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Some peculiarities of linear growth and scale structure of Pacific salmon.

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Assuming the knowledge of the general biological regularities of a given species, examination of the scales on a fish is, as it is known, an important means of clarifying those ecological peculiarities which are inaccessible to direct observation due to the specific aspects of the object.

The examination of scales on the Pacific salmon, as a rule, does not involve great difficulty, Nevertheless, there are controversies concerning some of the details of the scales which have not been clarified as yet. Some of the authors (Vedenskii, 1954; Lapin, 1963, 1964) dispute the generally accepted opinion about the two-year life cycle of the salmon and accept as growth rings those formations which are disregarded in the determination of the age of the salmon by other authors. It is obvious that the revision of the question concerning the age leads to the revision of other concepts in the biology of the salmon, and also leading to attempts to find new solutions to some of the problems of population dynamics of this fish. Consequently, the question of the nature, conditions and time of

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annular formation and similar formations is not only of theoretical but also of practical interest. In addition to this, without the clarification of this question a correct description of the periodicity of the growth is not possible.

The nature of the annuli

It is generally accepted that the annuli of the Pacific salmon are the direct result of retardation or total stagnation in growth during winter, due to low temperature or unfavorable feeding conditions. On the basis of the width of the annuli which is, as already known, a narrow zone of connected sclerites, it was attempted to establish even the longitudinal growth of the body of the salmon during winter; in some of the papers after the word "sclerites" of the annuli the term "winter" has remained even until the present time. If we were to be guided by such calculated values of growth we would come to the absolutely false conclusion that the various species of salmon differing significantly from each other as far as their summer growth is concerned, would then have uniformly slow growth in winter (Table 1.).

Material contradictory to this concept concerning the origin of the annuli of the Pacific salmon

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Revisor's Note: For "growth ring" read "annulus."

Table 1.

Average length increase in the body of humback salmon and the red salmon during the first year of their life in the sea [cm] (according to data of back calculation)

Таблица 1

Средние (по данным обратного расчисления) приросты длины тела горбуши и красной на первом году жизни в море (см)

1 Период роста	Горбуша 2		Красная оз. Дальнего (по Крогиус, 1960) 3	
	Приморье (по Миловидовой-Дубровской, 1937) 4	Бассейн Амура (по Енютиной, 1954) 5	возрастные группы 3_1+ и 4_1+ 6	возрастные группы 4_2+ и 5_2+ 7
8 Лето	24,2	24,3	14,5	15,0
9 Зима	3,2	3,6	3,6	3,5
10 За год	27,4	27,9	18,1	18,4

1 - period of growth; 2 - humback salmon; 3 - red salmon, Lake Dal'nee (according to Krogius); 4 - seacoast (according to Milovidova - Dubrovskaya, 1937; 5 - Amur-basin (according to Enyutina, 1964; 6 - age groups; 7 - age groups; 8 - summer; 9 - winter; 10 - during a year.

was first compiled in 1959. As it was reported (Birman, 1960-a), on 47 specimens caught in April of that year in the waters south of the Western part of the Aleutian ridge, annuli were found on their scales and, in addition to this, 7-13 (on the average 9,7) wide "summer" type sclerites in the second year growth (Fig.1.). About the same conditions were found on the silver salmon. On the other hand, a portion of the keta salmon and red back salmon caught at the same time had no annuli at all, whereas other fish had them but without the slightest sign of further growth. Thus, it was concluded that the humpback salmon (as well as the silver salmon) grows well in winter, the growth rings form not later than the middle of January and consequently these are not characteristic of the winter growth. On the keta salmon and redback salmon the growth rings form during spring: on the former generally in March, on the latter in April. For this reason, neither in this case do the growth rings characterize the winter growth conditions. In all four species (and obviously in the other salmon) the growth rings form only at the beginning of a new growth period, and are the result of same.

Kobayashi (1959). whose work we learned about belatedly, also indicates that in May a portion of the four-year-old keta salmon still did have the outer growth ring and that these differed from those in the fourth year (3+) only by the higher number (6-18 against 4-5) of sclerites in the last year's growth.

Concerning the Atlantic salmon (from the rivers of Scotland and Finland),it should be noted that there are earlier indications from Jarvy and Mensies, 1936 (quoted according to G.P. Barach, 1946) that during winter no condensed sclerites on their scale i.e., no formation of growth ring, but only growth stagnation was observed, Consequently, the growth rings are the result of a subsequent renewal of growth. It is true that these indications relate to the fresh water period, however,these may also apply to the period spent in the sea, since it is probable that the seasonal variations of the environment (temperature, food supply) will influence in the same way the growth of scales in fresh water and in sea water as well.

It was proven very convincingly by Lapin (1965) by histological investigations of the scale structure of herring and carp that during the stagnation of the growth of scales in winter no mark was formed on their edge, and that the growth rings were only the result of the renewal of growth.

Concerning the humpback salmon, Vedenskii (1954) has reached similar conclusion, i.e., that the growth rings do not reflect the growth conditions during winter; however, he was of the opinion that the humpback salmon do not grow in winter at all, and that their growth rings form either before the total growth stagnation during winter, or after the renewal of growth during the first weeks of spring. Vedenskii was more inclined to the second variant; he has supposed that during winter the humpback salmon stays in the cold water which is impoverished in plankton; however we already know that this is not true. The assumption of Kaganovskii (1949) has been proven, according to which the humpback salmon migrate into relatively warn waters during winter. Observations (Birman,1960 b) have indicated that in winter the humpback salmon migrate into the blending

zone of subarctic and subtropical waters, further south than the 3-5° isotherms. The majority of the humpback salmon hibernate in the 5-8° isotherm range, whereas other fish will spend the winter further south, and there the hibernating regions of the humpback salmon are not so poor in nourishment. As it was proven by Mednikov,1961), till the end of April the blending zone has sufficiently high quantity of plamktonic biomass. During winter, in December-January, the
16/17 propagation of some species of copepods Calanus cristatus, C. plumchrus) takes place in mass. In addition to this, there are abundant quantities of pteropoda mollusks present as well as other important foods for the salmon. This means that the salmon(in the first place the humpback and silver salmon) hibernating in the blending zone are under adequately favourable food conditions.

As far as the second assumption of Vedenskii is concerned according to which it is possible that the growth rings are formed before the total growth stagnation in winter, this is contradictory to the data of some other authors (Milovidova-Dubroskaya,1937; Dvinin, 1952; Kitida,1952 (quoted according to Miyaguchi, 1957); these data point out that the humpback salmon obtains the approximative measurements of the one-year-old salmon already by November-December, and that their scales have the number of "summer" sclerites which are characteristic of the one-year old salmon; however, the scales have no growth rings, and any marks of the retardation of the growth may be observed. During this time the growth is either not intensive enough as yet, or it has just stopped. Evidently, at this time there can not be any growth rings as yet.

This means, that the question about the formation time of the growth rings of the humpback salmon was approached by Vedenskii with the conviction that the width of the ring is too great for winter, since in his opinion the humpback salmon do not grow in winter at all. Actually, this width is too small to correspond with the winter growth of the salmon, and as was shown by us, it only indicates the very beginning of the winter growth. This is now an established fact without any doubt. Ricker,1964 , has stated in his last paper that three humpback salmon caught in the Alaska-bay on January the 24th, 1963 already had growth ring on their scales, and in addition to this two of them had two sclerites each in the second year growth. By this fact as it is noted by Ricker, our assumption (Birman,1960) is fully proven, that the growth rings of the humpback salmon are formed not later than the middle of January. The same indication was found on the scales collected during the passage of the ship "Amethyst" in the Southern part of the Sea of Japan.

We have planned the route of the ship "Amethyst" so we could repeat the catching of salmon on the one and the same station at about one-month intervals. The result of this repetition of the route was that we had the possibility of clarifying the dynamics of the main quality characteristics (length, weight, stages of gonad) of the humpback salmon, and the pattern of the growth of scales for the hibernating period, perhaps even including the very beginning of the spawning migration in April. Here we present only the data relating to the growth of scales (Table 2.).

Table 2.

Change in the number of sclerites in the growth of scales during the second year of humpback salmon in the Sea of Japan from February to April 1965

Таблица 2

Изменение числа склеритов в приросте чешуи за второй год у горбуши Японского моря с февраля по апрель 1965 года

Дата	Число склеритов в приросте второго года				Число рыб	Длина горбуши, см	
	в пределах годового кольца		в последующем приросте				
	пределы колебаний	среднее	пределы колебаний	среднее		M	Число рыб
8—11/II	1—3	1,8	3—8,5	5,3	23	34,5	70
11—12/III	1—3	1,5	5—11	8,0	28	36,1	128
10—14/IV	0—3	1,5	7—14	10,3	27	38,2	202

1 - data; 2 - number pf sclerites in the second year growth; 3 - within the annuli 4 - variation limits; 5 - on average; 6 - in subsequent growth; 7 - number of fish ; 8 - length of the salmon, cm.

As we may see from the data presented in Table 2. between February 8-11 the humpback salmon already had about five new growth sclerites above the growth ring (Fig.2.).

After a month (March 11-12) there were already eight of these, i.e. on the average three more sclerites were formed. Supposing the same rate of scales growth during January, it is clear that the growth rings should have been formed at approximately the beginning of January. Assuming a lower rate of scales growth for January, we would find that the ring was formed already in December, however as it has been stated above, a growth ring has never been observed
17/18 yet on a humpback salmon caught in December.

Thus, the scales of the humpback salmon grow fast during almost the entire winter (maybe not slower than during summer); their growth rings do not form either before or during the growing period but after a short stagnation which seems to occur at the end of December.

Evidently, the same applies to the silver salmon, too; although we do not have any such detailed data for this fish. On some silver salmon caught further south from the Aleutian Ridge in April 1959, up to 11-12 wide summer sclerites were counted in the second sea-year growth above the growth ring. The silver salmon migrate further south, pass the 5° isotherm, and it may be assumed that their food supply is not worse than that of the humpback salmon. Their growth stagnation is as brief as that of the humpback salmon.

Nevertheless, the time of growth renewal at the wintering area does not only depend on the specific external conditions. The winter range of other species (especially that of the Keta salmon) coincide partly with the winter range of the humpback salmon and silver salmon (Birman, 1960 b.); nevertheless, the annular rings form at different times. It should be assumed that under the same ecological conditions the times of growth renewal of the different salmon species could be quite different after their migration to the place where they overwinter.

As far as the reason for growth retardation is concerned, it seems to be probable that this is connected with the expenditure of food energy for other processes, for example, on the intensification of fat storage before the onset of winter. The consideration of this question is beyond the scope of this paper.

Time of formation of annuli and age

The time of ending the growth stagnation in winter and the formation of annuli in salmon, as well as in other fish (Chugunova,1959), is connected with their age. However, when discussing the migrating salmon, the majority of which spend a significant part of their life cycle in fresh water, we have to clarify whether the formation time of the growth ring in the sea depends on the number of years spent in sea.

It is quite possible that the formation time of the growth rings in fresh water depends on the years spent in fresh water. In order to clarify this question, let us analyze the scales of fish caught in the spring of 1959 in the region South from the Aleutian ridge.

R e d b a c k s a l m o n . On the majority of the four-year old fish (Table 3.) which have spent two years in fresh water and two years in the sea (4_2+), the scales were finished were the corresponding number of growth rings and, over these with four, wide summer-type sclerites. But fish were also caught which did not have this formation. More than half of the five-year-old fish (Table 4.) having spend the same period in fresh water and three years in the sea (5_2+), on the average had 3,5 sclerites in the next (sixth) year growth over the growth ring; however a portion of the fish did not yet have this formation, and one fish was found on which even the growth ring was not formed.

Thus, the conclusion may be drawn that on the red back salmon the second and third growth rings in the sea do not form exactly at the same time. The second ring will obviously appear not later than March, whereas the formation of the third ring may be delayed in some fish until May.

K e t a salmon (Tables 5,6). Eleven of the fourteen three-year-old fish caught already had the next growth ring

in the second half of April, and in addition to this more than the half of the fish had 2-3 "summer" sclerites in the fourth year growth. At the same time the majority of the four-year-old fish did not have the next growth ring, whereas on those which had it not even the slightest mark of further
18/19 growing was observed. In the first half of May almost every three-year-old fish already had the new growth ring, but among the four-year-old fish it was present in only a little more than half of the specimens. This means that there is a significant difference in the formation times of the growth ring between the three-year-old and the four-year-old Keta salmon. The third growth ring is formed mostly at the beginning of April, and on some of the fish, obviously even in March, whereas the fourth ring is formed generally in May, however at times it may be delayed until June. Now and then even in June some four-year-old specimen may be found which does not have the next growth ring; this fish may be erroneously considered salmon in their fourth year (3+) if we do not take note of the large number of sclerites which are too numerous for the beginning of summer.

Analyzing the data of Kobayashi (1959) published in the quoted paper, Ricker has drawn the conclusion that the third growth ring on the Keta salmon is formed at
19/20 about April 12 and the fourth ring at about April 25, i.e., significantly earlier than it follows from our data; but

this way or an other, the later formation of the growth ring on the older fish is an established fact.

Table 3.

Characteristics of scales on the four-year-old redback salmon which has spent two years in fresh water and was cought in April 1959

Таблица 3

Характеристика чешуи четырехгодовалой красной с двумя пресноводными годами, пойманной в апреле 1959 года

Без четвёртого (второго морского) годового кольца	С четвертым годовым кольцом (экз.)		Общее число рыб (экз.)	Среднее число склеритов в приросте 5-го года, сверх годового кольца
	без последующего прироста	с последующим приростом		
—	1	13	14	3,6

1 - without the fourth (in the sea the second) growth ring; 2 - having the fourth growth ring (specimens); 3 - without next year's growth; 4 - with next year's growth; 5 - total number of fishes (specimens); 6 - average number of sclerites in the fifth year growth above the growth ring.

Table 4.

Characteristics of scales on the five-year-old redback salmon which has spent two years in fres water and was cought in April 1959.

Таблица 4

Характеристика чешуи пятигодовалой красной с двумя пресноводными годами, пойманной в апреле 1959 года

Без пятого (третьего морского) годового кольца (экз.)	С пятым (третьим морским) годовым кольцом (экз.)		Общее число рыб (экз.)	Среднее число склеритов в приросте 6-го года, сверх годового кольца
	без последующего прироста	с последующим приростом		
1	2	4	7	3,5

1- without the fifth(in the sea the third) growth ring, specimens; 2 - having the fifth (in the sea the third) growth ring, specimens; 3 - without next year's growth; 4 - with next year's growth; 5 - total number of fishes, Specimens; 6 - average number of the sclerites in the sixth year growth above the growth ring.

Table 5.

Characteristics of scales on the three-year-old keta salmon caught farther south from the Aleutian Ridge in April-May 1959

Таблица 5

Характеристика чешуи трехгодовалой кеты, пойманной в апреле—мае 1959 года южнее Алеутской гряды

Дата	Ед. изм.	Без третьего годового кольца	С третьим годовым кольцом		Общее число рыб (экз.)
			без последующего прироста	с последующим приростом	
15—30/IV	шт.	14	16	34	64
	%	21,9	25,0	53,1	100,0
3—12/V	шт.	5	33	63	101
	%	4,9	32,7	62,4	100,0

L - data; 2 measuring units; 3 - without the third growth ring; 4 - with the third growth ring; 5 - without next year's growth; 6 - with next year's growth; 7 - total number of fishes (specimens); 8 - pieces.

Table 6.

Characteristics of scales on the four-year-old keta salmon caught farther south from the Aleutian Ridge in April-May 1959

Таблица 6

Характеристика чешуи четырехгодовалой кеты, пойманной в апреле—мае 1959 года южнее Алеутской гряды

Дата	Без четвертого годового кольца (экз.)	С четвертым годовым кольцом (экз.)		Общее число рыб (экз.)
		без последующего прироста	с последующим приростом	
10—30/IV	11	3	—	14
3—12/V	6	6	2	14

1 - data; 2 - without the fourth growth ring (specimens); with the fourth growth ring (specimens); 4 - without next year's growth; 5 - with next year's growth; 6 - total number of fishes (specimens).

Thus, the younger the fish, or (more precisely) the shorter the time spent in the sea the earlier will the growth rings form. This means, that on the fish which has spent a shorter period in the sea, the retardation of the winter growth will be finished earlier, and it is probable that the retardation period is shorter as well.

On February 26,1964, in the region of N. lat. $46^{\circ}16'$ and of E. long. 174° the ship "Amethyst" has caught a 3_1+ old redback salmon, 38,5 cm long and weighing 550 g. There already were five typical "summer" sclerites superimposed on the two marine annuli. Another specimen of 4_2+ age already had three "summer" sclerites at this time. As we may see in the case of these two fish their growth was renewed very early. In any case, they were doing well in February, and it is probable that their last growth ring was formed in January, i.e., only somewhat later than that on the humpback salmon. Consequently, in the case of the redback salmon which has spent only one year in the sea, it is possible that the growth ring would form at an earlier time, i.e. at the same time as that of the humpback salmon, but not on all individuals. On the scale illustrated in Fig.3.,the growth ring was evidently formed not earlier than February. All this means that the material collected in 1964 brings a significant correction into our earlier

concept concerning the time of annulus formation.
If we have stated earlier that the growth rings of the redback salmon are formed in spring, now we have to qualify that in the first place this is true only for the fish in the older age categories. In some fish of the younger age bracket, the growth ring may form already in winter, sometimes much earlier than the onset of spring.

As far as the keta salmon is concerned, we may not say the same with as much conviction, on the other hand, if we take into account the size of the scale growth on the two-year-old (1+) keta salmon during the second summer (Fig.4), then it may be assumed that their growth rings are already formed during the winter months. However, on the redback salmon which has spent exactly as much summer time in the sea, the growth ring is evidently formed (on an average) earlier than on the keta salmon which w i n te rs in the same region. This means that the redback salmon renews the growth earlier. It is also possible that their winter growth stagnation is shorter, provided of course, that it does not start earlier than that of the keta salmon. However, taking into consideration the good capability of the redback salmon to resist the cold, this is not very likely.

Concerning the redback and keta salmon, it may be stated that the fewer years they have spent in the sea, the more they will approach the formation time of growth rings on the humpback and silver salmon, which are distinguished by the shortest period in the sea. This is also true of all other salmon. For example, on five specimens of three-year-old Oncorhynchus masu which have spent one year in the sea (3_2+) and were caught in the Sea of Japan on February 11,1965, the growth ring was clearly visible on the edge of the scale (Fig.5); whereas on the fish which has lived two or three years in the sea the growth rings seldom form during the winter but most frequently in May or June (Table 7.).

An Oncorhynchus masu caught on the high seas in winter may be assumed to be a fish which spent two years in the sea, provided that on its scale, in the zone representing the second year in the sea, it has at least eight-nine "summer" sclerites, since the minimum number of sclerites formed in this zone in a year is equal to seven. A fish which has lived only one year in the sea usually was found to have not more than six sclerites in the second year growth by March or April that have spent two or three years in the sea may not have the last growth ring as yet, and for this reason when swimming up the rivers their age may be understated by one year.

By the way, the assumption that the Oncorhynchus masu matures only in the third or fourth year of their life cycle (Navozov-Lavrov,1927 and others), is certainly not true. Semko has pointed out (1956) that the Oncorhynchus masu from Kamchatka also matures in the fifth year, but such late maturity, according to the author, is peculiar to the Oncorhynchus masu on the Northern boundary line of their habitat.. However, our observations have shown that these fish are also found in the Tumnin river, in the very center of their range, during their fifth year and at their fourth year of age, when the fourth annulus had not yet been able to form. In addition to this, as it is presented in Table 7., there are older fish here as well, i.e., five and six year olds, and even fish in the sixth or seventh year of their life cycle. This species is not as early-maturing as it used to be assumed.

Table 7.

Age and scale characteristics of the Oncorhynchus masu from the Tumnin river, June 19-30, 1959.

Таблица 7

Характеристика возраста и чешуи симы из р. Тумнин 19—30 июня 1959 года

Число лет, прожитых в море	Возраст	Число рыб без последнего годового кольца	Число рыб с последним годовым кольцом		Число склеритов в «плюсе»	
			без «плюса»	с «плюсом»	от до	среднее
2	3(3_1)	—	1	—	—	—
	4(4_2)	1	4	10	2—6	4
	5(5_3)	—	2	—	—	—
	Сумма	1	7	10		
3	5(5_2)	3	6	1	—	1
	6(6_3)	—	2	1	—	3
	Сумма	3	8	2		

1 - years spent in sea; 2 - age; 3 - number of fish without the next year's growth ring; 4 - number of fish with the next year's growth ring; 5 - without "plus"; 6 - with "plus"; 7 - number of sclerites among the "plus"; 8 - from - to; 9 - on an average; 10 - total.

From all the above consideration it follows that the explanation concerning the early growth ring formation of the humpback and silver salmon is that this ring is just the first one. The second growth ring sometimes found on humpback and silver salmon is probably formed later in the year than the first one. This assumption may be evidently extended also to the formation of the growth ring in fresh water to the case of humpback and silver salmon, as well as to the other species staying for a longer period in fresh water.

The growth rings and the periodicity of the growth

Thus, with age, and, according to the general retardation of linear growth, the growth renewal after the winter stagnation will be more and more delayed, or it will proceed at an ever decreasing rate. In a given age category the slower the growth of a given species which has spent a definite number of years in the sea the later will be the formation of the growth rings. It follows from this that the yearly scale growth, which for the majority of salmon is a decreasing value with age, characterizes not only the retardation, but also the constantly later occurring growth after winter stagnation. From the second year of its life spent in the sea, the younger the fish, the relatively greater will be the portion of the so-called summer scales growth up to the early spring or the winter period. In other words, beginning with their second year in the sea in case of the keta and redback salmon (and probably the king salmon and the Oncorhynchus masu as well), each subsequent "annual" increment will correspond to a shorter period of time than the preceding one.

It is also without any doubt that for all these salmon the first year marine growth corresponds to a shorter time period than the second. Assuming, for example, that the great majority of the keta salmon descend into the sea in June, and that their growth stagnation begins in December, then the first year marine growth will be formed over 5 or 6 months, whereas the second over 9-10 months, taking into account that the growth renews at about March and becomes retarded again in November or December. It is no wonder that, with regard to the keta salmon, the second year's growth is sometimes almost equal to the first year's growth.

On some other salmon species ("Kamchatka trout," king salmon) not only the second, but also the other subsequent yearly marine growth of the scale are equal, or almost equal to the first year growth. This is easy to explain when we take into account the late descent of these salmon into the sea and the possibility of an early growth renewal in the second and third year of their life cycle in the sea.

It should be noted that when determining the longitudinal growth of the fish by the back counting method, we usually exaggerate the length of the one-year old fish and understate the length of the two year-old fish on the assumption that the growth ring signifies a finished year, whereas it denotes the beginning of a new one. It is evident that we must carry out the back counting in the same way in the future in order to allow

comparison with the data of past years, however we have to find some other designation for the age categories. If we have designated by 1+, 2+, 3+, and so on those fish which in addition to the growth ring also have some "summer" sclerite growths, then now in the same way we should also mark those fish which only have an annulus on the scale, this in itself is a new growth.

Finally, we should note the following. Since the annulus marks the beginning of new growth, it is evident that these would not appear at all if the growth was continuous. The formation of the growth ring indicates that a growth stagnation has taken place. In order to clarify the period of the stagnation, it is necessary to determine when the growth was stopped, however, this it is impossible to say on the basis of the scales. The scales give only the possibility to state approximately when the growth was renewed.

On the other hand, when comparing the different age categories and the different species of salmon with each other, this is quite enough for our purpose. Without any doubt the winter stagnation of growth of the older fish, Since the growth ring on these forms later, is of longer duration that that on the young fish, even when taking into account a simultaneous growth stoppage (although in our opinion the growth stagnation of the older fish sets in earlier than that of the younger fish). Comparing the different salmon species with each other, then, since the first growth ring of the humpback salmon and silver salmon in the sea are formed earlier than that of the other species, it may be stated that their growth stagnation period is of shorter duration. Generally speaking, the younger the fish and the faster it matures, evidently the shorter will be its growth retardation in winter.

Reasons for the differences in the legibility and width of the growth rings

As it is known, the legibility of the growth ring on the scales of the Pacific salmon varies. In some cases the ring consists of one, two or more narrow sclerites differing sharply in their width from that of the previous and subsequent ring, whereas in other cases the contraction of the sclerites is hardly noticeable and the limits of the growth rings are difficult to distinguish. To clarify all these reasons, we have to note the following.

The illegibility, or the total absence of the growth rings may be most frequently observed on the humpback salmon and on the silver salmon, i.e., on salmon which grow more in winter than other species. Concerning the bad legibility of the growth rings on the humpback salmon, Vedenskii (1954) has already noted it at that time.

The illegibility of the growth ring in sea is less frequent on the redback salmon, and only exceptionally on the keta salmon. On the other hand, as it has been pointed out by Krogius (1959), the unclear legibility of the growth rings is a typical phenomenon for some less numerous shoals of redback salmon (e.g. in the Dal'nee and Blizhnee Lakes in Kamchatka.

22/23 In the case of the redback salmon, most frequently, the first growth ring in the sea used to be unclear. In this respect there is an undoubted similarity with the humpback salmon and silver salmon having only one ring. It may be stated that the illegibility of the ring on the redback salmon occurs most frequently when their growing is the fastest.

To summarise, the illegibility of the growth rings may be the most frequently observed on the young fast growing fish, in the first place on those species which also grow well in winter. Probably the ring indicates either that the total growth stagnation did not set in at all, or that it was short and was followed by a very intensive growth renewal. It may be said especially about the redback salmon in the Dal'nee and Blizhnee Lakes, that the starting rate of the growth renewal is higher than in the individuals of other shoals. However, it is also possible that these winter in warmer waters.

As a rule, the first growth ring on the redback salmon is wider and consists of more sclerites than the others. The same may be said about the keta salmon: with age the width of the annuli and the number of the sclerites in them will continously decrease (Table 8.). As a rule, the first growth ring is the widest on the keta salmon.

The explanation for all these is that the growth renewal and the formation of the growth ring takes place earlier on the younger fish than on the older, and at lower temperatures, therefore, at a lower starting rate. If this is true, then evidently the more sclerites there are present in a given growth ring, the earlier was its formation. On the basis of data in Table 8, it may be assumed that the growth renewal of the Amur and Hokkaido keta salmon in their second and third year starts somewhat later than in the keta salmon in the rivers of Kamchatka and Northern Okhotsk.

Table 8.

Number of sclerites in the annuli and in the "summer" zones of growth

Таблица 8

Число склеритов в годовых кольцах и в «летних» зонах роста кеты

Район	Год	Возраст	1-й год «летних» склеритов M	от — до	2-й год склериты в годовом кольце M	от — до	2-й год «летних» склеритов M	от — до	3-й год склериты в годовом кольце M	от — до	3-й год «летних» склеритов M	от — до	4-й год склериты в годовом кольце M	от — до	4-й год «летних» склеритов M	от — до	Сроки сбора чешуи
Зал. Корфа	1963	3+	19,1	15—23	5,5	4—7	14	10—18	3,7	2—6	11	8—15	2,6	2—5	6,4	4—10	25/VII—12/VIII
Р. Камчатка	1963	3+	18,5	15—22	6,1	4—7	14,4	8—18	3,9	2—7	11,4	7—16	2,9	2—6	6,6	4—10	15/VII—19/VIII
Р. Большая	1963	3+	18,4	17—24	5,3	3—7	15,3	10—21	3,6	3—5	10,6	7—15	3,1	2—6	7,8	3—12	26/VII—10/VIII
Р. Гижига	1963	3+	19,7	17—22	5,4	4—7	15,2	11—20	3,3	2—5	11,7	8—14	2,6	2—4	5,9	3—10	2/VIII
Р. Ола	1963	3+	17,4	11—23	5.1	3—7	14,1	9—17	3,4	2—5	9,9	6—15	2,7	2—4	7,0	3—11	7—9/VIII
Р. Яма	1963	3+	18,2	14—21	5.6	4—7	15,1	8—19	3,8	2—6	10.2	7—14	3,1	2—5	7,1	5—11	2/VIII
Р. Тауй	1963	3+	10,4	17—25	5.3	3—7	15,0	10—19	4,0	2—6	10,1	7—13	3,0	2—5	7,7	-	VIII
Р. Амур (летняя кета)	1963	3+	22,8	19—27	4,9	3—7	14,4	10—20	3,4	2—6	10,7	7—15	3,0	2—5	5,3	2—8	29/VII
Р. Амур (осенняя кета)	1963	3+	20.9	18—25	4,8	3—7	15,0	11—19	2.9	2—5	10,3	6—15	3,1	2—6	9,1	3—13	7/IX
Р. Абасири* (Хоккайдо)	1959	3+	29,2	25—33	3,4	2—5	13.6	9—17	2,6	2—4	9,7	5—13	2,2	2—4	9,2	2—13	X
Р. Сибецу (Хоккайдо)	1959	3+	27,7	23—32	4,0	3—6	15,6	10—19	2,4	2—4	11,6	9—16	2,4	2—4	6,9	3—12	X

* Сборы чешуи кеты из рек Хоккайдо взяты из материалов Советско-Японской рыболовной комиссии.

1 - region; 2 - year; 3 - age; 4 - first year; 5 - second year; 6 - third year; 7 - fourth year; 8 - "summer" sclerites; 9 - sclerites in the growth ring; 10 data of the collection of the scales; 11 - from-to; 12 - Korfa-Bay; 13 - Kamchatka river; 14 - Bol'shaya river; 15 - Gizhiga river; 16 - Ola river; 17 - Yama river; 18 - Taui river; 19 - Amur river, (summer keta; 20 -Amur river (autumn keta); 21 - Abasiri river (Hokkaido); 22 - Sibetsu river (Hokkaido); 23 - Data concerning the collection of scales from the rivers in Hokkaido were taken from the material of the Soviet-Japanese Fishery Commission.

Supplementary rings

As it is known, in addition to the typical growth rings, other rings which consist of connected sclerites occur on the scales of the Pacific salmon. The form of these resemble that of the growth ring; however, these are usually not so clearly defined. In the case of keta and humpback salmon these rings may be most frequently observed in the region of the first growth ring. As far as the other salmon are concerned, the supplementary rings occur seldom on these, and these are usually located just after the "freshwater" ~~zone~~ , and restricted to two or three sea-type sclerites. For these reason those are less noticable an to the best of our knowledge, no attention was ever paid to them .

The occurance of the supplementary rings frequently gives rise to uncertainty in correct age determination; thus, the clarification of their character is undoubtedly of significant interest.

K e t a s a l m o n . The supplementary rings in the kernel of the scales of the keta salmon, sometimes called "estuary" rings, are known to those who are engaged in the study of the age of this salmon; however, the structure and the origin was not taken into specific consideration as yet.

We have stated (Birman,1958) that there are a great number of fish in the keta shoals in the Kamchatka river and Penzhinski Bay which have these supplementary rings, whereas the keta shoals in the Bol'shaya river do not have these. The data relating to other years indicate, however, that such rings may be also found on the keta salmon in the Bol'shaya river although seldom (Table 9.). This means, that we may speak about the frequency of occurrence of fish having " estuary" rings in the kernel of their scales as a distinguishing mark of some shoals.

The material at hand substatiates the high frequency of occurrence of this ring on Keta salmon in a number of other rivers, for example in the Vyvenka, Anadyr', Ola, Taui, also in some other rivers.

The general structural peculiarity of these rings concerns the followings: while the sclerite in the zzone of the rings is sometimes of the same width as the subsequent "summer" sclerites of the first-year zone, nevertheless these are mostly narrower, indicating different growth conditions. In some cases the width of the sclerites approximates that of the "fresh water" sclerites; and in this way the total zone becomes similar to the "fresh water zone" on the scales of the redback, king or silver salmon. Frequently some of the last sclerites in this zone are narrower than the others and on the edge of the zone these are similar to the growth ring; in other cases, the width of all the sclerites in the "estuary" zone is about the same and these are not separated from the other and wider sclerites of the first year zone.

Table 9.

The relative quantity of fish in different keta salmon shoals having "fresh water" and "estuary" rings on the scales

Таблица 9

Относительное количество рыб с речным и «эстуарным» кольцом на чешуе в различных стадах кеты

Водоем	Год	Сроки сбора	Исследовано рыб	Рыб с речным кольцом, %	Рыб с «эстуарным» кольцом, %	Число склеритов в «эстуарной» зоне	
						пределы колебаний	среднее
Зал. Корфа	1963	VII—VIII	101	4,9	70,3	5—15	11,0
Р. Камчатка	1945	VIII	44	100	22,8	—	—
»	1947	VII—VIII	85	52,9	59,3	—	—
»	1955	VIII	94	?	33,0	—	—
»	1963	VII	67	71,0	26,8	8—16	11,8
»	1964	VII—VIII	321	24,6	24,0	7—16	10,4
Р. Большая	1940	?	46	4,3	10,9	7—15	11,6
»	1955	VII—VIII	100	0,0	0,0	—	—
»	1963	VII—VIII	394	2,8	3,0	7—12	9,1
»	1964	VII—VIII	305	2,3	8,5	7—15	11,0
Р. Гижига	1963	VIII	100	0,0	54,0	6—15	9,6
Р. Пенжина	1931	?	33	0,0	66,6		
Р. Ола	1963	VIII	50	0,0	12,0	6—14	11,3
Р. Яма	1963	VIII	19	0,0	42,0	8—10	8,6

1 - basin. 2 - year; 3 - data of collection; 4 - number of the investigated fish; 5 - with "fresh water" ring,%; 6 - with "estuary" ring, %; 7 - number of sclerites in the "estuary" zone; 8 - variation limits; 9 - on an average; 10 - Korfa-Bay; 11 - Kamchatka river; 12 - Bol'shaya river; 13 - Kizhiga river; 14 - Penzhina river; 15 - Ola river; 16 - Yama river.

The number of sclerites in the "estuary" zone varies generally from 5-to 16 with an average value of 9-11; in this aspect the various shoals of keta salmon differ only insignificantly from each other (Table 9.).

The field of narrow sclerites on the edge of the "estuary" zone sometimes resembles the form of the growth ring and could be taken for a growth ring; however, the following two circumstances should be taken into account;

1/ The number of sclerites in the first year zone on the scales of the keta salmon is of sufficiently cone stant value; even the various keta shoals do not differ from each other in this aspect. (Table 8.) The number of sclerites is generally much higher than in the "estuary" zone. For example, in the case of keta salmon from the Kamchatka river, the average number of the sclerites in the first year zone, according to the data of a number of years, varies between 25-27; at the same time there are only 10-12 sclerites in the "estuary" zone of the keta salmon.

2/ Taking into account that the "estuary" ring frequently involves a maximum of 6-7 "summer" sclerites (Figures 6,7,8), and that the growth ring indicates the renewal of growth, as it has been stated above, therefore it does not belong to the previous but to the subsequent (next) year zone, so by taking the "estuary" rings for growth rings we would have assumed the possibility of only a 5-10 cm growth per year for the significant majority of the fish, whereas other fish will reach 25-30 cm length in one year. Of course, cases of such a weak growth are theoretically possible, but these do not occur on a mass scale. In addition to this, the survival of such fish hardly can be considerable.

The question concerning the formation time of the "estuary" ring is not clarified until the present time, since we had no information about the places where the young fish live during the first months. Now, however, we have already some data concerning this question.

During the passage of the ship "Amethyst" in the Sea of Okhotsk in the region of the station N.lat. of 53°10', E. long. of 143° 53', on September 21, 1964, eighteen keta salmon of 15-19 cm length from that year's brood were caught with a fine-mesh net (mesh size: 22 mm from knot to knot) set overnight. At least four of these fish had clearly noticeable "estuary" rings in their scales involving from 9 to 13 sclerites in the core zone. In one case these sclerites were of the same width as the subsequent ones, whereas in the other cases these were significantly narrower (Figures 9,10,11). The size of the young fish corresponding to these rings, according to the data of backcounting* would be 10,3,11,6, 12,2 and 13,2 cm. /25

* At the back counting we have assumed that the scales will be formed on young fish of 3,5-4 cm length.

The young fish evidently could not reach this length in the river, consequently, this zone could not be a "fresh water" zone but an "estuary" zone.

The proximity of this fishing ground to Sakhalin Bay gives rise to the assumption that these fish originate from the Amur river, and that their "estuary" zone was formed in the fresh waters of the Amur estuary.

The formation time of the "estuary" zone was evidently July-August, since the other, clearly sea-type sclerites could not have formed in less than a month.

The terms "estuary zone" and "estuary ring" are, of course, very conditional. These may be applied to the Amur-keta, but not acceptable for other shoals. For this reason it would be better to call this zone a transient sea zone (abb.MPZ), and the annulus which limits this zone a transient marine annulus (abb. MPK), in consideration that these are formed in the coastal waters under circumstances differing significantly from those where the subsequent growth takes place.

Naturally, the existing differences between the river and the high sea (or if expressed in time: from spring to summer), under the condition of not one but two or more sufficiently abrupt differences in water temperature and salinity, may be correspondingly result in the formation of not only one transient zone on the scales.

The percentage ratio of fish having "estuary" rings on their scales is variable for every keta shoal from year to year (Table 9.). This is quite natural, since the environmental conditions are changing as well.

However, in the analysis of these year to year variations and in the comparison of the shoals from the different rivers with each other, the time of material collection should be taken into account, considering that the relative quantity of fish with "estuary" ring also varies during the season, i.e. decreasing from the beginning to the end of the season (Table 10.)

Table 10.

Relative quantity of fish with "estuary" and "fresh Water" zones on their scales during the run of keta salmon in the Kamchatka river (1964)

Таблица 10

Относительное количество рыб с «эстуарной» и речной зоной на чешуе на протяжении хода кеты в р. Камчатку (1964 г.)

Дата	Рыб с «эстуарной» зоной, %	Рыб с речной зоной, %	Общее число рыб
29/VI	69,2	10,3	39
6/VII	52,8	58,3	36
13/VII	10,3	82,7	58

1 - data; 2 - fish having "estuary" zone,%; 3 - fish having "fresh water" zone,%; 4 - the total quantity of the fish.

The following curious peculiarity has been clarified from this. As it is known, the migration of the keta fry into the sea is sufficiently extended and obviously depends not so much on the hatching time of the fry from the eggs as on their number, on the hydrological conditions and on the food supply in the spawning-breeding place of the given river basin.

On the basis of the scales of the mature fish it may be determined which have migrated earlier and which later into the sea. The portion of the fry which spends longer time in the river will migrate into the sea with already scales on them, whereas the others without scales; thus, on the scales of some fish the "fresh water" zone which consist of some (usually 5-6) small, fresh water sclerites is well visible, whereas on the others it is not.

The number of the fish having the "fresh water" zone also varies during the season. It was established that the number of the fish with "estuary" zone decreases from the beginning to the end of the run, whereas the number of fish with "fresh water" zone increases (Table 10.). In other words, the "estuary" zone may be more frequently observed on the fish which has arrived first, whereas the "fresh water " zone on the fish which has arrived last*. This shows that the "estuary" ring

* The result is that the fish descending later into the sea will also ascend later to spawn.

is most frequent on the fish which descended early from the river. How to explain this? It seems to me that the only explanation is that the fry which descend early arrive in the sea at a fairly low temperature, weakly developed plankton and in conditions of considerable freshening of the water along the coastline due to the melting of snow and the spring flood of the rivers. This is evidently the main reason for the formation of the "estuary" ring.

From all the above consideration it may be concluded that at the same external conditions the quantity variation of the fish over the year, i.e., fish having an "estuary" ring, depends on the time of descent of the young fry. In years of earlier descent the relative quantity of fish with "estuary" ring should increase.

Evidently, this is also the reason, as well as the hydrological conditions of the sea-water along the coast line, that the occurrence of fish with "estuary" zone is not the same in the shoals in different rivers.

Undoubtedly, the most favourable conditions for the forming of the "estuary" zone exist when the young fish lives in bays, inlets, and firths where the influence of the fresh water is stronger than in the high sea. Possibly this is the expanation for the high occurence of fish with the "estuary" zone in the rivers of the East coast of Kamchatka (very broken terrain), and for the low occurence on the West coast in the region of the Bol'saya river.

Finally, it should be noted, that the this year's brood keta having "estuary" ring on their scale do not differ in length from that which does not have it and sometimes it is even bigger (Table 11). This means, that the young fish having descended later from the river, by the end of the year will catch up in growth with the fish descended earlier. Undoubtedly, the explanation is that the former arrive in the sea under conditions which are more favourable for feeding and growth, i.e., when the water is already warmer and the plankton for food is better developed.

Naturally it is also possible to assume that in the case of an early descent not the fish themselves will develop but only their scales; but in that case the fish which has descended earlier should be significantly bigger /28 than that which descended later. This, however, was not observed by us.

H u m p b a c k s a l m o n . The occurrence of the supplementary ring of connected sclerites in the core part of the scale of the humpback salmon was noted at first by Gilbert in 1914. Pravdin called it a fry ring in the assumption that it was formed while in the river.

Table 11.

Length of this year's brood keta salmon with and without "estuary" zone (according to the data of back-counting; collection 1963).

Таблица 11

Длина годовиков кеты с «эстуарной» зоной на чешуе и без нее
(по данным обратного расчисления, сборы 1963 г.)

Водоем	С «эстуарной» зоной			Без «эстуарной» зоны		
	пределы колебаний, см	среднее	число экз.	пределы колебаний, см	среднее	число экз.
Р. Камчатка	20,8—29,3	25,2	33	20,7—30,6	24,9	34
Зал. Корфа	22,3—32,4	26,2	22	19,7—29,6	24,1	14

1- basin. 2 - with "estuary" zone; 3 - without "estuary" zone; 4 - variation limits, cm; 5 - on average; 6 - number of specimens; 7 - Kamchatka river; 8 - Korfa-Bay.

However, it was later established that the young humpback salmon descend from the river without scales. Consequently, this term may be only conditionally applied. Navozov- Lavrov (1927), Pritchard (1931) and Milovidova - Dubrovskaya (1937) were of the opinion that this ring on the humpback salmon is formed during the migration from the fresh water to the sea, in the freshened water of the bays and firths. It was assumed by Navozov-Lavrov, for example, that this ring on the humpback salmon in the Amur is partly formed due to the insufficiency of food in the estuary of the Amur.Against this it should be pointed out that the river ending in a bay or inlet is not an indispensable condition for the forming of the "fry" rings.

From Milovidova-Dubrovskaya and Navozov-Lavrov point of view the mouth of the Amur river with its high fresh water content has to be considered, without any doubt, as the ideal basin for the forming of the "fry" ring; nevertheless this ring is not so often found on the humpback salmon in the Amur river.

According to Enyutina (Table 12.) the relative quantity of the fish having "fry" rings in the Amgun' river has varied over different years (1955-1960) between 0 and 19% and on an average it is only 6,1%, while the quantity of such fish in the My river which flows directly into the southwestern part of the Amur estuary, on an average was not higher than 8% over the same years.

Milovidova-Dubrovskaya did not observe any fish having "fry" ring among the humpback salmon in the Tumnin river flowing into the Datta Bay, and according to the data of A.S. Nikolaev in 1962 these totaled only 8%.

On the other hand, the quantity of such fish sometimes is high enough in some of the rivers of West Kamchatka flowing directly into the sea. In the Kikhchik river, for example in 1934 according to the data of Semko, their ratio was 48% of the entire shoal, and in the Icha river in 1939 (according to our determination) 23,7% all of the fish (Table 12.).

This means, that the conditions for the formation of the "fry" ring are present in the bays, inlets, and estuaries of the rivers as well as in the open coastal regions.

Table 12.

Occurence of the humpback salmon with "fry" ring in various regions of the Far East.

Таблица 12

Встречаемость горбуши с «мальковым» кольцом в разных районах Дальнего Востока

1 Река	2 Автор	3 Год	4 Встречаемость «малькового кольца», %	5 Исследовано рыб (экз.)
6 Р. Сибецугава (Хоккайдо)	16 К. Миягучи, 1959	1953	15,4	26
		1954	91,0	83
		1955	16,6	86
7 Р. Тумнин (Приморье)	17 А. С. Николаев*	1962	8,0	100
8 Р. Амгунь (Амурский бассейн)	18 Р. И. Енютина, 1962	1953	19,2	151
»	»	1954	3,3	122
»	»	1956	11,1	45
»	»	1958	0	128
»	»	1959	5,5	108
»	»	1960	2,7	226
9 Западная Камчатка				
10 Р. Ича	19 Собств. определения	1929	23,7	144
11 Р. Кихчик	20 Р. С. Семко, 1939	1934	48,0	100
12 Р. Большая	»	1935	0,0	100
»	»	1936	100,0	101
»	21 И. Б. Бирман, 1958	1955	0,0	100
»	17 А. С. Николаев*	1960	0,0	100
»	»	1961	1,0	100
»	»	1962	6,0	100
13 Восточная Камчатка				
14 Тихий океан в районе Камчатского залива	21 И. Б. Бирман, 1958	1955	63,0	81
15 Зал. Корфа	17 А. С. Николаев*	1962	59,0	100
»	»	1963	41,0	149

* Фонды КоТИНРО. 22

1 - river; 2 - author; 3 - year; 4 - occurence of the "fry" ring,%; 5 - total number of the examined fish (specimens); 6 - Sibetsugava (Hokkaido) ; 7 - Tumnin river (Coastal region); 8- Amgun' river (Amur-basin); 9 - West Kamchatka; 10 - Icha river; 11 - Kikhchik river; 12 - Bol'shaya river; 13 - East Kamchatka; 14 - Pacific Ocean in the region of the Kamchatka Bay; 15 - Korfa Bay; 16 - K. Miyaguchi,; 17 - A.S. Nikolaev; 18 - R.I. Enyutina; 19 - own determination; 20 - R.S. Semko; 21 - I.B. Birman; 22 - KoTINRO stock.

It is important to note that the ring on all the fish of a given generation was never observed at all and, as a rule, the majority of the fish do not have it. The most probable explanation for this is that the conditions affecting the formation of the "fry" ring are temporary and only a portion of the descending young fish are affected by them.

As it is known, some of the authors (Vedenskii,1954; Lapin. 1963, 1964) assume that these rings are growth rings. Fish having these are assumed by Lapin to be in the third year (2+), whereas according to Vedenskii they are the fourth year (3+). Vedenskii was of the opinion that if there is no ring present, this should be taken into account as an invisibly existing ring; the reason for its non-formation should be only the late renewal of the growth in the spring of the next year, and that the growth began immediately with wide sclerites. Now we know, however, that the growth renewal of the humpback salmon begins as early as in the winter. In view of this, Vedenskii's assumption cannot be accepted.

The size of the zone involved in the "fry" ring is, naturally, very small for a growth ring. Usually it is barely half of the typical growth ring. Lapin has assumed that the explanation for this is a late descent of the fish. The character of this ring, however, is not the mark of the changed duration but of the changed conditions of the growth. Undoubtedly the narrowness of the sclerites covering this zone indicates that the fish which have this ring were growing more poorly than the others for some period after the migration to the sea. /29

As it is known, the factors retarding the growth may be the high fresh water content of the coastal waters, the low water temperature and the insufficient development of the plankton serving as food. All these circumstances may be usually observed at the beginning of the summer season, and the fish which descend early are most affected by these influences. Thus, we cannot accept the assumption of Lapin.

As we have seen, the "estuary" ring on the keta salmon is the consequence of an early descent. The similarity of the "estuary" rings on the keta salmon to the "fry" ring of the humpback salmon is undoubted. As far as the regions are concerned, the occurence of these rings is also sufficiently similar for both species. For example, in the Kamchatka river, in Korfa Bay, and generally in eastern Kamchatka, these rings on both species occur quite frequently, whereas in the Bol'shaya river, at least for the time being, these are rare enough or even totally absent on both species (see Tables 9. and 12.).

It is also important to note that the sizes of the young fish with and without these rings are about the same for both the keta salmon and the humpback salmon (Tables 12. and 13.)

All this indicates that the origin of the supplementary ring is the same for both species. The formation of the "fry" rings on the humpback salmon and the formation of the "estuary" rings on the keta salmon is undoubtedly the result of early descent. It is absolutely evident that the young humpback salmon descended early , for a period of time will grow slower than the others. At the beginning of this period this is probably caused by the insufficient warming up of the water and inadequate development of the plankton, and in addition, by the longer existence in the narrow coastal zone cooled by the coastal drainage which also increases the fresh water content. In the bays and inlets the influence of the coastal drainage is naturally more effective than in the regions of open coast; for this reason it is not excluded that on regions with bays and inlets the occurence of fish with "fry" rings is more constant. This will be evident when if a comparison is made between shoals of keta and humpback salmon in Western and Eastern Kamchatka. In one way or another, the early descent of the fish having on their scales "fry" ring is undoubted, otherwise it would not be understandable how these could reach the same (sometimes even bigger) size than the other fish by winter, in spite of their longer growth stagnation.

Table 13.

Body sizes and the quantity of sclerites on the scales of humpback salmon, spawning in 1963, in the first year of life (according to Enyutina, 1962)

Таблица 13

Размеры тела и количество склеритов на чешуе у горбуши нерестовых подходов 1963 года на первом году жизни
(по Енютиной, 1962)

1 Показатели	2 Р. Иски		3 Р. Амгунь		4 Р. Мы	
	1+	1 (1+)	1+	1 (1+)	1+	1 (1+)
5 Число экземпляров	124	37	122	20	129	70
6 Длина (АС), *см*						
7 колебания	22—43	24—39	22—35	20—38	19—38	24—40
8 среднее	30,4	30,1	27,0	26,7	29,1	28,9
9 Количество склеритов						
7 колебания	14—26	16—25	15—23	17—22	15—25	16—25
8 среднее	19,6	20,2	19,7	19,6	20,7	20,4

Примечание. 1+ — чешуя обычного типа без дополнительного кольца в ядерной части; 1 (1+) — чешуя с дополнительным кольцом или зоной суженных склеритов в ядерной части.

1 - characteristics; Iski river; 3 - Amgun' river; 4 - My river; 5 - number of samples/ 6 - length (AC),cm; 7 - variation; 8 on an average; 9 - number of sclerites.

N o t e: 1+ indicates a usual type scale without supplementary ring in the kernel; 1(1+) indicates a scale with supplementary ring or zone of contracted sclerites in the kernel.

It follows from all the above considerations, that at given hydrological conditions in the coastal zone the number of fish with "fry" ring should depend, on the one hand, on the time of descent of the young fish and on the time dynamics of the descended fish, and, on the other hand, on the distribution rate of the descended population of young fish at which they go from the coast to the high seas. Naturally this factors vary from year to year.

On the other hand, the time of descent and its mass character during the season depends on two main factors: the variation of the water level in the rivers and on the abundance of the generation. Under the same hydrological conditions the descent of the majority of young fish will evidently be completed earlier when their numbers are fewer.* But, the lower the population density of the young fish descending into the sea, other things being equal, the slower they will go away from the coast in search of food. It follows, therefore, that in a small humpback salmon generation in a given river basin, as a rule fish having "fry" ring will be found more frequently than in a numerous generation. Although Enyutina(1962), on the basis of studying the occurence of "fry" ring on the Amur humpback salmon, denies the connection between its occurence and the number of fish in the generation, nevertheless theoretically speaking this connection should be observable in period of relatively low variations in the hydrological conditions over the year. Lapin(1963) has /31

* In this case the food supply of the young fish is of no importance, since the salmon fry hardly feed at all.

pointed out this type of connection with regard to the Amur humpback salmon as well, mainly on the basis of the data supplied by Enyutina. As it was said already, Lapin assumes that the "fry" rings are growth rings, and that the fish which have these are in their third year (2+). Lapin points out that there are more such fish in the not so numerous spawning shoals of the Amur humpback salmon (odd years) than in the more numerous ones (even years). Lapin is of the opinion that a portion of the fish from the foregoing abundant generation are retarded in their maturity by one year. He tries to explain the mechanism of alternating generations of the humpback salmon by similar "interpenetration" of the generations. However, as it was stated, the fish which were assumed by Lapin to be in the third year, in fact were not. The higher occurrence of these fish in years of poor run may be explained by the fact that these are in the second year and are individuals from the numerically poor generation among which, due to the above considerations, there should be a higher ratio.

While this paper was in print, Ivankov (1965) published a paper in which he also deals with the question concerning the nature of the "fry" ring. Ivankov, like the present author, considers this to be the result of an early descent.

We may agree with Ivankov's opinion, according to which the mortality of the early descended young fish should be higher than that of the fish descended later, however, this may be hardly the explanation for the higher occurance of the fish with "fry" ring in the not so numerous generations. In the first place the not numerous humpback generation, as a rule, originate from a not-numerous generation as well, secondly, it would be incorrect to think that the occurence of the fish with "fry" ring may be high only in less numerous generations. According to the already-quoted data of Semko, among the humpback salmon of West Kamchatka there were large numbers of fish with "fry" ring in 1934 and 1936, although during these years the number of the humpback salmon in West Kamchatka was fairly high. Conversely, for the time being, while the number of humpback salmon in West Kamchatka is very low, the occurence of fish with "fry" ring in the spawning shoals is insignificant for a number of years. This indicates that the time of descent and the duration of stay of the young fish at the coast does not depend exclusively on the number of fish in the generations.

Finally, it should be noted that the absence of any significant difference in the length of a particular year's brood humpback salmon with and without "fry" ring contradicts the point of view of Krykhtin and Smirnov (1962), according to which the different sizes of that particular year's brood in a generation of approximately equal numbers may be explained by the differences in the time of descent. Obviously, an interval of one ortwo weeks between the peaks of descent does not play any significant part. By the same analogy the size variation of the particular year's brood in any given generation does not depend on the time of descent, i.e., the sizes of the early descended and late descended fish are about the same.

Frequently on the edge of the second years zone on the scales of the humpback salmon another ring of connected sclerites may be found; these rings may be easily confused with growth rings (Figures 12,13). This ring is unusual on humpback salmon of an early run; it may be observed only at the end of July, August or September, and its occurence increases with time. This ring should not be considered a growth ring. Before the forming of a growth ring a stagnation in growth should occur, but there is no stagnation in the growth of the humpback salmon during the summer months of their second year of life. As it was already stated (Birman, 1960-a), only some retardation of linear growth may be observed in comparison to that of the first year, while the growth of the scales is somewhat retarded as well. Evidently the connection of the sclerites is just the end result of these and indicates a general slow-down of the linear growth in the humpback salmon by the end of the second year. During this period the total food energy is taken up by the intensive weight increase 132 and by the vigorous maturing of the gonads.

In addition to this we already know that on a portion of redback salmon, although their growth is slower than that of the humpback salmon, the second growth ring in the sea is still formed in midwinter. In the case of the keta salmon even the fourth and the fifth growth ring are formed not later than May. It is so much less probable that the second growth ring could form only in July; this ring should appear not later than April at least, and most probably even earlier.

Nevertheless sometimes humpback salmon may be found which are undoubtedly two-year-old, but quite certainly all these have a significant number of summer formations in addition to the second growth ring.

Summary

1/ The growth rings on salmon are formed after the winter stagnation of growth and characterize the beginning of new growth. These rings do not delineate the year zone of the scale growth but denote the beginning of the next one. In this relation the marking of the age should be somewhat modified: after the number of full years completed by a given individual the "plus" sign should be added even in that case when the scales are bordered by the growth ring, since this ring itself already represents new growth.

2/ The growth rings on the humpback salmon and silver salmon form not later than the first half of January. Before this time there is a very short growth stagnation. The duration of the winter growth stagnation and the time of growth renewal (formation of the growth ring) of other salmon species depend on the age of the fish: the younger the fish the more it will resemble that of the silver salmon and humpback salmon, with respect to the duration of winter stagnation and the time of growth renewal:

a/ the formation of the third growth ring in the sea takes place most frequently in March but it may be delayed till May; whereas the second growth ring in the sea forms not later than March and on some fish even in January and February;

b/ the formation of the fourth growth ring of the keta salmon most frequently takes place in May, however, it may be delayed till June; whereas the third growth ring usually is formed in April and the second evidently even earlier;

c/ The formation of the growth ring in the sea on the redback salmon of the one and the same series takes place, on an average, earlier than that of the keta salmon, i.e., the winter growth stagnation of the redback-salmon is evidently shorter;

d/ the formation of the first growth ring in the sea on the redback salmon, keta salmon, Oncorhynchus masu, and probably also the king salmon takes place during the winter months, and in some cases not much later than on the humpback and silver salmon. The young individuals of these species keep on growing over the major part of the winter. In case of humpback and silver salmon the short duration of growth stagnation and the early renewal of growth is, in this way, the consequence of the "youth" of these fish;

e/ the formation of the second and, especially the third growth ring on the Oncorhynchus masu in the sea may be delayed till June. For this reason it is possible to understate the age of this fish by one year in the case of early spawning. This salmon returns for spawning after spending one, two or three years in the sea.

3/ The size of the yearly scale growth decreases with age; this is the consequence of not only the retardation of growth but also that the renewal of the growth

takes place always later after the winter retardation. The younger the fish (beginning from its second year in the sea) the relatively bigger portion of its "summer growth of scales (and the body reppectively) will 13
occur during early spring or the winter period. In other words, in the case of keta, redback and king salmon and _Oncorhynchus masu_, from their second year in the sea onward, each subsequent yearly growth of their scales and bodies, on an average, will correspond to a shorter time period than previously.

4/ The second year growth on the above mentioned salmon species corresponds to a longer time period than the first one, especially in the case of fish which descended from the rivers at the height or at the end of summer.

5/The equality or slight increase with age of the yearly growth of the scales observed on some salmon (for example on king salmon and on _Salmo penshinensis_ Pallas) may be evidently explained by the late descent of the young fish and by the early growth renewal in the subsequent years. It may be assumed that the growth stagnations are very insignificant.

6/ The growing periods of the humpback and silver salmon in their first and second year in the sea are almost equal.

7/ When considering the growth in length of the body of salmon during their first year in the sea, the data usually obtained by the back counting method should be considered as exaggerated, since in the analysis the growth ring is also taken into account.

8/ The illegibility of the growth ring may be mostly found on young, fast growing fish, in the first place on species which are fast growing in winter as well; this indicates either the continuity of the growth or that the renewal of the growth was not slow.

9/ The first growth ring on the salmon is represented by a higher number of connected sclerites than the second. This may be explained by a growth renewal taking place earlier (and at a lower water temperature) in their second year in sea.

10/ The supplementary ("estuary") ring within the first year growth zone of the keta salmon forms about July-August; it may be observed on fish descended early from the river and having no fresh water zone on their scales. From the beginning of the run to its end the number of fish with "estuary" ring (i.e,the number of the early descended fish) decreases, and the number of fish with fresh water ring (i.e., the number of the late descended fish) increases.

11/ The keta salmon with and without "estuary" zone on their scales (i.e., the early and the late descended fish), like the humpback salmon with and without "fry" ring, will reach about the same sizes by winter. This circumstance as well as the similarity of both rings indicates that these have the same origin. Both of these are evidently the consequence of an early descent and longer stay under conditions which slow down the growth (low temperature, high fresh water content of the coastal zone, et c.)

12/ Other conditions being equal, the occurence of fish with "fry" ring in the not numerous humpback salmon generation should be higher than in the numerous generation. This is the probable explanation for the predominance of such fish observed by Lapin (1963) in the case of Amur humpback salmon in the years of weak run. This condition, however is not obligatory. Sometimes a high occurence of fish with "fry" ring may be observed in abundant years as well, and vice versa, may not be found in poor years.

13/ In the keta and humpback salmon the time of descent does not determine the size variation of young fish in the population of a given year and the length differences between the young fish of adjoining generation.

14/ It is proposed that the zone of the scales bordered by the "estuary" or "fry" ring should be called transient sea zone (abb. MPZ).

15/ The contraction of the sclerites of the humpback salmon, as sometimes observed at the edge of the second years zone, should not be considered as a growth ring, since this ring is formed at the end of summer or not much earlier, whereas in the slower growing other salmon species the second growth ring is formed at spring or during the winter months. This is a supplementary ring, evidently indicating the abrupt retardation of the linear growth in connection with a fast increase of weight and vigorous maturing of the gonads before the ascent to the rivers.

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<u>Fig.1.</u> Scale of a humpback salmon; April 18,1959; N.lat. 43°00' E. long. 173°37'. Length of the fish (AC) 51,5 cm; weight 700g.
<u>Fig.2.</u> Scale of a humpback salmon; Febr.11,1965. Sea of Japan N. lat. 38°36'. E long. 130° 27'. Length of the fish (AC) 29,5 cm, weight 250 g.
<u>Fig.3.</u> Scale of a redback salmon with one growth ring in sea; March 18, 1964; N.lat. 49° 00', E. long. 177° 22'.
<u>Fig.4.</u> Scale of a keta salmon; July 12, 1959. Length of the fish 32 cm, age 1+.
<u>Fig.5.</u> Scale of an Oncorhynchus masu with one growth ring in sea; Febr.11,1965. Sea of Japan; N.lat. 38° 36' E. long. 130° 27'. Length of the fish 34 cm; weight 500 g.
<u>Fig.6.</u> Scale of a keta salmon with "estuary" ring (Korfa-Bay).

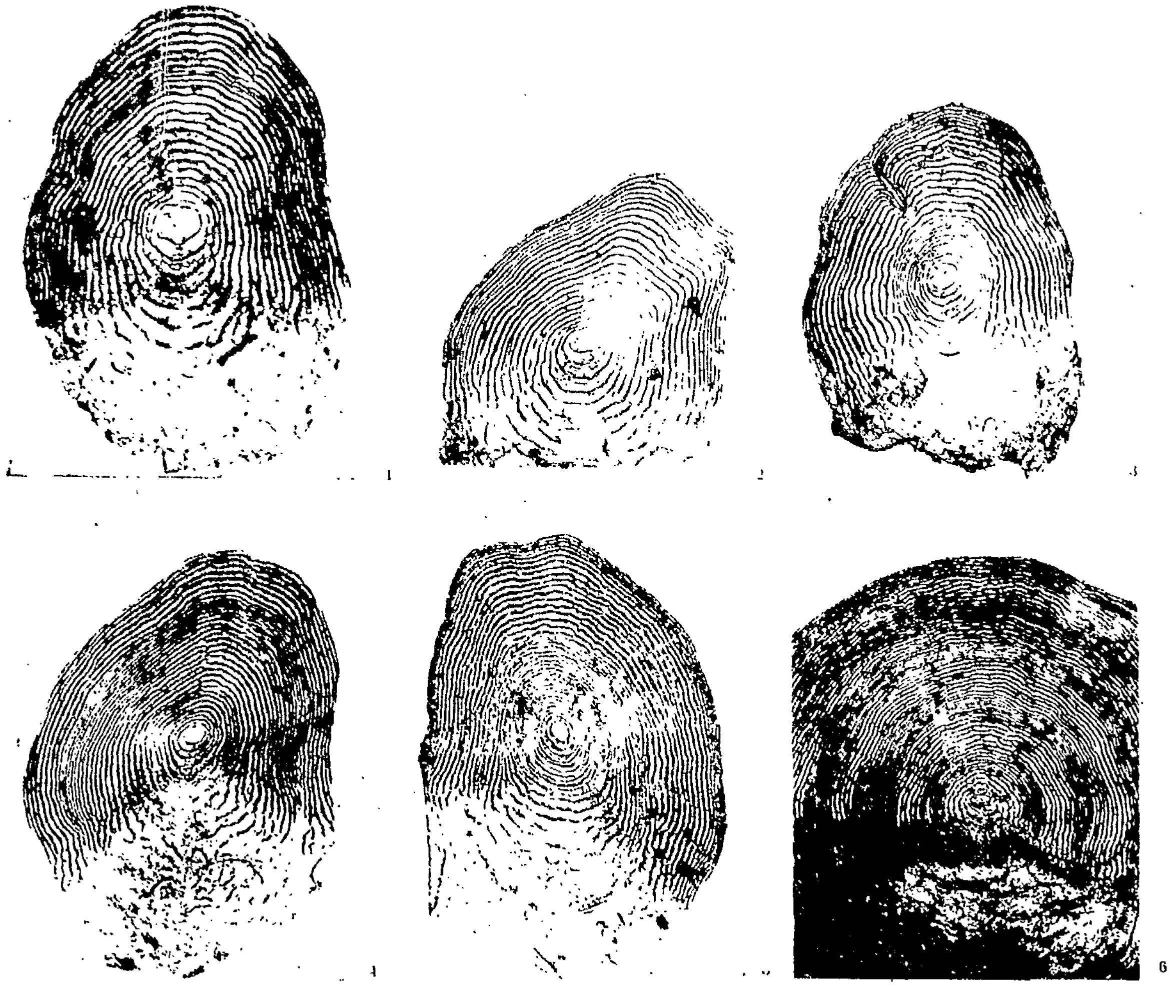

Fig.7. Scale of a keta salmon with "estuary" ring (Kamchatka river).
Fig.8. Scale of a keta salmon with fresh water and "estuary" ring (Kamchatka river).
Fig.9. Scale of this year's brood keta salmon with "estuary" zone. Sept. 21,1964; Sea of Okhotsk; length of the fish 14,7 cm.
Fig.10. Scale of this year's brood keta salmon with "estuary" zone and ring; Sept.21,1964. Sea of Okhotsk; Length of the fish 17,8 cm.

Рис. 6. Чешуя кеты с «эстуарным» кольцом зал. Корфа.
Рис. 7. Чешуя кеты с «эстуарным» кольцом, р. Камчатка
Рис. 8. Чешуя кеты с речным и «эстуарным» кольцом, р. Камчатка

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Fig.11. Scale of this year's brood keta salmon with "estuary" zone and ring; Sept. 21, 1964; Sea of Okhotsk; Length of the fish 17,8 cm

Fig.12. Scale of a humpback salmon 1+ with supplementary ring on the front edge of the scale; Sept.8.,1956; high sea South from the Commander Islands; length of the fish 52 cm; weight 1500 g.

Fig.13. Scale of a humpback salmon 1+ with "fry" ring and supplementary ring on the front edge of the scale; Aug.6,1939; Kamchatka river.


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Рис. 9. Чешуя сеголетка кеты с «эстуарной» зоной. 21/IX 1964 г., Охотское море Длина рыбы 11.7 *см*.

Рис. 10. Чешуя сеголетка кеты с «эстуарной» зоной и кольцом. 21/IX 1964 г., Охотское море. Длина рыбы 17.8 *см*.

Рис. 11. Чешуя сеголетка кеты с «эстуарной» зоной и кольцом. 21/IX 1964 г., Охотское море. Длина рыбы 17,8 *см*.

Рис. 12. Чешуя горбуши 1+ с дополнительным кольцом на переднем крае чешуи. 8/IX 1956 г., открытое море к югу от Командорских островов. Длина рыбы 52 *см*, вес — 1 500 *г*.

Рис. 13 Чешуя горбуши 1+ с «мальковым» кольцом и дополнительным кольцом на переднем крае чешуи. 6/VIII 1939 г. Р. Камчатка.

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