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by Yu. A. Smirnov

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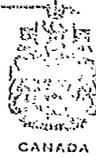
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Yu. A. SMIRNOV

THE SALMON OF LAKE ONEGA

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FOREWORD

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Some results of a study of the salmon inhabiting Lake Onega are set out in this pamphlet. The materials on which the work is based were collected in the years 1959--1965 when the author was studying the spawning grounds of the salmon in the basin of Lake Onega and was at the same time making observations on the commercial stocks. The estimate of the abundance of stocks and of the entire population is based on the state in 1965. Materials and observations of later years have not been included in the pamphlet.

This book could not have appeared but for the great and varied assistance of very many individuals. The bulk of the work was carried out in the Karelian Fish Plant (Karelrybvod) and subsequently in the department of zoology and Darwinism at Petrozavodsk State University.

The author is sincerely indebted to all who assisted him in his work.

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\* Numbers in right margin indicate corresponding pages in original text.

In Memory of  
Viktor Viktorovich Azbelev (1905--1968)  
and Leonid Pavlovich Kriulin (1941--1967),  
students of the Atlantic salmon ,

### INTRODUCTION

The lake form of the Atlantic salmon /Salmo salar L. morpha sebago (Girard)/ is found within the range occupied by the Atlantic salmon (S. salar L.) now or in the recent past when the migratory paths of the Atlantic salmon extended farther into the mainland.

Land-locked forms of the salmon are known to exist in some lakes in North America, Newfoundland, Norway, Sweden and Finland.

In the USSR the lake salmon is confined to Karelia, where it inhabits Lakes Onega, Ladoga, Sandal, Yanis''yarvi, Vygozero, Segozero, the Kuito Lakes (Upper, Middle and Lower), Nyukozero and Kamennoye. It is possible that very small, but independent stocks will still be discovered in two to four lakes of Central and Northern Karelia.

Although the salmon has long been specially fished in the above lakes, the scale of fishing and its economic importance have been slight in most instances. The two largest lakes, Ladoga and Onega, are an exception; in them the role of the salmon fishery has been of more than purely local significance. Old fisheries statistics show that the salmon catch reached 2500 centners<sup>1</sup> in Lake Ladoga 30 years ago and 1000 centners and possibly more in Lake Onega in the 1890s. The salmon populations in both lakes were

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<sup>1</sup> Translator's note. One Soviet centner = 100 kg.

subsequently sharply reduced for various reasons, although to differing degrees. It is now only in Lake Onega that the salmon has retained its independent commercial importance, but even in this lake the position of its stocks is extremely unfavourable.

The lake salmon is of great interest both economically and from the point of view of an understanding of its biology, a feature of which is extreme adaptability ('plastichnost'). This feature makes the salmon an extremely promising subject in rational lake management. It enables us to select those stocks which are found to be the most convenient and advantageous. Nor is the possibility excluded that it may be cultivated in special fish farms of a type in which the fish are kept in containers; some success has already been achieved along these lines abroad. /6/

In the interests of development of the fish industry it is essential that urgent measures should be taken to increase the abundance both of the salmon and of other valuable fishes of this family. Correct management is, however, impossible without precise knowledge of the biological features of a fish and of the demand which it makes on environmental conditions.

What is the present level of investigation of the Onega salmon and to what extent does our knowledge of it enable us to solve practical problems?

Isolated pieces of information and references to the salmon are scattered throughout a large number of sources, but the overwhelming majority are devoted to salmon fishing. The most valuable and extensive information is to be found in the writings of K. F. Kessler (1868), N. Ya. Danilevskii (1875) and in a number of the works of N. N. Pushkarev and N. I. Kozhin. The research directed by M. I. Tikhii in connection with the construction of a hydroelectric power station on the Svir' River has yielded a great deal of information. In particular, the assumption earlier made by K. F. Kessler

that the Ladoga and Onega salmon populations are incapable of mixing has been confirmed by tagging.

There have been only two articles specially devoted to the Onega salmon: by M. B. Zborovskaya (1935) and by Z. V. Prozorova (1951). The last of these authors considered only the salmon of the Shuya River (size, age, growth and catches from materials for 1948--1949; 257 fish). M. B. Zborovskaya studied the Onega salmon from 1931 and obtained the first material on age (838 fish), feeding and nutrition (57 fish) and fecundity (18 fish). On this basis M. B. Zborovskaya compiled a valuable summary of information on the Onega salmon fishery and on the biology of the Onega salmon (1948), in which she dealt with the population as a whole.

The investigation of the spawning rivers and of the stocks associated with them which has been carried out since 1959 has made it possible to attempt to describe the population in terms of local stocks, to understand the causes of the profound depression of salmon stocks and to propose the first measures which are urgently needed to correct the situation.

Unfortunately, it is impossible as yet to say that the data now at our disposal satisfy us, since they are far from adequate even for an approximate calculation of the optimum volume and structure of lake salmon management. A number of aspects of the biology of the lake salmon remain to be clarified; these include such important characteristics as the survival in different stages of development, the assortment of food items consumed, the return on feeding and also the state of the food resources, the productivity of spawning-growing grounds, the parasitological situation and other aspects without which a quantitative description of the population regime is impossible. The foregoing questions should therefore be the subject of further investigation.

## Chapter 1

### PROCEDURAL QUESTIONS

#### I. Investigation of the Spawning Rivers.

The object of the investigation was to take stock of the spawning grounds and to estimate their state and, where possible, their utilization.

There is no generally-accepted procedure for taking stock of spawning grounds. Data on the fall of a river, on the length of the rapids in it and on mean annual water discharges provide only a general representation of the river and do not allow its value for the reproduction of the salmon to be assessed, especially in the absence of reliable information on the size of the stock and on its distribution in the river.

For various reasons (unsuitable bottom material, natural and artificial obstacles to migration etc.) far from all the rapids in a river are capable of being utilized by salmon for egg laying. As a result of investigation we separate from the total number of rapids the "spawning" rapids, or spawning grounds. By a "spawning ground" we understand a rapid (or a small bank, the dialect word for which is kareshka, or a shallow) where salmon spawn (or used to spawn) year after year. The spawning grounds were subdivided into "existing", i.e. used by the salmon at the present time, and "potential", i.e. which for some reason are not used by the salmon at the present time but are quite suitable for spawning. Spawning grounds may lose their importance as a result of pollution of the water and the bottom material, alteration of the hydrologic regime, silting and becoming overgrown; special mention has been made of such cases.

The salmon does not use any part of a spawning rapid for egg laying, but strictly defined localities distinguished by their microregime. The salmon frequently excavate their redds at the same points year after year. There may, therefore, be fairly permanent areas of redds within a spawning ground. In most instances it is impossible to estimate the size of the area occupied by redds owing to the considerable depth and low transparency of our rivers. What some investigators have in mind when they refer to a "spawning ground" is essentially an area containing redds.

Determination of the area over which the young spread out is no less important than determination of the spawning area proper. The area in which growth takes place may include all stretches of rapids (except for waterfalls), including stretches unsuitable for spawning which may be entered by the young salmon as a result of migrations.

It is desirable for practical reasons to use the concept of a "spawning-growth area", including in it the entire area of the rapids in which spawning takes place and which is continuously inhabited by young. Because the size of this area alters in relation to the amount of water in the river in the year concerned, its observed size when discharge is minimum should be taken as its basic size. /8/

The following rivers were examined between 1959 and 1964: Shuya, Syapsya, Kutizhma (in part), Upper and Lower Lizhma, Elgamka, Sordiya, Sheichuga, Syargezhka, Kumsa, Oster, Vichka, Nemina, Pazha, Pyal'ma, Zhilaya Tambitsa, Tuna, Tuba, Vama, Vodla and a number of trout streams and brooks. The total length of the stretches investigated is more than 500 km and almost all the rivers were examined twice, at different water levels. Boats (wooden or rubber) were used to move along the large rivers; small

rivers were investigated on foot. The record which was made of the number and size of spawning grounds gave an idea of the effect of logging, uncontrolled removal and alteration of the regime of the rivers on the reproduction of the salmon. In addition, observations were made on spawning and on salmon redds in the Syapsya, Lower Lizhma, Tuba and Vama Rivers.

## II. Collection of Materials on the Structure of the Stocks and Determination of the Age of the Salmon.

Sampling to determine the structure of the stocks. Since it was assumed that the composition of the stocks was not the same at different periods of the spawning run, samples for determination of the structure of the stocks were taken throughout the entire run. All the fish in small catches were measured as a rule. If the catch exceeded 50 fish, the proportion of the catch which constituted the sample has been noted. The samples were fully representative; they were from 25 to 80 % of the total catch. An adequately complete picture of the structure of the stocks is therefore arrived at by simple addition of the mean samples. Furthermore, since the rate of removal is considerably in excess of 50 % in the Shuya and the Pyal'ma, and around this figure in the Vodla, the samples characterize the structure of the stocks quite adequately in all instances.

The sex of the migratory salmon was determined by the external appearance; the correctness of the determination was, as a rule, confirmed by the control dissections which were sometimes carried out. It is impossible to determine the sex of a salmon during the feeding period by appearance since sexual dimorphism is not so clearly expressed as it is in the migrating fish. If dissection was impossible, the sex was not recorded.

The material collected for determination of the structure of the

stocks between 1958 and 1965 totalled 5496 fish, of which 4666 were collected personally by the author or with his participation and 830 were kindly supplied by Karelrybvod. The material on the salmon during the feeding period was small in quantity (200 fish). The explanation for this is the banning of "garva"<sup>1</sup> fishing since 1958; this salmon is not often found in catches of other fishes. /9/

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<sup>1</sup> The "garva" is a large-mesh net used in Lake Omega to catch feeding salmon in the upper horizons of the water.

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Special consideration should be given to the determination of age. For comparable results to be obtained it was essential that all investigators should adhere to a standard procedure. Unfortunately, this does not invariably happen in work with the salmon.

The "stumbling blocks" to determination of the age of the salmon are the "transitional" zones lying between the river zones and the feeding zones, the spawning marks and also the areas of damage ("epitheliomatous erosion") caused by some disease of the epithelium, which are extremely similar to spawning marks.

Transitional zone. Elucidation of the time at which and the conditions under which the "transitional" ring (or "transitional" growth zone) forms is of great importance for its correct interpretation and, consequently, for correct determination of the age of the salmon.

Some authors count the transitional ring as a year of the river period (Zborovskaya, 1948, p. 130), others count it as a year of the feeding (marine) period (Kuchina, 1939; Svetovidova, 1941), while yet others do not

regard the transitional ring as an annulus and include it in the first year of the feeding period (Yankovskaya, 1958; Mel'nikova, 1959; Birman, 1960; Enyutina, 1962; Bilton and Ricker, 1965). The comparison of age characteristics is thereby complicated.

The fact that a "transitional ring" is to be found both in the marine and in the lake salmon removes the basis for the assumption of some authors (Kuchina, 1939; Svetovidova, 1941) that the formation of a "transitional" ring is due either to an alteration of salinity or to retention of the salmon in semi-freshened parts of the sea.

L. A. Yankovskaya (1958) relates the formation of the "transitional" ring to the time of downstream migration of the smolts. Were this to be so the percentage of fish with transitional rings should be lower in stocks with a shorter downstream migratory path, but this is not found in the rivers of Lake Onega.

The different frequency of fish with "transitional" rings and differences in the structure of these rings in salmon of the different stocks of Lake Onega justify the assumption that there is a connection between the formation of the "transitional" ring and the feeding conditions which the smolts encounter after downstream migration. This view is confirmed by the elegant experiments on the rainbow trout conducted by Bhatia (1932), who demonstrated that scale structure precisely reflects alterations in the availability of food. All kinds of rings, including "transitional" rings, were obtained in these experiments in relation to feeding. Bilton and Ricker (1965) used tagging to demonstrate that the supernumerary ring of a pink salmon is not an annulus. The same point of view is held concerning the Atlantic salmon by L. A. Yankovskaya (1958) and M. N. Mel'nikova (1959).

The few sclerites (2--4) of spring growth which form in a small proportion of the smolts while still in the river, before the time of downstream migration to the lake, may in essence also be included in the transitional zone. According to our materials, the vast majority of downstream migrants do not have springtime river growth. This is in agreement with the conclusions of A. R. Mitans (1965; for the Salatsa River in Latvia).

In determination of the age of the Onega salmon, we included the transitional zones and spring growth of downstream migrants in the first year of the feeding period. Even although M. B. Zborovskaya regarded the transitional zone as a year of river life, her materials are quite suitable for comparative use. The point is that the percentage of fish with transitional zones in the salmon stock of the Shuya River, for which M. B. Zborovskaya collected the greatest amount of material, is very small, no more than 16 %, and consequently the error will be slight. This remark should be borne in mind in the analysis of the annual variations of population structure given in section VII of chapter 3.

Spawning marks (Russian terms: nerestovye metki, otmetki, znaki)<sup>1</sup>, which are, in the first instance, a reflexion of the fishing rate (and possibly, also, of the special features of the rivers), are encountered with widely varying frequency in different years, from 50 % to 5 % or less. Some

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<sup>1</sup> Spawning marks are areas of damage to scales caused by the modification of metabolism connected with preparation of the fish for spawning.

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authors, including Z. V. Prozorova(1951), do not consider the age of fish which have spawning marks, but merely refer to their percentage in the catch. The reason for this is the lack of any precise understanding as to the period of

time to which a spawning mark corresponds, i.e. by how much the number of years must be increased after the annual zones have been counted. However, by refusing to consider the age of fish which have spawned previously we deprive ourselves of the possibility of estimating the abundance of spawning stocks in past years and the extent to which these stocks were fished.

The lake salmon, which enters the river with a completed annual zone (additions are extremely rare !), passes 6--12 months in it since a proportion of the "val'chiki"<sup>2</sup> migrate downstream immediately after spawning, and the remainder in the following spring, in the beginning of May -- beginning of June.

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<sup>2</sup> Val'chiki are spawned salmon leaving the river.

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In any case the val'chiki cannot begin to feed intensively until May when the smelt approaches the river mouths. A fish needs to spend at least a year (12--16 months), and sometimes 2 years in the lake for restoration of its weight (the weight loss reaches 40 %) and development of the gonads. When salmon were tagged in Cross Lake (Maine, USA) it was found that the lake salmon spawned in the next year but one and only exceptionally in the year after spawning (Warner, 1962). The spawning mark should therefore be regarded as equal to one year for the lake salmon which does not have a hiemal autumn form. This is confirmed by the results of the tagging of val'chiki in Lake Ladoga (Tikhii, 1931c; Pravdin, 1948b). T. I. Privol'nev (1933) takes the spawning mark to be 2 years in the autumn Atlantic salmon, and we should evidently agree with this.

Scales with spawning marks should be examined very closely since erosion frequently covers several peripheral annual zones, especially in males.

The age may be understated if the last zones are not noted. To avoid this, scales must be taken in two places: firstly, as is normal, below the dorsal fin where the scales become submerged in the skin in the post-spawning condition ("loshanie")<sup>1</sup> and are heavily eroded, with the result that the spawning marks are excellently apparent on them, but the peripheral annual zones are frequently "overlooked"; secondly, from around the pelvic fin where the scales are not submerged and spawning marks are weakly expressed on them or may even be completely absent, but all the zones are preserved. Such material was

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<sup>1</sup> The Russian word loshanie (from "lokh", a male in spawning colours), here translated as post-spawning condition, is connected with the alteration in the colour and external appearance of the salmon in connection with the preparation for spawning.

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collected from 1960, since the defects of the former method were already apparent in the first year of the operations.

Pectoral-fin rays and otoliths were also taken to check that the zones had been correctly counted in fish with spawning marks, but the amount of material involved was small, since salmon are not prepared at the fishing places.

"Epitheliomatous erosion" is a term used provisionally to designate destruction of the scales caused by some disease of the epithelium, the nature of which has not been established. This disease has not previously been recorded for Lake Onega. In the opinion of O. N. Bauer, who examined a diseased fish sent by the author, the condition is "epithelioma", i.e. a viral disease. To judge by the description, M. I. Vladimirskaia (1957) encountered the same disease in the Pechora, but only in dwarf males, and also called it epithelioma. Calderwood (1906) and Menzies (1931) refer to "white spot

disease" found among salmon in the rivers on the western coast of the British Isles (Scotland). This disease is seen in fish inhabiting small rivers in a hot summer; the salmon are covered by white spots, but when the river floods they are cleansed. None of the authors cited refers to the effect of this disease on the scales.

Some of the foregoing information is in agreement with our observations. Immature parrs are subject to the disease as well as dwarf males. Infected fingerlings (up to 20 % in the catch) are encountered in August and September. They later disappear somewhere and it may be that they are in fact cured in connexion with the autumn flood or the drop in temperature. The disease was not noticed to cause the death of a fish or to occasion severe suffering. Even those fingerlings in which up to a half of the body surface was affected were able to maintain themselves in a fast current, were active and took the bait well. Infected dwarf males are found around the redds together with healthy fish. The disease was not noted in smolts or in silvery parr and it was, in general, not encountered in the first half of the summer. /12/

Several adult fish were recorded with white spots on the head and body. These fish were caught in the Pyal'ma River or near its mouth in August and September. Although we did not find infected immature fish feeding in the lake, they undoubtedly exist, as is convincingly shown by an analysis of the scales. The point is that there is no stock of the Onega salmon including fish which mature after one year of life in the lake, like the grilse of the Atlantic salmon or the Ladoga grilse ("sinyushka"). This is confirmed by observations covering many years, by fencing off in the Pyal'ma and by catching in the spawning grounds. The earliest time of maturation is after 4 years in the lake, but usually after 5--6 years. However, "spawning marks" are found on some fish after 1, 2 or 3 years in the lake but not on all scales even around the dorsal

fin. All that can be assumed in such instances is that we are once again confronted with epithelioma. It is curious that such fish are very rare in the stock of the Shuya, but usual and even plentiful in the stocks of the Pyal'ma and the Vodla. If the disease is in some way connected with feeding conditions, the unequal frequency of sick and recovered fish (with traces on the scales) in the different stocks may indicate that feeding takes place in different regions of the lake. A. M. Gulyaeva (1966) notes that a disease of the vendace which affected the epithelium and the scales was prevalent in the northeastern part of Lake Onega between 1961 and 1965; she suggests that this disease was "whitefish pestilence". However, may it not have been connected with the disease of the feeding salmon, which is in constant contact with the vendace, all the more so because the description of the external stigmata of the disease is very similar to that of "epithelioma"?

The disease observed by us both in fingerlings and in adult salmon was expressed in the formation of slight whitish swellings accompanied by petechial haemorrhages on the body of the fish. Such "white spots" are most often scattered above the lateral line and sometimes merge together and cover up to half the surface of the body, not excluding the fins. The scales within the "spots" become ragged and are eroded, sometimes almost entirely. In adult fish considerable portions of the body are sometimes covered by patches of very small (1--2 mm long), abnormally located scales which apparently grow where the scales have been completely eroded. Were the erosion of a scale to be partial, a false spawning mark would form on it after the fish recovered and it would not always be possible to distinguish it from a true spawning mark. In general, however, the difference between a spawning mark and epitheliomatous erosion is very considerable. Epitheliomatous erosion may be found on the same fish in

different annual zones, for example two years in succession, i.e. there is evidently no development of immunity.

The correct identification of "epitheliomatous erosion" is of great importance. Its confusion with spawning marks will lead to overstatement of the proportion of the carry-over in the stock and this will distort calculations of the size of spawning stocks and of the rate of removals.

The taking of scales in two places, around the dorsal and pelvic fins, reduces the probability of error.

### III. Observations on Young Fish. Tagging.

Young salmon were observed in the Shuya, Syapsya, Upper and Lower Lizhma, Elganka, Kumsa, Nemina, Pazha, Pyal'ma, Tambitsa, Tuba and Vodla Rivers. All ages were represented in the collections, from the time of completion of morphogenesis (as defined by Nikiforov, 1959a, from the fourth stage) to smolts from the lake. These materials are in course of processing.

Observation of the distribution of young in the rivers and the results of test fishing (by a small trap net for fingerlings, by hand net and by rod and line) made it possible to estimate the population density of the parr in some instances.

Tagging has been begun in the Pyal'ma and Tuba Rivers to study movements, behaviour and survival. Smolts, silvery parr and parr, including dwarf males, and grayling fingerlings and adult dace have been tagged. The tag used was an individual celluloid tag 0.5 mm thick and 4 x 11 mm in size described by B. Carlin (1955). The tag has a wire and an end piece of nickel-chrome wire 0.15 mm in diameter. The end piece was inserted into the body by means of two needles of the type used for subcutaneous injection fastened together. The tag

was attached beneath the dorsal fin encircling the basal bones. In some of the fish only the adipose fin was clipped (in the Tuba River). The smallest size of the tagged fish (ad) was 4 cm.

To lessen the damage to the fish they were tagged under anaesthetic. The anaesthetic used was the imported product chinoldin recommended to the author by L. A. Petrenko, a scientific officer of the State Research Institute for Lake and River Fisheries (GOSNIORKh) (Leningrad). The preparation was added to the water immediately before tagging. The optimum concentration is approximately 1 : 100 000; at this concentration the fish is anaesthetized for 1--2 min at a water temperature of 10--20°C. When a lesser dose is used the narcosis is shallow and the fish struggles and is injured. A dose 3 to 4 times larger leads to the death of the fish. Fish should not be kept in the solution for more than 5 min. After tagging the fish were placed in pure water where they recovered within 5 to 15 min and adopted a normal position. The fish were then kept for up to 2 days in running-water containers, after which they were released into the river; this period may be reduced to one hour. Some fish were kept in the containers for up to two weeks for observation of the healing of the wounds, after which they were released. /14/

Subsequent observations on the behaviour of the tagged fishes have shown that the parr and the young grayling remained within a radius of up to 50 m from the point of release for a month (September). This is in agreement with the observations of other authors (Vladimirskaya, 1957; Saunders and Gee, 1964) in which tagging was used. When fish were recaptured the tags had kept their position well and the wounds from the punctures had healed.

The use of an anaesthetic makes it possible to obtain material on the size and age composition of the young in addition to tagging. Scales are removed with needles. Weight is determined from the amount of water displaced

in a measuring cylinder. The wastage in catching and tagging was 2 %.

The method may be used under expedition conditions and in work at stations on rivers.

Chapter 2

THE SPAWNING RIVERS OF THE BASIN OF LAKE OMEGA: COMPARATIVE  
DESCRIPTION, STATE AND REPRODUCTIVE VALUE

I. A List of the Spawning Rivers.

We know for certain that the following rivers are utilized (or have been utilized) by the Onega salmon for breeding:

Lososinka,

Shuya (to Lake Salon-yarvi), its tributaries the Syapsya and the

Malaya Suna,

Suna (to the Kivach Falls), its tributaries the Sandalka and the

Tivdiika,

Lizhma, its parts the Upper, Middle and Lower Lizhma and its tributary the Elgamka,

Unitsa,

Kumsa,

Povenchanka,

Nemina, its tributary the Pazha,

Pyal'ma, its tributaries the Zhilaya Tambitsa and the Tuna,

Tuba,

Vodla, its source the Vama and its tributary the Koloda,

Andoma, its tributary the Samina,

Vytegra,

Megra,

Vodlitsa.

In addition to these 15 rivers with their 12 tributaries, according to N. N. Pushkarev (1900a), the salmon previously entered a further 7 rivers: the Shoksha, the Tambitsa (around Tambitsy-Nos) and all the rivers of any size between the Pyal'ma and Orov Bay, i.e. the Arzhema, Vozritsa, Nelyuksa, Issel'ga (Tambitsa) and Filippa Rivers. The salmon disappeared from these rivers at the end of the last century, but the trout continued to enter them; they remain trout rivers down to the present. The transition of rivers from the category of salmon rivers to that of trout rivers has been noted for the basin of Lake Ladoga by D. K. Khalturin (1966).

According to unverified information, the salmon now enters the Syargezhka (a tributary of the Lizhma) and the Somba (a tributary of the Vodla). In 1963 and 1964 there were isolated instances of salmon being caught in the Ragnuksa (a tributary of the Vodla) and in the Chernaya stream (around Besov Nos /Cape Besov/), where it had previously never been caught; this was evidently an instance of straying.

M. B. Zborovskaya (1948) included the Oshta among the rivers which the salmon may possibly enter. Whether or not this is so has not as yet been established. Nor is it known whether the salmon previously entered the tributaries of Vodlozero -- the Ileksa, the Kelka and the Okhtomreka. M. B. Zborovskaya (1948) considers that it did enter these tributaries, but B. S. Lukash (1939), to whom she refers, does not state anything definite on the matter but refers to these rivers as spawning grounds of the whitefish, the bream and the dace and notes that the spawning grounds of the salmon are in the Vama, and that in Vodlozero the salmon is occasionally taken in the Lakhta (near the source of the Vama) and in the middle part of the lake. There are still rare instances of the catching of salmon in Vodlozero (2 fish in 1962 and

3 in 1963), when the salmon succeeds in negotiating the Vama dam when the backwater is relatively low. However, all the catches of the salmon relate to the southern or middle part of the lake and there are no known instances of salmon being caught in the three tributaries mentioned.

The Irsta, a tributary of the Shuya, is a river which the salmon may possibly have entered, but since the construction of a hydroelectric power station near the settlement of Ignoilo this river has, like the upper reaches of the Shuya, become inaccessible to it.

If, therefore, we disregard the last 9 rivers, for which there is no verified information, the salmon has bred in only 34 rivers, including tributaries. It is these rivers which will be considered subsequently.

## II. Physiographic Description of the Spawning Rivers

It is appropriate at this point to give a general description of the rivers, without entering into detailed descriptions of each of them.

Structural features. The drainage system of Karelia is distinctive by virtue of topographic features and the youth of the system itself. The territory is one of quite rugged topography and intricate structure. The main features of its present-day appearance were formed under the influence of three main relief-forming factors: tectonic movements, denudation and glaciation (glacial exaration and accumulation, glaciofluvial accretion). The surface of Karelia is covered by a mantle of Quaternary deposits, interrupted in places by exposures of the underlying bedrock. The deposits are thickest in areas where there are glacial and glaciofluvial accretional forms and in major depressions in the surface of the pre-Quaternary rocks (Biske, 1959).

Many of the rivers, especially the small ones, are practically like

mountain streams. They have large gradients (average fall from 0.001 to 0.007), a stony, little-eroded bed, as a result of which there are numerous waterfalls, rapids, kareshki<sup>1</sup> and shallows, alternating with pools and at times with lake-like widenings and true lakes. The rivers of Karelia are

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<sup>1</sup> Kareshki are small gentle rapids.

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essentially not rivers in the strict sense, but lake-river systems consisting of alternating lakes and river reaches.

The rapids which dam the pools and lakes are found in places where crystalline rocks outcrop in the river bed or in those places where the river cuts its way through a moraine or glaciofluvial deposits containing boulders. In the latter case the formation of rapids consisting of an accumulation of boulders has been due to the work of the river which has carried away the fine-grained material and left behind the larger size categories. /17/

The valleys of most of the rivers are faults and fissures in the crystalline rocks. For example, the narrow valley of the Kumsa River (reaching a width of 300 m in the region of Kol'ozero) is a tectonic depression; it has high, steep slopes consisting of crystalline rocks. In those places where the river cuts through a body of Quaternary deposits the valley is more developed. On the whole the river valleys are distinguished by features found in young valleys: the longitudinal and transverse profiles have not been elaborated. In some instances the transverse profile is V-shaped or trapezoidal, but the valley is not invariably expressed throughout the length of the river. Cyclic terraces developed throughout the length of the river are as a rule absent (Karandeeva, 1957).

Terraces are found in those parts of the valleys where the rivers flow through unconsolidated deposits subjected to greater erosion than the bedrock. They are clearly expressed in the lower reaches of the rivers owing to the lowering of the base level of erosion. Terraces are to be seen along the Suna, Shuya, Vodla, Nemina, Samina and Lososinka Rivers; in the Lososinka there are terraces within the town of Petrozavodsk.

The floodplain of the rivers is a relatively narrow, interrupted area of bog or meadow. Its surface may be level or hummocked. The floodplain is frequently overgrown with shrubs or forest.

Bogs and lakes occupy a considerable area in the river basins. The ratios of lake surface and bog area to drainage area stand in inverse proportion (Gritsevskaya, 1964).

Water regime. The water regime of the rivers may have a decisive influence on the reproduction of the salmon. Rivers with higher and more stable levels in the summer and winter low-water periods are of greater value, since the size of the feeding grounds and the preservation of the eggs in the redds during the winter are dependent on the stability of level.

A. V. Shnitnikov (1962) arrived at the following conclusions in an analysis of the variability of general moisture conditions in the Neva basin, to which the basin of Lake Onega belongs.

1. There is a well-expressed intrasecular cyclicality of general moisture conditions corresponding to the long-term regime of atmospheric precipitation; over the period from 1850 to 1960 there were four phases of reduced moisture and four phases of increased moisture; the duration of the cycle is between 27 and 31 years.

2. The intrasecular variability of general moisture conditions occurs against a background of suprasedecular variability; over the secular

period the total moisture clearly tends to reduce.

3. In the secular regime of total moisture the effect of man's economic activity is increasingly manifested as time passes.

These extremely interesting and important conclusions should certainly be borne in mind when analyzing the causes for fluctuations in the abundance of the salmon.

The rivers are fed from a combination of sources: snow, rain and groundwater. A. N. Malyavkin (1962) has estimated that groundwater accounts for between 10 and 25 % of the mean long-term discharge.

The elements which are distinguished in the annual variation of the water level of the rivers are the spring flood (peak in May), a short summer low-water period, a rise, usually of short duration, in the autumn (due to rain) and a winter low-water period with levels falling gradually to April. Levels are usually lowest at the end of March and in the first half of April. Groundwater feeding plays a large role in the formation of discharge in the winter low-water period.

The lakes incorporated in the river systems strongly regulate (smooth) the annual variation of level and discharge. The size of the maximum and minimum discharges and of the specific rates of flow is dependent on the ratio of lake surface to drainage area. As the percentage of lake surface increases the maximum specific rates of flow are reduced and the minimum rates are increased. The most regulated rivers with a lake surface of more than 20 % have an annual graph of the fluctuation of discharges which is reminiscent in its smoothness of graphs of the variation of lake level (Malyavkin, 1947).

The regulating effect of lakes is dependent on their position in the basin; the closer a lake is to the line of river flow, the greater is its influence. The factors other than the ratio of lake surface to drainage area

which affect seasonal fluctuations of discharges are the size of the catchment (the flood is evened out when the catchment is larger), the area of bogs to the drainage area (its effect is similar to the effect of lakes, but to a lesser degree) and the afforestation.

The distribution of discharge over the course of the year has been affected by wholesale felling of forests in the basins of some small rivers with a low ratio of lake surface to drainage area. Such rivers as the Vilga, the Upper Lizhma, the Elgamka and the Zhilaya Tambitsa have begun to freeze in the winter, which is something which, in the words of old inhabitants, did not happen previously. This is apparently connected with alteration of the regime of bottom feeding as a result of the reduction of the forests.

In addition to their role in the regulation of the water regime of the rivers, the lakes are receivers of groundwater feeding. The proportion of groundwater in the balance of a river is proportional to the area of the lakes, since groundwater under pressure enters deep lake basins which frequently lie below sea level. This is well manifested in the minimum specific rates of flow in the winter.

A. N. Malyavkin (1962, 1965) has established a relationship between the degree of lake regulation (the ratio of lake surface to drainage area) and the amount of the minimum discharge. /19/

1. Rivers with slight lake regulation. Ratio of lake surface to drainage area 0--3 %. Minimum specific rates of flow 1--2 litres/sec/km<sup>2</sup>.

2. Rivers with intermediate lake regulation. Ratio of lake surface to drainage area 4--8 %. Minimum specific rates of flow 2--2.5 litres/sec/km<sup>2</sup>.

3. Rivers with medium lake regulation. Ratio of lake surface to drainage area 9--15 %. Minimum specific rates of flow 2.5--3 litres/sec/km<sup>2</sup>.

4. Highly-regulated rivers. Ratio of lake surface to drainage area 16--34 %. Minimum specific rates of flow 3--3.5 litres/sec/km<sup>2</sup>.

The variation of winter levels, which is largely dependent on groundwater and bottom feeding may in some instances have a decisive influence on the reproduction of salmonids. The freezing of the rapids when water level falls, which occurs in small rivers and in part also in large ones (the Vama and the Suna, mainly owing to the regulation of discharge) undoubtedly causes egg mortality.

Ice regime and thermal regime. The Petrozavodsk Observatory of the Meteorological Office has been studying the ice regime of rivers for the last few years (Ustinov, 1964, 1966a, 1966b; Gromov and Ustinov, 1965). Nevertheless, there is still no clarity on many points which are very important for a study of the conditions of reproduction of the salmon, in as much as these have remained outside the purview of the investigators. It should be noted that it is very difficult to set up direct observations on the effect of the ice regime on fishes and what is said on some points can only be tentative. Thus, in our opinion, frazil ice and sludge may be a cause of the death of spawned salmon. The oral cavity and gills of dead fish have been found to be clogged with ice which evidently interfered with respiration.

Bottom ice may sometimes cover the whole area of rapids in a continuous layer, the thickness of which ranges from 5--10 cm (Vama River, October 30--November 2, 1963) to 0.5--1.0 m. Such covering of the bottom undoubtedly causes "clogging" of the redds and, in consequence, a heavy reduction and possibly cessation of the flow and filtration of water through the redds, i.e. a deterioration of oxygen supply. It has not been possible to establish how long bottom ice may remain (for a short period or until the spring),

and it is therefore difficult to estimate the degree of the influence of this factor. When the bottom ice floats up to the surface of the water it carries with it bottom material, including large stones; this may cause destruction of the redds and egg mortality. Bottom ice is also troublesome in the artificial propagation of fishes (Novikov, 1932).

Plugs formed by the accumulation of sludge, ascending bottom ice and finely broken-up floes in the stream are no less important factor. Plugs in rapids may block off the whole cross-section of the stream for hundreds of metres and even kilometres; in such localities the water flows above the ice and bursts the banks. Here, as in the case of bottom ice, flow through the redds should be strongly reduced. It is not known what happens to fish which do not succeed in quitting the rapids, but it must be thought that their chances of survival are very low. In the winter of 1965--1966 there were very strong plugs on the Vama River, which burst its banks and flowed into the forest. In the spring of 1966 the Vodlozero Collective Farm attempted to catch fish in the river, but without success. The fishermen themselves consider that the harsh winter and the plugs were the cause of the reduction in the quantity of fish in the Vama. In 1966 a reduction in the quantity of indigenous fishes was noted for the whole of the Shuya River below Lake Vagat. /20/

V. V. Azbelev and B. I. Shuster (1965) consider that the survival of eggs in redds is wholly dependent on the winter regime and they refer to repeated observations of instances of the destruction not only of individual Atlantic salmon redds, but also of entire spawning grounds as a result of plugs.

Frazil ice forms every year in the rivers of Karelia; the plugs were strongest in 1949--1950, 1954--1955, 1962--1963 and 1965--1966.

Icing usually begins in the rivers of the basin of Lake Onega in the

second half of October and the beginning of November: bank ice in pools and frazil ice and sludge in rapids. The autumn ice run occurs in November. Permanent ice is usually observed in pools no earlier than the second half of November; by the end of the winter its thickness reaches 70 cm. The ice is thin and unstable in rapids. Waterfalls and the largest rapids do not freeze over and are centres of the formation of frazil ice since the excellent mixing and supercooling of water masses essential for this occur in them. The rapids become ice free earlier than the pools, sometimes by as early as March or the beginning of April. An ice run does not occur in all rivers; the ice frequently melts in situ in small rivers. Within two to three weeks of the river ice run the lakes connected to the rivers are opened and lake ice is carried into the river. There are no observations on the effect of the ice run on fishes. The rivers are completely freed of ice in the second half of April or the beginning of May, with the middle of May as a late period.

The temperature regime of the rivers is dependent not only on air temperature, but also on the hydrographic features of the basin and on the nature of the catchment. Rivers which have a marshy catchment are cooled faster in the autumn than those which include lakes. Rivers which flow from large lakes are more slowly cooled owing to the reserve of heat accumulated during the summer heating; the greater is the volume of the water mass of the lakes, the farther downstream does their influence extend. It is this factor which is responsible for the differences in the time of spawning of the salmon in different rivers of the Lake Onega basin (end of September--beginning of October in the Pyal'ma and the Tuba, middle--end of October in the Vama and the Shuya, sometimes extending to the beginning of November). Water temperature is measured in tenths of a degree or is around zero from November (December) until April. Following the supercooling of the water in rapids the temper-

ature becomes negative. This may evidently affect the embryonic development of the salmon and lower the survival rate of the eggs in the redds since the optimum development temperature lies in the range 2--5°C and fluctuations of temperatures to above 8°C and below 0°C are impermissible at critical periods (Vernidub, 1950, 1961, 1964; Monich, 1955), at all events the temperature should not be below -0.5°C (Lozina-Lozinskii and Lyubitskaya, 1940).

Admittedly, temperature was not measured in the redds, but it would appear to be slightly higher than in the river, possibly as a result of supply of heat from the bottom or as a result of spring waters, although this is in need of verification. The causes of the extremely high mortality of salmon eggs in the redds during incubation (on average 91.9 %, Nikiforov, 1959a, 1959b) have not been established. In our opinion, these causes might be supercooling of the water and the ice phenomena to which reference has been made above.

The upper temperature limit is no less important. According to N. D. Nikiforov (1959b), growth of young salmon in the summer takes place when temperature is not in excess of 25°C. McGrimmon (1954) has established that the heating of water to 25°C does not reveal a noticeable effect on survival rate, but that a temperature of 28.5°C is lethal for young Atlantic salmon of all ages. According to the observations of M. I. Vladimirskaia (1957), salmon in the Pechora in July 1954, when water temperature reached 22.4--24.2°C, behaved in an agitated manner and swam to streams in which the water was colder. Dying adult salmon which had no damage on the body were found at this time. Young Atlantic salmon move to places where the current is faster in the middle of the summer. According to the observations of N. V. Evropeitseva (1950), young salmon in ponds were depressed at 25°C and attempted to keep to places where there was greater flow.

M. N. Lishev and E. Ya. Rimsh (1961) established that the abundance

of the salmon was conditioned by the conditions of its existence during the first year of life, to the underyearling stage. Strong and average year-classes formed in years when the summer air temperature (from May through September) did not exceed 90--95 % of the period mean and when spring-summer discharge was at least 110 % of the usual (norm). The absolute index of the norm was  $14.6^{\circ}\text{C}$ ; a correlation was established between yield and temperature in 75--85 % of cases.

In the rivers of the basin of Lake Onega water temperature is highest in July and may reach a level at which the salmon become depressed. Thus, at the outflow of the Middle Lizhma from Lizhmozero a temperature of  $25.7^{\circ}\text{C}$  was recorded on July 31, 1938, while the mean maximum temperature (over 17 years) from this point was  $22.3^{\circ}\text{C}$ . A temperature of  $23.0^{\circ}\text{C}$  was recorded in the Kumsa near the mouth on July 10--11, 1954; the mean maximum over 11 years was  $21.1^{\circ}\text{C}$ . A maximum of  $24.5^{\circ}\text{C}$  was recorded for the Vodla and  $24.0^{\circ}\text{C}$  for the Shuya. /22/

Water quality. The water of rivers in the basin of Lake Onega belongs to the hydrocarbonate class. Such water is characterized by extremely slight mineralization, an increased content of coloured humic acids and by virtue of this a weakly acid reaction. The last two circumstances are caused by the considerable frequency of bogs, the overall area of which is approximately 30 % of the total area of Karelia (Lepin, 1957). Bogs and lakes have an opposite effect on the colour index and acidity of the water.

The Karelian rivers are characterized by extremely slight sediment discharge, which is explained by the resistance to erosion of the rocks forming the bed. Because of this the rivers have transparent water and the transportation and deposition of alluvium are slight. The reduction of the forests has not apparently affected the sediment discharge, since instances of soil

erosion have not been recorded in the former areas of forest.

The turbidity of the river water may be strongly increased in some instances by shallow "feeder" lakes or lakes with through flow. This happens when such lakes are subjected to strong wind mixing as a result of which silt and clay particles are stirred up and carried in suspension into the river. An effect of this kind is to be noted in a number of rivers: in the Shuya below Lake Vagat, in the Vama issuing from the Vavdepol'skaya arm of Vodlozero, in the Tuba flowing through Lake Egozero. The silt carried into the river settles in part in the spawning grounds in close proximity to the outflow and this may possibly lead to a deterioration of the incubation regime (observations on the Shuya and the Vama in the second and third decades of October, i.e. nearer the end of spawning). The suspended matter settles mainly in the pools and the water clears. This is largely facilitated in the Tuba by the dense reed beds in the shallows of the river, which function so efficiently as a filter that transparency increased from 0.4--0.5 m to 1.0 m in the course of 4.5 km below Lake Egozero, and at the mouth (9 km below Egozero) the bottom could be seen at a depth of down to 1.2 m (observations in August 1963).

Vegetation. The development of aquatic vegetation in rivers is dependent on a combination of different factors -- bottom material, flow rate, depth, the transparency of the water, and also logging, which have such a mechanical effect primarily on inshore and coarse vegetation that such vegetation does not as a rule form beds of considerable size in logging rivers (there is no logging in the Tuba). The largest beds of submerged soft vegetation are found in the Tuna, the Middle Lizhma and the Syapsya, which are highly transparent. Water moss is common in the rapids of all the rivers. There are reed beds, sometimes with bulrushes, around the mouths and outlets of the

rivers in lakes through which rivers flow; considerable aggregations of pike are common in such localities. For this reason aquatic vegetation is undesirable in salmon rivers. /23/

Groups of rivers. The salmon rivers of Lake Onega may be divided into three groups in relation to size and water content: large, medium and small.

The first group comprises only three rivers, the Vodla, the Shuya and the Suna, which were of very great economic importance to the salmon fisheries in the past. These rivers are at least 170 km long and the mean annual discharge of water is at least 70 m<sup>3</sup>/sec. The Vama, which is a reach of the Vodla, should not be separately distinguished, although this has been done in table 1.

The group of medium rivers comprises the Syapsya, Sandalka, Lizhma, Kumsa, Povenchanka, Nemina, Pyal'ma, Koloda, Andoma, Samina, Vytegra and Megra Rivers. These rivers are from 15 to 156 km long and have mean annual water discharges of between 6 and 25 m<sup>3</sup>/sec. The Sandalka, the Povenchanka and the Vytegra have been rendered completely unsuitable for the reproduction of the salmon owing to hydraulic engineering works. Only the Pyal'ma is at present of commercial significance; there are very few salmon in the other rivers and the salmon has disappeared completely from the Koloda.

The small rivers have mean annual water discharges of from 1 to 4 m<sup>3</sup>/sec and are between 15 and 57 km long. They include the Lososinka, Malaya (Lesser) Suna, Tivdiika, Upper Lizhma, Elgamka, Unitsa, Pazha, Zbilaya Tambitsa, Tuna, Tuba and Vodlitsa Rivers. Their role in the reproduction of the salmon is insignificant at the present time.

The area of rapids suitable to salmon was taken into consideration in addition to size and water content when dividing the rivers into groups. Thus,

although the mean annual discharge of water in the Tivdiika rose to  $62 \text{ m}^3/\text{sec}$  after the inclusion of a part of the catchment of the Suna, the reproductive potentialities of the river have not been increased and it has been left in the group of small rivers.

The main hydrographical and hydrologic characteristics of the spawning (salmon) rivers of the basin of Lake Onega are set out in table 1, a composite table compiled from the data of S. A. Bersonov (1960), S. V. Grigor'ev and G. L. Gritsevskaya (1959), S. A. Sovetov (1917) and L. I. Tsimbalenko (1918).

Information concerning those rivers which are entered only by chance by the salmon or for which entry is doubtful is set out in table 2. Those rivers which for various reasons have ceased to be breeding grounds of the salmon and have passed to the category of trout rivers are given at the end of this table. The other trout tributaries of Lake Onega have similar characteristics. In addition to the eastern shores of the lake, there are groups of trout rivers between the outflow of the Svir' and Petrozavodsk and between the Kondopoga and the Lizhma.

The differences between the salmon and trout rivers of Lake Onega may be summarized as follows.

1. Even when small, salmon rivers are larger than trout rivers; if the trout enters salmon rivers, it spawns either in the lower rapids or in the small tributaries nearest the mouth.

2. The salmon rivers are more gently flowing than the trout rivers, as was noted by K. F. Kessler (1868): "for preference the taimen (Hucho taimen) chooses the most stony rivers and streams with the most rapids for spawning, whereas the salmon to some extent avoids such eternally grumbling

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Таблица 1

2 Основные характеристики перестовых (пососевых) рек бассейна Онежского озера

3	4	5	6	7	8	9	10
Река, приток	Длина, км	Падение, м	Площадь водосбора, км <sup>2</sup>	Коэффициент озерности, %	Модуль стока, л/сек. км <sup>2</sup>	Расход воды, м <sup>3</sup> /сек.	Примечания
Дюссентика	23.3	123.0	322.5	5.7	11.3	3.66	(12) Сезонное вдхр в истоке и три русловых вдхр в нижн. течении, одно — с 1703 г.
Шуя	272.0	163.0	10267	10.3	9.4	96.27	(13) У пос. Шнойла (130 км от устья) с 1939 г. плотина ГЭС, русловое вдхр.
Сисья	34.0	17.0	1803	20.4	8.7	15.72	Плотин нет.
Мадан Суна	23.3	28.5	481.6	8.5	8.5	4.09	Силавная плотина в 7 км от устья.
Суна	281.6	325.2	7665	12.5	9.6	74.06	Сток переброшен от впадения в оз. Палье—оз. Саудал—Шугозеро—Кондопожская губа.
Сандава	14.9	20.8	1066	26.2	9.5	10.17	В 1926 г. исток закрыт глухой дамбой, река поресохла.
Тинцинка	16.0	10.0	449.7	24.7	9.4	4.41	(14) В 1952 г. приключена часть водосбора Суны площадью 5861 км <sup>2</sup> , расход воды возрос до 62 м <sup>3</sup> /сек.
Векма	68.3	114.0	717.6	19.4	10.6	7.61	(15) Плотины в верхнем, среднем и нижнем течении.
Верхняя Шижма	20.0	79.5	98.7	≤ 5	11.0	1.08	Силавная плотина.
Гламка	18.0	83.3	—	≤ 2	—	≤ 1	Плотины разрушены.
Унцида	56.7	141.4	394.3	2.4	10.0	3.95	Соединена с Шижмозеркой, плотины.
Кумса	60.2	126.6	745.4	8.5	10.0	7.45	Плотины в верхнем, среднем и нижнем течении.

35 Таблица 1 (продолжение)

3	4	5	6	7	8	9	10
Река, приток	Длина, км	Падение, м	Площадь водосбора, км <sup>2</sup>	Коэффициент озерности, %	Модуль стока, л/сек. км <sup>2</sup>	Расход воды, м <sup>3</sup> /сек.	Примечания
Повенчанка	16	60	822	—	—	≤ 10	(37) Вошла в состав Беломорско-Балтийского канала.
Неваля	79.4	144.6	635.2	2.8	10.0	6.35	(38) Плотина в 30 км от устья.
Пала	34.2	86.0	231.5	2.5	10.0	2.32	Плотины разрушены.
Писляя	68.0	125.0	922.2	1.7	10.0	9.22	То же.
Иволга Гамбона	48.0	89.6	266.5	5.6	10.0	2.67	Плотина разрушена.
Гуна	21.1	—	—	—	—	≤ 1.5	Плотин нет.
Губа	15.5	54.3	324.2	3.5	10.0	3.24	(40) Две плотины: в истоке из Вогозера разрушена, в нижн. течении не используется.
Водла	169.5	103.1	13655	5.5	10.0	136.55	(41) В обоих истоках плотины, Водлозеро — сезонное вдхр.
Вама	23.4	47.5	5814	8.8	10.0	58.14	(42) В истоке плотина.
Велюда	110.0	171.3	1283	2.2	10.0	12.83	(43) Три плотины — в верхней, средней и нижней частях реки.
Андоня	156	—	2570	1.5	10	25.7	Плотина ГЭС.
Самина	79	—	976	0.7	10	9.8	
Вытегра	66	—	1280	—	—	—	
Мегра	69	—	660	—	10.1	6.7	(44) Вошла в состав Волго-Балтийского пути, зашлюзована.
Веданца	43	—	411	—	10	4.1	

Key to Table 1: 1. Table 1 2. Main characteristics of spawning (salmon) rivers of the basin of Lake Onega 3. River, tributary 4. Length, km 5. Fall, m 6. Catchment area, km<sup>2</sup> 7. Ratio of lake surface to drainage area, % 8. Specific rate of flow, litres/sec/km<sup>2</sup> 9. Water discharge, m<sup>3</sup>/sec 10. Comment 11. Lcososinka 12. Seasonal reservoir at outflow and three river-bed reservoirs in lower reaches, one in existence since 1703 13. Shuya 14. Hydroelectric power station dam near the settlement of Ignoila (130 km from the mouth) since 1939, river bed reservoir 15. Syapsya 16. Malaya (Lesser) Suna 17. No dams 18. Suna 19. Logging dam 7 km from mouth 20. Discharge diverted from the Girvas Falls into Lake Pal'e -- Lake Sandal -- Nigozero -- Kondopozhskaya Bay 21. Sandalka 22. Outflow dammed off in 1926, river dried up 23. Tivdiika 24. A part of the catchment of the Suna to an area of 5861 km<sup>2</sup> was included in 1952 and the discharge of water rose to 62 m<sup>3</sup>/sec 25. Lizhma 26. Dams in upper, middle and lower reaches 27. Upper Lizhma 28. Elganka 29. Logging dam 30. Dams destroyed 31. Unitsa 32. Joined to the small lake Pigmozerka, dams 33. Kumsa 34. Dams in upper, middle and lower reaches. 35. Table 1 /25/ (continuation) 36. Povenchanka 37. Incorporated in the White Sea-Baltic canal 38. Nemina 39. Dam 30 km from mouth 40. Pazha 41. Dams destroyed 42. Pyal'ma 43. Zhilaya Tambitsa 44. Tuna 45. Dam destroyed 46. No dams 47. Tuba 48. Two dams: dam at outflow from Egozero destroyed, dam in lower reach not used. 49. Vodla 50. Dams at both outflows, Vodlozero is a seasonal reservoir 51. Vama 52. Koloda 53. Dam at outflow 54. Three dams -- in the upper, middle and lower parts of the river 55. Andoma 56. Samina 57. Hydroelectric power station dam 58. Vytegra 59. Incorporated in the Volga-Baltic waterway, locks on the river 60. Megra 61. Vodlitsa.

Таблица 2

Основные характеристики рек, в которых заход лосося случаен или не доказан

3 Река	4 Длина, км	5 Падение, м	6 Площадь водосбора, км <sup>2</sup>	7 Коэффициент осерпости, %	8 Модуль стока, л/сек/км <sup>2</sup>	9 Расход воды, м <sup>3</sup> /сек
10 Ирета	65.5	65.3	1802	4.4	9.3	16.86
11 Сыргежика	12.0	—	—	—	—	≤2
12 Илекса	206.0	72.7	3879	3.0	10.0	38.79
13 Келка	19.9	14.0	361.6	8.2	10.0	3.61
14 Охтомрека	24.4	16.0	210.3	2.0	10.0	2.10
15 Сомба	74.9	201.0	685.1	1.5	10.0	6.85
16 Рягнукса	45.6	100.8	450.7	4.3	10.0	4.51
17 Черная речка	90.0	65.0	585.6	0.7	10.0	5.86
18 Ошта	37	—	688	—	—	—
19 Вилга	21.2	128.3	136.1	0.2	9.0	1.22
20 Шокша*	21.2	120.8	116.0	1.2	8.5	0.99
21 Тамбница (у Тамбниц-Носа)*	20	42	—	—	—	—
22 Аржема*	12.5	117	—	—	—	—
23 Возрица*	12	17	—	—	—	—
24 Нелюкса*	11.6	—	—	—	—	—
25 Иссельга (Тамбница)*	34.5	112.0	152.1	1.2	10.0	1.52
26 Филиппа*	24.3	105	89.2	1.6	10.0	0.89

27 \* Во все эти реки сейчас заходит только форель.

Key to Table 2: 1. Table 2 2. Main characteristics of the rivers which the salmon enters by chance or for which entry has not been proved 3. river 4. Length, km 5. Fall, m 6. Catchment area, km<sup>2</sup> 7. Ratio of lake surface to drainage area, % 8. Specific rate of flow, litres/sec/km<sup>2</sup> 9. water discharge, m<sup>3</sup>/sec 10. Irsta 11. Syargezhka 12. Ilekxa 13. Kelka 14. Okhtomreka 15. Somba 16. Ragnuksa 17. Chernaya rechka 18. Oshta 19. Vilga 20. Shoksha\* 21. Tambitsa (near Tambits-Nosa)\* 22. Arzhema\* 23. Vozritsa\* 24. Nelyuksa\* 25. Issel'ga (Tambitsa)\* 26. Filippa\* 27.\* At the present time only the trout enters all these rivers.

waters<sup>11</sup>.

3. The trout is able to tolerate a higher degree of humification and is found even in peat ditches in which the water is heavily coloured and

has a pH of 6.0--6.5 (Pravdin and Kornilova, 1949).

Despite the traditional conviction, the trout is on the whole less demanding on conditions than is the salmon. It is able to breed in rivers which the salmon avoids entering, for example in the upper reaches of the Pyal'ma and the Nemina. By virtue of its greater adaptability (plasticity) it is able to form landlocked forms in heavily humified, swampy oxbows (lamby) (transparency 0.6--0.8 m; size up to 200--300 m long, bottom material ooze), which have long lost a connection with the sea, (Chernov, 1935). These valuable properties of the trout compel us to consider it at least as attentively as we consider the salmon.

Divergence within the genus Salmo has had the effect that its species have adapted themselves to the use as spawning grounds of watercourses within their range which differ in their nature, and the trout has even succeeded in occupying landlocked bodies of water. The high adaptability (plasticity) of Salmo species makes them extremely promising subjects for economic exploitation, especially in Karelia, which abounds with lakes and rivers with the most varied conditions.

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### III. The Fish Fauna of the Rivers.

#### Enemies and Competitors of the Salmon.

There has not previously been a special study of the fish fauna of the rivers in the basin of Lake Onega. Lists of fishes for many rivers are given in "The Natural and Economic Conditions of the Fishing Industry in Olonets gubernia" (1915), a report compiled from questionnaires filled in by the population. However, there are great inaccuracies in these lists and although commercially exploited species well known to the population are correctly listed in them, there is no mention of such species as the lamprey,

the minnow, the stone loach, the white bream, the miller's thumb, the dace and others. In some instances a local name is given without any explanation. For example, "korpuz", which is apparently the "korbitsu", i.e. the dace, is listed for the Shuya. The data in this report are therefore in need of verification and correction.

Because the scientific studies of recent years have been devoted to the lakes and have scarcely touched on the rivers, little can be extracted from them. The lakes of the Shuya basin have been most fully investigated; we have the most detailed information on the fishes of this river.

Our materials on the different rivers are of unequal value, but they do permit us to make some comparisons and draw some conclusions.

The rivers in the basin of Lake Onega differ significantly in the composition of the fish fauna and in the relative abundance of its components, including competitors and enemies of the salmon. The diversity of species in the fish fauna is dependent on the size of the river and on its hydrographical and hydrologic features. The smaller is a river, the more impoverished is the composition of the fish fauna. In rivers which abound in lakes through which there is flow the fish fauna is enriched by limnophilous fishes. The abundance of the pike and the extent of its effect on young salmon are connected with the existence in a river of such lakes in which the pike breeds. The predator forms considerable concentrations, which are a strong barrier to downstream migrants where the spawning tributaries join the river, in the lower reaches of the tributaries and in the outflow of the main river (Malaya (Lesser) Suna -- Syamozero -- Syapsya -- Vagatozero -- Shuya -- Logmozero; Upper Lizhma, Elgamka -- Lizmzero -- Middle Lizhma -- Kedrozero -- Lower Lizhma ("Kedroreka") -- Tarasmozero).

The nature of utilization of the river has a considerable influence on the composition of the fish fauna. There is, as a rule, reduction and sometimes total disappearance in the first instance of the most valuable species.

The species composition and frequency of individual species are given in table 3 only for those rivers which were investigated by us. Since we were unable to make lengthy observations at permanent stations, it is inevitable that these data will subsequently be corrected and expanded. Thus, it is evident that the sculpin Cottus poecilopus, which is known to exist in Lake Onega, will be found in the rivers.

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The largest number of species has been recorded for the Shuya (25 for the river and 31 for the basin as a whole) and the Vodla (20 and 25 respectively), which have the best conditions for thermophilous cyprinids. Such relicts as chub, zope, gudgeon, crucian carp and white bream are found in the basins of both rivers; the catfish, the rudd and the spiny loach are found in the Shuya; the pike-perch is found in the Shuya and the Vodla and is absent from the other rivers.

The number of species has been reduced in a number of rivers as a result of hydraulic engineering works by elimination of the most valuable species -- salmon, trout, whitefish and grayling (table 4).

The least number of species is found in the small, fast-flowing rivers, which are suitable only for typical rheophilous fishes (the Pazha -- 10 species; Upper Lizhma, Elgamka, Tuba -- 11 species). Thanks to the presence of lakes through which there is flow the other rivers have a richer fish fauna, but far from the same as that of the Shuya and the Vodla.

From among the fishes which inhabit the rivers we are primarily interested in those which are enemies and competitors of the salmon.

Таблица 3

Видовой состав и встречаемость рыб в лососевых реках бассейна Онежского озера

Вид и форма	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	Лососинка	Шуй (от Сяпек до Устья)	Суна (от впадения Кивы до Устья)	Верх. Дьяма, Елгама	Нижн. Дьяма	Уинца	Кумса	Нежина	Пажа	Пильма	Жилак Тамбца	Туба (ниже Егосера)	Волга (вс)	Вала			
<i>Leuciscus phariaticus</i> — много ручья	-	+	+1	-	+		?										*
<i>L. planeri</i> — много ручьевая	+	?	?				+										?
<i>Acipenser ruthenus</i> — стерлядь*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Salmo salar</i> m. <i>schago</i> — озерный лосось	=	+	=	1	+1	1	+1	1	1	+	+	+1	+	+			
<i>S. trutta</i> m. <i>lacustris</i> — озерная форель	=	+1	=	1	1	?	1	1	1	+	-	+1	+1				
<i>S. trutta</i> m. <i>fario</i> — ручьевая форель	1	1	=	1	1	?	+1	?	+1	+1	?	?	+1	-			
<i>Corygenus albula</i> — ряпушка***	-	1***	-	-	-***	-	-	-	-	-	-	-	?	-			
<i>C. tauricus tauricus</i> — озерно-речной сиг	-*	+	1	=	1	=?	=?	+1	-	+1	+1	=*	+	+1			
<i>Thymallus thymallus</i> — харюс	+1	+	=	1	1	?	+	+	+	+	+	1	+1	+			
<i>Oncorhynchus eperlanus</i> — корюшка	-	-*	-*	-	-***	-	-*	-	-	-	-	-*	-	-			
<i>O. eperlanus eperlanus</i> m. <i>spitzoi</i> — сигок	-	-	-	-	-	-	-	-	-	-	-	-	-	-			

29 Таблица 3 (продолжение)

Вид и форма	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	Лососинка	Шуй (от Сяпек до Устья)	Суна (от впадения Кивы до Устья)	Верх. Дьяма, Елгама	Нижн. Дьяма	Уинца	Кумса	Нежина	Пажа	Пильма	Жилак Тамбца	Туба (ниже Егосера)	Волга (вс)	Вала			
<i>Salmo trutta</i> — форель	+	+	+	+	+	1	+	1	+1	+	+1	+	+	+			
<i>Salmo trutta</i> — плотва	+	+	+	+1	+1	+	+	+1	+	+	+	+1	+	+			
<i>Salmo leuciscus</i> — елец	?	+	+1	-	-	?	?	+	+	+	+	?	+	+			
<i>Salmo gairdneri</i> — голец	-	1	-	-	-	-	-	-	-	-	-	-	1	1			
<i>Salmo trutta</i> — форель	-	+1	+1	?	?	+1	-	-	-	1	1	-	+1	+1			
<i>Salmo trutta</i> m. <i>phthalicus</i> — голец	?	?	-	+	1	+	+	?	?	+	+	+	+1	+1			
<i>Salmo trutta</i> m. <i>phthalicus</i> — голец	-	1	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Salmo trutta</i> — пескарь	-	+1	-	-	?	-	-	-	-	-	-	-	+1	-			
<i>Salmo trutta</i> m. <i>alpinus</i> — уклей	?	+1	+1	-	-***	?	+	?	?	+1	+1	-	+	+1			
<i>Salmo trutta</i> — густера	-	+1	?	-	-	-	-	-	-	-	-	-	?	?			
<i>Salmo trutta</i> — дум	1	+	+	-	1***	+	1	+	-	-	-	-	+	+1			
<i>Salmo trutta</i> — сигок	-	1	-	-	-	-	-	-	-	-	-	-	?	?			
<i>Salmo trutta</i> m. <i>trassiacus</i> — карась	-	?	-	-	-	-	-	-	-	-	-	-	1	-			
<i>Salmo trutta</i> m. <i>barbatulus</i> — голец усатый	+1	+1	?	?	?	+1	+1	+1	?	+1	+1	+1	+1	+			

Таблица 3 (продолжение)

Вид и форма	Лососинка	Шуя (от Слеса до устья)	Суня (от впадения Кивача до устья)	Верх. Лижма, Елгамка	Нижн. Лижма	Унитса	Кумса	Немина	Пазха	Пыльма	Жилых Тамбитса	Туба (выше Егозера)	Водла (вск)	Вана
<i>Cobitis taenia</i> — щиповка	—	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Silurus glanis</i> — сом	—	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anguilla anguilla</i> — угорь****	—	1	—	—	—	—	—	—	—	—	—	—	+	—
<i>Lota lota anadromus</i> — чалым	+1	+	+1	1	+1	+1	+1	+1	1	+1	+1	1	+	+
<i>Pungilius pungilius</i> — колюшка девятиглаз	—*	—*	—*	—	—	—	—*	—*	—	—*	—	—*	—*	—
<i>Gasterosteus aculeatus</i> — колюшка трехглаз	—*	—*	—*	—	—	—	—*	—*	—	—*	—	—*	—*	—
<i>Lucioperca lucioperca</i> — судак	—	1	—	—	—	—	—	—	—	—	—	—	+1	1
<i>Perca fluviatilis</i> — окунь	+	+	+	+1	+1	+	+	+	+1	+1	+	+1	+	+
<i>Acerina cernua</i> — ерш	+	+	+	1	+1	+	+	+	—	+1	+1	+1	+	+
<i>Myoxocephalus quadricornis onegensis</i> — рогатка четырехрогая	—	—	—	—	—	—	+1 <sup>00</sup>	—	—	—	—	—	—	—
<i>Cottus gobio</i> — подкаменщик	+1	+1	1	+1	+1	+1	+1	+1	+1	+1	+1	+1	+1	+1

Примечание. В таблице приняты следующие обозначения: знак + — рыба обычная, многозлазная; +1 — обычная, но немногочисленная; 1 — очень редкая, единично; — — не встречается; = — была, но исчезла; ? — возможно, встречается; \* — заходит в устье; \*\* — вселяется с 1954 г.; \*\*\* — спускается из озер; \*\*\*\* — после постройки плотины на Свири стал чрезвычайно редок; 0 — может спускаться из Водлозера; ∞ — в оз. Остер; <sup>00</sup> — есть в притоках лососевых рек; <sup>000</sup> — есть в Лижмазере, но очень редок. Если о рыбе нет никаких сведений, то графа оставлена пустой.

Key to Table 3: 1. Table 3 2. Species composition and occurrence of fishes in salmon rivers in the basin of Lake Onega 3. Species and form 4.

Lososinka 5. Shuya (from the Syapsya to the mouth) 6. Suna (from the Kivach Falls to the mouth) 7. Upper Lizhma, Elgamka 8. Lower Lizhma 9. Unitsa 10. Kumsa 11. Nemina 12. Pazha 13. Pyal'ma 14. Zhilaya Tambitsa 15. Tuba (below Egozero) 16. Vodla (the whole river) 17. Vama 18.

*Lampetra fluviatilis* -- river lamprey 19. *L. planeri* -- brook lamprey 20.

*Acipenser ruthenus* -- sterlet\* 21. *Salmo salar* m. *sebago* -- lake salmon

22. *S. trutta* m. *lacustris* -- lake trout 23. *S. trutta* m. *fario* -- brook trout<sup>000</sup>

24. *Coregonus albula* -- vendace\*\*\* 25. *C. lavaretus lavaretoides* -- migratory

lake-river whitefish 26. *Thymallus thymallus* -- grayling 27. *Osmerus*

*eperlanus eperlanus* -- smelt 28. *O. eperlanus eperlanus* m. *spirinchus* --

snetok (landlocked smelt) 29. Table 3 (continuation) 30. *Esox lucius* --

pike 31. Rutilus rutilus -- roach 32. Leuciscus leuciscus -- dace 33.  
L. cechalus -- chub 34. L. idus -- ide 35. Phoxinus phoxinus -- minnow  
36. Scardinus erythrophthalmus -- rudd 37. Gobio gobio -- gudgeon 38.  
Alburnus alburnus -- bleak 39. Blicca blicca -- white bream 40. Abramis  
brama -- bream 41. A. ballerus -- zope 42. Carassius carassius -- crucian  
carp 43. Mezochilus bartatulus -- stone loach 44. Cobitis taenia -- spiny  
loach 45. Silurus glanis -- catfish 46. Anguilla anguilla -- eel \*\*\*\*  
47. Lota lota quadromus -- burbot 48. Fungitius fungitius -- nine-spine  
stickleback 49. Gasterosteus aculeatus -- three-spine stickleback  
50. Lucionerca lucionerca -- pike-perch 51. Perca fluviatilis -- perch 52.  
Acerina cernua -- pope 53. Hyoocerhalus quadricornis onegensis -- fourhorn  
sculpin 54. Cottus gobio -- miller's thumb 55. Note. The following  
notations are adopted in the table: +, the fish is common and numerous; +1,  
common but not numerous; 1, very scarce, singly; --, not found; =, used to  
exist, but has disappeared; ?, possible, may be found; \*, enters the mouth;  
\*\*, present since 1954; \*\*\*, descends from the lakes; \*\*\*\*, became extremely  
rare after construction of dams on the Svir'; <sup>0</sup>, may descend from Vodlozero;  
<sup>00</sup>, present in Lake Oster; <sup>000</sup>, present in the tributaries of salmon rivers;  
<sup>0000</sup>, present in Lizhmozero but very rare. Where there was no information  
concerning a fish the column has been left blank.

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The competitors include young grayling, the dace, the minnow, the stone loach  
and the gudgeon; this combination of fishes is as a rule found in the same  
localities as young salmon and is caught together with them. Owing to  
differences in biology and behaviour the competitive capacity of these fishes  
is not the same. The grayling, the pike and the burbot should be regarded  
as the main enemies of young salmon in our rivers. However, according to

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Таблица 4

2. Количество видов и форм, встречающихся в лососевых реках бассейна Онежского озера

3 Встречаемость	4 Лососинка	5 Шуй (от Сяпсы до устья)	6 Суня (от Кивача до устья)	7 Верхняя Лижма, Елгамка	8 Нижняя Лижма	9 Уница	10 Кумса	11 Немина	12 Пазха	13 Пяльма	14 Жилая Тамбитца	15 Туба (ниже Егозера)	16 Водла (вся)	17 Всего
Постоянно встречается в реке в настоящее время	11	25	12	11	13	11	15	13	10	16	14	11	20	17
Были в прошлом, но исчезли	2	—	4	1	—	1	1	—	—	—	—	1	—	—
Входит из озер и притоков	3	6	3	—	4	2	4	3	—	2	1	4	5	1
Всего отмечено для бассейна	16	31	19	12	17	12	20	16	10	18	15	16	25	18

Key to Table 4: 1. Table 4 2. Number of species and forms found in the salmon rivers in the basin of Lake Onega 3. Frequency 4. Lososinka 5. Shuya (from the Syapsya to the mouth) 6. Suna (from the Kivach Falls to the mouth) 7. Upper Lizhma, Elgamka 8. Lower Lizhma 9. Unitsa 10. Kumsa 11. Nemina 12. Pazha 13. Pyal'ma 14. Zhilaya Tambitsa 15. Tuba (below Egozero) 16. Vodla (the whole river) 17. Vama 18. Invariably to be found in the river at the present time 19. Was present in the past but has disappeared 20. Enters from the lakes and tributaries 21. Total recorded for the basin.

published data, even such non-predatory fishes as the minnow and the dace may be not only competitors, but also enemies of the salmon and consume its larvae (Mikhin, 1959). Whitefish, ide, perch, pope and roach are common in the pools of the rivers and below the rapids, but these fishes may also enter the rapids and there enter into interrelationship with the young salmon.

The lamprey apparently inhabits all the rivers, with the exception of the upper reaches (Vama, Upper Lizhma, Elgamka). Its larvae are found both in soft bottoms and in shingle beds. There was an interesting instance of the discovery of a lamprey larva in a salmon redd in the Syapsya River. No eggs were found in this redd and there was a lot of tree bark in it. It is possible that this was a "test" redd in which no eggs were laid because of the heavy contamination of the bottom resulting from logging.

A river lamprey was observed at Chuporog on the Suna on May 26, 1960 keeping in the vicinity of a batch of eggs attached to the undersurface of stones; the eggs were in the mobile embryo stage.

The trout is not of commercial importance in salmon rivers, since it enters them in very small quantities. It breeds in shallow tributaries not entered by the salmon, but it is possible that it also utilizes the lower spawning grounds of the salmon in the main river. During the river period of existence and during the downstream migration the young of these fishes are to be found in the same reaches.

A number of investigators regard the trout as an undesirable fish in salmon rivers, in as much as it is a food competitor of parr and consumes salmon eggs. V. A. Abakumov (1960) found, additionally, that the hybrids which form under natural conditions between the salmon and the trout are inferior in growth rate to the salmon during the (marine) feeding period.

The lake-river whitefish is common, if not invariably present in salmon rivers, but its abundance has been sharply reduced, and it has practically disappeared along with the salmon from the Suna, Povenchanka and Unitsa Rivers. The sea whitefish of the Shuya appears in the river in July and remains in the pools of the Shuya and the Syapsya and below the rapids until spawning; fish which have overwintered in the river after spawning migrate downstream in

April--May, i.e. before the salmon larvae emerge from the redd. Young whitefish which have migrated downstream from the river are caught in Petrozavodsk Bay in July--August. It is evident that the whitefish is not an enemy or competitor of the salmon under the conditions of the Shuya. The Lizhma whitefish approaches the mouth of the Kedrozerka in May after having overwintered in Tarasmozero, but since it is not found in the locality in June it is also scarcely a threat to salmon larvae.

The grayling is a competitor and predator which invariably accompanies young salmon. Its abundance varies in different rivers. The grayling is, perhaps, the fish most sensitive to the effect of logging, since its spawning and spawning grounds are exposed to the effect of the intensive spring logging. The grayling has disappeared completely from the Suna. Its numbers were low in the Kumsa, but since logging was discontinued its stock has increased rapidly. The grayling is found far more often than young salmon in the Kumsa, Syapsya and Shuya Rivers. It is very rare in the Tuba and in the system of the Lizhma, whereas it is the fish which has the main effect in the rapids of the Pyal'ma and the Tambitsa and is possibly inferior in abundance only to the minnow. According to the data of test fishing in the middle of August 1963 the ratio of grayling and salmon in groups of underyearlings and yearlings in the rapids of the Pyal'ma and the Tambitsa was 4 : 1 in favour of the grayling. Although the grayling inhabits the same localities as young salmon, it extends over a greater area. The salmon is more active in search of food. According to the data of A. A. Zabolotskii (1959), the grayling consumes three times as much food as the parr and grows faster. There is a corresponding difference of 2--3 times in the weight of coeval young grayling and salmon. At the proportions of underyearlings and yearlings observed in the system of the Pyal'ma River, the

fish mass of the grayling is therefore 10 times that of the salmon parr. It is clear from this that unless the abundance of the grayling (and of other competitors) is reduced it is impossible to increase the productivity of the salmon spawning rivers.

The grayling is an active predator which continues to feed even when the river is ice covered. The stomach of a grayling 850 g in weight and 41.5 cm long which was caught on October 30, 1963 in the salmon spawning grounds in the Vama River contained 15 specimens of the landlocked smelt 5--6 cm long. The smelt had appeared in the river after a strong wind had been blowing toward the outflow. A week before this, at the height of salmon spawning, grayling which had been feeding on salmon eggs were caught in the Vama. The grayling undoubtedly also feeds on young salmon, which are more available in the early stages, down to the underyearling, when the young salmon are less mobile.

The pike inhabits all the salmon rivers, but its quantities vary in relation to the existence of spawning reaches suitable for it. In rivers in which conditions are not suited to the reproduction of the pike (Kumsa, Pazha, Pyal'ma) its abundance is slight.

Because the Kumsa has steep rocky and sandy banks in its lower reaches, where there are salmon spawning grounds, there are very few pike there and the pike cannot significantly affect the young salmon. In other rivers where the floodplain is subject to inundation (Shuya, Syapsya, Elgamka, Syargezhka) or where there are swampy streams, excellent conditions are created for the spawning of the pike, with the result that its abundance is high.

The pike usually concentrates in the grassy inlets around the river mouths, in the lower pools of the rivers, in places where the rivers are

obstructed and in the lower parts of the rapids, especially where the rapids are dammed. The influence of the pike is inversely proportional to the width of the river since it is a fish which keeps mainly to the banks. In a spawning tributary of slight width (less than 10 m) a single pike may control the entire width of the river bed, as was shown by spinning: the same pike rushed at two trolls cast from either bank. The concentration of the pike around the mouths of the spawning tributaries may be very high. Since there are as a rule very few other fishes in the spawning tributaries, the influence of the pike on the young salmon is undoubtedly of decisive importance for the fate of future salmon catches in such instances. The population density of the pike may be to some extent characterized by the following figures (data for the Lizhma River basin). Five pike between 0.3 and 1.0 kg in weight were caught in half a day in the mouth of the Sheichuga River in a stretch 50 m long where the river is 10 m wide, which was 1 pike per 100 m<sup>2</sup> of the river bed. In the reach around the mouth of the Sordiya River, where the river is 10 m wide, large pike were seen splashing every 10--15 metres. In the outflow of the Middle Lizhma up to 22 pike have been caught in a day with a single spinning rod. The young salmon are more available to the pike during the downstream migration.

Artificially reared young salmon released into unprepared bodies of water also become prey for the pike. According to a communication of S. P. Kitaev, who made observations between September 15 and October 21, 1963 on pond-reared underyearlings released into the Syus'kieka River (Lake Ladoga), salmon underyearlings formed a significant part of the food of pike caught for a month after the release of the young salmon.

Conditions for young salmon are greatly worsened by the construction of dams at rapids and by the obstruction of the river bed as a result of logging. This deterioration is due not only to the reduction of the feeding

grounds, but also to the improvement of hunting conditions for the pike. The dams and spits at the rapids are refuges from behind which the pike emerges to hunt in the shallows of the river bed inhabited by the young salmon.

The dace is extremely numerous in the rapids of the Vama, Syapsya and Pyal'ma Rivers but is not found in the Lizhma basin (there are two recorded instances of dace caught in the Lizhma inlet, in 1961 and 1962). There is no information concerning the interrelationship of the dace and the salmon in our rivers.

The minnow is evidently to be found in all the rivers in the basin of Lake Onega. It is noticeably less plentiful in the Tuba and the Lizhma than in the Pyal'ma.

In August 1963 we were able to observe the behaviour of a school of minnows in a pool in the Pyal'ma River. A school of minnows of different ages numbering up to 150--200 fish (estimated) occupies an area approximately 0.5--0.8 m wide and 2--2.5 m long. The minnows are arranged as follows: the largest fish (6--7 cm long) are at the head of the school, the underyearlings are at the tail and fish of intermediate sizes lie between them. When underyearlings caught with a net darted in front of the school, some of the large minnows seized and swallowed their own underyearlings. This may probably be regarded as confirmation of the predatory feeding of the minnow described by V. S. Mikhin (1959). In the Bol'shaya River (Baikal) the minnow destroys a considerable quantity of Arctic cisco larvae (Barbarovich et al., 1966).

/35/

The gudgeon is found only in the Shuya and the Vodla. The extension of the range of this species and the increase in its population which have been observed for probably no more than the last ten years are of interest.

In their reference manual "The Lakes of Karelia" (1959) K. I.

Belyaeva and V. V. Pokrovskii wrote: "The gudgeon is a very rare fish in Lake Onega and even then is confined to the southern part of the lake". In 1953 we found the gudgeon in the Ragnuksa, a tributary of the Vodla. Fishermen did not note its appearance in the Shuya before 1959. In 1961 the gudgeon was already to be caught from the mouth to the Vidanskii rapid, and it was then that the first communications concerning the appearance of a new fish unknown to the population were received from several fishermen (professionals and amateurs). In December 1961, I. A. Pesnin, the leader of a fishing brigade, took one specimen of the gudgeon from the region of the village of Shuya. When the Shuya River was examined in September 1962 we caught gudgeon at the Vidanskii rapid in the same localities as young salmon, but nearer the bank, where the current was more gentle (flow rate up to 0.5 m/sec) and where depth was between 10 and 40 cm, i.e. in the zone inhabited by salmon underyearlings. Thereafter the gudgeon penetrated up stream, overcame the Bol'shoi Tolli Falls (apparently by advancing along the quieter left branch) and is now caught (in tens by rod and line in the course of a day) at and above the Yumanishki rapids, but it has not been established whether it has reached Lake Vagat. In August 1962 a gudgeon was caught for the first time in the Lizhma inlet (taken by the author), where, like the dace, it had not previously been known to the local inhabitants.

These facts are of interest in themselves, and they have the further interest for us that the gudgeon may be a food competitor of young salmon (to the underyearling stage), since the gudgeon is clearly tending to increase in abundance in the Shuya.

The miller's thumb, like the very similar Cottus bairdii bairdii Girard in American rivers (Dineen, 1948), apparently feeds on the eggs of salmonids and is a competitor of the young mainly to the underyearling stage,

up to which time the young live on the bottom together with the miller's thumb.

The burbot is most plentiful in the Vodla and the Shuya and there are many small burbot in the Vama in the salmon spawning grounds. During the spawning period of the salmon the burbot consumes its eggs. When the water becomes colder in the autumn the burbot becomes more active and even such an active swimmer as the grayling is found in its food at this time. This suggests that the burbot may possibly also consume young salmon, although we do not as yet have direct observations of this. According to the observations of N. I. Vladimirskaia (1957), young Atlantic salmon were found in the winter in 8.8 % of burbot stomachs in quantities of up to 3 in one stomach. The burbot should be regarded as a dangerous predator in relation to young salmon. In rivers where the numbers of fishes of no food value are low (Tuba, Liza), the abundance of predators should be reduced to as low as possible, since their threat to parr is greater, the lower is the abundance of other fishes. The ideal solution would be to eliminate predatory fishes and fishes of no food value completely from salmon rivers and this is possible in principle by the use of ichthyocides. /36/

In speaking of the enemies of the salmon, reference should be made to fish-eating birds, among which young salmon are consumed by the dipper (Vladimirskaia, 1957) and especially by the goosander, which does considerable damage in the rivers of Canada and Sweden (Elson, 1950, 1962; Lindroth, 1955). Fortunately for our salmon, the numbers of these birds are now very low and they are incapable of having any significant effect on the survival of parr in the rivers of the basin of Lake Onega.

IV. The State of the Rivers in Connection with their Utilization. The Effect of Hydraulic Engineering Works and Logging.

The development of water use. The interests of different water users come into conflict in rivers and the demands which water users make on rivers are, as a rule, mutually exclusive.

In addition to their use by the fish industry, rivers are used for water transport (including logging), power supply, the discharge of industrial effluents, the discharge of water from drainage systems and for communal and domestic needs.

The stocks of the Omega salmon have been most affected by the use of the rivers for transport and as a source of power, which began in the 18th century in connexion with the development of the economy of the region.

So that use could be made of the energy of the rivers dams were constructed on them for metallurgical plants (after 1700 on the Lososinka, Tivdiika, Vichka, Povenchanka and Tuba Rivers), for sawmills (in the second half of the 18th century on the Shuya, Suna, Lizhma, and Kumsa Rivers and later on the Povenchanka) and for flour mills (on the Tuba and other rivers). Hydroelectric power stations were constructed on some rivers after 1900. The construction of the hydroelectric power station on the Lososinka had no effect on the reproduction of lake and river fishes in it, since they had disappeared long before that time, probably back in the 18th century because of the dams of the Petrovsk Plant and later the Aleksandrovsk Plant. On the Shuya the dam of the hydroelectric power station at Ignoila cut off the upper spawning grounds of the salmon, but their area does not exceed 10--15 % of the area of rapids utilized by the salmon in the basin of this river. In the Andoma the power station cut off the main spawning grounds, the "Mal'yanovskie rapids" and although spawning grounds have

remained in the Samina, a tributary of the Andoma, they do not compensate the loss of area which is at least  $2/3$  of the total area of salmon rapids in the Andoma basin.

The Suna is an example of the most serious consequences of hydraulic engineering works for the fish industry, consequences which have admittedly been made worse by logging. This river was of great importance to the fish industry in the past and took second place after the Vodla in terms of catches. In 1895--1900 whitefish catches in the Suna exceeded 300 centners (Pushkarev, 1913b)(translator's note. 1 Soviet centner = 100 kg). There is no information concerning the salmon catch in these years. In 1926--1930 when the Suna Fishery was already on the decline, salmon catches were 21--30 centners (Kozhin, 1927a; Zborovskaya, 1935). Thereafter there was a sharp reduction; 4 centners of salmon were caught in 1932 and after that time the Suna salmon and whitefish disappeared entirely from the commercial catch. Although whitefish still enter the river singly, the salmon had disappeared here as a species. /37/

Hydraulic engineering works on the Suna were carried out in stages. In 1926, the Sandalka (a tributary of the Suna), which was entered by a large quantity of salmon, was completely dammed and as a result a catchment with an area of 1017 km<sup>2</sup> was cut off.

The reach of the river below Girvas (65 km from the mouth) became in essence an independent river which approximates to the Kumsa and the Lizhma, which are salmon rivers, with respect to its main hydrographical and hydrologic characteristics (table 5, based on the data of Grigor'ev and Gritsevskaya, 1959 and of Bersonov, 1960).

The excellent natural regulation of the basin of the Lower Suna could ensure a uniformity of discharge within the year sufficient for the reproduction of salmon and whitefish. However, since the Suna is one of the main logging

water ways, its regime and especially the regulation of discharge are so determined by the interests of logging as completely to exclude the reproduction of lake-river fishes.

Таблица 5

2 Основные характеристики рек Лижма, Кумса и Суна (участок от Гирваса до устья)

3 Реки и створ	4 Длина участка, км	5 Площадь водосбора, км <sup>2</sup>	6 Площадь озер, км <sup>2</sup> число озер	7 Коэффициент озерности, %	8 Модуль стока, л/сек./км <sup>2</sup>	9 Расход воды, м <sup>3</sup> /сек.
10 Лижма (устье)	68.3	717.6	$\frac{138.54}{76}$	19.4	10.6	7.61
11 Кумса (устье)	60.2	745.4	$\frac{63.62}{159}$	8.5	10.0	7.45
12 Суна (д. Шушки)	25.5	513	$\frac{77.3}{64}$	15.1	8.5	4.36
13 Суна (устье)	65.0	787	$\frac{89.0}{77}$	11.3	8.5	6.70

Key to Table 5: 1. Table 5 2. Main characteristics of the Lizhma, Kumsa and Suna Rivers (the reach of the Suna from Girvas to the mouth) 3. River and reach 4. Length of reach, km 5. Catchment area, km<sup>2</sup> 6. Lake area, km<sup>2</sup>/number of lakes 7. Ratio of lake surface to drainage area, % 8. Specific rate of flow, litres/sec/km<sup>2</sup> 9. Water discharge, m<sup>3</sup>/sec 10. Lizhma (mouth) 11. Kumsa (mouth) 12. Suna (village of Shushki) 13. Suna (mouth).

Navigation is on the whole poorly developed in the rivers. The use of the Povenchanka and Vytegra Rivers as parts of the White Sea-Baltic and Volga-Baltic waterways is an exception, but the salmon stocks in these rivers had already been adversely affected in the last century (owing to the dam of a timber plant and to overfishing in the Povenchanka), so that the loss to the

fish industry from this form of utilization of the rivers has been slight.

The effect of logging. The transport of timber by water is the main form of utilization of the rivers in the basin of Lake Onega, as it is in general of Karelian rivers. Even quite recently logging was carried on in all the salmon rivers in the basin of Lake Onega. Naturally, therefore, the greatest contradictions arise where the interests of the fish industry come into conflict with those of logging. The cessation of logging on a number of rivers (Lizhma, Kumsa, Tuba and Pyal'ma) has been due primarily to the fact that the forests have been felled in their basins, and to a lesser degree to conversion to another form of transport (Shuya).

Logging appeared in the rivers in the basin of Lake Onega with the rise of the sawmilling industry in the first quarter of the 18th century, but the volume of logging was slight by comparison with the present-day volume down to the beginning of the 1920s (1.76 million cubic metres for Karelia as a whole in 1913, approximately 3.5 million in 1928 and reaching 9 million in 1961; Grigor'ev, 1961).

Whereas previously when the volume of felling was slight logging was carried out only during the flood period, the duration of logging has been extended as the volume of felling has increased and it has become necessary to create seasonal reservoirs.

The effect of logging was therefore far weaker in the earlier period than in the subsequent years, especially because it was the forests nearest the river mouths which were initially felled and therefore the upper spawning grounds were initially not affected by logging. However, it was already realized in the last century that the fish were adversely affected both by logging itself (Pushkarev, 1900a) and by substances extracted from the timber (Borzdynskii, 1867). Admittedly, N. Ya. Danilevskii (1875) regarded drift

floating as a positive feature on the grounds that it greatly interfered with river fishing and therefore prevented overfishing. However, this is more an example of the "cure being worse than the disease". Pushkarev, who investigated the Vođla 20 years after Danilevskii, reached opposite conclusions. He recommended measures to limit the harm caused to the fish industry by the timber industry (limitation of the logging period, barking of the logs, controlled operation of the boom, inadmissibility of the dumping of sawmill waste in rivers and the construction of fish ways at sawmill dams). It was evidently Pushkarev who was the first to formulate the demands of the fish industry on the timber industry. However, it cannot be said that even one of these reasonable aspirations has been met in the years which have since elapsed. Furthermore, right down to the present, water-use legislation has not ensured effective protection of the interests of the fish industry which have suffered from the effect of the timber industry.

The development of the timber industry and the simultaneous reduction in the abundance of diadromous fishes compelled many investigators both in our country and abroad to refer to the connexion between these events. Almost all investigators of fishes and fishing who have worked in Lake Onega refer to the use of spawning rivers for the needs of the timber industry as one of the adversely operating factors. It would take too much space to list these investigators. /39/

Two authors (Stroganov, 1937; Artimo, 1961) doubted whether timber extracts and bark were harmful, but they were not concerned with salmon rivers. Artimo, who observed the development of pike-perch and pike eggs laid on bark, concluded that the opinion that the bark which peeled off during logging was harmful had been greatly exaggerated. The data of Alm (1923) and of A. G. Gusev (1950, 1952, 1953) force us to disagree with the opinion of this author.

Two other authors, namely H. Jürnefelt (1931) and N. A. Ostroumov (1944, 1947), went even further and asserted that the pollution of rivers by logging waste was beneficial. Ostroumov based his conclusion on the fact that the biomass of the benthos was increased on a timber substrate and that consequently the food supply of fishes was improved; he stressed the positive nature of these changes (from his point of view). Without investigating the other influences of logging, he concluded: "Until it has exceeded a certain maximum, logging is a progressive factor in northern rivers". However, he did not state what this "certain maximum" might be. In the opinion of Ostroumov "Logging in rivers does not have an inhibiting effect on fishes".

Although an increase in the biomass of the benthos is also to be observed in our rivers (in pools and below rapids, where the bark settles and is washed by sand and silt), we cannot accept the opinion of Ostroumov that logging is beneficial, at all events for salmon rivers of the Karelian type.

Although some benefit is obtained from this by the indigenous fishes of little value inhabiting the pools, it is our most valuable food fishes, salmon, trout and whitefish, which suffer as a result of logging.

Many investigators who acknowledge the harm caused to the fish industry by the timber industry, in particular the harm caused by logging, emphasize some one aspect of the influence, either the obstacle to the migration of the fishes, or the pollution and the deterioration in the quality of the water, or only the interference to the industry.

The first attempt at an overall estimate of the effect of logging was undertaken by Alm (1923), who reached the conclusion that logging affected fishes and fishing simultaneously in various ways: biocoenoses were modified,

spawning grounds were polluted, a fungal and bacterial flora developed, the quality of the water was changed and there was mortality of eggs (reaching 92.2 % in salmon) and fingerlings. Alm concluded: "The effect of logging is directly proportional to the amount of timber floated down the river, the duration of logging, the number of dams etc. and inversely proportional to the water discharge of the given system" (retranslated, cited from Kozhin, 1929a).

From among other works in which a similar approach is adopted to the study and assessment of logging, we may mention the articles of I. F. Pravdin (1948a; Karelia, the North West), G. D. Dul'keit and Yu. I. Zapekina-Dul'keit (1965; the mountain rivers of Siberia) and the research of A. G. Gusev (1953) on the rivers of Southern Karelia. These publications contain the results of original observations, on the basis of which the authors conclude that logging is undoubtedly harmful to the fish industry. /40/

Observations on rivers in the basin of Lake Onega. The salmon rivers in the basin of Lake Onega have been most intensively used for logging. This to some extent facilitated our observations which were made beginning with 1959. Investigation of the rivers showed that logging had a diverse and extremely strong effect on the reproduction of salmon, trout and whitefish. The conditions of reproduction of these fishes are worsened in all instances and sometimes reproduction becomes completely impossible. Logging is regarded as the most economical form of the transportation of timber under our conditions, but no allowance is made in calculations of the cost of logging for the vast damage caused to the fish industry.

The effect of logging is compounded of a combination of the following factors: deformation of the river bed; the mechanical effect on the fish; pollution of the river bed; alteration of the water, thermal, ice and chemical

regimes; alteration of biocoenoses. As a result of the effect of these factors there is an alteration of the fish fauna affecting its composition and the proportions of the species. Different species are found to react differently to alteration of the state of the river.

If an attempt is made to distinguish the chief factors among the various factors which modify the conditions of reproduction of diadromous fishes, it has to be acknowledged that the erection of dams (for logging purposes and for power supply) has been the decisive cause of the disruption of stocks. The construction of other logging facilities and the pollution of the rivers greatly worsen the conditions of reproduction, but when there are no dams these factors alone are evidently incapable of leading to the complete destruction of stocks of diadromous fishes.

Commercial stocks of the Onega salmon are now maintained exclusively by the spawning grounds in the Shuya (below Lake Vagat and in the Syapsya), in the Vama and in the Pyal'ma, including its tributary the Zhilaya Tambitsa.

#### V. The Location and Nature of the Spawning and Rearing Reaches.

The location of spawning and rearing reaches, which is conditioned by the distribution of rocks in the river basin, determines their nature and value and also, apparently, the time of the spawning migration of the salmon (see section IV of chapter 3).

The location of the spawning grounds in the basin of Lake Onega is as follows (fig. 1).

Lososinka. The most suitable reaches lie within 16 km of the mouth; for the whole of this distance pools are an insignificant proportion, less than 20 %. Information on the distribution of the salmon in this river has not been

preserved; it may possibly have ascended the river as far as Lake Lososinoye (23.3 km from the mouth).

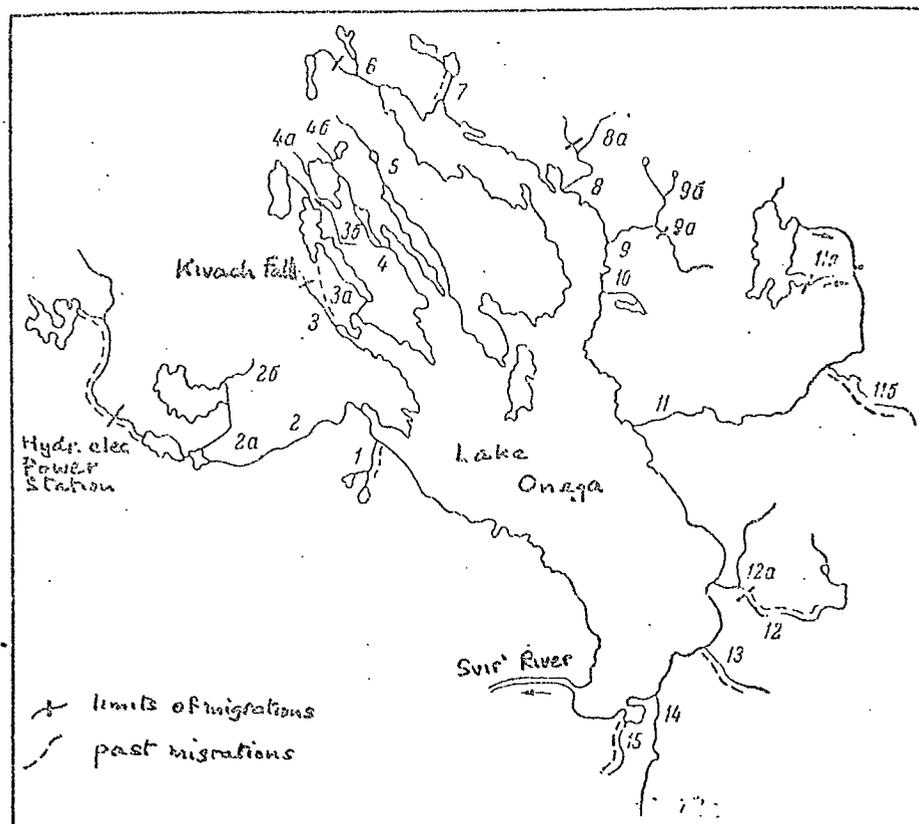


Fig. 1. Diagram of the location of spawning and rearing stretches in the basin of Lake Onega. 1) Lososinka; 2) Shuya, 2a) Syapsya; 2b) Malaya (Lesser) Suna; 3) Suna, 3a) Sandalka, 3b) Tivdiika; 4) Lizhma, 4a) Upper Lizhma, 4b) Elgamka; 5) Unitsa; 6) Kumsa; 7) Povenchanka; 8) Nemina, 8a) Pazha; 9) Pyal'ma, 9a) Zhilaya Tambitsa, 9b) Tuna; 10) Tuba; 11) Vodla, 11a) Vama, 11b) Koloda; 12) Andoma, 12a) Samina; 13) Vytegra; 14) Megra; 15) Vodlitsa.

Shuya. The reaches now in use are in three places: in the Syapsya (between 124 and 102 km from the mouth of the Shuya) and in the Shuya itself below Lake Vagat (between 84 and 76 and 60 and 20 km from the mouth). Before construction of the hydroelectric power station at the settlement of Ignoila (130 km from the mouth) the salmon ascended to Lake Salon''yarvi (208 km from the mouth), and its spawning grounds were in the rapids of the Karatsalma arm (4 km long) linking this lake to Lake Suoyarvi, and below Lake Suoyarvi (between 192.7 and 130.0 km from the mouth). In the Malaya (Lesser) Suna there used to be spawning grounds in the middle reaches of the river (between 154 and 143 km from the mouth of the Shuya). /42/

Suna. Here there were three groups of spawning grounds: in the Tivdiika between Krivozero and Sandal, the main spawning grounds between Khizhozero and Lake Sandal (63.7--62.7 km from the mouth of the Suna), in the Sandalka (between 38.2 and 26.3 km from the mouth of the Suna) and in the Suna itself below the Kivach Falls (between 30.0 and 0.1 km from the mouth). The lower spawning ground (the Nizhka rapid) was practically in the river mouth.

Lizhma. The spawning grounds are in the lower half of the Upper Lizhma (between 60.0 and 51.3 km from the mouth of the Lizhma), in the Elgamka (between 63 and 57 km from the mouth of the Lizhma) and in the Lower Lizhma (from 4.3 km from the mouth to the mouth). There are two suitable rapids in the Middle Lizhma, the Srednii (Middle) rapid (31 km from the mouth) and the Zalonnii rapid (28 km from the mouth), but their total area is slight (0.33 ha) and there is no reliable information concerning spawning. According to unverified information, the salmon enters the Syargezhka, which flows into Kedrozero, in which there are small rapids (kareshki) (between 33 and 26 km from the mouth of the Lizhma).

Unitsa. According to replies to questionnaires, salmon are caught for a distance of approximately 40 km from the mouth, but there are also rapids higher up; the river has not been investigated.

Kumsa. The spawning grounds lie between the mouth of the Oster River and the lower rapid (Zakhar'evskii, or Zavodskii ; between 15.3 and 2.7 km from the mouth of the Kumsa) and possibly extend for up to 37 km from the mouth (6 rapids with a total length of 1350 m, an average width of 12 m and an area of 1.6 ha), but no higher than the Bugma Falls (38 km from the mouth) since the bottom of the upper rapids is quite unsuitable. Adult salmon and fingerlings have been caught below the confluence of the Oster and spawning has been observed; there is no information concerning salmon catches and spawning for the reach above the Oster.

Povenchanka. There were spawning grounds between 10 km and 0.3 km from the mouth to a total length of as much as 8 km.

Nemina. There are spawning grounds in the tributary, the Pazha (between 46 and 40 km from the mouth of the Nemina) and in the Nemina itself (between 22 and 8 km from the mouth). Because the salmon has never ascended to the upper reaches of the Nemina above the confluence of the Pazha (30 km from the mouth), the logging dam 0.3 km above the mouth of the Pazha does not affect reproduction.

Pyal'ma. The main spawning grounds are in the tributary, the Zhilaya Tambitsa (between 30 and 22 km from the mouth of the Pyal'ma) and in the Pyal'ma itself (between 6.0 and 0.4 km from the mouth). The rapids between the mouth of the Zhilaya Tambitsa and the Krivoi rapid (between 17.9 and 7.5 km from the mouth) are unsuitable because of the bottom material. In the Tuna, a tributary of the Zhilaya Tambitsa (it enters the Tambitsa 17 km from its mouth) there are suitable rapids and shallows (kareshki) only for a distance of 4.5 km in the

lower third of the river (between 40 and 35 km from the mouth of the Pyal'ma), but their area is very slight. According to information yielded by questionnaires, the salmon sometimes enters the Koda, a tributary of the Tuna (it enters the Tuna 12 km from the mouth), but nothing is known concerning its spawning there and spawning would scarcely be possible in this stream. The salmon does not ascend to the upper reaches of the Pyal'ma (above the confluence of the Zhilaya Tambitsa); only the trout ascends. /43/

Tuba. There are four spawning rapids confined to the first 4.5 km from the mouth, the chief of which is the Velikii kamen' rapid (between 4.5 and 2.5 km from the mouth). Because the rapids above this reach are unsuitable for spawning (blocks, large boulders and rocks), their area has not been included in the resources of spawning grounds, although the salmon occasionally ascends to Tubozero (15.5 km from the mouth); but this is evidently a loss of direction.

Vodla. The spawning grounds of the Vodla salmon are concentrated in the Vama (between 169.5 and 147 km from the mouth of the Vodla) and are now the only spawning grounds in the Vodla basin. Spawning previously took place in a tributary, the Koloda, but salmon have not been seen in this river since 1957 because the Koloda became unsuitable for spawning owing to the construction of logging dams and to intensive logging. The area of rapids in the Koloda is far smaller than in the Vama. There is no information concerning the other tributaries of the Vodla to confirm that salmon regularly enter them and spawn in them. There are no salmon spawning grounds in the Vodla itself, including the Sukhaya Vodla, because of the unsuitable nature of the rapids and the bottom material.

The reference work "Lakes of Karelia" (1959) lists as spawning grounds the Fadun, the Vodla, Ust'-Koloda, Ostrov, Podporozh'e and the mouth of the Shalitsa, but this is a mistake. These points are mentioned in the writings of M. V.

Logashov (1931), E. A. Veselov (1932) and M. B. Zborovskaya (1935) as places where the migrating salmon is caught. A paper by E. A. Veselov and V. M. Korovina (1932) contains the direct statement that: "...it (the salmon, -- Yu. S.) ascends above the Padun rapids to spawn and is caught en route to the spawning grounds at Castrov, Ust'-Koloda and at catching weirs actually in the Padun rapids."

Andora. The spawning grounds in the Andoma itself (Mal'yanovskie rapids, between 60 and 50 km from the mouth) have been cut off by a hydro-electric power station dam; spawning grounds remain in a tributary, the Samina.

Vytogra. Before 1961 there was still a very small spawning ground below the first dam at the town of Vytogra, but even it disappeared after reconstruction of the canal.

Merra. The spawning grounds lie more than 12 km above the mouth; the migration of the salmon is obstructed by the dam here; the stock is extremely small.

Vodlitsa. According to the data of N. N. Pushkarev (1915), the river was entered for spawning by salmon and whitefish, which passed through Lakes Megorskoe and Vodlitskoe, i.e. more than 10 km above the mouth. Nothing is now known concerning these fishes and they have evidently disappeared since the river is not included among the salmon rivers protected by the "Fishing Regulations" (1960).

The spawning reaches of the rivers are characterized in table 6, in the compilation of which use was made of the data of S. A. Bersonov (1960).

The bottom material of the spawning and rearing reaches is uniform on the whole: blocks, large, medium and small boulders, pebbles, gravel, sand; the spawning grounds are sometimes silted (figs. 2--4). The areas of redds

/44/

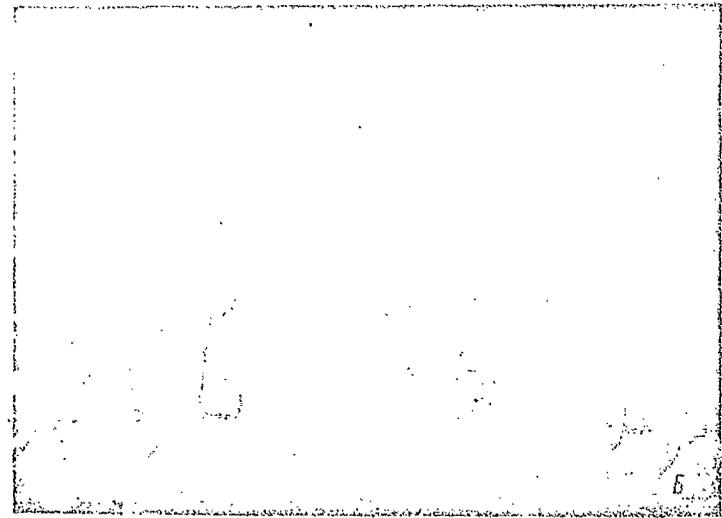
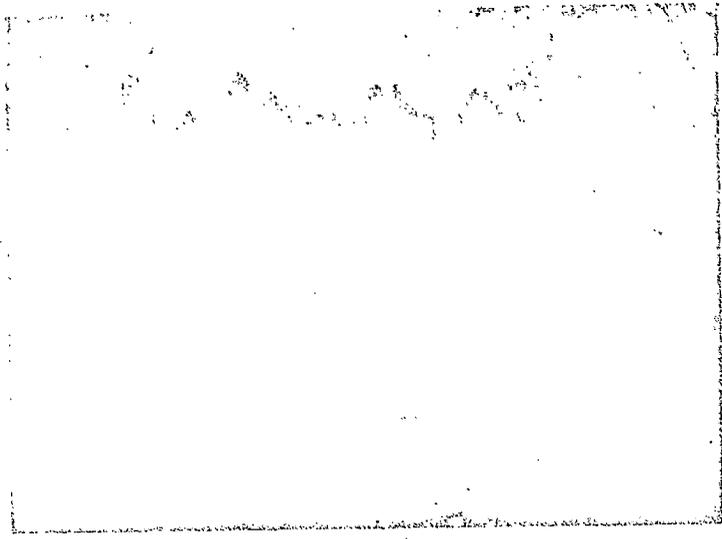


Fig. 2. Kumsa, Berezovyi rapid. General appearance of spawning ground (A) and example of bottom material (ruler 20 cm long)(B).

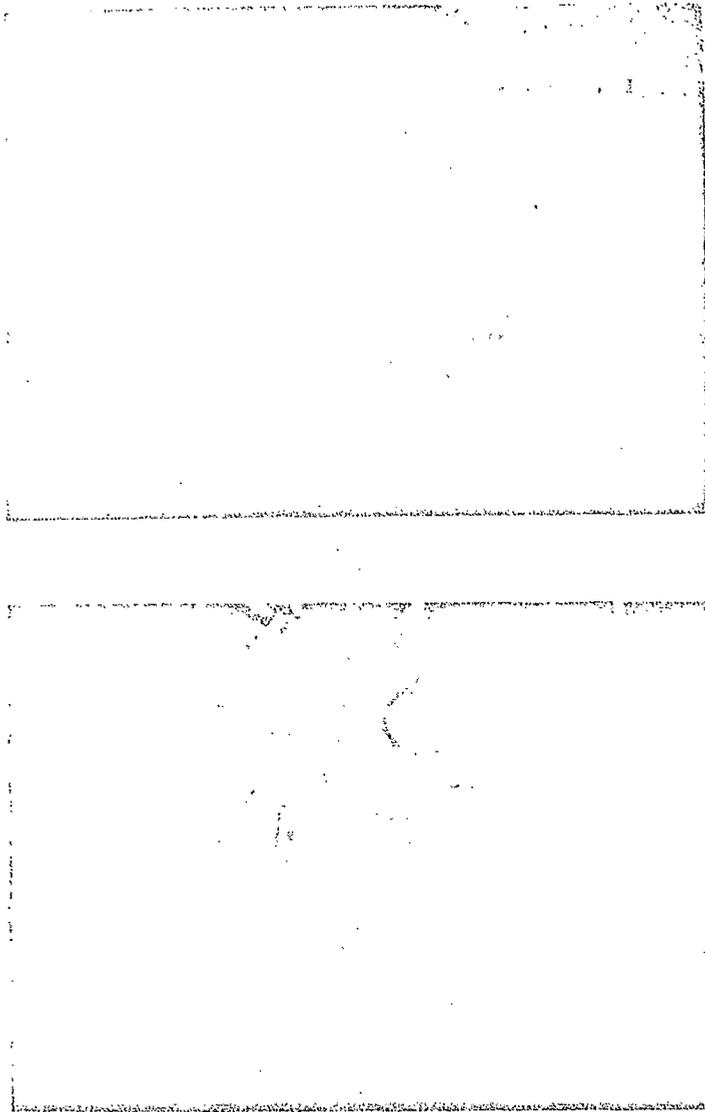


Fig. 3. Nemina, Dolgii rapid. View of a portion of the spawning ground (A) and example of the bottom material (the matchbox shows the scale)(B).

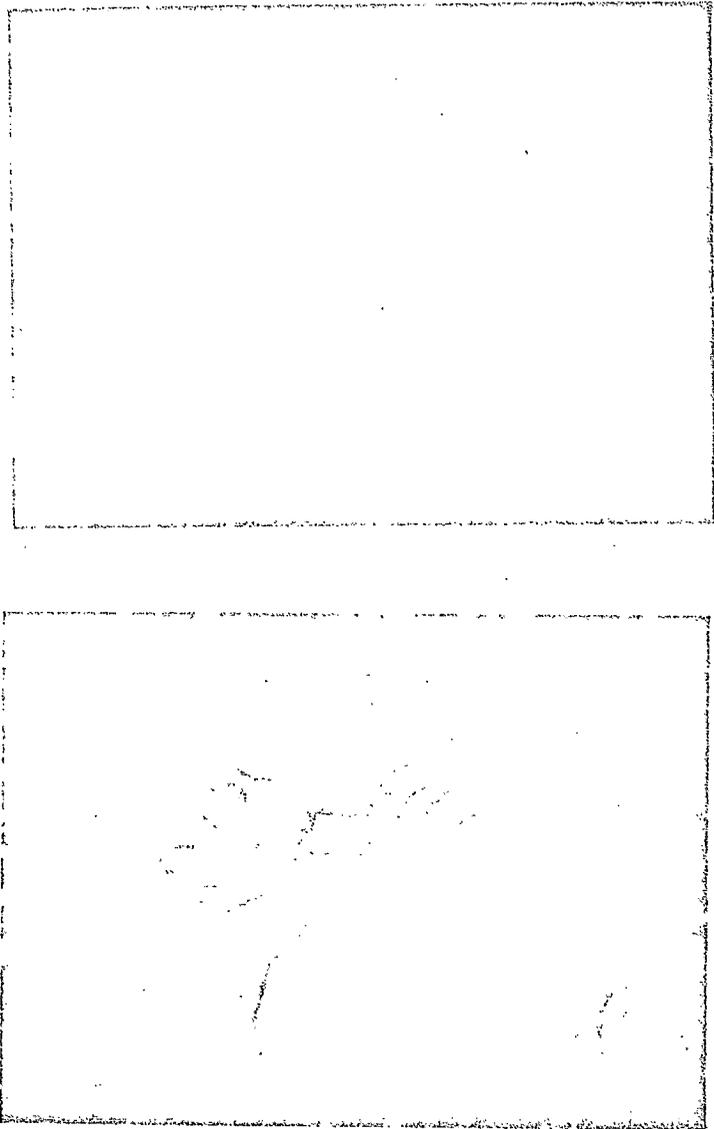


Fig. 4. Tuba, Velikii kamen! rapid. View of a portion of the spawning ground (A) and sample of bottom material (B).

Таблица 6

## 2. Характеристика нерестовых участков рек

Рекa $\bar{S}$	Длина участка, км $l_r$	Расход воды, м <sup>3</sup> /сек. $\bar{S}$		Падение, м $\bar{S}$	Уклон, ‰ $q$	Порожнистость, % $10$
		в начале участка $6$	в конце участка $7$			
11 Нососинка . . . . .	16.0	3.05	3.66	123.0	7.7	80
12 Шуя (ниже Вагат) . . . . .	86.7	71.15	96.27	57.5	0.7	22
13 Сяпси . . . . .	34.0	14.00	15.72	17.0	0.5	8
14 Малая Суна . . . . .	17.6	2.42	4.09	23.5	1.3	10
15 Верхняя Лижма . . . . .	11.7	0.40	1.08	35.0	3.0	29
16 Елгамка . . . . .	18.0	—	≤ 1	83.3	4.6	44
17 Средняя Лижма . . . . .	12.2	4.99	5.51	5.0	0.4	2
18 Нижняя Лижма . . . . .	4.3	7.41	7.61	29.5	6.9	42
19 Ушца . . . . .	39.5	0.95	3.95	107.0	2.7	—
20 Кумса . . . . .	15.3	6.61	7.45	42.5	2.8	43
21 Немца . . . . .	29.7	5.30	6.35	46.3	1.5	21
22 Пазха . . . . .	16.5	0.75	2.32	51.0	3.1	31
23 Пялма . . . . .	17.9	8.15	9.22	49.7	2.8	56
24 Жилая Тамбца . . . . .	12.5	2.45	2.67	54.0	4.3	48
25 Туба . . . . .	7.6	3.00	3.24	39.0	5.1	61
26 Вама . . . . .	23.4	52.99	58.14	47.5	2.0	34
27 Колода . . . . .	76.3	2.31	12.83	101.0	1.3	—

Key to Table 6: 1. Table 6 2. Characteristics of the spawning reaches of the rivers 3. River 4. Length of reach, km 5. Water discharge, m<sup>3</sup>/sec 6. At start of reach 7. At end of reach 8. Fall, m 9. Gradient, ‰ 10. Length of rapids, % 11. Lososinka 12. Shuya (below Lake Vagat) 13. Syapsya 14. Malaya (Lesser) Suna 15. Upper Lizhma 16. Elgamka 17. Middle Lizhma 18. Lower Lizhma 19. Unitsa 20. Kumsa 21. Nemina 22. Pazha 23. Fyal'ma 24. Zhilaya Tambitsa 25. Tuba 26. Vama 27. Koloda.

are among small boulders and shingle, frequently immediately adjacent to large boulders and blocks. In one case, in the Pazha, the bottom of the spawning rapids was strewn with flagstones of all sizes, from blocks to gravel. The spawning of salmon on flagstones, admittedly of a slightly different nature, has been described by T. I. Privol'nev (1962) for the Narva River; there the

salmon were unable to excavate mounds. In the Pazha the bottom material is such that it is quite possible for mounds to be excavated and the accumulation of flags on the stream bed provides an excellent refuge both for the young and for adult fish (fig. 5).

In the Upper and Lower Lizhna and in the Elgamka we observed (June 23--27, 1962 and June 18, 1963) that, after emerging from the nest mounds, the young salmon remained above silty bottoms close into the bank in the upper layer of the water (down to 10cm from the surface) where the water was 0.3--0.6 m deep and where flow rate at the surface was 0.25--0.5 m/sec. In general, the prevailing flow rates in the spawning and rearing reaches are 0.3--1.0--1.5 m/sec and the prevailing depths are 0.2--0.8--1.2 m, but under-yearlings and parr are sometimes also found at lesser depths, as little as 10 cm in the Tuba in the summer of 1963, a year when there was little water. A similar distribution of young has been observed by G. G. Galkin (1955) in the Salatsa River.

We should pause to consider the role of lakes in the basins of the spawning rivers and their effect on the regime and value of the spawning and rearing reaches. The quality of a spawning river is determined by the stability of the water regime, by the possibility of silting, by conditions for the existence of predators and worthless fishes and by their abundance, by feeding conditions etc.; all these factors are related to the existence of lakes in the river basin. /48/

Seasonal and annual fluctuations of level, which are responsible for alteration in the size of the spawning and rearing areas, are the most important characteristics. In years when there is little water the water content may play a decisive role, since the freezing of the redds in the winter and the drying out of the rapids in the summer lead to the formation of weak

year-classes. The stability of level is increased with increase in the size of the river and in the ratio of lake surface to drainage area. The water-level regime is most favourable in the spawning grounds in the Syapsya (ratio of lake surface to drainage area 20.4 %), the Shuya (below Lake Vagat, 11.3--10.3 %), the Lower Lizhma (19.4 %) and the Vama (8.8 %). However, in the last two cases the rapids dry out completely (an unusual phenomenon for our rivers), owing to the incorrect use which is made of the dams (Kedrozerskaya and Vamskaya) from the point of view of the interests of the fish industry.

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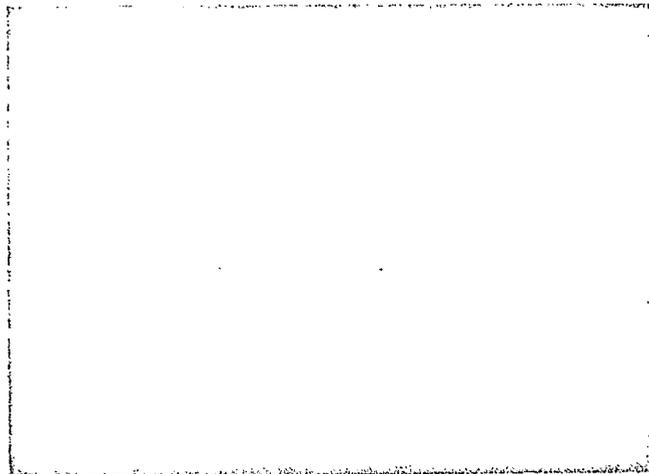


Fig. 5. Pazha, Babii rapid. Example of bottom material in a spawning ground.

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The extent of the effect of water content as a factor is not the same in rivers of different size and different natural regulation. In small rivers with a slight lake area the river bed sometimes dries out completely in the reaches of rapids in years when there is little water. Not only does this make the rapids unsuitable as a habitat for the young, which are obliged to

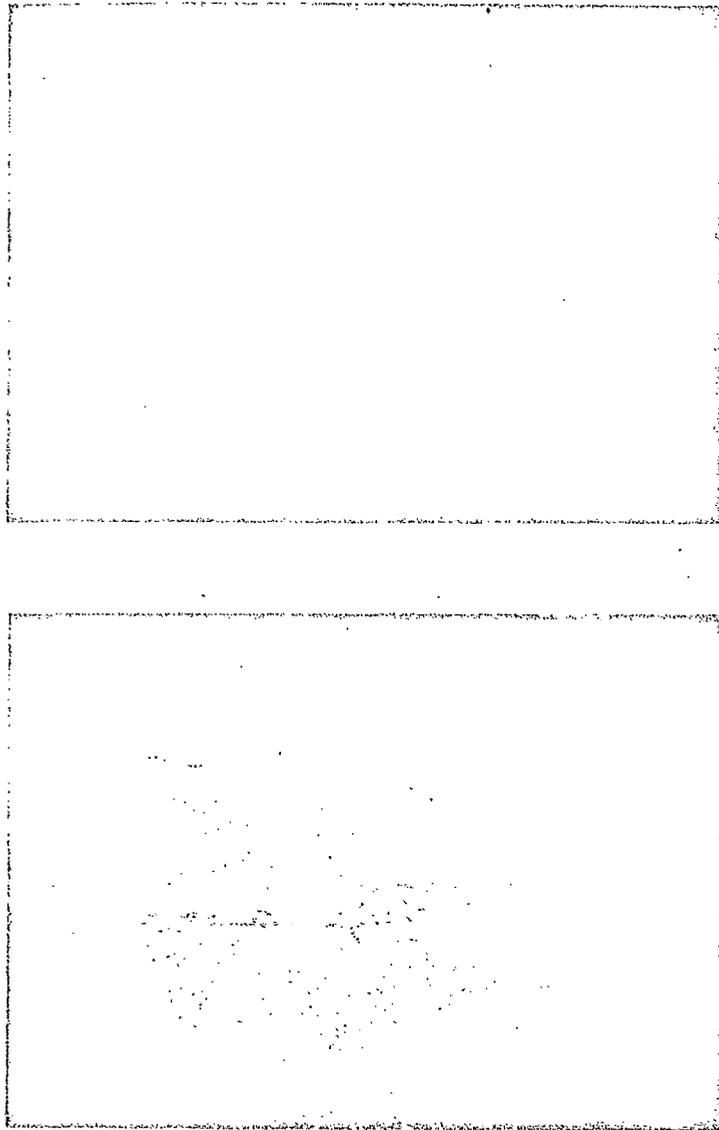


Fig. 6. Relationship between the area of rapids and water content. A) the kumsa in a year of little water (1960); B) in a year of plenty of water (1962). Both photographs were taken in the first decade of August.

move into the pools, but it also increases their mortality and even leads to mass mortality (e.g. in the Elganka, according to information from questionnaires). In directly regulated rivers of average size (Fyal'ma, Kumsa) the area of rapids may be practically halved in years when there is little water by comparison with the area in years when there is plenty of water (fig. 6). In large rivers with a high ratio of lake surface to drainage area the reduction in the area of the rapids in years when there is little water is relatively slight: probably no more than 20--25 %.

/50/

Another positive result of the existence of lakes through which the river flows is that plankton is carried out, thereby increasing the feeding capacity of the river.

Among the negative results we should include increased turbidity, silting and an increase in the pressure of predators. The spawning grounds situated below shallow lakes which are readily subjected to wind mixing (Lake Kandasovskoe on the Shuya, the upper lakes on the Vama and to a lesser extent the spawning grounds of the Tuba) are in an unfavourable position in relation to silting. In the period between the commencement of salmon spawning and the freezing of the lakes autumn gales cause silting of the spawning grounds, which undoubtedly affects the incubation of the eggs and their survival and may subsequently make the emergence of the larvae from the nest mounds more difficult. The high turbidity in the summer hinders the young salmon in the search for food, since the fingerlings are mainly guided by sight in taking food.

The extent of the effect of enemies on young salmon is determined both by the relative abundance of predator and prey and by the hunting conditions of the predatory fishes, which are influenced by the mutual

disposition of lakes and spawning grounds in the river basin, by the development of aquatic vegetation and by obstruction of the river bed. The abundance of the pike is increased in rivers on which there are many lakes through which the river flows. The pike concentrate around the inflow and outflow (where there are normally beds of water plants) and the predator forms a barrier for smolts migrating downstream through the lakes. In this respect the spawning grounds of the Kumsa have a considerable advantage over those of the Lizhma (which is very similar to the Kumsa with respect to overall characteristics): the spawning grounds in the Kumsa are located below the lakes and the abundance of the pike in the river is very low owing to the lack of suitable spawning grounds for it. Another advantage of the Kumsa is that the location of the spawning grounds in a compact group in the lower reaches of the river greatly facilitates the carrying out of improvement and conservation works and fish management.

To sum up, it may be said that of rivers which are equal in the area of the spawning grounds and in water content, the best for reproduction of the salmon are rivers in which the spawning grounds are concentrated nearer the mouth and lie considerably below the lakes through which the river flows. In this case the regulating effect of the lakes is felt, the consumption of downstream migrants by lake predators is excluded, the feeding capacity of the river is increased by plankton carried out of the lakes, the possibility that the spawning grounds may be silted as a result of wind mixing in the lakes is reduced and, finally, inspection and positive active intervention by man in the reproduction of the salmon is facilitated.

VI. Principles for the Assessment of Spawning Rivers  
and Their Reproductive Value.

When there is a need to assess the role of any river in the reproduction of the salmon, difficulty will usually be encountered owing to the lack of a generally accepted criterion, as is evident from the extensive literature on the salmon. Nevertheless, assessment of reproductive capacity is of practical importance since it is reproductive capacity which should be the guiding principle in the selection of rivers for improvement works and fish management; the return on the capital investment is dependent on the correctness of the choice.

The generally correct principle of assessment of the importance of the rivers in relation to size is inapplicable given their present state and the nature of their use. Gradients and the quantity of rapids are an indication of the nature of a river, but they do not give an idea of its reproductive capacity, which is dependent on the existence of suitable bottom materials, and this cannot be established without a detailed investigation of the river. The quality of the spawning and growth regions, i.e. their reproductive value, is dependent on a combination of many factors whose effect cannot be quantitatively evaluated.

What is therefore needed for a comparison of the conditions of reproduction in different rivers, in addition to the general considerations set out at the end of the last section, is an objective index which provides an overall evaluation of the productivity of a unit of the spawning and growth area. The gross return of adult fish per hectare of the spawning and growth area may provide such an index.

The information on catches needed for the calculation of this index is not always available, especially for rivers from which the salmon has long disappeared. But even at present the statistics are a poor reflexion of the

real catches, which are invariably considerably higher than those recorded. In the case of large-scale catching of the feeding salmon (as has occurred in Lake Onega) catches in the rivers give a very approximate indication of the role of most of them in the total balance. It is sometimes completely impossible to decide to which stock the catches should be ascribed. For example, the salmon caught in the autumn around Saloostrov may belong to the stocks of the Pyal'ma, Tuba, Nemina, Kumsa and possibly other rivers, whereas there is organized salmon fishing and recording of the catches in this region only in the Pyal'ma. Similar doubt arises with respect to the salmon from the region of Besov Nos, which may be inhabited by the Andoma salmon in addition to the Vodla salmon.

The present catches are, as a rule, a consequence of the state of the rivers, which has been altered as a result of their use. These catches cannot therefore be used to assess the potentialities. However, an alteration of catches is not invariably due to an alteration of abundance as is shown, for example, by the Pyal'ma, where the fishing rate has been sharply reduced since 1961. It is clear that catches alone cannot be a reliable criterion for assessment of the importance of a river in the absence of an idea of the alteration in the size of the stocks. /52/

When there is more or less reliable information both on catches (which reflect abundance) and on the spawning and growth area, simultaneous use of both indices will yield the best characterization of the reproductive value of the river. Then, after indices of the relative gross return have been obtained for rivers of various nature, we shall be able to make an assessment by analogy of other rivers of a similar type for which there is no information on catches.

The growth rate of young salmon in rivers of various nature may also be used as an index for assessment, but its value is lower since the consequences of differences in the population density of the young may overlap differences in the productivity of the rivers. Moreover, it takes far more expenditure of labour and time to obtain satisfactory data in this case and this is something which is far from invariably possible.

The information on the abundance of stocks needed for assessment of the reproductive potentiality of the rivers was determined from the maximum catches. Such an approach seems completely correct, since the maximum abundance should approximate to some extent to the abundance which the stocks had before the conditions of reproduction in the rivers were altered. The present mean abundance was calculated at the same time.

The maximum return per 1 ha of the spawning and growth area was 20 fish or more in the Vodla, 25--27 in the Shuya, 35--47 and 45--60 in the Suna, 60--75 in the Pyal'ma and, lastly, 200 fish or more in the Lizhma; the mean return was 19 fish/ha for the Shuya and 37 for the Pyal'ma. Unfortunately, it is impossible to make a comparison with other basins, since there are no such estimates for them.

The number of downstream migrants may be calculated from the return of mature fish. When allowance is made for the coefficients of natural mortality in the river period, which are known for the Atlantic salmon, this yields the number of parr and, finally, their population density.

According to the data of Swedish investigators (Carlin, 1955, 1964), the return of the Baltic salmon from smolts reached 15.7--17.3--37.6 % and even 41.4 % in some instances and was on average no less than 10--12 %. There is every reason to expect that the survival of the lake salmon over the feeding period will be no lower than that of the salmon in the sea. The population

density of the parr was therefore calculated for a return of 10 %, separately for the maximum and mean abundance.

According to the calculations of N. F. Nikiforov (1959a), the mortality of parr at an age of 1+ and older should not exceed 16 % a year on average. Mortality in earlier stages has been established by the experiments of McCrimmon, (1954) and was found to be 30 % for the age from 0+ to 1+ and on average (three experiments) 87 % for the stages from the larva to the under-yearling 0+; overall mortality by the spring of the third year was 97 % of the initial quantity of larvae. /53/

These data enable us to reconstruct not only the quantity of parr, but also the initial quantity of eggs from the quantity of smolts (fig. 7). Since the ratio of downstream migrants 2+ and 3+ years old in our salmon is on average 67 : 33, the quantity of parr (1 and 2 years old -- 1. and 2.) needed to obtain a definite number of downstream migrants (N) should exceed the number of the latter by approximately 1.6 times ( $1.64 N$ ); the quantity of larvae should amount to approximately 15 N and of eggs to 150 N. /54/

The latter circumstance signifies that if mortality over the feeding period is approximately 90 % of the initial quantity of downstream migrants (which is on average approximately so in the Atlantic salmon according to the results of tagging), the return of mature fish per pair of spawners will be 3--4 fish, or 1 : 1.5--1 : 2 when fecundity is 5000 eggs and 6--7 fish, or 1 : 3--1 : 3.5 when fecundity is 10 000 eggs.

The mean ratio of spawners and return calculated by us from the data of V. V. Azbelev and B. I. Shuster (1965) for the Atlantic salmon of the Kola Peninsula was 1 : 2.5 (average over 14 years) for the stock of the Tuloma River and 1 : 2.7 (average over 11 years) for the stock of the Kolvitsa River.

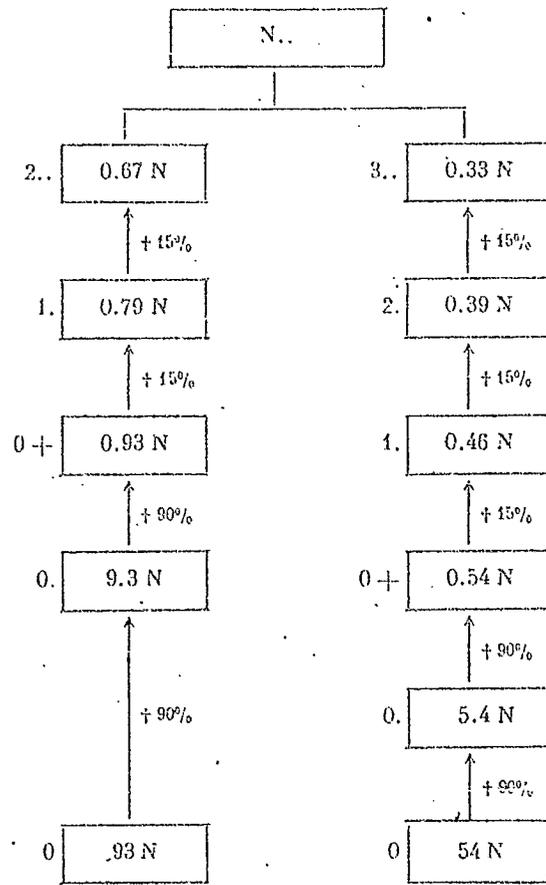


Fig. 7. Survival of the salmon by stages of the river period. Smolts -- 2..+3.. = 0.67 N+0.33 N =N; parr -- 1.+1.+2.=0.79 N+0.46 N+0.39 N=1.64 N; larvae -- 0.+0.=9.3 N+5.4 N=14.7 N; eggs -- 0+0=93 N+54 N=147 N; † -- mortality. Explanation in text.

The fecundity of the Kola salmon lies in the range 5--10 thousand eggs, i.e. the calculated ratios are in good agreement with those actually observed. This signifies that the mean value of 90 % for mortality over the embryonic period established by N. D. Nikiforov is not overstated, since mortality in

the subsequent stages has been experimentally determined and is confirmed by the practice of the artificial rearing of young salmon.

A quantity of parr should be separately calculated for the spring (1.--2.) and for the autumn (0+--2+), and the population density should be calculated without the smolts which leave the river in the spring. Toward the autumn the number of fingerlings and their density are approximately doubled by the arrival of underyearlings (1.47 N). It may naturally be conceded that the mortality of parr 1+ and 2+ over the summer will not exceed the mortality over the remainder of the year, i.e. will not be more than 7 % of the 15 % for the whole year. Therefore, the number of fingerlings (0+) + (1+) + (2+) in the autumn will be  $(0.93+0.54) + (0.79 \times 0.93 + 0.46 \times 0.93) + (0.39 \times 0.93) = 2.99 N$ .

The maximum calculated population density for the autumn with a 10 % return was  $17 \text{ m}^2$  per 1 fingerling in the Vodla, 12--13 in the Shuya, 7--10 and 5.5--7.5 in the Suna, 5.5--4.5 in the Pyal'ma and 1.7 in the Lizhma; the mean density was  $18 \text{ m}^2$  per fingerling for the Shuya and  $9 \text{ m}^2$  for the Pyal'ma. The density of fingerlings observed in the Pyal'ma in its lower rapids between 1963 and 1965 was around the mean established for this river by calculation, approximately  $10 \text{ m}^2$  per fingerling. Density is far less in all the other rivers (apart from the Tuba). In the Nemina, for example, there are hundreds of square metres per fingerling; as a result of the practically complete disappearance of the stock salmon fingerlings are extremely rare in this river. It was only in the Tuba, in the Velikii kamen' rapids that we were able to observe a high fingerling density, no more than  $2 \text{ m}^2$  per fingerling, in August--September 1963--1964. However, the density had decreased perceptibly in 1965, most probably because of the effects of uncontrolled removal (the catching of spawners in the autumn of 1963 and 1964 and the wide-

spread practice of catching young salmon), since due attention was not paid to the conservation of the river.

Published data make it possible to compare the rivers in the basin of Lake Onega with other rivers with respect to the population density of fingerlings. In the Atlantic salmon spawning grounds in the upper reaches of the Pechora there is on average approximately  $9 \text{ m}^2$  per fingerling in the second half of the summer in places where the concentration of fish is greatest (Vladimirskaya, 1957).

According to the results of an investigation of 11 rivers in the province of New Brunswick, there are approximately  $1.4 \text{ m}^2$  per parr (between 0+ and 2+) in Canadian rivers (Elson and Kerswill, 1964).

There is at least 1 young salmon, including underyearlings, per  $1 \text{ m}^2$  in the Daugava (Lishev and Rimsh, 1961). According to the observations of A. R. Mitans (1962), the concentration of underyearlings and yearlings (not counting other fishes) reached  $0.74 \text{ m}^2$  per fish in the Daugava in September 1960.

This comparison indicates that the spawning and growth areas in the basin of Lake Onega are very little utilized. The cause of this is the small number of fish spawning, not to mention those instances in which migration to the spawning grounds is completely excluded.

This raises the question of the number of spawners per hectare which should be regarded as the optimum. It has been established from the mean abundance and from the structure of the stocks in the Shuya and the Pyal'ma that the mean density of egg laying in these rivers is 5 eggs per  $1 \text{ m}^2$ . This density cannot be regarded as high, since with a wastage of 90 % 1 larva per  $2 \text{ m}^2$  will remain by the spring, and the density of the fingerlings (0+--2+) will not subsequently exceed  $9.5 \text{ m}^2$  per fish. To obtain a density of  $1 \text{ m}^2$  per

fingerling 50 eggs per 1 m<sup>2</sup> would be needed or 200 m<sup>2</sup> of spawning ground per pair of spawners at a fecundity of 10 000 eggs.

In the absence of a salmon hatchery in Lake Onega the only way of increasing the abundance of the salmon and salmon catches is to intensify the utilization of the spawning and growth areas. Technical and biotic improvement (the elimination of enemies and competitors), which it is easier to carry out in medium and small rivers, may play a large role in increasing their productivity. The ideal solution would, of course, be to combine these operations with artificial propagation, in particular with the introduction of hatchery young into growth areas which are becoming depopulated or are weakly populated, which would accelerate the formation of stocks of high abundance. In relation to the stock of the Shuya, where there is overfishing, it is desirable that in order to improve the utilization of the areas a quota should be fixed of one fish let through to every fish caught and also that protection of the river against uncontrollable removals should be intensified.

The importance of a river to the salmon fishery and its potential value are determined at the present time not so much by its size as by the nature and intensity of its utilization. The role of medium and small rivers in the reproduction of salmonids is therefore increased, especially after logging is discontinued in these rivers and they can become fully available to the fish industry. It is quite possible that the improvement and cultivation of these rivers (for example, salmon monoculture) will so increase their productivity as to make it possible largely to compensate the lost part of the resources of spawning grounds.

## Chapter 3

### COMPARATIVE DESCRIPTION OF THE SALMON STOCKS OF LAKE ONEGA

#### I. The Life Cycle of the Salmon.

The life cycle of the salmon of the Onega population has some distinctive features. Firstly, in contrast to the Ladoga salmon (Sabunaev, 1956), no form similar to the hiemal race in the Atlantic salmon has been discovered. Also absent are the stages found in the Ladoga population of grilse and especially pre-grilse or post-smolt, in which return to the rivers and spawning occur at a duration of the feeding (marine) period of respectively 1+ and 0+. It is interesting that the pre-grilse stage found in males and described by Saunders and Henderson (1965) is not known for the rivers of Canada and the basin of the Arctic Ocean, is extremely rare in the rivers of Newfoundland (three authenticated cases in the Little Codroy River cited by Saunders and Henderson, 1965) and in the Baltic (one male in the Lagan River (Sweden) cited by Carlin, (1955), but is fairly common in British rivers (Richardson, 1836; Day, 1884; Hutton, 1949; Shearer, 1963).

It has been found on the basis of long-term observations on different stocks that the predominant duration of the river period is two years -- in 66 % of fish. Downstream migrants 3 years old comprise approximately 33 %, and the downstream migration takes place at 4 years old in no more than 1 %. No fish have been found for which the duration of the river period is 1 year or 5 years.

The feeding period in the recruits (fish maturing for the first time which are the recruitment of the spawning stock) lasts for no less than 4 years

and no more than 9 and is 5--6 years for the majority. The percentage ratio of the age groups varies in different stocks and in different years, as will be stated in greater detail below.

Growth in the year of the spawning migration is encountered very rarely and as an exception. Fish entering the river have a completed annual zone even if the migration is not in the spring but in the autumn (Pyal'ma). The explanation for this may be found in the behaviour of the fish. The salmon remains in the estuarine zone of the Pyal'ma throughout the summer, but is unable to enter the river owing to the low level. When in the estuarine zone it does not feed, i.e. it behaves like a fish which has already entered the river and is keeping to a pool.

Females account for at least  $2/3$  of the adult part of the spawning stocks. The lack of large males is made good by their dwarf substitutes which are present in excess in the rapids during the spawning period. /58/

It is probable that dwarf males are able to take part in spawning more than once. G. V. Nikol'skii (Nikol'skii et al., 1947) tells of a dwarf male 5+ years old which had a spawning mark on the scales, i.e. which had spawned in the previous year. However, this erosion could have been caused by an epithelioma, which is a common occurrence for the Pechora (Vladimirskaya, 1957). We have found fish with destruction on two river zones in succession. It is impossible to infer for certain from this erosion that spawning had taken place in the past, although epithelioma is also to be found in dwarf males. This consideration, naturally, in no way rules out the possibility that dwarf males may spawn twice or even three times (for example, successively at an age of 1+, 2+ and 3+).

For reasons which are unclear the post-spawning mortality of spawned salmon leaving the river is slight in comparison to that of the salmon in the

sea. Although the proportion of the carry-over, i.e. fishes spawning repeatedly, is governed in the first instance by the fishing rate, it is difficult to explain a high percentage of carry-over solely by "weak" exploitation. Fish with 2 and 3 spawning marks and even with 5, i.e. fish coming to spawn for the 6th time, have been found among the carry-over. However, the carry-over may disappear completely in the case of heavy over-fishing. V. B. Sabunaev (1956) also concludes on the basis of observations of the salmon of the Vuoksa River (Lake Ladoga) that post-spawning mortality is very slight.

The type of population (as defined by Monastyrskii, 1953) is not a stable entity. Depending on the rate of removal and possibly on the conditions determining post-spawning mortality (for example, on distinctive features of the regime of the rivers), a population will belong either to the second type, with a considerable proportion of carry-over, or may be converted to the first type, in which the spawning stock consists almost entirely of recruits alone. The third type is possible in principle, but only as a rare exception at the present time, only when fishing has been neglected for a long time, as for example in the Kuito Lakes, where the carry-over is a half of the stock and includes old fish which have spawned several times (A. F. Smirnov, 1965).

The lake salmon, which should be regarded as an adaptive relict, has very effective adaptive capabilities. High adaptational plasticity is characteristic for all salmonids (Gerbil'skii, 1961, 1965), but among this family it is evidently only members of the genera Salmo and Oncorhynchus which are most eurybiontic and which possess the most perfected adaptational mechanisms by means of which they maintain their numbers when the conditions of reproduction worsen. If there has long been an almost universal reduction in the abundance of the salmon, what is responsible for this is not its biology, but its

extremely high value, which creates the desire to over-exploit all the fish, and also those fundamental and frequently irreversible changes in the state of rivers which have accompanied the settlement and industrialization of uninhabited territories with their untouched wild life.

It may be stated confidently that were the life cycle of Salmo to be simpler and were the "reserve of strength" to be lower, these fish would long ago have disappeared as a species. Double bonds play a special role in "strengthening" the cycle: dwarf males which successfully replace adult fish in the spawning grounds and repeated spawning which is not found in salmon of the genus Oncorhynchus. The distinctive features of the life cycle in the genus Salmo therefore ensure its species "protection in time" (Bakshanskii, 1967), i.e. they enable even very small populations and stocks to exist.

The life cycle of the salmon falls naturally into five periods which include individual stanzas of ontogeny (in a slightly different sense to that of Vasnetsov, 1953 and Nikol'skii, 1965). The stanzas consist, in their turn, of stages, the study and isolation of which is far from complete both in the salmon and in other fishes, as is evident from the literature on embryology, physiology and histology. The periods and stanzas are as follows.

I. River period, from fertilization of the egg to the downstream migrants.

Stanzas:

- 1) embryonic,
- 2) larval,
- 3) fingerling (underyearlings, parr),
- 3a) "neotenic" (dwarf males),
- 4) downstream migrants (smolts).

II. Feeding period (= stanza 5), from the smolt to commencement of the spawning migration.

III. Breeding period.

Stanzas:

6) migratory,

7) spawning. These stanzas are understood in the sense in which they are defined by A. I. Smirnov (1965), but the boundary of the period has been shifted: it is more logical to transfer the post-spawning downstream migration (downstream-migrant stanza) to the following period.

IV. Recovery period.

Stanzas:

8) downstream-migrant,

9) additional feeding, which is not identical to the feeding period, since the state of the organism is different and the rates of weight increase are also different and are very high in fish which have spawned and left the river.

V. Period of natural mortality (= stanza 10). The old fish finally die from senility and exhaustion of the organism after several spawnings, either immediately in the spawning grounds or during the post-spawning downstream migration.

The greatest mortality in the course of ontogeny is connected with the times of transition from one stanza to another, i.e. at vulnerable moments in the reconstruction of the organism and alteration in ecological requirements. The greatest relative mortality is noted in the course of the embryonic stanza, on transition from the larval to the fingerling stanza and from the downstream-migrant stanza to the feeding period: in the first two instances it may reach practically 90 % (McCrimmon, 1954; Nikiforov, 1959a, 1959b), and in the third 80 % (Parker, 1965).

If the life cycle of the salmon is depicted in a diagram, the "double bonds", to which reference has been made, which increase the viability of the species, are revealed with greater clarity (fig. 8).

Resistance to commercial loading, to excessive removal, is increased in populations with a longer life cycle in which the spawning stocks are formed from fish of several year-classes, the number of which is greater, the longer is the cycle. Differences in the time at which the recruits reach maturity also have a smoothing influence. For this reason several weak generations in succession may still not lead to a catastrophic reduction of the population. Therefore, considerable inertia is a feature of the population dynamics of the salmon. However, this inertia also includes a negative property: increase in the abundance of the adult part of the population when conditions become favourable will be equally slow.

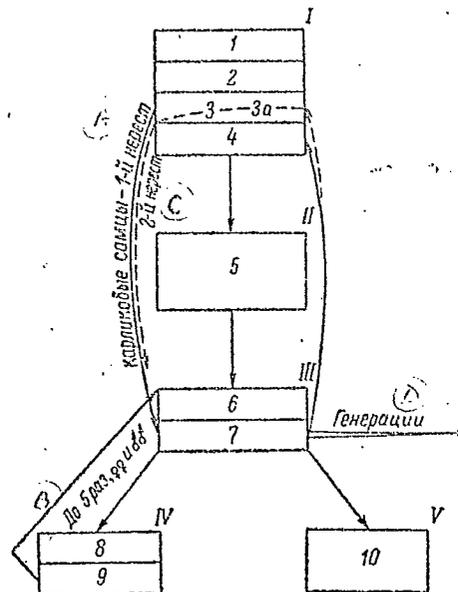


Fig. 8. Diagram of the life cycle of the salmon. Roman numerals --- periods in the life cycle; arabic numerals --- stanzas. See the text for explanation.

Keyed on figure: A. Dwarf males -- first spawning B. Up to 5 times, females and males C. Second spawning D. Generations.

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This should be borne in mind, since the life cycle in the Omega salmon is apparently the longest of the cycles in the populations known to us. Succession of generations in the Omega population takes place on average only at intervals of 8--10 years. It is after such a period that the effect of return will be obtained if the spawning rivers are improved. However, the return will be accelerated in hatchery rearing which reduces the river period. The selection for fish breeding of stocks with a shorter cycle and the selection of spawners in relation to growth rate and the rate of maturation would appear to be a promising approach which might significantly increase the effectiveness of artificial propagation.

## II. Habitats of the Salmon.

/61/

In the river. A general description of the rivers as a habitat of the salmon has been given in the previous chapter. Here we shall discuss the distribution and behaviour of the salmon.

During the period spent in the river before spawning the adult fish remain in pools and when the weather is hot they emerge into the faster current, in the rapids. In rivers which do not have deep pools and in which the rapids are greatly shallowed in the summer instances have been observed of spawners burying their head in beds of water plants, apparently in search of shade. The probable reason is excessive insolation (not only overheating as such), which was shown long ago to have an inhibiting effect, at all events on the young (Davis, 1946).

Fish which have spawned and which do not succeed in migrating down-

stream before the river freezes over probably spend the winter in pools or above the rapids, since ice jams would make their presence in the rapids unthinkable.

The habitats of the young alter with age. During the period spent in the river young salmon form small schools (between 10 and 3 fish) on only two occasions, i.e. after emerging from the nest mound before dispersal over the "fishing areas" and at the time of downstream migration of the smolts. At these times the young have the least chance of concealing themselves when a predator attacks. Schooling is evidently a protective adaptation in these instances, the role of which is regarded as proved for other fishes (Redakov, 1961; Nikol'skii, 1965).

On emerging from the nest mounds the young remain during the second and third decades of June in small schools close in to the bank in the upper layer of the water (0--10 cm). The current is uniform in such places, flow rate does not exceed 0.25--0.5 m/sec, and the bottom is frequently silted. In August underyearlings are solitary. Although they are to be found not far from the bank at this time, it is now in places with a more lively current and gentle nicks. In the Tuba River underyearlings and older parr were found at the time of the summer low water (August 1963 and 1964) at a minimum depth of 10 cm, i.e. close to the bank. Profuse development of water moss was noted in the river; the fingerlings may possibly have taken refuge from the bright sun beneath the clumps of moss. According to the observations of H. I. Vladimirskaia (1957), fingerlings avoided remaining around vegetation.

Older parr are to be found all over the river bed, but for preference at greater depths and where the current is stronger than in the case of underyearlings. The largest are to be found in the current where it is livelier.

In places where the bottom is uneven the parr are usually to be

found on top of a stone, apparently with the abdomen resting on it. In other instances the fish lie slightly curled to the side of a stone, completely motionless, in such a position that the current presses them against the stone. Some newly tagged and released small fish also behaved in this manner. /62/

In places with a level bottom of shingle and gravel the parr take up position approximately in the centre of an area with a radius of approximately 0.5 m with a depression of the bottom in the middle; it is from here that the fish makes sorties after food. If frightened, it departs almost invariably sideways and downward, but returns to its position after some time.

As has been noted by many investigators (McCrimmon, 1954; Vladimirskaia, 1957; Saunders and Gee, 1964), parr everywhere reveal amazing constancy of association with one place throughout the summer. In our experiments on the Pyal'ma tagged parr were not found more than 50 m from the point of release for a month (September) after release. Young grayling of the same age are everywhere found accompanying salmon fingerlings during the summer.

In the fall, in late September--early October, the fingerlings leave the rapids and it is difficult to find sexually immature parr in the rapids. Only dwarf males, which have already reached stage V of maturity by around September 10 (Pyal'ma) are found in the rapids. Dwarf males assemble in the spawning grounds before the mature fish appear.

Although the wintering localities of the young are unknown, they should be pools, since the chances of the survival of fish in the rapids would be slight during the period of ice jams. It is possible that this migration should be regarded as a protective adaptation. There is no information concerning the behaviour of the young during wintering and the spring ice run.

After wintering, the fish enter the opening rapids in the second half of April, as may be assessed from what happened when the Vama dam was closed at this time; salmon fingerlings were left behind on the drained bed of the river. A yearling (length as defined by Smitt --- ac 7.1 cm, weight 3.8 g) was taken by net in the Syapsya in the Terva-koski rapid on April 29, 1961. In April--May the young advance upstream and in so doing occupy localities where spawning has not taken place. Thus, the rapids of the upper part of the Vama, where spawning has become impossible owing to the regime of the dam, are occupied every spring. The fingerlings may also enter small tributaries. In the Shuya they enter a stream which flows into the Yumanishki spawning rapid; to judge by the catches of "amateur" fishermen, the concentration of fingerlings in the stream is ultimately very high.

Smolts and silvery parr appear in the lower reaches of the rivers at the end of May. Their downstream migration from the rivers is apparently complete toward the middle of June, since we were not able to find them in the rivers after June 15. After June 20 smolts are already to be found at some considerable distance (more than 10 km) from the river mouths: as far as Khedostrov in the region of Onega around the Pyal'ma River and as far as Besov Nos in the region around the Shala River. From the middle of June smolts are taken in fine-mesh traps ("merezhi" and trap nets) set up in the spring to catch firstly the smelt and later the vendace. /63/

The weight of smolts is usually 15--30 g, and in rare instances more. A smolt weighing 175 g (a female, not a dwarf male !), which had 3 complete annuli and large growth of the 4th (3+) was caught in the Lizhma on June 10, 1964; the arrangement of the sclerites in the 3rd and 4th zones was reminiscent of that characteristic for the feeding period. The stomach and esophagus of the smolt were gorged with insect larvae and, despite this, it took the hook

with a large piece of worm. According to statements by inhabitants, these large smolts are often found in the Lizhma. The existence of lakes in the basin (headwater lakes, Lizmzero, Kedrozzero, Tarasmozzero), which not only increase the feeding capacity of the river, but may also provide a place for the partial or preliminary feeding of the smolts, may be mentioned as a probable cause. In this respect attention should be paid to the local view that there is a separate Lizmzero salmon (like the Lake Seltskoe salmon in the system of the Lizhma and the Tikhtozero salmon in the system of the Pista, both of which are in the White Sea basin).

Such large smolts are either very rare or not found at all in other rivers of Lake Onega. A smolt of similar size caught in the Shula in 1964 caused astonishment among local fishermen, since downstream migrants are small here and are found from a weight of 11 g.

The smolts grow rapidly in the lake and their weight reaches 200--500 g and possibly more by October (1958 data).

Is downstream migration into the lake in the parr stage possible? Downstream migrants caught in the lake were either complete smolts or silvery parr with clearly showing transverse bands. We did not find parr in lake catches. G. V. Pishchula (1951) gives facts of the migration of under-yearlings to the sea for Latvian rivers and assumes on this basis that the Baltic salmon generally descends downstream in the parr stage. We know of only one instance in which fishermen took a parr ("troutlet") in May 1965 around the mouth of the Pyal'ma. However, this instance is in no sense evidence in support of the possibility of such downstream migration. The point is that when the lower spawning grounds are practically in the river mouth, as in the Pyal'ma, parr may move into the zone around the mouth for the winter and then return to the river in the spring, in the same way as from an ordinary

winter pool.

In the lake. The feeding salmon is found throughout the lake" . . . with the exception of the shallowest heavily isolated bays such as Svyatukha and Keften'-guba, the northern part of Gorskaya Bay and the northern part of Unitskaya Bay, where it is found extremely rarely. Nor are there salmon in the cliff area, in the strait formed by Klimetskii Island and the mainland" (Zborovskaya, 1948).

The following may be added to this general description of the distribution of the salmon over the lake. The salmon is in fact extremely rare in the bays listed above. A feeding sexually immature salmon (weight 2.4 kg, age 3+3) with the stomach filled with bleak, was taken on June 3, 1965 in the heavily overgrown, swampy Matguba Bay (in the northern part of Unitskaya Bay), which is a typical bream spawning ground. Local inhabitants state that there have been a further two cases of salmon being caught here in the past (oral communication from Z. N. Smirnova, Karelrybvod). /64/

There are some distinctive features to the distribution of the salmon in the lake in the course of the year. As soon as the ice breaks away from the shore in the spring the salmon move from under the ice into the opening shore leads. They remain close to the shore (within 100--200 m) and right at the surface, so that the head and dorsal fin show above the water. If there is a return movement of the ice, the salmon in shallow places are unable to move back into deep water because, in the opinion of fishermen, they are afraid of the noise made by the ice. As a result fish have been pressed into the shore and have perished; this has been noted around Peschanyi and Derevyannyi.

Although approach of the salmon to the shores in the spring has been noted in many parts of the lake, and not only in the zones around the mouths of the spawning rivers, it has only been around Besov Nos that this approach of the

salmon has been used for special and highly successful fishing. The salmon (both migratory and feeding) does not usually remain for more than 15 days close to the shore here and is better taken from the beginning in fine-mesh nets (merezhi) close into the shore than in those farther out. More than 7 centners were caught in 7 days of fishing (between 24 and 31 May) in 1963; 5 centners of this quantity were taken on 3 days (May 26--28). In 1962 the catch was 18 centners, 12 centners of which were taken before May 30. There was previously a case in which 5 centners of salmon were taken in a night. Westerlies which pile up cold water from the lake are conducive to fishing in this region. There was no fishing around Besov Nos in the summer since salmon were rarely taken there.

According to the observations of N. B. Zborovskaya (1948, p. 94), when the water along the shores heats to above 14°C the salmon move out into the open lake. In a cold spring they remain for longer around the shores, until the beginning of June.

The feeding salmon and spawned salmon descending from the rivers feed at this time on spawning smelts (Veshchezerov, 1931; Zborovskaya, 1948). In the summer the salmon feeds on the vendace and is therefore to be found where the vendace is found and is taken in fine-mesh fixed nets. Autumnal feeding concentrations of the salmon are associated with spawning concentrations of the vendace. There is a close correlation between the runs of these fishes which has been noted by N. N. Pushkarev (1914a, 1914b) and V. V. Veshchezerov (1931). Autumn concentrations of the salmon are known for the regions of Brusno, Saloostrov and Cape Petropavlovsk.

When the lake is ice-free the salmon keep to the upper layer of the water, from the surface to a depth of no more than 10 m, as has been established by the age-old practice of "garva" fishing and rod and line fishing; "garva."

fishing was practised until the lake froze over. In calm clear weather salmon may be seen sporting at the surface. The presence of the salmon in the upper layers of the water explains why the vendace predominates in its diet, rather than the smelt, which keeps to the deeper horizons. We know nothing concerning the habitats of the stickleback, which has also been recorded in the diet of the feeding salmon. Nor do we know where the salmon winter.

Although the pattern of the scales is slightly different in different local stocks (different percentage of occurrence of transitional zones and of epitheliomatous erosion), these differences are not so significant as to enable us to infer from the scales of a salmon caught in the lake to which river stock it belongs. Admittedly, some difference which has been noted in the structure of the transitional zones may possibly enable us to make a tentative judgment of the stocks to which the fish belongs, but this is still in need of classification. Therefore, materials on the feeding salmon unaccompanied by tagging may be used only for an overall description of the feeding part of the entire population (nutrition, growth etc.).

### III. The Spawning Migration and the Factors Affecting It.

It is not known how the salmon is guided in the open lake in the search for the way to the parent river. To judge by foreign research data (Fagerlund et al., 1963; Woodhead, 1963; Andersen, 1965; Sockeye salmon... 1965), the salmon are guided in the sea by smell, by taste and even by orientation by the sun, and that in the approach to the river and in the river itself they are guided in seeking out their spawning tributary by smell and by taste.

In the zone off the river mouth where the continuation of the river

flow can still be traced, the run of fish is determined by the currents. This has been established by dyeing the water of rivers flowing into Bristol Bay and by observing the movement of the sockeye in the bay (Sockeye salmon... 1965). According to the observations of V. M. Nadezhin (1964) on the behaviour of the Atlantic salmon in Pechora Bay, the run of the salmon is governed by the discharge current. Offshore winds intensify the discharge current as a result of drift and this intensifies the entry of the Atlantic salmon into the river. Conversely, "backing" winds deprive the fish of a guideline, since the current is lost.

B. Carlin (1955) holds similar views on the effect of the current and the wind on the behaviour of the salmon in the zone off a river mouth.

Our observations on the movement of salmon in Petrozavodsk Bay do not contradict what has been said above. On entering the bay, the salmon definitely keeps to the current of the Shuya, which hugs the southern shore on leaving Solomenoe Strait (Litinskaya, 1960). Salmon traps were erected in the past all along the southern shore of the bay. Nowadays they are placed in the inlet area on both sides of the strait, but by far the greater part of the catch is yielded by the traps along the southern shore. The largest catches here are taken when the winds are northerly and easterly. The north wind intensifies the discharge current and increases the entry of fish into the river. The east wind apparently operates in a different way: without blocking off the current it forces it closer to the shore in the region of Peskov which is where the main traps are installed. In addition, mixing causes a slight reduction of transparency which makes the traps less noticeable. A south wind is a backing wind, and a west wind shifts the current away from the shore, i.e. away from the traps.

/66/

In general the wind has a strong influence on the behaviour of salmon

in the areas off river mouths. However, this effect is exerted mainly on daily catches (occasionally on catches over 10-day periods) and does not alter the general picture of the spawning run -- the number and time of the peaks.

There is a very well manifested correlation between the run of the salmon and water content. The most intensive ascent of fish into the rivers occurs during floods (spring and autumn); the ascent decreases as water discharges are reduced and ceases entirely in small and medium-sized rivers during the low-water period. The run may be renewed in such rivers in the summer when level rises after rain (Pyal'ma and Kumsa) or when there is abrupt discharge from reservoirs (Lizhma), when salmon from the zone around the river mouth rush into the stream. In Kondopoga Bay salmon entered a stream flowing from a power station, the strength of which was 10 times greater than the current in the old river bed. Owing to the extremely low levels in the summer and autumn of 1963 and 1964 the obstacles in the mouths of the Tuba and Kumsa Rivers (dam and bay-mouth bar) were insurmountable to the salmon.

The decisive effect of the water content of rivers on the time of the spawning run and on the quantity of spawners entering the rivers is referred to by A. N. Derzhavin (1922, 1953), I. Krussel' (1962) and A. I. Sherstyuk (1958).

The connexion between the run and water temperature has been inadequately investigated. M. B. Zborovskaya (1935) noted three periods of mass run with successively lowering intensity in the Shuya salmon. The first run, which is the largest, coincides with a mean water temperature of 7°C, the middle run occurs when temperature is 10--12°C and the third and smallest run occurs when temperature is 14°C. "Within each of these periods the run of the salmon is reduced when there is a temporary rise in water temperature".

On the other hand, P.I. Novikov (1947), who studied the run of the summer and autumn Atlantic salmon in the Kem' River, concludes that "no relationship is to be observed between the intensity of the run and water temperature".

Our materials do not at present suffice for final conclusions. It would apparently not be mistaken to suggest that water temperature within the normal temperature range plays a lesser role than water content and the wind.

The rate of advance of the salmon upstream in different rivers is /67/  
apparently different and is dependent on many factors (on the remoteness of the spawning grounds, on the total fall and gradients, on water content, on the existence of logging etc.). Because there have not been any direct experiments involving tagging, the mean rate of advance may be assessed from the time of appearance of the salmon in different reaches of the rivers.

The Vodla salmon reaches the Upper Vama (170 km from the mouth of the Vodla) toward the middle of July, i.e. in 2--2.5 months. In this case the mean rate of ascent is 2--3 km a day with a rise of approximately 1.5 m.

The Pyal'ma salmon appears in the Zhilaya Tambitsa in the region of the settlement (30 km from the mouth of the Pyal'ma) approximately between the 15th and the 20th of May or 10--15 days after commencement of the run from the lake. Here also the mean rate of ascent is 2--3 km per day, but the rise is 7--10 m.

According to tagging data (Tikhii, 1931c), the mean rate of ascent in the Svir' was 1--4 km per day and the maximum rate was 8.5 km per day (one instance). In the lower reaches of the Kem', also according to tagging data (Novikov, 1950), the mean rate was approximately 2.5 km per day; similar results were yielded by tagging and by observation of the behaviour of the fish in different reaches of the river (as in our example with the Vodla and the Pyal'ma). In the lower reaches of the Vyg (Gorskii, 1935) the salmon advanced 3--6 km per day, and in the Nezen' (Danil'chenko, 1935) it advanced 14--19 km per day. No more rapid advance has been recorded.

IV. Types of Spawning Migrations of the Lake Onega Salmon.

The study of spawning migrations has a direct bearing on consideration of the question of localization. There are stable differences in the time of the spawning run of the Lake Onega salmon entering the different rivers (figs. 9--13). This is not connected with membership of different biological groups, as in the salmon from the sea, in which there is a hiemal form and a grilse ("tinga").

The information to be found in the literature concerning the time and pattern of the spawning run of the Lake Onega salmon is far from plentiful. The material assembled by M. B. Zborovskaya (1935, 1948) contains a table which includes half the salmon rivers (eight), but in which the periods when the run is intensified are not distinguished.

On the basis of M. B. Zborovskaya's table, P. I. Novikov (1957) compiled his own table which, in his own words, contained "some clarifications". However, the new table contains a number of mistakes not to be found in the original table: 1) the time of the mass run for Petrozavodsk Bay and the mouth of the Shala is given as "September and the first half of October" which does not correspond to reality; 2) there is no mention of the autumn run in the Fyal'ma, which was known long ago by N. Ya. Ozeretskovskii (1812); 3) the time of the mass run for the region of the Vama dam, as for the mouth of the Shala, is indicated as "September and the first half of October". In fact the salmon appears in the upper part of the Vama from the middle of July and does not advance any further, but remains to spawn where it is. Moreover, it is physically incapable of covering the distance of 170 km from the mouth to the headwaters in the time stated by P. I. Novikov.

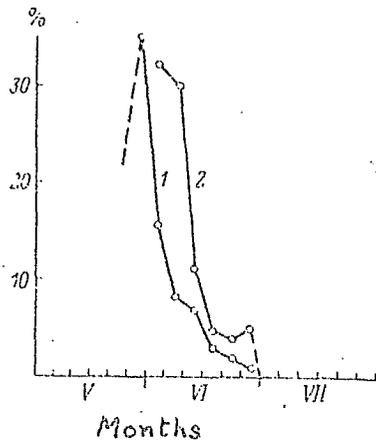


Рис. 9. Интенсивность хода лосося по пятидневкам в % от улова за сезон в р. Водле.  
1 -- 1927 г.; 2 -- 1964 г.

Fig. 9. Intensity of the salmon run by 5-day periods as percentages of the catch over the season in the Vodla River.  
1 -- 1927, 2 -- 1964.

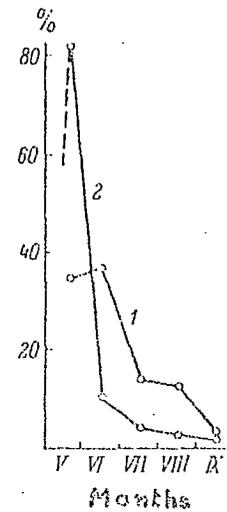


Рис. 10. Интенсивность хода лосося по месяцам в % от улова за сезон в р. Водле.  
1 -- 1927 г.; 2 -- 1930 г.

Fig. 10. Intensity of the salmon run by months as percentages of the catch over the season in the Vodla River.  
1 -- 1927, 2 -- 1930.

There follows an account of all that is known concerning the time of the run from published data and from our own observations.

Lososinka. It is stated in the chronicle of Andrei Likhachev (1563; cited by M. N. Pravdin, 1915) that salmon and trout are caught throughout the summer in the river ("...v Lososinnitse lososi i torpa vo vse leto"). It may apparently be considered that this reference to some extent characterizes the time of entry into the river, since in those far-off times the bulk of the catch in rivers was taken with racks of traps installed near the mouth. There is no later information concerning the Lososinka; salmon have long disappeared from it.

Shuya. An excellent description of the run was given by M. B. Zborovskaya (1935): "Three periods of mass run are annually observed in the migrations of the salmon into Petrozavodsk Bay and into the Shuya River. These periods do not coincide in time in different years, but are nevertheless close. The first period of the largest run of the salmon lasts from May 15--20 to June 5--10. The second rise in the intensity of the run is noted from June 10--15 to June 25--July 5.

/69/

The third ascent takes place between June 30 and July 10. Single salmon are caught in the autumn."

Our observations of the Shuya salmon were made in years which differed markedly in the size of the run, in water content and in temperature conditions. It is noteworthy that the pattern of the run remains constant on the whole, as described by M. B. Zborovskaya. It was only in 1964 that the run began ten days later than usual and that the decline in its intensity in July was not as sharp as in previous years (fig. 12); the cause of this is not clear at present.

Suna. A description of the salmon run when the Suna was in its natural state before its regulation was given by N. I. Kozhin (1927a, p. 227): "The first run of the salmon begins immediately after the passage of the ice, while the water is still high (in the condition known locally as "scouring" water). According to statements by fishermen, it is small salmon weighing 3 to 5 lbs. which arrive at this time. These salmon, which are known as "Lake Sandal" salmon are distinguished by lighter colouring. The second run occurs at the beginning and in the middle of June by the new calendar.<sup>1</sup>

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<sup>1</sup> Translator's note. The reference to the new calendar means that the date has been adjusted by the addition of 13 days to bring the Julian calendar into line with the Gregorian calendar. The Gregorian calendar was introduced in Russia on February 1, 1918. As the date of Kozhin's paper, from which this quotation is taken, is given as 1927, Kozhin must have been drawing

on sources before 1918.

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This run coincides with the spawning of the bleak (known locally as the "salaga"). It is larger salmon with darker colouring, known locally as the "Suna salmon" which run at this time. This run also lasts for 2--3 weeks; "Lake Sandal salmon" are taken together with "Suna salmon". The "Lake Sandal salmon" is no longer to be found in the subsequent runs. The salmon run subsequently continues intermittently for the whole of the summer. The run begins to intensify at the beginning of September by the new calendar and the third and most considerable run takes place between the middle of September and October 15. The salmon in this run are already spawning salmon, since spawning is observed around October 10--15 by the new calendar, or to be more precise salmon with ripe eggs are caught. Salmon ascend the Suna River to the Kivach Falls, which they cannot surmount, and they previously entered the Sandalka River in large numbers (before 1926)."

Therefore, there were three intensity peaks to the run in the Suna, as in the Shuya; the only difference is that the third run in the Suna occurred considerably later, when the run had already ended in the Shuya.

M. B. Zborovskaya cited observations made when the Suna had already been regulated. She writes (1948): "In the greater part of the rivers (of Lake Onega -- Yu. S.) the main run is observed in the spring, in the month of May. It is only in the Suna and Lizhma Rivers that salmon are caught in the river mouths only in the autumn, at the end of September and in the beginning of October. In these rivers the salmon does not ascend far upstream to spawn." According to the data of the Suna fishing station for the period from 1959 to 1962, the migratory salmon arrived between August 20 and October 15, mainly at

the end of August and the beginning of September.

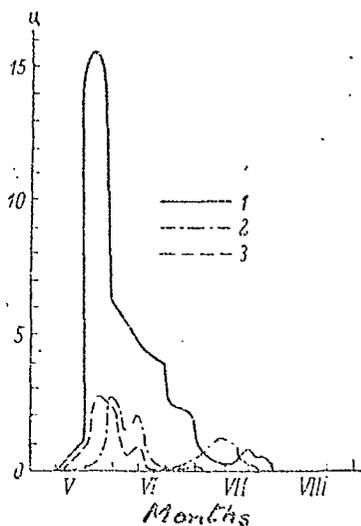
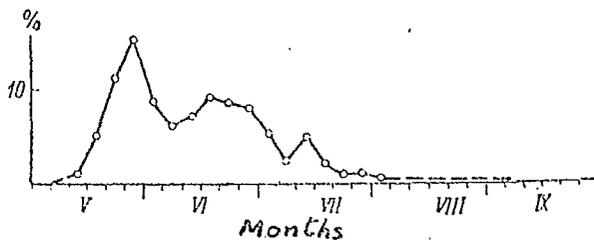


Рис. 11. Улов лосося в цч Шальском промысловом районе в 1932 г. (По: Зборовская, 1948).  
 1 — в устье Водлы; 2 — у Бесова Носа; 3 — у Муромского мыса.

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Fig. 11. Salmon catch in centners in the Shala fishing area in 1932 (taken from Zborovskaya, 1948).

1 -- In the mouth of the Vodla; 2 -- around Besov Nos; 3 -- around Cape Murom.



/70/

Fig. 12. Intensity of the salmon run as percentages of the catch over the season in the Shuya River (mean long-term data).

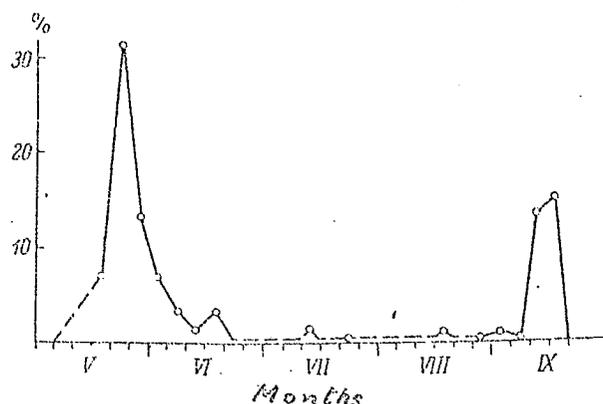


Fig. 13. Intensity of the salmon run as percentages of the catch over the 1963 season in the Fyala River.

Information from questionnaires filled in by old inhabitants who were fishermen confirms the statement of N. I. Kozhin concerning the spring-summer run which previously took place. If the spring "Lake Sandal" salmon in fact entered the Sandalka and the Tivdiika (that this was so is reported by K. F. Kessler (1868) and P. F. Domrachev (1929)), its disappearance after hydraulic engineering works have been carried out is understandable since it did not reach these spawning grounds.

Therefore, the pattern of the spawning run was initially simplified (the number of peaks in the run was reduced), and subsequently around 1962 the Suna stock finally disappeared.

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Lizhna. The salmon now enters this river from June through October; the main run occurs in August and the beginning of September and is strongly affected by the operational regime of the Kedrozero dam. When the dam is closed the salmon hardly enters the river at all but remains in the zone around the mouth. When there is a sharp discharge of water from the reservoir the salmon rushes into the stream. For this reason it is impossible to give a precise

indication of the time when the run is at its peak.

Old inhabitants state that there was in the past an even earlier run in May in which the salmon had already reached the dam in the upper part of the Elgamka at the end of May. However, these upper spawning grounds in the Elgamka and the Upper Lishma have long been practically inaccessible owing to the obstacles produced by logging (dams and obstructions). Spawning now takes place only in the reach below the Kedrozero dam; the path to the spawning grounds has therefore been shortened from 50--60 km to 4 km, i.e. to 1/12--1/15.

Unitsa. Amateur fishermen caught several fish 5--6 km from the mouth in September 1963 and several more in November 1962, but approximately 40 km from the mouth. The time of the run cannot be assessed from these data and there is no information in the literature.

Kumsa. According to observations made by a fisheries inspector, H. F. Pavlov, over several years, the main run of the salmon occurs between the second half of July and the beginning of September. There are no published data and no fisheries records.

Povenchanka. N. N. Pushkarev (1900a) has the following to state concerning this river: "Even now the salmon enters the Povenchanka occasionally, beginning in July (by the old calendar, -- Yu. S.)", and he continues: "Up to 15 salmon are caught in the course of the summer...at the dam near the sawmill (in the river mouth -- Yu. S.)." As in the neighbouring Kumsa, the run was evidently not early here.

Nemina. A number of authors give original information on the spawning run of the salmon in this river. N. Ya. Danilevskii (1875): "... the run of the pike-perch...to the end of June to Peter's Day. At this time the salmon and the taimen enter the bay (Cholmuzhskaya Bay -- Yu. S.), and subsequently the Nemena River. The run of these fishes continues until

the autumn...". L. N. Zverintsev (1899): "Their basis (the basis of the Cholmuzhskaya Fisheries -- Yu. S.) is the spring run of the pike-perch and the salmon...". N. N. Pushkarev (1900a): "The salmon...is also caught in Cholmuzhskaya Bay in the autumn, and in the Nemina River and in front of the Cholmuzhskii Strait in considerable quantity in the spring." V. V. Pokrovskii (1936): "The run of the salmon into Cholmuzhskaya Bay also occurs in the spring: the run begins between the first and the 15th of May, is greatest between May 15 and June 1, and ends in September. From Cholmuzhskaya Bay the salmon ascends the Nemina River...".

According to replies to questionnaires obtained when the river was inspected in 1964, salmon are caught at the beginning of June and in September in the region of the upper spawning grounds in the tributary, the Fazha. No movement of salmon was noted in the summer; only those fish which had remained in the pools since the spring were caught. /72/

It may be concluded from the foregoing information that there are two peaks, a spring and an autumn peak, in the run of the salmon into the Nemina, and that the spring peak is the main one.

Pyal'ma. N. Ya. Ozeretskovskii (1812) reports the run in the spring and autumn: "A fence has been erected in the Pyal'ma River at which many whitefish, salmon and "torpy"\* are taken in the spring and autumn...". For some reason, none of the other authors who refer in their writings to the Pyal'ma salmon say anything about an autumn run. It is stated in the reference work "The Lakes of Karelia" (1959) that the run ends in July. Nevertheless, an autumn run exists and is well known to the entire local population and not only to professional fishermen.

Karelrybvod maintained an observation point and control nets across the river bed on the Pyal'ma from 1958 through 1964 with interruptions.

\* Translator's note. Apparently a dialect word. Not in the latest edition of Nikol'skii: Chastnaya ikhtologiya (Moscow, 1971). Not in Ryby SSSR.

According to the observations in 1963 and 1964, the autumn run, which coincides with a rise of level, begins from the end of August and ends by September 20; the bulk of the salmon run between September 14 and 18. In 1963 more than 100 salmon accumulated below the control nets across the river bed on September 15 and 16. The autumn run was weaker in 1964, possibly owing to the absence of an autumn flood and the extremely low level of the water, which was more characteristic of the summer low water in a dry year with little water in the river.

The spring run lasts from the beginning of May (immediately after the ice run) to the middle of June; the peak is between May 20 and June 5 and the run is larger than the autumn run. The ascent of the river by the salmon ceases entirely at times between the spring and autumn runs, but may be renewed after rain as a result of the rise of level. The first salmon of the spring run appear in the tributary, the Zhilaya Tambitsa, in the region of the settlement around May 15--20. The pattern and time of the run in the Pyal'ma are therefore very similar to the pattern and time in the Nemina (fig. 13).

Tuba. There is no published information. Before 1964 the salmon was able to ascend the river only in the spring, during the flood. The dam dries up during the low-water period and the autumn rise of level is insufficient to permit of the passage of the salmon, which remains below the dam (observations in 1963 and 1964). A passage which was cut through the dam in the autumn of 1964 will facilitate the passage into the river both of the salmon and of undesirable fishes.

Vodla. Several authors give information concerning the time of the run. N. Ya. Danilevskii (1875): "The pike and the salmon begin to ascend from the end or from halfway through April (old-style calendar -- Yu. S.), depending on the year. The salmon run continues throughout the summer...". N. N.

Pushkarev (1900a): "The Shala fishermen find the salmon in their catches from May through July"; "...the first salmon appear in the Vodla in "Nicol'skaya" week, i.e. between May 1 and 6"; "Both around Podporozh'e and below, right to the mouth of the Vodla River, there are three periods of fishing: the spring salmon catch, the autumn whitefish catch and the winter burbot catch." Trap nets were usually used for fishing at Podporozh'e from the end of April until the end of May and salmon were taken in them with other fishes; it was mainly whitefish and a few salmon which were taken in the summer and only whitefish and burbot in the autumn. M. V. Logashev (1931): "The salmon run in the Vodla...begins at the time when the river opens or a few days before it...". V. V. Pokrovskii and A. F. Skirnov (1932): "It (the salmon -- Yu. S.) begins to ascend the Vodla River in the spring, frequently before the lake and the lower reaches of the river are free of ice. The run continues throughout May and half of June, after which the salmon is no longer taken in the river and only isolated specimens are taken in Shala Bay. There is no autumn run of the salmon here...". M. B. Zborovskaya (1935) gives the following times for the run: start May 1--15, mass run May 15--20, end of run June 1--15. According to A. A. Zabolotskii (1936) the peak level of catches in 1932 was between May 20 and 30.

Our observations are in full agreement with the conclusions of M.B. Zborovskaya. The spawning run ends in June, around the middle of the month, at the section in the mouth of the river. In this respect it is very similar to the first peak of the run in the Shuya. In the following months, down to September, only feeding salmon are caught along the Shala shore, where they are to be found in general from the spring, from the time of approach of the smelt (see figs. 9--11 based on the materials of E. A. Veselov (1932) and M. B. Zborovskaya (1948)).

Andoma. Original information is given only by V. V. Veshchezarov

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(1931); other authors repeat him. Veshchezerov notes that there are three salmon runs to the region of the shore around the Andoma, in the spring, the summer and the autumn; the first of these is a spawning run (entry into the river), while the other two are assumed to be feeding migrations. The first run takes place from halfway through May and entry into the river is particularly intensive in the first 7--10 days. In 1929 the run was recorded from May 29 and lasted 5--8 days. Fishing used to last for 15--30 days in the spring and autumn during the period of the run. The second run is at the beginning of June -- "It must be assumed that this migration is of the nature of a feeding migration, but it is possible that some proportion of the salmon move directly into the river". "The third run of the salmon, which is also of the nature of a feeding migration, takes place in the autumn during the migration of the vendace. At the present time, in connexion with the heavy reduction (since 1926) in the arrival of the vendace to spawn around Cape Fetrovavlovsk and the shores adjacent to it, the autumn run of the salmon has also disappeared."

There have not been any subsequent observations of the Andoma salmon. The data obtained from the control nets set up across the river bed by Sevzaprybvod (Leningrad) have not completely clarified the pattern of the run. According to replies to questionnaires, there is an autumn run in September, which is not clearly stated by Veshchezerov, and in the autumn the salmon also enters the tributary, the Samina. Nothing reliable is known concerning the summer run. /74/

Vytegra. V. V. Veshchezerov (1931): "...between 50 and 70 fish were caught...around the town of Vytegra...in the spring of 1924...". There is no other information.

Megra. Control nets were stretched across the river bed 3 km from the mouth by Sevzaprybvod between May 13 and September 25 1964. Salmon and

trout arrived singly between May and July; the main run was in August and the first half of September and the last catch was on September 18. There were approximately 7 times as many lake trout as salmon in the catch (observations of I. I. Ryzhev).

Vodlitsa. There is no information concerning the time of the run.

Comparison of the time and pattern of the salmon run in the different rivers in the basin of Lake Onega reveals considerable similarity in some instances. The following three types of spawning run may be distinguished on this basis (figs. 14, 15):

- 1) spring run with one peak (Vodla);
- 2) spring-autumn run with two peaks (Pyal'ma, Memina);
- 3) spring-autumn run with three peaks (the Shuya and, in the past, the Suna);
- 4) protracted summer-autumn run (Kumsa).

Because there is at present no reliable information for the other rivers it is premature to accord them to any of the types, although provisional judgments may be expressed.

The intensity or density of the run is connected with the type and is dependent on the number of peaks into which the entire run is subdivided. The density of the run is greatest in the Vodla, followed by the Pyal'ma, where the peaks are sharply expressed, and then by the Shuya, which has gentler peaks. Thus, almost as many salmon were caught in five days in the Vodla in May 1927 (between May 27 and 31) as in the whole of the following June (according to the materials of E. A. Veselov, 1932).

The pattern of the run is related to (or coincides with?) the location of the spawning grounds in all the rivers for which there are reliable data. This correlation is expressed in the agreement between the number of peaks of the run and the number of groups of spawning grounds and in a less

expressed correlation between the time of the run and the remoteness of the spawning grounds. It may therefore be suggested that the location of the spawning grounds is the cause of the difference in the types of run in the different rivers.

In fact, the spawning grounds of the Vodla salmon are concentrated in the Vodla between 170 and 147 km from the mouth. No such arrangement exists in the other rivers and it is only in the Vodla that there is a short, dense spring run (first type).

In the Pyal'ma the main spawning grounds lie in two groups, in the tributary, the Zhilaya Tambitsa (between 30 and 22 km from the mouth of the Pyal'ma) and in the lower reaches of the Pyal'ma itself (between 6.0 and 0.4 km from the mouth). Even here, however, despite the short migratory path, two peaks are clearly expressed in the run. It has been noted that the salmon of the spring run mainly occupy the upper spawning grounds, in the Zhilaya Tambitsa, and that a few of them even ascend the Tuna, a tributary of the Tambitsa, as far as the Koda (up to 50 km from the mouth of the Pyal'ma). Salmon of the autumn run, in which the males frequently enter the river with runny milt, do not succeed in ascending far up the river and utilize the lower spawning grounds, beginning 400 m from the mouth.

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The arrangement of spawning grounds in the Nemina is similar to their arrangement in the Pyal'ma and there are correspondingly two peaks of the run -- in the spring and in the autumn.

There used to be three groups of spawning grounds in the Suna (see the section on the location of spawning and growth areas) and three peaks to the run; the salmon of the first run were definitely connected with the most remote spawning grounds and were known as the "Lake Sandal" salmon (Kozhin, 1927a; see above). The salmon of the last run, which entered the river with

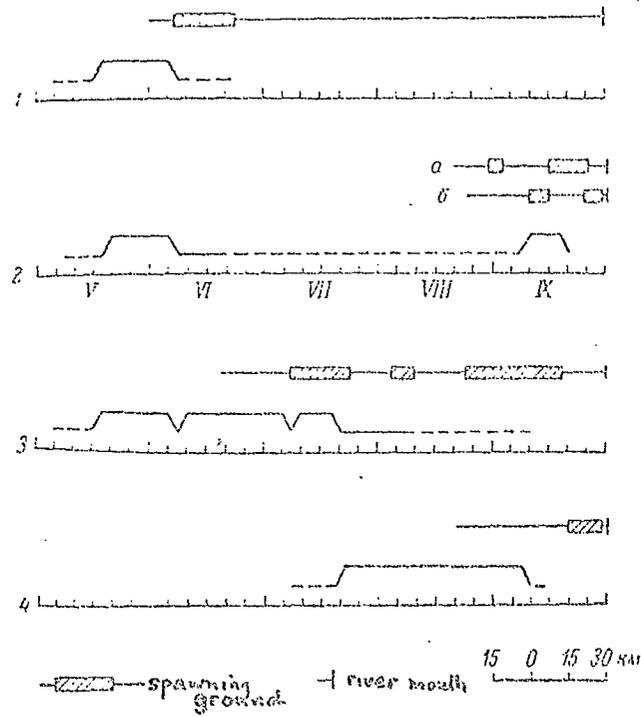


Fig. 14. The type of spawning migration of the salmon and the location of the spawning grounds.

1 -- Vedla; 2a -- Nemina; 2b -- Pyal'ma; 3 -- Shuya; 4 -- Kumsa.

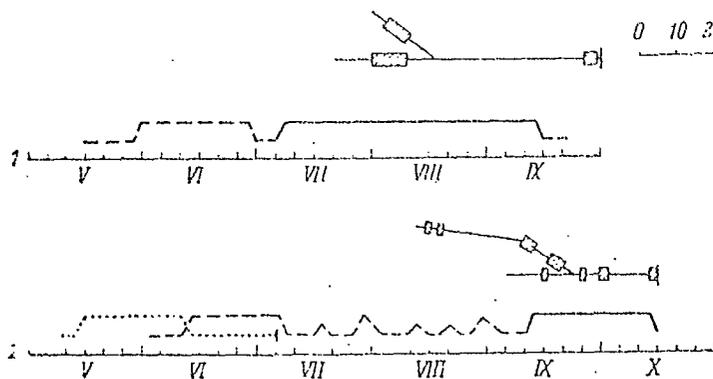


Fig. 15. The type of spawning migration of the salmon and the location of the spawning grounds.

1 -- Lizhma; 2 -- Suna. See fig. 14 for the key.

running sexual products, spawned in the lowest rapids.

There are three main groups of spawning grounds in the Shuya and also three peaks to the run annually expressed with great constancy.

In the Kumsa the spawning grounds are essentially located in one group covering 13 km of the lower reach of the river and there is here a protracted summer-autumn run in which no sharp peaks are noted.

It is highly curious that the elimination of groups of spawning grounds (the upper spawning grounds in the Lizhma and the Suna) leads to a simplification of the pattern of the run: the spring run ceased in the Lizhma and the spring and summer runs in the Suna (before the stock disappeared completely).

After the hydroelectric power station at Ignoila had cut off the small upper spawning grounds in the Shuya, the salmon ceased ascending to the upper reach of the river (above Lake Vagat), with only isolated instances of wandering.

All this suggests that there may possibly be "small-scale localization", i.e. that within the stock of an individual river there may be smaller groupings associated with definite spawning grounds. Admittedly, it would be risky to assert a priori that, for instance, "the salmon of the second peak is firmly related to the second group of spawning grounds", but such a possibility must be conceded, especially because there are similar examples for other basins. Thus, the sockeye stock in the Bystraya River (Kamchatka) consists of four "substocks" which differ in spawning localities and in the time of the run; instances of wandering are exceptional. The independence of these substocks, which had previously been established on the basis of ordinary ichthyological analyses, has been confirmed by serological analysis (Zaks and Sokolova, 1961).

This question is of great significance and there is no need to demonstrate its topicality. We know what practical benefits have been derived from the study of intraspecific biological groups in the Acipenseridae (the work of the laboratory of M. L. Gerbil'skii).

The first step towards elucidation of this important and extremely interesting question should be a broadly conceived and executed tagging of salmon of different peaks of the run and young salmon in different spawning and growth areas, and also the use of sensitive biological methods (immunological, biochemical etc.).

V. Alteration in the Structure of the Stock during the Run of the Salmon.

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Although alteration in the structure of a stock during the run may be an indication of its heterogeneity, constancy of structure is not, on the other hand, a reliable indication to the contrary.

No significant differences in the structure of the population during the run were discovered in the Shuya from materials for the period 1959--1965. There were slight fluctuations in the mean weight of the fish without any definite trend; M. B. Zborovskaya (1948) reached the same conclusion. The apparent reduction in the number of large fish (and in the proportion of carry-over) in August is due solely to the fact that few fish are taken at this time and that the fishermen keep the best for themselves.

In the Suna, according to the data of N. I. Kozhin (1927a), salmon from different peaks of the run differed significantly in size and colouration (see the previous section); the spring salmon was the smallest at 3--5 lbs. The possibility of establishing the cause has been lost now that the Suna stock has disappeared; there are no old records.

Larger salmon enter the Pyal'ma in the autumn than in the spring (according to records for 1963 and 1964): 5.1--5.3 kg as against 4.4--4.6 kg (table 7). This is due to the fact that the carry-over constitutes a greater proportion in the autumn (up to 40 % of the number of migrants as against 20--30 % in the spring) and that there are more large old females (although these are smaller than coeval males); in the autumn run females account for up to 81--86 % as against 67 % in the spring. The mean weight of recruits is practically the same in the spring and the autumn, 4.3--4.6 kg; their age composition and mean age (7.3 years) are absolutely the same.

Таблица 7

<sup>2</sup> Вес лосося, идущего в Пыльму весной и осенью

3 Сезон	4 Вес, кг								5 Число рыб	6 Колебл. для веса, кг	7 Средний вес, кг
	2	3	4	5	6	7	8	9			
1963											
♂ Весна . . .	2	43	82	46	9	—	—	182	2.7--7.0	4.64	
♀ Осень . . .	2	7	14	20	4	1	2	50	2.7--8.5	5.10	
1964											
♂ Весна . . .	—	62	77	36	2	—	—	177	3.1--6.25	4.43	
♀ Осень . . .	—	5	28	43	15	1	—	92	3.7--7.2	5.32	

Key to Table 7: 1. Table 7 2. Weight of salmon entering the Pyal'ma in the spring and autumn 3. Season 4. Weight, kg 5. Number of fish 6. Weight range, kg 7. Mean weight, kg 8. Spring 9. Autumn.

For the region around the mouth of the Vodla N. N. Pushkarev (1900a) and N. B. Zborovskaya (1948) note a strong reduction of mean weight between the start of the run and July; according to Pushkarev as much as 5--7 lbs. This

is due solely to the fact that after the migrating salmon enter the river only small sexually immature salmon remain along the shore around Shala and are caught there till September.

The same cause was responsible for the reduction noted by V. V. Veshchezerov (1931) in the mean weight of the salmon in the Andoma region from 3--7 kg in May to 1.8--2.5 kg in June; in the summer the bulk of the salmon weighed between 0.55 and 2.5 kg (Tikhii, 1931a, the table on p. 11), i.e. were obviously sexually immature, since the minimum weight of adult fish caught in the spawning grounds is 3 kg, according to the data of Veshchezerov (females 3--6 kg, males 5 kg).

In the Vuoksa the mean weight of adult fish increases in the course of the run from April through October by 2--2.5 times as a result of reduction in the proportion of grilse (Sabunaev, 1956). It is impossible to use this material or the large amount of material on salmon of different populations from the sea for purposes of comparison because of the significant differences in biology (grilse, hiemal form).

#### VI. Spawning, Time of Spawning and Behaviour of The Salmon.

Published information on the time of spawning is extremely sparse and fragmentary because no special observations have been made.

K. F. Kessler (1868): "...it does not begin spawning until the late autumn after the festival of "Pokrov"...The salmon also spawns earlier in the Povenchanka, already in the month of September." N. I. Kozhin (1929a): "Spawning of the salmon began in the mouth of the Suna River on October 25" (in 1927 -- Yu. S.). V. V. Veshchezerov (1931): "The spawning period lasts up to 20 days, from approximately September 25--27 to October 14" (in the Andoma -- Yu. S.). V. V. Pokrovskii and A. F. Smirnov (1932): "Spawning of the salmon

was noted for the Suna in the first half of October. It is interesting to note that salmon kept in the autumn of 1931 in the live containers of the Ust'-Suna hatchery of the Karelian Fish Breeding Research Station (KNIIRS) did not yield eggs until November 16--13, i.e. their spawning was delayed for a whole month. The life of the fish in captivity apparently had a retarding influence on maturation of the sexual products in this case." B. S. Lukash (1939):

"Spawning is noted in the second half of October and in the beginning of November at a depth of approximately 1 m..."(in the Vama --- Yu. S.). H. B. Zborovskaya (1948): "Spawning of the salmon is usually observed in October and the beginning of November. Thus, in the Suna River in 1927 spawning took place under natural conditions from October 21 and was at its height on October 25, which was, according to the observations of fishermen, slightly later than in other years, since spawning begins, depending on weather conditions, either before October 14 or from October 20.

The time of spawning of the salmon in different years was as follows: the salmon began to spawn on October 15 in the Suna in 1931; in the middle of October in the Lizhma River in 1932; on October 20 in the Shuya River in 1933; on October 15 in the Shuya River in 1936; on October 13 in the Shuya River in 1946. /79/

Our observations in the spawning grounds contribute little that is new to clarification of the time of spawning. The rate at which the water in the river cools is dependent on the existence of lakes in the river and their position. Where cooling proceeds more rapidly spawning begins slightly earlier: end of September--beginning of October in the Pyal'ma and the Tuba, middle--end of October in the Vama and the Shuya. Attention was first drawn to this by K. F. Kessler (1868) in relation to the Poverchanka. In England spawning occurs earlier in the northern rivers than in the southern rivers

(Menzies, 1931).

We have the following observations in our possession. Adult and dwarf males with running milt were found in the Fyal'ma and the Tuba in 1954 from September 8; adult males were caught in the lake, approximately 1 km from the mouth of the Fyal'ma. Females were still in stage IV of maturity at this time. Spawning occurred after September 20. In 1965 dwarf males in stage V of maturity were found in the Fyal'ma from September 13. Salmon were seen sporting in the lower spawning ground of the Fyal'ma on September 30. A large redd was found in the Tuba on the following day at the lower end of the Velikii Kamen' rapid. There were some ten dwarf males in stage V of maturity around this redd (eight were caught); there were no traces of adult salmon which had in all probability been caught by "amateur" fishermen, traces of whose activity could be seen both in the river and along the banks.

Redds were found in the Syapsya on November 1--2, 1960 in the Tervakoski and Kover-porog rapids, but it is possible that the salmon had spawned previously, but that the commencement had not been noticed. Redds were noted on October 18 of the same autumn in the Lower Lizhma, but spawning was still not complete since the salmon remained around the redds in pairs; nine days later there were no females in the spawning grounds and only males remained around the redds.

In the Vama in 1963 spawning was complete by November 1, only males remained around the redds in the rapids, while the females had already left the spawning grounds (only one female which had laid its eggs was found).

Salmon were kept in containers at the Suna hatchery from the third decade of August until the middle of September. Eggs were obtained on October 18--19 in 1959, on October 18 and 27 and November 1 in 1960, on October 13, 17, 20, 23 and 27 in 1961 and on October 22 in 1962. We do not know to what

extent the maturation of salmon in captivity lags behind natural maturation.

Redds may be located in different parts of a rapid (shallow), including its upper and lower ends. Spawning usually takes place at a depth of down to 1.5 m, but a redd was found in the Vama at a depth of approximately 2 m. According to replies to questionnaires, spawning formerly took place in the Suna in the Vidansk rapid at a depth of 2 m and even deeper. Such a depth seems very unusual and slightly too great. However, M. I. Vladimirskaia (1957) notes that there were redds in the Pechora at a depth of down to 2 m, and V. B. Sabunaev (1956) even says that the maximum depth for the Vuoksa is 4 m (!). However, the majority of the fish evidently excavate their redds in the depth range 0.5--1.2 m, as may be assessed from our not-very-extensive observations in the rivers. The reaction of the fish to an alteration of water level when spawning has already begun is of interest in this respect. At the time when spawning began in the Vama (1963) level in the river was high owing to discharge from the reservoir and the salmon therefore began to excavate their redds practically along the bank. However, the discharge of water proceeded rapidly, so that the salmon were unable to finish spawning and were obliged to move to the middle of the river bed. There were rows of incomplete, essentially trial redds along both banks, which were found to be at too shallow a depth as the level fell and were therefore abandoned. Finally, the salmon moved 5--10 m away from the first redds and spawned at a depth of between 0.5--0.7 m and the very middle of the bed at down to 1.5--2.0 m. Such behaviour of the salmon has been observed in the spawning grounds of the Vuoksa by V. B. Sabunaev. /80/

If the reservoir is discharged after spawning has finished, as is more often the case in the Vama, the redds along the banks dry out; this has been the case since the first years after construction of the dam (Lukash, 1939).

A large number of trial redds may be a result not only of an alteration of level, but also of unsuitable or contaminated bottom material. There were six trial redds in a chain, 1--2 m apart, along a crib in the Syapsya in the Terva-koski rapid, where the shingle was mixed with bark; the redd actually used was in the middle of the river bed 20 m higher upstream from the trial redds.

There is in general no consensus of opinion concerning the number of trial redds and redds actually used which may be excavated by a single female. Because there are few observations (Greeley, 1932; Hobbs, 1937; Jones and King, 1949, 1950; Nikiforov, 1960; Grinyuk, 1963; Hardy, 1963), there is inadequate basis for any categorical assertion (e.g. "one trial redd + 3 redds actually used").

In as much as the behaviour of the fish at the time of spawning and its choice of site for the redd are determined by fluctuations of level and by the quality of the spawning area, and since either may be highly variable, it is difficult to expect an identical number of redds in all circumstances. The suggestion of M. I. Vladimirskaia (1957) that the Atlantic salmon may excavate between 1 and 7 redds actually used seems quite realistic in our view. There is evidence in support of this from observations abroad under natural conditions and in experimental ponds.

Dwarf males appear first in the spawning grounds before the adult fish arrive. They are essentially in the same place where they have passed the summer; immature parr have already departed to overwinter before spawning begins.

Although large males comprise only  $1/3$  of the stock, and sometimes even less (falling to 15 % in the autumn run in the Pyal'ma), there is no lack of males owing to the abundance of dwarf substitutes. Some of the females undoubtedly spawn with dwarf males, the more so because a single female is

sometimes accompanied by several large males (up to nine, according to the observations of Young (cited by Smitt, 1895)). It is not very probable that a large male could spawn successively with several females as is usual in other species of fishes, since all the known observations show that males exhibit an attachment both to a redd and to a female.

When several large males approach a single female a contest takes place between the males in which the largest is the winner. K. F. Kessler (1864): "...several males almost invariably accompany the female...they frequently begin to fight savagely amongst themselves." Similar observations are cited by V. B. SabunaeV (1956) and V. K. Soldatov (cited from Novikov, 1953). We have also heard tell of this from fishermen who have caught salmon in the spawning grounds. We have not observed scraps between large males, but have seen a large male repelling dwarf males of which up to ten assemble around a redd (they take up position below the redd). On occasion large males are to be seen with wounds along both sides of the body around the dorsal fin. The explanation which fishermen offer for this is that during a scrap the adversaries seize ("bite") each other by the back with their hook-shaped curved jaws.

While the large males are settling things amongst themselves, the female may spawn with a dwarf male, without waiting for the victor. The eggs in different mounds of the same redd may therefore be fertilized by different males. This is supported by experimental observations (Jones and King, 1952).

In those rivers where the spawning grounds of the salmon and the trout coincide (see below), a dwarf male around a female may be a trout and this will result in hybrid progeny. Females are apparently not very selective and may spawn in case of need with a large male trout, as is indicated by the observations of Young, to which reference has been made above (Young, cited by Smitt, 1895): "...one female salmon was accompanied by nine males, which were

all caught one after the other, and when the last had been caught, the female returned to the redd with a large male trout" (re-translated from the author's translation into Russian, retaining the author's emphasis). Furthermore:

"Most of the small trout usually remain at a respectful distance below the redd and seek out eggs carried down by the current, but from time to time a dwarf male will seize the opportunity to take part in spawning while the partner of the female salmon fights with a rival."

We have not succeeded in observing the actual act of spawning.

According to observations in the Lower Lizhma and the Vama, females forsake the spawning grounds immediately after spawning and only males remain around the redds. We have seen them in the Lizhma in the same places around their redds (there was a single large redd near each male) for two weeks after spawning, after which observations were discontinued. Menzies (1931) also states that in practice only males may be caught in the rivers after spawning. /82/

After spawning the males are relatively immobile and react weakly to danger, in contrast to their behaviour at other times. It is difficult to say what precisely is responsible for such a state and for post-spawning mortality. It may possibly be that the modification of metabolism associated with spawning proves to be irreversible in older fish. Emaciation in the usual sense cannot be the cause of their death, since the condition and fat content are higher in males than in females after spawning. Dead males driven into the bank and frozen into the ice have been found in many spawning grounds at the time of formation of frazil ice; their gills and mouth were packed with frazil ice.

In contrast to males, females are extremely mobile after spawning and move actively away from the spawning grounds. Many of those who have fished for salmon in the post-spawning condition with harpoons state that it is very rarely that a female can be caught, whereas there is no difficulty in harpooning males. It is possible that females begin to feed while still in the river.

M. I. Vladimirskaia cites an instance in which the stomach of a female caught before the end of spawning contained a half-digested dwarf male. May it not be that some females behave like the pike in consuming their less elusive partners ?

The spawned fish may migrate downstream into the lake soon after spawning, in the same autumn, in small rivers and from the lower spawning grounds of large rivers. However, the downstream migration from the upper spawning grounds involves overwintering in the river, is renewed at the end of April--beginning of May and ends by the third decade of May or at the latest in the first decade of June. More fish apparently perish in downstream migration from the upper spawning grounds than from the lower ones.

To judge by the rate of exploitation and the fairly high percentage of the carry-over, mortality among spawned fish migrating downstream is on the whole slight. This is the opinion of V. B. Sabunaev in relation to the Vuoksa salmon (Lake Ladoga).

Females and males with two, three and even four spawning marks, i.e. the latter had come for the fifth spawning, have been found in the stocks of different rivers in the basin of Lake Onega. The weight of such old fish does not usually exceed 10 kg. However, according to the testimony of several individuals, a spawned salmon weighing 17 kg was harpooned in the Lizhma in 1958. If this is so, it should have weighed at least 20 kg before spawning since, as determined by Z. E. Tilik (1932), the loss of weight in males by the beginning of spawning is on average 14 %. It is difficult to imagine how many times this male had come to spawn.

The largest fish measured by the author was a female which had fed after spawning; it had two spawning marks and weighed 13 kg and its body length as defined by Smitt was ac 105 cm. Fish with four spawning marks weighed between

7 and 11 kg.

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VII. The Structure of Spawning Stocks and Its Annual Variations.

The treatment of this question is based on materials for the stocks of the Shuya, the Vodla and the Pyal'ma, which have been studied in the greatest detail owing to their commercial importance. Materials on the still-remaining, but small stocks of other rivers are so insignificant as to be essentially incapable of providing any characterization; the same applies to materials on the now non-existent Suna salmon.

The first thing which may be noted in the comparison of salmon of different stocks and of the same stock, but for different years, is the difference in size, which is best reflected in the mean weight of a fish in a stock (table 8). The salmon of the Pyal'ma is considerably smaller than that of the Vodla and the Shuya.

The mean weight of a fish in a stock is determined above all by the special features of growth, but is additionally influenced by two ratios: 1) the ratio of the recruitment and the carry-over, since the old fish are as a rule larger than the recruits (table 9) and 2) the ratio of males and females in the stock, since males are larger than females of the same age (table 10).

Fluctuations in the ratio of the recruitment and the carry-over may be very considerable. The carry-over in the Shuya between 1959 and 1965 was successively 16.0, 19.0, 20.0, 10.7, 5.6, 31.0, and 17.0 %. In the Pyal'ma between 1963 and 1965 the carry-over was 35.0, 37.0, and 17 %; in the Vodla between 1963 and 1965 it was 30.0, 50.0 and 35.0 %, but the possibility is not excluded in this case that the proportion of the carry-over has been overstated as a result of epitheliomatous erosion which was taken for a spawning mark.

This is scarcely possible in the stock of the Shuya, since such damage is hardly

ever found on the scales of the Shuya salmon.

Таблица 8

Средний вес особи в стадах разных лет, кг

3 Река	1931-1933 гг.	1948 г.	1949 г.	1950 г.	1951 г.	1959 г.	1960 г.	1961 г.	1962 г.	1963 г.	1964 г.	1965 г.
4 Шuya	5.4 (66)	6.4 (58)	6.7 (199)	6.8 (88)	6.9 (626)	6.5 (606)	6.4 (445)	5.9 (250)	6.3 (250)	6.3 (500)	6.0 (550)	5.8 (350)
5 Водла	—	—	—	—	—	—	—	—	—	7.0 (79)	5.9 (111)	5.9 (92)
6 Пяльма	—	—	—	—	—	—	—	—	—	4.7 (233)	4.7 (270)	5.0 (66)

7 Примечание. Данные за 1931—1933 гг. М. Б. Зборовской (1935), за 1948—1951 гг. З. В. Прозоровой (1951 и из отчета «Промысловые карты...», 1952); по Шuye за 1964—1965 гг. — с использованием материалов Карельского рыбохозяйства (отчеты Онежского икhtiологического пункта); по Водле и Пяльме за 1931—1962 гг. данных нет. Цифры в скобках — число исследованных рыб.

Key to Table 8: 1. Table 8 2. Mean weight of a fish in stocks of different years, kg 3. River 4. Shuya 5. Vodla 6. Pyal'ma 7. Note. Data for 1931--1933 taken from M. B. Zborovskaya (1935), data for 1948--1951 taken from Z. V. Prozorova (1951) and from the report "Fisheries Maps...", (1952); materials of Karelrybvod used for the Shuya in 1964--1965 (reports of the Onega Ichthyological Station); no data for the Vodla and the Pyal'ma for 1931--1962. The figures in brackets denote the number of fish examined.

Fluctuations in the proportion of the carry-over are due primarily to alterations in the fishing rate, but the influence of distinctive features of the rivers on the post-spawning mortality of the spawned fish is not excluded; mortality should be less when the downstream migration is short. /85/

The proportion of the carry-over provides a good indication of alteration in the fishing rate in the case of a number of year-classes of approximately the same abundance. When there are sharp fluctuations of abundance the use of this index may lead to incorrect conclusions. Thus, when

Таблица 9  
 Весовой состав пополнения и остатка Водлы в 1964 г. и в 1965 г.

	3 Вес, кг										4 Число рыб	5 Колесба- ния веса, кг	6 Средний вес, кг
	3-4	5	6	7	8	9	10	11					
1964 г.													
7 Пополнение	1	12	30	10	2	—	—	—	—	—	55	4.0—7.4	5.57
8 Остаток	—	7	12	13	8	5	3	1	—	—	49	4.1—11.0	6.65
1965 г.													
9 Пополнение	6	12	28	11	3	—	—	—	—	—	60	3.3*—7.8	5.43
10 Остаток	1	4	7	7	6	4	3	—	—	—	32	4.0—9.4	6.71

// \* Возможна незначительная примесь нагульного.

Key to Table 9: 1. Table 9 2. Weight composition of recruitment and carry-over in the Vodla in 1964 and in 1965 3. Weight, kg 4. Number of fish 5. Weight range, kg 6. Mean weight, kg 7. Recruitment 8. Carry-over 9. Recruitment 10. Carry-over 11.\* A small admixture of feeding salmon is possible.

the rate of exploitation is the same the proportion of the carry-over will be overstated when a strong year-class is followed a year later by a weak year-class and it will be understated in the opposite case. It will therefore be more correct to determine the abundance of the carry-over in each case and to relate it to the abundance of the catch in the year of the previous spawning run. This was done in estimation of the abundance of the Shuya stock.

The ratio of the sexes in salmon entering a river is characterized by invariable predominance of females in all stocks. It was 75 % in the Vodla in all three years of the observations (1963--1966). It was 72 % in the Pyal'ma in 1963 and 1965 and 66 % in 1964. The fullest information on annual

Таблица 10

2 Размеры самцов и самок Шуй, рекрутов (по материалам 1961 г.)

3	Возраст (речные и озерные годы)	4 Пол	5 Число рыб	6 Длина ос, см	7 Длина ад, см	8 Вес, кг
6	{	♀♀	9	74.7	70.0	4.93
		♂♂	1	74.5	69.5	4.80
7	{	♀♀	48	78.3	73.5	5.40
		♂♂	11	81.0	79.0	6.16
8	{	♀♀	63	81.4	76.2	5.95
		♂♂	25	87.7	82.5	6.87
9	{	♀♀	24	83.1	77.5	6.20
		♂♂	10	92.0	85.25	7.70
10	{	♀♀	5	81.7	76.0	5.74
		♂♂	2	89.0	83.25	7.10
11		♂♂	2	87.25	81.25	6.70

Key to Table 10: 1. Table 10 2. Size of males and females in the Shuya, recruits (according to 1961 materials) 3. Age (years in the river and in the lake) 4. Sex 5. Number of fish 6. Length ac, cm 7. Length ad, cm 8. Weight, kg

variations in the sexual composition of the stock exists for the Shuya (table 11).

The comparison of stocks by the first fish to mature may be very indicative.

On the whole the weight composition of recruits duplicates what is characteristic for the whole stock: the salmon of the Pyal'ma is always smaller than that of the Vodla and the Shuya (e.g. 4.59, 6.55 and 6.24 kg respectively in 1963 -- table 12).

Таблица 11

/84/

2 Половой состав стада Шуй, %

Пол 3	1931-1933 гг.	1959 г.	1960 г.	1961 г.
4 Самки . . . . .	75 ± 3.0	61 ± 2.0	64 ± 2.3	74 ± 3.1
5 Самцы . . . . .	25 (146)	39 (597)	36 (441)	26 (200)

6 Таблица 11 (продолжение)

Пол 3	1962 г.	1963 г.	1964 г.	1965 г.	Среднее 8
4 Самки . . . . .	80 ± 2.5	70 ± 3.0	75 ± 1.9	63 ± 4.3	70.4 ± 1.0
5 Самцы . . . . .	20 (252)	30 (236)	25 (500)	37 (123)	29.6

7 Примечание. Цифры в скобках — число исследованных рыб.

Key to Table 11: 1. Table 11 2. Sexual composition of the Shuya stock, %  
 3. Sex 4. Females 5. Males 6. Table 11 (continuation) 7. Note. The  
 figures in brackets denote the number of fish examined. 8. Mean.

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Таблица 12

2 Весовой состав рекрутов Шуй, Водлы и Пяльмы в 1963 г.

3 Реки	Вес, кг 4										5 Число рыб	6 Колебания веса, кг	7 Средний вес, кг
	2	3	4	5	6	7	8	9	10				
8 Шуй	—	2	36	74	64	40	17	2			235	3.6—9.3	6.24
9 Водла	—	—	6	13	18	8	4	3			50	4.65—9.6	6.55
10 Пяльма	3	36	66	39	6	—	—	—			150	2.7—7.0	4.59

Key to Table 12: 1. Table 12 2. Weight composition of recruits in the  
 Shuya, the Vodla and the Pyal'ma in 1963 3. River 4. Weight, kg 5.  
 Number of fish 6. Weight range, kg 7. Mean weight, kg 8. Shuya 9.  
 Vodla 10. Pyal'ma.

The salmon of all other stocks, for example of the Nemina, the Lizhma and the Suna (in the past), are also smaller than the Vodla and Shuya salmon. It is possible that the cause of this difference is to be found in the length of the migratory path. The spawning grounds are most remote in the Vodla and the Shuya and are moreover at a considerable elevation. Because the way to them requires greater expenditure of energy than in the other rivers, the fish here should be stronger and larger, i.e. the remoteness of the spawning grounds evidently determined the trend of selection. Moreover, the age of maturity is slightly greater in the salmon of the Vodla and the Shuya, i.e. the increase in their size is due to some extension of the feeding period taken in conjunction with slightly faster growth.

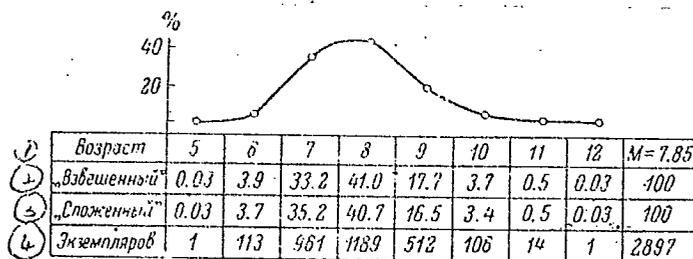


Fig. 16. The course of maturation of the Shuya salmon expressed as percentages of the occurrence of age groups of recruits (mean long-term data). Numbered on figure: 1. Age 2. "Weighted" 3. "Composite" 4. Number of fish.

The average course of maturation may be represented in terms of the percentage proportion of the different age groups among the recruits obtained on the basis of long-term data. This evens out variations due to differences

in the abundance of different year-classes and in the growth rate in different years. Thanks to the work of M. B. Zborovskaya and Z. V. Prozorova we now have material of this type for the Shuya stock for 14 years.

The average course of maturation was calculated from the age composition of recruits in the Shuya (table 13) as percentages of the occurrence of different age groups. It is noteworthy that both the mean "weighted" and the mean "composite" frequency of occurrence established from the percentage composition for individual years yield practically the same picture: an almost symmetrical distribution is obtained in both cases (fig. 16). Although similar material exists for the stocks of the Vodla and the Pyal'ma, the sequence of observations is very short (tables 14 and 15).

It is evident from the information given here that the age composition of fish maturing for the first time may differ considerably in different years. It is also apparent that maturation is not so protracted in the Pyal'ma salmon (no age groups 10--11 years) and that maturity is reached slightly earlier on average than in the salmon of the Vodla and the Shuya.

It is fairly difficult to compare the rate of maturation from the percentage proportions of the age groups. It is far more convenient to use mean age characteristics for this purpose. In this case the alteration in the age composition of the recruits becomes very obvious (fig. 17). /88/

It is possible that the cause of the difference in the age of recruits of different stocks and of the same stock but in different years will be successfully established from the age structure, i.e. by comparing the duration of the river and lake period, which together characterize the living conditions of the salmon in the river and in the lake. Taken in conjunction with the mean weight of a recruit, these characteristics reflect primarily the availability of food and possibly other environmental factors, i.e. this /89/

approach enables the characteristics of individual year-classes to be related to the general ecological background.

Fluctuations in the mean length of the river period (tables 16--18) are slight by comparison with the fluctuations in the mean age of recruits. This suggests that the fluctuations in age are due mainly to feeding conditions in the lake. We arrive at the somewhat unexpected conclusion that the conditions determining the growth of the salmon in the river are typified by greater constancy than conditions in the lake. This evidently means that the availability of food for the salmon in the lake may be subject to very strong variation.

The duration of the lake period of recruits in the stocks in 1963 is given in table 19. All the mean characteristics given above for changes in the course of maturation and in the age structure in salmon of the different stocks are given in table 20, which is a composite table, and in a graph (fig. 18). The lake period of the Pyal'ma salmon was found to be the shortest in all instances. The alteration in the duration of the lake period from 1963 was not uniform: maturation of the Shuya and Pyal'ma salmon was retarded while maturation of the Vodla salmon was accelerated. The duration of the river period altered slightly and had practically no modifying effect on total age. /90/

Does not the different pattern of variation in the duration of the lake period indicate different feeding conditions, a difference in the feeding grounds of the stocks in the lake? This suspicion is strengthened by the different frequency of occurrence in the stocks of transitional zones on the scales (in 1963: 16 % in the Shuya, 48 % in the Vodla and 42 % in the Pyal'ma) and of epitheliomatous erosion, and also differences in the rate of weight increase (see below).

Таблица 13

2 Возрастной состав рекрутов Шуй (эка.)

3 Годы наблюдений	4- Возраст (речные и озерные годы)								5 Число рыб	6 Средний возраст
	5	6	7	8	9	10	11	12		
1931--1933	--	9 (6.2)	31 (23.6)	65 (45.2)	24 (16.7)	12 (8.3)	--	--	144	7.97
1948	--	1 (1.8)	21 (33.2)	17 (30.9)	14 (25.5)	1 (1.8)	1 (1.8)	--	55	7.93
1949	--	1 (0.6)	61 (37.9)	67 (41.6)	30 (18.7)	1 (0.6)	1 (0.6)	--	161	7.83
1950	--	2 (2.1)	32 (33.2)	46 (48.0)	10 (10.4)	6 (6.3)	--	--	96	7.85
1951	--	36 (9.7)	141 (37.8)	134 (36.0)	58 (15.4)	4 (1.1)	--	--	373	7.61
1959	--	2 (0.4)	52 (10.3)	258 (51.3)	151 (30.0)	35 (7.0)	5 (1.0)	--	503	8.36
1960	1 (0.3)	2 (0.6)	62 (17.4)	143 (40.0)	114 (32.0)	30 (8.4)	4 (1.0)	1 (0.3)	357	8.34
1961	--	10 (5.0)	59 (29.5)	88 (44.0)	34 (17.0)	7 (3.5)	2 (1.0)	--	200	7.88
1962	--	14 (6.2)	104 (46.2)	89 (39.6)	15 (6.7)	3 (1.3)	--	--	225	7.51
1963	--	14 (5.9)	134 (61.0)	63 (26.7)	14 (5.9)	1 (0.5)	--	--	236	7.34
1964	--	20 (6.0)	170 (50.0)	124 (36.5)	20 (6.0)	4 (1.2)	1 (0.3)	--	339	7.47
1965	--	2 (1.0)	81 (38.0)	95 (46.0)	28 (14.0)	2 (1.2)	--	--	208	7.75
7 Всего:	1	113	961	1189	512	106	14		2897	7.85

8  
Примечание. За 1931-1933 гг. - материалы М. Б. Зборовской, за 1948-1951 гг. - З. В. Проzorовой. Распределение особей по годовым классам за 1950 и 1951 гг. вычислено по процентному составу. Цифры в скобках - число рыб определенного возраста, выраженное в процентах от общего числа, исследованных за данный год (или годы) рыб.

Key to Table 13: 1. Table 13 2. Age composition of recruits in the Shuya (number of fish) 3. Years of observations 4. Age (years in the river and in the lake) 5. Number of fish 6. Mean age 7. Total 8. Note. Materials of M. B. Zborovskaya for 1931--1933 and of Z. V. Prozorova for 1948--1951. The distribution of fish by year-classes for 1950 and 1951 was calculated from the percentage composition. The figures in brackets denote the number of fish of a given age expressed as a percentage of the total number examined in the year (or years) concerned.

Таблица 14  
2. Возрастной состав рекрутов Водлы (%)

3 Год наблюдений	4. Возраст (речные и озерные годы)							5 Число рыб	6 Средний возраст
	5	6	7	8	9	10	11		
1963	—	—	24	28	28	18	2	50	8.46
1964	—	2	16	50	30	2	—	50	8.14
1965	1.5	7	26.5	36.5	21.5	7	—	60	7.90

Key to Table 14: 1. Table 14 2. Age composition of recruits in the Vodla (%) 3. Year of observations 4. Age (years in the river and in the lake) 5. Number of fish 6. Mean age.

Таблица 15  
2. Возрастной состав рекрутов Пяльмы (%)

3 Год наблюдений	4. Возраст (речные и озерные годы)					5 Число рыб	6 Средний возраст
	5	6	7	8	9		
1963	—	9	52	36	3	151	7.33
1964	—	4.5	45.0	39.0	11.5	159	7.57
1965	—	2	50.0	42.5	5.5	54	7.52

Key to Table 15: 1. Table 15 2. Age composition of recruits in the Pyal'ma (%) 3. Year of observations 4. Age (years in the river and in the lake) 5. Number of fish 6. Mean age.

We need to verify by tagging whether the salmon of the different stocks in fact feed in different parts of the lake. If this is so it must necessarily be taken into consideration in the release of downstream-migrants from hatcheries so that uniform use is made of the food resources of all

Таблица 16

2 Соотношение рыб с различной длительностью речного периода в стаде Шуйи (%)

3 Год наблюдений	4 Речной период, годы			5 Число рыб	6 Средний возраст
	2	3	4		
1948	52.8	43.6	3.6	55	2.51
1949	59.0	39.9	1.1	161	2.42
1959	64.0	34.5	1.5	600	2.38
1960	68.2	30.8	1.0	443	2.33
1961	67.5	32.5	—	250	2.32
1962	72.6	27.0	0.4	252	2.28
1963	84.5	15.1	0.4	236	2.16
1964	75.0	24.4	0.6	336	2.26
1965	72.0	26.7	1.3	75	2.29

Key to Table 16: 1. Table 16 2. Proportions (%) of fish with river periods of different duration in the Shuya stock 3. Year of observations 4. River period, years 5. Number of fish 6. Mean age.

/89/

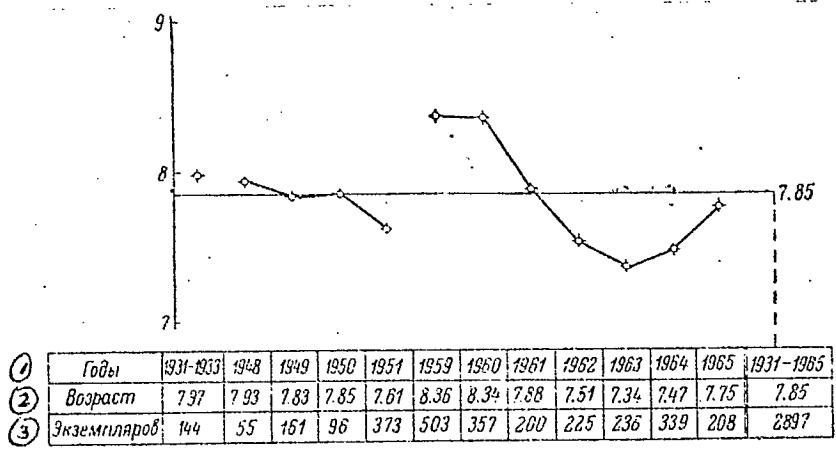


Fig. 17. Mean age of recruits in the Shuya over a number of years.

Numbered on figure: 1. Years 2. Age 3. Number of fish.

① Таблица 17

② Соотношение рыб с различной длительностью речного периода в стаде Водлы (%)

③ Год наблюдений	④ Речной период, годы			⑤ Число рыб	⑥ Средний возраст
	2	3	4		
1963	70	28	2	50	2.32
1964	72	26	2	50	2.30
1965	75	25	—	60	2.25

Key to Table 17: 1. Table 17 2. Proportions (%) of fish with river periods of different duration in the Vodla stock 3. Year of observations 4. River period, years 5. Number of fish 6. Mean age.

/90/

① Таблица 18

② Соотношение рыб с различной длительностью речного периода в стаде Пяльмы (%)

③ Год наблюдений	④ Речной период, годы			⑤ Число рыб	⑥ Средний возраст
	2	3	4		
1963	66	34	—	151	2.33
1964	56	44	—	153	2.44
1965	65	35	—	54	2.35

Key to Table 18: 1. Table 18 2. Proportions (%) of fish with river periods of different duration in the Pyal'ma stock 3. Year of observations 4. River period, years 5. Number of fish 6. Mean age.

areas of the lake.

Data on fecundity exist only for the Shuya and Pyal'ma salmon.

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According to the data of M. B. Zborovskaya (1935), the mean fecundity of the Shuya salmon is 12 thousand eggs and the range is from 8 to 15 thousand. A

Таблица 19

Соотношение рыб с различной длительностью озерного периода рекрутов в стадах Шуй, Водлы и Пяльмы 1963 г. (%)

Рекa	Озерный период, годы							Число рыб	Средний возраст
	3	4	5	6	7	8	9		
Шуй	—	7	70	22	1	—	—	236	5.18
Водла	—	4	24	34	32	4	2	50	6.14
Пяльма	0.5	11	77	11	0.5	—	—	151	5.00

Key to Table 19: 1. Table 19 2. Proportion (%) of fish for which the duration of the lake period of recruits is different in the stocks of the Shuya, the Vodla and the Pyal'ma in 1963 3. River 4. Lake period, years 5. Number of fish 6. Mean age 7. Shuya 8. Vodla 9. Pyal'ma.

mean fecundity of 12 630 and a range of from 3447 to 23 962 eggs are given for the Shuya salmon in the reference work "Lakes of Karelia" (1959). According to the data of Z. V. Prozorova, to be found in the same reference work, the mean fecundity of the Pyal'ma salmon is 5300 eggs and the range from 2196 to 9186. According to our materials for the autumn run of the salmon in 1964, the mean fecundity of the Pyal'ma salmon was 8155 eggs with a range of from 5355 to 9900 eggs and the mean weight of the females examined was 5.14 kg. It should be noted that the salmon of the autumn run is noticeably larger than the salmon of the spring run (5.2 kg on average as against 4.4--4.6 kg), which is due to the larger proportion of the carry-over in the autumn run. In the reference work "Lakes of Karelia" it is not stated from which run of the salmon samples were taken for the measurement of fecundity, but it must be thought that it was the spring run.

Таблица 20

Изменения структуры возраста рекрутов Шуи, Водлы и Пильмы, в годах

Рева	Возраст	1931--1933 гг.	1948 г.	1949 г.	1950 г.	1951 г.	1959 г.	1960 г.	1961 г.	1962 г.	1963 г.	1964 г.	1965 г.
Шуи	Полный	7.97	7.93	7.83	7.55	7.61	8.36	8.34	7.88	7.51	7.34	7.47	7.75
	Речной	—	2.51	2.42	—	—	2.38	2.33	2.32	2.28	2.16	2.26	2.29
	Озерный	—	5.12	5.41	—	—	5.98	6.01	5.56	5.23	5.18	5.21	5.46
Водла	Полный	—	—	—	—	—	—	—	—	—	8.46	8.44	7.90
	Речной	—	—	—	—	—	—	—	—	—	2.32	2.30	2.25
	Озерный	—	—	—	—	—	—	—	—	—	6.14	5.84	5.65
Пильма	Полный	—	—	—	—	—	—	—	—	—	7.33	7.57	7.52
	Речной	—	—	—	—	—	—	—	—	—	2.33	2.44	2.35
	Озерный	—	—	—	—	—	—	—	—	—	5.00	5.13	5.17

Key to Table 20: 1. Table 20 2. Alterations in the age structure of recruits in the Shuya, the Vodla and the Pyal'ma, in years 3. River 4. Age 5. Shuya 6. Total 7. River 8. Lake 9. Vodla 10. Pyal'ma.

VIII. Growth of the Salmon in the Lake.

M. B. Zborovskaya and Z. V. Prozorova studied the growth of the salmon by back calculation. Conclusions on growth based on our materials are not at variance with what is generally known. There are perceptible differences between fish of the same age which have a different combination of the number of years spent in the river and in the lake: the longer a salmon

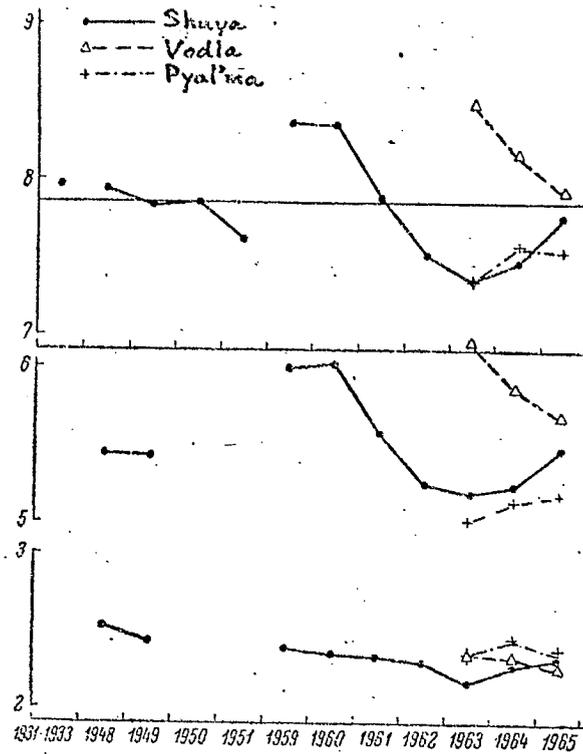


Fig. 18. Alteration in the age structure of recruits in the Shuya, the Vodla and the Pyal'ma. Years along x-axis; age structure along y-axis (7--9, total age; 5--6, lake period; 2--3, river period).

had lived in the river, the smaller was its ultimate size, although the downstream migrants were larger. Thus, the body length as defined by Smitt (ac) of eight-year-old fish was 86.8 cm when 2 years had been spent in the river and 82.3 cm when 3 years had been spent in the river; the corresponding lengths for nine-year-old fish were 90.5 and 86.5 cm (table 21). The reason here is that fish which migrate downstream at 2 years have an advantage of one feeding season.

If, however, we take fish with a different river age but the same duration of the feeding period, no tendency toward faster growth is found in

fish with a river age of 3 years by comparison with fish with a river age of 2 years despite the greater size of the downstream migrants (figs. 19--21).

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The same feature is observed in the group with a river age of 4 years. Growth in the feeding period is therefore not dependent on the initial size, although survival rate is dependent on it. The ultimate size is slightly greater in fish with a lake age of 6 and 7 years than in fish with a lake age of 5 years, although the latter grow slightly faster. This is apparent from table 22 and fig. 22, in which average data are given for the river period and for a feeding period of equal duration for the groups 2+5 and 3+5, 2+6 and 3+6, 2+7 and 3+7. Males grow noticeably faster than females (table 23).

This feature was taken into consideration in the compilation of table 21, where an equal number of males and females (13 of each) was taken for the most abundant age groups (2+5, 6, 7 and 3+5, 6, 7).

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The practical conclusion which stems from the distinctive features of growth is not an original one: in artificial culture of the salmon transition of the fingerlings to the downstream-migrant state must be stimulated at the earliest possible age -- at 2 years, and even better at 1 year.

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Data on length increase alone are not sufficient for the assessment of weight increase, which is intensified in the second half of the feeding period, in contrast to length increase. The mistaken view of a number of authors that weight increase is sharply reduced with age is based on a failure to allow for differences in the nature of growth in weight and length.

If the alteration in the relationship between body length and weight is traced in the salmon, it may readily be noted that this relationship is far from linear (fig. 23) and that young fish have a more fusiform body than those

Таблица 21

Темп роста (длина *ac*, см) шуйского лосося (по обратному расчету) по материалам 1959 г.

3) Число лет		4) Возраст, годы											7) Число рыб
		1	2	3	4	5	6	7	8	9	10	11	
5) реках	6) озерах												
		2	4	3.84	13.4	34.6	42.3	61.0	82.5	—	—	—	—
5	6.85		13.7	33.7	46.0	60.2	72.8	82.8	—	—	—	—	26
6	6.25		14.0	29.8	42.5	54.0	65.9	77.5	86.8	—	—	—	26
7	6.38		16.7	30.4	40.3	53.0	62.3	74.5	82.5	90.5	—	—	26
8	7.85		16.7	31.0	38.0	48.7	58.5	67.0	78.0	87.5	93.0	—	3
3	9	5.50	15.3	28.5	38.5	49.0	56.5	63.0	71.0	77.5	83.0	86.0	1
	4	3.90	8.1	13.4	35.3	55.0	65.3	76.8	—	—	—	—	2
	5	5.60	10.3	17.4	37.1	48.3	61.3	71.5	82.3	—	—	—	26
	6	5.80	11.4	17.1	36.2	47.5	58.3	70.0	80.0	86.5	—	—	26
4	7	5.25	9.9	15.1	35.6	45.5	54.8	65.8	74.3	83.3	88.5	—	26
	4	5.00	10.4	12.6	16.4	33.8	51.5	72.5	85.0	—	—	—	1
	5	5.80	9.7	13.0	16.3	37.4	49.0	64.0	76.7	83.6	—	—	5
	6	4.81	10.2	13.6	18.4	37.4	47.5	62.0	76.2	83.7	88.0	—	2
												168	

Key to Table 21: 1. Table 21 2. Growth rate (length *ac*, cm) of the Shuya salmon (back calculated) from materials for 1959 3. Number of years 4. Age, years 5. In the river 6. In the lake 7. Number of fish.

close to maturity. But this signifies that the same length increase will be accompanied in fish of different sizes (ages) by a different weight increase. The graph was compiled solely for feeding salmon which had no spawning marks and which did not mature in the year when the material was collected; fish of the maximum weight (up to 10 kg inclusive) could have entered the river no earlier than the following year.

Such a graph may be used to reconstruct weight increase by back calculation of linear growth.

The weight increase (in kg) in the feeding period may be represented approximately as follows, with heavy averaging (data for the entire

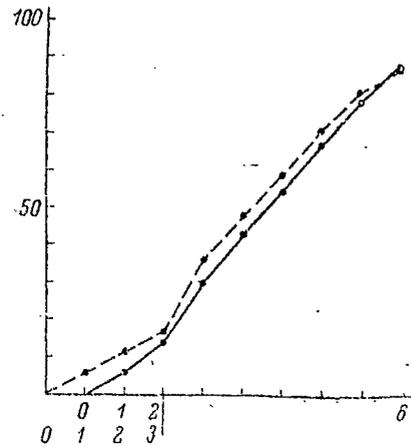
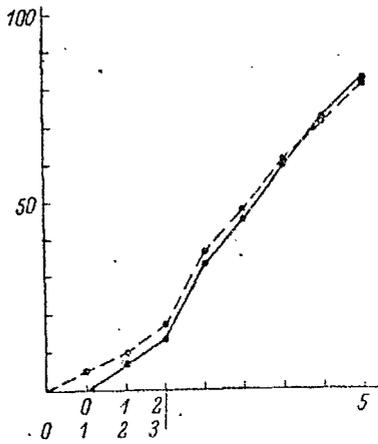


Fig. 19. Growth of the age groups 2+5 and 3+5. Age in years along x-axis; body length as defined by Smitt (ac), cm along y-axis.

Fig. 20. Growth of the age groups 2+6 and 3+6. Key as in fig. 19.

Таблица 22

2. Линейный рост (длина ac, см) лосося в реке и в озере (по обратному расчислению, 156 экз., 1959 г.)

3 Речной период, годы		4 Средняя длина лососа	5 Озерный период, годы						
2	3		1	2	3	4	5	6	7
6.5	5.5	15.6	35.4	47.1	60.7	72.1	82.5	—	—
14.8	10.5		33.0	45.0	56.1	68.0	78.8	86.6	—
	16.5		33.0	42.9	53.9	64.0	74.4	82.9	89.5
6 Средний рост . . .			33.8	45.0	57.0	68.0	78.6	84.7	89.5

Key to Table 22: 1. Table 22 2. Length increase (length ac, cm) of the salmon in the river and in the lake (back calculated, 156 fish, 1959) 3. River period, years 4. Mean length of downstream migrant 5. Lake period, years 6. Mean length increase.

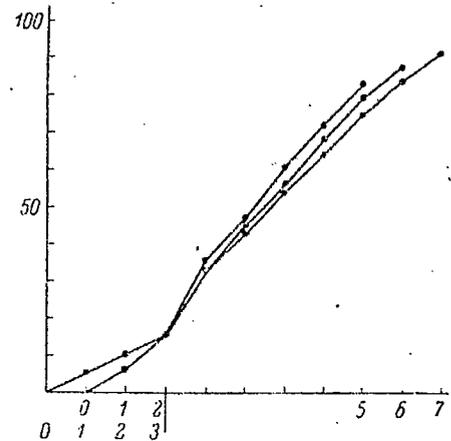
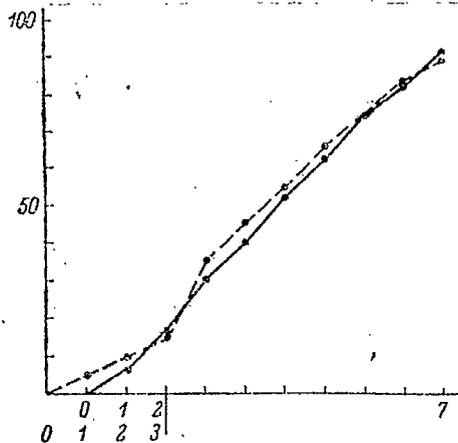


Fig. 21. Growth of the age groups 2+7 and 3+7. Key as in fig. 19.

Fig. 22. Growth with a feeding period of 5, 6 and 7 years. Key as in fig. 19.

population).

0+	1+	2+	3+	4+	5+	6+
0.4	1.0	2.0	3.5	5.5	6.5	7.5

According to our materials, the relationship between the length and weight increase of the salmon in the feeding period appears as follows (fig. 24). The total increase in length and in weight follows a practically parallel course until the very end of the feeding period, after which loss of weight commences in connexion with the spawning migration. Conversely, growth rates (increments of length and weight) vary "independently" of each other: the most rapid increase in length during the first season is accompanied by the least increase in weight. From the third to the fifth season inclusive the rate of length increase remains practically unaltered, but there is rapid increase of weight at this time. Both rates decline after the fifth season, apparently in

Таблица 23

2 Темп роста (длина *ac*, в см) самцов и самок шуйского лосося (по обратному расчислению) по материалам 1959 г.

3 Число лет		6 Пол	7 Возраст. годы									8 Число рыб
4 реч-ных	5 озерных		1	2	3	4	5	6	7	8	9	
2	5	♂♂	7.4	13.8	35.2	46.5	63.0	76.0	86.0	—	—	13
		♀♀	6.3	13.7	32.2	45.5	57.5	69.5	79.5	—	—	13
	6	♂♂	6.2	14.0	30.5	44.0	56.0	69.5	81.5	90.0	—	13
		♀♀	6.4	14.1	29.0	41.0	52.0	62.3	74.0	83.5	—	13
	7	♂♂	7.0	19.0	32.2	43.0	57.0	66.0	80.0	88.0	94.0	13
		♀♀	5.8	14.4	28.6	37.6	49.0	59.0	69.0	77.0	87.0	13
3	5	♂♂	5.6	10.4	17.7	38.8	51.0	63.0	74.0	86.5	—	13
		♀♀	5.6	10.2	17.0	35.4	45.5	59.5	69.0	78.0	—	13
	6	♂♂	6.5	11.4	17.4	37.6	51.0	63.5	77.0	86.5	91.5	13
		♀♀	5.1	11.3	16.8	34.8	44.5	53.0	63.0	73.5	81.5	13

Key to Table 23: 1. Table 23 2. Growth rate (length *ac*, in cm) of male and female Shuya salmon (back calculated) from materials for 1959 3. Number of years 4. In the river 5. In the lake 6. Sex 7. Age, years 8. Number of fish.

connexion with the approach of maturation.

The following approach was used for comparative estimation of the weight increase of individual stocks in the feeding period. Mean annual weight increments were calculated from the mean weight of the recruits and the mean duration of their feeding period. The weight of downstream migrants was not taken into consideration, since its value falls within the range of error in weighing. It was found that the Shuya salmon had the best growth rate, with the Vodla salmon in second place, and that growth was worse in the Pyal'ma salmon for which the mean annual weight increment was approximately 20% less than for the Shuya salmon (table 24). However, even the Pyal'ma salmon grows

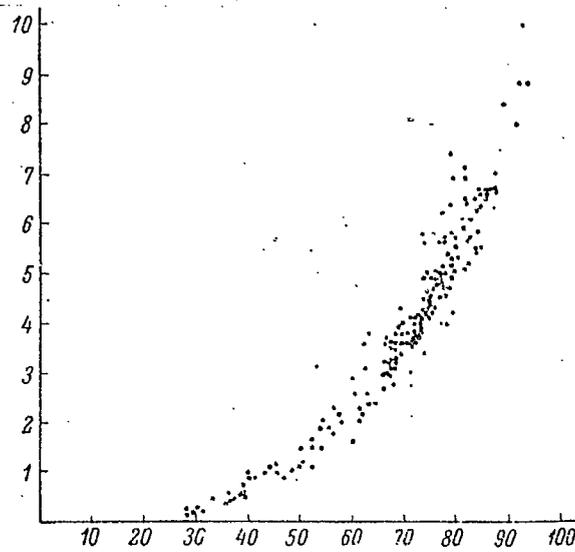


Fig. 23. Relationship between weight and body length (ac) in the feeding salmon of Lake Onega. Body length as defined by Smitt (ac), cm along x-axis; weight, kg along y-axis.

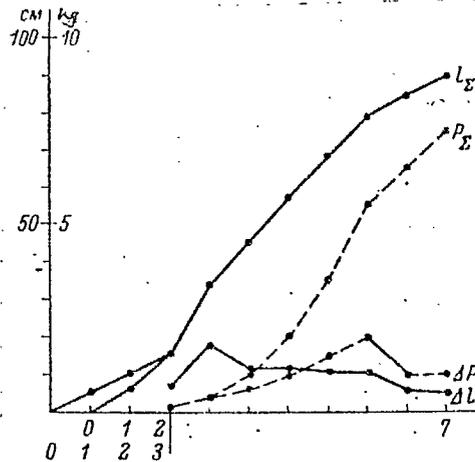


Fig. 24. Relationship between length increase and weight increase of the salmon in the feeding period.  $l_{\Sigma}$  -- total length increase, cm;  $\Delta l$  -- growth rate (increments), cm/yr;  $P_{\Sigma}$  -- total weight increase, kg;  $\Delta P$  --

growth rate (weight increments), kg/yr. Age, years along x-axis; length, cm and weight, kg along y-axis.

Таблица 24

## 2 Средний годовой привес (кг/год) лосося разных стад

3 Река	1943 г.	1949 г.	1963 г.	1964 г.	1965 г.
4 Шуйа . . .	$\frac{6.37^*}{5.42} = 1.17$	$\frac{6.70^*}{5.41} = 1.24$	$\frac{6.24}{5.18} = 1.20$	$\frac{5.91}{5.21} = 1.13$	$\frac{5.92}{5.46} = 1.08$
5 Водла . . .	—	—	$\frac{6.55}{6.14} = 1.07$	$\frac{5.57}{5.84} = 0.96$	$\frac{5.43}{5.65} = 0.96$
6 Пяльма . .	—	—	$\frac{4.59}{5.0} = 0.92$	$\frac{4.72}{6.13} = 0.92$	$\frac{5.01}{5.17} = 0.97$

7 \* С остатком, но доля его мала — 5.2% и 15.6%. В числителе дроби — средний вес рекрута, кг; в знаменателе — средняя продолжительность нагульного периода, годы.

Key to Table 24: 1. Table 24 2. Mean annual weight increase (kg/yr) of the salmon of different stocks 3. River 4. Shuya 5. Vodla 6. Pyal'ma 7. \* Including the carry-over, but its proportion was small (5.2 % and 15.6 %). Mean weight of a recruit, kg in the numerator of the fractions; mean duration of feeding period, years in the denominator.

far faster than any other Karelian freshwater fish.

It is at present impossible to say anything definite concerning the causes of difference in the growth of the different stocks. The matter may possibly have to do with different feeding grounds, but there is another suspicion in relation to the Pyal'ma salmon (see below). In the case of artificial salmon culture it must be borne in mind that the Shuya stock is economically more advantageous because of faster growth.

Z. V. Prozorova (1951) noted significant differences in the rate of length increase when she compared her materials with those of M. B. Zborovskaya (1935). She related these differences to an improvement in the food supply of

the salmon due to the decline in vendace and smelt fishing during the war years. However, length increase is a very poor indication of the real situation. In such cases it is more convenient to use the mean weight increase of recruits over the feeding period, which is an overall indication of living conditions, including the availability of food. If significant differences are found in the weight increase in different years, the year of the feeding period in which the deviation of growth (from the long-term norm) occurred may be established by back calculation, i.e. this deviation may be related to the ecological background.

#### IX. Morphological Description of the Salmon.

An enthusiasm for biometric analysis without the use of other criteria has led to the establishment of a multitude of different taxa of rank below the species, including subspecies and forms below subspecies ("infrapodvidovye"), and this has led to considerable confusion in systematics. A clear example is the situation with whitefishes, among which up to a hundred subspecies, varieties, forms, races and breeds have been distinguished within the USSR alone. In a number of instances descriptions have been given not only of individual populations, but of their constituent stocks.

There are many grounds for doubting the taxonomic value of morphometric analysis in the study of the salmon. The proportions of the body vary greatly in fish of different sizes and age. In the past this has even led to salmon of different development stages being classified as different species (Richardson, 1836) or to uncertainty as to how to classify them (Günther, 1866). There is overlapping of almost all the characters of the salmon and the trout. Smitt (1895) wrote in this connexion: "The relationship between these forms (between S. salar and S. trutta) is the same as that between

different age groups and between the sexes" (re-translated from the author's Russian translation with brackets inserted by the author -- translator). All these difficulties have been best set out by K. F. Kessler (1864, p. 163).

I shall take the liberty of giving his statement in full:

"Fish belonging to this genus (Salmo -- Yu. S.) are subject to very considerable variations in body constitution and in colour, variations which are related partly to their age and sex and partly to the properties of the waters which they inhabit; but, furthermore, immature fish which cannot be separately distinguished are frequently found among them and these, in their turn, are more or less different from fertile fish which also cannot be distinguished. For these reasons great difficulties are encountered in the identification and description of species of this genus and misunderstandings and contradictions have frequently arisen between zoologists in this respect; in particular, fish of different ages and of the same species have often been classified as belonging to different species."

V. V. Abramov (1953), who studied the development of the spawning colours in Pacific salmon, established that almost all the morphological characters undergo modification in the post-spawning condition. The snout-to-vent length is, of course, relatively invariable and only the post-dorsal distance and the depth of the caudal peduncle remain. Abramov considers that these characters may be used for the analysis of races and to establish local stocks. However, these three characteristics are evidently too few for such purposes.

This is why morphological analysis must be used very circumspectly in the study of salmon. It is far from invariably that the test of statistical significance ( $\text{diff} \geq 3$ ) will reflect the real biological differences which should be taken as the basis.

Furthermore, it is far from clear to what extent ordinary measurement errors are capable of affecting the end result. Accuracy is reduced both in the measurement of the smallest fish (the relative error is increased even when the absolute magnitude of the error is slight) and in measurement of the largest fish (owing to the readjustments of the calipers). The result will also be slightly different in measurement of the freshest fish (some "spreading" of the fish owing to the mobility of the tissues which yield under the calipers) and in the measurement of rigid fish (muscle contraction in frozen and preserved fish; the "accuracy" of the actual measurement is higher in such "hard" fish). Since the absolute magnitude of the discrepancy in the means which are compared is usually very slight, these measurement errors may yield quite statistically "significant" differences if the requirement of uniformity has not been observed in collection of the material.

Great doubt attaches to the value of such a character as eye diameter (horizontal and vertical): firstly, the actual measurement of the eyeball cannot be very precise; secondly, the probability of artefact is very great. The point is that salmon taken from the trap are killed by a blow on the head, as a result of which even if the eyes do not emerge completely from the sockets, the diameter of the eyeball is invariably increased. The orbital diameter would therefore be a far more reliable character since the bone may be measured with greater accuracy (the measurement of fixed points).

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Finally, body length as defined by Smitt (ac), which is taken as a standard for comparison, cannot be regarded as satisfactory since it includes the length of the head, which varies strongly with age (especially in males). Only comparison of the snout-to-vent length\*(the length of the backbone) can yield a true picture of the variation of proportions. Americans turned to this standard 30 years ago (Davidson and Shostrom, 1936), but it has regrettably not yet established itself with us, despite the recommendations of I. F.

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\*Translator's note. Term taken from Fish. Res. Bd. Circular No. 65. Incorrect?

Pravdin (1929, 1949), which have been used by the American authors just cited.

By some strange concatenation of circumstances the salmon has avoided the lot of whitefishes. Moreover, until now there has still not been a detailed morphological description of its lake form, especially at the level of populations and stocks. K. F. Kessler (1868) compares the colouration of the Onega and Ladoga salmon. Mean values of some meristic and morphological characters are given for both sexes combined on the basis of M. B. Zborovskaya's materials in a paper by I. F. Pravdin (1954), but there is no indication of the river of the stock and no description of the material (amount and the stage of maturity of the fish).

We have at our disposal fairly extensive material for a morphological description of the stocks of the Shuya, the Vodla and the Pyal'ma (more than 300 fish). Only mature migratory fish in stage III of maturity were taken for the measurements. An approximately equal quantity of females and males was taken for the general description (of both sexes), since there are already perceptible differences between them even in stage III of maturity, although it was still a long time before the appearance of spawning colours -- the collections were made between May and July. Because it is impossible to make full use of all the material here, certain information which is given (on the Shuya stock, table 25) is of a provisional nature. All that can be stated is that no significant difference was discovered between the sexes in meristic characters. The apparent reduction of the snout-to-vent length in males (diff = 9) is due to the fact that males have a larger head. This is an example of the way in which the accepted standard (ac) reflects actual relationships in an inverted form. It is for the same reason that no differences are detected between the sexes in the length of the body minus the caudal fin (ad), since the head is included in both lengths (ac and ad). The value

obtained for the length ad is in full agreement with that established by D. K. Khahturin (1965) for the salmon of the Pasha and the Oyata (Lake Ladoga).

Таблица 25  
 2) Некоторые морфологические признаки лосося р. Шуй в средних показателях

3) Признаки	4) Оба пола (59 экз.)		7) Самки (27 экз.)	8) Самцы (32 экз.)
	5) колебания	6) средние		
9) Длина тела по Смитту (ac), см	75.5—97.0	86.4	83.7	89.9
10) Число ветвистых лучей:				
in P	12—14	12.76	—	—
in V	7—9	7.95	—	—
in A	7—9	7.22	—	—
in D	9—11	10.51	—	—
11) Формула боковой линии	116 $\frac{21-27}{21-26}$ 122	118.54 $\frac{24.00}{24.20}$	—	—
12) Чешуй по боку хвостового стебля	28—33	30.30	—	—
13) Жаберных тычинок на 1 дуге	18—22	20.02	—	—
14) в % длины тела по Смитту:				
15) длина туловища (od)	64.7—76.1	71.99	73.56	70.72
16) длина тела без С (ad)	82.6—97.8	93.39	93.47	93.33
17) длина рыла	7.1—10.3	8.68	7.77	9.44
18) диаметр глаза горизонтальный	1.9—2.5	2.25	2.24	2.26
19) заглазничный отдел головы	10.8—13.2	12.11	11.87	12.32
20) длина головы	20.1—24.7	22.62	21.42	23.54
21) длина верхнечелюстной кости	7.5—9.6	8.42	7.99	8.78

Key to Table 25: 1. Table 25 2. Some morphological characters of the salmon of the Shuya River expressed as mean characteristics 3. Characters 4. Both sexes (59 fish) 5. Range 6. Mean 7. Females (27 fish) 8. Males (32 fish) 9. Body length as defined by Smitt (ac), cm 10. Number of branched rays 11. Lateral-line formula 12. Scales alongside of caudal peduncle 13. Gill rakers per one arch 14. As percentages of body length as defined by Smitt: 15. Snout-to-vent length (od) 16. Body length minus C (ad) 17. Snout length 18. Horizontal diameter of eye 19. Postorbital

head length 20. Head length 21. Length of maxillary.

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It is at present impossible to make a convincing comparison of the Shuya, Vodla and Pyal'ma stocks by morphological characters. The point is that the actual relationships will be distorted owing to the different sizes of the salmon of these stocks, especially because the indices were calculated in relation to body length as defined by Smitt. Reliable comparisons may be made only when the snout-to-vent length has been taken as the basis, as has been proposed by I. F. Pravdin.

X. The Possibility of Infringement of the Reproductive  
Isolation between the Salmon and the Trout.

The demands which trout and salmon make on spawning conditions differ perceptibly, as is also reflected in the use of the terms "trout" and "salmon" rivers. Should both fishes enter a single large "salmon" river, their spawning grounds do not coincide even here: the trout breed in the shallow tributaries of the main river, principally in those which join the river not far from its mouth, since the trout (sea trout) in general makes shorter migrations than the salmon. The quantity of trout in large salmon rivers is very small. All these features are to be observed not only in the basin of Lake Onega (and Lake Ladoga), but also in the basins of the Baltic, White and Barents Seas. /102/

The situation may be different in small rivers. In the Pyal'ma, for example, the relative abundance of the trout is very high. Its main spawning grounds are situated in the upper reaches of the main river, to which the salmon does not go for some reason. In addition to these spawning grounds

the trout also utilizes streams which flow into the lower reach of the river, in the zone of the salmon spawning grounds. In years when there is little water and these tributaries dry up, and when not only the spawning of the trout but the entry of the trout into them becomes impossible (as happened, for example, in 1963 and 1964), the trout lays its eggs in the salmon spawning grounds in the main river. The possibility is not excluded that hybrids will occur when this happens. How this may occur is discussed in the section on spawning.

It is not by accident that this question has arisen. The point is that the Pyal'ma salmon has some features which cast doubt on its purity as a species. In general, there are references to natural hybrids between salmon and trout in many publications, especially foreign ones. There is an interesting statement in a paper by V. A. Abakumov (1960) to the effect that hybrids have not been found in the large rivers of the Baltic region (Daugava, Gauya), in contrast to small rivers in which the spawning grounds are superimposed when discharge is reduced, i.e. a situation similar to that created in the Pyal'ma.

This is a very interesting question and one of practical importance. A reliable method, for preference karyological analysis, is needed for its solution. Other stocks apart from the Pyal'ma salmon are in need of such verification. This applies not only to the Onega population, but also to the populations of the northern lakes (Kuito, Topozero, Nyuk).

Chapter 4

SALMON FISHING, CATCHES AND THE  
STATE OF THE SALMON STOCKS

I. The History of the Development of the Salmon Fishery and Catches.

Fish entering the rivers are readily accessible even to the most primitive fishery. It is not accidental that there are among the neolithic rock paintings at Besov Nos (2nd--3rd millennium B.C.) drawings of the burbot (catfish, in the opinion of Lebedev, 1960), sterlet, apparently sturgeon and some kind of salmonid. There are also drawings of fishing gear -- a harpoon and a 3-pronged fish spear. A. M. Linevskii (1939), who interpreted these petroglyphs, also considers that there may be a hook and line, a basket trap and a trap fence.

The first reference to fishing in the Mnevetskii rapid on the Vodla River is to be found in the cadastre of Yurii Saburov (1496); (cited from Pushkarev, 1900a), in which there is also a reference to the levying of quit rent in salmon and whitefish and to the existence of the hamlet of Shuiskii pogost (Shuya graveyard), around which a trap fence was later used for fishing (references in the books of Andrei Likhachev, 1563 and Nikita Panin, 1627--1629).

All the fishing places were re-enumerated in 1563 and a tax was imposed. This is evidently the first statement of which fish species were caught in the fishing places and with what fishing gear, but there is no indication of the size of the catches. Salmon were caught in the Lososinka, the Shuya and the Suna, in the Sandal stream and in Lake Sandal, in Lake Lizmoo (Lizmoozero), in an inlet on the Cherka (Chorga) and in the Sosnovets, in Lake Onega around Klimenetskii Island, in the Elovets, in the Mnevets rapid (Vodla),

in the Cholmozha (Nemina ?), the Pyal'ya (Pyal'ma ?), in the Sukhoi navolok (translator's note -- navolok is a dialect word for a shallow lake produced by the spring flood), in the Andoma, the Vytegra and the Megra. Fishing gear: fences ("stakes"), of which there were several in the Shuya ("stakes" are also noted for the Kumsa, Cholmozha, Fyal'ya, Nikema, Suna, Vodla and Andoma Rivers; whitefish nets and harpoons, river and lake trap nets, "trains"<sup>1</sup> and undoubtedly fish spears, although they are not mentioned.

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<sup>1</sup> A "train" (poezd) or "belt" (poyas) is a small trap net for catching salmon in rapids.

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We do not know the size of the salmon catches or how they were obtained. It is mentioned in the Tikhvin Customs Book that the goods brought to the fair by Andrei Chusov, a leading Olonets merchant, included "...two barrels of Shuya whitefishes, 17 fresh Onega salmon and 17 cured salmon..." (cited by Müller, 1947), but this fact does not tell us much. /104/

Sawmills and metallurgical plants using water power were constructed on a number of rivers in the 18th century, especially in its second half. Apart from hindering the upstream migration of fishes, dams can be used to catch them, and this undoubtedly happened at the time.

There is information on fishing only for 1785, when N. Ya. Ozeretskovskii and G. R. Derzhavin carried out an investigation of the territory almost simultaneously and quite independently. N. Ya. Ozeretskovskii records among the fishing gear "kerevody"<sup>1</sup>, which had not previously been mentioned, and hook and line. He reports that salmon, trout, char, whitefish and pike

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<sup>1</sup> A "kerevod" is a single-winged lake net used in Karelia.

were sold salted in St. Petersburg, that a trap fence was erected in the Pyal'ma where "many whitefishes, salmon and trout were taken in the spring and autumn", and he gives other interesting information.

G. R. Derzhavin gives a list of the food fishes of Lake Onega in his "Diary" (Pimenov and Epshtein, 1958) and describes the fishing at Podporozh'e: "...before it was forbidden to erect trap fences, there was very successful fishing for salmon, whitefishes, bream, pike, burbot, pike-perch and other fishes; large "muzzles" (drag nets) were used for fishing and up to 500 whitefishes and sometimes up to 30 poods of salmon (translator's note: 1 pood = 36 lbs.) were taken in a day, but now the catch is extremely small." It would appear from what follows that the ban was imposed in 1785, but the reason is not stated. This measure was apparently enacted in the interests of the developing timber industry and of logging, which was hindered when the rivers were sealed off all across. The erection of trap fences all across logging rivers was prohibited for the same reason in the 1870s (Pushkarev, 1900a). We may therefore agree with N. Ya. Danilevskii (1875) that logging prevented overfishing at that period and thus helped to maintain salmon stocks.

There is no information on fishing for the first half of the 19th century.

K. F. Kessler (1868) noted a heavy reduction of salmon in the Povenchanka due to the construction of a sawmill.

According to N. Ya. Danilevskii (1875), the salmon catch in good years reached 800 fish or approximately 150 poods at the Pyal'ma trap fence and 30 poods at the Nemina fence; up to 1862 trap fences were erected all across these rivers. The salmon catch in the Vodla at this time was at least 400 poods a year. Danilevskii noted the strong development of fishing with

large drag nets known as "matki" in imitation of the Ladoga fishermen.

In 1854 drag nets appeared in the Suna, where they replaced the trap fence which previously existed in the river. Their use subsequently spread throughout the entire lake and they became the principal fishing gear for the in-shore salmon fishery.

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/ Таблица 27

2 Регистрируемые уловы лосося в Онежском озере за 1930—1965 гг., ц (по данным Карелрыбвода и Карельского отд. ГосНИОРХ)

3 Год	4 Улов		3 Год	4 Улов		3 Год	4 Улов	
	5 за год	6 средне- годовой		5 за год	6 средне- годовой		5 за год	6 средне- годовой
1930	272	} 197	1946	280	} 233	1956	166	} 174
1932	247		1947	272		1957	189	
1933	193		1948	174		1958	130	
1934	186		1949	217		1959	221	
1935	86		1950	222		1960	166	
1936	150	} 226	1951	204	} 229	1961	69	} 95
1937	182		1952	184		1962	71	
1938	177		1953	319		1963	109	
1939	305		1954	233		1964	132	
1940	321		1955	204		1965	93	

7 Примечание. Данные об уловах за 1933--1940 гг. взяты из диссертации М. Б. Зборовской (1949).

Key to Table 26: 1. Table 26 2. Salmon catches in Lake Onega according to data in the "Olonets Gubernia News" (taken from Zborovskaya, 1948, p. 140)  
 3. Year 4. Catch 5. Over the year, in poods 6. Over the year, in centners 7. Mean annual catch in centners 8. Comment 9. 1876 -- "abundant catch of fish". 10. 1879 - "more successful than in previous years".

The first estimates of the salmon catch for the entire lake appeared in the "Olonets Gubernia News"; we have data only for the period 1875--1890 (table 26). The catches recorded for this period are no different from the

catches in the period 1930--1960 (table 27), but what the actual catch was is not known. Because of difficulties in sale a considerable part of the catch was undoubtedly consumed in the localities.

The establishment of regular communication with St. Petersburg by steamboat and the improvement of marketing led to extensive development of the salmon fishery. When the salmon fishery was at its height in the 1890s salmon catches in Lake Onega reached 1000 centners, as may be assessed from the data of N. N. Pushkarev (1900a). The figure given above should be increased because Pushkarev did not investigate such important salmon fisheries areas as the Shuya, Suna, Lizhma and Andoma Rivers, Chorga and Unitskaya Bays and the region of Cape Besov Nos, but it should evidently not be increased to more than 1500 centners.

Salmon were fished in the following ways at this period:

- 1) fishing for migratory salmon with large drag nets in the river mouths and with trap fences in the rivers;
- 2) special types of net fishing<sup>1</sup> in pools occupied by the salmon on arrival; fishing with "trains" (small trap nets), trap nets and fixed gill nets in the rivers;

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<sup>1</sup> Kalezhen'e and brozhenie are the local terms for fishing with special nets ("kalega" and "brodil'naya" net) practised in small and medium-sized rivers.

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- 3) harpoon fishing for spawning and spawned fish;
- 4) fishing for feeding salmon (largely immature fish) in the open lake using "garvy" (large-mesh nets for use in the upper horizons of the water) and "prodol'niki"<sup>1</sup>, mainly along the western shore of the lake around Brusno Island.

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<sup>1</sup> Translator's note. No equivalent found; presumably a long thin net.

Таблица 26

2 Уловы лосося в Онежском озере, по данным «Олонецких губернских ведомостей» (по Зборовской, 1948, стр. 140)

3 Год	Улов 4			Примечание 8
	за год, 5 в пудах	за год, 6 в ц	средне- годовой, в ц 7	
1875	1025	169	} 189	1876 г. — «улов рыбы обильный». 9 1879 г. — «более удачный, чем предыдущие годы». 10
1876	1196	198		
1879	1248	206		
1880	1173	184		
1881	1516	250	} 223	—
1882	1209	199		
1883	1335	220		
1889	1082	178	} 172	—
1890	997	165		

Key to Table 27: 1. Table 27 2. Salmon catches recorded in Lake Onega in the period 1930--1965, centners (100 kg) (from the data of Karelyrbvod and the Karelian Department of GosNIORKh -- the State Scientific Research Institute for Lake and River Fisheries) 3. Year 4. Catch 5. Over the year 6. Mean annual 7. Note. Data on catches for the period 1933--1940 were taken from the thesis of M. B. Zborovskaya (1948).

Trap fences for the catching of salmon and other fishes were constructed in 1895 in the Shuya (at the village of Nizhnyaya), in the Suna (below the sawmill dam) and in the Shoksha and the Pyal'ma. Trap fences were prohibited in the Nemina from the 1870s because of logging. "Considerable quantities" of salmon were caught in Cholmuga Bay and in the Nemina in the spring and autumn; including trout the catch amounted to 50 poods a year. Fish stocks in Cholmuga Bay were reduced by overfishing and pollution of the waters of the bay and its tributaries by the floating of timber which had not

been barked, the amount of which increased every year. The principal salmon catch in the Pyal'ma was taken in the spring and the autumn. The salmon run occurred immediately after the ice run, after May 9 (May 22 by the new calendar) and lasted until "Peter's Day" (July 12 by the new calendar). A catch of up to 440-550 fish was taken at this time with "kalega" nets and a further 90 fish in drag nets near the mouth. During the low-water period the salmon were "stalked" in the pools and those which had escaped the "kalega" fishing were taken. From August until the late autumn fishing was carried out with trap fences erected near the mouth. In the opinion of Pushkarev (1900a), the salmon was completely fished out in the Pyal'ma, since adult fish and spawned fish migrating downstream were not found here: "The Pyal'ma River is a grave for all the fish which enter it...The present fishing must be regulated."

In 1871 there were trap fences in the Vodla in many rapids above the Mnevetskii rapid (Polyakov, 1873), and they were used for catching fish migrating both upstream and downstream, for example in the Padun rapid. /107/

Although fishing for feeding salmon is highly destructive, it was of the greatest economic importance in the 1890s. Pushkarev wrote: "...garvy fishing should be regarded as one of the most important types of fishing...". This type of fishing, which constituted the bulk of the salmon catches at this period, yielded between 400 and 1000 centners, on average more than 500 centners (figure arrived at by conversion of the value of the catches given by Pushkarev).

At the beginning of the present century there was a sharp reduction of catches which was noted by a number of investigators (Pushkarev, 1914a, 1914b; Petrov, 1926; Tikhii, 1931a). N. N. Pushkarev (1914b) wrote that fishing with garvy nets had practically ceased along the western shore of Lake Onega and had been halved in other places. Fishing had therefore ceased in what had once been the main fishing grounds. Pushkarev, like other authors,

does not give precise figures for the catch throughout the lake and there are no such figures from the beginning of the 20th century until 1930. It should be noted that the statistics of catches were never satisfactory.

There is more or less reliable information for the period from 1930 down to the present, with the exception of the war years of 1941--1945. The most significant aspects of the salmon fishery during this period were:

- 1) the re-establishment of garvy fishing from 1932 in the area of Brusno Island; this fishing attained its greatest development in the post-war years and has been discontinued since 1958;
- 2) the use of trap nets in place of drag nets since 1953;
- 3) the institution of a number of conservation measures in the last decade.

Let us dwell on this last point in greater detail. Commercial and amateur fishing, including fishing with rod and line, has been prohibited in the rivers since 1956; this ban has been confirmed by the 1960 "Fishing Regulations". In 1958 an area in which garvy fishing was banned was designated in the area of Brusno Island. By the new "Fishing Regulations..." (1960) there is a general ban on the use of nets to catch feeding salmon in the lake. The main salmon catch is now taken with trap nets in the estuarine reaches no nearer than 1 km from the mouth. There was no limit on the number of traps before 1964 and this led to overfishing of the Shuya stock (Yu. A. Smirnov, 1964).

The use of trap nets for salmon fishing was begun in Lake Onega in 1948--1949, but these were initially only shore traps of the Kuban' River type. In 1953 the fishing brigade of A. A. Stafeev caught 70 centners of salmon by the middle of July with a single trap net in Logmozero (Shuya River). Such a successful catch enabled the fishermen to dispense with drag net fishing.

The fish industry took an interest in the development of the new type of fishing (Cherkasov, 1953). Since 1955 trap nets have been included in the gear of other fishing brigades operating around Solomennoye. Two types of trap nets are used commercially: two-pot deepwater nets ("giganty" -- "giants") and inshore single-pot nets ("Kuban River nets"). The number of both types of net continued to increase until 1960 (8 "giants" and 12 "Kuban River nets"), after which it remained at the same level. In 1964 Karelrybvod reduced the number of permitted places around Peskov. The traps from Peskov were shifted 1--1.5 km to the east of the Solomennoye Strait, to Loi Island, but there was hardly any change in the total number. The rate of exploitation was reduced by reduction in the number of traps at the point of greatest concentration of the fish in front of the river mouth (Solomennoye Strait).

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Trap nets did not begin to be used in the Shala until 1961; in 1964 and 1965 there were 4 of them (2 local brigades each had 2). Salmon continue to be caught about Pyal'ma with drag nets; the local brigade has still not received a trap net.

During the years since Pushkarev's investigation there have only been three occasions (1939, 1940 and 1953) when the salmon catch for the whole lake has exceeded 300 centners. In the last quinquennium catches have fallen to the lowest level over the whole time known to us (table 27 and fig. 25) and but for the ban on the taking of sexually immature salmon in the open lake, catches would have been even lower. This situation is characteristic not only for the lake as a whole, but also for individual stocks. It should be noted that the salmon fishery is now based on the stocks of three rivers -- the Shuya, the Vodla and the Pyal'ma. The Shuya stock is the most numerous. It has yielded catches of between 40 and 140 centners, on average approximately 80 centners (up to 1960) and no marked reduction in the abundance of the stock has been noted over a period of 30 years (from 1932 through 1960).

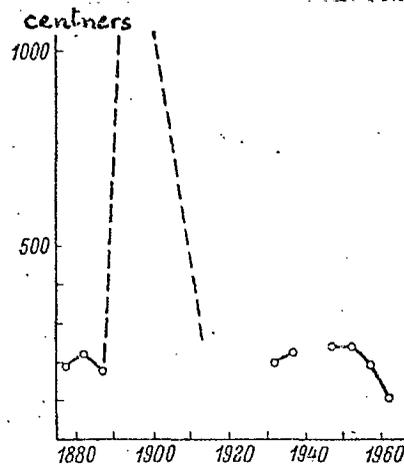


Fig. 25. Salmon catches in Lake Onega between 1875 and 1965.

Catches of the Shuya salmon have been divided into three groups on the basis of long-term data: high -- more than 100 centners, medium -- from 70 to 100 centners and low -- from 40 to 70 centners. However, there has been occasion in recent years to distinguish a new group of catches, namely "catastrophic" (less than 40 centners), which have been found to be considerably lower even than the mean low catches (table 28). As was to be expected, there has not been any increase in catches of the Shuya salmon in the subsequent years. On the contrary, there was a new decline to "catastrophic" beginning in 1967, which was a consequence of overfishing in 1959--1961 accompanied by a deterioration in the conditions of reproduction.

Salmon catches in the Pyla'ma River are summarized in table 29. The sharp reduction of catches in 1961 was due mainly to a reduction in the rate of exploitation owing to the banning of fishing in the river and in the lake within 1 km from the mouth. However, there was heavy overfishing in

Таблица 28

2. Уловы шуйского лосося в Петрозаводской губе, ц

3	Группа уловов	4	Год	5	Улов за год	6	Средний улов по группе	7	Число лет
8	Высокие		1939		102.4	}	121		3
			1940		140.4				
			1959		120.0				
9	Средние		1932		85.0	}	85		7
			1949		75.5				
			1950		79.5				
			1951		85.6				
			1956		84.0				
			1957		99.7				
			1960		85.5				
10	Низкие		1933		53.0	}	55		11
			1937		56.5				
			1938		55.5				
			1946		58.5				
			1947		69.5				
			1948		61.3				
			1955		64.6				
			1953		43.6				
			1963		61.0				
			1964		58.0				
			1965		59.0				
11	Катастрофические		1961		26.0	}	25		4
			1962		38.0				
			1967		30.5				
			1968		7.0				

Key to Table 28: 1. Table 28 2. Catches of the Shuya salmon in Petrozavodsk Bay, centners 3. Group of catches 4. Year 5. Catch over the year 6. Mean catch by groups 7. Number of years 8. High 9. Average 10. Low 11. Catastrophic.

1959 and 1960 which should have an effect on the state of the stock in 1967--  
--1970.

Since the end of the last century the main salmon fishing in the Vodla has been conducted around the mouth of the river, in the Shala district. According to the data of E. A. Veselov (1932), the catch was 992 kg in 1927,

1350 kg in 1928, 3179 kg in 1929 and 4491 kg in 1930. With these catches in mind, N. V. Logashev (1931) wrote: "Although the salmon catch has not been reduced in the last three years, it has declined by comparison with catches before the revolution."

The catch in 1932 was either 52 centners (Zborovskaya, 1935) or 70 centners (Zabolotskii, 1936). From 1948 through 1957 catches ranged between 10 and 40 centners and were on average 20 centners ("Lakes of Karelia", 1959). The catches for the period 1955--1965 are set out in table 30. /110/

2 Уловы лосося р. Пяльмы, ц (по данным Карелрыбвода) Таблица 29

3 Год	4 Улов						
1932	24	1948	23	1954	20	1958	10
1938	18	1949	11	1955	17	1959	34
1939	45	1950	29	1956	24	1960	33
1940	34	1951	25	1957	14	1961	5

5 Примечание. Данные за 1962--1965 гг. не репрезентативны.

Key to Table 29: 1. Table 29 2. Salmon catches in the Pyal'ma River, centners (data of Karelrybvod) 3. Year 4. Catch 5. Note. The data for 1962--1965 are not representative.

2 Уловы лосося в районе Шалы, ц Таблица 30

3 Место лова	1955 г.	1956 г.	1957 г.	1958 г.	1959 г.	1960 г.	1961 г.	1962 г.	1963 г.	1964 г.	1965 г.
4 Район устья Водлы . . .	11	5	5	7	12	12	20	17	7	21	15
5 Район Бесова Носа . . .	6 Нет данных						8	18	7	—	4

Key to Table 30: 1. Table 30 2. Salmon catches in the Shala district, centners 3. Locality 4. Around the mouth of the Vodla 5. Around Cape Besov Nos 6. No data.

The salmon catch in the Shala is mainly dependent at the present time on the catch of the smelt. The better are the runs of the smelt, the greater is the amount of attention and energy paid to catching it and the less are the possibilities for catching salmon. Salmon trap nets are not installed until the end of May--beginning of June during the smelt run. However, the mass run of the salmon into the Vodla is already ending at this time and later, from the second half of June, it is only feeding salmon which are caught along the Shala shore and then in small quantity. It may therefore be that the catches of recent years reflect not so much fluctuations in the abundance of the salmon as the smelt runs. The 1963 fishing season was particularly disastrous (owing to ice conditions, the abundance of the smelt and organizational failings) and the fishermen had no time for the salmon. The increase in catches from 1961 is to be explained by the use of trap nets, which have a higher catching capacity than the drag nets previously used. Very small quantities of salmon are also taken in smelt drag nets. Some of the Vodla salmon catch (migratory and feeding salmon) are taken around Cape Besov Nos, but feeding salmon from other rivers, for example from the neighbouring Andoma, may be present here. Once again fishing is heavily dependent on ice conditions, which were particularly unfavourable in both areas in 1963. One of the two trap nets near the mouth of the Vodla was destroyed by ice at the end of May in 1965 and this immediately had an effect on the catches.

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To judge by the proportion of the carry-over in the Vodla salmon stock, no more than 50 % of the fish are caught. The present fishery cannot therefore be regarded as a factor limiting the abundance of this stock.

In the past salmon and whitefish were the basis of fishing in the Suna and Nemina Rivers. In 1964 the salmon catch in the Chholmuga Bay area was only 1.3 centners (25--30 fish). It has been estimated by N. I. Kozhin

(1927a) that the catch in the Suna in 1926 was 21--23 centners, and that the salmon catch had been reduced by one third by comparison with the 1870s. Thirty centners were caught in 1930 (Zborovskaya, 1935), but this was the last considerable catch: no more than 4 centners were caught in 1932, 4 centners in 1953, 2 centners in 1955 and 3 centners in 1956. Traps were set in the river mouth in the years 1958--1962 to catch salmon spawners: in no year were more than 20 fish caught and in 1962 only 4 salmon were taken, after which the fish station on the Suna was closed.

Like the Suna and the Nemina, all salmon rivers apart from the Shuya, the Vodla and the Pyal'ma have lost their commercial importance. This is evident from the distribution of catches for the 1961 fishing season by areas of Lake Onega (table 31). The migratory salmon of the three main rivers accounted for 75 % (51 centners) of the total catch of 69.45 centners; the migratory salmon (Vodla and Andoma) is caught mainly in May around Cape Besov Nos (850 kg, 12 %) and in the Andoma area (280 kg, 4 %). The migratory salmon of the Suna accounted for 90 kg (1.3 %) and feeding salmon from the remaining parts of the lake accounted for 616 kg (approximately 8 %).

The restrictions on commercial and amateur fishing introduced from 1956 were the first measures to maintain salmon stocks in Lake Onega. However, it is clear that, given the present state of the spawning resources, these measures can do no more than halt a further decline in abundance<sup>and</sup>/are inadequate for the restoration of stocks. /112/

## II. The Causes of Reduction in the Abundance of the Salmon in Lake Onega.

Salmon stocks have been brought to their present state by the following causes:

Таблица 31

## 2. Распределение уловов лосося в Онежском озере в 1961 г., кг

3 Место лова	4 Месяцы							5 Улов за май-декабрь	
	V	VI	VII	VIII	IX	X	XI	6 в кг	7 в %, от общего улова
8 Шала . . . . .	1311	513	136	32	—	—	—	1992	28.7
9 Бесов Нос . . . . .	850	—	—	—	—	—	—	850	12.2
10 Петрозаводская губа . . . . .	615	1200	747	27	—	—	—	2589	37.3
11 Пяльма . . . . .	485	43	—	—	—	—	—	528	7.6
12 Район о. Брусно, Леликово . . . . .	—	—	6	—	—	—	—	6	0.1
13 Леликово . . . . .	—	—	—	11	143	11	—	165	2.4
14 Толвуйское Онего, Челмужи . . . . .	106	49	4	4	62	83	79	387	5.6
15 Суня . . . . .	—	—	—	—	90	—	—	90	1.3
16 Уницкая губа . . . . .	—	—	—	—	—	—	—	58	0.8
17 Андомский р-н . . . . .	280	—	—	—	—	—	—	280	4.0
18 Всего . . . . .	3647	1805	893	74	295	94	79	6945	

Key to Table 31: 1. Table 31 2. Distribution of salmon catches in Lake Onega in 1961, kg 3. Locality 4. Months 5. Catch for May--December 6. In kg 7. As a percentage of the total catch 8. Shala 9. Besov Nos 10. Petrozavodsk Bay 11. Pyal'ma 12. Around the Island of Brusno, 13. Lelikovo 14. Tolvuiskoe Onego, Chelmuzhi 15. Suna 16. Unitskaya Bay 17. Andoma area 18. Total.

1) alteration of the regime of the rivers and reduction of the spawning and rearing areas as a result of the construction of dams for power generation and logging and of the construction of other hydraulic engineering works;

2) pollution of the spawning rivers by logging waste;

3) irrational commercial fishing;

4) unchecked removals of spawners in the spawning grounds and what is loosely called "amateur" fishing for young salmon in the rivers.

Different combinations of these factors have had the effect that some rivers have completely lost their role in the reproduction of the salmon. The resources of spawning grounds have undergone considerable modifications since the last century; not only have the spawning and rearing areas been reduced, but there have been changes in their quality, not for the better.

Great harm has been done to salmon stocks by irrational fishing, i.e. by fishing for immature feeding salmon in the open lake with garvy nets and long nets ("prodol'niki").

K. M. Ber (1860) worked out principles on which fishing for Caspian diadromous fishes should be based: catching should be concentrated in the rivers, sufficient spawners should be let through to maintain stable stocks and, finally, sturgeon and other valuable fish should not be caught in the open sea. He wrote: "I regard it as my duty to warn against extending fishing too far out into the sea", by which he meant that removals of immature diadromous fishes should be limited. It is not only to the Caspian that these remarks of K. M. Ber apply.

It would seem that the "collapse" of catches in Lake Onega after 1900 should have dictated a cautious approach to the re-establishment of fishing for small salmon. Instead, however, it was recommended that fishing with garvy nets should be intensified (Pokrovskii, 1947; Pravdin, 1954), and this was done.

According to the evidence of N. N. Pushkarev (1900a, 1914b), the average weight of the salmon in the years when the fishery flourished was only 5--6 lbs., or 2--2.4 kg. This weight is an indication of the intensity of fishing for immature salmon, if it is borne in mind that the average weight of fishes maturing for the first time ranges in the different stocks from 4.5 to 6.5 kg and is as a rule not less than 4 kg. This explains the sharp decline

in catches after 1900; the industry had exhausted several generations of feeding salmon.

A clear idea of the composition of catches of feeding salmon is given by the materials of M. I. Tikhii (1931a, the table on p. 11) for the area of Andoma Bay where 48 centners were caught in 1929 in long nets ("prodol'niki"). According to these materials, the catches comprised fish weighing between 0.55 and 0.85 kg, on average 2.6 kg (sic), and fish weighing more than 4 kg accounted for only 17 %. It therefore follows that more than 1500 of the 1850 fish comprising a catch of 48 centners were sexually mature, i.e. that the quantity of young in the catch was more than 5 times the quantity of adult fish.

According to the data of P. E. Vasil'kovskii (1927), who visited the area of Cape Petropavlovsk, where salmon were caught with "kerevody" (single-winged lake nets) from August through November, the usual weight of the salmon in these catches was 2.8--3.2 kg.

There are also similar data for subsequent years. In 1932, when fishing was renewed in the area of Brusno Island, 27 centners were caught. The average weight was 3.5 kg and fish weighing more than 5 kg accounted for only 8 % (Zborovskaya, 1935, table on p. 272), i.e. the quantity of young was more than 10 times the quantity of adult fish: there were more than 700 young among the 770 fish caught.

In 1958, the year when this fishing around Brusno was banned, young accounted for from 50 to 90 % of the catch. Salmon which were feeding in the lake for the first summer were also found in the catch. These fish, which accounted for 13 % of the total catch, weighed between 200 and 500 g. The average weight in this year was 2.3 kg.

Such a low mean weight is an indication that all size-age groups are fished with practically equal intensity with this type of fishing. Although doubts may be expressed concerning this conclusion, it is supported by direct observations. Salmon which could have passed through the mesh are entangled in the nets by the jaws. It therefore happened that garvy nets with 80-millimetre mesh were equally efficient in catching adult salmon and smolts weighing 200 g or more.

Salmon feed in the lake for 6 years on average. Toward the end of the feeding season the eight groups in the lake range from 0+ to 5+ (lake age); fish of the oldest group enter the rivers in the spring of the following year.

Study of the survival of the pink salmon after downstream migration to the sea has shown that 77 % of the downstream migrants perish in the first 40 days and that 78 % of the remainder, or 18 % of the initial quantity of downstream migrants, perish in the following 410 days (Parker, 1965). Out of a total mortality of 95 % during the period spent in the sea, 81 % of the fish die during the first feeding season.

It is quite permissible to stipulate that all salmon which survive to the end of the first feeding season may reach maturity, i.e. that the "age pyramid" approximates to a column. When the level of reproduction is constant the abundance of all age groups of the feeding salmon will then be approximately the same. /114/

In such a situation each of the 6 age groups in the case of the Onega salmon should account for approximately 16.7 % of the number of feeding fish (excluding fish which have spawned and returned to feed). In the autumn of 1958 the group 0+ accounted for 13 % of the total catch and 14 % of fish which had not yet matured in the area of Brusno Island; these figures are close to

the stated figure of 16.7 %.

The mean weight of a fish in the catch is 3 kg only if all the age groups are equally exploited. The mean weight for different years which has already been given ranged from 2.0 to 3.5 kg. This indicates that immature fish accounted for up to 80 % on average in the catch of feeding salmon, which is 4 times the number of fish maturing for the following year (the 5+ group and part of the 4+ group).

The effect of this fishing may be approximately estimated by comparing catches in the area of Brusno Island and in Petrozavodsk Bay (table 32) and by using the mean weights to convert them to the number of fish caught.

Таблица 32

2 Уловы лосося, ц

Место лова 3	1948 г.	1949 г.	1950 г.	1951 г.	1955 г.	1956 г.	1957 г.	1958 г.	Сред- ний улов 4
<sup>5</sup> Район о. Брусно . . .	71	46	85	34	38	27	48	18	46
<sup>6</sup> Петрозаводская губа .	61	75	79	86	65	84	100	44	75

Key to Table 32: 1. Table 32 2. Salmon catches, centners 3. Locality  
4. Mean catch 5. Area of Brusno Island 6. Petrozavodsk Bay.

If the mean weight of a fish is taken to be 3 kg for the area of Brusno Island and 6 kg for fish entering the Shuya, we find that catches over the period under consideration, converted to the number of fish, are slightly higher in the first area (1530 fish) than in the second (1250 fish). It should be noted that the situation was in fact worse than in our calculations: the actual catch of feeding salmon was higher since the large number of undersized

fish and of fish which had perished in the nets and begun to rot, which is inevitable in such fishing, were not taken into store and were not recorded. Fishing of this type has been carried on in the Tolvuisloe Onego area and in other places, as well as around Brusno Island, but admittedly on a lesser scale. It is undoubtedly one of the reasons for the decline in catches which began in 1956, i.e. a situation similar to that at the beginning of the century. If this fishing had not been prohibited, there would evidently now be nothing to catch.

Another adverse feature of the fishery, in this case in relation to the Shuya salmon, is overfishing of the spawning stock, which was particularly heavy in the years 1959--1961 because rather too many trap nets were used, (Yu. A. Smirnov, 1964). In the following years the fishing rate was slightly lower: in 1962 because traps were broken by floating logs and towed rafts of timber, in 1964--1965 because of the limitations placed by Karelrybvod on the number of fishing places in the Peskov area. /115/

It must be stated that I. F. Pravdin (1957) warned against the excessive use of trap nets because these might disrupt salmon and whitefish stocks, but this warning was not heeded. At the same time Pravdin himself (1954) recommended that fishing with garvy nets should be intensified.

In the opinion of V. I. Lastochkin (1959), the Svir' River and especially the Vuoksa River, in which the spawning grounds are unaffected by hydraulic engineering works, are the clearest examples of the almost total destruction of salmon stocks as a result of overfishing with trap nets. These nets began to be used in Svir' Bay in 1950. Their high catching capacity led to a rapid increase in the number used, from 9 in 1951 to 74 in 1955. The largest catch, 700 centners, was obtained in 1952; thereafter catches began to decline rapidly, despite an increase in the number of trap nets, and had fallen

to 66.5 centners by 1957. In 1958 the fishing collectives themselves began to curtail fishing since it had become unprofitable. In 1958 the Svir' fish hatchery was itself obliged to organize special catching of spawners (these had previously been taken from commercial catches) and from that time down to the present no more than 10 spawners have ever been caught in a season. The Svir' stock, which was the largest of all the lake salmon stocks, was destroyed within 8 years of the intensification of fishing, i.e. within the cycle of one year-class.

The salmon of the Shuya River will apparently avoid such a fate since the use of trap nets was here begun later and certain limitations were placed on fishing in 1961 and in 1964--1965. Nevertheless, it is to be expected that the abundance of the stocks arriving at the river mouth in the period 1967--1970 will be extremely low owing to overfishing in 1959--1961. Even after 1970 catches are hardly likely to reach the level of average catches (over the period 1932--1960).

Under conditions in which commercial fishing is very intensive and few fish are let through to spawn, uncontrollable removals in the spawning grounds do particularly great damage, but unfortunately this cannot be assessed.

Another form of uncontrollable removal is fishing for salmon fingerlings. This made an appearance in Karelia at the end of the 1930s in connexion with the development of fishing as a sport, became widely prevalent in the post-war years and is still continuing although it is banned by the "Fishing Regulations..." (1960). An approximate estimate of amateur catches shows that several thousand fingerlings of the downstream-migrant size may be caught in a single river during the summer. At its present level this fishing does at least as much harm as the uncontrollable removal of spawners (Yu. A. Smirnov, 1965).

III. An Estimate of the Abundance of Omega Salmon Stocks.

A rough estimate of the abundance of individual salmon stocks may be given by a "number" scale:

- 1) the stock has disappeared completely (0);
- 2) the stock contains less than 10 or 10 fish (1--10);
- 3) tens--hundreds (10--100);
- 4) hundreds--thousands (100--1000).

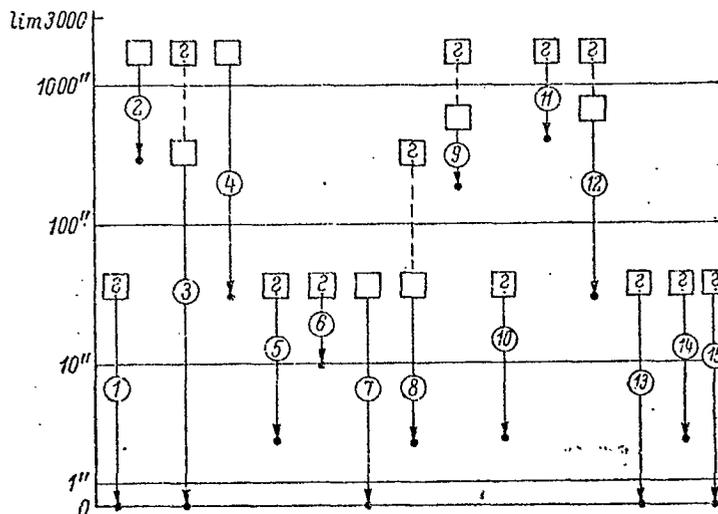


Fig. 26. Alteration in the abundance of salmon stocks.

1 -- Lososinka; 2 -- Shuya; 3 -- Suna; 4 -- Lizhma; 5 -- Unitsa;  
 6 -- Kumsa; 7 -- Povenchanka; 8 -- Nemina; 9 -- Pyal'ma; 10 --  
 Tuba; 11 -- Vodla; 12 -- Andoma; 13 -- Vytegra; 14 -- Megra; 15 --  
 Vodlitsa. Levels of abundance are plotted along the y-axis (a square denotes the abundance in the past and an arrow the present abundance).

A scale of this type may be used to estimate not only the present state of stocks, but also the alteration in their abundance over the time known to us; this is reflected in fig. 26. When there was no information on the state of the stock in the past its assumed abundance has been indicated by a question mark.

Only those stocks which are numbered in hundreds--thousands of fish are of independent commercial importance. There are now only three such stocks, those of the Shuya, the Pyal'ma and the Vodla. The stocks of the Suna, the Lizhma and the Andoma were included in this category comparatively recently, in this century, but the first has completely disappeared and the other two have lost their commercial importance. Stocks which have disappeared also include those of the Lososinka, Iovenchanka and Vytegra Rivers and probably that of the Vodlitsa. There is no information concerning the past commercial importance of the stocks of the Unitsa, Kunska, Nemina, Tuba and Megra Rivers; their present numbers are extremely low. /117/

V. V. Veshchezerov (1951) gives a physical estimate of the catch for the Andoma of up to 500--750 salmon in a season. The results of a calculation made by Sevzaprybvod (Leningrad) suggest that this stock has been greatly reduced; only 41 fish were recorded in 1963 (communication of I. I. Ryzhov), but this is not the entire stock, since salmon also enter the Samina, a tributary of the Andoma, and there were no counting fences in this tributary.

N. A. Borodin (1916) put the catch in the Suna at 220 fish. According to figures given by N. I. Kozhin (1927a), the catch in 1926 may be estimated at 400--500 fish; according to the data of M. B. Zborovskaya, the catch in 1930 (30 centners) was 500--600 fish. In the latter case, as in the Andoma, the whole stock may have numbered up to 1000 fish, since considerably less than the entire catch was recorded and not all the fish were caught.

V. V. Petrov (1926) gives a figure of 2000 fish for the catch in the Lizhma (around the year 1916); the entire stock does not exceed 200 fish at the present time.

It is possible to have more precise information on abundance in some instances when reliable commercial statistics are supplemented by materials on the structure of the stocks. It may be considered with confidence that the abundance of the stock approaching any river has not exceeded 300 fish since 1900. Materials for the last few years enable us to give a quite accurate estimate of the Shuya, Fyal'ma and Vodla stocks.

The salmon stocks approaching the mouth of the Shuya in the period 1957--1963 numbered 900--2500 fish with an average of 1700.<sup>1</sup> Between 60 and

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<sup>1</sup> Translator's note. These figures contradict the statement in the last paragraph in which 300 should perhaps read 3000.

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90 % of the stocks were taken by the industry and approximately 10 % by "amateur" fishermen. Very few fish spawned, especially from 1959 onward, when the rate of exploitation in Petrozavodsk Bay reached the limit. The exception was 1962 when the trap nets in the best fishing place ("Lipa") were torn away by logs at the height of the run and were not restored for two weeks. This enabled a large number of salmon, up to one third of the stock, to migrate upstream without hindrance. There are a number of facts which indicate that the number of salmon entering the Shuya has been sharply reduced from 1959 onward. Salmon and salmon redds have become a rarity in the Syapsya, a tributary of the Shuya. Our search for redds in this river in October 1959 was fruitless: no redds were found even in those rapids where the salmon always spawned previously. Up until 1958 inclusive local

inhabitants found dead salmon which had perished after spawning in the Kindasovskoe spawning ground; this was not observed in the following years. After 1960 it became very rare for spawned salmon which had migrated downstream in the spring after overwintering in the river to be caught in Petrozavodsk Bay and none were caught in 1961 and 1962. Nets were specially erected around the mouth of the Shuya at the beginning of May 1966 but only 5 spawned salmon were taken. This information enables us to improve the accuracy of the estimates of abundance. /118/

A counting fence was installed in the Pyal'ma River in 1963 and 1964 although admittedly not for the entire run. On the basis of these data and taking the catch and the wastage into consideration, the stocks of these years are estimated at 500--1000 fish (Smirnov and Smirnova, 1965). According to N. Ya. Danilevskii (1875), up to 800 salmon were taken in the summer in good years at the trap fence erected at that time in the Pyal'ma, i.e. the abundance of the stock in those years was within the same range as at present. Admittedly, we know nothing concerning catches in the more distant past, but they may have been far higher.

According to Danilevskii, the catch in the Vodla was at least 400 poods, which corresponds to 1000 fish, and in addition some of the fish entered the river. Including the catch, the wastage and the proportion of the carry-over the stocks of 1962--1965 may be estimated at 500--1000 fish.

The abundance of the mature part of the entire population of the Onega salmon in the quinquennium 1961--1965 did not exceed 4--5 thousand fish; in the following quinquennium the abundance was at least halved.

WAYS OF INCREASING THE ABUNDANCE OF THE SALMON IN

LAKE ONEGA

I. Conservation of Stocks and Regulation of Fishing.

The purpose of conservation measures is primarily to halt the reduction in abundance and not to permit stocks whose numbers have become very low to disappear. This latter point is very important, since owing to the high plasticity (adaptability) of the salmon and its tendency to form local groupings, there are evidently no completely identical stocks and each stock possesses a combination of properties specific to it alone. Because of this different stocks are of unequal value for intensive artificial culture. In the conditions which have developed in the Onega basin conservation measures alone not combined with improvement works and artificial culture cannot lead to a significant increase in abundance, especially within a short period, but this in no way detracts from their significance, which is now overriding. The putting of our rivers into order must be begun with the systematic implementation of the main measures for the conservation of stocks and the regulation of fishing. The following should be included in the conservation measures.

Discontinuation of logging in those rivers where conversion to another form of transport (for example road transport) is possible: firstly the Nemina and the Suna; unfortunately this is at present impossible in the Vodla.

The establishment of a working regime of dams which is in accordance with the interests of the fish industry. This applies in the first instance to the Vama dam (Vodla), where discharge of water from the reservoir should

cease by the end of September and where at the end of October the dam at the head of the Sukhaya Vodla should be sealed so that the entire discharge is directed into the Vama. In the spring the Vama dam should not be closed before the beginning of the flood, i.e. not before the first of May, to avoid drying out of the upper reach of the river and the mass death of fish, including young salmon moving to the upper rapids after overwintering. The regime of the dam at Shushki (Sura) has not been established; complete closing of the dam for the winter is permitted there. The question of the Kedrozero dam (Lizhma), which prevents the passage of salmon to the upper spawning grounds, has not so far been solved.

Systematization of the exploitation of commercial stocks, namely /120/  
transition to concentrated fishing with appropriate modification of the industry so that the ratio of removals to escapement should in fact be 1 : 1 and not as it was in the Pyal'ma in 1963 and 1964 where, owing to the continuation of lake fishing, the actual removals were 3 times the escapement, 3 : 1. This measure will not only ensure against overfishing, but will promote an increase in abundance (long-term experience in the rivers of the Kola Peninsula); because it completely justifies itself economically it is practised in the Atlantic salmon rivers of Murmansk and Archangel Provinces, including the largest Atlantic salmon river, the Pechora.

The principles and merits of concentrated fishing were set out more than a century ago by K. M. Ber (1860). If we wish the rational exploitation of stocks of lake-river fishes and to be certain of future catches we must convert to what is known as concentrated fishing, in which catching is concentrated in the river mouths. When this is done we shall have accurate knowledge of the abundance of the stocks, which will permit accurate calculations of the effectiveness of natural reproduction and make it possible

to keep a check on the state of the entire population. After the abundance of the stocks has increased to the maximum possible for each river, the proportion of removals may be increased. After the maximum abundance for the stock has been reached it is evident that a constant number of spawners (or a number which varies slightly in relation to the amount of water in the year) must be let through to spawn; this number will be related to the spawning and growth area and the whole of the remainder of the stock will be removed.

Concentrated fishing is quite feasible at the present time in the Shuya and the Pyal'ma, but needs prior preparation, special traps and strict recording, without which the very principle of fishing is lost. A repetition of what took place in the Pyal'ma in 1963 and 1964 under the guise of concentrated fishing is impermissible.

It is highly desirable that all fish allowed to pass the counting fence should be tagged. This operation will not constitute a large amount of work since the abundance of the stocks is slight.

The suppression of uncontrollable removals is an urgent and pressing problem since the consequences of the catching of spawners in the spawning grounds are particularly grave given the present smallness of the spawning stocks. Major obstacles ("fences") are constructed in the Vodla to catch migrating salmon; there were up to 50 in the reach between Padun and the settlement of Vodla in 1963. Nets, spinning and harpoons are used in all rivers. We have observed unfinished empty salmon redds in the spawning grounds in the Lower Lizhma and the Tuba because the spawners had been caught.

In the case of concentrated fishing and the calculated escapement of spawners uncontrollable removals will distort calculations of the commercial return in addition to reducing the future catch.

Another form of uncontrollable removal on a larger scale is the catching of salmon fingerlings by rod and line, which is practised both by adults and by children. It occurs in all rivers with the exception of the Vama and in part the Fyal'ma. According to our calculations, this fishing does at least as much harm as the catching of spawners. Tens of thousands of smolts and large parr are caught in the rivers between the spring and the autumn; the losses to future catches from each thousand fingerlings will be at least 5--10 centners.

Improvement of the Fishing Regulations is necessary because enemies and competitors of the salmon are protected by the total ban on amateur fishing in salmon rivers established by the existing regulations (1960), and this runs counter to what is intended.

In those rivers where no measures of biotic improvement will be carried out rod fishing and fishing with live bait (but not trolling!) should be permitted, but only in reaches that do not provide pools for salmon and whitefish. This is needed in the first instance to put down pike. Such fishing may be permitted in all rivers before improvement works are carried out in them.

In order to minimize the possibility of uncontrollable removals in salmon rivers, it is possible, firstly, to allocate certain reaches of the rivers (apart from the rapids) on a contractual basis to teams of fishermen and, secondly, to permit fishing in salmon rivers on only two days a week (for example, on Saturday and Sunday), which will facilitate the conservation of the rivers.

## II. Improvement Works.

The purpose of improvement works is to increase the productivity

of spawning and growth areas and thus to compensate the reduction in the resources of spawning grounds. Such operations were until recently impossible and undesirable since there was intensive logging in almost all the rivers of Southern Karelia. With the cessation of logging it is becoming necessary to carry out a combination of improvement works and not merely to clean up the rivers. When deciding on the allocation of resources for improvement works it is naturally essential to take into consideration, in addition to the natural features of the river, the prospects of its economic exploitation and the technical potentialities of improvement works.

Because there is no hatchery in Lake Ohenga the abundance of the salmon may be increased only by natural reproduction in the rivers not used for logging. It is shown by foreign research and experience that the carrying out of biotic improvement (the suppression or total elimination of enemies and competitors) may sharply increase the productivity of spawning and rearing grounds. /122/

A number of investigators (Foerster, 1938; Ricker and Foerster, 1948; Elson, 1950, 1962; Allen, 1951; Ricker, 1954; Smith, 1955; Watt, 1955; Horton, 1961) have established the high level of losses due to the destruction of young fishes by predators. Thus, according to the estimate of Allen, the losses of young sea trout (Salmo trutta) by the end of the second year of life reach 80--93 %, and in the case concerned (New Zealand) eels are the greatest predator. The only way to increase the productivity of a body of water is to destroy the predators (fishes, birds and mammals) which consume the fish which are of concern to us, and no other measures can correct the position. The experience of Canadians (Smith, 1955) has shown that the fertilization of trout lakes and the introduction of hatchery-reared young did not produce an increased yield until the predators (eels and fish-eating birds)

which had consumed the whole of the addition to the yield began to be destroyed. However, once the predators had been destroyed the yield of the trout increased by 6.5 times at the former stocking density and by 11 times at double the density, although admittedly the growth rate was slightly lowered in the latter case. The measures for control of predators are fishing out, the construction of insurmountable barriers (dams with penstocks for the removal of water) at the river head, and the shooting of birds.

The fertilization of lakes may yield very good results. Thus, the size of downstream-migrating red salmon was increased by this measure in Bare Lake (Alaska) and, as a result, survival in the sea was increased and the return rose from 3.26 to 7.89 %, (Nelson, 1959). This measure may be recommended for our source lakes which are the origin of small spawning rivers (e.g. the Upper Lizhma and the Elgamka). The food supply of the young will be increased by plankton carried out of the lake, which is very important in the transition to active feeding. An attempt may also be made to introduce young directly into the lakes after undesirable fishes have been eliminated from them (chemical means make this an easy matter). However, it must be remembered that over-fertilization is far worse than inadequate fertilization, since it may lead to total mortality of the fish as a result of oxygen starvation.

According to the observations of A. A. Zabolotskii (1959), parr are able to grow well even in small lakes without an outlet, in which they transfer to predatory feeding (on minnows). It might be appropriate to stock some fishless source lakes with the smelt or the minnow in order to provide food of suitable size for parr.

The destruction of undesirable fishes in salmon rivers will permit of an extension of the use of such a measure as the stocking of the vacated areas with young. Failures in the release of larvae due to predators have

obliged a switch-over to the release of older young with which, for example, vacated areas in the Gamryroy River were filled (Smith, 1963), and this stocking has led to a positive result. But in the absence of predators, as is the case above the dam in the Lower River, the release of larvae yields an excellent commercial return, in which uniform distribution of the larvae over the whole of the suitable area goes hand in hand with success (Larsen, 1959). It is far simpler to transport and release salmon as larvae than as older young. /123/

After enemies and competitors have been suppressed in rivers obstacles must be erected to keep these fishes out of the river. In some cases it may apparently be possible to use rotating net drums or webbing of the type used abroad (Isaev, 1962). However, in our view, small dams with a drop of 1.5--2 m, which are insurmountable to all fish except the salmon, will be most effective. It is precisely because of such a dam that the salmon in the Tuba has existed under conditions approximating to monoculture.

Before the downstream migration of the smolts begins the reaches of the rivers below the obstacles must be fished out to remove predators or chemical repellents must be used.

The following improvement works need to be carried out in the rivers of the basin of Lake Onega.

Rubble, submerged logs and unnecessary logging structures must be removed from the river beds. It is an unrealistic undertaking to remove bark from the river bed, since not only are there no machines for this purpose, but none are being designed, and even the raising of submerged logs is carried out manually.

The cutting of vegetation in bays around the river mouths and in the

lower reaches, which is needed to worsen environmental conditions for the pike.

The suppression of predatory and worthless fishes. The different approaches which are practicable in different rivers include, for example;

- a) the fishing out of all fishes entering the river between the ice run and the start of the salmon and whitefish run, for which purpose the bed is completely fenced across with fine-mesh traps;
- b) amateur live-bait fishing in the pools;
- c) use of the chemical method or electrofishing for the complete treatment of small rivers.

Spawning rivers cannot be brought into a proper state unless a specialized fish breeding and improvement station is organized. The principles worked out by G. V. Nikol'skii (1956) for the operation of such stations for the salmon rivers of the Soviet Far East are largely also applicable to the conditions of Karelia. As yet, however, it is not planned to set up an improvement station in Karelia and to carry out improvement of the salmon rivers.

One of the causes of the underestimation of improvement works is the lack (both in our country and abroad) of precise data for estimation of the possible yield of downstream-migrating salmon per hectare of spawning and growth area after the improvement of the river. It is therefore not clear to what extent the loss of spawning grounds (and catches) throughout the basin of Lake Onega may be made good by the improvement of the remaining small and medium-sized rivers. It was solely for this reason that improvement works were not included in the "General Outline of the Development of Lake and Pond Fishing in the Karelian ASSR" (Gidroribproekt, 1964).

The supposed high cost and the lack of mechanization are serious arguments against melioration. The point is that the existing legislation on water use does not provide means of obliging logging organizations to clean the rivers. The results of the mismanagement of the timber industry are therefore

turned into great losses and great expenditure for the fish industry.

Were the situation to be different, the expenditure on fisheries improvement would be very slight: it would reduce mainly to biological measures, to elimination of the enemies and competitors of young salmon and whitefish. This is quite feasible with the existing methods in small and medium-sized rivers. The carrying out of biotic improvement to increase the efficiency of natural reproduction will therefore be desirable and undoubtedly advantageous in those rivers in which technical improvement is not required or where the amount of technical improvements needed is small.

### III. The Possible Abundance of the Salmon in Lake Onega.

In looking at the size of the lake, its productive potentialities should not be overestimated. At the present level of development of the resources of the industry, Lake Onega cannot be regarded as more than a "live container", from which the contents may always be exhausted. It is therefore extremely important to determine the maximum quantity of predatory fishes, including salmon, which may be fed on the plankton-feeding fishes (vendace and smelt) and how intensive vendace and smelt fishing should be if reproduction is not to be disrupted.

It is essential to determine this in order not to allow the productive properties of the valuable predators to be lowered (slowing down of growth and maturation which will lead to an increase of the feeding ratio). This will occur if the abundance of predators is excessive with limited food resources, i.e. if the food supply is inadequate. Such a feature has been observed in the breeding of trout, not only in the system of small lakes of the Solovetskie Islands (Gul'el'mi, 1888), but also in fairly large and productive lakes of New Zealand (Percival and Burnet, 1963).

How many salmon may be fed in Lake Onega? Unfortunately, we are unable to give a clear answer based on a knowledge of the abundance of plankton-feeding fishes. However, a knowledge of the changes occurring in Lake Onega does permit of an approximate estimate of the permissible abundance of salmon based on fisheries data. This figure may possibly turn out to be understated, but in this case understatement is less risky than overstatement. /125/

The following remarks should be made concerning the planned catch in the General Outline (2000 centners). This figure is not supported by calculations on the food resources. It is apparently overstated, at all events for the present condition of the lake.

The point is not only that there has been no increase in the abundance of the vendace and the smelt, which are the food of salmon and other valuable predators, since the end of the last century, i.e. since the time when maximum salmon catches were fixed. N. N. Pushkarev (1914a) noted such a heavy reduction in vendace catches that the vendace fishery had become unprofitable. Complaints by fishermen of a reduction in vendace catches had earlier been noted by K. F. Kessler (1868) and N. Ya. Danilevskii (1875).

In addition to the disappearance or reduction of some stocks of vendace and smelt, there has been a heavy increase in the rate of exploitation and in the catches of these fishes throughout the lake by comparison with the last century and a corresponding reduction in the proportion of them available for predators. However, it was noted as long as 50 years ago by N. N. Pushkarev and slightly later by V. V. Veshchezerov that salmon catches were dependent on the abundance of the vendace.

At their present low level of abundance salmon do not experience lack of food, as is evident from the growth rate and the time of maturation. However, the existing food resources will be inadequate with the present trend

of the industry for a tenfold increase in the fish mass of the population.

The following facts are indicative of a reduction in the food resources of predators.

1. The vendace stock in Kondopoga Bay has been destroyed by effluent discharged by a pulp and paper combine (catches reached 1000 centners in the past).

2. The entry of the smelt into Petrozavodsk Bay has been reduced in recent years owing to its pollution. The vendace, which was previously plentiful here (Pushkarev, 1900a), has practically disappeared.

3. The vendace stock in the area of Velikaya Bay has ceased to be of commercial importance (according to the data of Karelrybvod, pre-war catches were more than 2.5 thousand centners); overfishing is a possible cause.

4. The abundance of the southern vendace stock in the area of Cape Petropavlovsk has been reduced, apparently as a result of overfishing: the catch, which was of the order of 3000 centners in 1898 (21000 poods, Pushkarev, 1914a), fell to 1000 centners in 1934--1935, 943--233 centners in 1956--1961, only 97 centners in 1962 and 170--650 centners in 1963--1965.

The assumed cause of reduction in the abundance of the stock in recent years is the heavy silting observed in 1961 and later as a result of the dumping of bottom material from dredging of the Volga-Baltic canal: /126/

a) the increased turbidity greatly impeded fishing;

b) the increased turbidity may have forced the vendace to alter the usual paths of its spawning migrations.

5. Removals of the vendace and smelt have been increased.

a) According to K. F. Kessler (1868), vendace catches at Tolvuiskoe Onego (the main fishing ground) did not exceed 15000 poods + 1200 poods of vendace roe = 2600 centners; in 1870--1871 (Danilevskii, 1875) the catch was

4800 poods of vendace + 400 poods of vendace roe = 830 centners. In the period 1948--1951 catches in the same area ranged between 3212 and 8366 centners and were on average 5300 centners. Therefore, the average catch of these years was more than twice the record catch in the past.

b) Nerezha (hoop net) fishing for the smelt in the Shala area, which was begun in the 1870s, was initially carried out on a small scale limited to the needs of the fishermen and the not-very-numerous local population. The 1928 catch of 826 centners was regarded as extremely successful: the smelt "asked to be caught" (Logashov, 1931). In 1948--1951 the smelt catch in this area was 1572--2286 centners, on average 1940 centners, or 2.3 times the former record catch. In 1962--1965 the catch by the fishing brigades of the fish combine alone varied between 1890 and 3270 centners, on average 2500 centners, or 3 times the catch in 1928.

c) A similar pattern is also observed in the southern part of the lake -- in the Petropavlovsk, Vytegra and Andoma fishing grounds. In 1928 the catch here was only 600 centners (Veshchezerov, 1931). In 1948--1951 catches ranged from 1572 to 2845 centners, on average 2400 centners. Smelt catches in this area were even further increased in the subsequent years: in the period 1956--1965 they were between 2669 and 5324 centners, on average 3700 centners.

Such an increase in the smelt catch is characteristic for the lake as a whole. The smelt catch now exceeds the demand: a) the demand of the population is low; b) far less is required for canning and other forms of processing than is caught; c) state fur farms prefer sea fish because it is cheaper.

By continuing to fish for the smelt on the present scale we are

reducing the food resources of more valuable predatory fishes -- salmon, trout, char, pike-perch and whitefish (a facultative predator). The economic expediency of continuing such fishing is doubtful.

6. Special fishing for pope (with "mutniki"), which was earlier practised, has long been abandoned since it is commercially unprofitable and forbidden for the population. According to available observations (Pokrovskii, 1953), the abundance of the vendace may be largely limited by the pope which consumes its eggs in the spawning ground.

We are, therefore, faced with the disappearance or sharp reduction of a number of stocks of the vendace and with fishing for it and for the smelt which is extremely intensive by comparison with the last century, i.e. with an overall reduction in the food resources of predators. Although, on the other hand, the abundance of pike-perch, burbot, char, trout and whitefish has been heavily reduced, we cannot be certain that the food resources thus "freed" will make it possible to support a salmon stock which will equal in fish mass the lost catch of predators. Given the present trend and rate of exploitation in Lake Onega there are therefore no grounds for counting on a salmon catch of 2000 centners, especially because such catches are not known even for the best times in the past (tables 26 and 27; fig. 25). /127/

A very rough calculation may be made of the food (smelt and vendace) needed to obtain 2000 centners of salmon. The food ratio for the salmon has still not been established. In rainbow trout reared on fish meal the food ratio ranges from 5 to 7. It should undoubtedly be considerably higher in the salmon (longer feeding period, expenditure of energy in the search for food) and at all events at least 10. Therefore, to obtain stable salmon catches of 2000 centners at least 20 000 centners of smelt and vendace should be left annually for the salmon. In addition, some quantity of these fishes is essential for

fishing, for other predators and, finally, for reproduction. What part of the smelt and vendace populations should be left for reproduction to prevent a decline in their abundance has not as yet been established. But even were this to be known, we could not give clear recommendations on the reconstruction of the fishery. The point is that no attempts have hitherto been made to estimate the abundance of stocks of plankton feeders in Lake Onega and the extent to which they are exploited by the industry.

In recent years (1953--1965) the industry has taken between 10.3 and 16.5 thousand centners a year of vendace and smelt combined (table 33), on average approximately 15 thousand centners. Food ratios may be used to make an admittedly very approximate estimate of the proportion of these fishes which will remain for predators. The vendace and the smelt are consumed by salmon, trout, char, burbot, pike-perch and to a lesser extent pike, perch and whitefish. The last two species have not been considered in examination of catches of predators.

The catch of predators was 2874 centners in 1930; between 1953 and 1965 catches ranged from 1274 centners to 3887 centners (table 33), on average approximately 2300 centners. The last-mentioned figure should be increased to 2.5--3 thousand centners to account for the developed amateur fishing and the wastage of catches. If  $\frac{1}{3}$  of the stocks escapes being caught, the total fish mass of predators may be estimated at 4--5 thousand centners. With a food ratio of 10, 40--50 thousand centners of plankton feeders are needed to support such a quantity of predators. Unfortunately, no estimates have hitherto been made of the remaining reproductive part of the stocks. It may be assumed that at the present rate of exploitation of the vendace in the main fishing grounds, Tolvuiskoe Onego, no more than  $\frac{1}{3}$  of the stocks approaching the spawning grounds avoids being caught. The situation is apparently the same with the smelt in the Shala area.

Таблица 33

2 Структура уловов по Онежскому озеру.  
Соотношение планктофагов и хищников

	1953 г.	1954 г.	1955 г.	1956 г.	1957 г.	1958 г.	1959 г.
3 Общий улов по озеру, ц	21140	26040	21686	25578	18906	21120	22240
4 Улов ряпушки и корюшки, ц	13922	16537	12851	16801	12512	14034	14255
5 Доля ряпушки и корюшки в улове, %	66	64	59	66	66	66	64
6 Улов хищников, ц	3147	3410	3887	2945	2027	2331	1935
7 Отношение улова хищников к улову планктофагов, %	23	21	30	18	16	17	14

8 Таблица 33 (продолжение)

	1960 г.	1961 г.	1962 г.	1963 г.	1964 г.	1965 г.	(10) Средние
3 Общий улов по озеру, ц	17190	16355	19600	20371	15838	18645	~ 20 тыс. ц
4 Улов ряпушки и корюшки, ц	13429	12974	15100	15969	10283	14160	~ 15 тыс. ц
5 Доля ряпушки и корюшки в улове, %	78	79	77	79	65	76	~ 70%
6 Улов хищников, ц	1274	1755	1739	1807	2018	1708	~ 2.3 тыс. ц
7 Отношение улова хищников к улову планктофагов, %	9	14	12	11	20	12	~ 15%

Key to Table 33: 1. Table 33 2. Structure of catches throughout Lake Onega. Proportion of plankton-feeders and predators 3. Total catch throughout the lake, centners 4. Catch of vendace and smelt, centners 5. Proportion of vendace and smelt in the catch, % 6. Catch of predators, centners 7. Catch of predators as a percentage of the catch of plankton-feeders 8. Table 33 (continuation) 9. thousands of centners 10. Means.

If the "avoidance" is extended to 1/3 (i.e. approximately 7000 centners) of the catch of vendace and smelt throughout the entire lake, the

annual balance of gross production of plankton-feeders appears as follows: 40--50 thousand centners are consumed by predators (natural mortality); 15000 centners are removed by fishing; 5--10 thousand centners remain for reproduction; a total of 60--70 thousand centners is the annual "turnover" of plankton-feeders.

Is a considerable increase in the abundance of plankton-feeders possible, for example to 2--3--5 times the existing level? There is as yet no answer to this question, primarily because we do not know the extent to which plankton feeders are supplied with food and whether there are "free" resources of plankton. There may be random causes for the reciprocal relationship observed between vendace and smelt catches (fig. 27). But, on the other hand, we know that such a pattern may characterize competitive relations when the food resources are under pressure. /129/

On the basis of all that has been said, we should not plan to obtain a gross return of salmon (catch + number of fish for reproduction) of more than 1000 centners a year, at all events not until the food resources have been clarified.

A relative excess of feeding salmon with limited food resources may lead to an undesirable deterioration in growth and to retardation of maturation and, consequently, slow down the rate of return, the recouping of resources expended on fish management. However, if the food resources are subsequently found to be adequate, the number of salmon could be increased.

In order to make better use of the food resources in the lake the abundance of other salmonids (trout, char and whitefish) should also be increased. The most desirable and suitable whitefish are lake-river forms which are readily accessible for fishing and whose abundance can be regulated. There is no clarity concerning the possible (or maximum permissible) abundance

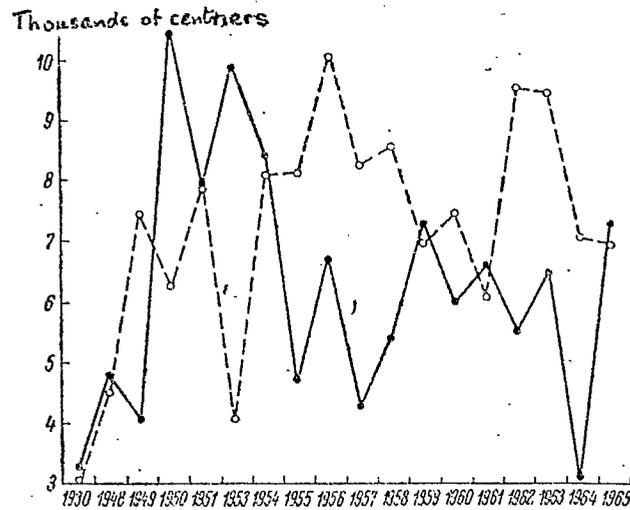


Fig. 27. Relationship between vendace and smelt catches in Lake Onega.  
Continuous line -- vendace, broken line --- smelt.

of these fishes. Solution of this question depends on what will be accepted as the optimum structure of catches throughout the lake. In addition, as in the case of the vendace and the smelt, it is not clear what part of the stocks should be left for reproduction if we count upon natural reproduction.

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#### IV. The Fish Hatchery and Natural Reproduction of the Salmon.

The need to construct a fish hatchery to maintain and restore stocks of the Onega salmon was already apparent more than half a century ago (Pushkarev, 1914b, 1914c; Borodin, 1916). This need has now become even more acute. The profitability of salmon fishing under present-day conditions is confirmed by the calculations of GosNIORKh (State Research Institute for Lake and River Fisheries) (Khalturin, Leizerovich and Yandovskaya, 1966) and by foreign experience (Carlin, 1964).

The construction of a hatchery and conversion to the artificial propagation of the greater part of the population while making simultaneous use of the rivers (spawning and stocking) will make it possible to resolve a number of difficulties and holds out tempting prospects.

To begin with, it is only in this way that the number of fish may be increased in a short period to the desired limits (in conformity with the food resources). Secondly, the size of the removal (catch) increases, and in the case of hatchery propagation alone becomes practically equal to the return, since a small quantity of spawners is needed for reproduction. Thirdly, by annually releasing a regular quantity of standard downstream migrants it is possible to count on obtaining more stable catches in the future, since the fluctuation in the yield of young in years when conditions differ, which is a feature of natural reproduction, is excluded. Fourthly, selection which will subsequently increase the efficiency of fish culture becomes possible. Fifthly, if more young are reared than are needed for Lake Onega they may be introduced into other suitable bodies of water. Finally, the construction of a hatchery will make it possible to use vacated growth areas in those rivers where the salmon stock has disappeared or is on the verge of disappearing. In this case previous preparation will be necessary (destruction of enemies and competitors), after which such rivers (mainly small and medium-sized rivers) may be stocked even with larvae, quite apart from older young. This form of combination of hatchery and natural reproduction will be particularly desirable if the contribution of hatchery propagation to the maintenance of numbers is not overwhelming, for example if initially there are insufficient growth areas (ponds) or insufficient food for the production of smolts.

Even were we to be able to replace natural reproduction completely by

hatchery reproduction, there would be no justification for refusing to use the rivers. The task of fish management is to make effective use of bodies of water and not to leave them in a chaotic state. /131/

At the present time natural reproduction can do no more than maintain the population of the Onega salmon at the present low level and we cannot count on an increase in catches. Moreover, catches will be extremely low by the beginning of the 1970s and even in the subsequent quinquennium they will not rise above the mean. Every measure must be taken to conserve the stocks which still exist so that there should be material for the hatchery when it is constructed. The salmon of the Shuya River and the autumn salmon of the Pyal'ma River are most suitable for propagation. The salmon is the most valuable and fast-growing of the lake predators. Accelerated hatchery rearing of smolts, i.e. reduction of the river period, is one way of hastening the return and recovering the investment. The selection of fast-growing and maturing forms is another way which is also unthinkable without hatchery propagation. Should a fish hatchery be constructed and begin mass propagation of the salmon by 1975 a commercial return will be obtained by 1985 and the size of the catch will depend on the intensity of fish culture.

Irrespective of the prospects for the construction of a hatchery it is essential to proceed with improvement and intensify the utilization of the spawning and growth areas, since for the next 15 years at the very least the catches will be provided exclusively by natural reproduction and their amount will be determined by the state of the resources of spawning grounds.

BibliographyA. Russian publications

Translator's note. For ease of use the titles in this list have been rearranged in English alphabetical order of the author of each title (first author, if more than one). The following journals, occasional publications and publishing houses are given in transliterated form.

AN -- Imperial Russian Academy of Sciences  
AN SSSR -- USSR Academy of Sciences

Byull. rybn. khoz. -- Fisheries Bulletin  
Byull. rybn. khoz. KP SSR -- Fisheries Bulletin Karelo-Finnish SSR

Dokl. AN SSSR -- Proceedings of the USSR Academy of Sciences

Ekon. i stat. Karelii -- Karelian Economy and Statistics

GGI -- State Hydrological Institute

Gos. izd. KASSR -- State Publ. House of the Karelian ASSR

Gos. izd. KP SSR -- State Publ. House of the Karelo-Finnish SSR

Gos. VNIORKh -- State Res. Inst. for Lake and River Fisheries

Izv. Bakinsk. ikhtiol. lab. -- Bull. Baku Ichthyological Lab.

Izv. KE fil. AN SSSR -- Bull. Karelo-Finnish Branch USSR Acad. Sci.

Izv. KP n.-i. bazy AN SSSR -- Bull. Karelo-Finnish Sci. Res. Base USSR Acad. Sci.

Izv. Leningr. n.-i. ikhtiol. inst. -- Bull. Leningrad Ichthyological Res. Inst.

Izv. Min. zemled. i gos. imushchestv -- Bull. Min. Agriculture & State Lands

Izv. Nauchn. inst. im. P. F. Lesgaft -- Bull. P. F. Lesgaft Science Inst.

Izv. N.-i. ikhtiol. inst. -- Bull. Ichthyological Res. Inst.

Izv. Obshch. izuch. Olon. gub. -- Bull. Soc. for the Study of Olonets Guberniya

Izv. Otd. prikl. ikhtiol. -- Bull. Dept. Applied Ichthyol.

Izv. Otd. pril. ikhtiol. i nauchno-promysl. issled. -- Bull. Dept. Applied  
Ichthyol. & Fishery Research

Izv. Tikhookeansk. nauchno-promysl. issl. st. -- Bull. Pacific Fishery Research  
Station

Izv. Vses. n.-i. inst. ozern. i rechn. rybn. khoz-va (VNIORKh) -- Bull. All-  
-Union Res. Inst. for Lake & River Fisheries

Karelrybvod -- Karelian Fisheries Trust

Karel'sk n.-i. rybokhoz. st. -- Karelian Fisheries Res. Station

Kargosindat -- Karelian State Publishing House

KP otd. VNIORKh -- Karelo-Finnish Division All-Union Res. Inst. for Lake &  
River Fisheries

Khoz. S.-Z. Kraya -- Economy of the Northwestern Territory

Leninskaya pravda -- Lenin's Truth (Republican newspaper)

Leninskoe znaniya -- Lenin's Banner (Republican newspaper)

- Mat. rybolchoz. issl. Severnogo bass. --- Materials of Fisheries Research in  
the Northern Basin  
MGU --- Moscow State University  
Min. gos. imushchestv. --- Ministry of State Property  
Mosk. obshch. priro. i OI. upr. po zapovedn., otd. zool. --- Moscow Naturalists'  
Society and Chief Administration for Reservations, zool. div.
- Nauchn.-tekhnich. byull. GosNIOBKh --- Scientific Technical Bull. State Res.  
Inst. for Lake & River Fisheries  
Nauka --- Science Publishing House
- Olon. gubern. zemstva --- Olonets Guberniya Zemsto (elected rural council)  
Olon. sb. --- Occasional Papers on the Olonets Guberniya
- Pgr. tip. Mor. min. --- Peterhof Printing Works of the Naval Ministry
- Rybn. khoz. --- The Fish Industry  
Rybn. khoz. Karelii --- The Karelian Fish Industry
- Sb. nauchn. inf. VNIRO --- Collected Items of Scientific Information, All-Union  
Res. Inst. for Sea Fisheries & Oceanography  
SNKh Leningr. ekon. r-na --- National Economic Council of the Leningrad Economic  
Region
- Tr. Boredinsk. biol. st. --- Transactions Borodino Biological Station  
Tr. Karelo-Finsk. otd. VNIORKh --- Transactions Karelo-Finnish Div. All-Union  
Res. Inst. for Lake & River Fisheries  
Tr. Karel. n.-i. rybolchoz. st. --- Transactions Karelian Fisheries Res. Station  
Tr. Karel'sk. fil. AN SSSR --- Transactions Karelo-Finnish Branch USSR Academy  
of Sciences  
Tr. Karel'sk. gos. ped. inst. --- Transactions Karelian State Pedagogical Inst.  
Tr. Leningr. obl. po izuch. mestn. kraya --- Transactions Leningrad Regional  
Territorial Studies (? Society -- reference defective).  
Tr. N.-i. inst. rybn. khoz. Latv. SSR --- Transactions Latvian Fisheries  
Research Institute  
Tr. Olonets. nauch. ekspeditsii --- Transactions of the Olonets Scientific  
Expedition  
Tr. Pechoro-Ilychskogo gos. zapovedn. --- Transactions Pechora-Ilych State  
Reservation  
Tr. VNIRO --- Transactions All-Union Res. Inst. for Sea Fisheries and  
Oceanography  
Ts BII --- Central Office of Technical Information
- Uch. zap. KF gos. univ. --- Scientific Annals Karelo-Finnish State Univ.  
Uch. zap. Leningr. gos. ped. inst. im. A. I. Gertsena --- Scientific Annals A. I.  
Hertzen State Pedagogical Inst., Leningrad  
Uch. zap. MGU --- Scientific Annals Moscow State Univ.  
Uch. zap. Petrozavodsk. gos. univ. --- Scientific Annals Petrozavodsk State Univ.
- Vestn. Karelo-Murmansk. kraya --- Journal of the Karelo-Murmansk Territory  
Vestn. LGU --- Journal Leningrad State Univ.  
Vestn. N.-i. inst. ozern. i rechn. rybn. khoz. --- Journal Res. Inst. for Lake  
& River Fisheries

Vestn. Olon. gub. zemstva -- Journal Olonets Guberniya Zemstvo

Vestn. rybopromyshl. -- Fish Industry Journal

Vopr. ikhtiol. -- Problems of Ichthyology (Translator's note. Title of  
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No. 1, 1970).

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Zap. Russk. geogr. obshch. -- Annals Russian Geogr. Soc.

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