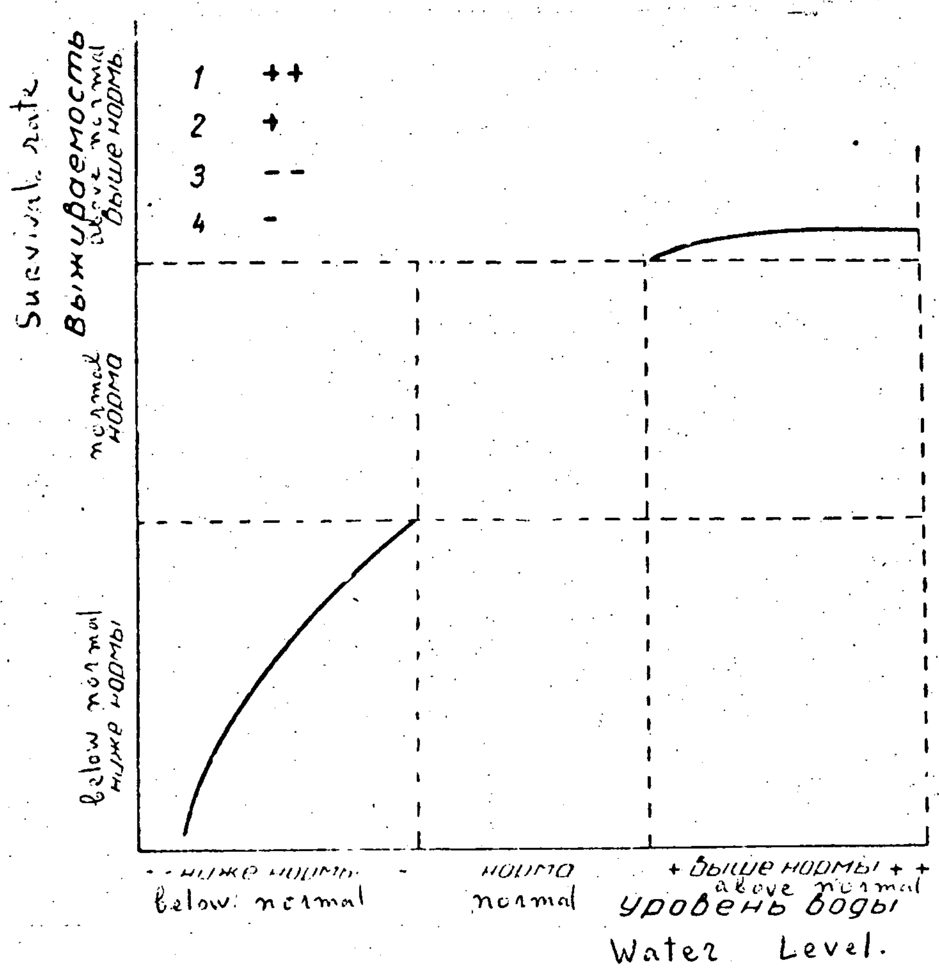

Fig. 2. Relation between the water level and the survival rate of salmons.

Favourable factors of the environments: 1. – very strong, 2 – significant.

Unfavourable factors of the environments: 3 – very strong, 4 – significant.

Thus, we may consider the climatic fluctuations to be the main cause of fluctuations in the chum and pink salmon yield in fresh waters. However, it is necessary to stress the fact that changes in the hydrometeorological factors affect the numbers of chum and pink salmon during the fingerling period of life, but they do not affect the qualitative indices of the chum fingerlings which contrary to pink salmon feed intensely in fresh water. In salmons whose juveniles spend a year or more in fresh waters the relation of the survival rate during the period of embryogenesis to the hydrometeorological conditions, at the time when the downstream migration starts, is disguised by biotic factors affecting the population in fresh water for a period of several years.

The Effect of Biotic Factors upon the Efficiency of Natural Reproduction.

Predatory fish are the main factor in the natural mortality of salmon fingerlings. At the initial stage of the research the main problem was reduced to determination of the species composition of predators devouring the salmon juveniles. In the basin of the Amur River such studies were carried out by I.I. Kuznetsov (1928, 1937). The same author also enumerated the predators devouring the salmon fingerlings among the Kamchatka fishes (1928).

At the Conference on the problems of the salmon economy, in 1953, I presented a diagram of food relations between the chum fingerlings and the freshwater fishes in the tributaries of the Amur River (Levanidov, 1954a).

Detailed quantitative research on the effect of predatory fish upon the population of salmon fingerlings in small spawning water bodies was carried out by Cameron (1941), Pritchard (1948), Wickett (1952), R.S. Semko (1954), Hunter (1959) by complete censusing of the downstream migration of the salmon fingerlings. Data obtained by these scientists, particularly those obtained by R.S. Semko, indicate an exceptionally heavy pressure from the side of predators. Thus, according to the data of Semko, chars aged 1^+ and 2^+, yearlings and two-year-old coho salmons, and to a lesser degree the sockeye yearlings devoured in the Karymaysk Spring from 20% to 85% of all the fattened fingerlings of pink salmon, chum, sockeye, coho and char, thus destroying on the average 1.5 million fingerlings annually. The elimination percentage fluctuates in the following manner from species to species: pink salmon, from 11 to 100%, chum from 2 to 68%, sockeye, from 13 to 91%, coho, from 6 to 86%. The number of predators fluctuates in the Karymaysk Spring extremely much from year to year: from 14,000 in 1947, to 222,000 in 1945, the average being about 67,000 fish. The average density of predators was two predators per one square metre of the spring area, while their maximum density reached six. /p.43

According to Wickett's data (1952) in a small section partitioned by small dams the predators destroy during the fattening period from 44 to 46% of chum fingerlings emerged from the ground.

Hunter indicates the following predators occurring at Hooknose Creek: Coho salmon, Dolly Verden char, trout, steelhead (S. gairdneri Richardson), "prickly" sculpin (Cottus asper Richardson) and the Aleutian sculpin (Cottus aleuticus Gilbert). Only the yearlings of coho and the "prickly" sculpins attain considerable numbers. Destruction of chum and pink salmon fingerlings by predators in the Hookmose Creek fluctuates from 282,000 to 837,000 individuals, 500,000 on the average; the average percentage of the elimination is 45.4% with fluctuations ranging from 22.6 to 85.5%.

The annihilation percent of fingerlings by predators in all the springs constitutes a value of same order, but the amplitude of fluctuations is very different: in the Karymaysk Spring the maximum amount of devoured fingerlings exceeds the minimum amount by 13 times (over a period of 8 years), but at Hookmose Creek, by three times (over a period of 10 years of observations).

Gradually one began to doubt whether the elimination of fingerlings in the partitioned section of the spring really corresponds to what is taking place under natural conditions. Thus, Hunter points out that Pritchard's data indicating that in the stomach of a coho yearling, in 1931, an average of 2.7 pink salmon fingerlings was found, but 3.7 fingerlings in 1933, are obtained under conditions of an artificial concentration of fingerlings. Similar artificially high concentrations of fingerlings, according to him, were also created in Hookmose Creek, where he was carrying out his observations. Hunter refers to the data of MacDonald, according to which under natural conditions a coho salmon's stomach contains only one half of the amount of pink salmon fingerlings, than in the springs partitioned by censusing barriers. Ricker (1962a) also mentions the artificial concentration of pink salmon in the MacClinton and their intensified devouring.

Vernon (1962) did not try to analyze practically the data on the elimination of pink salmon and chum fingerlings in the springs, where a complete censusing was carried out; he points out that the activity of predators is an important factor in small populations in small rivers, but that it is not an important factor in large rivers, where the amount of migrating pink salmon fingerlings is so considerable, that predators are unable to inflict any substantial damage to the population.

In 1960, at the Georgievsk spawning grounds in the Khor River we have organized together with the Georgievsk fishery-melioration station a complete censusing of fall chum fingerlings. During the first half of May, while the barrier was still standing, the stomachs of fish spending all their life in the river, who were in the partitioned-off space, were filled with chum fingerlings. In 400 gudgeons (Gobio gobio L.), eight to thirteen centimetres long, which were cut open, the frequency of the occurrence of chum fingerlings was 71%, while the average number of fingerlings per stomach was 1.7.

In 200 Amur minnows (Phoxinus lagowskii Dyb.) the occurrence frequency of fingerlings was 96% and the average number of fingerlings in the intestines of one fish was 2.1.

In the same spawning ground, but when the amount of spawned chum was considerably greater over a period of some years, during which no barriers were erected (1950 to 1955), completely different results were obtained. Out of 2000 gudgeons cut open during these years we found only in three large males larvae of fall chum (one larva in each). In 1200 Amur minnows the average occurrence frequency was 32% during these years, the average number of chum fingerlings in intestines was 1.3 (the material was collected at the end of April and in the first half of May). The conclusion that under artificial conditions, i.e. when the spawning ground is partitioned off from the river, the elimination of the salmon juveniles increases quite substantially, forces itself upon us. /p.44

Most probably, it is the disturbance of the natural life conditions that explain the intense devouring of salmon fingerlings in the Karymaysk Spring. Erection of a stationary censusing set-up converts the spring into a sort of a fish-tank with an area of about 3.5 hectares, but very shallow. Up to six predatory fish occur per one square metre of this water body. Usually the predators begin their migration from the water bodies of the tributary system to the river channel soon after the breaking up of the ice, but in the Karymaysk Spring this is prevented by the barrier; the latter being opened only four times a day to count the fingerlings. Relatively large and careful yearlings and two-year-old cohoes and chars, still far from the migration period, avoid entering the traps and stay in the spring. The seasonal dynamics of the downstream migration of chum and pink salmon fingerlings, not to mention those of other salmons, are likewise disturbed because of the barrier on their route. Approaching the closed barrier the fingerlings may go up the spring and re-approach the barrier only after a period of several days, or even several weeks.

In the experiments of McKinnon and Brett (1955) the chum fingerlings caught in the outlet of a small artificial lake and transplanted to its upper portion, were returning during the entire period of experiment (one week) to the location where they had been caught. A total of 14.4% of chum and 30.8% of pink salmon returned. It is not very probable that those who did not return were eaten by predators, it is more likely to assume that they were detained somewhere along their way.

Data of I.I. Kurenkov (1964) show that the consumption of salmon fingerlings by the coho yearlings is not very high under natural conditions. According to these data of 947 studied coho yearlings only 15% (143 individuals) contained salmon fingerlings in their stomachs. The analyzed coho salmons also included cohoes from the Karymaysk Spring, the latter having a complete barrier.

According to some unpublished data of L.P. Tikhomirova, the coho salmon in the Utka River (western coast of the Kamchatka Peninsula) aged 1^+ and 2^+ during the period of downstream migration fed on benthic organisms and air insects (699 yearlings and two-year-old were opened); the occurrence rate of salmon fingerlings in the food of char fingerlings was in April and May 18% and in June 17%.

In the basin of the Ichi River (western coast of the Kamchatka Peninsula, in springs and tributaries, the yearlings and two-year-old coho salmons, and char yearlings feed during the period of downstream migration upon benthos and adult insects. The Utka and Ichi are rivers into which numerous pink salmon and chum populations enter, therefore, there is no reason for explaining the absence of salmon fingerlings in the food spectrum of predators by small number of salmon juveniles.

In the same years, according to L.P. Tikhomirova's data, in the Karymaysk Spring with stationaty barrier, salmon fingerlings constituted up to 30% (by weight) of the food of coho yearlings, and even 58% of the food of two-year-olds, regardless the fact that the number of fingerlings in the Karymaysk Spring was considerably lower than in the period described in the article of R.S. Semko.

Under natural conditions the constant consumption of one and the same quantity of fingerlings by predators takes place only when the numbers of fingerlings exceed considerably the food requirements of the predators. In cases, when the new generation of pink salmon or chum is low in numbers, the absolute value of the consumption of fingerlings by predators must decrease considerably, although the percentage of them being devoured may increase. And, finally, at a very low population density of chum or pink salmon fingerlings, not only the absolute number of devoured fingerlings decreases, but also their relative number. Facultative predators switch to benthos feeding in other stations of the water body, and the new generation of salmons avoids its complete annihilations.

It is worth mentioning that the results of the study on the efficiency of salmon reproduction in the Karymaysk /p.45 Spring, carried out by R.S. Semko, oppose his theoretical viewpoints. According to R.S. Semko (1961) the Pacific salmon has "biological compensatory system", i.e. an ability of restoring the numbers of the population. This is carried out by increasing the survival rate from eggs to fingerling and by general increase of the coefficient of downstream migration.

It is shown in table 13 how the efficiency of natural reproduction changed when the abundance of salmon in the Karymaysk Spring (according to the data of R.S. Semko, 1954) was low.

Table 13.

Dynamics of the numbers of adult salmon and of its offspring in the Karymaysk Spring (numbers of individuals).

	Years 1943 to 1950	Years 1954 to 1964
Chum		
Average numbers of adult fish	16,100	486*
Fingerlings per one female	53	5
Sockeye		
Average numbers of adult fish	2,400	96*
Fingerlings per one female.	608	7
Coho		
Average numbers of adult fish	2,100	341
Fingerlings per one female	302	11

* starting with 1955.

** starting with 1957.

Data in this table indicate that in the spring converted to fish-tank, when the numbers decrease the reproduction efficiency also decreases, and the latter decreases to the extent, at which annihilation of the population takes place. This naturally does not refute the generally correct thesis on the increased reproductive ability of scarce salmon populations, but indicates once more the shortcomings of the so-called complete censusing of fingerlings, when natural conditions of the existance of salmon fingerlings are disturbed.

In the basin of the Amur River the special composition of fish that spend all its life in the river is considerably more numerous than in rivers in Kamchatka or at the American coast of the Pacific Ocean. Thus, for example, in the Khor River, we find 37 species of freshwater fishes (Levanidov, 1959). Only two of these species (pike and taimen) are typical predators starting with the age of one year.

The majority of the species are the so-called facultative predators, who predominantly feed upon invertebrates, but who devour also fish more or less intensively. Among such predators we find:

lenok (Brachymystax lenok Pallas),
Amur whitefish (Coregonus ussuriensis Berg),
arctic grayling (Thymallus arcticus Grubei),
Amur ide (Leuciscus waleckii Dyb),
Amur minnow (Phoxinus lagowskii Dyb),
Amur flathead asp (Pseudoaspius leptocephalus Pallas),
Hemibarbus labeo Pallas (a cyprinid fish),
skygazer (Erythroculter erythropterus Basilewsky)

two species of gobies: (*Mesocottus haitej* Dyb)
(*Cottus poecilopus* Haeckel)
and burbot (*Lota lota* L.).

Thermophylic *Cyprinidae* occur in the lower reaches of the Khor River and in other large rivers, but are absent in the semi-mountaneous tributaries (the Amur minnow and the Amur ide are exceptions).

In the lower reaches of the Amur River the facultative predators are, according to L.V. Kokhmenko (1965), multitudinous:
Dolly Varden char (*Salvelinus malma* Walbaum)
Siberian char (*Salvelinus leucomaenis* Pallas), and also
Asiatic arctic smelt (*Osmerus eperlanus* dentex Steindachner).

In the rivers of the Kamchatka Peninsula the predatory fishes are basically represented by three facultative predators: arctic char (*Salvelinun alpinus* L.), coho and chinook salmons. /p.46 Only one facultative predator, the arctic char, is important in the rivers on the continental coast of the Sea of Okhotsk. And, finally, in the rivers of the Sakhalin Island live the following facultative predators: Dolly Varden char, Sakhalin taimen (*Hucho perryi*, Brev.), Siberian char and yearlings of masu salmon.

Hunter (1959) notes that in the Hooknose River gobies less than 5 centimetres long do not eat chum or pink salmon fingerlings. Only in stomachs of gobies longer than 6 centimetres did the fingerlings of chum and pink salmon occur regularly. The number of fingerlings in the stomachs increased proportionally with the size of the predator. The most dangerous predators were the large gobies longer than 12 centimetres.

A.N. Kanidyev (1966) when studying the effect of predators upon the reproduction of Sakhalin salmons came to the conclusion that large chum juveniles are practically invulnerable by predators.

I (Levanidov, 1964c) have shown experimentally that small predators (fish and birds) eat the smallest fingerlings of fall chum. Thus, the predators act selectively upon the generation of chum and pink salmon fingerlings by destroying predominantly those that are retarded in growth.

In order to study the effect of predatory fish upon the reproduction of the Amur salmons, we have used a methodology for a period of 14 years, based upon the study of food spectra, of food requirements and of the numbers of fish spending all their life in rivers, without disturbance of natural life conditions, both of the latter fish, and of chum and pink salmon fingerlings. The observations were predominantly carried out at the Georgiyevsk Springs in the Khor River.

The winter concentration in springs and channels of fish who spend all their life without migration, is characteristic of the tributaries of the Amur River, where fall chum multiplies. These non-migrating fish concentrate in the channels from the end of fall and leave for the river bed only after the ice breaks up in the first half of the month of May.

The most numerous predators in the system of the Georgiyevsk Springs are the Amur minnows, lenoks and taimens. The numbers of other predators are very small compared to the numbers of the three mentioned species. The period of predatory activity in the spring channels of the Amur tributaries begins with the first days of April, when the fingerlings of fall chum leave the spawning nests and switch to active feeding.

In the calculations shown below, owing to incompleteness of information on the numbers of fish spending all their lives in the rivers, for various years and for individual spawning and growing water bodies, the data are used according to their average ichtyomass and numbers considered over a period of several years and obtained by means of systematic catches.

Taimen is one of the most typical predators in the basin of the Amur River (table 14). In the Georgiyevsk channels the taimen juveniles concentrate during the winter and spring period at the spawning grounds of chum, while the adult individuals migrate to the Ussuri River. Taimens older than three years do not feed upon fish as small as chum fingerlings, and in the spring they do not enter channels and springs serving as fall chum spawning grounds (Levanidov, 1951b).

According to L.V. Kokhmenko's data (1962) in the Teploye Lake the young taimens feed exclusively on chum fingerlings in April and May. The occurrence frequency in April and May of this food in their stomachs is 100%, however, in June it is 42%. By weight chum fingerlings constitute in the food over a period of three months: 99.8%, 99.9% and 81.8% respectively. In the Bira River below the estuary of the river connecting Bira to the Teploye Lake, the occurrence frequency of chum fingerlings in the taimen stomachs, was 38% in May, and 28% in June.

According to the data of fingerling catches by means of seine in the spring channels of the Khor River, the biomass of taimen juveniles, in April and in May, was 7.9 and 2.8 kilogram per hectare respectively, and the abundance 225 and 70 individuals per one hectare. The average occurrence frequency of chum fingerlings in the stomachs (excluding the years 1951 and 1954, which had a very low yield of fingerlings) was 78%; the average quantity of fingerlings per stomach was 3.7. The weight of consumed fingerlings was approximately 3.5% of the taimen's weight; one may assume that /p.47

Table 14

Chum fingerling consumption by taimens in the channels of the Khor River in April.

Indices.	1951	1954	1956	1957	1958	1959	1960	1961
Chum fingerling numbers thousands per hectare	12	80	120	450	300	160	180	250
Occurrence frequency of fingerlings in stomachs, %	10	40	52	93	90	67	75	90
Average number of fingerlings per stomach *	3,0	2,8	3,1	3,5	3,9	4,0	3,6	3,9

* Both here, and in tables 16 and 18, the average value is calculated by division of the total number of the devoured fingerlings by the number of stomachs in which chum fingerlings were found.

this value corresponds to the daily ration (in percents of the body weight). According to L.V. Kokhmenko's data (1962), in May, when the water temperature in the Teploye Lake was higher, the daily ration of taimen was 5% of its body weight.

On the basis of these assumptions we may calculate the value of the chum fingerling annihilation (n) by the population of young taimens in April in the channels and springs.

n = 225 x 0.78 x 3.7 x 30 = 19,480 individuals per hectare.

In May the numbers of taimens decrease to 70 individuals per hectare; the occurrence frequency drops to 43%, and the number of fingerlings per stomach drops to 2.8. Consequently, the total consumption of the chum fingerlings by taimen, in the month of May, is:

n = 70 x 0.43 x 2.8 x 30 = 2528 individuals per hectare.

In total during the fattening period of the chum fingerlings, at an average abundance of 250,000 fingerlings per hectare the taimen population destroys 21,700 fingerlings per hectare, or approximately 9% of the average initial numbers.

Lenok is one of the most common fishes in the tributaries of the Amur River right from the source of the estuary. As our (Levanidov, 1951a) and O.A. Klyuchareva's research (1952) shows, the lenok in the basin of the Amur River is a facultative predator; both adult lenoks and their juveniles feed on chum fingerlings.

In taimens the abundance of that portion of the population, which feeds upon the salmon fingerlings, is subjected, depending on the yield, to more or less sharp fluctuations, insofar as this population consists only of two age groups. Contrary to this, the effect of lenoks upon the reproduction of the Amur salmons is a less changeable factor, since the multi-age-level population of lenoks consists of eight or nine age groups.

The basin of the Amur River contains two forms of lenok. A typical form migrates for the winter downstream to the Amur and Ussuri Rivers, and migrates back to the spawning rivers during the downstream migration period of the salmon juveniles. Young individuals of the typical form hibernate at the spawning grounds together with the so-called "local" form, which does not migrate for the winter downstream to the Amur River, the latter form is morphologically characterized by a subterminal mouth. This form is a very dangerous predator to the fingerlings of fall chum during their transition from the ground stage of life to the demersal one.

Table 15 shows the average occurrence frequency of the chum fingerlings in the stomach's of lenoks in the month of April. The average biomass of lenok juveniles measured over a period of several years in the spawning and growing water bodies in the Khor River was in April, 8.4 kilograms per hectare or 400 fishes per hectare. The average occurrence frequency of chum fingerlings in their stomachs, except in years with very low yield of juveniles (1951 to 1954), is 15%; the average number of fingerlings per stomach /p48 is approximately 3. This quantity (weight 750 milligrams) is close to the daily ration of young lenoks. In the 30 days of the month of April the yearlings and two-year-old lenoks destroy on the average /p.48

$$400 \times 0.15 \times 3 \times 30 = 5400$$ chum fingerlings per one hectare.

Table 15

Consumption of chum fingerlings by lenoks in the Georgiyevsk channels in the Khor River

Indices	1951	1954	1956	1957	1958	1959	1960	1961
yearlings and two-year old lenoks								
Numbers of chum fingerlings, thousand per hectare	12	80	120	450	300	160	180	250
Occurrence frequency of fingerlings in stomachs %	0	4,2	7,9	22,8	16,3	11,6	14,2	17,0
Average number of fingerlings per stomach	0	1,4	2,3	3,2	2,7	3,1	3,0	3,3
adult lenoks								
Occurrence frequency of fingerlings in stomachs %	0	3	8	34	23	11	14	54
Average number of fingerlings per stomach	0	11,4	19,6	12,3	19,0	17,2	14,8	25,0

In May the occurrence rate decreases to 5.1%, the average number of chum fingerlings per stomach is 2.1, and the average biomass and numbers of the lenok juveniles in the channels and springs decreases to 5 kilograms per hectare or to 200 fish per hectare.

The average number of chum fingerlings devoured by the lenok juveniles per month is 200 x 0.05 x 2.1 x 30 = 630 fingerlings per hectare.

The biomass of adult local lenoks in April constitutes 10 kilograms per hectare, or 14 fish per hectare, the occurrence frequency of fingerlings in their stomachs is 26%; the average amount of fingerlings per one stomach is 17. The fingerlings constitute approximately 30% of the weight of the food lump, which is on the average 16 grams, i.e. 2.2% of a lenok's weight. Evidently, this is the value of a lenok's daily ration at low water temperatures. Thus, during the thirty days of the month of April the consumption of chum fingerlings by adult lenoks is 14 x 0.26 x 16 x 30 = 1747 fingerlings per one hectare.

In May the chum fingerlings are not found in the stomachs of lenoks, because at that time of the year the lenoks are spawning. Thus the lenoks destroy at the spawning grounds, during the entire pre-migrational period on the average a total of 7750 fingerlings per hectare of the fattening area. At initial abundance of fingerlings of 250,000 per hectare this constitutes 3% of the total number. In years of very low chum fingerling abundance, their annihilation percent is different. Thus, for example, in the spring of 1954, the decrease in the number of chum fingerlings was 200 fingerlings per hectare or 0.4%. At a very scarce fingerling density, such as observed in the spring of 1951 (1.2 fingerlings per one square metre), the chum fingerlings did not occur at all as food of lenoks. The stomachs of the latter were filled with minnows, sticklebacks and gudgeons.

The most numerous enemy of the fall chum juveniles in the spawning water basins is the Amur minnow, which is a facultative predator with very high indices of predatory activity, in respect to the salmon juveniles. When studying 550 sets of intestines of the Amur minnows from tributaries of the Amur River, during seasons when those tributaries do not contain any salmon fingerlings, the fish remains are found only in 1.3% of individuals.

According to G.V. Nikolsky's data (1956b), the occurrence frequency of fish food (other than salmon fingerlings) in the minnows from various tributaries of the Amur River constitutes 13.1% (122 stomachs were opened), while according to L.V. Kokhmenko's data, it constitutes 1.6%. The problem of the predatory activity of minnows in respect to chum fingerlings remained unclear for a (long period of) time. /p.49 It is true, I.I. Kuznetosov, (1937) indicated that in the stomach of almost every large minnow there is from one to five chum fingerlings, but this information presented without any numerical data received no attention. O. Ya. Baykova (1954) opened 50 Amur minnows caught at the end of the month of March, and found in one of the intestines a fingerling of fall chum (the occurrence frequency thus being 2%).

As we see from a comparison of the results of the opening of the intestines in minnows, it is, as a rule, those individuals who feed upon the chum fingerlings, whose body lenght exceeds 11 centimetres. The chum fingerling have never been found in the food of Amur minnows shorter than 10 centimetres; in the minnows between 10 and 11 centimetres the occurrence frequency is only 2.7%. In Amur minnows from 11 to 16 centimetres long the chum fingerlings are a common food found in the intestines (table 16).

Table 16.

Consumption of the Amur chum fingerlings by minnows 11 to 16 centimetres long.

Indices	1951	1954	1956	1957	1958	1959	1960	1961
Number of chum fingerlings, thousands per hectare	12	80	120	450	300	160	180	250
Occurrence frequency of fingerlings in stomachs, in %	0	5	13	33	28	15	20	20
Average number of fingerlings per one stomach	0	1.0	1.5	2.0	1.9	1.8	2.0	1.9

The biomass of the Amur minnows at the spawning grounds constitutes, in the month of April, approximately 150 kilograms per hectare, in other words, 17,000 individuals, 10% of which are fish longer than 11 centimetres. Consequently, the number of minnows devouring chum fingerlings is only 1700 individuals, the occurrence frequency in the stomachs (again excluding the two low-yield years) is 21%; the average number of fingerlings per one stomach is 1.9; the waste $n = 1700 \times 0.21 \times 1.9 \times 30 = 20{,}349$ fingerlings per hectare. In May the occurrence frequency of fingerlings in a minnow's food is 1%, on the average a stomach contains 1.2 fingerlings, while the biomass and the numbers decrease to 46 kilograms per hectare and 5200 fingerlings per one hectare; in this case 1872 fingerlings are eaten per one hectare. All in all, the Amur minnows destroy in spring channels 22,000 chum fingerlings per hectare or 9% of the total number.

Thus, the three numerically most important predators destroy approximately 20% of the original quantity of juveniles. A certain small quantity is devoured by gobies, graylings, pikes, but jointly they hardly destroy more than 2% of the fingerling populations of average size. Consequently, the decrease in chum fingerlings is determined by extensive openings of predators during the fattening period and is 20 to 22% of the initial numbers.

The effect of the predators is a rather constant factor, since this is a multi-species and multi-age complex, for which the chum fingerlings are a seasonal food not determining the numbers of the predators.

Mortality Rate of the Amur Salmon Fingerlings during the Period of Downstream Migration

The move from spawning ground to the river bed, or the beginning of the downstream migration, differs from species to species in the Amur salmons in the degree to which the conditions change. Fall chum fingerlings, which fatten in limnocrens, or spring beds, during their transition to the spawning river get into water which differs being less transparent and having a faster current, and occasionally also having a different temperature. In a considerable number of spawning channels, because of water entry through outlets, similar changes in the hydrological /p.50 conditions take place at the spawning grounds themselves: the spring channel turns into a river channel.

Summer chum fingerlings, when starting the downstream migration, suffer a change in the conditions which is considerably less sharp, since the spawning grounds of summer chum are located in river channels and at the banks of the main river bed. Pink salmon juveniles emerging from the ground in the main river channel leave almost without changing the customary living conditions at the beginning of the downstream migration. Change in the living conditions requires a definite reconstruction of conditional reflexes in a school, in other words it requries an adaptation to the new environment. It has already been noted above, that in such periods the mortality of juveniles sharply increases. Therefore, it may be assumed that at the initial stage of the downstream migration the mortality rate must be highest in fall chum fingerlings connected to limnocrens.

We know that when the concentration of downstream migrating juveniles of fall chum at the exit from a limnocren to a river is very high and constant from year to year, the predatory fish accumulate at such locations in considerable numbers. Such a phenomenon is observed in the estuary of the Teplovskaya River along which hatchery-raised chum juveniles migrate downstream. In the period from 1946 to 1951, an annual accumulation of lenoks was observed there at the end of April, when the downstream migration of chum fingerlings began, and when, furthermore, a flowing away of its larvae was taking place. In 1948, 200 lenoks were caught in the estuary of the channel; in 25 opened lenoks chum fingerlings were found in 18 stomachs; the average number of fingerlings per stomach was 111, or 25 grams; with the average weight of a lenok of 600 grams and a daily ration of 2% of the body weight the stomack content constitutes a two-day food reserve. The total number of lenoks calculated on the basis of regular accumulations in the estuary was approximately 1000. This lenok population was capable of consuming a total of up to 800,000 juveniles during 20 days of the downstream migration. The total number of the downstream-migrated fingerlings was 8 million in the spring of 1949, consequently, the mortality rate in the estuarian space of the Teplovskaya River was 10% of the migrating juveniles.

In 1950, on 11th and 12th of April, more than 500 lenoks were caught in the estuary, 19 of these were opened. The occurrence frequency of chum juveniles in the lenok stomachs was 90%, an average of 232 juveniles was found in one stomach. It is true, in this particular case, judging from the time of the season, it was not the downstream-migrating fingerlings that were eaten, but larvae at final stages of development carried out by the water current. The downstream-migration of the hatchery-raised fall chum fingerlings was 35 million in 1950. If we assume that the lenok population in this year destroyed twice as many fingerlings as in 1949, even then the mortality rate of fingerlings in the estuarian area constitutes 5% of the fingerlings.

Thus, we can see that when the population of the downstream-migrating chum fingerlings is excessively high in relation to the size of the population of fish living their entire life in the river, the loss inflicted by the latter appears insignificant.

At natural spawning grounds of fall chum the concentration of juveniles does not attain such dimensions as in the Teplovsk fish hatchery, therefore, we neither observe any concentration of predators in the estuarian areas of the spawning channels. In the majority of cases the transition from the spawning water body to the river bed is not accompanied by any considerable increase in mortality.

During the downstream-migration stage the juveniles of fall and summer chum live in two stations in the spawning river, namely, in the water mass of the river channel, when migrating along with the current, and among pebbles at the banks, when in process of feeding (predominantly in day time).

The pink salmon larvae also migrate downstream in the water mass, but during time of the migrationary movement only a fraction of them approaches the banks, while the remainder hides among pebbles along the entire river bed. It is not the food factor (search for food) that dominates them, but the defense factor (search for cover).

Downstream migration of fall chum in the Khor, Bira and other rivers takes place mainly at night, when predatory fish of /p.51 the large water channels usually stays in the tributary system (channels, bays etc.). At day time the non-anadromour predators leave the banks, while the chum fingerlings approach the latter to feed. This phenomenon is probably the explanation of the rare occurrence of fall chum fingerlings in the stomachs of predatory fish during the downstream migration along the spawning river from April 25 to May 30th. Thus, the chum fingerlings, as a rule, did not occur every year and only in small amounts in the stomachs of lenoks caught in the bed of the Khor River. The same may be said about the intestines of pikes. In the alimentary tracts of taimens, graylings, gobies, and minnows caught in river sections, the fingerlings did not occur at all.

In high-yield years (1952, 1956 and 1957) the fall chum fingerlings were relatively frequently found in the stomachs of lenoks. In years, when the numbers of downstream-migrating fingerlings were very low (1951, 1955 and 1959) they were not found at all in the stomachs of predators (table 17). The pressure of the mentioned predators upon fall chum fingerlings in the Khor River and in other tributaries of the Ussuri River is weakened by certain peculiarities of their ecology. At the beginning of the downstream migration, when the water level in a river is still low and the water is clear, the predators being in the pre-spawning state eat poorly. As a rule, until they emerge in the river current, where the downstream migration of chum fingerlings continues under conditions of spring flood and a considerable increase in the turbidity, but stay in the gulfs and in the flooded areas, where they are ensured a rich food base (minnows, gudgeons, bitterlings and other small cyprinids.).

Table 17.

Consumption of chum fingerlings by predators during the downstream migration along the spawning river.

Indices	1951	1952	1954	1955	1956	1957	1958	1959	1960
Lenok									
Number of fish	30	25	40	22	100	34	11	25	55
Occurrence frequency, %	0	12,0	2,5	0	11,0	11,7	9,0	0	7,3
Number of fingerlings per stomach	0	1,7	3,0	0	1,8	2,0	1,0	0	1,5
Pike									
Number of fish	10	20	26	69	70	50	40	37	19
Occurrence frequency, %	0	5,0	0	0	21,4	18,0	7,5	0	3,4
Number of fingerlings per stomach	0	3,0	0	0	2,0	1,7	1,7	0	2,0

Towards the end of the downstream migration of chum fingerlings (end of June) the Khor River and other rivers of similar type are entered by populations of Amur whitefish and of Mongolian false-asp, but not a single chum fingerling was found in their stomachs, although 347 intestines of whitefish and 184 of false-asp were studied in the years 1951 to 1962.

The abundance of pike in the Khor River is considerably lower than of lenok: in the spring the pike does almost not occur in the middle and upper reaches of the river, while in the lower reaches, according to the results of annual control catches (1950 to 1962) the abundance of pike constitutes 60% of the numbers of lenok. The scale of the pike's consumption of chum fingerling in the lower reaches of the river and the consumption scale of them by the lenok are very close. Thus, it should be accepted that in the large tributaries of the Ussuri River, of the Middle and Lower Amur, where the fall chum reproduces, annihilation of fingerlings during the downstream migration is very insignificant along the spawning river.

A different picture is observed in the small tributaries of the lower reaches of the Amur River and in the rivers of the liman, i.e. in the spawning area of pink salmon and summer chum.

According to the data of V.V. Abramov (1954), in the tributaries of the Amguni, i.e. in the Somna and Im Rivers, /p.52 the major rise of the Amur ide coincides in time with the intensive downstream migration of salmon juveniles, this fish is a serious enemy of summer chum and particularly of pink salmon fingerlings.

According to our observations, in small rivers of mountaneous or foothill type, such as Khivanda, Beshenaya, Gera and other rivers, the lenoks are more dangerous enemies of the salmon juveniles than in large tributaries. The population density of lenoks in such rivers is considerably higher and the conditions for catching juveniles are much more favourable. The occurrence frequency of chum and pink salmon fingerlings in the stomachs of lenoks in the collections from the Khivanda River, in the years 1949 and 1950, was 18% and 28% respectively (50 individuals were opened), one stomach contained, on the average, 17 fingerlings in 1949, and 12 in 1950. The taimens and Amur minnows are relatively scarce in these rivers. Minor tributaries of the Amur River often run into small flood-bed lakes; like for example: Khivanda, Bystraya, Krivaya Kenzha, Gera, Aksha and other rivers. Depending on the water level in the Amur River the basins of these rivers are predominantly filled either with cold and clear water from the mentioned rivers, or with the warmer turbid water of the Amur River; the current in the channels connecting the lake with the Amur River is also changing the direction depending on the level of the Amur River. Migrating down to such lakes the salmon fingerlings find themselves under different ecological conditions and a certain period of time is required for an adjustment to the conditions. If this takes place during high-waters in the Amur River and during the filling out of the lake basins with water from the Amur River, numerous predatory fish come here and destroy salmon juveniles in the estuarian sections.

Very considerable accumulations of predatory fish, particularly of pike, are also observed at the estuary of small rivers running directly into the Amur River. Because of the insignificant rate of the water current in such rivers, the current is now completely mixed with the Amur water in the estuarian sections. Therefore, we observe here a very considerable concentration of salmon juveniles migrated from the river. These juveniles attract predators, particularly pikes.

In the rivers of the Amur liman, according to the studies of L.V. Kokhmenko (1964), the predatory fish play a relatively important role in the decrease of the efficiency of the natural reproduction of salmons. Basically, we have here as predators: Asiatic arctic smelt (extremely numerous and feeding during the downstream migration on chum fingerlings, in June, almost exclusively), the Amur whitefish and, to a lesser degree, the lenok (table 18).

Table 18.

Consumption of the downstream-migrating salmon juveniles by predatory fish in the rivers of the Amur liman.

Species	Occurrence frequency, %.	Average occurrence per one stomach, individuals	Consumption Intensity
Asiatic arctic smelt	83.8	25.8	20.8
Amur whitefish	60.0	6.0	3.6
Lenok	50.0	102.5	51.3

It should be mentioned that in a smelt the weight of devoured fingerlings constitutes almost 10% of the body weight, in lenok it is even 15%. It is obvious that these are not the daily rations, because the water temperatures at the end of May and in the month of June in the rivers of the liman are only four to seven degrees (C^0), therefore, the daily food rations of fish cannot be high. The high frequency of occurrence and the overfilling of stomachs of predators with salmon fingerlings indicate that the latter are an easily available food in the rivers of the liman.

In the rivers of the liman, the most dangerous predators to the salmon juveniles are the Asiatic arctic smelts. Their numbers in the basin of the Amur River are high, according to the data of G.V. Nikolsky (1956) their yield, even when the fishery is operated at low intensity, is 8000 to 10,000 centners /TR: 800 to 1000 metric tons/ per year (eleven to fourteen million fish). The total number of the population, according to a conservative estimate, is 30 to 40 million fish. According to L.V. Kokhmenko's data, the smelt feeds intensely after the spawning upon salmon fingerlings in the rivers of the liman. /p.53

Such fish like Dolly Varden and Siberian chars, who were earlier strongly "stigmatised" in respect to their predatory habits, are now to a considerable degree rehabilitated by L.V. Kokhmenko's studies. Both species, particularly the Dolly Varden char mainly feed upon benthos and only very rarely do they eat salmon fingerlings.

All the above-said leads to the conclusion that the biotic elimination factors of Amur salmon fingerlings in the tributaries of the lower reaches of the Amur River and in the rivers of the liman may be of greater significance than the tributaries, where the fall chum alone is reproduced. Of greatest importance for the decrease in reproduction efficiency are the "diadromous" predatory fish migrating to the spawning rivers from the Amur or from the liman. Predators constitute a relatively stable factor: on the average they diminish the salmon fingerlings numbers during the period of fattening and downstream migration by 15 to 30%; an annihilation of 50% of the population is, apparently, only rarely observed and may happen owing to a combination of circumstances unfavourable to the natural reproduction conditions.

We have determined the amount of salmon fingerlings devoured by predators for a low level period of chum and pink salmon resources. When the abundance of fingerlings is high (appearance of "high-yield" generations) the importance of predators as a elimination factor decreases, and in a number of cases this factor becomes a secondary factor of natural mortality.

Juveniles of chinook, coho and sockey live in fresh water for a period of one to three years and during this entire period they are being eliminated by predators. As a result of this the amount of migrating sockeye juveniles (Krogius, 1951; Foerster, 1955) and of coho salmon (Foerster, 1955) constitutes a value of approximately one tenth of the amount of migrating chum and pink salmon fingerlings.

Foerster and Ricker (1941 and 1953) demonstrated the efficiency of the annihilation of predators in lakes to increase the abundance of migrating sockeye juveniles (but not of their qualitative indices), as well as of coho salmon. Predators may affect the qualitative indices of pink salmon, who hardly feed in fresh water, only by eliminating a greater percentage of small juveniles. However, the pink salmon fingerling population is very homogemous in size, but the dimensions of fingerling change according to Smid (1955) during the downstream migration; the larger fingerlings migrate first.

The matter is considerably more complicated in respect to the chum fingerlings. G.V. Nikolsky (1950b) discussed the problem of the effect of predators upon the reproduction of fish and pointed out the complexity of this phenomenon: the predator does not only destroy fish of a given species, but also its competitors for food. Thus arctic char devours not only the sockeye juveniles, but also the stickleback, which competes for food with the former. Therefore, when the effect of a predator upon the salmon reproduction is being determined, one must consider not only the direct influence upon the numbers, but also the indirect effect upon the food base, which in a number of cases is even more important.

The period of the direct effect of predatory fish upon the Amur chum fingerling population is limited by the brief period of their fattening and migration. During the remainder of the year the food relations of predatory fish are formed along the line of feeding upon the non-migrating fishes and upon benthos. From this viewpoint, we will discuss the main predators in the basin of the Amur River.

Taimen. During their first year of life taimen juveniles feed to a considerable degree upon the same benthic organisms as the chum juveniles, but owing to their small numbers they do not present any significant competition for food to the chum finger- /p.54 lings. Yearlings and two-year old taimens at the beginning of the period of downstream migration of chum fingerlings feed predominantly upon the latter; but during the entire summer, fall and partly winter they devour small cyprinids, who are benthophages and who use the same food as chum juveniles. Adult taimens eat intensely predators and competitors of chum fingerlings.

Lenok. Feeds basically on relatively large aquatic invertebrates, who do not form a part of the food spectrum of chum fingerlings; they also feed on cyprinids.

Lenok, taimen, and a number of large facultative predators (benthophages) devour competitors, thus on the whole, they increase the food supply of chum fingerlings, a factor that must have a beneficial effect upon their growth rate.

Amur minnow. The predominant part of its population feeds upon benthos or algae. The food spectra of the minnow and of the chum fingerlings coincide to a considerable degree. Owing to its high abundance the minnows are the basic food competitor of the chum fingerlings. Furthermore, the large minnows, as already indicated, devour a considerable number of fingerlings. Owing to competition the growth of fingerlings is inhibited and the latter remain for a long period of time subjected to pressure from predators, primarily from the minnows themselves.

Amur ide. In the lower section of the spawning area of the Amur salmons, this fish is simultaneously both competitor, and predator in respect to the summer chum juveniles.

Thus, the Amur minnow and the Amur ide are the most important negative biotic factor in the chum reproduction.

The Effect of the Juveniles Quality upon the Dynamics of the Salmon Population during the Marine Period of Life.

In the analysis of the problem of the relation of the abundance of parental stock and its progeny, G.V. Nikolsky (1965) justly concludes that in many instances the absence of direct correlation between the number of spawned eggs and the size of the juvenile harvest is explained by the fact that the researchers do not take into consideration the quality of laid eggs. Undoubtedly, of still greater importance to the survival rate at sea is the quality of the downstream-migrated fingerlings or juveniles of salmon.

It may seem that juveniles of pink salmon migrating from the spawning rivers at the end of the larval period must be relatively uniform. Actually the heterogeneity of these juveniles is founded already in the unequal quality of eggs and, furthermore, in the unequal environmental conditions in the period of embryogenesis also contributes to the appearance of a heterogeneous generation.

Thus, Skud (1955) notes that during the time of the downstream migration from the rivers of southeastern Alaska the weight of pink salmon fingerlings decreases progressively. He believes that the eggs that are laid early develop under more favourable thermal conditions, this causes hatching of relatively larger larvae.

The connection comes very sharply between the dimensions of the juveniles migrating to the sea and the return of adult salmons with a prolonged freshwater period of fattening.

Foerster (1954) found a very high positive correlation between the weight and lenght of sockeye juveniles migrating downstream from the Cultus Lake and the return percent;the correlation coefficients were $^{+}$0.66 and $^{+}$0.83 respectively.

On the basis of Foerster's data, Ricker (1962b) calculated that for sockeye juveniles with an average lenght of 63 millimetres the return rate of adult sockeyes is 1.20%, but for juveniles 107 millimetres long this rate is 14.74%, in other words 12 times greater! /p.55

Burgner (1962), determined when studying the downstream migration of sockeye yearlings from the Wood River, determined that in 1955 the length variation series indicated a sharply pronounced bimodality (70 and 90 millimetres). The return coefficient of small yearlings in 1957 to 1958 turned out to be only half as great, as the one of the large ones. The return percent in the latter instance increased approximately proportionally to the weight of the yearling, but in Ricker's calculations the survival rate increased faster than the weight (approximately by $\sqrt{p^3}$

times, where p is the weight of a downstream-migrating individual).

As Foerster (1944), Krogius and Krokhin (1948), and Burgner (1962) have shown, the growth rate of sockeye juveniles in lakes and the dimensions of migrating juveniles are determined by a population's food supply.

One may maintain that between the dimensions of the migrating juveniles of such salmons, as chinook and coho, and the survival rate at sea exist the same pattern as in sockeye.

The matters are more complicated in respect to chum. As we know, the chum feed very intensely in the fresh waters, but stays there only two to three months. A considerable part of chum fingerlings leaves the spawning rivers already prior to the formation of scales, consequently, according to data collected at sea it is difficult to judge the various survival rates in different sizes of fingerlings. However, we have some indirect proof that it is mostly the smaller individuals that are subject to elimination. This assumption may be considered proven for fresh waters. (Levanidov, 1964c). Most probably it is also correct for the coastal period of life of fingerlings after their migration to the sea. In the coastal zone live numerous small predators to whom the small fingerlings are more readily accessible. It is already mentioned that according to Parker's calculations (1962a) approximately 95% (?) of all the downstream migrated chum and of pink salmon fingerlings perish here. Insofar as the predators in a number of cases devour the small and weakened individuals, we may assume that the survival rate of juveniles is correlated to their dimensions.

Practice of acclimatizational and fish-raising operations shows that the older and, consequently, the larger the juveniles are when released, the higher is the survival rate. Thus, B.I. Ponedelko (1963) showed that the survival rate of the first year peled during acclimatization depends primarily upon the size of the first-year fish: the larger they are, the higher is the survival rate. G.D. Polyakov (1958, 1960, 1961, 1962) proved that when feeding conditions deteriorate for the multitudinous population of fish juveniles, then better feeding and growing conditions are created for the largest individuals.

In his studies of the survival rate of Pacific salmons, Neave came to the conclusion that the factors diminishing the growth rate also have unfavourable effect upon their survivability.

According to our observations large fingerlings and first -year chums (weighing from two to five grams) survive under experimental conditions a water temperature increase of up to 28 to 30°C, and a transfer without any acclimatization period into water with a 25°/00 salinity, as well as a decrease in oxygen content in water down to 2.5 to 2.7 milligrams per litre. Brett (1952) found that the mortality of salmon juveniles owing to low water temperatures is highest among the smallest individuals. The presented data confirm the fact that large, fast-growing fall chum individuals are better adapted to the very sharp fluctuations in the factors of abiotic environment, than are the small individuals. Consequently, in the case of Pacific salmon the return rate is the higher, the larger are the migrating juveniles.

Results of research at the Teplovsk fish hatchery in the basin of the Amur River during the period from 1928 to 1952, serve as an example of the dominant importance of the food supply and the growth rate of fingerlings in the growth water bodies. During this period the chum fingerlings after being released from fish tanks, fattened in the river, which was rich in food invertebrates, but had a river bed area only slightly more than one hectare. When less then ten million larvae were released, the return rate of adult chums to the fish hatchery was 0.19% (12 years of observations), when, however, an average of 25 million larvae was released, then the return rate was 0.10%. /p.56

In the case of such a small population the intrapopulational competition could not have had any effect upon the growth and survival rate; therefore, we may assume that a higher food supply, and thus higher qualitative indices during the downstream migration have secured a better survivability of scarce generations.

In 1954 to 1959, at the Teplovsk fish hatchery, a number of measures were carried out, as recommended by us, to increase the productivity of the growth water basins (Levanidov and Levanidova, 1962).

In the period from 1955 to 1961 an increase in the weight of the migrating fingerlings was recorded. The return coefficient of the hatchery reached in the years 1960 to 1963 0.3% (at a release of 30 to 50 million fingerlings annually) against 0.11% during the period of 1938 to 1952, in other words this coefficient increased by 2.7 times, regardless of the origin of a new, and a very strong factor for decrease in the abundance of chum, namely the origin of Japanese fisheries.

The Sakhalin pisciculturists achieved a very considerable increase in the survival rate in chum in fresh water and at sea by feeding chum fingerlings at the hatchery. They have thus organized a release of fingerlings with twice as great weight, as in the first period of their operation. As a result, the numbers in the populations reproduced by the hatchery method in the rivers, where there are almost no natural spawning grounds, increased by several times.

Table 19.

The relation between the fluctuations in the numbers of fall chum and the growth rate during the first year of life.*

Year of spawning	Length of a yearling, centimetres	Change in numbers
1952	27,5	+
1933	27,8	=
1954	28.0	+
1948	28,2	+
1953	29,0	=
1928	30,0	+
1947	30,0	+
1925	30,7	+
1932	25,8	—
1942	25,9	—
1943	26,3	—
1944	26,9	—
1950	27,0	—
1951	27,0	—
1945	27,1	+
1949	27,2	—
		—

* Symbol – (minus) indicates drop in the numbers compared to the parental population; + indicates an increase in the numbers; = indicates stability of the numbers.

Let us show one example more illustrating the effect of the dimensions attained by chum towards the end of the first year of life upon its future abundance (table 19).

The data on the growth rate are taken from E.S. Lovetskaya (1948), I.B. Birman (1951b), M.L. Krykhtin and A.C. Smirnov (1962). As shown by the data in table 19, when the final size of a yearling is less than 27 centimetres the numbers of the population decrease, i.e. a slow growth rate in the first years of life is accompanied by higher mortality rate.

The examples discussed above indicate that the qualitative indices of the chum fingerlings during the migration period do not have less importance in the survival of these fingerlings, than the dimensions of sockeye juveniles have in the survival of salmon. The size and weight of the migrating chum fingerlings are also determined by the food supply, same as in the sockeye or in the chinook juveniles. G.V. Nikolsky includes in the concept "food supply" the value and quality of the food base of the food availability, the /p.57 abiotic conditions of the fattening, numbers of the populations of the competitors and predators. The dynamics of the food base, according to Nikolsky, determines in many respects the dynamics of the yield of the generations and the growth rate of fish. We agree with him and thus in the study of natural reproduction of the salmons must consider the study of the food base, feeding and food ratios to be one of the most important tasks. We are going to study these problems in the subsequent part of this book.

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Part Two.

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PART TWO

FOOD SUPPLY OF THE AMUR SALMONS IN FRESH WATERS.

FOOD RESOURCES OF THE AMUR SALMONS AND THEIR UTILIZATION.

Spawning and Growing Water Bodies of the Amur Chum and the Conditions of the Fattening of Fingerling.

The food supply depends on the food base, food ratio and abiotic conditions of the fattening. G.V. Nikolsky (1950a; 1965) believes that one can evaluate the food supply without knowing anything but the biological indices. This is true to a certain degree, but with this approach it is impossible to understand the possible causes of one or another level of the resources, the biological patterns and the ecological relations detemined the observed biological indices, and the possibilities of the intervention by men.

A characteristic feature of the ecology of chum is the fact that the spawning of adult fish and the fattening of fingerlings takes place in one and the same water body and, usually, at the same stations,although a greater part of the water body is used for the fattening, than for the spawning. Thus, from the emergence from the ground to the downstream migration to the river bed, the chum fingerlings live in the natural spawning and growing water basin.

The spawning grounds of the fall chum in the basin of the Amur River may be divided according to their hydrological conditions into several types united by one common feature; a considerable debit of relatively deep ground waters. The following types of the spawning grounds belong to the basic types.

1. Spring channels, which are temporary river branches, more or less isolated from river bed at the outlet. Depending on the degree of isolation during the summer a more or less considerable amount of water enters them. When the water level decreases, usually in October, the outlets of the channels are separated from the river and their beds are filled with ground waters. Consequently the spring channels, over considerable stretches, are not covered with ice during the winter even when the current rate is low.

Spring channels are the most important and the widest occurring type of fall chum spawning grounds, particularly in the tributaries of the Ussuri River and in such large tributaries of the Amur River as Anyuy, Khungari, Koor, as well as in the upper reaches of the Argun' River.

2. Spawning springs are running water bodies isolated at the sources from the river bed the entire year round. Their water expenditure and their thermal conditions are determined by the debit of ground waters. Such a type of springs is described in detail by E.M. Krokhin for the Kamchatka (Krokhin and Krogius, 1937).

3. Limnocrens or lake basins filled with ground waters, are usually located in the upper floodland of a river. They occur relatively rarely, but are exceptionally productive /p.62 spawning and growing water bodies for the fall chum.

4. Spring gulfs are water bodies connected the year round with the river bed. Their debit of ground waters compared with the total volume of water masses in the gulf is small. Because of this phenomenon and because of poor water movement in these bodies during the summer, the water in these gulfs is warmer than in the river; in winter these gulfs are covered with a thick layer of ice. Their spawning importance is small; they are located mostly in the lower reaches of large tributaries of the Ussuri and Amur Rivers.

5. The lake lithoral. In cases, when we have in large flood-land lakes of the Amur River sections with rock and pebble lithoral and exit of ground water (remains of ancient cones of deposit), the fall chum uses them for its spawning. Such spawning grounds occur in lakes of the lower reaches of the Amur River, where the annual fluctuations in the water level are relatively small (Kizi and Kadi Lakes, and others).

6. River beds and permanent river branches. In these water bodies with typical river conditions the fall chum spawns at locations with dispersal outlets of ground waters. These spawning grounds do not have any significant importance in the reproduction of fall chum.

The summer chum multiplies only at the spawning grounds of the latter type. The spawning of summer chum in a river and in river beds near the banks, at places where visible outlets of ground waters are absent, gave us reason to assume that the chum, like the pink salmon, buries its eggs in the fluvial sub-bed current without any admixture of ground water. However, during the winter months, in all the tributaries of the Amur River, where spawning nests of pink salmon and summer chum were studied, it was established that at equal depth of egg deposition (20 to 30 centimetres from the bottom) the water temperature in the pink salmon nests was 0.2 to 0.3°C., and in the chum nests 0.9 to 1.7°C (end of January and February). The difference in the thermal conditions may only be explained by the presence of ground waters.

Pink salmon spawning in the current below the river bed with an extremely low winter temperature has an adaptive significance. The development of pink salmon under such temperatures progresses very slowly, and towards the moment of the downstream migration (in May and June) the pink salmon is still completing its larval period of development; the summer chum, which spawns later than the pink salmon, had by that time achieved the fingerling stage long ago. At such development rate the pink salmon must either start its feeding while in fresh water, or migrate down to the sea still under ice and arrive to the sea coast area during a period of unfavourable living conditions (possibly even at negative water termperatures /TR: i.e. below 0°C/).

The temperature factor should be considered as the main factor in a water body's hydrological conditions determining the fattening conditions.

The current rate and the turbidity of the water become important only with the rise of the spring flooding.

The gas conditions are interesting, insofar as they show to which breeding conditions the chum fingerlings have adapted themselves. In tables 20 and 21 information is given on the thermal conditions and oxygen content in water in typical spawning and growing water bodies of the fall chum *).

The fattening stage of the chum fingerlings in the spawning and fattening water bodies begins in spring channels starting with the first days of April, and in the limnocrens, already in the middle of March and continues to the middle of June, although the bulk of the fingerlings leaves the water bodies in May. Thus, the fingerlings of fall chum fatten at water temperatures of 5 to $10^{\circ}C$. Chum begins to feed upon exterior food already while still having considerable yolk reserves at the larval stage. At that time the chum switches from the obligatory ground form of life to the facultative ground life. The larvae emerge from the mounds /p.65 for a brief period of time and hide again inside the mounds; gradually they keep expanding their hunting area and towards the end of the larval period hide in the pebbles at any section of the bottom.

Already N.P. Navozov-Lavrov (1927) was finding out about the facultative-ground life form of the fall chum larvae; he wrote that "the fingerling tries to make several excursions from its

* In tables 20 and 21 the Bolshay channel in the river bed of Khor River, the Teploye Lake and the Orekhov Spring are limnocrens, all the other water bodies are spring channels.

Thermal conditions of the fall chum's spawning water bodies, in degrees (Celsius)

Name of Water body (Название водоема)	Years (Годы)	Jan. (Январь)	Feb (Февраль)	Mar (Март)	April (Апрель)	May (Май)	June (Июнь)	July (Июль)	Aug (Август)	Sept. (Сентябрь)	Oct. (Октябрь)	Nov (Ноябрь)	Dec. (Декабрь)	Annual Total of Heat
Bolshaya Channel	1950	0,1	0,1	0,1	2,0	9,4	14,9	16,9	19,5	14,2	7,9	1,2	0,1	2640
"	1956	0,1	0,1	0,2	2,0	7,6	14,5	16,0	15,5	12,4	4,3	0,3	0,1	2240
Pavlinovsky Spring	1950	2,3	2,6	5,0	7,7	10,0	11,0	11,2	11,0	10,0	8,2	5,2	3,6	2675
"	1956	2,5	1,8	2,9	5,1	8,1	11,5	14,0	15,0	12,6	7,6	5,4	3,1	2703
Sumasshedshaya	1956	2,1	1,7	2,4	3,6	8,5	14,0	15,1	15,6	12,4	9,0	5,6	2,8	2832
Potopilis	1956	5,0	4,5	4,7	5,6	10,1	14,6	15,5	16,0	12,5	8,9	5,7	5,6	3311
Telefon	1950	2,1	2,5	3,0	4,0	10,0	16,0	17,3	20,0	10,5	8,1	5,6	3,0	3118
"	1956	4,3	2,6	3,0	4,0	7,3	14,5	16,0	15,5	11,6	4,3	4,0	2,8	2740
Kryuchki	1956	4,2	4,5	4,5	4,5	7,2	13,6	16,0	15,5	12,4	4,5	4,2	4,2	2902
Kovalchikha	1955	1,4	1,1	2,3	6,2	8,0	12,2	13,6	14,2	12,5	6,2	2,5	1,5	2493
Boidyrikha	1955	3,4	2,6	2,6	5,4	7,8	11,5	13,5	13,5	12,4	8,1	5,0	3,6	2725
Teploye Lake	1955	3,2	3,3	3,5	4,3	6,2	8,0	9,8	8,0	6,4	4,1	4,0	3,2	1944
Orekhov Spring	1957	3,5	3,3	3,3	5,0	8,0	11,2	12,3	11,4	7,9	4,2	4,0	3,6	2363

Table 20

Oxygen content in the surface waters in spawning water bodies of fall chum*

Название водоема / Name of Water Body	Показатели / Indices	Январь / Jan.	Февраль / Feb.	Март / Mar.	Апрель / Apr.	Май / May	Июнь / June	Июль / July	Август / Aug.	Сентябрь / Sept.	Октябрь / Oct.	Ноябрь / Nov.	Декабрь / Dec.
Протока Большая / Bolshaya Channel	t° воды 1	0,1	0,1	0,2	1,0	8,8	11,0	15,8	14,0	13,0	4,5	0,3	0,1
	O_2 мг/л 2	8,8	8,7	9,5	10,8	10,5	10,0	9,4	9,6	9,0	9,5	8,8	9,7
	% насыщ. 3	61,6	60,2	65,8	76,6	90,0	91,0	94,9	93,3	85,6	73,7	61,2	67,1
Телефон / Telefon	t° воды 1	4,7	3,2	3,8	3,8	6,8	12,8	16,0	14,2	13,4	4,6	2,8	0,4
	O_2 мг/л 2	6,9	7,8	8,7	10,2	10,0	9,4	8,9	8,8	9,3	9,4	8,7	9,7
	% насыщ. 3	53,9	53,7	66,5	77,9	83,3	89,1	90,2	85,9	89,2	73,2	64,8	69,4
Павленовский ключ / Pavlenovsky Spr.	t° воды 1	3,1	2,0	2,8	4,8	7,8	11,2	13,2	14,9	14,0	7,6	6,0	3,2
	O_2 мг/л 2	9,0	8,9	8,4	9,0	9,2	9,1	9,2	8,0	8,2	7,6	7,4	9,4
	% насыщ. 3	67,5	64,9	62,5	70,5	77,7	82,3	88,0	79,2	79,7	64,0	59,8	70,7
Сумасшедшая / Sumasshedshaya	t° воды 1	2,0	1,8	2,3	3,2	8,8	12,0	16,2	15,0	13,8	9,2	6,6	3,0
	O_2 мг/л 2	9,0	9,0	9,5	10,0	9,6	9,2	9,0	9,3	8,6	7,8	8,4	9,2
	% насыщ. 3	65,6	65,2	69,7	75,2	83,2	85,7	91,5	92,8	83,3	68,2	69,7	68,8
Потопились / Potopilis	t° воды 1	7,2	4,6	6,6	4,8	9,2	13,4	16,4	16,2	13,9	9,4	6,8	5,2
	O_2 мг/л 2	7,8	6,2	4,4	7,2	8,8	8,2	8,6	7,9	7,8	6,8	5,8	6,6
	% насыщ. 3	64,9	48,4	36,1	56,4	76,9	78,6	87,9	80,4	75,2	59,7	47,8	52,3
Крючки / Kryuchki	t° воды 1	4,4	5,0	4,4	4,2	5,8	11,2	15,6	14,1	13,2	4,8	4,0	4,1
	O_2 мг/л 2	5,8	1,6	1,8	3,2	8,0	8,2	8,4	8,1	7,6	7,4	8,2	6,8
	% насыщ. 3	45,0	12,6	13,9	24,8	62,7	75,2	84,4	78,8	72,7	58,0	62,9	52,3
Теплое озеро / Teploye Lake	t° воды 1	3,2	3,3	3,5	4,9	6,2	8,0	9,8	8,0	6,4	4,1	4,0	3,2
	O_2 мг/л 2	5,46	5,68	6,51	9,04	9,88	9,88	9,93	9,62	9,47	9,37	8,04	6,20
	% насыщ. 3	40,5	42,3	50,0	77,7	79,0	82,3	86,2	80,2	76,0	70,9	60,9	46,0

Captions: 1 - t° of water
2 - O_2 milligrams per litre
3 - % of saturation

*) The analyses were carried out on the 14th to 16th of each month, at 1 to 3 p.m., for a period of 3 years. Average values are shown in the the table.

Table 21

nest and every time endevours to return". I.I. Kuznetsov (1928) observed that "the fingerlings emerged from pebbles do not leave their nests immediately. Taking trips along the spring they return to the original point where new fingerlings gradually join them."

I succeeded to observe the facultative-ground form of life of the fall chum larvae under experimental conditions. At that time the average lenght of a larva was 29 millimetres and the weight 235 milligrams.

The downstream migration of chum from the limnocrens and spring channels begins in the end of April, continues the entire month of May and ends in June, therefore, it is difficult to judge the individual changes in the weight of fingerlings during the fattening period. From table 22 we see that in many spring channels the average weight of a fingerling migrating seawards is only slightly above the average weight of a larva at the end of March. This is explained by the irregular rates in the embryogenesis, by different dates of spawning and by the fluctuating lenght of the fattening period.

Experimental studies of feeding and growth of fall chum fingerlings indicate, that they feed intensely and grow fast under favourable food conditions. (Levanidov, 1954b, 1955).

Table 22

Size (in millimetres) and weight (in milligrams) of fingerlings leaving spawning water bodies.

Водоем Water body	Год year		Апрель April 25—30	Май May 1—10	11—20	21—31
Sumasshedshaya Channel	1958	длина 1	33,0	33,0	33,3	33,2
		вес 2	235	244	233	242
Pavlinovsky Spring	1960	длина	34,5	34,0	34,3	34,2
		вес 2	285	294	275	280
Ambansk Channel	1954	длина 1	31,1	31,2	32,6	33,9
		вес 2	242	236	247	260
Sokhonto Channel	1962	длина 1	32,4	31,4	32,1	31,7
		вес 2	250	266	268	242
Great Bidzhan Spring	1954	длина 1	36,0	35,8	37,2	35,8
		вес 2	300	325	365	353
Teploye Lake	1954	длина 1	31,6	31,4	32,0	33,0
		вес 2	220	234	226	260
Teploye Lake	1953	длина 1	31,7	34,0	34,8	35,8
		вес 2	226	273	322	375
Doldzo Channel	1958	длина 1	—	34,9	35,1	34,3
		вес 2	—	369	366	342

Captions:

1. length
2. weight.

Food Base of the Amur Salmons in Fresh Waters

The food resources in water bodies where the juveniles fatten are the least studied ones of all the cardinal problems of the natural reproduction of Pacific salmons. Such a complex biological phenomenon as the food base of salmons in fresh water is poorly studied even from the viewpoint of its fauna, not to mention the study of the reproduction of organisms constituting this base. The laws of the biomass dynamics and of the dynamics of the numbers of invertebrate populations (in particular their production), their life cycles and ecological peculiarities are practically unknown. /p.66

The food base of the benthophages, i.e. fingerlings of chum, chinook, coho and of sockeye is so poorly studied that the researchers of the population dynamics of these salmons disregard it. In respect to the salmons of the Asiatic coast we can mention only two or three works on this subject (Levanidov and Levanidova, 1962; Kurenkov, 1964; Levanidova, 1964a). However, the importance of this basic element of the food supply the dynamics of the biomass and of the numbers of the food invertebrates is decisive for the efficiency of the reproduction and to a considerable degree for the dynamics of the numbers of the salmon population at sea. Of this reason we have given considerable attention to the study of the food base of salmons in the Amur basin.

The plankton and the benthos of the bed of the Amur River and particularly of the water bodies of its floodland, including large lakes, are to a considerable degree studied both from the point of view of the special composition, and from the numerical viewpoint. The initial reconnaissance research of the benthos and plankton biomass of the lower reaches of the Amur River was carried out by the TINRO /Pacific Research Institute for Marine Fisheries and Oceanography/ expedition in 1933 and in 1935 (Mikulich, 1948; Lovetskaya and Mikulich, 1948). This work gave an idea of the order of values in the benthos and sestone biomass in the river bed of the Amur River and of its floodland lakes. The taxonomical composition of the bottom population remained unknown because the determinations usually were carried out merely down to the "group" rarely to the genus, except for some well-known species*).

The expedition of the Moscow University carried out, in the years 1945 to 1949, a thorough study of benthos and plankton of the Amur River and its floodland, as the food resource of fish (Konstantinov, 1950; Borutsky, Klyuchareva, Nikolsky, 1952; Borutsky, 1952; Chernova, 1952; Klyuchareva, 1952). The main task of the expedition was to study the biology

*) The first substantial contribution to our knowledge of the taxonomical composition of the aquatic invertebrates was carried out by the expedition of the Zoological Institute of the USSR Academy of Sciences in 1927 (Rezvoy, 1930). A number of monographs is completed from the material of the expedition (Martynov, 1934, 1935; Sokolov, 1940 and others).

of the freshwater Amur-fish living in the floodland and in the river bed of the Amur and Ussuri Rivers, therefore, the tributaries of these rivers were studied relatively little.

Samples of the benthos and plankton in the tributaries were usually taken in the estuarian sections, where the hydrological conditions of the tributary are most affected by the river into which the latter runs out. In meantime the hydrological conditions of the lower and the middle reaches of the Amur and Ussuri Rivers on the one hand, and of their tributaries, on the other hand, are very different.

The Amur River, in its lower and partly in its middle reaches, is a flatland river of the monsoon type running through a wide, in sections narrowing, valley among mountain ridges of Sikhote-Alin', Burein, Badzhal and others, from which rivers of a foot-hill or mountaneous type are running down. These tributaries, which are spawning rivers for the Amur salmon, differ from the Amur River in their thermal conditions (in summer the difference in the temperature between the water in the Amur River and the water brought by its tributaries reaches 5 to 10°C, and individual cases 15°C), in the character of the bottom ground (pebble and rock in the tributaries and sandy in the Amur River), in the transparency of water and in the current rate.

Such a difference in the physical-geographical character in a river and in the majority of its tributaries is probably a rather rare phenomenon. Usually a river of the flatland type has tributaries also of the flatland type (for example, Volga River other scientists carried out the collections of benthos according to our program in various tributaries of the Amur River parallel with their main tasks. (L.V. Kokhmenko, L.S. Rubanenkova, M.D. Zazhigina, N.V. Tolmacheva, N.I. Kulikova, V.I. Gudzenko, A.M. Kolgayev, O.Ya. Baykova, A.P. Ivanova, Yu.S. Roslyý, B.B. Vronsky, I.A. Nosova, L.A. Rostovtseva, L.A. Slobodchikova, A.F. Isayeva).

Particiaption of L.V. Kokhmenko in the accumulation of material on the river bottom fauna deserves our special attention. While studying the food and food interrelation of fish in the channels of the Amur River, she carried out simultaneously regular quantitative and qualitative collections of benthos in these water bodies. L.S. Rubanenkova, chief laborant, later fishery-technician of the laboratory, deserves considerable praise in the study of benthos from the tributaries of the Amur River. Starting with 1954, she carried out, in addition to her participation in the collection of material, a significant part of the indoors processing, and in the later years participated in the completion of individual section of the subject.

Besides the scientists of our laboratory mentioned above, associates of the fishery-meliorative station of Amurgosrybvod participated in the operations. Among the latter, A.P. Fadina-Lavrova, director of the fishery-meliorative station on the Khor River, deserves special mentioning for her long and conscienceious work.

Determination of benthos species was carried out by the following persons: turbellarians were done by Z.I. Zabusova-Zhdanova; oligochatae by N.L. Sokolskaya and O.V. Chekanovskaya; leeches by E.I. Lukin; mollusks by Ya. I. Starobogatov; crustaceans by V.Ya. Levanidov; water mites by A.I. Yankovskaya; dragonflies (imago) by B.F. Belyshev; dragonflies (larvae) by I.M. Levanidova with consultation of B.F. Belyshev; mayflies (for years 1949 and 1950) by O.A. Chernova *), data for the years 1957 to 1961 are processed by I.M. Levanidova (consulted and assisted by O.A.Chernova and R.S. Kazlauskas) and utilised in the present compendium **); stoneflies by Yu.I. Zapekina-Dulkeit and I.M. Levanidova under consultation with L.A. Zhiltsova; collection of water bugs were forwarded to professor T.L. Yachevsky for classification are still not finally processed (the determinations shown below of several species were carried out by V.Ya. Levanidov, of

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*) The results of the processing were included in the compilation by O.A. Chernova on the mayflies of the Amur River(1952).

**) Data collected rom 1950 to 1956 were forwarded to O.Ya. Baykova for classification. As these classifications were not completed by the time of the present compilation, we were not able to use them but partly (mainly on the basin of the Iman River.).

Micronectinae by A. Vroblevsky); water beetles by V.B. Zakharenko*), /p.68 caddis-flies by I.M. Levanidova; collections of chironomids during various periods and from various water bodies were classified by several specialists. A considerable part of material from the basin of the Khor River and from the water bodies of the Teplovsky fish hatchery, as well as chironomids from the stomachs of the salmon fingerlings are determined by the author, the other collections from the Teplovsk channel and lake were determined by I.M. Levanidova and L.S. Rubanenkova under consultation with A.I. Shilova and A.A. Linevish; about 40 collections from the Khor River, as well as collections from the Teplovsk channel and lake , for the years 1960 and 1961, were done by I.I. Darova; a portion of the collections from the spawning tributaries by L.V. Kokhmenko (under direction of A.A. Linevish and I.I. Darova); 76 samples from various tributaries of the Amur River were classified by A.V. Sycheva; tipilids by E.N. Savchenko, the larvae of other diptera by I.M. Levanidova.

Part of material on a number of groups is still not finally processed, therefore, the species determination of certain forms, including some playing a significant role in the benthos and in feeding, has still not been finalized.

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*) An extensive beetle collection collected during the first operation years at the Amur River and sent to professor F.A. Zaytsev was, most probably, not processed because of F.A. Zaytsev's death.

The authors brings his heartfelt gratitude to all the collegues who participated in collections and in laboratory processing of the material, as well as to the specialists, who took upon themselves the difficult task of the species determination of the bottom invertebrates in a poorly studied basin.

Methodology

The main difficulty in the study of the biomass of benthos in the tributaries of the Amur River consists in the collection of quantitative samples from stony grounds predominant in these rivers. Sandy and sandy-silt grounds, upon which one could operate with bottom grabs of Petersen or Ekman-Berdzhi type only occur in gulfs, in estuarion sections and in limnocrens.

We did not have such relatively complicated implements for the stony ground like the quantitative Greze drag, thus we used somewhat less complicated, but sufficiently catching quantitative apparatuses, which gave fully reliable results in shallow spawning rivers. One of such instruments, "catching prism" has much in common with A.A. Sadovsky's (1948) benthometer. The catching-prism was primarily used at sandbanks, on stony and on flat portions between sandbars, it was used on a ground of fine or medium-sized pebbles. In the latter instance the biomass of the benthos is usually small, but it contains large representatives of benthofauna, therefore, the catching over a large area (1200 square centimetres) presents certain advantages.

Another extensively used collection apparatus is the pipe of stratimetric type with a diameter of 3.6 to 5 centimetres. It was used on fine-pebbled, pebbled, clayed, sandy-silty and silty grounds, as well as on sections of the bottom, where pebbles and stones do not lie solidly side by side, but with sections of finer fractions in between. In the latter instance collection from the finer fractions by means of a tube is complemented by the collection from individual stones and pebbles.

Quantitative collection from individual stones and further calculations were carried out according to V.I. Zhadin's method (1940, 1960).

In the limnocrens and in the rivers flowing from the former a peculiar biocoenosis takes place consisting of solid accumulations of filiform algae Rhizoclonium, which swim on the surface of the water body, particularly in calm places, or are accumulated around objects protruding from water. Occasionally they reach areas of many square metres and are abundantly populated with invertebrates. On shallow places Gerd's (1951) quantitative frames were used; on deep spots a paper square of 10 by 10 centimetres was placed on top of algae and according to this "pattern" a corresponding piece of "float" was cut out with scissors. A total of 2000 quantitive samples and more than 1200 qualitative ones were taken in the tributaries of the Amur River by means of various methods. /p.69

Parallel to the collections of benthos along the banks of the water bodies regular entomological catches were conducted to determine the species composition of amphibiotic insects and for the control of the dynamics of their flights.

To determine the size and character of the bio-flow in the Khor and Teplovsk Rivers, as well as in several other tributaries (Nizhnyaya Uda, Namptu), in the Amur and Ussuri Rivers collections of "planktobenthos" were carried out (bottom invertebrates in the mass of the river current). These collections were carried out by fingerling traps, egg nets and by specially designed nets of guaze No. 16 and 27 (Levanidova and Levanidov, 1962; Levanidova and Lenvanidov, 1965).

Plankton, Planktobenthos and Microbenthos

Periphyton (mainly diatomic) is the main producer of the organic substance in the foothill tributaries. A.A. Sadovsky (1949, 1963), S.N. Skadovsky (1955) and V.N. Greze (1957) indicate the leading role of the periphyton in rivers.

Fouling with diatomic and green algae and lichen covers the stony and pebbled grounds of the rivers. Bottom algae are developed only in the tributary system of the rivers, where the higher aquatic vegetation is also developed. The latter forms a heavy overgrowth in the flatland rivers. Masses of organic substance enter the rivers from water accumulation area; the importance of fallen leaves is particularly great (Levanidov, 1949).

Plankton. In the mountaneous and foothill tributaries of the Amur River the true phytoplankton and zooplankton are absent. Only during the summer flooding, when the river covers the floodland, rather many cyclops and several cladocerans were caught in each of the plankton-nets erected in the main channel of the Khor River. Usually their number was 0.5 to 1 specimen per one cubin metre of water. Here both the cyclops and the cladocerans were represented by forms belonging to the bottom plankton or planktobenthos (Cyclops strenuus Fisch., Chydorus spaericus O.F.M. and Sida O.F.M.).

E.V. Borutsky (1952) recorded the following amounts of Copepoda and Cladocera in one cubic metre of water in the semi-mountaneous tributaries of the Upper and the Lower Amur River: Onon River: 0; Ingoda River; 4; Shilka River: 8; Khalzan River:

Copepoda - 0, Cladocera - 83 (Chydorus spaericus); Bichi River: Copepoda - 13, Cladocera - 3 individuals. E.V. Borutsky presents no species classification except for the mentioned one, but it can be assumed that all these forms belong to the benthopelagic plankton or plantobenthos. As. V.I. Zhadin (1950) justly pointed out, the autochthonous part of the river plankton is formed almost exclusively by the representatives of the planktobenthos.

Planktobenthos and microbenthos. As our and E.V. Borutsky's mentioned data on the Khor River show, in the bed of semimountaneous and foothill rivers the planktobenthos is practically absent (at any rate its value as food resource at a concentration of 0 to 1 individual per cubic metre is zero). However, in the limnocrens and in certain spring channels the planktobenthos develops in considerable quantities. Thus in the Teploye Lake, in quiet silty gulfs, among the vegeration remains, the total numbers of the planktobenthic organisms reaches 42,000 individuals per one square metre, including the cyclops (Cyclops strenuus) 25,000 harpacticids (Canthocamptus sp.) 750 Chydorus spaericus 9300, Bosmina 2500, Ostracoda 2500. Mites belonging to the microbenthos category are mainly represented by species of the genus Lebertia, as well as by Hygrobates octopus (Dad), Sperchon glandulosus (Koen), Eylais sp.sp. Particualrly numerous are the mites in the biotopes of the filiform algae and of pondweed, where they in some areas reach an abundance of 1000 specimens and a biomass of 1 to 3 grams persquare metre.

/p.70

In the Orekhov Spring lindocren the species composition and the numbers of this category of benthos are:

Cyclopoida –	Acanthocyclops viridis (Jur.)	5400
Harpacticoida –	Canthocamptus sp.	1600
Cladocera –	Chydorus sphaericus	800
	Sida crystallina O.F.M.	1200
Ostracoda –	Eucypris sp.	14600
	Candona candida O.F.M.	38400
Hydracarina –	Lebertia sp. sp.	500

A total of 62500 individuals per square metre.

Among the spring channels the greatest abundance of planktobenthos and microbenthos was observed in Polevaya channel of the Khor River, which is distinguished by its slow current (about 40 metres per hour) and by its considerable accumulation of silt and detritus.

The species composition of the microbenthos in this channel is the same in the limnocrens, but the numerical ratios are different. Per one square metre of bottom we find:

Cyclopoida –	Acanthocyclops viridis	260
Harpacticoida –	Canthocamptus sp.	20
Cladocera –	Sida crystallina	30
	Chydorus crystallina	30
Ostracoda –	Candona candida	50
Hydracarina –	Lebertia sp.sp.	10

Total 400 individuals per one square metre.

In other spring channels the microbenthos occurs in an abundance of 200 to 400 specimens per one square metre.

In the beds of cold-water semimountaneous rivers the microplanktobenthos occurs only in individuals instances. The most common among the mites here are: Hydorbates octupus, Atractides nodipalpis constrictus Sokol., Sperchon glandulosus and certain species of the genus Lebertia.

V.N. Greze (1957) having studied the connection between the microbenthos of the Yenisey River and the speed of the current pointed out that the abundance of the benthopelagic plankton or the micronektobenthos (planktobenthos according to V.I. Zhadin) is proportional to the speed of current, other conditions being equal. The planktobenthos attains a considerable density in the channels: 10,869 specimens per square metre on the silt and only 102 specimens per square metre on the pebbles.

Benthos in the Tributaries of the Amur River

The Fauna of Bottom Invertebrates in the Amur Basin and its Connection to the Hydrofauna of the Adjoining Territories

The zoogeographical analysis of the invertebrate fauna of the Amur basin is outside our task. We may touch upon this question only insofar as classification of a species to one or another zoogeographical complex determines to a considerable degree their ecological features and the distribution pattern according to the water bodies.

The problems of the zoogeography of individual groups of the aquatic invertebrates in the Amur basin were discussed in monographs and articles of a number of authors (Martynov, 1924, 1929; Zhadin, 1952; Chernova, 1952, 1958; Zaytsev, 1953; Lukin, 1955, 1960; Sokolskaya, 1958; Chekanovskaya, 1962; Levanidova, 1964b and others). The zoogeography of freshwater fish is discussed in works of A.Ya. Taranets (1939a), G.U. Lindberg (1947) and of L.S. Berg (1949).

As we know, the Amur basin is located in the Amurian (Manshurian) transitional zoogeographical subprovince of the Palearctic (province according to L.S. Berg). Of this reason its fauna is genetically heterogeneous and consists of Palearctic /p.71 Sina-Indian and Arctic species.

Fish in the Amur River were subject to the most complete zoogeographical analysis among the freshwater animals; they were studied earlier and better than other groups. G.V. Nikolsky (1956b) went very successfully into the depth of the zoogeographical analysis of the ichtyofauna of the Amur River using the ecological method. G.V. Nikolsky took the fanunistic group of species that was connected by common geographical origin and development within one geographical zone as a unit; he substantiated the belonging of the Amur fish to six faunistic complexes. The first four complexes are Palearctic: the ancient Upper-Tertiary consisting of thermophilic relicts characterized in the contemporary epoch by areas interrupted on the territoty of Siberia, the Boreal flatland complex and the Boreal foothill complex formed of less thermophilic elements of the Tertiary fauna, who have preserved continuous Transpalearctic areas, and the Arctic freshwater complex, the most cold-loving element in the Palearctic fauna. Species of Sino-Indian origin are distributed in two complexes: the Chinese flatland complex and the Indian flatland complex.

This ecological-geographical classification, we believe is fully acceptable also in the case of invertebrates, who for a long geological period were developing under the same climatic conditions in the water bodies which were precursers of the Amur River. Among them are found representatives of all the complexes segregated by G.V. Nikolsky, plus, probably, the elements of the Sino-Indian foothill complex.

Contrary to fish, the species composition of the fauna of aquatic invertebrates in the Amur River is still far from being fully clarified and in a very different degree in different taxonomical groups. The boundaries of their areas on the territory of our country /the USSR/ and particularly of the adjoining countries of the southeastern Asia remain still only partly known for a whole number of species. However it is extremely important to note that owing to intense faunistic studies in the later years carried out in Siberia (Zapekina-Dulkeit, 1961; Vershinin, 1962; Golyshkina, 1962; Sukatskene, 1962; Kazlauskas, 1963), as well as the publishing of the results of the faunistic development of the earlier collected extensive data (Greze, 1957; Chernova, 1958) the boundary of the areas of a number of "Amurian" species, particularly of mayflies and caddis flies, "moved" far to the northwest. In a number of instances the areas of European species and even of genera have "expanded" to the east. A characteristic example of this is the occurrence of the representatives of the European genus Torleya (mayflies) in the Angara River (Sukatskene, 1962; Kazlauskas, 1963), and later in the Elbanka River (Amur basin) and in the Khor River (Lavanidova and Levanidov, 1965)*).

However, at the contemporary stage of the faunistic knowledge of Asia a more precise determination of the belonging of a species to one or another zoogeographical complex often causes difficulties. On the other hand, the presence in a considerable number of invertebrates living in the Amur basin of extra-

*) R.S. Kazlauskas made the species determination of T. padunica Kazl.

ordinary extensive areas*) stretching mainly in the longitudinal direction, is now beyond any doubt. Here, naturally, the number of the Amurian "endemic species" decreased, and the degree of the commonness of fauna with the adjoining territories increased (Levanidova, 1964b), a fact of high importance in the determination of the ecological peculiarities of the Amur benthos and of the distribution pattern of its representatives within the hydrographical grid.

Species with areas stretching in latitudinal direction belong mainly to the complexes of cold-loving forms of G.V. Nikolsky: the Boreal foothill, the Boreal flatland and, possibly, the foothill Sina-Indian complexes. A small portion of species belongs to the thermophilic Sino-Indian fauna (Macronema radiatum, Aethaloptera rossica and others).**) /p.72

Table 23 shows data on the occurrence of species with extensive areas of habitat, belonging to the relatively stenobiontic groups of invertebrates, who as a rule do not have the capacity for extensive propagation (mayflies, stoneflies, caddis flies).***) However, a considerable part of the species of bottom invertebrates of the Amur basin do not leave the confines of the Amur zoogeographic subprovince. /p.73

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*) The meridional stretching of these areas in the territory of Siberia is determined only for a few forms.

**) The authors of the species are indicated in tables 23, 25, and 26; authors of the species not included in these tables are quoted in the text.

***) For the compilation of the table, in addition to the published data, including those of I.M. Levanidova and me, our unpublished data were used. Certain data on the Sakhalin fauna are based on the collections of E.I. Zhuykova determined by I.M. Levanidova.

Comparing the extent of occurrence of the individual taxonomical groups in total, we can say that the more eurybiontic groups are characterized by the most extensive geographical occurrence. The chironomids are the extreme member of this series, a phenomenon explained by their widely known biological characteristics. Therefore, it is quite natural that the commonness of the fauna of this group must be great, particularly in the Chironominae subfamily.

The list of chironomids from the Amur tributaries contains, at the present time, 200 forms (table 25) not counting the clearly new ones that are not yet described. Thus, while the work of A.S. Konstantinov (1950) was published this list was enlarged by 80 forms. The enlargement took place mostly because of the Orthocladiinae subfamily, whose species live in foothill tributaries (which were) relatively poorly covered by operations of the expedition of the Moscow State University. However, it is difficult to compare the faunistic lists of the chironomids from different territories, insofar as besides species they also contain determination down to a group of species (according to larvae). It /p.78 should be also noted here that from one larval form, when hatched by us, we always obtained gnats of only one species, while it is known that from one form of larvae adult gnats emerge belonging to two or three different species (Chernovsky, 1949). Almost in all our cases these turned out to be species widely occurring or known from other territories of the Soviet Union, such as: Paratendipes albitibia, Lauterbornia chlorophita, Micropsectra viridis - scutellata, Syndiamesa orientalis, S. nivosa (Levanidov and Levanidova, 1962).

Table 23

The geographical occurrence of certain major species of the bottom invertebrates in the tributaries of the Amur River.

Species Виды	Europe Европа	European North of the USSR Европейский Север СССР	Altay Алтай	Yenisey Basin Бассейн Енисея
1	2	3	4	5
Веснянки				
Pteronarcys reticulata Burm.			Zapekina Запекина, 1955	Коропеп, 1949 Запекина, 1955 Zapekina Грезе, 1957 Greze
Rhabdiopteryx quadrata Kopon.				Коропеп, 1949 Запекина, 1957 Zapekina
Amphinemura borealis Mort.	Brinck, 1952	Zhiltsova Жильцова, 1964	Запекина, 1955	Запекина, 1958
Capnia nigra Pict.	Бианки, 1905 Bianki		Запекина, 1955 (Syn. Capnia conica.)	Запекина, 1958
Capnia pygmaea (Zett.)	Бианки, 1905	Жильцова, 1964		Запекина, 1958
Isoperla lunigera (Klap.)			Запекина, 1955	Запекина, 1958
Isoperla obscura Zett.		Klapalek, 1914 (Сев. Урал)		Запекина, 1958
Arcynopteryx brevis Kopon.				Коропеп, 1949 Запекина, 1958
Arcynopteryx compacta McL.	Brinck, 1952	Жильцова, 1964	Запекина, 1955	Запекина, 1958
Diura nanseni Kemphy	Brinck, 1952	Жильцова, 1964		Запекина, 1958
Chloroperla mediata Navas				Запекина, 1958
Haploperla ussurica Navas				Грезе, 1957 Greze Запекина, 1958

Baykal rivers, Angara to Bratsk Реки Прибайкалья, Ангара до Братска	Amur Basin Бассейн Амура	Ussuri River, rivers south of the Coastal area Река Уссури, реки южного Приморья	Other habitats Прочие места обитания	
6	7	8	9	
Бианки, 1905	Леванидов, 1951а	Запекина, 1959		
	Леванидова (в печати) (in print)	Леванидова (в печати) (in print)	Ю. Сахалин (сборы Е. И. Жуйковой). Камчатка (материалы И. М. Леванидовой)	S. Sakhalin (collected by E.I. Zhuykova) Kamchatka (I.M. Levanidova's data)
	Запекина, 1959	Леванидова, 1964б	Ю. Сахалин (сборы Е. И. Жуйковой)	S. Sakhalin (collected by E.I. Zhuykova).
Запекина, 1957	Запекина, 1959 (Syn. G. conica)	Леванидова (в печати) (in print)	Япония, Туркестан (Бианки, 1905), Кавказ (Жильцова, 1964), Камчатка (материалы И. М. Леванидовой)	Japan, Turkestan (Bianki, 1905), Caucasus (Zhiltsova, 1964). Kamchatka (I.M. Levanidova's data).
		Запекина, 1959		
Klapalek, 1923 Запекина, 1957	Запекина, 1959	Запекина, 1959		
	Запекина, 1959	Леванидова (in litt.)		
Запекина, 1957 (Syn. A. dichroa var. polaris) (?)	Запекина, 1959	Запекина, 1959	Охотское побережье (Запекина, 1959), Камчатка (материалы И. М. Леванидовой)	Okhotsk Sea coast (Zapekina, 1959). Kamchatka (I.M. Levanidova's data)
Запекина, 1957 (Syn. A. dichroa)	Леванидова, 1964б	Леванидова, 1964б	р. Лена, о. Сахалин (Klapalek, 1912), Камчатка (материалы И. М. Леванидовой)	Lena River, Sakhalin Is. (Klapalek, 1912), Kamchatka (I.M. Levanidova's data)
	Запекина, 1959	Запекина, 1959	Камчатка (материалы И. М. Леванидовой)	"
	Леванидова (in litt.)	Navas, 1925 Запекина, 1959	Камчатка (материалы И. М. Леванидовой)	"
Запекина, 1957 (Syn. Isopteryx sp.)	Леванидова, 1964б	Navas, 1925, Запекина, 1959	Ю. Сахалин (сборы Е. И. Жуйковой).	S. Sakhalin (collected by E.I. Zhuykova).

1	2	3	4	5
Neophasganophora brevipennis Navas				Коропеп, 1949
Клопы Water Bugs				
Micronecta wui Lundblad				Wroblewski, 1963
Micronecta guttata Matsumura				Wroblewski, 1963
Поденки Mayflies				
Ephemera amurensis Navas				Chernova Чернова, 1952
Epeorus latifolium Ueno			Chernova Чернова, 1949	Greze Грезе, 1957, Запекина, 1961 Zapekina
Iron maculatus Tshern.			Чернова, 1949	
Heptagenia soldatovi Tshern.				Greze Грезе, 1957 Запекина, 1961 Zapekina
Heptagenia arsenjevi Tshern.				Запекина, 1961
Heptagenia yoshidae Takahashi			Чернова, 1952	
Acanthametropus nikolskii Tshern.				
Pseudocloeon tuberculatum Kazlauskas				
Pseudocloeon sibibricum Kazlauskas				
Chitonophora mucronata Bngtss.	Chernova Чернова, 1952	Chernova Чернова, 1952		Грезе, 1957
Ephemerella triacantha Tshern.			Чернова, 1949	Greze Грезе, 1957
Ephemerella latipes Tshern.				
Ephemerella thymalli Tshern.				Zapekina Запекина, 1961 Грезе, 1957, Greze
Ephemerella ignita Poda (=sibirica Tshern).	Bianki Бианки, 1905	Chernova Чернова, 1941		Запекина, 1961 Zapekina
Ephemerella lenoki Tshern.				Грезе, 1957, Greze Запекина, 1961
Ephemerella rufa Iman.				
Ephemerella lepnevae Tshern.			Chernova Чернова, 1949	Zapekina Запекина, 1961
Ручейники Caddis flies				
Rhyacophila impar Mart.			Martynov Мартынов, 1934	Lepneva Лепнева, 1948, Запекина, Zapekina 1961
Rhyacophila retracta Mart.			Lepneva Лепнева, 1949б,	Мартынов, Martynov 1914б Минусинский кр. Minusinsk region.

6	7	8	9	
	Navas, 1912	Zapevina Запекина, 1959 (р. Хор) (Khor riv.) Леванидова, 1964 (р. Иман) Levanidova (Iman riv.)		
		Wroblewski, 1963		
Wroblewski, 1963		Wroblewski, 1963	Казахская ССР, Китай, Япония (Wroblewski, 1963)	Kazakh SSR, China, Japan.
Chernova Чернова, 1952	Chernova Чернова, 1952	Chernova Чернова, 1952	р. Вилюй (Вершинин, 1962); оз. Зайсан, Япония, Корея, Китай (Чернова, 1952)	Vilyuy River (Vershinin, 1962); Zaysan Lake, Japan, Korea, China (Chernova, 1952)
Sukatskene Сукацкене, 1962	Levanidova Леванидова, 1964а	Levanidov Леванидов, 1959 (р. Хор) (Khor r.) Леванидова, 1964б (р. Иман) Levanidova (Iman riv.)	Ю. Сахалин, Япония, (Чернова, 1952)	S. Sakhalin, Japan, (Chernova, 1952)
Сукацкене, 1962	Леванидова, 1964а	Леванидова, 1964б	Камчатка (материалы И. М. Леванидовой)	Kamchatka (I.M. Levanidova's data).
Сукацкене, 1962	Чернова, 1952	Baykova Байкова, 1954 (Khor r.) (р. Хор)	Камчатка (материалы И. М. Леванидовой)	
	Chernova	Леванидова, 1964б (Иман) Levanidova (Iman)		
Сукацкене, 1962	Чернова, 1952	Леванидов, 1951в Levanidov	Ю. Сахалин, Маньчжурия (Чернова, 1952)	S. Sakhalin, Manchuria (Chernova, 1952)
Сукацкене, 1962	Чернова, 1952	Леванидова, 1964б	Япония (Чернова, 1952)	Japan (Chernova, 1952)
Sukatskene Сукацкене, 1962	Chernova Чернова, 1948	Levanidova Леванидова, 1964б		
Kazlauskas Казлаускас, 1963	Леванидова, 1964а Levanidova	Леванидова, 1964б	Сахалин (Казлаускас, 1963)	Sakhalin (Kazlauskas, 1963).
Kazlauskas Казлаускас, 1963	Леванидова, 1964а	Леванидова, 1964б		
Сукацкене, 1962	Чернова, 1952	Chernova Чернова, 1952	Камчатка (материалы И. М. Леванидовой)	Kamchatka (I.M. Levanidova's data)
Sukatskene Сукацкене, 1962	Chernova Чернова, 1952	Baykova (Khor r.) Байкова, 1954 (р. Хор). Леванидова, 1964б (р. Иман) Levanidova (Iman riv.)	Япония (Чернова, 1952), Камчатка (материалы И. М. Леванидовой)	Japan (Chernova, 1952) Kamchatka (Levanidova's data)
	Levanidova Леванидова, 1968	Леванидова, 1968	Ю. Сахалин, Корея (Чернова, 1952)	S. Sakhalin, Korea (Chernova, 1952)
Сукайкене, 1962	Чернова, 1952	Леванидова, 1964б		
Сукацкене, 1962	Chernova Чернова, 1952	Levanidova & Levanidov Леванидова и Леванидов, 1965	Ю. Сахалин (Чернова, 1952)	S. Sakhalin (Chernova, 1952)
Sukatskene Сукацкене, 1962	Чернова, 1952	Чернова, 1952 Chernov		
Сукацкене, 1962			Сахалин, Япония, Корея (Чернова, 1952)	Sakhalin, Japan, Korea (Chernova, 1952)
Сукацкене, 1962	Леванидова, 1964а	Levanidova Леванидова, 1964б		
	Levanidova Леванидова, 1964а	Martynov Мартынов, 1934, Леванидов, 1959 (р. Хор) Levanidov (Khor riv.)		
	Леванидова, 1964а	Мартынов, 1934 Martynov		

1	2	3	4	5
Rhyacophila lata Mart.				Леванидова, 1962 [Levanidova]
Mystrophora altaica Mart.			Лепнева, 1949а, Мартынов, 1934 [Lepneva; Martynov]	Лепнева, 1948 [Lepneva]
Mystrophora intermedia Klap.	Лепнева, 1964 (северная и средняя) [Lepneva (northern & central)]	Лепнева, 1964 [Lepneva]		Сборы Запекиной (определены Леванидовой) [Zapekina's collections (determined by Levanidova)]
Mystrophora ussurica Mart.				Запекина, 1961 [Zapekina]
Mystrophora angarica Levanidova				
Diploglossa nylanderi McL.	Мартынов, 1934 [Martynov]	Мартынов, 1934	Лепнева, 1949а, Мартынов, 1934 [Lepneva]	Мартынов, 1934 [Martynov] Лепнева, 1948 [Lepneva]
Agapetus sibiricus Mart.			Мартынов, 1934 [Martynov]	Мартынов, 1934 [Martynov]
Agapetus jakutorum Mart.				Запекина, 1961 [Zapekina]
Padunia forcipata Mart.				
Padunia bikinensis Mart.				
Padunia adelungi Mart.			Мартынов, 1934 [Martynov]	Мартынов, 1934 [Martynov]
Padunia lepnevae Mart.			Мартынов, 1934	
Stenopsyche griseipennis McL.			Мартынов, 1934,	Лепнева, 1948 [Lepneva]
Psychomyiella composita Mart.			Мартынов, 1934	Мартынов, 1934 (Н. Тунгуска) [Martynov (Lower Tunguska R.)]
Psychomyiella minima Mart.			Мартынов, 1934	Мартынов, 1934 (Н. Тунгуска)
Paduniella uralensis Mart.			[Martynov] Мартынов, 1934	
Hydropsyche kozhantshikovi Mart.				Мартынов, 1934, [Martynov] Запекина, 1961 [Zapekina]
Cheumatopsyche czekanowskii Mart.				Мартынов, 1934 [Martynov] Лепнева, 1948
Macronoma radiatum McL.				Лепнева, 1947 [Lepneva]
Aethaloptera rossica Mart.				Мартынов, 1934 [Martynov]
Apatania zonella Zett.	Мартынов, 1924 [Martynov]	Мартынов, 1924	Лепнева, 1949 [Lepneva]	
Neophylax ussuriensis Mart.			Лепнева, 1949	Лепнева, 1918 [Lepneva]
Oligoplectrodes potanini Mart.			Мартынов, 1924 [Martynov]	

6	7	8	9
	Levanidova Леванидова, 1962	Levanidova Леванидова, 1962	Ю. Сахалин (сборы Е. И. Жуйковой, определен И. М. Леванидовой) S. Sakhalin (collected by E.I. Zhuykova determined by Levanidova)
Golyshkina Голышкина, 1962	Леванидова, 1964а	Lepneva Лепнева, 1949	
Levanidova Леванидова, 1964б	Леванидова, 1964б	Levanidova Леванидова, 1964б	Камчатка (Мартынов, 1934) Kamchatka (Martynov)
Golyshkina Голышкина, 1962, Леванидова, 1964б	Леванидова, 1964б а	Martynov Мартынов, 1934	
Levanidova Леванидова, 1964б	Леванидова, 1964б	Леванидова, 1964б Levanidova	
Голышкина, 1962 Golyshkina	Леванидова, 1964б	Леванидова, 1964б	
	Леванидова, 1964б	Леванидова, 1964б	
	Леванидова, 1964б	Леванидова, 1964б	Якутия (Мартынов, 1934) Yakutia (Martynov)
	Леванидова, 1964б а	Леванидова, 1964б	Якутия (Мартынов, 1934)
Леванидова, 1964а	Levanidova	Martynov Мартынов, 1934	
Леванидова, 1964а Levanidova	Леванидова, 1964а	Леванидова, 1964б	
	Леванидова, 1964а		
Martynov Мартынов, 1934 Голышкина, 1962 Golyshkina	Мартынов, 1934 Martynov	Мартынов, 1934	Сахалин, Япония, Корея, Китай, Индия, Формоза (Мартынов, 1934) Sakhalin, Japan, Korea, China, India, Formosa (Martynov, 1934)
Bas. of Ingoda riv. Басс. р. Ингода, Леванидова Levanidova (in litt.)	Леванидова, 1964а Levanidova	Мартынов, 1934	
Н. Ангара Lower Angara Леванидова (in litt.) Levanidova	Леванидова, 1964а	Мартынов, 1934	Якутия (Мартынов, 1934) Yakutia (Martynov)
Леванидова, 1964а	Леванидова, 1964а	Мартынов, 1934	Ю. Урал (Мартынов, 1934) S. Urals (Martynov)
Голышкина, 1962 Golyshkina	Леванидова (in litt.)	Мартынов, 1934 Martynov	р. Вилюй (Вершинин, 1962) Vilyuy river (Vershinin)
Голышкина, 1962	Мартынов, 1934 Martynov	Мартынов, 1934 Lepneva	Верхняя Обь (Мартынов, 1934) Upper Ob' (Martynov)
Голышкина, 1962	Мартынов, 1934 Лепнева, 1947 Lepneva	Лепнева, 1947	Обь, Якутия, Маньчжурия (Мартынов, 1934) Ob', Yakutia, Manchuria (Martynov)
	Мартынов, 1934 Martynov	Мартынов, 1934 Martynov	Обь, Маньчжурия, Китай (Мартынов, 1934) Ob, Manchuria, China (Martynov)
	Леванидова, 1960 Levanidova	Мартынов, 1935	Сев. Урал, Командорские о-ва, Сибирь (Мартынов, 1935), Камчатка, определение Леванидовой N. Urals, Comandores, Siberia (Martynov) Kamchatka determined by Levanidova
Levanidova Леванидова, 1964б	Леванидова, 1964а	Мартынов, 1914 Леванидова, 1964б Levanidova	Ю. Сахалин (сборы Е. И. Жуйковой) S. Sakhalin (collected by E.I. Zhuykova)
Лепнева, 1949 Lepneva	Леванидова, 1964а	Лепнева, 1948 Lepneva	Северо-западная Сибирь, Камчатка, Монголия (Мартынов, 1924) N.W. Siberia, Kamchatka, Mongolia (Martynov, 1924)

Characteristic Features of the Geographical Distribution of Bottom Invertebrates in the Amur River Basin.

A considerable number of species of bottom invertebrates is found in all the large tributaries of the Amur River, as well as in many medium-sized and small tributaries of the same, in the rivers on the western coast of the Sea of Japan and of the Peter the Great Gulf. In table 24, this commonness of hydrofauna can be traced from the southeastern border of the country to the tributaries of the Middle Amur. Faunistic data on the basin of the upper current are almost absent, but many of the species shown in the table are found in the upper reaches of the Amur River (Borutsky, Klyuchareva, Nikolsky, 1952; Chernova, 1952).

The number of species and forms of invertebrates widely occurring in the Amur basin is considerably greater than shown in table 24, which includes only the major species or species numerous in the water bodies among the most stenobiontic orders (mayflies, stoneflies, caddis flies) and among the latter, only representatives of the most stenobiontic families or genera.

Among groups, that are most cosmopolitan in their character (chironomids, oligochaetae, leeches) the similarity of the species-composition of the fauna in individual rivers within the basin is still greater.

The irregular completion of columns in the table is partly explained by unequal degree of the knowledge of fauna. Thus, to the poorly studied ones belong the rivers in the southern Pacific Coast province (the first two columns), the Koor River, the Anyun' basin is less studied than the Khor and Iman Rivers. The data on the benthos in the river bed of the Amur and the Ussuri Rivers are fragmental and partly based on the collections from the water mass. Consequently, in the course of further research, a still greater similarity in fauna will probably manifest itself. It is natural, that the first prerequisite for such a commonness must be the extent of the habitat areas of many species constituting the Amur fauna, as already discussed.

In all the taxonomical groups we observe a certain impoverishment in the species composition from south to north, and from east to west, in connection with the disappearance of those species of the Sino-Indian complex, whose areas cover only the southeastern part of the Amur basin, or only the rivers on the coast of the Sea of Japan. Thus, the larvae of the caddis flies Psilotreta kisoensis Iwata have been found only in water bodies in the environments of Vladivostok; the caddis fly Apsilochorema sutschanum Mart. has not been found north of the water-shed between the rivers Bikin and Khor; mayflies Chankgenesia natans Buld. lives only in the Khanka Lake and in the tributaries of the Lower Amur; the stoneflies of the genus Kamimuria, the mollusks Polypylis hemisphaerula (Bens.), Camptoceras rezvoji (Lindh.) and certain other caddis flies were not found north of the Iman basin. A part of these species, as we often see at a boundary of habitats, occur in the Amur basin ubiquitously, but in individual numbers.

Table 24. Occurrence of certain major species of the bottom invertebrates in the Amur basin.

Species	Rivers of the Peter the Great Gulf and of the western coast of the Sea of Japan			Basin of the Ussuri River						Rivers of the Amur Liman and of Schast'ye Gulf		Amgun'	Basin of the Lower Amur				Basin of Middle Amur	River bed of Amur
	Sedanka, Lyanchikhe, Chernaya	Mongugay (Gakkelevsky spring)	Avvakumovka, Sudzukhe, Vangou and others	Iman	Khor	Kiya, Birushka	Bychikha, Zakharovka	Shivki River, springs between Khor and Bikin rivers	River bed of Ussuri	My	Iski		Khivanda, Beshenaya	Elbanka, Great Nanaysky Spring (Bolon')	Nemptu	Koor	Bira, Bidzhan	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ephemera amurensis			+	+	+	+			+	+	+	+		+	+	+	+	+
Heptagenia arsenjevi				+	+	+		+	+						+	+	+	+
Heptagenia soldatovi				+	+	+			+						+	+	+	+
Heptagenia yoshidae			+	+	+	+		+	+				+		+	+		+
Heptagenia kibunensis				+	+				+		+	+						
Ecdyonurus tobiironis		+		+	+			+									+	
Rhithrogena unicolor	+		+	+	+					+	+	+	+			+	+	+
Rhithrogena sp. № 1				+	+				+	+	+						+	
Cinygmula grandifolia				+	+					+	+	+			+	+		
Cinygmula altaica				+	+		+				+	+			+			
Cinygmula hirasana	+	+																
Epeorus aesculus	+		+	+			+	+			+				+			
Epeorus latifolium	+	+	+	+	+	+	+	+	+	+	+		+		+	+		
Iron maculatus		+		+			+	+		+	+		+					
Iron sp. № 1					+				+	+	+	+						
Siphlonurus zetterstedti			+	+	+	+			+	+		+	+		+		+	+
Isonychia japonica	+			+	+	+			+			+	+				+	+
Ameletus montanus				+	+						+		+	+	+			+
Ameletus sp. № 1		+					+			+		+						
Parameletus minor				+	+				+			+						
Baetis thermicus				+	+	+			+	+	+		+		+		+	+
Paraleptophlebia chocolata					+					+	+	+		+	+			
Paraleptophlebia lunata	+			+	+	+				+	+	+		+	+	+	+	+
Chitonophora mucronata				+	+				+	+	+	+	+	+	+		+	
Chitonophora sp. № 1			+	+	+					+	+	+			+	+	+	
Ephemerella basalis	+		+	+	+					+	+	+	+	+	+	+	+	

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ephemerella triacantha			+	+	+				+	+	+	+		+	+	+	+	
Ephemerella latipes	+			+	+			+			+			+	+			
Ephemerella ignita	+		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+
Ephemerella sp. «naz»	+			+	+	+				+	+		+	+		+	+	
Ephemerella thymalli				+	+					+	+	+						
Ephemerella lepnevae	+		+	+						+	+		+		+	+		
Ephemerella taeniata			+	+	+	+	+			+	+	+	+	+	+	+	+	
Pteronarcys reticulata	+		+	+	+							+	+		+	+	+	
Rhyacophila impar			+	+	+			+		+		+	+			+	+	
Rhyacophila narvae	+		+		+							+	+		+		+	
Rhyacophila retracta				+			+				+	+			+			
Rhyacophila lata	+	+	+	+	+			+			+	+			+	+	+	
Diploglossa nylanderi		+		+	+							+				+	+	
Mystrophora intermedia	+							+		+			+			+	+	
Mystrophora ussurica	+			+			+	+		+	+		+					
Mystrophora angarica	+		+	+	+		+	+					+					
Agapetus sibiricus	+			+	+		+			+		+	+					
Agapetus jakutorum				+	+					+	+	+					+	
Stenopsyche griseipennis	+		+	+	+	+				+	+	+	+		+	+	+	
Arctopsyche palpata	+		+	+	+			+		+	+	+	+		+	+	+	
Arctopsyche amurensis				+	+					+	+	+	+		+	+	+	
Hydropsyche nevae			+	+	+	+		+				+			+	+	+	
Macronema radiatum				+	+	+		+	+			+				+		+
Goera sajanensis	+		+	+	+		+	+		+	+	+	+	+	+	+	+	
Oligoplectrodes potanini			+	+	+		+	+		+	+	+	+	+	+	+	+	
Apatania crymophila	+				+					+	+	+	+		+		+	
Dicosmoecus palatus		+	+		+			+		+	+	+	+				+	
Neophylax ussuriensis	+	+	+	+	+		+	+		+	+	+	+		+	+	+	
Hydatophylax nigrovittatus	+		+	+	+		+	+		+	+	+	+	+	+	+	+	
Arctoecia servata	+			+	+	+		+		+	+	+	+			+	+	

Being unable to discuss the zoogeographical problems connected with the boundaries of the habitat areas of individual species, let us merely note the following. The occurrence boundaries of the representatives of thermophilic invertebrates of the Sino-Indian complex (for example, many caddis-flies, certain mollusks, leeches and others) may be associated with the insufficiently high summer temperatures of the water. What concerns the boundaries of the occurrence of the denizens in foothill rivers, which are cool in the summer, for example of caddis flies A. sutschanum, many Ephemerella, representatives of Heptageniidae, such boundaries may be linked with the temperature merely in the general climatic sense (seasonal dynamics of the temperatures, heat total etc.).

Among the tributaries of the Amur River studied by us, the flatland tributaries of Kiy, Naytsukhe and others, which are geographically restricted to the Ussuri Territory, are reservoirs of the thermophilic Indochina fauna /sic! TR; probably: Sino-Indian fauna/. It is natural that the benthofauna of these rivers contains the lowest (although still considerable) amount of species in common with the foothill rivers. These common species belong to relatively eurythermal invertebrates.

Thus, we come to the conclusion that the geographical factor does not play any considerable part in the faunitic peculiarities of the bottom fauna of the foothill rivers. However, the determination of the faunistic composition of the benthofauna in individual basins and rivers is only the first step towards understanding of the pattern in the distribution of the invertebrates.

The commonness of the fauna of the rivers in the Amur basin, shown above, is governed in addition to the geographical factor also by the fact that the majority of these rivers belong to one large hydrological category, namely: they are foothill and semi-mountaneous rivers, this also determines the common type of the hydrochemical and thermal conditions and of the grounds. However, as the below-stated data indicate the conditions of the environment in these rivers are not identical. Individual sections of the rivers, as well as various biotopes within the confines of a single river section differ still more from one another. These differences in the conditions of the environment govern not merely the difference in the qualitative composition of the benthos in rivers and their sections, but also the quantitative relation between its individual components. The wider the ecological spectrum of the species is, the greater the number of various categories of the water bodies and of various stations which this spectrum inhabits.

Distribution of Bottom Invertebrates within the River Systems of the Amur Basin.

Environmental factors affecting the life of organisms in the river are: the rate of the current, grounds, transparency of water, its chemism, development of vegetation and other factors. However, these factors do not have equal effect upon invertebrates; furthermore, some of them are to a considerable degree determined by other factors.

V.I. Zhadin (1940, 1950) believes that the current is the main factor in the distribution of the fauna in a river; he points out that the role of the current consists not only in the hydraulic pressure, but also in the transportation of alluvia, food, oxygen, and for removal of waste products of life-activity. The current sorts out the grounds and thus determines the distribution of entire biocoenoses along the river bed. Thus, the most important factor in the formation of the river biotopes and bottom communities is the character of the ground distribution, which is more constant in time, than the rate of current. Therefore, in the classification of the river biocoenoses of the benthos developed by V.I. Zhadin (1940, 1950, 1960) the ground character*) is used as the distinguishing feature and not the differences in the rate of current.

/p.82

V.I. Zhadin segregated five basic biocoenoses: lithorheophile, phytorheophile, argillorheophile, psammorheophile and pelorheophile, and a few intermediate types. This classification principle was accepted in a number of hydrobiological monographs (Lipin, 1950; Greze, 1957; Yaroshenko, 1957; Sokolova, 1963).

In his monograph on the Yenisey River (1957) V.N. Greze distinguishes the following three sharply differing biocoenoses; the lithorheophile, the psammorheophile and the pelophile; with intermediate forms: the litho-psammorheophile, the psammo-pelophile (in the lower reaches of the rivers) and the phytophile (in the tributary system). The author, however, indicates that because of the presence in the rivers of numerous transitions between various grounds and because of the extensive adaptability of many organisms to these transitional types, the classification of the bottom invertebrates to one or another ecological category is often difficult. This assumption is justified to a still greater degree in respect to the tributaries of the Amur River. On the one hand, the environmental conditions in the tributaries of the Amur

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*) More correctly, the character of the substratum, insofar as together with the population of various grounds we also discuss the population of lichen growth, of higher vegetation, of tree stumps etc.

River are more variegated and the spatial change in them takes place considerably more often, than in the Yenisey River. On the other hand, the adaptability of the invertebrates, as we shall see further below, is higher in the tributaries of the Amur River. Accepting in the present work V.I. Zhadin's classification we have introduced several additional gradations of bottom substrata.

The preferance by the bottom invertebrates of one or another ground is associated with their adaptations to the life in respect to the current, feeding character or the methods of hiding from enemies. Experiments of Eriksen (1963a, 1963b) show how important is the quality of the ground to the life of invertebrates and how fine the selectivity may be in respect to the bottom factor. The optimal substratum for the digging larvae of mayflies Ephemera simulans Walker and Hexagenia limbata (Serville) was the ground with particle size of two to four millimetres, the digging activity being easier at this substratum. An increase or a decrease in the diameter of the ground particles produced a noticeable increase in the respiration coefficient.

Tables 25 and 26 reflect the diversity of the life conditions of bottom invertebrates and the ecological spectra of species that are the most significant in the benthos in respect to the two most important factors of the environment: the substratum and the current.

The use of the term "biocoenosis" (in V.I. Zhadin's understanding, 1950; page 53) for large ecological groupings, such as the lithorheophiles, or psammorheophiles, we believe to be more justifiable. But in a number of instances this term is to a considerable degree conditional, because of our poor knowledge of the ecology of the majority of aquatic invertebrates, of their biocoenotic relations, and of the environmental conditions in the microbiotopes of the water bodies. Thus, the term "rheophile" is usually used for invertebrates living at the bottom of the riverbeds characterized by considerable rate of current. However, as Ambühl (1959, 1962) pointed out, the rate of current at points of immediate distribution of invertebrates is often small, sometimes it equals zero.

Taking the gaps in our knowledge into consideration, evidently, we must consider here not the biocoenosis, but the complex of organisms*) populating the biotope, although from the terminological point of view this is not completely accurate**).

The predominant ground in the foothill and semi-mountaneous tributaries of the Amur River is a stony one consisting of large and medium pebbles and stones. This typical ground for the salmon rivers covers 80 to 90% of the entire area of the river bottom. To the stony ground with current a vast complex of invertebrates, lithorheophiles, is characteristic, for the majority of which the presence of very clearly pronounced adaptations to the environmental conditions is characteristic (such adaptations are: flattened body shape, suckers, /p.83 sclerotized spiny body covers etc.). Besides this category among the stones and pebbles lives a considerable number of facultative lithorheophiles, who do not have such sharp adaptations to the current. The latter do not stand up to the current, but hide from it in crevices, under stones, in vegetations.

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*) This term is accepted in a number of cases also by V.N. Greze (1957).

**) As we know, it is accepted to call the place where a biocoenosis lives "biotope".

Owing to high biomass of the stony grounds, particularly at the sandbanks of the middle and upper portion of the lower reaches of a river, as well as the predominance of such grounds over the other, the lithorheophiles play the leading role in the fauna of the tributaries of the Amur River.

The stones and pebbles in the river bed are almost never completely naked. Even at a strong current their surface is covered with an incrustation of algae or with a thin silt deposition, a phenomenon to which the invertebrates contribute much by attaching their huts or catching nets to the stones. Furthermore, other variations of stoney grounds are extensively developed in the tributaries of the Amur River.

At shallow sections of the river bed, particularly at the sandbanks and in small foothill rivers, the stones in the current grow over with water moss and with algae (Ulothrix, Draparnaldia, diatoms) and form a special biotope which offers the animals completely different possibilities for the existence in the river stream. Here they are able to stay by means of claws on their legs (mayflies, stoneflies); small animals like the Helmintinae beetles, Orthocladiinae chironomids, Tanytarsini and others constituting the algobryorheophile complex are particularly characteristic of this biotope. The biomass of overgrowth benthos in the tributaries of the Amur River is, as a rule, considerable.

In the lower reaches and in the reaches of the foothill rivers, in the sections of the slow current the ground is formed of medium-coarse or fine pebbles with a considerable sand admixture, the latter sometimes even forms the main component of its surface layer. This kind of biotope is populated, as also pointed out for the Yenisey River by V.N. Greze, by a complex of a transitory type, the psammolithorheophile complex. In addition to the relatively eurytopic invertebrates occurring on stones, and in the sand, a kind of mosaic (according to V.I. Zhadin's terminology) biocoenosis is formed here, in which live stenotope animals, like caddis flies of the Stenopsyche genus, while in the sand and gravel between and under the pebbles live the mayflies of the Ephemera genus.

Purely sandy grounds occur very seldom in the foothill rivers; usually these are temporary deposits formed as a result of eddies, which are rapidly washed away when the level and current flows are changed. The population in these sections has a relatively small number of typical psammorheophiles (such as mayflies of the Ametropodidae family and certain oligochaetae). The biomass of the benthos at the unsilted sands is small.

In open gulfs of the rivers and in very slow flatland rivers deposits of pure and almost unsilted sand are formed. This biotope occupies a small area, its macrobenthos is poor in species, and its biomass is small.

The biotope of the silted sand occurs in the river in sections, where the rate of current is getting so slow, that not only the sand, but also the silt precipitates from the suspension. This takes place in the sandy ripal in the lower and occasionally in the middle reaches of the rivers, as well as in their closed gulfs and in the estuarian sections of the limnocrens. The accumulation of detritus in a river is usually formed on the sand or in the silty ground, behind the sand spits or shallows, along the banks of the rheocrens and of the spring channels, where the current weakens and reverse flows and eddies are formed.

The last two biotopes are populated by ecologically heterogeneous organisms, whose species composition and quantitative relations between individual components of benthos change in relation to the content of detritus and silt, the chemical composition of the latter, and in relation to the rate of the current. The same factors also determine the biomass of benthos, but usually it is rather high. The areas occupied by these biotopes are very small. /p.84

In the gulfs of spawning channels and at the banks of limnocrens, under conditions of weak flow, coarse detritus accumulates on the silty bottom. Here, lives besides the pelophiles, a number of species ecologically connected with detritus, particularly the caddis-flies (Artoecia servata, Ganonema extensum and others), who build their hut out of the detritus.

The very extensively occurring transitional type, which occupies considerable areas in the rivers and particularly in the tributary system, the biotope of silted stones in the current. The silt is formed in this case of decomposed aquatic vegetation and contains an admixture of allochthonous detritus (sometimes a little of sand).

We find in this biotope representatives of various ecological complexes, the specific ratios of which change depending on the silting, the current rate and the temperature conditions of the water body. In the river bed and in the major channels the silt layer does usually not exceed a few centimetres; the lithorheophiles predominate here, a considerable number of them withstands the silting in the rivers of the Amur basin, if the current rate is maintained. In the limnocrens, in the coastal area and in the reaches of the streams running from them, and in the ripals of the reaches of the spring channels under conditions of sharp drop in the rate of current, and in places of an insignificant depth, a considerable layer of silt with detritus admixture is deposited upon the pebbles. The population of this biotope is from the ecological point of view, still more heterogeneous than on the silt-covered stones in the river bed. We observe here all the gradations of the transition from a pelolithophile complex to the pelo(rheo)phile and pelophile ones*).

The composition and structure of the silt in various sections of these water bodies is highly variegated, a phenomenon reflecting upon the composition and the biomass of the benthos. Furthermore, for a considerable number of organisms the selective factor here (under conditions of uniform ground) is the current. All this does not allow any segregation of a complex of organisms specific to the given biotope (or rather, to the series of related biotopes).

Besides the limnocrens the pelophile complex of the bottom invertebrates is characteristic of the river bays, but its specific composition differs considerably from the limnocrens because of the high summer temperatures of water. A number of eurythermal species are common to the fauna of silts of both types of water bodies (leeches, part of

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*) The category of the pelorheophiles is segregated by E.S. Neizvestnova-Zhadina (1937). However, we agree with V.N. Greze (1957) that all these are organisms for which the current rate is not compulsory, therefore, we designate this group of organisms as pelo(rheo)philes.

oligochatae, aquatic isopods and others), but the more stenothermal invertebrates cause material differences in the species composition of the population of these sections of the river system.

The biotopes of stones outside of the current in the system of foothill rivers occur only in limnocrens where the ground waters emerge. These stones are usually covered with a thin layer of silt deposit or an incrustation of green algae. Their fauna is very poor and poorly studied in the ecological respect. The areas covered with this biotope are insignificant.

Very small areas in the river beds, but rather considerable ones in the limnocrens, streams running from the limnocrens, and in spring channels are occupied by higher aquatic vegetation (pondweeds, coontail-grass, eel-grass), as well as by filiform algae (Spirogyra, Rhizoclonium). For the limnocrens and for the streams emerging from the same the water moss is particularly characteristic; the latter reaches occasionally a height of 1 to 1.5 metres. This vegetation develops both on the silty sand, as well as on the stony-sandy silty ground. Phytorheophiles and /p.85 phytophiles are characteristic of the thickets of the higher vegetations, namely those consisting of mayflies, chironomids and caddis-flies, but the highest biomass of benthos is formed on the grounds located below the thickets; it consists basically of phytophiles and pelorheophiles.

The accumulations of green filamentous algae, often overgrown with diatoms, are usually characterized by a high biomass of benthos basically formed of litho(rheo)philes (the Apatania zonella caddis fly), pelophiles (aquatic isopod), eurytopic mollusks (Pisidium casernatum and Gyraulus acronious sibiricus) and of other unspecified species.

Tree remains (submerged trees, parts of them, root system of bushes and trees undercut by the river) are one of the varieties of the hard ground of the river; along the river flow they are populated by a complex of invertebrates close to the lithorheophile. However, in the foothill rivers the population of the tree stumps differs from the population of the stony grounds by a smaller diversity of species composition and by the presence of dendrophile forms that are biologically connected to decomposing wood.*) Thus, for example, certain larvae of chironomids are feeding upon the protozoic fauna and bacteria developing on the decaying wood remains. In the flatland rivers, where the hard substratum occupies relatively small part of the bottom, all the lithorheophiles occurring in this section settle upon tree stumps.

In the tributaries of the Amur River argillaceous grounds are almost non-existent, since the river bed here is mainly stony. The argillaceous bottom of individual sections of the ripal of the main bank is almost always covered with silt, sand or gravel. The population of these sections is ecologically unspecified. In the lower flatland section of the river the argillophiles (particularly the digging larvae of the Ephemera mayflies and others) occur in the argillaceous bank-scarps.

A peculiar impermanent argillo-vegetative substratum is formed in the basin of the Amur River during the summer owing to the prolonged

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*) O.S. Zvereva (1947, 1950) records the latter peculiarity for the northern rivers.

floodings covering the floodland. Such sections are particularly extensive in the lower reaches of the rivers. The water overflowing its banks inundates the coastal vegetation of various type: grassy meadow vegetation or vegetation bordering water with marshy sedge-covered hummocks.

Soils along the river banks are mostly argillaceous or argillaceously sandy. When flooded these soils are rapidly covered with silt deposit, which is particularly heavy at the constantly inundated sections of the bank.

The flooded sections are intensely populated with invertebrates brought here with water; this process proceeds particularly intensively because of the presence of nocturnal migrations by aquatic insects (Levanidova and Levanidov, 1962, 1965), as well as by means of ovipositions by flying imagos. We have not included this peculiar biotope in the table, since it is a temporary biotope existing outside of the water basin's permanent boundaries, of this reason we will briefly enumerate here its composition.

The benthos of flooded sections of the bank consists mainly of certain nektobenthic forms: mayflies and amphipods. It is distinguished by its paucity in species composition, but by occasionally high biomass indices. Thus, in the Sigov Gulf of the Amgun' River the biomass of the mayflies alone was at the end of June, from 7.8 to 18 grams per square metre. The mayflies were exclusively represented by the Siphlonuridae family (mainly: Siphlonurus zetterstedti, and by individual specimens of Parameletus minor and Ameletus montanus). Upon the vegetation proper develop phytophile larvae of chirotomids. S. zetterstedti mayflies constantly populate similar biotopes also in the Khor River and in other rivers. In addition to what has already been enumerated, in the ground /p.86 and in the silt deposit of the flooded participants we found pupae of chironomids, of Helophorus sp. beetles, of the Helophorus sp. beetles, of the Limnaea auricularia plicata and of others.

The population of the inundated terrestrial vegetation represents an impoverished complex of the biotope of the higher subaquatic vegetation of the supplemental system.

The fauna of the tributaries, as well as of the Amur River itself, is extremely variegated: of the chironomids alone (see table 25) we find about 200 species and species-groups. A list of bottom invertebrates belonging to other taxonomical groups (see table 26) includes mainly only the major and ordinary forms of benthos (327 species) and mainly from the river beds, from the river channels and from the limnocrens*). A complete list of the bottom invertebrates of the Amur tributaries known today is considerably greater. The tables are compiled with consideration of two environmental factors: the ground (or of the substratum) and the current.

Data shown in tables 25 and 26 reveal that the larvae of amphibiotic insects are the predominant group of invertebrates according to the species composition and also, as we will see below, according to the biomass particularly on the stony grounds of the river bed. In the mountain rivers and in the rivers that are full of rapids in the western

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*) In tables 25 and 26, the symbol + symbolizes the usual form; ++ indicates the often occurring form; +++ is the "mass", i.e. major form.

part of the Soviet Union larvae of three insect orders predominate, these are: caddis flies, mayflies and stoneflies (Zhadin, 1940), but in the foothill tributaries of the Amur River, because of the powerful development of the overgrowth by lichens and algae the chironomid larvae (mainly Orthocladiinae) are added to the former three orders.

The following must be said, when we evaluate the role of the thermal conditions in the distribution of invertebrates in various water bodies and according to various morphological elements of the river. The difference in the mean monthly summer water temperatures between the extreme variations of the thermal series of the rivers reaches 9 to 10°C (for example, the Kiya and the Khivanda Rivers). The temperature difference between the rivers of moderate thermal conditions (Khor and Iman Rivers in their middle and lower reaches) and the cold ones is considerably less, only 3 to 6°C. A difference of same order exists between the middle and the lower reaches of such rivers, as Khor, Iman and Bikin.

Comparing the species composition of benthos in these rivers and in their sections, we find that along considerable stretches of these rivers and in rivers differing in thermal conditions the species composition of the benthofauna changes relatively little, mainly in stenothermal species*). Thus, moving from the lower reaches to the sources, certain species become scarce and are replaced by other species, often by closely related ones (<u>Arctopsyche amurensis</u> by <u>A. palpata</u>;

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*) There are no eurybiontic and eurythermal species in the proper sense among the denizens of running waters, but a number of forms in the basin of the Amur River are relatively eurythermal.

Stenopsyche bergeri by S. griseipennis etc.).

The difference in the species composition of benthos in the moderately warm rivers (the middle and the lower reaches of the Khor and Iman Rivers) and in such a warm-water river flatland river as the Kiy River this is considerably more significant: in addition to the thermal conditions also other differences in the character of the rivers are reflected here. However, the presence in these rivers of a number of common species from theophiles permits us to consider the latter as relative eurytherms and even as eurybionts. Such are, for example, Heptagenia soldatovi, H. arsenjevi, H. kibunensis, Choroterpes trifurcatus, Ephemerella taeniata, E. ignita*), E. "naz" Imanishi, Siphlonurus sp., possibly Epeorus latifolium**), Macronema radiatum, Stenopsyche bergeri, Psychomyiella composita, P. minima. p.111

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*) This species described by O.A. Chernova (1952) from the basin of the Amur River according to a larva such as Ephemerella sibirica is considered by R.S. Kazlauskas (1963), who had imagos of analogous larvae from the basin of the Angara River, to be identical with E. ignita Poda (an extensively occurring European species).

**) In the tributaries of the Amur River occur two forms, both well-distinguishable morphologically, and, especially, ecologically, which earlier (Levanidova, 1964a, 1964b) were classified as separate species. However, later R.S. Kaslauskas and O.A. Chernova having studied an extensive series of larvae from the tributaries of the Amur River came to a conclusion that all these forms belong to a single species: Epeorus latifolium (personal information). This conclusion is based upon the presence of transitions between the morphological types of larvae from the cold-water and warm-water rivers. The population of larvae from the rapidly flowing cold-water tributaries of the Amur River are morphologically close to the Altayan specimens, according to which the description of the species E. latifolium was carried out (Chernova, 1949). The populations living in the warm-water flatland rivers of the Kiy River type on the contrary, differ, considerably from the Altayan ones.

The benthofauna in the thoroughly warmed bays and in the medial of the river beds have almost no species in common. Common species in the fauna of the bays and in the river ripal belong to the category of eurybionts. A considerable number of common species occurs in the bays of rivers and in the limnocrens. All these are typical eurytherms from various groups (leeches, oligochaetae, mites, mollusks and others).

We may conclude from the said that the fauna of bottom invertebrates of homogeneous stations (for example, stony ground in the medial of the middle reaches of the foothill rivers) contains a considerable nucleus of common species in the entire basin of the Amur River, while in the heterogeneous stations, even those located in the same section of some river, differ in the species composition to a considerably greater extent.

Therefore, further down in the text we are going to discuss the biomass of the benthos and the main species of the invertebrates as applicable to individual morphological elements of the river bed and of the floodland. Such elements are the following: the estuarian section and the lower reaches of a river, the foothill section, which usually occupies a considerable portion of the river, the semi-mountaneous section (most often the upper reaches of the river), side-branches of the river. Spring channels, bays, limnocrens and rheocrens.

Table 25.

Distribution of the chironomid larvae in the tributaries of the Amur River according to biotopes.

Species	Bodies of Running Water									Water bodies with slow run-off.				
	Stony grounds on rapid current	Stones overgrown with moss or algae	Stony-Sandy grounds	Silty stony grounds	Aquatic vegetation	Sandy grounds	Silty sand	Stumps, tree roots, logs etc.	Coarse plant detritus on slow current	Stony grounds	Silty grounds	Aquatic vegetation	Coarse plant detritus	Sandy grounds
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Подсем. *Chironominae*														
Corynocera ambigua Zett.		+		+			+					++	++	
Lauterbornia chlorophita Kieff.				+			++			++				
Lauterbornia sp.				++						+				
Micropsectra curvicornis Tshern.	+	++												
Micropsectra gr. praecox Mg.	+	+	+	+	+	+	+	+	+	+	+	+		
Micropsectra viridis — scutellata Goetgh.				++		+			+		+			+
Stempelina gr. bausei Kieff.				+			++							
Stempelina septentrionalis Tshern.				+		+	+							
Tanytarsus aequidens Tshern.	++													
Tanytarsus gr. exiguus John.	+				++							+		
Tanytarsus gr. gregarius Kieff.	+				+	+								
Tanytarsus gr. lobatifrons Kieff.					+			+			+			
Tanytarsus gr. mancus v. d. Wulp.	++	+	+											
Tanytarsus типа mancus № 3 Zvereva			+			++								
Tanytarsus типа mancus № 5 Zvereva		++		++										
Tanytarsus типа mancus № 7 Zvereva			++			+								
Tanytarsus monodentatus Konst.	++		++											
Tanytarsus nikolskyi Konst.	++		+											
Tanytarsus sexdentatus Tshern.	++													
Tanytarsus tetradentatus Konst.	++			+										
Tanytarsus gr. lauterborni Kieff.	+				+				+		+			
Tanytarsus sp.	+	++			+	+								
Zaurelia sp.			+	++		+								
Stictochironomus sp. (=Allochironomus)				+	+		+			+		+	+	
Cryptochironomus gr. anomalus Kieff.							+							+
Cryptochironomus gr. brevipalpis Konst.						++	+							

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Cryptochironomus borysthenicus Tshern.	+		++	+		++								
Cryptochironomus borutzkii Konst.						+	++							
Cryptochironomus gr. camptolabis Kieff.	+			++		++	++							
Cryptochironomus gr. conjungens Kieff.										+				+
Cryptochironomus defectus Kieff.				+			++							
Cryptochironomus demeijerei Krus.			++				+							
Cryptochironomus dnepricus Tshern.			++											
Cryptochironomus gr. fuscimanus Kieff.							+			++				
Cryptochironomus fridmanae Tshern.														++
Cryptochironomus latidentatus Tshern.						+	++							
Cryptochironomus macropodus Ljach.	+					++								
Cryptochironomus ussouriensis Goetgh. (=nigridens Tshern.)										++	+		+	++
Cryptochironomus gr. pararostratus Lenz.			+	++	+			+						
Cryptochironomus monstrosus Tshern.			++	+										
Cryptochironomus rolli Kiritshenko						++								
Cryptochironomus viridulus Fabr.				++										
Cryptochironomus gr. vulneratus Zett.			+		+	++	+			+				+
Cryptochironomus gr. zabolotzkyi Goetgh.			+		+	++								
Parachironomus vitiosus Goetgh. (=Chironomini gen. № 7 Lipina)						++	+							
Chironomini «gen. № 9» Lipina.			+	+		++	+							
Einfeldia gr. carbonaria Meig.								+		++		+		+
Endochironomus tendens F. Kieff.										+	++		+	
Endochironomus gr. dispar Meig.	+	++	+					+			++		+	
Endochironomus albipennis Mg.											++	+		+
Endochironomus stackelbergi Goetgh.										+	++			
Endochironomus sp. № 1.							+				+	++		
Glyptotendipes gr. gripekoveni Kieff.					+						++	+	+	
Glyptotendipes paripes Edw.				+++								+	++	+
Glyptotendipes sp.								+			++			
Phytochironomus sp.										++	+			++

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Lauterborniella gr. agrailoides Kieff.		+									++	+		
Lauterborniella brachylabis Edw.					+	+	++				+		+	++
Lauterborniella marmorata v. d. Wulp.		++		+							++			
Limnochironomus gr. nervosus Staeg.		+			++			+			++	+		
Limnochironomus albipes Kieff.			+	+	++						+			
Limnochironomus gr. tritomus Kieff.			+		++					+		+	+	
Microtendipes gr. chloris Meig.	+		++		+	+								
Microtendipes gr. tarsalis Wolk.			++	+	++	+								
Paratendipes gr. albimanus Meig.			++		+		++							
Paratendipes albitibia Kieff.		+	+	+	+	+	++		+		+			
Pentapedilum exectum Kieff.					+	+	+	++				+	++	
Polypedilum breviantennatum Tshern.	+		+	++		+	++			+				
Polypedilum (Chironominae. gen. № 3 Lipina)	+		+	++		+		+						
Polypedilum convictum Walk.	+	++			+	+					++			
Polypedilum gr. pedestre Meig.	+	++					+	++	+			+		
Polypedilum monodentatum Konst.							++							
Polypedilum tridentatum Konst.			+				++							
Polypedilum gr. nubeculosum Meig.	+	+	++			+	++							
Polypedilum gr. scalaenum Schr.	+		+	++		+								
Pseudochironomus gr. prasinatus Mall.											++			+
Stenochironomus sp.	+							++						
Stictochironomus («connectens № 2») Lipina			+			+	++							
Stictochironomus gr. histrio Fabr.	+		+		++	+			+					+
Stictochironomus psammophilus Tshern.					+		+		+	++			+	+
Stictochironomus sp.								+		+	++			
Sergentia? flavondentata Tshern.				+			+							
Sergentia gr. longiventris Kieff.		+			+	++								
Sergentia lv. ordinaria**						+				+			++	++
Sergentia? baicalensis Tshern.	+			++					+	+	++			++
Sergentia sp.											++			
Chironomus f. lv. bathophilus Kieff.				+				++						
Chironomus f. lv. plumosus L.						+	+		+	++	+			
Chironomus f. lv. plumosus reductus Lipina										++				+

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Chironomus f. lv. reductus Lipina			+				++			+				
Chironomus f. lv. thummi Kieff.				++			+							
Chironomus salinarius Kieff.				+						++				
Chironomini gen? macrophtalma Tshern.				+						+	+			
Lipiniella sp.							++			+				
Chironomini lv. minuta Kruglova				++										
Xenochironomus xenolabis Kieff.										++		+		
Subfamily **Подсем.** ***Orthocladiinae*** *														
Abiskomia virgo Edw.						++	++							
Brillia gr. modesta Mg.		+	+											
Brillia pallida Sparck.	+	++			+		+	+						
Brillia dendrophila Zvereva								++				+		
Cricotopus biformis Edw.	+	+			+									
Cricotopus brevipalpis Kieff.	+			+										
Cricotopus gr. silvestris Fabr.	+				++			+			+			
Cricotopus gr. algarum Kieff.	++	++			++	+								
Cricotopus? versidentatus Tshern.				+					++			+		
Cricotopus sp. № 1 **		+	++	+										
Cricotopus sp. № 2 **		+		++		+								
Diplocladius cultriger Kieff.		++		++					++				+	+
Eukiefferiella bicolor Zett.	+		++	+	+	+								
Eukiefferiella coerulescens Kieff.		++		+										
Eukiefferiella hospita Edw.	++													
Eukiefferiella discoloripes Tshern.	++	+		+										
Eukiefferiella longicalcar Kieff.	++													
Eukiefferiella alpestris Goetgh.			+											
Eukiefferiella longipes Tshern.		+												
Eukiefferiella gr. lobifera Tshern.		++	+											
Eukiefferiella quadridentata Tshern.	+	++	+											
Eukiefferiella cf. similis (Savrel)	+	+												
Eukiefferiella cf. tridentata Linevitsh	+	++												
Krenosmittia ginocera Edw.		+												
Limnophyes gr. pusillus Eaton			+		+	+								
Limnophyes gr. prolongatus Kieff.										+		++	+	
Limnophyes septentrionalis Tshern.	+	+												

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Metriocnemus gr. marcidus Walk.			++	+		+	++							
Metriocnemus gr. hygropetricus Kieff.							+	+						
Metriocnemus sp.	+	+												
Orthocladius gr. bathophilus Kieff.			+	+										
Orthocladius corosinensis Tshern.													++	
Orthocladius gr. dorieri Goetgh.	+	++		+										
Orthocladius nudipennis Kieff.		+				++								
Orthocladius oxyrhynchus Linevitsh	+	+												
Orthocladius gr. olivaceus Potth.		++	+	+										
Orthocladius gr. piger Goetgh.		++			+									
Orthocladius paratatricus Tschern.	+		++			+								
Orthocladius potamophilus Tshern.		+	+	+		++			+					
Orthocladius reofilus Linevitsh	++	+												
Orthocladius saxicola Kieff.	++	++	+		+	+	+							
Orthocladius gr. semivirens Edw.	+	+	+	+	++	+								
Orthocladius thienemanni Kieff.	+	++	+											
Orthocladius lv. abundans **		++		++					+					+
Orthocladius lv. carbonaria **		++												
Orthocladius lv. cyaneus **		++							+					
Psectrocladius gr. dilatatus v. d. Wulp.	++	+		+										
Psectrocladius gr. dendrophila Zvereva								+				++		
Psectrocladius gr. psilopterus Kieff.			+	+	+				+			+		
Psectrocladius septentrionalis Tshern.			+		+				++					
Pseudoorthocladius curtistylus Goetgh.												++	++	
Smittia ephemerae Kieff.	++	+	+	++									++	
Smittia microcera Konst.													++	
Smittia gr. stercoraria Degeer													++	
Smittia muscicola Kieff.													++	
Smittia septentrionalis Tshern.													++	
Smittia sedula Konst.													++	
Smittia tshernovskii Konst.													++	
Trichocladius inaequalis Kieff.				+		++	+							
Trichocladius gr. lucidus Staeg.	+	++		+										
Orthocladiinae gen? acutilabis Konst.								++				+	+	
Orthocladiinae gen? lv. karelica Tshern.			+		+	++								

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Orthocladiinae gen? lv. macrocera Tshern.		+				++								
Orthocladiinae gen lv. triquetra Tshern.					++		++							
Orthocladiinae gen? lv. zalutshicola Lipina	+								+	++			++	
Orthocladiinae gen? sp.	++		+											
Diamesa baicalensis Tshern.	+	++	+											
Diamesa campestris Edw.		++		+		++	+							
Diamesa coronata Tshern.	++	+												
Diamesa gaedi Mg.	++	+	+	+										
Diamesa cf. longicaptis Linevitsh	+	++	++	+										
Diamesa gr. prolongata Kieff.	++	++	+											
Diamesa quadridens Linevitsh	++	+												
Prodiamesa gr. bathyphila Kieff.	+			++		+	++							+
Odontomesa fulva Kieff. (=Prodiamesa flabellata Kieff).				+			+						+	
Prodiamesa olivacea Mg.	+			++					+	+		++	+	+
Prodiamesa rufovittata Goetgh.			+	+	+							++		
Prodiamesa (Monodiamesa) sp. ***		++		++	+					+		+	+	+
Protanypus morio Zett.			++	+								+	+	+
Syndiamesa hydropetrica Kieff.	++	+		+										
Syndiamesa gr. nivosa Goetgh.	++	+	+		++				++	+	++			+
Syndiamesa orientalis Tshern.	+	++	+						++	+				+
Syndiamesa jacutica Zvereva									+				++	
Syndiamesa sp.	++	+												
Thinemaniella flaviforceps Kieff.	+	++			++									
Thinemaniella sp.		+			+									
Corynoneura celeripes Winn.	++	++			+									
Corynoneura sp.	++				+				+					
Subfamily Подсем. *Pelopiinae*														
Ablabesmia curticalcar Kieff.												+	+	+
Ablabesmia gr. lentiginosa Fabr.	+					+	++	+				++	+	
Ablabesmia gr. tetrasticta Kieff.		+	+									+		
Ablabesmia gr. monilis L.					+			++			+		+	
Ablabesmia flavida Kieff.	+	++			+			+			+			

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ablabesmia fulva Kieff.							++					+		
Anatopynia sibirica Tshern.	++	+	+											
Apsectrotanypus trifascipennis Zett.			+	+		++			+					
Clinotanypus nervosus Mg.				++								++	+	
Pelopia punctipennis Mg.				+						++	+		+	
Pelopia sp.														
Procladius sp. № 1 **	+		++	+		+			+	++				
Procladius sp. № 2 **	+			+	+	++						+	+	

*) We follow the newest taxonomy for the Chironomidae family created by Brundin (1956) and Fittkau (1962) quoted according to A.I.Shilova (1966). Brundin and Fittkau, in particular, have excluded the subfamilies Diamesinae and Corynoneurinae and species constituting these subfamilies are now included in the Orthocladiinae subfamily. Species of the Diamesinae subfamily are separated into Diamesini tribe, and species of the Corynoneurinae subfamily, into Metriocnemini tribe.

**) New larvae (Levanidov and Levanidova, 1962).

***) Species new to the science; it is determined by its adult phase by A.A.Linevich.

Table 26.

Distribution of the bottom invertebrates in the tributaries of the Amur according to the biotopes (except the chironomid larvae).

Species	Bodies of Running Water										Water bodies with slow run-off				
	Stony grounds on rapid current	Stones overgrown with moss or algae	Stony sandy grounds	Silty stony grounds	Aquatic vegetation	Sandy grounds	Silty clay with sand admixture	Silty sand	Stumps, tree roots, logs etc.	Coarse plant detritus on slow current	Stony grounds	Silty grounds	Aquatic vegetation	Coarse plant detritus	Sandy grounds
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Веснянки Stoneflies															
Fam Сем. Nemoridae															
Amphinemura borealis Mort.	+++	+	+	++		+++			+++						
Nemoura cinerea Retz.	++		++	++					+						
Nemoura sp.	+	+		++	+++		+		++	+					
Capnia nigra Pict.	+++		+	++											
Capnia sp. № 1 (sp. nova)	+++			++											
Isocapnia sibirica Zap.-Dulk (?)	++			+											
Isocapnia sp. № 1	++		+	++											
Fam Сем. Taeniopterygidae															
Rhabdiopteryx quadrata Kopon.	+	+		+					++						
Fam Сем. Pteronarcydae															
Pteronarcys reticulata Burm.	+++	++		++					+++						
Fam Сем. Perlodidae															
Arcynopteryx brevis Kopon.	++			++					++						
Arcynopteryx compacta (McL)	+++			++					+++						
Arcynopteryx (Megarcys) ochracea Klap.	+			++					+						
Diura nanseni Kemphy	+++		+	++					+						
Diura sp.	++			+					+						
Isogenus sp.				++					++						
Isoperla obscura Zett.	+		+	+											

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Isoperla lunigera (Klap.)	++	+		+++					+++						
Isoperla sp. № 1 lv. nova	++			++					+++						
Isoperla sp. № 2 lv. nova	++	++	++	+++					++						
Isoperla sp. № 3 lv. nova	+			+											
Fam. Сем. Chloroperlidae															
Chloroperla mediata Navas	+		++	++					+++	+					
Chloroperla sp. № 1	+	+	+++	++			+		+	+					
Haploperla ussurica Navas	+	+	+++	++	+		++		+	+			+		
Haploperla sp. nova	+	+	++	+			++		+	++			+		
Paraperla sp.			+	++											
Fam. Сем. Perlidae															
Neophasganophora brevipennis Navas	+++			++					+++						
Oyamia amurica Klap.?	+			+					+++						
Acroneuria sp.	+								+						
Поденки Mayflies															
Fam. Сем. Ephemeridae															
Ephemera amurensis Navas			+++				+++	++	+	+		+		+	
Ephemera formosana Ulmer			+	+				+							
Ephemera strigata Eaton			+												
Ephemera sachalinensis Mats?			+					+						++	++
Fam. Сем. Potamanthidae															
Potamanthus luteus L.	+		+	+					+						
Fam. Сем. Ephoronidae															
Polymitarcys sp. (virgo+nigridorsum)			+	+			++								

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fam. Сем. Heptageniidae															
Rhithrogena unicolor Tshern.	+++		++	++		+									
Rhithrogena sp. № 1	++			+											
Epeorus aesculus Ueno	+			+											
Epeorus latifolium Ueno	+++			+++					++						
Heptagenia arsenjevi Tshern.	+	++	+++	+++	+		++		+++	++			+		
Heptagenia kibunensis Iman.	++		++												
Heptagenia soldatovi Tshern.	+	++	++	++					+++						
Heptagenia yoshidae Takahashi	+++	+	+++	+++					+++	+++	+			+	
Ecdyonurus tobiironis Takahashi	+	+		+					+						
Cinygma sp.							++								
Cinygmula grandifolia Tshern.	+++						+		++						
Cinygmula altaica Tshern.	+++	+		+					+						
Iron maculatus Tshern.	++	++	+	++											
Iron sp. № 1	++														
Fam. Сем. Ametropodidae															
Metretopus sp.		+	+			++									
Fam. Сем. Siphlonuridae															
Acanthametropus nikolskii Tshern.			+		+										
Siphlonurus zetterstedti Bngtss.	+	++	+	++	+++		+++		++	+	+	+++		++	
Siphlonurus sp.	+	+			++				+	+			++		
Parameletus minor Bngtss.						+++	+++			+			+++	+++	+++
Ameletus montanus Iman.			+	+		+++				+					
Ameletus sp. № 1						+++	+	+							
Isonychia japonica Ulmer				++			+		++						
Fam. Сем. Baetididae															
Centroptilum pennulatum Etn.				+	+	++									
Baetis sp. № 1 из гр. B rhodani			+			++									
Baetis sp. № 2 из гр. B. chinononis	++		+												
Baetis tricolor Tshern.	++			+			++		+						

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Baetis sp. № 3 из гр. B. carpatica	++	+	+			++									
Baetis vernus Curt.	+++	+	+				+		++						
Baetis thermicus Ueno	+++	+	++				+		++						
Pseudocloeon sibiricum Kazlauskas	++	++		+					+						
Pseudocloeon tuberculatum Kazlauskas	+			+					++						
Fam. Сем. Leptophlebiidae															
Choroterpes trifurcatus Ueno	++		+	+					+						
Paraleptophlebia lunata Tshern.	+++	+++	+++				++		+	+					
Paraleptophlebia chocolata Iman.			++			+			+++						
Fam. Сем. Ephemerellidae															
Ephemerella basalis Iman.			+++	++					+++	++					
Ephemerella triacantha Tshern.	++	+	++			+			+++						
Ephemerella lv. nova из гр. triacantha	+														
Ephemerella sp. № 3	++	+	++						+						
Ephemerella lepnevae Tshern.	+++	++	++						++						
Ephemerella levanidovae Tshern.	++		+	++			+		++						
Ephemerella tshernovae Baik.			+												
Ephemerella lenoki Tshern.			++	++											
Ephemerella thymalli Tshern.	+		+						++						
Ephemerella ignita Poda		++	+++	+++	++	+	+++		++	++		+		+	
Ephemerella sp. № 1 (lv. «naz» Iman.)			+	++					+						
Ephemerella taeniata Tshern.	+	++	++	++	++	+	++		+++	++	+	+		+	
Chitonophora sp. lv. № 2			+	+											
Torleya padunica Kazlauskas		+			+		+			+					
Chitonophora mucronata Bngtss.			++		+	++			+	+					
Chitonophora sp. № 1	++	+++	+++	++	+		++		+	+					
Chitonophora sp. № 2								+							

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ручейники Caddis flies															
Fam Сем. Rhyacophilidae															
Rhyacophila impar Mart.	++	+	+	++			+		+	+					
Rhyacophila narvae Navas	++	++	+	++					+	+					
Rhyacophila lata Mart.	++	+		+											
Rhyacophila kardakoffi Mart.	+++	+++	++	++					+						
Rhyacophila depressa Mart.	+														
Rhyacophila retracta Mart.	++								+						
Rhyacophila sp. № 1	++			+		+			+						
Apsilochorema sutschanum Mart.	+														
Fam Сем. Glossosomatidae															
Diploglossa nylanderi Mcl.	+++														
Mystrophora altaica Mart.	++	+							++						
Mystrophora ussurica Mart.	++								+						
Mystrophora intermedia Klap.	++														
Mystrophora angarica Levanidova	+++	+													
Agapetus sibiricus Mart.	+++			+					+						
Agapetus jakutorum Mart.	+++			+											
Padunia lepnevae Mart.	++			++											
Fam. Сем. Philopotamidae															
Dolophilodes sp.	++	+		+											
Fam. Сем. Stenopsychidae															
Stenopsyche griseipennis McL.	+++		+	+					+						
Stenopsyche bergeri Mart.	+++		+	++					++						
Fam. Сем. Psychomyidae															
Psychomyiella minima Mart.	+++			++											
Psychomyiella composita Mart.	+++			++											

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fam. Сем. Ecnomidae															
Ecnomus tenellus Ramb.	+			++									+		
Pseudoneureclipsis sp.							++								
Fam. Сем. Polycentropodidae															
Plectrocnemia kusnezovi Mart.	++	+		+					+						
Neureclipsis bimaculata L.	+				+				+						
Fam. Сем. Arctopsychidae															
Arctopsyche amurensis Mart.	++			+											
Arctopsyche palpata Mart.	+++	++		+					++						
Fam. Сем. Hydropsychidae															
Hydropsyche nevae Kol.	+++			++					++						
Hydropsyche kozhantchikovi Mart.	++			+					+						
Cheumatopsyche infascia Mart.	++			+											
Cheumatopsyche sp.	++			+											
Macronema radiatum McL.	+		+	+					+						
Amphipsyche proluta McL.				+			+++			+					
Fam. Сем. Phryganeidae															
Phryganea sinensis McL.		+		+	+				+						
Holostomis atrata Gmel.		+		+		+			+	+					
Holostomis phalaenoides L.		++		++	++				+++	++					
Сем. Limnophilidae															
Apatania zonella Zett.	+	+++	++	++	+++		++			++					
Apatania parvula Mart.	++			++											
Apatania crymophila Wall.	++	+		+++					+++						
Apatania sp. № 1.	++			+++					+++						
Imania sichotalinensis Mart.	+			+											
Neophylax ussuriensis Mart.	+++			+											
Dicosmoecus palatus McL.	+			++					++	+					

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Nemotaulius admorsus McL.				+++	+				+++	++					
Arctoecia servata McL.				++		+	++		+++	+++		++		+++	
Limnophilus correptus McL.				++	++				+++						
Hydatophylax magnus Mart.	++			++					+++						
Hydatophylax nigrovittatus McL.		+		+++	+	+	++		+++	++	++				
Hydatophylax soldatovi Mart.									++						
Hydatophylax grammicus McL.				+					+++	+					
Сем. Goeridae															
Goera sajanensis Mart.	+++		++	++					+		++				
Goera squamifera Mart.	++	+	+	+											
Сем. Lepidostomatidae															
Lepidostoma hirtum Fabr.			+	++			+		++	++					
Lepidostoma sp.				++					+	+					
Сем. Brachycentridae															
Brachycentrus subnubilus Curt.									+						
Brachycentrus bilobatus Mart.	++								++						
Oligoplectrodes potanini Mart.	+++	+		+					++						
Micrasema sp.	++	+		+					+						
Сем. Calamoceratidae															
Ganonema extensum Mart.				+++		+	++		++				+	++	
Anisocentropus pallidus Mart.		+	+	+	+++				++						
Molannidae															
Molanna angustata Curt.				+			+		+						
Molanna submarginalis McL.						+	+					+			
Leptoceridae															
Leptocerus variabilis Mart.	++			++											
Leptocerus excisus Mart.				++			++		++						

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Leptocerus annulicornis Steph.		+		++					+						
Leptocerus sp. № 1.				+			+		+						
Leptocerus sp. № 3.	+			++					++						
Mystacides dentata Mart.				+											
Oecetis testacea Curt.				++					++						
Oecetis notata Ramb.				+					++						
Стрекозы Dragonflies															
Fam. Сем. Calopterygidae															
Calopteryx virgo japonica Selys					++										
Fam. Сем. Agrionidae															
Agrion lanceolatum Selys													+		
Lestes sponsa Hans.													+		
Supra fam. Надсем. Aeschnoidea															
Nihonogomphus heterostilus Bart.				+			+	+				+			
Anisogomphus amurensis Bart?															
Ophiogomphus cecilia obscura Bart.			+			++	+++	++	+			+			
Trigomphus anormolobatus Bart.						+	+	+							
Sieboldius albardae Selys							+								
Gomphidia gen. sp.			+									+			
Aeschna crenata Hag.													++		
Aeschna juncea orientalis Bart.															
Fam. Сем. Libellulidae															
Macromia amphigena Selys		+		+	+				+				++	++	++
Epitheca bimaculata Charp.				+	+								++		
Cordulia aenea amurensis Selys		+		+											

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Somatochlora metallica exuberata Bart.		++		++				+	+			+	+		
Leucorrhinia rubicunda intermedia Bart.					+							+	++		
Sympetrum sp.												+	++	+	
Жуки Beetles															
Fam. Сем. Haliplidae															
Haliplus lineolatus Mnnh				+	+							+	++		
Haliplus sibiricus Motsch.												++	+		
Fam. Сем. Dytiscidae															
Noterus japonicus Sharp.												+	+		
Bidessus japonicus Sharp.												+	+		
Hydroporus tristis (Payk)												+	++		
Hydroporus sp.					+										
Oreodytes rivalis Gyll.		+		+	+				+						
Gaurodytes adpressus (Aube.)		++							+		+				
Ilibius lateralis (Gebl)							+	+				++	++	+	
Ilibius crassus Thoms.					+								++		
Ilibius poppiusi Zaitz.												+	+		
Rhantus notaticollis Aube												+	+		
Eretes sticticus (L.)												+	+		
Hydaticus laeviusculus Popp.												++	+	+	+
Acilius canaliculatus Nic.												+	+		
Ditiscus dahuricus Gebl.												++	+	++	
Ditiscus distans Feng.				+	+										
Ditiscus delictus Zaitz.													++		+
Fam. Сем. Hydrophilidae															
Helophorus sp.													+		
Hydraena riparia Kugel	+	++			+				+	+					
Hydraena sp.		+											+		
Berosus signaticollis Sharp.												+	+		+
Hydrobius fuscipes L.												+			

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Anacaena limbata F.												+	++		
Enochrus sp.												+	+		
Laccobius bedeli Sharp.												++			
Laccobius czerskii Zaitz.													+		
Limnebius truncatulus Thoms.												+	++		
Fam Сем. Driopidae															
Helmintinae gen. sp.		+++		++											
Fam Сем. Psephenidae															
Psephenus sp.	+														
Большекрылые Macroptera.															
Sialis sp.															
Diptera (except chironomids) **Двукрылые (кроме хирономид)**															
Fam Сем. Cilindrotomidae															
Triogma sp.		+			+								+		
Fam. Сем. Limoniidae															
Eriocera sp.		+		++		+	++								
Dicranota sp.	++	++	+	+++			+	+	+	+					
Dicranomia sp.		++		+											
Dactylolabis sp.		+		++			++		+			+		+	
Ormosia sp.				+			+	+				+		+	
Fam. Сем. Tipulidae															
Tipula (Arctotipula) sp. sp.	+++			++											
Tipula (Yamatotipula) sp. sp.	+	+		+		+			+						
Tipula (subgen?) sp.	+		++												
Fam Сем. Psychodidae															
Pericoma? sp.		+				+		+		+					

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fam. Сем. Culicidae															
Dixa amphibia Deg.							+								
Fam. Сем. Melusinidae															
Prosimulium irritans Rubz.	++														
Eusimulium bicorne Dor. et Rubz.	+++														
Eusimulium pigmaeum Zett?	++														
Gnus malyshevi Dor. et Rubz.	+++								+						
Gnus pavlovskii Rubz.	++				+										
Fam. Сем. Blepharoceridae															
Blepharocera sp.	+++			+											
Philorus sp.	++														
Bibiocephala sp.	+++								+						
Thaumaleidae gen? sp.									+						
Tanyderiidae gen? sp.									+						
Stratiomyiidae gen? sp.		+										+	+		
Fam. Сем. Rhagionidae															
Atherix sp.	+			+++					+++	+					
Fam. Сем. Tabanidae															
Tabanus sp.	+			++											
Chrysops sp.															+
Fam. Сем. Ephydridae															
Ephydra sp.		++													
Клопы Water bugs															
Fam. Сем. Micronectidae															
Micronecta wui Lundblad					++		++			+				+	+

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fam. Сем. Corixidae															
Sigara sp.					+										
Corixa sp.													+		
Fam. Сем. Nepidae															
Ranathra chinensis Mayr.					+								+		
Fam. Сем. Aphelochiridae															
Aphelochirus amurensis Kir.				++		++		++	+						
Aphelochirus ussuriensis Kir.		+		+	+			+							
Fam. Сем. Gerridae															
Gerris sp. sp.					++		++								
Ракообразные Crustaceans															
Order Отряд Isopoda															
Asellus hilgendorfii Bov.							+			+		++	+++	+	
Asellus dentifer Birst. et Levan.							+								
Livoneca amurensis (Gerst.)			+												
Order Отряд Amphipoda															
Crangonyx arsenjevi (Derzh.)				+			+								
Gammarus lacustris G. O. Sars.		+	+		++				+++	++		+	+		
Order Отряд Decapoda															
Cambaroides schrenkii (Kessler)			+		++								++		
Palaemonetes sinensis (Sollaud)			+		++								++		
Водяные клещи Water mites															
Fam. Сем. Eylaidae															
Eylais rimosa Piers.													++		

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Eylais mülleri Koenike												+	+		
Eylais tantilliformis Sokol.												+	+		
Fam. Сем. Sperchonidae															
Sperchon glandulosus (Koen)				++			++								
Fam. Сем. Lebertidae															
Lebertia sp. sp.		+++	+++	+++		++	+++		+	++					
Fam. Сем. Atractideidae															
Atractides nodipalpis constrictus Sokol.				+			+	+							
Fam. Сем. Hydrobatidae															
Hydrobates octoporus (Dad)				++						+				+	
Hydrobates foreli (Lebert)			+			+				+					
Fam. Сем. Unionicolidae															
Unionicola ypsilophora (Bonz)	На жабрах Margaritana (много)														
Моллюски Mollusks															
Fam. Сем. Limnaeidae															
Limnaea auricularia (L.) plicatula Bens.	++	+		++	+		+		+++	+		+	++		+
Limnaea peregra (Müll)		+											++	+	
Limnaea palustris liogyra West.												+	+	+	
Limnaea pervia (Martens).		+													
Fam. Сем. Planorbidae															
Gyraulus acronicus var. sibiricus	+		+								++	+	++	+	+
Gyraulus acronicus var?	++			+			++		++						
Gyraulus filiaris (Gredl.)		+		+			++				+	+	++		
Polypylis hemisphaerula (Bens)									+						
Camptoceras rezvoji (Ldn)													+		

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fam. Сем. Ancylidae															
Acroloxus lacustris (L.)	+	+		+											
Acroloxus lacustris var.	+			+					+						
Fam. Сем. Valvatidae															
Valvata stelleri (Dyb.)	++								+			+		+	+
Valvata sibirica Midd.												+			
Fam. Сем. Viviparidae															
Viviparus praerosus (Gerst)							++		+		+	++	+		+
Viviparus ussuriensis (Gerst.)			+	++							+	++		+	
Fam. Сем. Hydrobiidae															
Amnicola sp. nova											+				
Bithynia ussuriensis Ehrm.											+	+	+		
Fam. Сем. Melaniidae															
Semisulcospira cancellata (Bens)	++			++					++						
Semisulcospira cancellata f. amurensis Gerst.				++					++			++			++
Semisulcospira laevigata (Gerst.)	++			+											
Semisulcospira libertina (Gould)	+			+		+			+						
Fam. Сем. Margaritanidae															
Margaritana dahurica (Midd.)	++			+											
Fam. Сем. Unionidae															
Unio douglasiae Griff. et Pidg.			+	+											+
Anodonta woodiana (Leach)															+
Cristaria plicata (Leach)															+
Fam. Сем. Sphaeriidae															
Sphaerium nitidum Clessin.		+					+								
Sphaerium compressum Mouss													+	+	+
Pisidium amnicum (Mull.)						+									

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Pisidium casertanum (Poli)		+	+++		+++		++		+	+		++			
Pisidium punctatum Sterki								+							
Pisidium pulchelluin Yen.				+						+		+			
Турбеллярии Turbellaria															
Fam. Сем. Dendrocoelidae															
Bdellocephala grubeiformis Z. Sab.	+														
Bdellocephala parva Z. Sab.									+						
Bdellocephala mediobuccalis Z. Sab.	+			+											
Bdellocephala sp.	+++			+					+						
Baicalobia guttata Gerst.	+			+											
Baicalobia sp.				+											
Dendrocoelum sp.									+						
Fam. Сем. Planariidae															
Seidlia schmidti H. Sab.	++										++				
Penecurva sibirica H. Sab.	+++	++	+	+++			+			+					
Penecurva mesorchis Liv. et Z. Sab.	++			+			+		+						
Penecurva teletzkiana v. longopharyngea Liv. et Z. Sab.	++	++	+	++					+						
Dugesia lugubris v. wytegrensis H. Sab.	+			+											
Dugesia lugubris v. amurensis Z. Sab.	+														
Волосатики Nematomorpha															
Fam. Сем. Gordioidae															
Gordius sp.				+			+								

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Олигохеты Oligochaetae															
Fam Сем. Naididae															
Specaria josinae (Vejdovsky)			+												
Uncinais uncinata (Orsted)			+												
Stylaria lacustris (L)			+		+										
Dero sp.			+												
Fam Сем. Enchytraeidae sp. sp.		+	++	++		++	+++					++	+++		
Fam. Сем. Tubificidae															
Branchiura sowerbyi Beddard				+											
Rhyacodrilus coccineus (Veid)			+++	++								++			+
Rhyacodrilus sinicus (Chen)		+		+								+		+	
Bothrioneurum vejdovskyanum												++			
Limnodrilus udekemianus Claparede		+	+	+			+++								
Tubifex tubifex (Müller)							+					+			
Peloscolex nikolskyi Lastockin			+++	++			++						+++		
Peloscolex apapillatus Lastockin				++			++						++		
Peloscolex sp.				+											
Aulodrilus sp.			+				++								
Fam. Сем. Haplotaxidae gen? sp.?		+	++	++											
Fam Сем. Lumbriculidae															
Lumbriculus variegatus (Müller)				+											
Lumbriculidae sp.		+		++			++	+							
Пиявки Leeches															
Fam Сем. Ichtyobdellidae															
Piscicola geometra L.	На карповых и лососевых рыбах (Upon carps and salmons)														
Trachelobdella taimeni Epstein	На лососевых рыбах (Upon salmons)														

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fam. Сем. Glossiphoniidae															
Hemiclepsis marginata (O. F. M.)	+	+	+	++	++		also upon fish а также на рыбах				++	++	++		
Glossiphonia complanata (L.)	+	+		+	+						+	++	++		
Glossiphonia heteroclita (L.)		+		++								+	++	+	
Glossiphonia weberi lata (Oka)				+	+								+		
Helobdella stagnalis (L.)													+		
Fam. Сем. Gnathobdellidae															
Haemopis sanquisuga (L.)	+			+								+	+		
Whitmania laevis (Baird.)												+	+		
Fam. Сем. Herpobdellidae															
Herpobdella octoculata (L.)	+	++	+	++	+				+++	+	++	+++	+++	++	

QUANTITATIVE CHARACTERISTICS OF THE BENTHOS IN THE TRIBUTARIES OF VARIOUS HYDROLOGICAL TYPES AND IN THEIR SECTION.

The Lower Reaches of the Foothill Tributaries (Moderately Warm-Water Type).

The benthos in the lower reaches of the Ussuri and the Amur Rivers was studied by an expedition of the Moscow University in the years 1946 to 1959 (Borutsky, Klyuchareva, Nikolsky, 1952). The results of these studies are shown in table 27.

Insofar as all the quoted figures are based on one-day observations carried out on different days, it is impossible to judge the comparative value of the biomass of the benthos in these rivers.

The authors present lists of the benthofauna determinations from which we may conclude that in the lower reaches of the large rivers such as Khor, Bikin and Amgun', which completely have a flatland character, the following forms predominate: Chironomus f.lv. plumosus, Ch. f.lv. thummi, Lipiniella sp., Prodiamesa gr. bathyphila, Lauteborniella brachylabis, mollusks Viviparus praerosus, mayflies Ephemera amurensis, E. strigata, Heptagenia kibunensis.

In the lower reaches of the rivers Khalzana, Khivanda and Dzhappi, which are distinguished by their small size, low summer temperatures of the water (13 to 14°C) and by a relatively fast current, the fauna composition was different. Among the chironomids predominated orthocladines (Orthocladius gr. saxicola, Cricotopus biformis, Cr. gr. silvestris, Diamesa gaedi and others). Mayflies are represented by ecologically heterogeneous species (Siphlonurus zetterstedti, Heptagenia yoshidae, Epeorus sp., Ephemerella tenax).

Our material is collected 70 kilometres from the estuary of the Amgun' River, it supports the data of the Moscow University expedition. /p.112 Thus, several summer series of samples taken by means of the Petersen's bottom grab in the main channel of the river in 1958, permitted a determination of the summer biomass of the benthos to be 0.88 gram per square metre, including the chironomid larvae as 0.73 gram per square metre, larvae of other diptera, 0.11, mayflies, 0.02 and of oligochaetae, 0.02 gram per square metre. Consequently, the biomass of benthos in the lower reaches of the Amur tributaries, as well as in the Amur River proper (according to the data of the Moscow University expedition) is extremely low and ranges between 0.01 and 0.32 gram per square metre (excluding the mollusks). If the salmon fingerlings at this stage of the migration route continued to feed on benthos, then their food supply would be much lower than in the spawning rivers, particularly, because the biomass of fish, which are competitors and feed upon the benthos in the channel of the Amur River, is greater than the one in the tributaries. Further down, in the chapter on the feeding of the fingerlings, it will be shown how the character of fingerling feeding changes along the migration route.

Table 27.

The Summer Biomass of the Benthos in the Estuarian Sections of the Amur Tributaries, in grams per square metre.

Groups of Invertebrates	Bikin one kilometre from estuary Aug. 13	Khor channel, estuary Aug. 17	Khalzan 200 m. from estuary June 9	Khivanda, estuary July 27	Bichi, 200 m. from estuary July 21	Dzhappi, estuary July 17	Amgun' 5 kilometres from estuary July 14
Chironomids	0.09	2.11	0.44	0.38	0.14	0.12	0.03
Geleids	-	-	-	-	0.01	-	0.01
Other diptera	0.03	-	-	-	-	-	0.01
Mayflies	1.10	-	0.39	0.11	0.09	0.28	0.01
Caddis flies	0.24	-	-	0.14	-	-	-
Orlflies	-	-	0.15	-	-	-	-
Dragonflies	0.01	-	-	-	-	-	-
Water bugs	-	-	0.01	0.01	-	-	-
Amphipods	-	-	-	0.23	-	0.01	0.01
Oligochaetae	-	0.11	-	0.01	0.21	0.12	-
Nematods	-	-	-	-	-	0.01	-
Total without mollusks	1.47	2.22	0.99	0.88	0.45	0.54	0.07
Mollusks	0.20	0.08	-	-	0.09	0.05	0.34

Foothill Sections of the Tributaries of the Amur River.

(Moderately-cold-water type).

In the foothill sections the falls, rapids (deep sections of the river with narrow bed), reaches, which are clearly divided into a medial and a ripal, as well as small open bays are distinctly pronounced. To each morphologically distinct element of the river bed corresponds a rate of current, ground dispersion, intensity of the deposition of suspended and carried deposits, which are characteristic of it and distinguishable from the adjoining elements. The invertebrates of the medial live in the main channel and are less dependent on the fluctuations in the river level. At the same time, the denizens of the shallow ripal (usually developed near one of the banks) must be adapted to a periodic drying of a considerable zone of the bottom. However, as we shall see in the following, a considerable amount of invertebrates in the foothill rivers is not strictly restricted to the individual sections of the river profile. The potamophile group is characterized by the greatest stenotopicity among the number of deep medial denizens (Macronema radiatum, Amphipsyche proluta), who do not live in the ripal or in the falls of a foothill river.

In the tributaries the absence in a considerable portion of the invertebrates of a strict restriction to one or another station is explained primarily by a high dynamicity of the environmental conditions, /p.113 particularly in the river sections. Sharp changes in the water level in a river, several times a year erase the boundaries between the falls and the rapid, ripal and medial. Thus, the invertebrates living at the falls, during a period of a few days, often happen to be (and occasionally for a prolonged period of time) under a water layer of two to three metres, in other words, under completely different ecological conditions.

The animals, if they by chance happen to be under unfavourable environmental conditions, may to a certain degree avoid such conditions by means of nocturnal migrations, but the pupae or larvae in the nymphal stage (caddis flies, black flies and certain other diptera) are deprived of such a possibility and must adapt themselves to these conditions. Thus, the environmental conditions in the foothill rivers form populations of invertebrates with a wider ecological spectrum.

The ripal is divided into two categories according to its character of ground and its rate of current. Grounds in the ripal, at a shallow bank, are characterized by a development of smaller fractions, such as, fine silted pebbles, gravel with a considerable admixture of sand; in spots, particularly where channels and streams enter, and in open bays the sandy-silty grounds predominate. The current, compared to the medial, is very slow, therefore the water temperature here in the summer is higher than in other sections of the river bed. A narrow ripal at a deep bank is usually distinguished by its large-pebbled or stony bottom. In areas, where the basic rocks are washed out into the ripal the clay, sand and humus are periodically precipitated. The current here is considerably faster than in the ripal at a shallow bank.

The ripal, particularly its upper level, if compared with other elements of the river profile, has a smaller number of forms that are characteristic of it alone. These forms will primarily be the larvae of mayflies (Ephemerella ignita, Chitonophora mucronata, certain Baetidae), stoneflies Amphinemura borealis, larvae of the diptera Arctotipula, bugs Micronecta wui, mollusks Semisulcospira cancellata and certain other invertebrates. Furthermore, here occur invertebrates, which are more characteristic of the medial and falls, but their density is much lesser in the ripal. They occur in the ripal mainly at the early stages of their development. The latter phenomenon, apparently, is connected with the generally known biological peculiarity of the majority of aquatic invertebrates consisting in the fact that at early stages they are less demanding in respect to environmental conditions, in other words, they are more eurybiontic. In the ripal a number of biotopes may be segregated differing mainly in the character of ground and in the strength of current. These factors determine the quantitative and special distribution of benthos, a phenomenon illustrating the data of the hydrobiological series carried out at the end of June, 1960 (table 28) at the shallow bank. The samples were taken three to six days after the flooding. The mayflies are represented here mainly by young Baetis sp.sp, and individually by very young Ephemerella tricantha, Rhithrogena unicolor and Rh. sp. No.1; the stoneflies are represented by adult larvae of Amphinemura borealis.

The next two stations are characterized by close indices of biomass, but differ in the composition of population. In a stony ripal located in immediate proximity to a fall, forms predominate which are restricted to strong and medium-strong current: Epeorus latifolium, Rhithrogena unicolor, Rh. sp No.1, Heptagenia soldatovi, Pseudocloeon sibiricum, Baetis sp. sp., Ameletus montanus. Ephemerellidae were represented only by very young E. triacantha; scarce caddis-flies are represented by large forms of Stenopsyche griseipennis, Hydropsyche nevae: stoneflies, by larvae of Amphinemura borealis and Haploperla ussurica, mollusks, by large Semisulcospira cancellata.

Section with pebbles and sand, far away from the falls, was characterized by a slower current and a lesser diversity in forms. Mayflies were represented only by young Baetis sp. The benthos at the section of sand and clay is also very poor in the special and quantitative respect. /p.114 The richest biotope, namely, stones in the falls, differs from the biotope of stones located below the falls only in the strength of the current. Here we find basically the same species (except chironomids), but Heptagenia soldatovi (a form characteristic of a moderate current) and the mollusks and amphipods are absent.

The benthos of the ripal (like the one of the entire river) is subjected to considerable qualitative and quantitative changes. The June series shown in table 28 characterize the minimum period of the biomass originating after the spring flight of a considerable number of species of amphibiotic insects. Insofar as the benthos of the ripal consists to a considerable extent of mayflies, the seasonal fluctuations of its biomass correlates in the majority of cases to their life-cycle. A high biomass of mayflies is observed in April and May, when the species of Ephemerellidae with a one-year life-cycle (E. taeniata, Chitonophora mucrinata, Ch. sp. No.1) attain their medium or maximum dimensions. In June the biomass of the ripal is decreased as a result of the metamorphosis of a considerable part of the population of this species; in July the biomass increases again, mainly owing to the growth of Ephemerella ignita reaching even at the poorest section (pebbles at the shallow bank) 4 grams per one square metre, including 1.5 grams constituted by E. ignita. In August E. ignita flies and the biomass of the benthos of the ripal decreases again. In table 29 we see certain data characterizing the May and August benthos in the ripal. In this table we primarily see the original biotope located on almost the vertical sections of the forest bank underwashed by the river. The denuded intertwinings of willow roots are located 1.5 to 2 metres from the water level. During the flood-time large and fine detritus, river refuse and silt accumulate here. During high waters the last-year's grassy dry-stand of the river terrace is inundated. The mayflies E. taeniata, Ch. mucrinata, Ch. sp. No.1, Ephemera amurensis, E. sachalinensis, as well as Caenis sp., Baetis sp. predominate in the benthos. Among stoneflies, in addition to A. borealis and the species of the genus Chloroperla, which are common here, prior to the metamorphosis to the winged stage, the large species Arcynopteryx, Isoperla, Diura gather here. The large mollusks S. cancellata are also characteristic of this station, they usually occur in accumulations among the roots and are almost never caught by the quantitative catching devices. A significant part of the /p.115 invertebrates in this biotope belong to dendrophiles. In May, on the sandy and pebbled ground and on sandy ground a high ratio of mayflies is likewise characteristic. The more dendrophile (and lithophile) Ephemerella taeniata cedes the leading role in the sandy biotopes to Chitonophora mucronata, Siphlonurus zetterstedti, Ephemera amurensis, *E. sachalinensis*, very many *S. cancellata*; beetles *Ilybius lateralis* also occur. The larvae *Ameletus montanus* are frequent on the pebbles among sand. In August, after the flight of *Ephemerellidae* the benthos consists mainly of mayflies *Ephemera* to which the larvae of *Metretopus* sp., *Centroptilum pennulatum*, oligochatae, chironomid larvae are added; there are still many mollusks.

Table 28.

Abundance (A) and biomass, in grams per square metre (B) in benthos in various biotopes in the ripal of the Khor River, June 24th to 30th, 1960.

Group of organisms		Section of the rapid current: Shallow bank — Fine slightly silted pebbles with sand	Section of the rapid current: Deep bank below sandbank — Fine stones	Section of the rapid current: Deep bank below sandbank — Pebbles with sand	Section of the rapid current: Deep bank along the reach — pebbles with sand and clay	Sandbank near deep bank — small stones
Chironomids	A	330		104	312	2059
	B	0.17		0.1	0.2	1.1
Other diptera	A	60			104	
	B	0.44			0.8	
Mayflies	A	150	257	520		489
	B	0.48	0.9	1.4		6.3
Stoneflies	A	15	32	104		56
	B	0.06	0.1	0.4		0.6
Caddis flies	A	45	46			12
	B	0.35	1.7			0.2
Amphipods	A		43	104		
	B		0.7	1.7		
Total without mollusks	A	600	522	832	416	2616
	B	1.5	3.3	3.6	1.0	8.2
Mollusks	A		144			
	B		39.8			

The medial is more homogeneous according to the environmental conditions than the ripal. Its population depends less upon the changes in the water level of the river. According to depth we segregate the following sections in the medial: falls, medial of rapid sections and the medial of the reaches. Almost all the large forms of aquatic insects are characteristic of the rapid sections. The caddis flies are represented by *Arctopsyche amurensis*, *A. palpata*, *Hydropsyche navae*, *Diploglossa nylanderi*, by species of the genera *Psychomyiella*, *Padunia* and others. The mayflies are represented by larvae of the genera *Ephemera*, *Ephemerella* (*E. latipes*, *E. triacantha*, *E. basalis*), *Heptageniidae* (*Cinygmula grandifolia*, *Cinegmula altaica*, *Heptagenia soldatovi*, *H. arsenjevi*, *Rhithrogena unicolor*, *Rh.* sp. No.1), *Baëtididae* (species of the genus *Pseudocloeon*) and others. Almost all the large stoneflies (*Arcynopteryx*, *Neophasganophora*, *Diura*, *Pteronarcys* and others) are also restricted to this zone of the river. Of chiromids the following are common here: *Stictochironomus histrio*, *Polypedilum* gr. *convictum*, *Tanytarsus* gr. *lauterborni*, *Tanytarsus* gr. *mancus*, *Orthocladius* gr. *saxicola*, *Cricotopus silvestris*, *Cr.* gr. *algarum*, species of the genus *Eukiefferiella*, various representatives of the genus *Diamesa* (*D. prolongata*, *D. gaedi* and others).

Almost all these forms constitute also the medial fauna of the falls, but the latter are usually denser populated and are characterized by a greater biomass than the medial of the rapids or of the reach. Particularly characteristic of the falls are the caddis flies *Stenopsyche bergeri* and

Table 29.

Abundance (A) and biomass in grams per one square metre (B) of benthos in the ripal of the Khor River in 1957 and in 1958.

Groups of organisms		Rapid section	Reach		
		Soil, roots, inundated grass	Pebbles and sand, slightly silted	Slightly silted sand, detritus	
		End of May		August	
Chironomids	A	550	200	400	52
	B	0.3	0.3	0.2	0.05
Other diptera	A		100		104
	B		1.7		0.36
Mayflies	A	800	700	900	468
	B	9.7	8.3	29.2	2.0
Stoneflies	A	1050		200	
	B	2.0		0.3	
Caddis flies					
Beetles	A		50		
	B		2.6		
Amphipods	A	250		200	
	B	3.3		0.7	
Oligochaetae	A				364
	B				0.47
Total without mollusks	A	2650	1050	1700	1508
	B	15.3	12.9	30.4	3.9
Mollusks	A		100		520
	B		43.3		20.2

S. griseipennis, diptera Simuliidae, Blepharoceridae and mayflies Epeorus latifolium.

In deep sections of the medial (deeper than two metres) live mainly the larvae of caddis flies, particularly the potamophiles Macronema radiatum, Amphipsyche proluta, as well as Oligoplectrodes potanini, Brachycentrus subnibilus, S. griseipennis, mayflies occur less frequently. For all the sections of the medial the station of the submerged tree-remains, such as: trunks or stumps, is characteristic. Wood that stayed in the river for a long period of time is usually populated very densely, specially with mayflies (occurrence 22%), caddis-flies, chironomids and mollusks. The most dendrophilic ones: among the mayflies are: Heptagenia soldatovi, H. arsenjevi, Rhithrogena unicolor, Rh. sp. No.1, Ephemerella taeniata, E. basalis, E. latipes, E. leonevae, Chitonophora mucronata, Chitonophora sp. No.1, among caddis-flies: Hydatophylax magnus, H. nigrovittatus, Arctoecia servata; among stoneflies: Pteronarcys reticulata, species of the genus Arcynopteryx, Isoperla; among chironomids: Brillia pallida, Polypedilum gr. pedestre, Pentapedilum exectum; among mollusks: Semisulcospira cancellata, Limnaea auricularia plicatula. About one half of the stumps is populated with amphipods G. lacustris. /p.116

The biomass of the benthos medial (table 30) is greater than of the ripal and on the average constitutes 13 to 19 grams per square metre.

In the fall and winter period the biomass of the benthos both in the ripal, and in the medial is higher than in the summer; it increases particularly at the falls. With the fall decrease in the river level a considerable part of the ripal goes dry, the rate of current, particularly at the falls, decreases sharply, a massive development of the fouling algae takes place. The difference between the ripal and the medial, particularly at the falls, is levelled off to a considerable extent. All these factors contribute to a mixing of fauna from various stations and to its concentration at the falls. The biomass increases also owing to the growth of the insect larvae of the new generation. Thus, towards the end of October the biomass of benthos at the Shishlov Falls (the Khor River) was 40 grams per square metre, 13 of which were mayflies and 25.5 grams were amphipods. In the ripal of the high bank, in one of the poor sections (sandy talus) the biomass of benthos consisting of amphipods and oligochaetae was as high as 8.3 grams per square metre. The ecological differentiation of the benthofauna according to various sections of the river bed takes place in April with the first rise in the water level and is carried out basically by means of migrations of invertebrates in the mass of the river flow (Levanidova and Levanidov, 1962, 1965).

On an average the biomass of benthos in the foothill sections is of an order of 10 grams per square metre.

The average biomass of benthos in the lithorheophile biocoenoses of the Yenisey River, in the section running from sources to estuary of the Nizhnyaya Tunguska River, fluctuates within the range of 0.7 to 2.2 grams per square metre, while in the lithopsammorheophile biocoenoses it fluctuates between 0.2 and 0.4 gram per square metre (Greze, 1957). The biomass of benthos in pebble and boulder ground in the Podcherem River (a tributary to the Pechora River) was 3.59 grams per square metre (Zabolotsky, 1959). Thus, the biomass of benthos in these rivers is considerably inferior to the same in the foothill sections of the Amur tributaries.

Foothill sections of the river bed of many Amur tributaries, for example, of Iman, Khor, Anyuy, Bira, Khungari and Amgun' Rivers serve as spawning grounds of the fall chum. Particularly significant are the spawning grounds in the river bed of the Iman River stretching 100 kilometres.

Among the freshwater benthos-eating fish in the foothill sections of the rivers the following fish are fattening: lenoks, whitefish, graylings, Amur minnow; also predatory fish live here, such as taimen and pike. The benthos of foothill sections is relatively accessible to fish, since the moderate rate of current does not prevent their search for food. A relatively high biomass of benthos and considerable areas of these sections give a leading position to these sections for the fattening of non-migrating fish.

Bays. Bays deeply indented into the banks are mainly located along the middle and the lower reaches of the foothill rivers, there where the latter emerge into the flatland. The bays may be divided into spring bays, which have an inflow of ground waters (as a rule, a very insignificant one compared to the water masses of the bay) and the river bays, the water exchange of which takes place exclusively with the river (its degree changes in relation to the river level). According to hydrological conditions bays are /p.118
to a considerable degree close to stagnant water bodies. During the open water period under conditions of a hot summer, characteristic of the Amur basin, the water in the bays warms up considerably more than the water in a river; in July and August the difference in the water temperature reaches 5 to 6°C. The bottom of the bays is covered, with a layer of silt up to 0.5 metre thick; here and there, coarse detritus is accumulated together with large tree remains. In the estuarian part the sandy-silty grounds predominate. The higher vegetation attains considerable development.

Table 30.

Average summer biomass of benthos in grams per square metre in the foothill sections of large tributaries to the Amur River (1957 to 1961).

Groups of Organisms	Khor River						Iman River				Tatibe River	Tuda-Vak River	Bira River	
	Ripal			Medial			Ripal			Medial	Ripal	Medial	Ripal	Medial
	Reach, Sand	Rapid section, sand and pebbles	Falls, sand and pebbles	Reach, pebbles	Rapid section, stones and pebbles	Falls, stones	Reach, Sand	Reach, Pebbles and Sand	Falls, stones and pebbles	Falls, stones	Falls, pebbles	Falls	Falls, sand and pebbles	Falls, stones
Chironomids	0,05	1,20	0,73	0,13	0,22	1,32	—	0,22	0,18	0,74	1,05	0,29	0,02	—
Black flies ...	—	—	—	—	—	0,22	—	0,03	0,03	—	—	0,55	—	—
Other diptera ...	0,36	3,64	0,62	0,70	1,03	0,50	—	0,06	3,10	0,21	1,84	1,58	—	0,47
Mayflies ...	1,98	1,20	6,35	0,88	3,08	5,28	5,62	1,40	2,06	7,80	0,85	6,01	0,47	1,76
Stoneflies ...	—	0,05	—	0,91	2,44	6,20	—	0,58	—	3,06	—	7,89	0,20	0,33
Caddis flies ...	—	0,26	—	4,49	9,12	5,26	—	0,80	1,05	1,61	1,24	0,74	0,02	0,25
Mites ...	—	0,11	—	—	—	—	—	—	—	—	—	—	—	—
Amphipods ...	—	0,11	—	—	—	—	—	—	—	—	—	—	—	—
Oligochaetae ...	0,47	—	0,83	—	—	—	—	—	—	—	—	—	0,40	—
Total without molluscs	2,86	6,57	8,53	7,11	15,89	18,78	5,62	3.09	6,42	13,42	4.98	17,06	1,11	2,81
Molluscs ...	19.80	—	—	—	—	—	—	0,55	—	—	—	—	—	—

The bottom fauna is formed predominantly of pelophiles, detritophiles and dendrophiles, which belong to the thermophile and to the eurythermal forms. Almost total absense of oxyphile species, like stoneflies and caddis flies, and the abundance of dragonflies, which live on the silty grounds and among the higher vegetation are characteristic.

To the majority of dragonfly species such water bodies serve as the main habitats in the floodland of the foothill rivers (*Lestes sponsa*, *Aeschna crenata*, *Cordulia aenea amurensis*, *Epitheca bimaculata*, *Lebellula quadrimaculata orientalis*, *Leucorrhinia rubicunda intermedia*, *Sympetrum* sp.sp. and others).

Among other amphibiotic insects the orlflies *Sialis* are characteristic. Mayflies are represented in the bays by a few forms: larvae of the genera *Ephemera*, *Siphlonurus*, eurybiontic *Ephemerella ignita*. Among the chironomids *Stictochirinomus*, *Phytochironomus*, *Endochironomus* gr. dispar, *Cryptochironomus conjugens*, *Cr.* gr. *vulneratus Tendipes* f.lv. *plumosus* and the predatory *Ablabesmyia* gr. *monilis* and *Procladius* are common. A considerable quantitative development is achieved by the oligochaetae: *Peloscolex nikolskyi*, *P. apapillatus*, *Bothrioneurum* sp., *Limnodrilus* sp., *Rhyacodrilus coccineus*, as well as leeches: *Piscicola geomethra*, *Herpobdella octoculata*, *Hemiclepsis*, *Hemiclepsis marginata*. Among the mollusks predominate: *Valvata sibirica*, *Bithynia ussuriensis*, *Limnaea auricularia*. Aquatic isopods are numerous.

As data in table 31 show, the biomass of benthos in the bays is rather considerable, but here the proportion of the large forms that are not used by the chum fingerlings is high; forms such as: leeches, dragonfly larvae, mollusks. A characteristic peculiarity of the bottom fauna in the bays is the high proportion in the biomass of predatory invertebrates. The benthos in the bays is an important food reserve for cyprinids and freshwater salmonids (Amur ide, carp, lenok and others). Certain fish, such as, for example, crucian carp, Pseudobagrus fulvidraco, live constantly in large bays in the lower reaches of the Khor, Iman and Bikin Rivers.

The chum fingerlings enter bays in small numbers. In some cases, when the chum spawns in the upper reaches of a "spring" bay, this water body becomes a growing water body for the juveniles.

Secondary Water Bodies in the Foothill Sections of the Amur Tributaries.

The spring channels are of the greatest importance to the reproduction of fall chum. In summer, when they function as river channels, their current speed is slower than in the main bed, the amount of suspended material entering with them is also lower than in the water of the river bed. As a result of this, aquatic vegetation can establish itself therein. Pebbles and stones occupy in the spring channels from 50 to 70% of the entire area of the river bottom; the silty sections are extensively developed. Peculiar "dual" conditions of the spring channels (river conditions in the summer and spring conditions in the winter) make its imprint upon the special composition and biomass of their bottom population. The most characteristic and well-studied in this respect are the Georgievsk channels in the Khor River.

The biomass of the benthos in the spring channels is greater in the majority of the biotopes than in the main channel and in the river branches; the algal foulings, stones at the falls and the remains of tree vegetation are distinguished by a particularly high biomass of the benthos (table 32). /p.121

On stony grounds, the leading forms are the caddis fly larvae: Stenopsyche bergeri, Hydropsyche nevae, Agapetus jacutorum, A. sibiricus. Rhyacophila lata, Plectrocnemia kuznezovi, larvae of mayflies: Ephemerella basalis, larvae of stoneflies: Pteronarcys reticulata. The chironomids are represented by numerous Orthocladiinae and Tanytarsini; the larvae Syndiamesa orientalis and S. nivosa occur frequently. On the tree stumps predominate the larvae of caddis flies: Holostomis phalaenoides, Nemotaulius admorsus, Arctoecia servata, Hydatophylax nigrovittatus, Apatania crymophyla. Mayflies are represented by species Ephemerella basalis, E. taeniata, E. levanidovae, Heptagenia arsenjevi, Heptagenia soldatovi.

It is necessary to note that the seasonal changes in biomass of benthos are determined not merely by the processes of growth and natural decrease, but also by migrations of bottom organisms. Particularly significant are the seasonal migrations of the benthic animals noticeable in spring channels, where the summer and winter living conditions are sharply distinguished. During the summer, when the channel functions as a river branch, the bottom organisms, except the forms typical of the falls, spread along its bed populating bays and the temporarily inundated zone. In the winter the animals continue to feed and grow in the water bodies that are copiously fed with ground waters. The water level during this season is lowest, and the animals concentrate in the main river bed selecting the most suitable biotopes.

A characteristic feature of the conditions in the spring channels, which are not covered with ice during the entire winter, is the development of algal and mossy foulings reaching their maximum towards the end of March and in the beginning of April. The rise in the vegetation is caused by considerable transparency of the channels and by the increased concentration of carbon

Table 31. Average summer biomass of the benthos in the bays of the foothill rivers, grams per square metre.

Groups of Organisms	Khor (Bolshaya Channel)											
	Lagerny Channel					Pogranichny Channel		Tombash Channel			Tunnelnaya Channel Bay	
	Detritus	Silt and Detritus	Soft silt	Detritus higher vegetation	Silty sand	Sand and silt	Silt and Detritus	Coarse silt, Detritus	Silty sand	Soft silt	Silt and Sand	Silt and Detritus
Chironomids	—	3,36	—	0,63	2,29	5,20	5,84	1,04	4,42	—	—	5,72
Other diptera	—	—	—	—	—	—	—	—	—	—	—	13,00
Mayflies	—	1,05	—	—	1,66	—	—	7,54	—	1,56	—	—
Dragonflies	—	—	—	12,22	—	—	—	—	—	—	—	—
Water beetles	—	—	—	—	—	—	—	—	—	0,78	—	—
Caddisflies	0,26	—	—	0,63	—	—	—	—	—	—	—	—
Aquatic isopod	2,60	0,63	11,44	16,40	—	1,04	—	—	—	4,40	—	—
Oligochaete	—	0,63	0,42	0,21	1,04	10,40	6,64	4,42	—	5,20	2,60	5,20
Leeches	—	—	—	0,63	7,30	—	—	—	—	—	—	—
Total without Mollusks	2,86	5,67	11,86	30,72	12,29	16,64	12,68	13,00	4,42	11,94	2,60	23,92
Mollusks	—	0,42	—	0,63	5,40	20,20	22,60	—	—	—	—	—

Table 32 (continuation)

Groups of Organisms	Khor (Bolshaya Channel)					Kiya	Bira		Amgun'			Average biomass
	Polevaya Channel Bay		Bay below the apiary	Lukashikha Bay	Shishlova falls	Pavlenovsky Bay	Bay above the apiary	Bay below the apiary	Sigovy Bay	Krugly Bay	Chernaya River Bay	
	Coarse silt and Detritus	Silt, Higher vegetation	Silt and Detritus	Silt and Detritus	Silt and Detritus	Silt	Silt and Detritus	Silt	Silt, Higher vegetation	Silt, Inundated Grass	Silt, Higher vegetation	
Chironomids	2,08	—	1,80	2,72	0,26	—	8,58	3,64	1,30	—	0,26	2.1
Other diptera	—	—	—	—	—	—	—	—	—	—	—	0,6
Mayflies	—	—	1,30	14,14	5,20	1,36	—	—	0,78	0,52	1,43	1,6
Dragonflies	—	16,40	85,00	—	—	2,82	—	—	—	—	33,60	6.5
Water beetles	—	—	—	—	1,30	—	—	—	—	—	—	0,9
Caddisflies	—	—	—	2,72	—	—	1,82	1.30	1,30	1,30	—	0.4
Aquatic isopods	1.04	—	—	1,46	2,08	—	—	—	1,70	3,38	0,92	2,0
Oligochaetae	3,12	9,10	—	0,83	3,90	4,20	—	0;78	0,13	10.68	—	2,9
Leeches	—	—	39,20	7,30	—	—	—	—	—	—	—	2,4
Total without Mollusks	6,24	16,40	126,80	29,07	12,74	8.38	10,40	5,72	5,21	15,88	36,21	19.4
Mollusks	9,10	—	—	5.85	—	—	39,30	—	—	—	2,34	4,5

dioxide. Algae (particularly the diatomous ones) develop intensely at the falls and on the surface of the fall chum spawning mounds which are restricted to the exits of the ground waters. In this biotope the biomass of the benthos also increases progressively from fall to the beginning of spring (owing to the individual growth of the bottom organisms and to their intense intrusion from other biotopes) and by March it achieves very significant values. Thus, for example, in the end of October, immediately after the spawning of fall chum in the Sumasshedshiy Channel, the biomass of the epifauna in the spawning mounds is 3.25 grams per square metre and consists of diptera and stonefly larvae; towards the end of December the epifauna is already 26.6 grams per square metre, and is formed of amphipods, and of stonefly, caddis-fly and chironomid larvae (the biomass of the latter larvae is only 0.27 gram per square metre); at the end of March, when the chum larvae emerge from the mounds and begin their active feeding, the biomass of the benthos in the spawning mounds attains 101 grams per square metre, including 35.4 grams per square metre of chironomids (10,650 individuals). In the "Potopilis" Channel the average biomass at the surface of the spawning mounds was at the end of October 2.16 grams per square metre (amphipods and mayfly larvae), at the end of March, 62.2 grams per square metre, thereof the chironomids constituted 29.9 grams per square metre (9970 individuals). At small falls located between the spawning mounds, in the fall, while the upper layers of pebbles are only slightly silted, the biomass of the chironomid larvae was only 0.27 gram per square metre (678 individuals). Towards the end of March when pebbles are covered with algal foulings, the biomass of the chironomids increases to 37.7 grams per square metre (12,330 individuals) with a total biomass of benthos of 68.8 grams per square metre. Data on the change in the numbers of larvae shown above indicate that the increase in the biomass of the chironomids, in this biotope, takes place basically because of an invasion from other biotopes.

The complex of chironomids living on the spawning mounds is formed of the following forms: Micropsectra gr. parecox, Cricotopus biformis, C. gr. silvestris, Orthocladius semivirens, O. potamophilus, Diplocladius cultriger, Metriocnemus gr. marcidus, Limnophies gr. pusilis, Eukief- /p.123
feriella gr. longicalcar, Smittia ephemerae, Orthocladiinae gen. sp. Diamesa gaedi, Syndiamesa nivosa. Besides the chironomids the stoneflies of the genera Capnia, Isoperla, Arcynopteryx, mayflies Rhithrogena unicolor, Rh. sp. No.1, Cinygmula grandifolia, C. altaica, Paraleptophlebia chocolata, P. lunata and amphipods are common.

Because of the increased migration to the fouling biotopes, from fall to spring a decrease in the biomass is taking place on the stony and stony-sandy grounds, which occupy the major part of the bottom area. In the end of April, when the water is rising, owing to the melting of the snow and to the merging of the exits of the channels to the river, the benthic organisms begin to spread along the bottom. During the May flooding the dissemination processes proceed very intensely, and already in June the biomass of benthos at the falls constitutes 27.4 grams per square metre, and only 0.27 gram per metre are formed by chironomids. On the former spawning mounds in the biotope consisting of pebbles with an admixture of sand the biomass of the epifauna in June is 7.89 grams per square metre including 0.14 gram per square metre (273 individuals) of chironomids. A sharp drop in the

Table 32. Average summer biomass of the benthos in the Georgiyevsk Springs in the channels of the Khor River, grams per square metre.

Groups of Organisms		Falls: Large Stones	Falls: Fine Stones and Pebbles	Falls: Higher Vegetation upon Pebbles with Sand	Rapid section: Stones overgrown with Algae	Reach: Stones and Pebbles	Reach: Stones overgrown with Algae	Reach: Silty Sand	Reach: Stumps and Tree remains	Reach: Pebbles and Sand
Хирономиды	Chironomids	1,32	2,38	5,93	2,94	0,45	50,00	0,66	0,18	1,42
Прочие двукрылые	Other Diptera	0,13	0,37	—	—	0,41	—	—	—	0,06
Поденки	May-flies	8,35	2,46	0,97	15,56	1,74	6,00	0,32	5,51	1,84
Веснянки	Stone flies	0,11	0,12	6,46	1,43	0,18	—	1,81	2,85	0,21
Ручейники	Caddis flies	29,67	9,60	7,13	4,39	2,23	—	0,65	13,05	4,48
Вислокрылки	Alderflies	—	—	0,12	0,03	—	—	—	—	0,05
Жуки	Beetles	0,02	0,05	0,01	—	0,01	0,80	—	—	—
Водяные клопы	Water bugs	—	—	0,19	—	—	—	—	—	—
Бокоплавы	Amphipods	0,50	0,15	0,57	0,23	0,04	—	—	10,28	0,65
Олигохеты	Oligochaetae	0,02	0,08	—	—	—	—	1,20	—	0,20
Пиявки	Leeches	—	—	0,04	2,08	0,84	—	—	—	0,26
Планарии	Planaria	0,10	—	—	—	—	—	—	—	—
Всего без моллюсков	Total without Mollusks	40,22	15,21	21,52	26,66	5,90	56,8	4,64	31,87	9,17
Моллюски	Mollusks	—	6,34	0,52		6,30	41,00	0,14		0,11

chironomid biomass, as well as of a number of other insect larvae is explained, naturally, not only by migration to other biotopes, but also by their flight, as well as by their being devoured by chum fingerlings.

Such dynamics of the biomass evidently observed only on spawning grounds of fall chum with their "dual" regimen are very favourable to the juveniles of fall chum. Chum larvae, on leaving the mounds, come under conditions of high concentration of food organisms and spend minimum energy on food search. In the future the larvæ of late stages and fingerlings are better adjusted to food search and to the defence against enemies, they spread now along the entire spawning ground, like the food organisms do.

Small running water bodies are divided into three groups: streams, rheocrens and rivers running out of limnocrens. In these water bodies, the ground usually consists of pebbles, which are more or less silted, of sandy sections of the bottom and of silt depositions. The aquatic vegetation reaches considerable development in springs running out of limnocrens and rheocrens, but are less developed in streams. Streams emerging from the limnocrens, the farther they are from the outlet, the more do they acquire the character of an ordinary stream. The streams of foothill tributaries, fast-running and with low water temperature, are populated predominantly with the lithorheophile forms. In streams and rheocrens the characteristic feature of the fauna is the diversity of species and the numerical predominance of caddis-fly and mayfly larvae over the larvae of chironomids and stoneflies. In the rheocrens the major form of crustaceans is the *Gammarus lacustris*, the planarians are sometimes numerous. In the rivers and streams emerging from limnocrens, the planarians are also numerous, but of crustaceans it is usually the aquatic isopods that develop (as a rule, the amphipods and the aquatic isopods do not live together). In the upper reaches of these streams the chironomid larvae predominate, these larvae cede their leading position to mayflies and caddis flies in the lower reaches.

Streams and rivers emerging from the limnocrens with their relatively rapid current and low depth illustrate excellently the process called by V.I. Zhadin (1940) the transit accumulation of organic matter. Very considerable food resources formed in the river, as well as those carried out of the limnocrens, are combined with the high concentration of oxygen and with considerable rates of current. Therefore, the breathing and feeding conditions of benthic animals are close to optimum the entire year round.

The Teplovskaya river is a typical example of the stream-river emerging from a limnocren; this river was described in detail earlier (Levanidov and Levanidova, 1962). In hydrology, composition of fauna and in its quantitative development the Teplovskaya River is divided into two sections: the upper section, the so-called Novaya /TR: "New"/channel, which is approximately 0.5 kilometre long, and the lower section, which is approximately 5 kiolmetres long, the so-called Staraya /TR: "Old"/channel. The Novaya channel is connected to the Bira River by means of an artificial river bed, and the main water mass runs along this channel. The pebble and sand bottom of this channel, at the banks and in the extensive bays ("holes") is heavily silted and contains much detritus; algae Rhizoclonium develop here copiously, so do the diatomous overgrowth upon stones, sand and moss. In the central part of the channel occur abundant thickets of pondweeds and hornwort.

The total biomass of benthos in the Novaya channel from December to April is 217 to 228 grams per square metre, in summer and fall it is 300 to 363 grams per square metre. In 1955, the average annual biomass of benthos was 252.5 grams per square metre, of which the chironomid larvae constituted 154.4 grams per square metre, i.e. 60% of the total biomass. The biomass of mayflies is very considerable (Chitonophora sp. No.2, Chitonophora sp. No. 1, Siphlonurus sp.) Among the larvae of the caddis flies predominate Apatania zonella, the predatory Rhyacophila impar and Rh. narvae are rather abundant, less frequently occur the stoneflies Capnia sp. and the orlflies (mainly in the bays). Aquatic isopods and small mollusks form a considerable biomass (Psidium casertanum, Gyraulus acronicus var. sibiricus), the oligochaetae play a somewhat lesser role. Predatory planarians are common and rather numerous: Penecurva sibirica, P. teletzkiana v. longipharyngea, P. mesorchis. The leeches occur rarely. On the whole the biomass of benthos is characterized by a relatively homogenous distribution over all the biotopes (the relative poverty distinguishes only the sections of "naked" pebbles in strong current). This homogeneity is explained by similar conditions of life: the ground of the channel consists everywhere of stones, pebbles and sand with varying degree of silting.

The Staraya channel is poorly connected at the outlet to the Novaya channel; in addition to the latter, it is also fed by emerging spring waters and is a fast-running shallow stream with a small water expenditure; it has a pebbled and slightly silted bottom. Its biomass (table 33) is incomparably lower than in the Novaya channel. The bottom fauna in the Staraya channel, is formed by several ecological groupings. The following caddis flies belong to cold-loving Rhithrophiles (denizens of cool streams and small rivers): Neophylax ussuriensis, Discomoecus palatus, Rhyacophila kardakoffi, Rh. impar, Rh. narvae, Holostomis atrata, Goera sajanensis, Mystrophora intermedia, mayflies: Ephemerella "naz", Ecdyonurus tobliironis, Epeorus aesculus, Cinygmula hirasan, Cinygmula altaica, beetles Oreodytes rivalis and others. To bottom invertebrates, which as a rule are connected to spring waters, belong: caddis flies A. zonella, chironomids Syndiamesa nivosa and Procladius, and, probably, the mayflies Chitonophora sp. No.2. Such species are considerably less frequent here, than near the outlet.

The most numerous group is formed by species occurring in various foothill rivers and in their tributary system. Such species are the caddis flies Arctopsyche amurensis, Stenopsyche griseipennis, Oligoplectrodes potanni, Hydatophylax nigrovittatus, stoneflies Amphinemura borealis, the beetle Gaurodites sp., chironomids Paratendipes albitibia, Prodiamesa olivacea, Cricotopus biformis, Stictochironomus psammophilus, Apsectrotanypus trifascipennis, Procladius sp., mayflies Chitonophora sp. No.1, Ephemerella taeniata, E. basalis, E. ignita, Paraleptophlebia lunata, Thithrogena unicolor, Siphlonurus sp. According to the species composition the chironomids represent an impoverished complex of the denizens of Novaya channel; among other groups many species do not occur near the outlet or occur only in individual numbers.

It is characteristic of the fauna of the both parts of the river that a whole number of species shows a considerable eurytropicity towards the ground (pebbles, silt, detritus), while some species manifest the same also towards the temperature. To such species belong, for example, the mayflies Chitonophora sp. No.1 and Chitonophora sp. No.2.

Table 33.

Average summer biomass of the benthos in streams and rheocrens in the Amur tributaries, grams per square metre.

Groups of Organisms	Streams						Rheocrens	
			Bezymyanny (Basin of Khor River)	Kimsky (Basin of Kiya River)	Staraya Channel (Basin of River Bira) 1957	Staraya Channel (Basin of River Bira) 1959	Ostakan spring (Basin of Amgun' River)	Lopatin Spring (Basin of Bidzhan River)
	Stones	Stones	Pebbles	Pebbles	Pebbles	Pebbles	Pebbles and Sand	Pebbles
Хирономиды Chironomids	0,13	—	0,30	—	1,87	4,32	1,92	1,28
Прочие двукрылые Other Diptera	—	—	—	—	0,88	0,36	—	—
Поденки May flies	1,65	1,22	1,40	—	10,56	9,43	17,41	6,34
Веснянки Stoneflies	0,07	0,01	0,30	—	—	0,75	—	—
Ручейники Caddis flies	—	—	0,70	—	12,19	1,69	2,56	13,22
Вислокрылки Owlflies	—	—	—	—	1,90	0,03	—	0,21
Жуки Water bugs	—	—	—	—	0,08	—	—	—
Бокоплавы Amphipods	0,66	5,55	—	4,03	—	—	3,07	5,11
Олигохеты Oligochaetae	—	—	0,90	3,85	—	2,37	—	—
Планарии planaria	—	—	—	—	—	—	—	0,78
Всего без моллюсков Total without Mollusks	2,51	6,78	3,60	7,88	27,48	19.57	24,96	26,94
Моллюски Mollusks	—	—	—	—	0,21	5,04	—	—

Table 33 indicates that the biomass of benthos in the streams with a pebble and sand bottom is relatively small and is by several times lesser than the biomass of the rheocrens, as well as of the streams and of the rivers emerging from the limnocrens. The cause of the small biomass in the streams is probably caused by the heavy freezing of the latter during the winter and partly by the lesser transportation of organic substances, which do not form any silty deposits in these streams. /p.126

As a rule, the rheocrens are used by the fall chum and by other Amur salmons for spawning; in the streams we merely observe spawning of a few specimens. The ichtyofauna of the rheocrens is not segregated from the ichtyofauna of a river; it consists of small freshwater fishes: Amur and ordinary minnows, and sticklebacks. These fish concentrate during certain seasons (early spring, fall) in the rheocrens, but leave mostly for the rivers during the summer. Besides these fish, the juveniles of lenok and grayling fatten in small quantities in the rheocrens.

The limnocrens are extraordinary original and productive spawning water bodies of fall chum; they are distinguished by high biomass of benthos. A typical limnocren and simultaneously also an important spawning ground of fall chum is the Teploye Lake; we have described it earlier (Levanidov and Levanidova, 1962). Therefore, we will not discuss its hydrological conditions in detail here, but we will merely remember that the main characteristic feature of the limnocrens is the stability in the conditions of the medium (small amplitudes of seasonal and diurnal temperature fluctuations, low oxygen content in the water, increased carbon dioxide concentration, high transparence, circulation of water and an almost unchangeable water level).

In the Teploye Lake we find all the grounds and growths of aquatic vegetation, as in the river emerging from this lake, but the biotopes corresponding to these are distinguished by an almost complete absence of current*), although the water circulation is considerable (the entire volume of water is renovated from 1.2 to 1.9 times per 24 hours). However, even this movement of water is sufficient for the transportation of dissolved oxygen and life products.

Thus, the Teploye Lake, like all the limnocrens in general, is characterized by the presence of biotopes that are intermediate ones according to the environmental conditions of the running and the stagnant water bodies. The degree of circulation determines the distribution of grounds and of the population. Thus, the left-bank part of the lake, where the main water flow runs, the bottom is covered with a thick layer of productive silt with an admixture of sand upon underlying pebbles. This zone has many common forms of invertebrates to the denizens of silt in a river running from a limnocren, but the species composition and the biomass of this zone's benthos is considerably poorer. The population of silts in the circulating part of the limnocrens belongs ecologically to the pelo(rheo)philes (According to V.I. Zhadin). The current, in the conditions under which these species live in the river, is, consequently, not a necessity to them. A typical representative of this group is the abundantly-occurring species of the chironomids <u>Stictochironomus psammophilus</u>.

The right-bank part of the Teploye Lake is distinguished by a thick <u>layer of poorly mineralized</u> silt with a considerable admixture of coarse

*) A noticeable current is observed only near the outlet from the lake; in other sections it equals one centimetre per second.

detritus. The benthofauna is basically formed of eurythermal pelophiles, it is relatively poor in species, the biomass of the benthos is relatively small. The complex of organisms living here may be called pelophilic. Compared with the pelophilic population of the bays and small lakes it is considerably poorer (a result of the selective effect of the thermal conditions).

The population of the biotopes of the vegetation (higher and filamentous alga) consists basically of phytophiles and detritophiles (aquatic isopod) and of phyto(rheo)philes, to which among the abundantly occurring forms belongs the caddis fly *Apatania zonella*. The biotopes of the vegetation and of the silts cover 80 to 90% of the limnocren area. The remainder is constituted by the stony and pebbled grounds. The silted pebble grounds are developed in the shallow part of the limnocren near the outlet. Owing to the current the leading role in the benthos is played by forms characteristic of the channel, /p.127 such as *Syndiamesa nivosa*, *Paratendipes albitia*, the biomass of which is great.

As data in table 34 show, even the poorest biotopes of the poorly silted stones and of the black silt, exceed considerably in the biomass the majority of river biotopes. A characteristic feature of the biomass of benthos in limnocrens is the domination of chironomid and oligochaeta larvae and the relatively small importance of mayflies, caddis flies and stoneflies. Often the biomass of the aquatic isopods and of the amphipods is very considerable. Compared with the river benthos, the limnocren benthos is more accessible to the chum fingerlings in respect to the dimensions of the invertebrates and to a considerable degree may be classified as belonging to the food benthos category. However, the availability of food invertebrates is decreased by the fact that a number of forms live in the silt, where the chum fingerlings cannot reach them. The chironomids, however, become an easily available food at the pupal stage when they float up to the surface of the water body.

Semimountaneous Sections (the Upper Reaches) of Large Tributaries of the Amur River (Cold-water Type).

In the semimountaneous sections of rivers the grounds with predominant large-stone fractions occur most extensively, although pebbles of various dimensions remain as their constant component.

The species composition of the bottom population of these grounds consists of an impoverished lithorheophile complex of foothill areas; the forms sensitive to the decrease in water temperature and to the increase in the current rate are sifted away, these forms populate not merely the foothill rivers but also the flatland ones.

The upper reaches of large tributaries being the least accessible for regular studies are considerable less known, than the other sections of the rivers. The average biomass of the benthos of stones in the upper reaches of the Iman and Khor Rivers is, according to the few available data, 2.56 grams per square metre, consisting of the following components: caddis flies: 0.89, mayflies: 0.72, stoneflies: 0.2, chironomids: 0.46, larvae of black flies: 0.03, larvae of other diptera: 0.26 gram per square metre; only individual oligochaetae and amphipods were found.

The numbers of salmons spawning in the foothill sections are small and the lower is the percentage of pebbles in the pebble-and-stone ground, the fewer salmons spawn here.

According to the average indices of the biomass the semimountaneous areas of large rivers in the Amur basin are close to the semimountaneous streams of the Transcarpathia, for which V.S. Ivlev and M.V. Ivasik (1961) show a biomass of benthos of 1.8 to 3.46 grams per square metre, as well as to the stone and pebble grounds of the rivers in the Kola Peninsula, where the average biomass according to V.I. Zhadin (1940) is 2.25 grams per square metre.

Foothill rivers (cold-water type) possess considerably lower depths, than the foothill sections of the large tributaries. Therefore, even at comparatively small rates of flow (0.5 to 0.8 metre per second) the movement of water distinguishes itself by such a high turbulence, that an impression of a turbulent stream is created.

S.G. Lepneva (1949a) writes about similar small running water bodies: "...in the majority of cases these are small turbulent and foaming torrents, however, the rate of current seldom rises in them to more than one metre per second."

At almost the identical rate of current (1 to 1.3 metres per second), characteristic of the Lower Amur, the movement of water takes place smoothly and, seemingly, not too fast, while in the Khor River's lower reaches, where the water moves at a speed of 2 metres per second, the movement remains an impetuous but smooth stream. The increased turbulence, apparently, ensures the intense exchange of suspended substances and deposits between the water and the bottom, i.e. it ensures an increased transportation of organic substances for benthic organisms.

In the foothill rivers the lithorheophile biocoenoses also predominate and occupy about 80% of the bottom area. The average size of stones forming /p.129

the ground of the river bottom is 50 to 60 square centimetres. At the falls over stony ground we often find algal or mossy overgrowth. In the foothill rivers a relatively greater area is covered by sandy-stony grounds (about 10%), as well as by sandy-silty grounds, than in the foothill sections of large tributaries. In the sandy-silty biotope, owing to the constant admixture of the detritus, besides the pelopsammophiles a considerable part is played by detritophile forms.

A distinctive characteristic of the bottom fauna in the foothill rivers in the Amur basin is the extensive distribution and a considerable biomass of the larvae of simuliids and of diptera of the Blepharoceridae family. The species composition of the larvae of caddis flies, mayflies, stoneflies, mollusks and of oligochaetae does not differ from the species composition in analogous biotopes of the large tributaries, but the numerical ratios between the individual species are different.

As examples, let us discuss data on the biomass of the benthos of some of the foothill rivers located in different sections of the spawning area of the Amur salmons.

The Nemptu River enters the Amur River from the latter's righthand bank slightly below the city of Khabarovsk. It starts in the mountains of the Sikhote-Alin.

The fauna of invertebrates developing in the algal overgrowth of stones is distinguished by its exceptionally high biomass (table 55). Larvae of the chironomids Diamesa gr. prolongata constitute here a biomass of 110 grams per square metre, while Orthocladius gr. saxicola constitutes 50 grams

Table 34. Benthos biomass in the limnocrens, grams per square metre.

Groups of Organisms	Teploye Lake (Bira River): End of June – Beginning of July	Teploye Lake (Bira River): Annual Average					Bidzhan Spring (Bidzhan River), end of September				Svetly Spring (Nemptu River); May		Orekhov Spring (Khor River) June, July, August		Ivanov Spring (Iman River), July
	Faintly silted stones at ground water outlets	Silty pebbles	Grey silt	Higher vegetation on silty sand	Silty sand at the ground water outlets	Dark silt with coarse detritus	Silty pebbles	Silt	Higher vegetation on silty sand	Silty sand	Silty pebbles, hornwort	Silty sand, detritus	Silty stones and pebbles	Higher vegetation on silt	Viscose dark silt
Хирономиды Chironomids	0,01	95,04	27,00	9,00	89,16	4,48	21,58	19,50	61,62	99,84	44,20	24,54	9,20	35,31	0,52
Поденки Mayflies	0,11	—	—	—	—	—	6,24	9,36	15,08	0,26	62,92	5,98	—	0,52	2,85
Веснянки Stone flies	2,16	0,54	—	—	—	—	—	—	—	—	13,52	1,82	—	—	—
Ручейники Caddis flies	5,53	5,43	0,72	5,40	0,72	—	20,54	—	26,26	4,94	2,86	—	0,51	—	31,98
Вислокрылки Alderflies	—	—	4,02	—	—	—	—	43,42	9,10	6,50	5,46	14,56	—	2,08	—
Личинки жуков Beetle larvae	1,25	—	—	—	—	0,96	—	—	—	—	—	—	—	—	—
Олигохеты Oligochaetae	0,03	4,50	0,42	7,42	13,44	1,34	44,20	1,56	11,70	3,12	13,52	5,98	0,51	45,49	2,04
Пиявки Leeches	7,43	2,00	11,00	6,75	0,36	7,52	—	—	—	—	—	—	0,32	0,70	—
Водяные ослики Aquatic Isopoda	0,73	5,90	4,80	92,84	9,60	7,01	—	—	—	—	—	—	—	—	—
Бокоплавы Amphipods	—	—	—	—	—	—	5,20	—	4,68	—	13,52	62,66	0,62	—	—
Планарии Planaria	0,12	1,96	2,02	2,47	—	—	—	—	0,52	—	7,80	—	—	—	—
Всего без моллюсков Total without Mollusks	17,37	115,37	49,98	123,88	113,28	21,31	97,76	73,84	128,96	114,66	163,8	115,54	11,16	84,10	37,40
Моллюски Mollusks	3,80	24,48	10,02	99,00	6,00	11,14	8,84	10,42	7,02				0,22		36,66

per square metre and the mayflies of the genus Ephemerella (E. basalis and others), 20 grams per square metre. The beetles Anacaena limbata were found in this biocoenosis only. The high biomass of the ripal, particularly of the tree remains, is usually composed of large larvae of the caddis flies Hydatophlax nigrovittatus and of mayflies Ephemerella taeniata.

In the tributary system of the river and in its tributaries (that are considerably lesser than the river itself) the biomass of the benthos is higher than in the river bed. Thus, the lithorheophile biocoenosis of the river channels gives a biomass of 30.3 grams per square metre, a considerable portion of which (18.4 grams) is comprised of the larvae of the black flies Simulium sp. sp. The biomass of the chironomid larvae is relatively high here (2.3 grams per square metre). The biomass of the caddis flies and of the mayflies in the branch channels is somewhat lower than in the main river channel.

The population of the sandy-silty grounds and of detritus in the tributaries and in the river bed has a high biomass. In the branch channels and in the tributaries it is mainly comprised of mollusks, while in the river bed predominate the larvae of caddis flies and of mayflies. The following species are common here: the mayflies Heptagenia soldatovi, Paraleptophlebia chocolata and various Ephemerella, the caddis flies Hydatophylax magnus and H. nigrovittatus, the mollusks Semisulcospira cancellata and particularly S. libertina.

Certain ideas concerning the seasonal dynamics of the biomass of the benthos present the following figures. The biomass in May and June was 20 grams per square metre (average value of 32 samples) and at the end of October, 15.1 grams per square metre (15 samples).

The My River studied by L.V. Kokhmenko which runs into the Amur liman south of the Amur estuary also belongs to the foothill type. The summer water temperature in the My River is relatively low: in May it is 0.2 to 4°C; in June, 6.7 to 9.4°C; in July 9.7 to 13.4°C. This river belongs to the liman type of rivers, which are still visited by a rather considerable number of salmons. The biomass of benthos in the My River is also high (table 36).

A characteristic feature of the benthos in the My River is the ubiquitous occurrence and the high numbers of the chironomid larvae. Among the lithorheophiles the larvae of the subfamily Orthocladiinae and in particular of Syndiamesa nivosa and S. orientalis predominate. Very numerous are also the Tanytarsini, particularly Micropsectra gr. praecox that plays the basic role in the biomass of benthos in the overgrowth, as well as Tanytarsus gr. mancus. The psammophiles and the pelophiles are mainly represented by Cryptochironomus borysthenicus, Polypedilum (Chironominae gen. No.3 Lipina), P. breviantennatum and P. gr pedestre. In the algae and mosses*) overgrowing the stones in the current, live in addition to the chironomids also larvae of caddis flies Micrasema, of mayflies Siphlonurus zetterstedti, Paraleptophlebia lunata and Baetis sp., the aquatic isopods and the oligochatae (Tubificidae gen. sp.). The larvae of the caddis flies Goera sajanensis, Arctopsyche palpata, Rhyacophila kardakoffi predominate on the stones; the mayflies are mainly represented by the family Ephemerellidae (Ephemerella

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*) Solid algal overgrowths (Draparnaldia, Ulothrix, blue-green algae of the order Hormonalis and others) with abundant population are very characteristic of the tributary system of the My River with slow current.

taeniata, Chitonophora mucronata). The Iski River is close in hydrological conditions to the My River, this river issues into the Schastye Gulf located north of the estuary of the Amur River. Studies of this river were carried out by L.V. Kokhmenko. The Iski River belongs to the cold-water foothill type, contrary to the My and Nemptu Rivers, the aquatic vegetation (overgrowth) is considerably more abundantly developed. The biomass of benthos in the Iski River is also high (table 37).

The seasonal fluctuations in the biomass of benthos on the stony, and on the pebble and sand grounds of the lower reaches of the Iski River (in grams per square metre) are the following: at the end of June and in the beginning of July, 23.1 (average value of 18 samples), in August, 38.4 (39 samples), and in September, 50.3 (6 samples).

The biomasses of benthos of the basic stone and pebble and other biotopes in the Iski and My Rivers are very close. In the Iski and My Rivers, even today, entering populations of pink salmon and summer chum number more than one million. The food base of summer chum fingerlings (pink salmon fingerlings feed very poorly in the liman rivers) is very great in these rivers; it mainly consists of the larvae of chironomids and aquatic isopods, to a lesser degree, of small larvae of mayflies and stoneflies. Besides the Pacific salmons multitudinous populations of Dolly Varden char and Siberian char fatten in these rivers, together with some non-migrating fish that feed upon benthos.

Table 35.

Benthos biomass in the Nemptu River and in its tributary Si during the second half of May and in the first half of June, grams per square metre.

Group of Organisms	Ripal				Medial			Si
	River Branch	Rapid Section	Reach		Falls		Rapid Section	River bed
	Slightly silted sand	Silty sand with detritus admixture	Pebbles with sand	Sand	Stones and pebbles	Stones overgrown with algae	Stones and pebbles	Silt and detritus
Хирономиды Chironomids	2,34	1,04	0,39	—	0,16	160,42	0,31	0,52
Мошки Black flies	18,40	—	—	—	1,91	—	1,45	—
Личинки др. двукрылых Larvae of other diptera	4,46	4,33	0,91	—	1,07	0,26	1,27	—
Поденки May flies	1,10	25,88	2,99	3,46	2,46	20,02	2,68	35,10
Веснянки Stone flies	—	0,17	0,13	—	0,20	—	0,83	—
Ручейники Caddis flies	3,90	19,02	0,65	—	0,56	—	7,03	—
Водяные жуки Water beetles	—	—	—	—	—	0,52	—	—
Бокоплавы Amphipods	—	3,97	2,34	—	0,21	—	0,17	—
Олигохеты Oligochaetae	—	0,73	—	1,56	—	—	—	2,60
Всего без моллюсков Total without Mollusks	30,20	56,14	7,41	5,02	6,57	181,22	13,74	38,22
Моллюски Mollusks	—	0,21	—	—	0,62	—	2,07	60,51

Table 30.

July biomass of benthos in the Ily River, grams per square metre.

Group of Organisms	River Branch	Ripal			Medial			
		Rapid section		Reach	Falls	Rapid Section		Reach
	Silty pebbles with sand.	Silty sand	Sand	Sand and detritus	Stones, overgrown with moss.	Stones and pebbles	Pebbles with sand	Shallow pebble, Detritus
Хирономиды Chironomids	1,30	17,91	2,08	15,92	17,47	2,86	6,55	6,11
Мошки Black flies	—	—	—	—	0,13	—	—	—
Личинки др. двукрылых Larvae of other Diptera	—	0,65	—	—	0,36	—	0,16	35,36
Поденки May flies	—	0,52	2,38	11,22	6,94	0,69	2,90	—
Веснянки Stone flies	—	—	—	0,43	1,13	0,17	0,39	—
Ручейники Caddis flies	25,22	—	—	3,97	9,44	26,64	3,20	1,43
Вислокрылки Celflies	—	—	—	—	1,17	—	—	—
Клещи Mites	—	—	0,63	0,30	—	—	0,05	—
Бокоплавы Amphipods	—	—	—	1,65	0,51	—	—	—
Олигохеты Oligochaetae	1,04	0,13	2,02	5,53	2,41	—	6,02	6,16
Водяные ослики Aquatic Isopoda	—	—	3,85	0,09	19,53	—	0,26	2,28
Всего без моллюсков Total without Molluscs	27,56	19,21	11,02	39,11	59,09	30,36	21,53	51,34
Моллюски Mollusks		98,00	1,04	—	1,39	—	—	—

Table 37.

Average Summer Biomass of the Benthos in the Iski River (in grams per square metre).

Groups of organisms	Falls			Reach				Malaya Iska River, river bed
	Stones and pebbles	Pebbles with sand	Silted pebbles	Sand	Silted sand	Sand and detritus	Stones fouled by algae and moss	Pebbles with sand
Chironomids	1.49	0.26	3.64	3.61	12.69	11.83	7.58	0.43
Black flies	1.15	-	-	-	-	-	-	-
Other diptera	1.61	2.45	1.65	0.07	0.68	-	-	43.68
Mayflies	4.66	2.96	1.21	0.39	3.25	1.82	11.78	8.79
Stoneflies	1.01	0.33	-	-	0.18	0.52	-	0.69
Caddis flies	23.68	2.60	4.16	0.19	0.86	1.98	0.65	1.04
Orlflies	-	-	-	-	0.20	-	-	-
Water bugs	0.01	-	-	-	-	-	-	-
Mites	0.02	0.13	0.08	0.07	0.18	-	-	-
Amphipods	0.02	1.56	-	0.39	0.29	1.75	0.65	1.65
Oligochaetae	0.12	0.36	3.99	0.78	3.24	2.15	3.25	-
Leeches	0.07	-	-	-	-	-	-	1.65
Planarians	0.10	-	-	-	-	-	-	-
Aquatic isopods	-	-	7.11	-	-	-	-	-
Total without mollusks	33.94	10.65	21.84	5.53	21.57	20.05	23.91	57.93
Mollusks	-	-	4.42	0.59	0.62	8.06	1.69	-

It may be assumed that in such small rivers as My and Iski, when /p.133 populations of millions of salmons multiply in them, that the productivity of the water body increases because of an introduction into it of organic and mineral substances with the bodies of salmons dead after the spawning (Krokhin, 1959). Evidently, the high biomass of the benthos in the liman rivers compared with larger tributaries of the Amur River is partly explained by this introduction.

Semimountaneous rivers (of cold-water type) include tributaries of the Khor, Imana and Bikin Rivers, as well as the Khivanda, Gera, Khilka and Beshenaya Rivers, the tributaries of the lower reaches of the Amgun', of Somnya and of Nizhnyaya Uda. In quantitative respect the benthos of these rivers is relatively poorly studied. In the Nizhnyaya Uda the low biomass of the caddis fly larvae (table 38) in the biotope of pebble grounds is explained by the fact that the collections were carried out by a strathimetric tube which only caught fine pebbles (less than five centimetres). Large larvae of caddis flies constitute the basic part of the benthos of the stones and are very important in the biomass of the stony grounds. Thus, five samples (in table 38, these are not included) from medium-sized and small stones have shown that the caddis flies Arctopsyche palpata, Rhyacophila impar, Hydropsychinae sp, sp, predominate upon them; the total biomass was 14.3 grams per square metre. The larvae of the diptera of the Blepharoceridae family occur in considerably lesser numbers, 4.1 grams per square metre and the larvae of the mayflies Heptageniidae, 1.1 grams per square metre (Cinygmula sp. and others).

The total biomass of benthos on the stones in the Nizhnyaya Uda River constitutes (according to five samples) 20.5 grams per square metre, in other words, the biomass in the foothill sections of large tributaries and in the small foothill tributaries of the Amur River is identical.

The Khivanda River, a right-bank tributory of the Amur, is a typical cold-water river of the semimountaneous type; the summer temperature of water does not exceed 13°C. In the Khivanda River all forms of the Amur salmon are multiplying, but only relatively few masu salmons or fall chums enter this river, the summer chum and pink salmon predominate. Only the lower reaches (approximately 2 kilometres) of this river are covered by quantitative hydrobiological studies; this part of the river constitutes a very considerable portion of its spawning stock.

The Knivanda River, in its lower reaches, is a rapid and shallow river with blurredly pronounced falls and reaches, ripal and medial. Owing to a poor morphological segregation of the river bed a distinct topological /p.134 division of the invertebrates belonging to various ecological groupings is absent. The bottom is almost everywhere of stone and pebbles; there are many tree stumps carried away by the current one may judge the composition and the abundance of animals in the studies section of this river by means of data in table 39.

Table 38.

The Average Summer Biomass in the Nizhnyaya Uda River (Tributary of the Amgun' River), in grams per square metre.

Groups of Organisms	Ripal					Medial	
	fall	reach				fall	reach
	pebbles with sand	sand	silted sand	open bay, highest vegetation	sand with detritus	pebbles	pebbles
Chironomids	0.88	0.61	0.64	0.05	0.87	0.04	0.77
mayflies	7.54	0.23	41.61	10.50	67.32	1.92	0.85
stoneflies	1.50	0.13	0.20	0.03	1.30	0.43	0.60
caddis flies	0.59	-	0.59	2.08	3.69	0.13	-
orlflies	-	0.01	3.11	-	-	-	-
dragonflies	-	-	-	-	1.95	-	-
Water bugs	-	-	-	-	0.02	-	-
water mites	-	-	0.21	0.03	-	-	-
amphipods	2.41	0.21	1.62	0.02	2.67	2.30	5.50
oligochatae	-	3.27	0.43	2.85	6.83	1.62	3.29
leeches	-	-	-	-	0.45	-	-
aquatic isopods	0.07	-	3.40	3.62	0.43	0.17	-
Total without mollusks	12.99	4.45	51.81	19.18	85.53	-	-
mollusks	-	-	9.56	3.55	-	6.61	11.01

For the extensive stone and pebble section of the rapids and falls the following forms are characteristic; on the one hand, the typical forms of the falls: mayflies Iron maculatus, Epeorus latifolium, Ephemerella lepnevae, larvae of diptera: Simulium and Bibiocephala, caddis flies Mystophora, Arctopsyche palpata, and on the other hand, denizens of areas with slow current and backwater places: larvae of mayflies Baetis thermicus, Ephemerella taeniata, Chitonophora mucronata, caddis flies Rhyacophila impar, Rh. narvae, Rh. retracta, Lepidosta hirtum, Agapetas sibiricus, Goesa sp., larvae of chironomids. The invertebrates of the second group are located behind stones circumfluxed by water, below such stones in dead zones formed between vortexes, and in the overgrowths. On stones overgrown with algae (preferably diatomous algae), the larvae of the mayflies Ephemerella triacantha, E. basalis, and species of Rhithrogena are numerous; larvae of chironomids: Tanytarsini, Diamesa gaedi; the amphipods constitute up to 80% of the biomass by weight.

The tree stumps are exceptionally densely populated, in particular with the larvae of the caddis-fly Hydatophylax nigrovittatus; larvae of the mayflies Ephemerella taeniata, Chitonophora mucronata, Ameletus montanus, amphipods and large stoneflies Pteronarcys reticulata are also numerous here.

Warm-water Flatland Rivers.

Such rivers occur most extensively in the basin of the Ussuri and the Middle Amur Rivers. These are short and shallow rivers with a small basin, they run through an area with flatland relief. Usually in the upper reaches of the basins of such rivers, we find rivers and streams of the foothill type, while in the tributary system we have tributaries with pebbled

Table 39.

Biomass of the Benthos in the Lower Reaches of the Khivanda River in the End of June and in the Beginning of July, (in grams per square metre).

Groups of organisms	Ripal						Medial	
	Fall		Reach				Rapids	Fall
	Stones and pebbles	Gravel and detritus	Stones and pebbles	Sand and gravel	Silted sand	Detritus and sand	Stones and pebbles	Stones overgrown with algae
Chironomids	2.00	0.05	0.29	0.10	0.10	7.80	0.08	0.10
Black flies	4.40	0.02	1.22	-	-	-	-	-
Larvae of other diptera	-	3.00	-	-	-	-	-	-
Mayflies	7.00	2.40	0.46	-	-	-	7.94	8.75
Stoneflies	-	6.60	-	-	-	-	5.76	0.65
Caddis flies	-	1.38	-	10.20	-	5.46	5.45	0.38
Amphipods	-	5.06	-	-	-	5.72	-	47.75
Oligochaetae	-	-	-	-	9.10	-	-	-
Plenarians	-	0.22	-	-	-	-	-	-
Total	13.40	18.73	1.97	10.30	9.20	19.98	19.23	57.63

bottom and even limnocrens; in the river beds we have sections of pebbled ground with outlets of ground waters, that sometimes are powerful outlets.

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The fall chum enters such rivers in small numbers to spawn. Apparently, the Kiya River, which runs through the same valley as the Khor River, had the greatest importance for the spawning among rivers of such type. According to information of V.K. Soldatov (1915), in the years before the war, up to 50,000 fall chums were caught annually in this river.

High development of aquatic vegetation is a characteristic of these rivers. A characteristic river of this type is the Kiya River mentioned above. Stony grounds occupy only small areas in the latter and are located at short falls only. The main areas of the bottom in the lower and middle reaches of the Kiya River are occupied by heavily silted pebbled grounds. In this biotope, which is the basic one in the Kiya River, the pelo(rheo) philes predominate.

The richest biotopes are the pebbled and pebble and sand sections of the bottom (table 40); the biomass of benthos in other biotopes is relatively small and is inferior to the biomass of analogous biotopes in the cold-water rivers.

According to the data of the Moscow University expedition (Borutsky, Klyuchareva, Nikolsky, 1952) the biomass of benthos in the flatland rivers running out into the Khanka Lake and into the Ussuri River (without large mollusks) reaches one to seven grams per square metre, but most often is determined by a value between 1 and 2 grams per square metre, in other words, it is close to the biomass of the psammorheophile and pelodetritophile complexes of the Kiya River.

Table 40.

Biomass in the benthos in the Kiya River at the end of July, (in grams per square metre).

Groups of organisms	Ripal reach	Medial				
		Fall	Reach			
	Silt and detritus	Pebbles	Sand and pebbles	Silted pebbles	Silted pebbles and detritus	Silted sand
Chironomids	-	-	-	1.22	2.00	-
Larvae of other diptera	0.21	-	-	-	-	-
Mayflies	-	8.16	12.02	3.08	0.40	6.39
Stoneflies	-	0.68	-	-	-	-
Caddis flies	-	1.36	-	-	-	1.36
Dragonflies	0.21	-	-	0.91	-	-
Amphipods	-	1.36	1.50	0.36	-	1.77
Oligochaetae	1.09	1.36	2.21	1.54	0.45	-
Total without mollusks	1.51	12.92	15.73	7.11	2.85	9.52
Mollusks	-	-	-	-	-	3.00

The benthofauna in the Kiya River, regardless of the presence of common species, differs sharply from the fauna of cold-water and temperate-cold-water rivers. Here predominate the thermophile representatives of the southeastern zoogeographic complex and the eurythermal palearcts. Among mayflies the major forms in the foothill rivers, the Heptagenia arsenjevi and H. soldatovi, relinquish their leading position to H. yoshidae; the large Epeorus latifolium are common and abundant at the falls. Polymitarcys virgo, Ephemera amurensis, Ephemera sachalinensis, Isonychia japonica, and the representatives of the Brychyceridae family are characteristic of the silty-sandy ground. The larvae of the mayflies Choroterpes trifurcata are characteristic of the sandy-stony grounds. The species composition of the Ephemerellidae is rich and original: Ephemerella lenoki, Ephemerella "naz", Ephemerella ignita and some more still undescribed species. The following caddis flies are characteristic of the macrophytes, which in places attain copious development (pondweeds, water chestnut, water lillies, cowlillies, water buckwheat and others): Phyraganea sinensis, Anisocentropus pallidus, Oecetis testacea, larvae of the butterlies Nymphula sp., larvae of the dragonflies Agrion glaciale, A. lanceolatum. On the silty-detritus ground and on the tree stumps live caddis flies Ganonema extensum, Oecetis notata, on the finely stoned ground with an admixture of detritus live large /p.136
larvae of Leptocerus sp. Birulia (Oecismus) orientalis. Stones and pebbles at the falls are populated with larvae of the caddis flies Stenopsyche bergeri, Macronema radiatum, Plectronemia sp. and others. At the sandy shallows, in the silted bank area and in the silted pebbles we find the mollusks Semisulcospira concellata, dragonflies Nihonogomphus heterostylus in abundance. In silty grounds live various oligochaetae: Peloscolex

nikolskyi, P. apapillatus, Lumbriculidae gen. sp. On tree stumps and in thickets of vegetations, sometimes among the silty pebbles, occur large larvae of the Japanese species of the dragonfly Macromia amphigena.

Among the small rivers of the flatland type of considerable interest is the Birushka River, a left-bank tributary of the Kiya River; this river runs between the Kiya and the Khor. It is a small river, 25 kilometres long; its basin is extremely small. The Birushka is fed with ground waters, which enter from springs along its upper reaches. This explains the constant water level in the Birushka (annual amplitude in the lower reaches are less than 50 centimetres). In summer the water of this river warms up to 25 or 28°C, in winter, rapid open falls remain along the entire length of the Birushka. Chum spawns in the lower reaches of the Birushka, but without rising higher than 5 kilometres from the estuary.

A characteristic feature of the grounds in the Birushka is the relative predominance of the medium-sized and large stones over the small stones and pebbles, this predominance is particularly sharply pronounced at the falls. It may be assumed that in the recent past the upper reaches of the Birushka were connected to the Khor River, and the former was an impetuous channel, from the falls of which fine pebbles were carried away. With the deepening of the Khor's river bed and lowering of the erosion base, the upper reaches of the Birushka became isolated from the Khor, the amount of water running through it decreased and it turned into a flatland river with quite moderate rates of current, even at the falls, and with a ground consisting of large stones. Apparently, the constant level and the character of the ground determine the high biomass of the falls in the Birushka, where the larvae of caddis flies are very abundant (table 41).

Table 41

Average Summer Biomass of Benthos in the Lower Reaches of the Birushka River. (in grams per square metre).

Groups of organisms	Falls		Bays and reaches	
	Large stones and pebbles	Pebbles and sand	Silted sand	Higher vegetation
Chironomids	0.48	-	-	-
Mayflies	4.34	17.27	0.13	-
Caddis flies	61.74	12.33	-	-
Amphipods	4.61	4.34	-	-
Oligochaetae	-	-	2.71	0.82
Leeches	-	-	8.02	-
Planarians	1.46	-	-	-
Aquatic isopods	0.04	-	-	-
Total without mollusks	72.67	33.94	10.86	0.82
Mollusks	17.20	-	-	38.90

Low water depth in this biotope at constant level creates favourable conditions for the existence of large and poorly mobile forms. The biomass of the larvae of the caddis fly Macronema radiatum, at the beginning of July, constitutes 35 grams per square metre, and of Stenopsyche bergeri, 16 grams per square metre. In addition to these two major-occurring species the stones are populated with larvae of Rhyacophila kardakoffi, Goera sp.; on the silted stones and tree stumps live Ganonema extensum; Limnophilus correptus, Stenopsyche sp. and others. Among the mayflies Epeorus latifolium, Ephemerella lenoki, Ephemerella sp. No.1 ("naz"), Heptagenia yoshidae, Polymitarcys virgo and others are numerous. Large mollusks Semisulcospira cancellata, Viviparus ussuriensis stay on the silted stones and among the vegetation. /p.137

On the average the biomass of benthos (without mollusks) was on stones and large pebbles: 98 grams per square metre at the beginning of June, 52.5 grams per square metre at the beginning of July, 13.4 grams per square metre on the fine-pebbled silted ground in August. The species composition of the bottom invertebrates is almost identical to the fauna in the Kiya River, but quantitatively the benthos is much richer. In the Bishkura River, like in the Kiya River, live thermophile fish: crucian carp, carp, snakehead, Opsaliichtis sinensis, also many pikes stay here.

Concluding the quantitative characteristics of the benthos in various typological sections of the Amur tributaries, let us determine the place the Amur tributaries have among other rivers with hard ground bottom. Published on the biomasses of benthos of such rivers are few. We find the following figures in the substantial monograph of V.I. Zhadin (1940). In Caucasus, in the Tskhal-Tsiteli River, this biomass is 4 grams per square metre; in the Karelian rivers, from 0.2 to 13.2 grams per square metre; in the Valdayka River (Central Russian Elevation), 2 grams per square metre. According to D.I. Kurvanidze (1949) the biomass of benthos on stones is in the Bakurianka River (Caucasus) from 6 to 20.7 grams per square metre.

The average biomass of the lithorheophile benthos on the pebble and boulder ground of the Atlantic salmon river Podcheryom (tributary of the Pechora River) constitutes 3.6 grams per square metre (Zabolotsky, 1959). The biomass of the lithorheophile biocoenoses of pebble grounds in the upper reaches of the Yenisey River is 2.2 grams per square metre, of the middle and lower reaches it is 0.7 gram per square metre (Greze, 1957). The biomass of the lithorheophile biocoenoses of the upper reaches of the Dnestr River (Yaroshenko, 1957) is 4.4 grams per square metre, 40% of the numbers of the benthos is comprised of mollusks.

While studying the mountain rivers of the Transcarpathia, the population of which consists almost exclusively of lithorheophiles, V.S. Ivlev established that their biomass fluctuates between 1.8 and 6.3 grams per square metre, reaching in individual cases 25 grams per square metre. This author points out that the biomass in small mountain rivers is higher than in the large ones, and that the slower the current is and the larger the ground particles are, the more abundant is the benthos. It should be noted that the latter conditions do not correspond to the typical relations in mountain rivers between the ground and the current. As a rule, the faster is the current, the larger are the particles of the ground, since the relatively small particles under such conditions are dragged along the river bottom. The conditions, pointed out by this author, may exist either in a stream running though a large-stone bed, or in those instances, when the water mass in the river or a river channel sharply decreased, but no increase in the small fractions has yet occurred.

A.A. Sadovsky (1949, 1963) established that in mountain rivers in Caucasus the biomass of benthos decreases from the upper reaches down to the estuary.

Recently appeared an extremely interesting and comprehensive work of N. Yu. Sokolova (1963), in which information is presented on the biomass of the lithorheophile benthos in the upper reaches of the Moscow River. At stony falls the biomass is 18.9 grams per square metre, including 7.2 grams per square metre of mollusks. The stony-sandy falls populated with psammolithorheophile complex were poorer, the biomass of benthos here was 9.1 grams per square metre.

Regardless of the small volume of the compared material, one may apparently assume that the complexes of lithorheophiles populating the basic areas of the bottom in the salmon tributaries of the Amur River attain a greater quantitative development than those in various rivers of the European part of the USSR and of the Siberia.

In the tributaries of the Amur River the maximum biomass of the lithorheophile benthos is observed at shallow falls with small speed of current and with a large-stone bottom. The deeper the fall, which gradually changes into rapids, the lower is the biomass of benthos. As a rule, the biomass of benthos is greater on the stony ground than on the pebbled ground; the fine pebble and gravel biotope is particularly poor in benthos.

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Psammo-lithorheophile complexes of the bottom population of the Amur River approximate in biomass (6.7 to 13 grams per square metre) the complexes in the Moscow River and are considerably richer than the complexes of the Yenisey River (0.2 to 0.4 gram per square metre).

The pelophile benthos in the tributary system of the Amur tributaries attains its highest development in the limnocrens, where it equals the most productive water bodies of the floodland in flatland rivers in the European part of the Soviet Union. Thus, the biomass in the floodland of the Oka River (excluding the mollusks) constitutes according to V.I. Zhadin (1940) from 133 to 153 grams per square metre, and of the Volkhov River, 38 grams per square metre.

Long-Term Fluctuations in the Biomass of Benthos in the Tributaries of the Amur River.

The late 1940-ies, when our studies were initiated, were a period of a relative shallowness in the tributaries of the Lower and the Middle Amur and in the Ussuri Rivers.

In the Khor River, the lowest summer water expenditures comprising only 48 to 75% of the average long-term expenditures were observed in 1949, 1950 and in 1951 (in August 1951 a considerable flooding took place). In the Iman River the period of low expenditures covered the years 1947 to 1951 (again, except the 1951 fall flooding) and in July, 1949 and 1951, as well as in June, 1950, the water expenditures were only 0 to 25% of the long-term average.

The average annual water expenditures in the Khor River, in 1949, was 64% of the long-term average, and in 1951, it was 70%. In the Irman River the average annual expenditure in 1947 was 77% of the long-term average, and in 1949, 38%, in 1950, 65%. In the Bira and Bidzhan Rivers (tributaries of the lower reaches of the Middle Amur) the shallow period also covered the years 1947 to 1952. In the Bira River the average annual expenditures in 1950, 1951 and 1952 were 32%, 72% and 48% of the long-term average, respectively.

This period lasted till 1954 (1953 was an exception), and starting with 1955 a high-water period began, which continued until the 1960-ies. The difference in water level from year to year, and from period to period has a relatively small effect upon the winter expenditures of water. Thus, in the

Khor River in the shallow period, only in January and in February of 1951, did the water expenditures differ materially from the long-term average forming 54% of the latter.

In the foothill rivers an increase in the run-off is accompanied by material changes in the hydrological conditions: the summer temperature of water decreases considerably and a moderately-warm-water section turns into a cold-water section, the turbidity and the amount of transported deposits increases. The channel-springs turn into river branches for the entire summer period; these river branches are filled with turbid river water; the development in them of higher vegetation and of algal overgrowth is inhibited or ceases. On the stones of the river beds and in deeply inundated falls sand, gravel and clay particles are deposited, a factor deteriorating the feeding conditions of the invertebrates, who are consumers of algae, detritus and of predators with catching nets.

The said phenomena permit us to expect that prolonged changes in the water mass (change of high and low water periods) must have a material effect upon the biomass and the species composition of bottom organisms. From the following examples we may judge the effect of the increased turbidity and of a considerable amount of suspended and transported deposits. The Bira River, in which the turbidity is considerable during the summer period (visibility to 25 or 30 centimetres), is at the present time considerably poorer in benthos than any other river we have studied, regardless of the similarity in current speed and thermal conditions. The summer biomass of the lithorheophile complexes in the Bira River constitutes 2 grams per square metre on the stones, and 1.2 grams per square metre on medium sized pebbles.

It is easy to see, that these data are slightly below those in other rivers.

We may, as another example, discuss one of the small channels called "Telefon" in the system of the Georgiyevsk spawning grounds in the Khor River. Until 1955, "Telefon" was poorly connected at the outlet to the river bed. After a deepening at the outlet it turned into a river branch. The summer biomass of benthos at the falls of this channel-spring, which in 1949 and 1950 averaged 20.7 grams per square metre, decreased in 1955 and in 1956 to 9.8 grams per square metre. The decrease in the biomass was primarily caused by the almost complete disappearance of the previously dominant forms of the caddis flies Stenopsyche griseipennis, Macronema radiatum. /p.139

Comparison of our observations on the benthos in the Khor River, in the years 1949 to 1951 and in 1957 to 1961, shows that in a river bed, when a shallow-water period is replaced by a high-water period, changes in the species composition and in the biomass of the lithorheophile benthos, are basically analogous to the ones described above. In the years 1949 to 1951, the larvae of the caddis flies Stenopsyche bergeri, Mystrophora altaica, Agapetus sibiricus, Arctopsyche amurensis, A. palpata, Hydropsyche nevae were very common; in the medial the larvae of Diploglossa nylanderi, Cheumatopsyche sp., Oligoplectrodes potanini, Psychomyiella composita, P. minima, young Arctopsyche are common, and in its deepest sections: Macronema radiatum, Amphipsyche proluta. The frequency of the occurrence of these species in the qualitative samples was between 60 and 85%. The average abundance of caddis flies at the falls was 1065 specimens per square metre in the summer. Very numerous were the larvae of the mayflies Ephemerella basalis, E. tricantha, Epeorus latifolium and others (the occurrence frequency in samples was between 75 and 90%.).

During the period 1957 to 1961 the occurrence rate of the larvae of caddis flies in samples dropped down to 20 to 24%, their average abundance at the same falls decreased to 430 individuals per square metre. The larvae of Psychomyiella became such a rarity, that one had to spend much time in order to find 1 or 2 larvae. In 1961, we observed no large imago of Macronema radiatum flying at the river. On the whole, the number of flying amphibiotic insects, particularly of mayflies and caddis flies, decreased sharply as compared to shallow period; the abundance of stoneflies decreased to a lesser degree.

The entomological collections were carried out particularly regularly during the summers 1949, 1950 and in 1961, and at the same sections of the bank. During the first two years the standard catch of ten throws of the net usually yielded several tens of adult insects: caddis flies, mayflies, stoneflies and others. Their species composition changed in accordance with the date of collection, but the abundance was the same during the entire summer starting with early spring.

In the summer of 1961, other conditions being equal, usually only the imagoes of stoneflies were caught, mayflies and caddis flies were caught only in individual numbers, most often there was not more than 2 to 3 species per catch.

The insects which have disappeared or whose numbers have been sharply curtailed belong to the group of species the larvae of which feed upon vegetation detritus and upon small animals and algae carried by the flow of water. Insofar as they live in the tributaries of the Amur River in a rather wide range of water temperatures and of the current rates, we must not consider these factors as the cause of the inhibition as much as the deterioration in the feeding conditions. Speaking of stoneflies, it must be pointed out that many of their species are predators or facultative predators.

Under conditions of sharp fluctuations in factors of the environments and primarily of the water level in the river, the species with the shortest life-span find themselves under the most favourable conditions, and, furthermore, within this group the advantage is on the side of those with the shortest period of active aquatic stages.

Among the amphibiotic insects many chironomids have more than one generation per year. The one-year life cycle is characteristic of a considerable number of other chironomid species, of the majority of stoneflies, mayflies and caddis flies. Thus, species of Ephemerella, numerous in /p.140
the basin of the Amur River, are characterized by a one-year cycle, however, their development type is varying (Levanidova and Rubanenkova, 1965). Ephemerella ignita has a long latent period at the egg stage, its juveniles appear in the water body in spring. During the period of the heaviest floodings, in the first half of the summer, E. ignita is represented in the benthos by young larvae, which are, as we know, less susceptible to the unfavourable influence of the environment. In August and September the entire population flies out. These peculiarities, as well as the relative eurybioticity of the larvae contribute to the progress of this species during the high-water periods. On the other hand, in years with unstable water level conditions and with all the unfavourable environmental factors accompanying such conditions, the insect species with an extended flight period have a definite advantage. In such species the processes of metamorphosis, egg-laying, development of juveniles have a chance, even in a fraction of

the population, to coincide with favourable periods of summer. As examples of a highly extended period of multiplication of amphibiontic insects may serve mayflies Epeorus latifolium, Heptagenia arsenjevi, Rhithrogena unicolor, Ecdyonurus tobiironis, Ephemerella lenoki, Chitonophora sp. No.1 and others; stoneflies Amphinemura borealis, Nemura sp, caddis flies Stenopsyche bergeri, S. griseipennis, Hydropsyche nevae, Agapetus sibiricus, as well as very many chironomids.

The flight periods, which restricted to early spring or fall, when usually there are no high floodings, are also favourable to the reproduction of species. To the late-fall species belongs, for example, the widely occurring and very numerous caddis fly Arctoecia servata, which emerges in the second half of September. Among the early-spring species we have many stoneflies (species of the genera Arcynopteryx, Diura, Rhabdiopteryx), as well as certain Chloroperlidae and Capniidae. Insofar as eggs of many species of stoneflies remain several months in a state of latency, the young generation of these species appears only at the end of the summer, in the fall or in winter, when the floods are over. It is interesting that a number of species emerge, at least partially, it seems, during the most unfavourable time of the year in respect to the air temperature. Thus, the mayflies Cinygmula sp., which moult at the stage of subimago, were found in the Tatiba River (a tributary of Iman) as late as October 12th; flight of Syndiamesa nivosa of the summer generation is stretched until November inclustively, while I found the imago of certain Orthocladiinae in the Khor River in December and January (!).

Many species with strong and mobile larvae, capable of active locomotion, have definite advantages during the high-water period. Such are the many species of stoneflies of the genera Pteronarcys, Arcynopteryx, Diura, Isoperla and the family Perlidae.

In the years with sharp fluctuations in the water level the larvae of insects with prolonged immobile stages, sensitive to the external conditions, are in a most unfavourable position. To this group primarily belong the larvae of caddis flies living at the falls and in other shallow sections. The prepupal and pupal stages during which the animal stays in a chamber or a closed casing last in the studied water bodies from four or five weeks to several months depending on the species (Arctopsyche, Stenopsyche, Mystrophora, Diploglossa and others). In this condition the invertebrates perish easily from desiccation, silting, freezing and other causes connected with the sharp fluctuations in the water level in the river.

We see from the said that in high-water periods stoneflies and chironomids have definite advantages over the other amphibiotic insects caused by the biology of these groups.

In low-water periods the picture of the benthos distribution changes along the transverse profile of the river. The low level of water in the summer causes a contraction in the ripal areas and approximation of the medial conditions in the sections of rapids to the conditions of the ripal. Therefore, the differentiation in the distribution of the bottom animals is less pronounced and the coastal areas (the ripal) are populated considerably more densely than in the high-water years, the greater constancy in the level, also contributes hereto. /p.141

In the high-water periods the species which are more stenobiontic reduce their numbers, the eurybiontic ones suffer less loss. The more thermophile species cede their place to the more cold-loving ones. Thus, instead of caddis flies *Stenopsyche bergeri* and *Arctopsyche amurensis*, in the Khor River predominate *S. griseipennis* and *A. palpata*; instead of mayflies *Ephemerella lenoki*, *E. thymalli* a high numerical development is achieved by *Chitonophora mucronata*, *Ephemerella ignita* etc. This pattern is much stronger pronounced in the lower reaches, and partly in the middle reaches, of the rivers. In the upper sections the high-water periods have a lesser effect upon the fauna because of a greater stability of hydrological conditions.

Alternation between high-water and low-water periods had no visible effect upon the bottom fauna in the limnocrens and bays in the rivers. This is understandable insofar as the fluctuations of their water level are insignificant and the environmental conditions are incomparably more stable.

Seasonal Dynamics of the Fluctuations in the Biomass of Benthos and the Growth of Invertebrates.

The size of the biomass of benthos in the foothill rivers changes under effect of counteracting processes: it increases with the increase in the individual weight of the aquatic organisms and with the rise in the numbers of the population, when a new generation appears, and decreases owing to natural mortality, including the predation of these organisms; in the amphibiotic insects it also decreases as a result of the transition to the winged phase.

The flight of amphibiotic insects gives a very acute character to the fluctuations in numbers of their larvae, the more so, since in many species such a flight takes place almost simultaneously. In insects with one-year cycle the larval biomass in many cases drops after the flight to zero, and for a certain period of time the entire species is excluded from the aquatic biocoenoses, this, of course, does not happen even at the heaviest devouring. This constitutes a material difference in the dynamics of the numbers of the aquatic stages of amphibiotic insects from the dynamics of crustaceans, mollusks, worms etc. However, if we consider separately one generation of the aquatic invertebrates, then at a constant decrease in numbers its biomass constitutes the resultant value between the rate of the individual growth and the rate of the natural mortality, the first value exceeds the second one at least in the beginning of the life cycle, and in many aquatic insects, it exceeds the latter right to the flight, as a result of this the biomass of the population increases continuously.

If we disregard the inhibitions in growth that are connected in the larvae of aquatic insects with moultings, then the rate of growth may, with certain admissions, be expressed by the following equation:

$$v = v_o \cdot e^{ct},$$

where v_o is the initial weight,

c is the specific rate of growth,

t is the growth period, and

e is the base of the natural logarithms (Schmalhausen, 1935).

Insofar as we speak here of very approximate calculations, an ordinary algebraic equation for compound interest may be used:

$$P_n = P_o (100 + q)^t,$$

where P_n and P_o are the initial and terminal weights for the period,

q is the average diurnal weight increase expressed in percents.

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The average natural mortality rate is expressed by the equation opposite to the growth equation:

$$n_t = n_o e^{-kt},$$

where n_t and n_o are the abundance at the beginning and at the end of the period (t).

k is the loss coefficient.

While comparing these equations, Ricker (1962_o) and Parker (1962_a) used for the determination of changes in the biomass of the sockeye population caused by the growth processes and by the natural mortality rate, the following equation:

$$N = e^{(g-i)^t} \cdot 100 \quad \text{and} \quad P_n = P_o \cdot N,$$

where g is the growth index of the average individual weight for the period (t),

i is the index of the "instantaneous" mortality for the same period (in fractions of one unit, for which the population abundance is accepted),

P_n and P_o are the biomass at the end and in the beginning of the period.

At the present time we have in the hydrobiological literature a relatively small numerical material on the rate of weight increase of fresh-water invertebrates.

In his monograph A.S. Konstantinov (1959) discussed the character and the growth rate of the chironomid larvae and presented data on the increase in the individual weight, i.e. the value showing by how many percents per day the weight of the larvae increases on the average. The author quotes data re six species. For Chironomus annularis the average index of the daily increase (q) is 1.44 (i.e. the larva increases its weight on the average by 44% every 24 hours !), but the rate of the weight increase decelerates with the age, and during the last 3 days (the entire development lasts 20 days) the index of the weight increase is 1.14. In larvae Chironomus plumosus during the 30 days of development q is 1.17, but during the last 10 days it is 1.06. For Ch. dorsalis q is 1.65 for the 13 days, while for the last 5 days it is 1.27. For Gliptotendipes pallens q = 1.53 for 17 days of development, but for the last five days it is 1.2. For Endochironomus tendens q = 1.63 for 14 days, and 1.25 for the last six days. And finally, for the larva Cricotopus silvestris, which is extensively occurring also in the tributaries of the Amur River q = 1.57 for the nine days of development and 1.3 for the last two days. Judging by these data, the chironomid larvae grow with a phenomenal speed: the average daily weight increase is during the period of development about 50% of the body weight, however, such an intensive growth is connected to a considerable degree with high water temperatures. Three species that showed the greatest relative growth rate (Ch. dorsalis, E. tendens, C. silvestris) were kept at a temperature of 24°C, G. pallens and Ch. annularis, at a temperature of 22°C. and Ch. plumosus, which showed the smallest growth rate, was kept at 18°C.

Of great importance to the calculation of the weight increase in chironomids is the stability of the ration of the weight to the cube of linear dimensions taken over the development period as proved by A.S. Konstantinov on a considerable factual material. It is known that with each moulting the linear dimensions (in particular the width of the head capsule) increases by a certain number of times. This coefficient, according to A.S. Konstantinov, is for the head capsule of the chironomid larvae 1.6 to 1.7. In the case of other aquatic insects the data on individual weight increase may be obtained for our purpose from immediate observations in the water body by means of measurements and weighings. A certain difficulty here consists only in the length of the emergence period of the new generation, but at a detailed analysis we always succeed in determining the time of major emergence of the new generation and to trace its growth during the entire period of development.

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The crustaceans seldom have a distinctly limited season for multiplication, after which a general destruction of the old generation would take place. Pontoporeia affinis is an exception in this respect, a phenomenon which allowed V.N. Greze (1951) to determine the individual weight, production, and to develop a method for the calculation of all the similar cases (in particular this method is applicable also to the larvae of insects with simultaneous emergence).

The matters are more complicated in the case of aquatic isopods, which multiply during the course of the year, at various intensity so that their population consists of sexually immature juveniles and adult individuals, a part of which, having achieved the maximum age, dies. Here an experimental determination of the growth rate in the aquariums and tanks is possible, as M.V. Zheltenkova (1952) did it for the aquatic isopod Asellus aquaticus L., or a determination of the average increase according to extensive measurements at certain intervals of time and exclusion from the comparison material of juveniles, who appeared after the beginning of the selection of samples. Here it is often convenient to evaluate the changes in the individual weight from the shift in the modulus of the variation series.

In table 42 data are shown on the individual weight increase in a number of insect and crustacean larvae in the period of intensive growth during spring and summer months.

Table 42.

Relative Speed in Weight Increase in Certain Bottom Invertebrates.

Species	Index of weight increase	Season of the year	Length of period in days	Water temperature	Source
1	2	3	4	5	6
Chironomid larvae					
Polypedilum gr. scalaenum	1.087	July-Aug.	30	19.9-22.8	A.S.Konstantinov (1950)
Tanytarsus gr. mancus	1.193	May-June	30	11-22	"
Chironomus plumosus	1.173	June-July	49	18	A.S.Konstantinov (1958)
Cricotopus silvestris	1.338	July	5	24	"
Syndiamesa orientalis	1.033	Dec.-April	120	3.0-6.0	Our data
Syndiamesa nivosa (winter generation)	1.029	Aug.-Feb.	180	9.0-3.0	"
Syndiamesa nivosa (summer gen.)	1.065	May-June	60	6.5-7.5	"
Diplocladius cultriger	1.031	Sep.-March	180	4.5-7.0	"

Continued:

1	2	3	4	5	6
Orthocladius lv. cyanesus	1.035	Jan.-April	80	3.0-7.0	Our data
Orthocladius lv. abundans	1.035	Jan.-April	80	3.0-7.0	"
Paratendipes albitibia	1.040	Jan.-June	150	4.5-6.5	"
Lauterbornia chloropthita	1.113	June-July	30	7.6-7.6	"
Stictochironomus psammophilus	1.030	June-Oct.	120	6.0-9.0	"
Larvae of Caddis flies					
Rhyacophila narvae	1.031	April-May	32	6.0-10.0	Our data
Rhyacophila impar	1.024	Aug.-Jan.	150	4.0-10.0	"
Hydatophylax nigrovittatus	1.050	July-Sep.	70	10-12.0	"
Larvae of mayflies					
Chitonophora sp.No2 (E.dentata Baik.)*	1.047	May-June	35	8 - 11	"
Crustaceans					
Asellus hilgendorfii	1.025	June-Sep.	92	8 - 11	"
Asellus aquaticus	1.031	May-Oct.	138	12 -20	M.V.Zheltenkova (1952)
Pontoporeia affinis	1.014	June-Feb.	240	-	V.N.Greze (1950)
Rivulogammarus lacustris	1.030	May-June	60	8 - 14	Our data

/Continued/

Continuation:

1	2	3	4	5	6
Gmelinoides fasciatus	1.022	June-Oct.	120	15	M.Yu.Bekman(1962)
Micruropus possolskii	1.035	June-Oct.	120	15	"

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*) The major species Ephemerellidae characteristic of the water flows with the lowest summer water temperature (Teplovskaya River, outlet of a limnocren, Nemptu River and others).

The growth rate taken over considerable periods of time is far from uniform; in many chironomids species the growth of larvae during the winter almost ceases, while in the early spring (in March and April), at the same water temperatures (or at slightly higher ones), the growth is very intensive. In Spring the rate of weight increase in the chironomid larvae, at a temperature of 4 to 8°C, is expressed by the following indices of the weight increase:

Syndiamesa orientalis	1.074	(February-March)
Diplocladius cultriger	1.111	(March-April)
Orthocladius sp. (lv.cyaneus)	1.102	(April-May)
Orthocladius sp. (lv.abundans)	1.108	(April-May)
Paratendipes albitibia	1.078	(March-April)
Lauterbornia chlorophita	1.098	(March-April)
Cricotopus silvestris	1.105	(April-May)

The daily weight increase in the chironomid larvae in spring is approximately three times as high as the average annual weight increase per 24 hour period; it is interesting to notice here that this exceptionally high relative growth rate is observed in larvae of older ages prior to moulting into pupa.

The relative growth rate of the chironomid larvae exceeds considerably the growth rate of chum fingerlings, who in the same water bodies increase their weight daily by 2.5 to 3% (Levanidov, 1955). The difference in the relative growth rate leads to the fact that during the fattening period of the chum fingerlings the number of the chironomid larvae of one and the same species devoured by one single fingerling in one day decreases with time.

Other larvae of aquatic insects such as: mayflies, caddis flies, stoneflies, and most probably, also of other orders, grow at identical temperature conditions approximately at the same rate as the higher crusta- /p.145 ceans, and considerably slower than the larvae of chironomids.

At such a high relative rate of weight increase, which is characteristic of the chironomid larvae ($q = 1.100$), these larvae can withstand a very considerable devouring, and their biomass will remain at the same level, or will even increase. Thus, at the mentioned index the natural mortality (including the devouring) may be 94% of the numbers of one generation per one single month, but the biomass will still remain at the same level. Under natural conditions the biomass of the chironomid larvae of each new generation continuously increases progressively, regardless of it being devoured, and the total biomass of the chironomids drops only in those periods, when there is an emergence of the most numerous forms.

The Orthocladiinae in the foothill tributaries, in the limnocrens and in other water bodies in the basin of the Amur River emerge in great numbers at the end of April and in May; it is exactly in May when the annual minimum of the chironomid biomass occurs. From June to August the biomass of the chironomid larvae is relatively small, since the emergence of various species continues; starting with September the biomass begins to increase owing to the growth of new generations of larvae. With some fluctuations this process continues throughout the winter, and in March (before the beginning of the major flight of the large Syndiamesa) the biomass of the chironomid larvae attains its annual maximum.

In the larvae of caddis flies, mayflies, stoneflies and other aquatic insects with one-year life-cycle the dynamics of the biomass differs somewhat from the described one, in the fact that after the summer minimum the biomass increases were slowly in the fall. While the biomass in the majority of chironomid species already in October differs only slightly from the maximum annual biomass*), in the larvae of caddis flies and mayflies, already at the beginning of the winter the biomass is, as a rule, very small; a considerable increase in this biomass takes place from February to April; it is also in April that the maximum annual biomass of the majority of the species occurs.

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*) Paratendipes albitibia larvae grow in fall and winter exceptionally slowly. Intensive growth begins from April (Levanidov and Levanidova, 1962).

In crustaceans, whose natural mortality is basically determined by the devouring and by the death at the end of the life-cycle (after repeated multiplications), the curve of the biomass dynamics has a smoother characteristic. The minimum of the biomass usually occurs at the end of winter, or in the beginning of fall, when the intensity of multiplication is weakened and the growth rate is decelerated. In the case of aquatic isopod the maximum of the biomass in the Teplovskaya River takes place in May and in September.

Fig.3 illustrates the dynamics of the biomass in the choronomid, caddis fly and crustacean larvae in the Teplovskaya River. As the graph shows, the larvae of Rh. narvae have biomass dynamics typical of the population with one-year life-cycle, namely: a compressed period of multiplication and complete destruction (disappearance) after the multiplication. For such a population the regular increase in the biomass and an increase in the abundance right to the multiplication period is characteristic (same type of dynamics is found in the population of the Far-Eastern salmons).

The population dynamics of the aquatic isopods have a more complicated character and is typical of all the species with a life-cycle of about one year and a year-round multiplication cycle with two maxima (in April and in July). From October to February the percentage of females with ovisacs fluctuates in the population from 1.7 to 3.5% of the numbers of females, while in March it rises to 8.1%, in April to 25.0%, in May and June it drops to 6.5%, but in the middle of July it is 26.5%, while in August and September it is 8.1 and 5.2% respectively. After the multiplication die only the largest

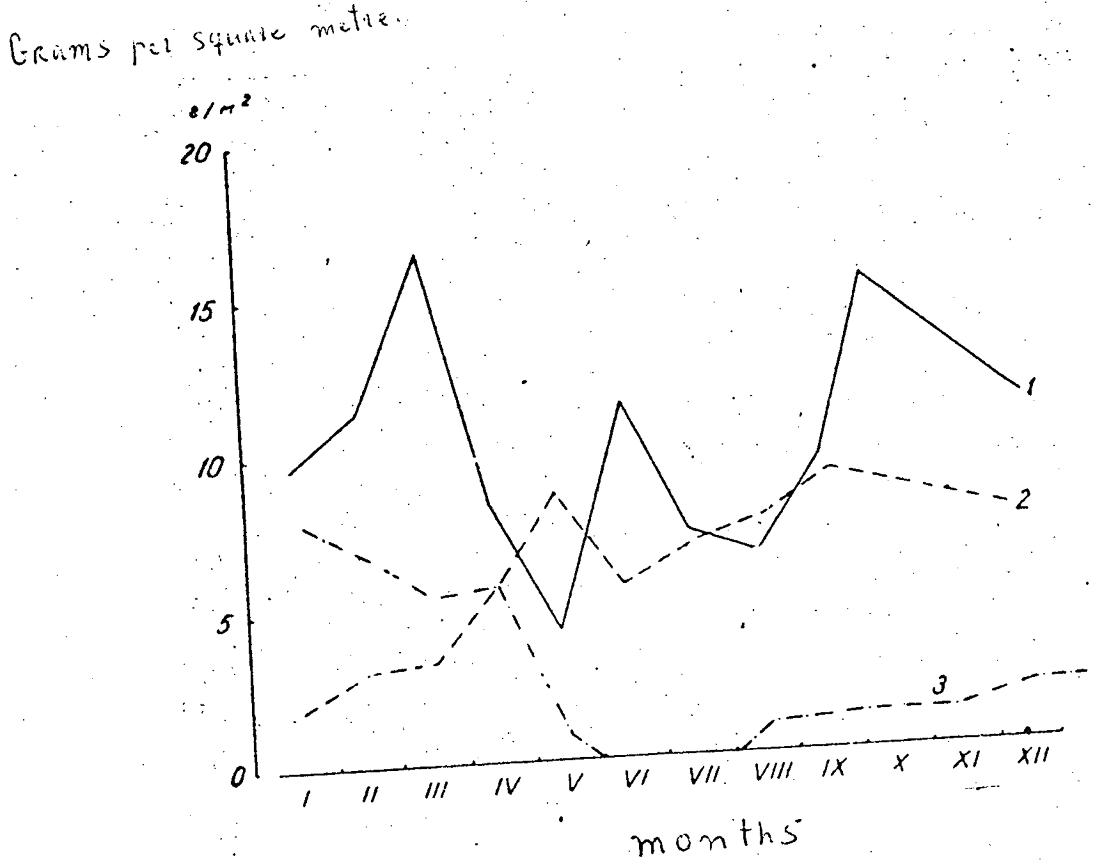

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Fig. 3. Seasonal dynamics in the population biomass of certain multitudinous invertebrates in the tributaries of the Amur River. 1 - chironomid larvae (10 species); 2 - aquatic isopod Asellus hilgendorfii; 3 - larvae of the caddis fly Rhyacophila narvae.

and, probably, the oldest individuals. The numbers of dead individuals after the multiplication are very high in April, but considerably lower in July. The dual peak curve is explained on the graph by the two periods of intensity in multiplication.

The total curve of the biomass of the chironomid larvae indicates, how the difference in species levels the extent of the fluctuations in groups of species, the abundance of larvae of each of them drops in the period of multiplication practically to zero. The dynamics of biomass in the individual species of chironomids from the Teplovskaya River are shown in the work of Levanidov and Levanidova (1962).

When the flight of the aquatic insects is stretched over a period of two to three months (as, for example, in the caddis flies Diploglossa nylanderi, Agapetus sibiricus, Hydropsyche nevae) or when the life cycle lasts several years, as in stoneflies Pteronarcys reticulata, Neophasganaphora brevipennis and certain other mayflies, then the seasonal fluctuations in biomass are expressed relatively poorly.

An increase in the biomass of benthos in a salmon river does not cease throughout the entire winter owing to the individual growth of the bottom invertebrates. The mortality caused by abiotic factors during the period of hibernation is, as a rule, small, although in the individual years, when there is a catastrophic drop in the level, in some rivers we observe death of benthic animals from starvation and freezing. Thus, in the winter of 1951/1952, we saw destruction of stonefly and caddis fly larvae in the frozen river-bed of the Amgun' River, but such phenomena are relatively few. The growth of invertebrates in the winter period particularly intensive in the limnocren and in the spring channels because of the relatively high water temperature.

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FEEDING OF THE BENTHIC ORGANISMS IN THE TRIBUTARIES OF THE AMUR RIVER.

The benthos animals (except the predators) are the first heterotrophic link in the food chain in the salmon rivers; they are the main consumers of the primary production of the autochtonous and allochtonous origin. The feeding character of the bottom organisms is determined to a considerable degree by the peculiarities of the biotope; forms living in swift current and on a stony ground, are relatively immobile; thus have developed a number of adaptations permitting them to feed upon the food transported by the current, as well as upon the overgrowth on the stones. The more mobile representatives of the epifauna of sandy and silty grounds, to whom the resistance to mechanical force of the current is not their main task, search their food by actively moving along the bottom.

The degree to which the feeding of the aquatic invertebrates of the mountaneous and semimountaneous rivers has been studied is insufficient for the compilation of food spectra and for the determination of the amount of food devoured by each species; however, the available material can already enable us to determine the difference in the feeding character of the organism category and the numerical ratios of them in various ecological complexes.

We follow the example of E.V. Borutsky (1955, 1959, 1961) and divide the aquatic invertebrates according to the feeding type into three groups: plantivorous (phytophages), animal eaters (zoophages) and omnivorous (phytozoophages), who in their turn are subdivided into smaller groupings.

Feeding of the caddis fly larvae. S.G. Lepneva (1964) indicates that on stones in the mountain streams live the algophages, such as larvae

Glossosomatidae, Apataniinae (where the current is slower). Larvae of the genus Rhyacophila, of the family Polycentropidae and of the subfamily Hydropsychinae occur as predators (the latter larvae, incidentally, feed also on plant food). Scott (1958) when studying the rheophile fauna of a small river determined, that the population on the stone biotope is 60.5% algophages (or rather: periphytophages), 7% of detritophages, and from 6.1 to 7.3% of predators.

Summing up all the known data, S.G. Lepneva (1964) comes to the following conclusion: "In the suborder of Annulipalpia ... the feeding of larvae is finely and diversely differentiated being connected with the character of one or another species: the microphages, the builders of tunnels, are omnivorous; free-living species, the builders of the catching nets, are predators; the carriers of the houses are plantivorous. In the suborder of Integripalpia, whose larvae consist entirely of house-carriers the feeding on decaying of fresh plant food predominate , which is characteristic of this order; this suborder contains no predators in the proper sense of the term.

This conclusion rests to a considerable degree on the work of L.V. Korolenkina (1951), in whose experiments the larvae of the family Phryganeidae, when plant food was available refused outright to take animal food. However, N.I. Kashkin (1958) proved, that under natural conditions the larvae of Phryganea grandis (L.) feed during the summer both on plant, and animal food, while in winter they feed on animal food alone (particularly on the larvae of dragonflies).

According to the data of O.L. Kachalova (1960) the larvae Phryganea striata feed both on algae, and on animal food: on larvae of chironomids Procladius, Limnochironomus gr. nervosus, on mayflies Caenis sp., on aquatic isopods, on microbenthos: Acroperus sp., Harpacticoida and Astracoda. In the feeding of other species of the same family (Agrypnia pagetana, A. obsoleta) also the larvae of mayflies, chironomids, aquatic isopods, cladocerans etc. are found in considerable amount together with the plant food.

Consequently, as O.L. Kachalova justly points out, these species of caddis flies are, under natural conditions, typical zoophtophages; they may be considered "facultative predators with low indices of predatoriness" (Levanidov, 1951a). /p.148

In our studies, we found the large larva Holostomis phalaenoides living in the spring-channels and in warm-water rivers to be a predator. In the alimentary tract of six larvae, opened by us, we found nothing but remains of animal organisms: larvae of stoneflies Capnia sp. (50%)*) and Chloroperla sp. (16), larvae of the mayfly Ephemerella taeniata (32), larvae of caddis fly Apatania sp. (16) and of numerous larvae and pupae of chironomids (90) belonging to the genera Diamesa, Psectrocladius and Tanytarsus. Besides the insect larvae, we found in the alimentary tract remains of aquatic isopods and planarians. Under aquarial conditions the large larvae Phryganea sinensis demonstrated the predatory way of feeding.

On the basis of the hypotheses that within the confines of one genus

*) Everywhere the brackets show the occurrence frequency in percent.

the feeding of different species, as a rule, is of one and the same character, we can, on the basis of S.G. Lepneva's data classify the lithorheophile caddis flies from the tributaries of the Amur River belonging to the genera Rhyacophila, Arctopsyche, Hydropsyche, Cheumatopsyche as facultative predators. Stenopsyche griseipennis and S. bergeri according to I.M. Levanidova's observations (Lepneva and Levanidova, 1953) feed by gathering from the surface of the catching net the microflora and microfauna organisms caught in the former together with organic substances brought with the current. In the intestines of these species, opened by me, the green and diatomous algae, detritus, minute animal organisms and small mineral particles predominated. S.G. Lepneva (1964) classifies the larva S. griseipennis as microphage, which is a part of the group of the omnivorous animals, the phytozoophages (Borutsky, 1961).

Such inhabitants of stony rapids and falls, as Mystrophora altaica, M. ussurica, as well as species of the genus Agapetus, belong to periphytophages. Living in water bodies with weak current and low water temperature on stone and pebble grounds, the larvae of the genus Apatania feed themselves by scratching off algal deposits from stones and may be classified as belonging to phytozoophages.

The limnophile caddis flies, which live in slowly running rivers, reaches, spring channels, river bays, limnocrens and other similar water bodies, and who comprise the dendrophile, detritophile and pelophile complexes of organisms, are basically phytophages according to their method of feeding themselves. Furthermore, as L.V. Kolenkina (1951) demonstrated, these larvae also feed upon the decaying leaves of trees. According to our observations the plant food (detritus and algae) is used by the larvae of the widely occurring species Hydatophylax nigrovittatus, Hydatophylax magnus, Arctoecia servata, Astenophylax sp., Nemotaulius admorsus and others. Among species that are common here, we find larva Ganonema extensum (the Calamoceratidae family), which lives in pieces of wood hollowed by itself or in reed canes, and it is a facultative benthophage belonging to a group of omnivorous animals. In its intestinal tract are found green algae and remains of the larvae of mayflies Heptagenia soldatovi and Ephemerella taeniata, of stoneflies Capnia sp., caddis flies Rhyacophila sp., chironomids Prodiamesa olivacea, Criptochironomus defectus, as well as of amphipods Gammarus lacustris.

Feeding of the mayfly larvae. Material on the feeding of the Amur mayflies is small. To obtain qualitative characteristics of the feeding of this group, I.M. Levanidova and I have opened intestines in larvae of major species (unpublished material) collected mainly during the warm period of the year. The feeding during the winter period of some of the most widely /p.149 occurring species of the Ephemerellidae family was studied by L.A. Slobodchikova (1964). Data on the feeding of larvae of the Amur Ephemera are presented in O.A. Chernova's work (1952).

In the group of digging (burying) larvae living in the sandy-pebbled, clayey-sandy and clayey grounds, we have studied the content of intestines in 15 specimens of Ephemera amurensis and Ephemera sachalinensis, collected from May to October. The intestines in all the larvae were filled and well-visible through skin-covers. The content consisted of rather homogeneous mass of fine organic substance mixed with a considerable quantity of quartz grains; occasionally valves of diatoms were found. Similar composition of the intestinal content of Ephemera is indicated by O.A. Chernova (1952), who believes with justification that the basic component in this mass are the bacteria. According to E.V. Borutsky's classification (1955) these larvae belong to plantivores (detritophages). According to O.L. Kachalova (1960), the larvae of Ephemera vulgata are fed with detritus and algae, and together with the detritus they also receive remains of dead plankters.

In the Ephemerellidae family we have determined the feeding of Ephemerella sibirica (a total of 11 larvae were opened in July and in August), Chitonophora mucronata (6 larvae of the three last stages, in May), E. levanidovae (2 larvae of medium age in May) and E. taeniata (18 larvae of various age from 4 to 11 millimetres in length collected from April to June). The intestines of all the Ephemerellidae also contain an unformed organic substance, but contrary to the Ephemera, we persistently find here also green algae in the form of long threads, and particularly in Ch. mucronata, we find valves of diatoms (sometimes the cells still contain coloured chloroplast) and even parts of insect larvae (probably semi-decayed remains), and also mineral particles. The content of intestines indicates that the larvae feed themselves by scratching off the overgrowth from the stones and from other objects. Conversely, in the homogenous organic unformed contents of two studied intestines of larvae Siphlonurus zetterstedti we found almost no mineral particles; this indicates that the larvae collect and not scratch off their food.

The intestines of three larvae of the Caenis sp. (Brachyceridae family) opened by us contained only rounded soft particles of organic origin.

Intestines of three larvae...../TR: Typographical error: First line of the previous paragraph is repeated here, but first line of this paragraph is, unfortunately, omitted/........biidae) species, which are extensively occurring in the Khor River, contained green algae and diatoms (July and August, six specimens).

In the Heptageniidae family we studied the feeding of larvae Epeorus latifolium. The intestines of the larvae of medium and older age (9 specimens) mainly contained filiform green algae and valves of diatoms.

Larvae Ephemerella taeniata, E. levanidovae and E. basalis, according to the data of L.A. Slobodchikova (1964) feed in winter upon fine plant and animal detritus, on diatoms and green filiform algae. In the food of E. taeniata fine detritus predominated, in E. levanidovae predominated diatomous algae, as well as filamentous algae; a seasonality was observed in the feeding of E. basalis: in December (young larvae) fine detritus and green filamentous algae predominated in the intestines; the diatoms were scarce. The intestines of May (adult) larvae, on the contrary, were filled mainly with diatomous algae of diverse species-composition. Ephemerella taeniata and E. basalis are very numerous in the benthos and live in many biotopes, particularly on the stones, pebbles and tree stumps.

According to data of a detailed research carried out by S.S. Ivanova (1958), the food of mayflies of the genera Heptagenia, Baetis, Potamanthus, Cloëon, Ephemerella and Siphlonurus consists of green, diatomous, desmids /p.150
and, to a lesser degree blue-green and Heterocontae algae, as well as of watermoss Fontinalis, of decaying higher aquatic plants and of detritus.

Furthermore, the larvae of the genera Heptagenia, Ephemerella and Leptophlebiidae feed upon decaying tree leaves that fall into the water. In