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Adaptive characteristics of the spawning
migration of Amur chum salmon

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The adaptive peculiarities of the spawning migration of the Amur chum
salmon.

(Amur section of TINRO - Pacific scientific Research Institute of
Fishing and Oceanography)

by I.B. Birman

The period which is spent by salmon in the sea, has hardly been studied; the data about the environment in the sea that influence the numerical strength of individual generations of salmon, determining the number of specimens that return to the rivers for spawning, are also meagre and unreliable. Regardless of the influence of marine environment upon the numerical strength of salmon, we are primarily interested in the "river period" of these fish; for it is in the rivers, where they multiply that we are in a position, in one way or another, to produce an effect upon their reserves, whereas in salt waters, in view of the present level of our knowledge and technical equipment we are deprived of this possibility.

The life of Pacific salmon in rivers consists of several separate stages; the ascent up stream the rivers, the distribution in the spawning grounds and the spawning itself, the development of the roe and of the larvae in spawning "nests", the departure from the spawning redds or mounds and the exodus of the fry to the sea. During each stage the salmon experience on themselves the action or effect of numerous extraneous factors of which some are of a greater or lesser significance for the development of salmon.

Undoubtedly the various stages in the life of salmon are mutually connected by causal ties, further, that on the conditions and the successful completion of one stage depends the completion of the subsequent stage by individuals and en masse. In connection with this the demands of these fish upon the conditions for existence in every stage and the use of them of these conditions are determined (at least in the more serious aspects), so it seems, by the demands of the subsequent stage of their life activities. Therefore it is important to know the direction of the causal ties or connections between the various links of the life cycle of these fish. Knowing them and affecting in one way or another the conditions for existence of salmon in one stage of their life, we could, perhaps, exert an indirect influence upon their further destiny. However, the laws that govern the mutual relations of salmon with their environment during the various stages of their "river life" have not yet been studied thoroughly. It is natural that the inter-relations of these stages or those of the river and salt water periods of salmon could not have been studied. Therefore it is necessary to study thoroughly and from all sides the ecology of every stage of the life cycle of these fish on the basis of the Michurin concept of the problem of "organism and environment". This study can be helped to a large extent by the light from a mass of factual data, which have been gathered throughout a half-century of studying the biology of the Amur salmon.

The work before us is dedicated to the spawning migrations of chum salmon within the basin of the Amur river.

The existing literature on the biology of this type of salmon contains many data in connection with this question. However, a number of the peculiarities of the river stage of the spawning migrations of chum salmon have not been studied, apparently, because special attention was not given them.

We shall try even if only partially, to clear up the laws that govern the dynamic of the spawning run and the conduct of behavior of salmon in connection with the biological condition and the condition of the water during the migrations and also the specificity of the ecology and the distribution of chum salmon of the summer and fall runs in the Amur basin in connection with the morpho-biological peculiarities of these seasonal races.

1. Temperature conditions of the spawning migrations of chum salmon in the Amur basin.

The current of warm water from the Amur river, when leaving the firth (primarily following the northern navigation channel), turns to the right; due to this the water in the eastern part of the Sakhalin gulf is warmer in summer, than in the western part. A strong layer of warm and "sweetened or freshened" water is also observed at the northern tip of the Sakhalin Island. It may be assumed that the currents of Amur water, which spread farther to the south serve as a guide for salmon to the Amur firth.

According to Brazhnikov (4) there is a steady increase of the temperature of the water in the Amur firth and in the adjoining waters;

the temperature increases gradually towards the estuary. Thus salmon proceeding for spawning to the Amur river and its tributaries move towards ever increasing temperatures.

Further the situation changes. Pink salmon and chum salmon enter a number of small streams in considerable numbers; these streams directly join the Amur firth. In these small streams, which flow from the northern foothills of the Skhote-Alin, the water is considerably colder than in the firth. Thus, according to our observations, on August 10, 1949, the water in the river Charrakh, which enters the bay between capes Ozerpakh and Kazakevich, approximately three km from the mouth, the temperature of the water was lower by 7.8° than in the firth at cape Ozerpakh. Soldatov (15) had also observed a drop in temperature in the upper reaches of that same river.

The difference in temperature between the Amur river and its tributaries is of no less significance. The boundary between the warm Amur waters and the cold waters of tributaries coming from the foothills is rather clearly marked.

The same thing is observed at the end of summer and in the fall during the run of fall chum salmon.

In summarizing the above it is necessary, with regard to temperature conditions to divide the river period of the spawning migration of Amur salmon into two stages: During the first stage salmon move from the colder waters of the Okhotsk Sea to the warmer waters of the Amur firth and of the Amur river in the direction of increasing temperatures; during the second stage they proceed from the warmer waters of the Amur firth, of the Amur and Ussuri rivers to the relatively

cold waters of the spawning rivers. During the first and also during the second stage the chum salmon and the pink salmon endure, as we have seen, rather considerable changes in temperature, within, at least, 10° , which can not but affect the intensity of the exchange of substances in the organism of fish as animals with a changeable body temperature and thereby also affect the consumption reserve of nutritive substances which had been accumulated during the stay in the sea. The salmon enter the first stage, as is known, in a well fed condition, in the second stage they enter showing the unmistakable symptoms of exhaustion.

The temperature conditions, which accompany the run of salmon are not always the same during the years and in some cases they differ greatly from one to another. Thus, for instance, in 1948 the fall chum salmon appeared in the Amur firth, in the Ozerpakh region, as individual specimens on August 10 and in small shoals on August 14, but in 1949 the run of fall chum salmon started with individual specimens on August 8 and with schools on August 15. Thus the run of fall chum salmon started almost at the same time as in 1948; but in water of a lower temperature. In general in 1948 it was observed that the temperatures in the firth during the run of salmon were higher than in 1949.

The temperature conditions of the year 1948 are unusual for the Amur firth. According to available data they had been observed in earlier years (for instance in 1938) and is of interest in connection with the influence which they exert upon the biological condition and the run of fish.

According to our observations the main body of the run of the fall chum salmon in 1948 entered the Amur river with more mature sexual or reproductive products than in 1949. There is no need to dwell upon details. Let us, however, note that in 1949 the females up to 68.2% had sexual or reproductive products in the II-III and III stages of maturity, whereas in 1948 in all the females that were examined they were only in the III-IV and IV stages. Such a rapid maturing of gonads has also been observed in other salmon. In the last shoals of pink salmon there occurred, for instance, males and females with running reproductive products before entering the river, which is an unusual phenomenon in the Amur firth; it is also abnormal. It is not to be wondered at that pink salmon in large numbers entered not only the rivers to which they were accustomed in the Amur firth; but also many of the smallest streams that under ordinary conditions are entered only by a few specimens. On the other hand regardless of the large numbers the pink salmon did not go up very high in the Amur river. According to data by V.V. Abramov the pink salmon entered the Amgun river in large numbers; but few were caught in the Amur river.

It is well also to note that the shoals that migrated under the highest temperatures showed the highest degree of sexual maturity. At the same time the number of specimens with clearly expressed "mating changes" and symptoms of exhaustion increased considerably. In the first runs such specimens composed, on the average, no more than 0.2, at the peak of the season or run - 5.8 and in the closing runs - 18.7% of the entire number of fish.

Almost every year a pre-spawning dying of summer chum salmon is being observed on the Amur. Frequently in years when the waters of the Amur firth and of the Amur river warm up to a high degree this

phenomenon assumes the proportional dimensions of an epidemic, in such cases it is observed that the fish do not reach the spawning rivers that are farther up; but almost all the fish strive for the tributaries of the lower reaches of the Amur river. Especially considerable was the mass dying of pre-spawning summer chum salmon in 1938 in the Amgun river, which had been entered by them in large numbers, whereas there were few fish in the rivers farther up the river.

A.G. Smirnov, who observed the run of summer chum salmon in 1938 is of the opinion that the failure to enter rivers above the Amgun river was caused or occasioned by the very high temperature of the water and the rapid maturing of the gonads. As is pointed out by I.I. Kuznetsov the commission that was appointed to study this phenomenon established, among other things, that due to the high temperature of the water and the weakening of the organism the chum salmon had to turn to the colder current of the Amgun water, which contained more oxygen. With regard to the cause for the dying of fish it was established by the commission that it had been caused by a disease of a furunculose nature. However, within the boundaries of the USSR a furunculosis of fish is not known. Therefore it must be assumed that the disease was not caused by infection but by the disturbed metabolism which was upset by high temperatures. Already Soldatov pointed out the pre-spawning dying of perfectly healthy summer chum salmon in the Amgun in the rivers emptying into the firth. In 1948 we also saw many dead summer chum salmon in the Amur firth in days when the temperature of the water was high. Outside of the firth the fish were healthy

The cause of this phenomenon must be sought, so it seems, in the radical disturbance of oxygen exchange at a time when the need for oxygen in connection with the increased temperature and the rapid maturing of the gonads increases.

The success of the spawning migration under famine conditions, especially with regard to the length of the spawning migrations, which is peculiar to the fall chum salmon of the Amur is decided, in the end, by the degree of the activity of the processes in the organism of the fish, in other words, by the intensity with which the nutritive substances accumulated in the sea are consumed. If this is true then the significance of the water temperatures for the spawning migration of salmon lies, so it seems, primarily in the influence which it exerts upon the exchange of substances and the consumption of energy by specimens migrating to spawning grounds.

As established by N.S. Stroganov, who studied the action of temperature upon the interrelation of the processes of the exchange of gases and of the exchange of nitrogen in the gambusia under temperatures which lie not beyond the adaptation of the given species the speed of the physiological processes is less dependent upon the temperature of outside environment, than beyond the limits of the adaptive temperature zone. The same author points out that "from the point of view of the energetics of vital processes, the vital processes take place more economically in the adaptive than if the temperatures had been removed from this zone".

It is without doubt that a rather high temperature of the water, which disturbs the normal course of metabolic changes and activates the processes in the organism, causes a rather quick consumption of

energy reserves and changes thereby the length of spawning migrations, shortens the period of the distribution of salmon in the Amur and forces them to enter rivers unnatural to them.

This situation, often aggravated by the dying of fish before they reach the spawning grounds, can not but affect, in one way or another, the reproduction or building up of the schools and from this point of view the study of the influence of the temperature factor upon spawning migrations of salmon is not just of theoretical interest.

Observations have also shown that at one and the same point in the Amur firth the temperature of the water was subjected during the run of salmon of every kind to rather significant variations (see drawings 1 & 2). Thus in 1948 the amplitude of the variations of average diurnal temperatures at cape Ozerpak (left shore of firth) in the upper or surface layer attained, during the run of summer chum salmon - 12° ; during the run of fall (chum salmon) - 11.4° . It must be noted that we have not ~~XXXXX~~ considered the run of the first individuals of pink salmon and the run of the last specimens of autumn chum salmon; therefore the amplitude of the variation of the temperature of the water for these salmon can be regarded as greatly underestimated. In 1949, according to observations made at this very same point, the amplitude of the variations in the temperature of the water was 7.8° during the run of summer chum salmon but during the run of autumn chum salmon - 10.6° . The last figure is also an under-estimation seeing that the lowest temperatures at the end of the run of fall chum salmon were not recorded by us.

Drawing 1. Variations of the temperature of the water and the changes in the average length of autumn chum salmon for each day of the run in 1948 in the Amur firth.

(Drawing is illegible)

It is observed from year to year that during the run of pink salmon the temperature of the water in the Amur firth rises gradually and that only towards the end of the run the temperature drops somewhat. During the run of summer chum salmon, if it starts at the usual time (13-15 July), the temperatures are not subject to "certain laws" and change quite radically. At the beginning of the run of all chum salmon the temperature of the water rises somewhat (apparently in connection with the flow of summer fish), and then after the beginning of the run and during the run fall chum salmon the temperature gradually decreases. The lowest temperatures, consequently, correspond with the run of the first schools of the smallest and the most poorly fed fall chum salmon. The highest temperature of the water is observed during the last approaches of especially large pink salmon, during the run of summer chum salmon and the first shoals of fall chum salmon, which consist of the largest and fattest fish.

In 1948 the temperature of the water rose from June 22 till July 16; however, the average size of lake pink salmon increases (from the beginning of the period indicated till July 24) by 5.7 cm, the average size of females by 2.7 cm. In the same year - from Aug. 18 till September 13, i.e. during the run of fall chum salmon the temperature of the water dropped and approximately during the same time the average size of males decreased by 12.8 cm and that of females by 8 cm. In the following year of 1949 the water at that point and at

about the same time the temperature of the water dropped and the average size of chum salmon decreased by 11.4 cm. From this follows that various schools of salmon depending upon the time of the run enter the Amur river under various temperature conditions, the fish themselves differ from each other with regard to size and state of nutrition (fleshing up).

Smaller specimens, as is known expend more energy per unit of body surface and weight unit than large fish that move with them simultaneously. Pentegov, Mentov, and Kurnaev (13) established, for instance, that the expenditure of energy of nutritive substances of male chum salmon for one kg. of living flesh and for 1 km, on the way from the Baidukov isle 2 to the Khor river is equal, on the average, to 605 small calories and that of females, that move simultaneously with them to 597 small calories. According to the opinion of the aforementioned authors one circumstance may be of significance, i.e. that the males are larger and heavier than the females and the relative body surface of the latter is larger than that of the former, which increases "the resistance of the habitat and the expenditure of energy.

Table 2. Variations of the temperature of the water and changes in the average length of fall chum salmon during the days of the run into the Amur firth on 1949. (Drawing is illegible)

At the same time specimens of the same size that moved under various timperatures showed that the activity of internal processes and the need for oxygen are different and hence there is, under identical conditions, also a difference in the expenditure of energy. Fish, which run in the early summer or in fall under lower temperatures display a less intensive use of oxygen and of a general metabolic

changes than fish which enter the Amur river when the waters are warmer. Their outward activity must also slow down and this has actually been observed. Thus the fall chum salmon of the first runs move somewhat faster than the chum salmon of later runs: from the Baidukov isle to the Sofiysk village (?) it takes six 24-hour-periods; it takes twelve 24-hour-periods for fish of the first runs to cover the distance from Sofiysk to the Khor river; but the latter runs require twenty-eight 24 hour periods. And this regardless of the fact, as we shall see below, that the chum salmon of the latter runs enter the Amur river and go upstream to the spawning grounds with a lower water level and a reduced current.

It is also known with regard to some other salmon that their activity is slowed down as the temperature drops. Thus, for instance, the sockeye salmon of the summer run move faster than the sockeye salmon of the fall run (Sheiring, 20), but the winter salmon of Scotland move faster in warm weather than in cold weather; in cold weather these salmon do not try to overcome waterfalls and a swift current (Schmidt, 17). It is evident that low winter temperatures of the water suppress the activity of the internal processes of these fish to such an extent that they lack energy for greater efforts.

If the autumn chum salmon move slower at lower temperatures, it may be observed at the same time that all the physiological processes take place in them on a more economical basis. We have no doubts that the run of small and less well-fed fish in lower temperatures of the water favours their reaching the spawning grounds with an expenditure of less energy which is in keeping with their relatively small reserve.

However, we hesitate to maintain that the run of the fish is strictly governed by the biological conditions of the fish and by thermic circumstances. The decrease in the size of fall chum salmon from the beginning of the run till the end of it, as we shall see further below is connected not only with the temperature; but, in the first place, with the variations of the water level and the volume of the flow in the Amur river and its tributaries. A favourable conformity has been observed only in the run of pink salmon and fall chum salmon in the size of the fish and the temperature of the water. With regard to the summer chum salmon it must be said that their size, though not always, yet not infrequently, similarly to that of the fall chum salmon, decreased from the beginning of the run towards the end of it (it is true, less noticeably) but at the same time the temperature variations are irregular age, therefore, there can be no connection between the coordination of the fish runs and the temperature changes. It is possible that by this very circumstance it can be explained that in the years when the waters get rather warm, the mass pre-spawning dying of fish together with a shrinking of the area of propagation were observed, primarily and in the largest numbers among (?) chum salmon. At any rate, there is no doubt that a rather high temperature of the water can change the normal course of the metabolic charges in the organism for salmon and thereby also lengthens the spawning migration forcing the salmon to enter rivers that are unnatural to them. It must be stated, however, that pre-spawning mass dying has been observed only among summer chum salmon, whereas the fall chum salmon seldom suffer from it.

II. The spawning run and the dynamics of the waters of the Amur river.

The attitude of various types of salmon to the water level and the speed of the current of their migrations varies; their size, their muscular energy and physiological condition, and the extent of their river migrations also vary. Already V.K. Braxhnikov (3), when speaking about the run of pink salmon and chum salmon in the Amur firth, noticed the different relation or attitude of these salmon to the water level. According to Reim the shallow banks of the Amur firth are completely inaccessible to fall chum salmon not only when the water is low, but also when the water is high. Summer chum salmon and pink salmon, in this respect, are less fastidious. It is also known that fall chum salmon, as a larger and stronger fish, follow those navigations channels in larger numbers, where the current is the strongest or keep to the edge of fairways, and only comparatively few specimens move closer to the shore. Summer chum salmon, particularly pink salmon prefer a less strong current for the run, near the shore, with relatively shallow places.

Such varying attitude of salmon to the water level and the speed of the current reflects also on the distribution of their schools over the diverse fishing areas of the firth. The runs of summer chum salmon and especially of fall chum salmon towards the fisheries on the right hand shore are intense only when the water level rises. When the water level is low in the firth the chum salmon sensing, so it seems, a slowing up of the current in the Sakhalin navigation waterway channel at the north-west coast of Sakhalin, evade moving in this direction and pass through to the mouth of the Amur river by way of the left, mainland coast along the Northern navigation channel.

Seeing that summer chum salmon are less particular with regard to the water level than the fall chum salmon, the catch of summer chum salmon by the fisheries plants on the right shore is always larger than that of fall chum salmon by the siad fisheries plants (Table 1). Least particular with regard to the water level, are pink salmon and their runs towards the fishing plants on the rights shores are the same in low and in high water. Most of them are caught precisely there from year to year.

The different behaviour of summer and fall chum salmon and of other species of salmon as regards the level of the water is seen in the fact that their run from the sea is determined or conditioned by a definite level of the waters of the Amur river.

Table 1 (Page 116, illustration is illegible)
Distribution of catches by fishing plants on the left and the right shores of the Amur firth in 1934-1945. (according to data by A.G. Smirnov, on a percentage basis).

The Amur river, like many other rivers, has two flood periods: one in the spring due to the thawing of the snow and one in the fall due to the abundant rainfall at the end of summer in the Amur valley. As has been pointed out by V.K. Brazhnikov the variations in the water level are largest in the upper section of the lower reaches of the Amur. As the flood waters move down the river they seem to "vanish"; this is also observed in the section from Niko laievsk to the mouth of the Amur, though on a smaller scale. Seeing that the snowfall in the Amur region is light and that the snow melts slowly the spring freshet is not large. The level of the water rises much higher as is seen in Fig. 3 as a result of flood waters in the fall.

The run of salmon in schools in the Amur firth, if it is to be studied as a whole from spring till late fall can be divided into two periods: the first- the spring-summer which embraces the run of salt water trout, of pink salmon and of summer chum salmon (end of May- beginning of August) and the second the fall run-corresponding with the mass run of fall chum salmon (end of August- beginning of October). Between these periods, i.e. between the end of the mass run of summer chum salmon and the appearance of schools of fall chum salmon lies a period of calm regarding runs, which continues from two to three weeks. During this time there is a movement of the last specimens of summer chum salmon and even of pink salmon and the appearance of individual specimens of fall chum salmon; but this does not change the picture: fishing has come to a standstill at this time.

Figure 3. (Page 117) (Drawing illegible). Variations and comparative height of the horizon of the water in the upper (2) and the lower (1) sections of the lower reaches of the Amur river from May till Nov. in 1945.

As is seen from the above no interruption or break between the runs of salt water trout, pink salmon and summer chum salmon was ever observed: on the contrary the termor dates of the run of pink salmon and that of summer chum salmon overlap and it often happens that large numbers of the one and the other enter the river simultaneously. On the other hand the run of fall chum salmon is separate from the run of other salmon.

One can not but see the relation between the periods in the run of salmon, of which mention was made above, and the two rises in the level of the water in the Amur rivers that were noted above. The

beginning of the spring-summer run (salt-water trout, pink salmon and summer chum salmon) follows the less significant rise of the water level in the spring. The run of fall chum salmon follows the second, more significant, rise in the water level in the Amur; the heavy run begins only after the water has attained a certain level. The period of calm in the run of salmon coincides with the low water level in the Amur river.

It must also be noted that the main body of summer chum salmon enters the Amur when the water level already has been considerably lowered. Figure 4 shows a comparison of the dynamics of the spawning run of summer and fall chum salmon and the "course" of the level of the water in the lower reaches of the Amguni river near the Sergiye-Mikhailovsk village. As is seen from the drawing the run of fall chum salmon coincided with a considerable rise of the water in the river. With regard to summer chum salmon it must be said that their main body proceeded upstream when the water was low; furthermore, large rises of the water level were accompanied by a decrease in the runs of summer chum salmon. It seems that summer chum salmon evaded moving against the current, which had grown stronger due to the higher water level. Thus fall chum salmon enter the Amur river and its tributaries at a higher water level and against a stronger current than summer chum salmon and pink salmon.

Fig. 4 (p. 118) - Variations in the water level and the dynamics of the spawning run of summer and fall chum salmon in the lower reaches of the Amguni river, 1949). (Illustration is illegible)

It is also necessary to point out the fact that the most important spawning rivers of fall chum salmon (the basins of the Ussuri,

Khungari, Aniuya, Kura, Biry, Bidzhana rivers) are within the area of the heaviest spring freshets; but the main non-spawning rivers of summer chum salmon (and of pink salmon) are within the area of the lowest spring freshets.

The following phenomenon is also being observed: among the fall chum salmon the largest specimens- "the runners" and the fish of the first runs enter the Amur river when the waters of the freshets are high; the smaller fish of the last runs enter the Amur river from the sea after the level in the river has started to redede. Thus the first ones succeed in getting to the spawning rivers whilst the level is still quite high and the current is fairly strong; but the latter ones - when the level is much lower and the current is less strong. Under such different conditions the specimens of various runs complete their further ascent to the spawning grounds: the specimens of the earlier runs go farther upstream in the spawning rivers (Navozov-Lavrov, 11).

The biological significance of the described peculiarities of the run of summer and fall chum salmon can be understood, it seems to us, from the following. Pink salmon and summer chum salmon, in comparison with the fall chum salmon, do not go up very far in the Amur river and its tributaries. The majority of the rivers visited by these salmon are not very long. The spawning grounds of pink salmon and summer chum salmon are located in the middle and lower reaches of these rivers, in the main riverbeds at that or in channels and quite less frequently in springs.

Fall chum salmon ascend much higher in the Amur river. The most important rivers, visited by them in the Amur basin, are of considerable

length and in these rivers a large number of fall chum salmon ascends to the very source or upper part of waters. In those rivers, which are visited by pink salmon as well as summer chum salmon, fall chum salmon, as a rule go up farthest.

Finally, fall chum salmon, in distinction from pink salmon and summer chum salmon, spawn not only in the main beds of spawning rivers; but to go up for spawning into the channels and springs that are remote from the main bed of the river, to places that abound with subsoil water. As has been said before, the specimens of the first runs go up exceptionally far in spawning rivers.

Fall chum salmon, so it seems, must to a larger extent than summer chum salmon, overcome on their way up numerous obstacles in the form of rapids, sandbars and wooden obstructions the number and dimensions of which grow the further they ascend in Siberian (sylvan) forest-mountain rivers. In connection with this it must be borne in mind that in order to overcome and the same natural obstacle the fall chum salmon, due to their larger size, require a higher water level to cover these obstacles than would be needed by pink salmon or summer chum salmon. It is natural that the penetration of fall chum salmon to the head-waters of spawning rivers and to remote springs and channels and their normal distribution over the spawning area in the basin of a given river- can only be safeguarded by a high water level, which must be higher than the one which meets the needs of summer chum salmon and of pink salmon.

G.V. Nikolski (12) expressed the opinion that the size of salmon and the rate of growing fit and fleshy clearly is coordinated with that distance, they must move when proceeding to their spawning grounds.

If that is so and there is no reason for doubting it, i.e. if we are to assume that there is a definite connection between the size and fatness of the transient fish, and the length of the spawning rivers as well as the distance they travel upstream, as was observed by many authors - it can be then stated with certainty that the supply of nutritive substances accumulated by salmon in the sea is strictly calculated for the migration route covered by them to the spawning grounds.

The river period of spawning migrations calls for the greatest efforts on the part of salmons; upon entering rivers the salmon cease to feed. A rather rapid burning up of nutritive substances may lead the organism of these fish to complete exhaustion and to death before they reach the spawning grounds and start to spawn. It is easily seen that the dates of the runs of salmon are timed with a certain water level and speed of the current which safeguard an economical expenditure of energy and a safe arrival in the native rivers, and distribution over the spawning grounds and, in the end, to a successful reproduction of progeny in such members for further continuation of the species.

III. About the origin of the fall form of chum salmon in connection with some peculiarities of their ecology and distribution.

"The main conclusion from the theory of Darwin, - as pointed out by V.V. Vasnetsov (5) - is the statement that all the traits of the species, its morphological and physiological peculiarities, the forms of the relations with the outside environment appear in the process of historical development, in the result of the action of natural selection, and consequently they are adaptable. Those must be regarded - the same author continues - as adaptive peculiarities of organism,

i.e, their structure, physiology, behaviour, which will safeguard the survival of a number that is necessary for the continuation of the species (individuals). In the light of these indisputable statements it is impossible not to see that the relation of salmon to the water level and to the currents of their migrations is adaptive. Therefore one may speak of a definite exaction towards these factors during the period of migration. It corresponds to the morphological peculiarities of every species of salmon. But the morphological differences of specimens of a given species, varieties, races etc. are shaped by themselves under the influence of "concrete" conditions of the outside environment. The organism, as pointed out by T.D. Lysenko (9), builds itself up from the conditions of the outside environment. (The last sentence may be still somewhat vague. Tr.) It becomes what it is as a result of the assimilation of the conditions of its existence. From this follows that the demands made by summer and fall chum salmon (and by other salmon) with regard to various factors of the outside environment are specific for them. They represent one unit together with the morphological peculiarities inherent in these fish.

L.S. Berg (1) has classified fall and summer chum salmon as seasonal races. The morphological differences that exist between them are generally known: a different rate in growth, hence different sizes, weight and fecundity; different conditions regarding the gonads when entering a river, different dates for running and spawning and a difference with regard to moving upstream the Amur river. The origin of both races, as already observed by P.Yu. Shmidt at one time (17) remained unclear, seeing that their connection with any ecological factors had thus far not been established.

After the above mentioned - as the most important ecological characteristic of fall chum salmon - its difference from summer chum salmon- it is possible to point out that the run of these fish is timed to the fall freshets, i.e. to the highest level, in the Amur river and its tributaries and, therefore, to the time of the heaviest run-off and the swiftest currents along the migration routes. The second, just as important an ecological peculiarity of the fall chum salmon is their spawning, in distinction from summer chum salmon, in areas, as has been said before, are noted for shallow depths and can be used to the fullest extent only during high water levels. These two ecological peculiarities represent essential advantages with regard to summer chum salmon - for the distribution in the Amur basin.

Summer chum salmon do not move upstream vary far in the Amur river - they grow in numbers making fishing worthwhile in the vicinity of Ulchi river (about 600 km from the estuary); their spawning rivers are "concentrated" in the lower stream reaches. Fall chum salmon spawn in the majority of rivers that are visited by summer chum salmon, but their overwhelming numbers move upstream much farther in the Amur river; in numbers making fishing unprofitable - near the Kumara river (200 km above Blagoveschensk). The main spawning rivers of fall chum salmon are: Khungari, Aniuy, Bikin, Iman, Khor, Kur, Bira and Bidzhan - are within the region of the Amur river that has a stronger run-off and the highest flood water level. Footnotes: 5. V. Lebedev, who was in this region in 1948, reported to us about the entering of fall chum salmon into the Kumaru (Khumarkhe) river.

6. One of the regions of increased run-off on the Amur is considered the Sikhote-Alin mountain range, being the source of the

first five tributaries - rivers; the other or the second to the (illegible) Burainsk mountain range) especially towards the upper reaches of the Selemdzhi river) the source of the other rivers. It is possible that the entering of the main body of fall chum salmon into these rivers is connected with the abundant flow of fall flood waters into the sea, which serve as a guide for fish that are headed for regions with an increased running.

The spawning area of fall chum salmon in the Amur basin stretches from north to south from the Langrova river and other rivers of the Amur firth to the sources of the Ussuri river (the Ulakhe and Daubikhe rivers) and from west to east from the Selemdzhi and the upper reaches of the Amguni river in the foothills of the Bureinsk mountain range to the upper reaches of the Khor, Bikin and Iman rivers in the eastern foothills of the Sikhote-Alin mountain range. Within the limits of such a large territory, it is natural to observe a variety of climatic conditions. The thickness of the ice-cover in the Amur basin also varies greatly. In the lower reaches of the Amur and Amgun rivers that have the heaviest snow-fall the ice-cover is considerably thinner than in the Khabarovsk region and in the basin of the Ussuri river, where the snow-precipitation is very light (V.B. Shostakovich, 18).

Returning to the distribution of summer and fall chum salmon in the Amur basin it can be noted that the spawning grounds of the first are within the area of the heaviest winter precipitation and of the slightest freezing up of rivers. The main body of fall chum salmon spawn in an area with a light rainfall in winter and where the rivers freeze to a greater depth.

It is observed every year on the Amur that the spawning grounds

of salmon freeze up, which is severest in cold winters with little snow. This freezing up, first of all, reaches the shallow sections of the beds of tributaries and brooks, which are remote from sources of subsoil waters.

In such areas, as has been said already, the spawning grounds of summer chum salmon are located; although their spawning rivers are located in a region with a relatively abundant rainfall, the ground in their spawning areas freezes to a depth of 1m and more (Smirnov, 14), which leads to a mass, at times, complete destruction of roe (?) in the nests of redos.

In the light of the above the adaptive significance of the fact that the spawning grounds of fall chum salmon are always located in areas that are fed, more or less, with subsoil water, it quite clear. Though such spawning grounds are characterized by shallow depths they are affected by frost to a much lesser extent; only the top layer of mounds or redds is touched. The adaptation to such spawning grounds for the purpose of natural increase has greatly diminished the loss of roe through frost or inter-destruction. The adaptive significance of the spawn of fall chum salmon in areas with subsoil feeding will become more evident, if we consider that the main spawning rivers of fall chum salmon are within a region with light snow-precipitation.

Thus if the adaptation to run up stream the river under conditions of a high fall flood level, and the swiftest current, provided fall chum salmon with an opportunity to move up stream farther in the spawning rivers and to occupy for spawning the largest aquatic territory within the basin, then the adaptation for propagation on spawning grounds with subsoil feeding made possible their successful

breeding in regions with light precipitations in winter and a greater frost penetration in the rivers.

It should be understood however, that the extension of the region of the distribution of summer chum salmon in the Amur basin to the limits or bounds, that are peculiar to fall chum salmon, could take place only if the summer chum salmon could adapt themselves to the ecological conditions under which the fall chum salmon migrate and reproduce. But then they would be no longer anadromous chum salmon.

Finally, it seems to us, that the autumn chum salmon, in distinction to summer chum salmon, is a race (or an ecotype) which is adapted: a) to reproducing in areas of spawning waters with, primarily, subsoil feeding and all the ecological conditions derived from them; b) to migrating under high flood conditions and greatest current speeds. In connection with such adaptation it became possible to the said race (ecotype) to spread most widely within the limits of every spawning river in the Amur basin, including the regions with light precipitations in winter, with the heaviest frost penetration and increased run-off.

The tremendous size of the aquatic territory within which the river migration and spawning of fall chum salmon take place, itself, undoubtedly, exerts a benevolent influence upon the reproduction of the reserves of this salmon; on the one hand - a large part is played here by the dimensions of the area, and on the other hand there is also the fact that in various rivers, in dependence upon their hydrological regime and local climatic conditions, these or other factors, that are harmful to roe and larvae, affect the yield of progeny in various ways: upon some their influence is stronger -

upon others it is weaker, and again for others the conditions may be so favourable for the development of progeny as to provide a sufficient numerical strength for the new generation.

In addition there exists another, apparently extremely favourable characteristic in the propagation of the autumn chum salmon. A hitherto unexplored aspect of the distribution of Pacific salmon in spawning of two or more species in one and the same spawning rivers, when their spawning grounds overlap, if the conditions for reproduction in a given area are, suitable, to a certain extent, to each type. There is every reason to believe that the use of one and the same spawning grounds by various types is a phenomenon, which limits (to a certain extent) their numbers. A similar statement was made at one time by I.I. Kuznetsov with regard to summer chum salmon and pink salmon (7). It is known that the spawning runs of these fish, to a remarkable degree, coincide with regard to time their spawning grounds are often the same, and they often spawn at the same time. In all rivers, that are jointly visited by these two species there has been observed a proportional conformity, with regard to their numbers: where there are pink salmon in abundance there are few summer chum salmon and, the other way around, where there are few pink salmon there are more summer chum salmon. In a word, in spawning rivers the various species of migratory salmon may, so it seems, coincide not only with "native" species but also with one another (by having a common spawning ground).

Fall chum salmon was the only species to avoid such encounters, on the one hand, due to its later arrival in the spawning rivers and, on the other, due to the separate, in most cases, spawning grounds within the limits of each spawning river and the distribution within the Amur basin far beyond the limits of distribution of other migratory

or transcient salmon. At the same time seeing that mostly all spawning rivers of summer chum salmon serve also as a place for the reproduction of pink salmon, 19 of the spawning rivers for fall chum salmon, the main ones at that, are not frequented by other salmon.

Thus the distribution grounds of fall chum salmon in the Amur basin beyond the limits of the distribution of other species as well as the appropriation of spawning grounds, that are fed by subsoil water, give them important advantages over the summer chum salmon, namely in that they safeguard a successful reproduction for progeny. Equally clear is also the adaptive significance of the wider distribution for the fall form of chum salmon and the entire species in general.

However significance of the described peculiarities of the distribution of summer and fall chum salmon are not yet exhausted by what has been just said. The varying latitude of distribution has, undoubtedly, determined the generally known morphological peculiarities of these fish. The lengthening of their migrations under conditions of a more powerful rise in the water level and against swiftest currents was obviously conducive to an increase in the tempo of fleshing up and of natural indicators of growth. The features that are peculiar to fall chum salmon were developed gradually and have become fixed by heredity and set them off advantageously over to summer chum salmon: a quicker rate of growth, larger size, fleshiness and, in dependence of size, also greater fecundity products of fall chum salmon at the time of entering the Amur river, is connected, so it seems, with the fact that they face a longer journey to the spawning grounds.

Thus if it were possible to compel summer chum salmon to reproduce under conditions under which the fall chum salmon reproduce, the dates and the durations of their river migrations would be changed gradually and subsequently also their morphological indicators.

The result would be a faster growing, a more productive form of chum salmon, with a more steady numerosity, i.e. fall chum salmon.

Fig. 5 (page 123) Distribution of fall chum salmon according to size (on a percentage basis with respect to the total number of specimens) in various rivers, 1948 and 1949: from the left 1) .. in the Amgun river from August 16 to September 15, 1948, 540 specimens and 2) _____ in the Khivanda river from September 16-27, 1948, 367 specimens; from right 1) _____ in the Amgun river from August 30 to Sept. 19, 1949, 2000 specimens and 2) _____ in the Khor river from October 3-25, 1949, 369 specimens. (Illustration is illegible)

Together with the tremendous spawning (illegible) territory goes the qualitative heterogeneity within the confines of each race. In order to become convinced of that it is sufficient to compare the sizes, let us say, of fall chum salmon from spawning rivers that are quite remote from each other. Table 2 and Fig. 5 show the size of in the runs of fall chum salmon in two rivers - Amgun and Khivand in 1948. The material of 1949 (Table 3 and fig.5) permitted us to compare the fall chum salmon from the Amguni river with fall chum salmon from the Khor river. But before entering upon a discussion of the data obtained it is necessary to say a few words about the rivers fore named.

The Amgun has its source in the Bureinsk mountain range and empties in the Amur on its left bank at about 200 km from the sea.

This is one of the larger rivers of the Amur basin (900 km). But regardless of its considerable length and its proximity to the sea its significance as a spawning ground for fall chum salmon is not great, though at the same time this river is one of chief spawning rivers for summer chum salmon.

The spawning ground of fall chum salmon are primarily located in the tributaries of the upper reaches of the Amgun river (Badzhal, Duki and others) and, therefore, the main body of them moves far upstream (illegible) the Amgun river.

Table 2, and Table 3 (page 124) are illegible.

Table 4, illegible.

The Khivanda river, a tributary of the right bank of the Amur river, about 500 km from the sea, is about 160 km long. Mass spawning is being observed in this river already at a short distance from the estuary. According to data, obtained the chums salmon do not move far upstream to spawn along the Khivanda river.

The Khor river is a tributary of the Ussuri river on its right bank; it is of considerable length (500 km). No data are available regarding the spawning area of the Khor river, but it is assumed that the area is very large. The significance of the Khor river with regard to the reproduction of fall chum salmon reserves is rather great and surpasses, so it seems, that of the other spawning tributaries along the right shore of the Amur and Ussuri rivers (Aniuy, Khuggari, Bikin, Iman) not to speak of the tributaries of the Amur on the left side such as the Bidzhan, Biraa(?) Tunguska rivers; their significance as spawning ground is negligible.

Let us now proceed to compare the dimensions of fall chum salmon from the rivers just mentioned. In 1948 chum salmon from the Amgun river were shorter or smaller than the fish from the Khivanda river by 2.7 cm. The correlation of various "size groups" in the school of fall chum salmon in the Amgun river varied from that which had been observed in the Khi vanda river; ub the latter the relative number of large specimens was considerably larger than in the Amgun river, but the number of small fish was correspondingly lower, which points to a rather big difference between the sizes of the fall chum salmon of the Amgun river and the Khivanda river. Still greater differences in size were seen, when with those of fall chum salmon from the Amgun and Khor rivers compared (according to material of 1949): on the average chum salmon from the Khor river was ~~KX~~ larger by 5.6 cm than the ones from the Amgun river. The distribution of specimens according to size in the above named rivers is altogether different in the Khor river the relative number of large fish would be much higher, but that of smaller fish - much lower than in the Amgun river.

The differences in the size of fall chum salmon were so great in various rivers that made us suspect whether or not these differences could have been due to the age groups. We had a chance to compare the correlation of the age groups of schools of fall chum salmon of the Amgun and Khivanda rivers. In both rivers (Table 4) the four-year-olds were the predominant age group (3 -), which has been observed year after year in the entire body of shum salmon of the Amur river. Relatively the number of fish that were younger (2 - and 3 -) was a little higher in the Amgun river than in the Khivanda river (by 2%).

It was evident however that it was not only the age difference which determined the smaller dimensions of chum salmon in the Amgun river. As is shown by Table 5 specimens of the same age (3 -) were of different dimensions in the Amgun and in the Khivanda rivers, which, in turn, maybe explained by their varying rate of growth during their second year of life.

It is easily seen from Table 6, which contains data about the condition of the sexual products and the fecundity of fall chum salmon in the Amgun and Khor rivers, that the fall chum salmon of various spawning rivers is distinguished by these signs or marks as much as by others. As in previous cases the material which is presented in Table 6 was compiled during the continuous run of chum salmon into each of the rivers afornamed.

Table 5 and Table 6 are illegible (page 125)

The differences in fecundity are particularly essential. With regard to the Amgun fall chum salmon in 1949 it was lower on the average - by 574 roe-corns than that from the Khor river. These differences, so it seems, depend not only on the size of the fish. It has been established that with the same length of body (65.5 - 66 cm) the average fecundity of females from the Amgun river was lower by 304 eggs than that of females from the Khor river.

One must also assume that because of the positive correlation (co-efficient 0.4) between the length of the body and the size of the roe-corns the Amgun river, the main mass of the spawn roe deposited in the ground was smaller than in the Khor river considering that the relative number of small fish in the first river was rather large and

considerably higher than in the latter, but the relative number of large fish was correspondingly smaller (Table 7).

Within the limits of the species a decrease in the size of eggs together with a decrease of the size of the body is, no doubt, of adaptive significance. This condition, it seems, does not cause a decrease in fecundity to a degree, which could reduce the numbers of the species, and in some cases it even safeguards a relatively high rate of fecundity. The above was confirmed by a comparison of summer and fall salmon (Table 8). The absolute fecundity of the Amgun fall chum salmon was higher by almost 1000 roe-corns than that of the summer chum salmon in the same river. Considering however, the identical body weight, the number of eggs was higher in the summer chum salmon, in this case by 239 eggs; this may be explained by the fact that the roe of the latter was smaller than that of the fall chum salmon: in 20 gr. of roe from summer chum salmon there were, on the average, 54 eggs more than in the roe of fall chum salmon with reproductive products in practically the same stage of development.

The morphological differences between the fall chum salmon of various rivers of the Amur basin, which, it is possible, point to the presence of biological groupings within the confines of the given generation or of local schools which usually remain in the largest tributaries of the Amur river, are, if not with respect to size, then with respect to their character similar to the differences between the summer and fall chum salmon.

The fact is that the summer and fall chum salmon differ in regard to size and fecundity; this is also observed when fall chum salmon from various rivers were compared. The summer and fall chum

salmon of the same river differ in respect to the size of the roe-corns. The fall chum salmon of various rivers is separated by means of this characteristic.

We emphasize once more, on the strength of the above, that the considerable dimensions of the spawning territory occupied by chum salmon in the Amur basin and the various bounds of distribution within its confines served as a foundation for the origin of the morphological peculiarities of chum salmon of the summer and fall runs.

Table 7 and Table 8 (page 126) are illegible.