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Peculiarities of embryonic and larval development of Atlantic and Pacific salmons of the genus Salmo with respect to their evolution

by

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Peculiarities of embryonic and larval development in Atlantic and Pacific salmons of the genus Salmo with respect to their evolution

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Significant differences have been established between the Atlantic and Pacific salmons of the genus Salmo in the degree of development of the larval organs (periblastic sinus, amnion, right yolk vessel, preanal fold) at the same stages of development, as well as in the number of body segments in the free-living embryo and the number of rays in the anal fin of the larva. We have outlined the evolutionary paths of early ontogenesis during the divergence of the Pacific and Atlantic salmons, and have hypothesized about the adaptive significance of an increase in growth rate in connection with the onset of spring spawning in the Pacific group of salmons. The embryological data point to the possibility of establishing the Pacific salmons in the subgenus Parasalmo.

The present system of the genus Salmo is based on the morphological characters of the adult forms, and has been verified by a number of physiological and biochemical investigations. Comparative embryological data have hardly been used for analyzing the taxonomic position of the species of this genus. Because of this, we undertook to compare the development of the species belonging to these two large groups of Salmo salmons indigenous to the Atlantic and Pacific oceans, and to interpret the results in accordance with the well-known concepts regarding the evolution and systematics of the genus Salmo.

This study deals with the embryonic and larval development of the following Atlantic species and forms: the Atlantic and Baltic salmon S. salar L., the anadromous and lake sea trout S. trutta L. and two races of the Sevan trout S. ischchan Kessler (gegarkuni and summer bakhtak). In the Pacific group, we have studied the development of the rainbow trout S. gairdneri Rich. and "mikizha" (S. mykiss Walbaum) of Western and Eastern Kamchatka.

The eggs of the Atlantic salmon and sea trout were collected from spawners in a number of rivers and lakes of Kandalaksha Bay on the White Sea. The eggs of the Kamchatka mikizha were collected from spawners of the Kishimshina and Baranya rivers (Kamchatka R. basin) and the Amchigach and Tundrovaya rivers (Bolshaya R. basin) by V.A. Maksimov, V.V. Zuyevsky and V.D. Nesterov of the Ichthyology Department of Moscow University, and by Yu.A. Biryukov of the Kazakh University. The eggs of the Murmansk Atlantic salmon were obtained from the harvesting centre on the Kola River, the eggs of the Baltic salmon - from the harvesting centre on the Daugava River, the eggs of the Sevan trouts - at the "Lichke" fish cannery of the Armenian SSR, and the eggs of the rainbow trout - from the "Banga" fishery co-operative of the Latvian SSR. After swelling, the salmon eggs were taken to the Ichthyology Department or White Sea station of Moscow University, where they were incubated in running water at several temperatures not exceeding the optimal range for each form.

Pavlov et Soin (1976) and Pavlov (1978) have described the procedure of the embryological investigations, the characteristics of the developmental stages of Salmo salmons and a number of embryonic organs which are of taxonomic importance (degree of development and length of existence). Not less than 30 eggs, prolarvae or larvae of each form were used to obtain the numerical data.

The species of the Atlantic and Pacific groups are distinguished by the following characteristics.

In the Atlantic group, the periblastic sinus, which appears at the gastrulation stage as in all Salmo salmons, is quite large for the greater part of the blastoderm epiboly process (fig. 1, a), and disappears when the blastoderm has grown about 4/5-5/6 of the yolk surface in the Atlantic and Baltic salmons and only by the end of epiboly or even after its completion in the rest of the species. The Pacific salmons are characterized by a decrease in the size of the periblastic sinus at the onset of epiboly (fig. 1, a) and the complete disappearance of this organ when the blastoderm has grown about 1/2-2/3 of the yolk.

The amnion (another larval organ) forms several days after the closing of the yolk plug in the Atlantic salmons, and when the blastoderm has grown about 1/2-2/3 of yolk in the Pacific salmons, and is clearly visible during the closing of the yolk plug (fig. 1, b_1).

The yolk plug in all the forms of Atlantic salmons (except for gegarkuni) closes when the body of the embryo averages 17-21 segments (fig. 1, b). At this stage, the brain begins to differentiate into three regions, slits form in the optic vesicles and auditory capsules appear. Despite the fact that the majority of Salmo species hardly differs in the plasma/yolk ratio, the embryo of the rainbow trout has 18-20 body segments during the closing of the yolk plug, and the number of body segments varies from 21 to 37 in the various forms of the mikizha (26-28 in the non-anadromous Western Kamchatka mikizha) (fig. 1, b_1). The optic receptors and the cavities of the auditory capsules appear at this stage, and neuromers begin to develop in the metencephalon.

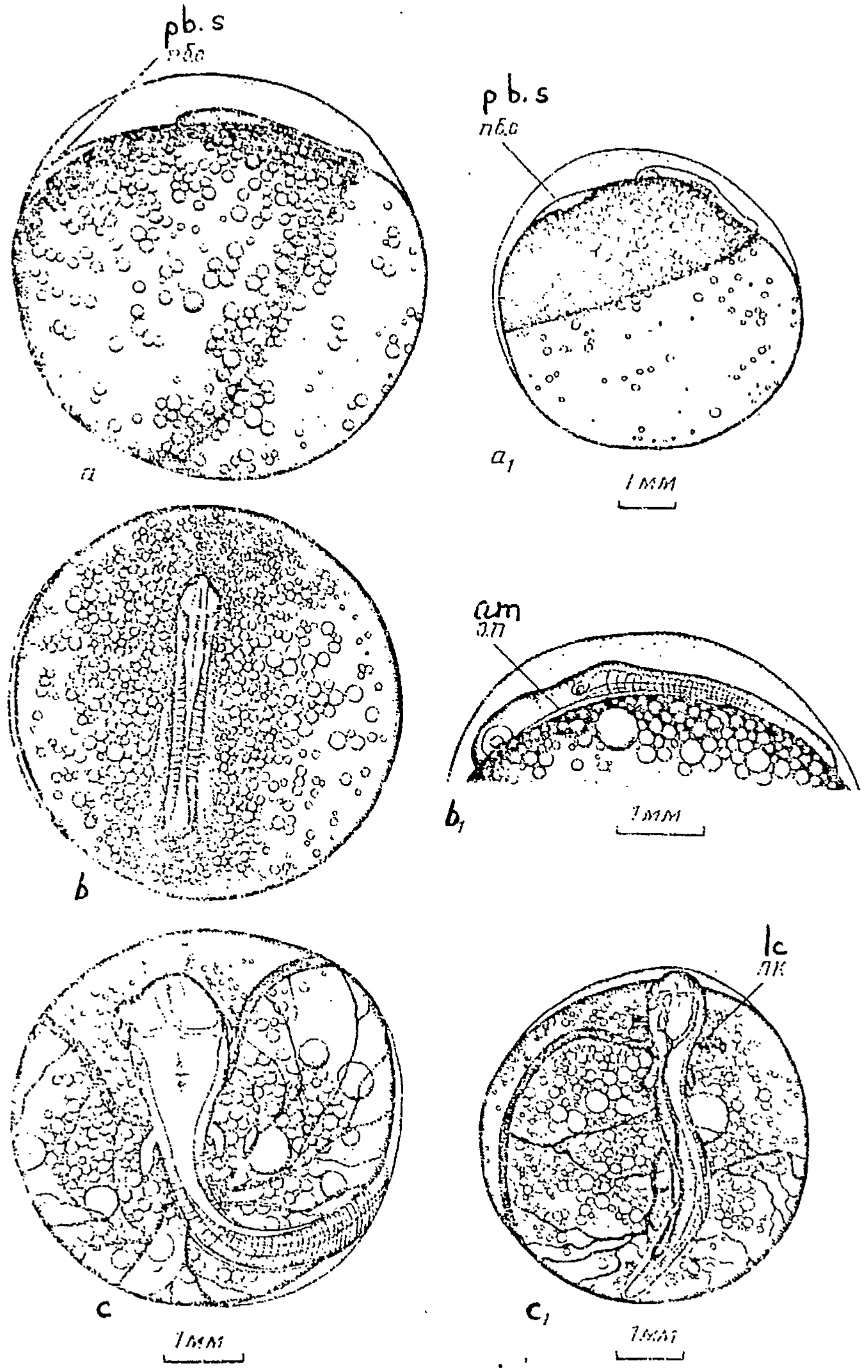

Fig. 1. Some stages of embryonic development in the Atlantic salmon of the White Sea (a-c) and the anadromous mikizha of Western Kamchatka (a_1-c_1): a - appearance of 9th somites, 2/3 of yolk covered with blastoderm (pb.s. - periblastic sinus); a_1 - appearance of 6th somites, 1/3 of yolk covered with blastoderm; b - appearance of 19th segments, closing of yolk plug; b_1 - formation of 28th segments, closing of yolk plug (am - amnion); c - beginning of hepatovitelline circulation, right blood vessel on yolk equal to left one in width; c_1 - appearance of a lacuna with blood (lc) on the right of the embryo, 1/3 of yolk vascularized

At the beginning of erythrocytic circulation, the yolk in the Atlantic species acquires (alongside the blood vessel falling into the heart on the left) a right vessel which, in the process of further development, undergoes more or less complete reduction (fig. 1, c), but is usually present in at least some of the eggs prior to the completion of yolk vascularization. The Pacific salmons are characterized by the disappearance of the right vessel at the onset of vascularization, or the absence of it. For example, in the majority of eggs from the non-anadromous Western Kamchatka mikizha, this vessel disappears when the yolk is 1/3 vascularized, and only a blood-filled lacuna, which falls into the heart, is preserved on the right of the embryo (fig. 1, c_1).

Free-living embryos of the Atlantic salmons average 54-59 body segments, whereas the Pacific species have 60-62 segments due to an increase in the number of both trunk and tail segments. Similar differences are observed in the number of vertebrae in the juveniles and adult forms; according to a number of authors (Vladimirov, 1940; Rounsefell, 1962; Savvaitova, 1975; etc.), it varies from 51 to 60 in salmons of the first group, and from 60 to 66 in species of the second group.

Within each of these groups of salmons, we observe variations in the degree of morphological development of the embryos at the stage of emergence from the membrane, as well as in the size of the juveniles and the nature and intensity of their colour at subsequent stages of development. However, the salmons of both groups are clearly distinguished by a character such as the degree of development of the preanal fold at the same stages of the subperiod of development outside the membrane and the larval period. In the Atlantic salmons, this organ disappears at the onset of mixed feeding, as in the Atlantic salmon (fig. 2, a), or simultaneously with yolk resorption which is characteristic of the majority of other forms. In the Pacific salmons of the genus Salmo, a wide preanal fold is retained during the stages of mixed (fig. 2, a_1) and exogenous feeding, and disappears only during the fingerling period of development.

There are 9-13 rays in the anal fin in larvae of the Atlantic salmons, and 13-14 in those of the Pacific species. The adult forms of these groups have 8-11 and 9-16 rays respectively (Vladimirov, 1940; Rounsefell, 1962; Savvaitova, 1975).

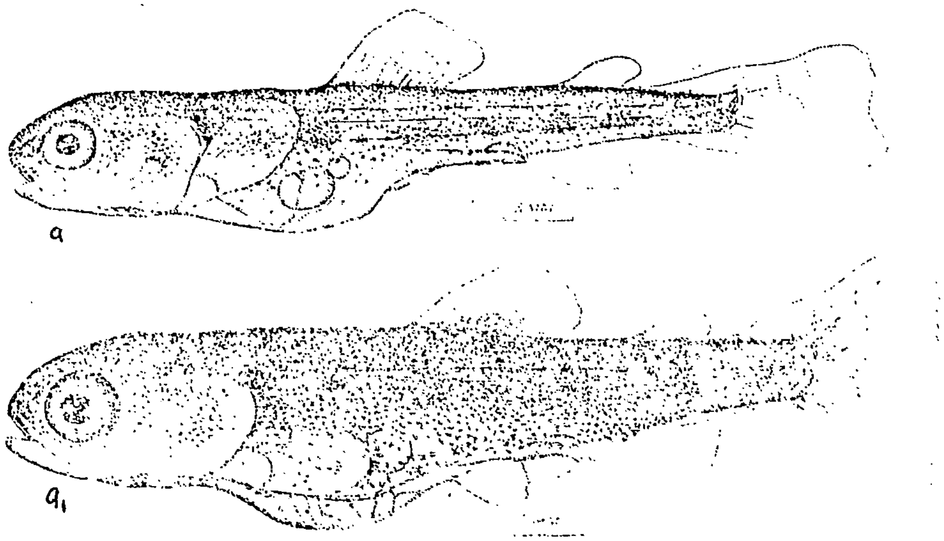

Fig. 2. Larvae of the White Sea Atlantic salmon (a) and the anadromous mikizha of Western Kamchatka (a_1) at the beginning of the mixed-feeding stage

The two groups of species differ in the rate of development from the earliest stages.

Ignat'yeva's paper (1970) indicates that, at similar temperatures, the duration of one mitotic cycle during synchronous fissions (τ_0) in the brook trout S. trutta m. fario is 70 min greater on the average, than in the rainbow trout. Our calculation of the τ_0 values for different species on the basis of published data has shown that the mikizha hardly differs from the rainbow trout in this index, whereas the same index calculated by Ignat'yeva for the rainbow trout exceeds τ_0 for the Atlantic species (fig. 3, A). Because the curves characterizing the dependence of τ_0 on temperature are approximately parallel to each other for different species, it follows that the value of τ_0 for any Atlantic species is greater than τ_0 for any Pacific species in a temperature range suitable for normal development.

The graph in fig. 3, B shows the dependence of the development span in the membrane on temperature in various species, plotted on the basis of our own and published data by means of the least-squares method and Mednikov's equation (1977) $\lg N = \lg A + k \cdot t$, where N denotes the development span in the membrane, t - temperature, A and k - the parameters. The reliability of the correlation coefficients for the sea trout and mikizha is below the 95% confidence level because of the small number of dots on the empirical lines of regression (see table). According to the correlation coefficient, the rainbow trout does not differ significantly from the mikizha, but each of these species differs significantly from each of the Atlantic species. At similar temperatures, the incubation period of the Pacific salmons is considerably shorter than that of the Atlantic species. During the incubation of eggs from species of these two groups (summer bakhtak and rainbow trout) at the optimal average temperature for these species (7.7°C), the development rate of the rainbow trout begins to accelerate drastically in comparison with the development rate of the summer bakhtak after the closing of the yolk plug (fig. 3, C). At the 8th stage of development, the difference in the development rates between these species increases more slowly; however, this difference reaches 10 days at the stage where the pectoral fins begin to move. A similar increase in the development rate and growth of Pacific salmons in comparison with Atlantic species is observed in free-living embryos and larvae. For example, at a temperature of 13°C, the rainbow trout switches to mixed feeding at the age of 16 days, and the gegarkuni - on the 23rd day after hatching.

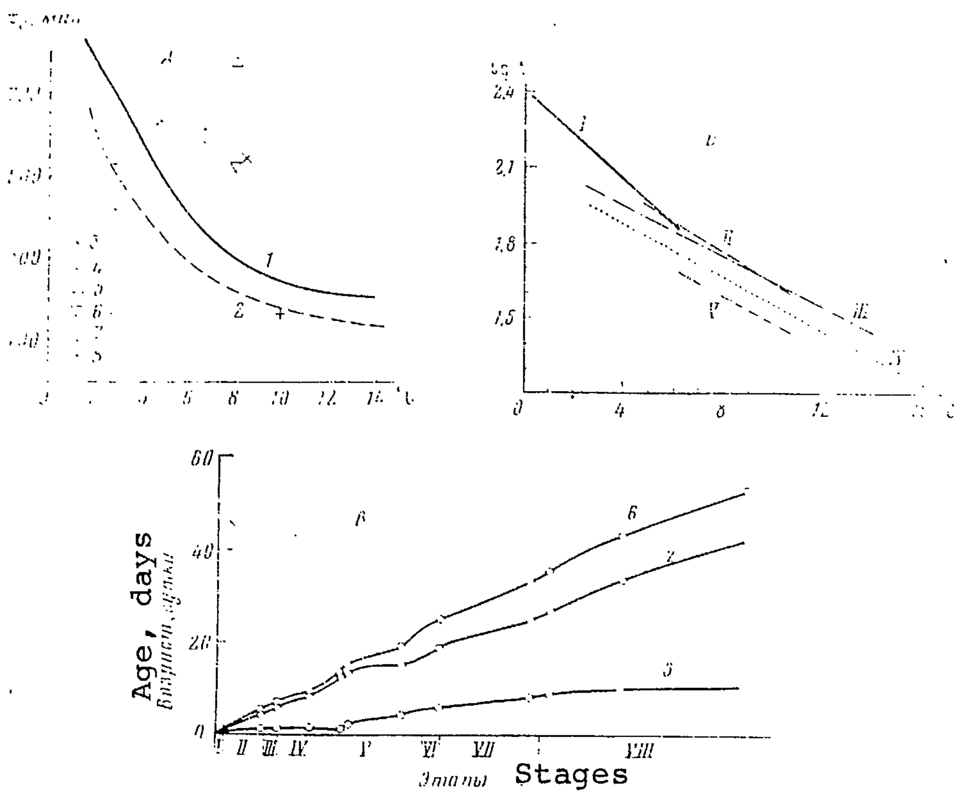

Fig. 3. Dependence of the length of the mitotic cycle (A) and the development in the membrane (B) on temperature in salmons of the genus Salmo, and the difference in the development rates of the summer bakhtak and rainbow trout at 7.7°C (C): 1 - brook trout, 2 - rainbow trout (after Ignat'yeva, 1970); 3 - Ladoga salmon, 4 - lake sea trout, 5 - gegarkuni, 6 - summer bakhtak, 7 - winter bakhtak, 8 - "mikizha", 9 - differences in the development span of the summer bakhtak and rainbow trout; I - Salmo salar, II - S. trutta, III - S. ischchan, IV - S. gairdneri, V - S. mykiss; X-axis (fig. C) - length of development stages of the summer bakhtak in % of its incubation period (development stages: I - swelling, formation of a perivitelline space, formation of a blastodisc; II - fission; III - blastulation; IV - gastrulation; V - organogenesis; VI - beginning of a heartbeat and mobility of the embryo; VII - beginning of erythrocytic circulation; VIII - hepatovitelline circulation and preparation for hatching)

The majority of researchers believes that the salmons of the genus Salmo are endemic to the North Atlantic. According to the opinions of some authors (Mottley, 1934; Balon, 1968; Nikol'sky, 1971), Salmo in the Atlantic and Oncorhynchus in the Pacific developed convergently during the Pleistocene. During the Interglacial Period, the salmons of the genus Salmo migrated from river to river across the continent to the Pacific Ocean (Mottley, 1934). Neave is of another opinion (Neave, 1958); he substantiated the hypothesis that the salmons of the genus Salmo migrated along the coast of North America to the Pacific Ocean during the early Pleistocene, and there the genus Oncorhynchus developed from the genus Salmo. After an unsuccessful rivalry with the genus Oncorhynchus for spawning grounds, the Pacific salmons of the genus Salmo switched to reproducing during the spring months. At the initial stages of evolution, they were apparently characterized only by spring spawning; later, in the process of assimilating the spawning grounds and as a result of lengthy selection for fishery purposes (Needham, Gard, 1959), a small part of the steelhead, rainbow trout and cutthroat trout populations switched to reproducing in winter.

Some are of the opinion that the sea trout is the most generalized species and the closest one to the ancestral form in the genus Salmo (Maksimov, Savvaitova, 1967; Balon, 1968; Dorofeyev, 1975; Akhundov, Meanikov, 1976). Our data have confirmed this point of view, as the sea trout has the largest number of developmental features common to other species. As in species of the Pacific group, the blood flow along the hyoid arch of the aorta in the sea trout appears at the beginning of the hepatovitelline circulation stage, when 3-4 branchial vessels are already functioning, in contrast to the Atlantic and Baltic salmons in which the blood begins to flow along the hyoid arch and two branchial vessels at the end of the preceding stage. The sea trout is compared to the Pacific salmons on the basis of the fairly lengthy existence of a preanal margin, as well as the value of the thermal stability coefficient (see table). At the same time, this species is similar to the Atlantic and Baltic salmons, and especially to the Sevan trout, in many of tne embryological indices.

Equation parameters of the development span of salmons in the membrane*

Species	l	A	k	m_y**	P_y
Salmo salar	13	260.0	-0.087	0.007	0.999
S. trutta	6	173.8	-0.060	0.023	0.950
S. ischchan	15	143.2	-0.051	0.036	0.999
S. gairdneri	14	121.3	-0.053	0.059	0.999
S. mykiss	7	120.2	-0.058	0.058	0.950

*l - the number of dots on the empirical line of regression, A - the value theoretically corresponding to the development span in days at t°C=0, k - the coefficient of thermal stability, m_y - the error of the theoretical values of function y=lg N, P_y - the reliability of the correlation coefficient.

**The error of the theoretical values of the function calculated by $m_y = \sqrt{\frac{\sum (y - y')^2}{l - n}}$, where y denotes the empirical values of the function, y' - the theoretical values of the function, l - the number of dots on the empirical line of regression, n - the number of equation coefficients, including the free term (Zaitsev, 1973).

With the possible evolution of the Pacific salmons of the genus Salmo from the same ancestor as the sea trout, the length of existence of the periblastic sinus diminished, and the right blood vessel on the yolk underwent almost complete reduction. The number of segments, which corresponds with the number of vertebrae, either increased or, what is more probable, was inherited from the ancestral form and diminished in the Atlantic salmons during the evolution of the Pacific species. The intensive development of the preanal fold in the larvae of the Pacific salmons is probably an adaptation to their development in summer at comparatively high temperatures. In warm water with a low density, this organ is, perhaps, necessary for better stabilization of the trunk. This conclusion is confirmed by the fact that the preanal fold is well-developed in the spring-spawning genus Brachymystax (similar to Salmo) (Smolyanov, 1961), the juveniles of which develop at relatively high temperatures. The increase in the development rate of the Pacific salmons is apparently due to spring spawning, and enables the juveniles to utilize to the utmost the spring-summer season for attaining the size and fatness required for overwintering.

On the basis of the differences in geographic distribution, the structure of the skeletal elements, pigmentation and mode of life, Vladykov (1963) singled out the Pacific salmons of the genus Salmo in the subgenus Parasalmo. The correctness of this is substantiated by the low survival of the crosses between species of the Atlantic and Pacific groups (Buss, James, 1956), the difference in the pigmentation of the juveniles (Bacon, 1954) and in the number of scales in the lateral line (Rounsefell, 1962), and by research into the osteology and karyotypes of various species (Dorofeyeva, 1965; Chernenko, 1969; Kaidanova, 1974; Vasil'yev, 1977). Embryological data also accord with this point of view.

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PECULIARITIES OF EMBRYONIC AND LARVAL DEVELOPMENT OF ATLANTIC AND PACIFIC SALMONS OF THE GENUS *SALMO* WITH RESPECT TO THEIR EVOLUTION

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Summary

Marked differences were found between the Atlantic and Pacific salmons of the genus *Salmo* by the degree of development of the larval organs: periblastic sinus, amnion, right yolk vessel, preanal fold, as well as by the number of segments in the free embryo body and the number of rays in the larval anal fin. Ways of evolution of the early ontogenesis upon the divergence of Atlantic and Pacific salmons are outlined. A suggestion is forwarded on the adaptive value of increase in developmental rate with respect to transition of Pacific salmons to spring spawning. The embryological data confirm the possibility of isolation of Pacific salmons into subgenus *Parasalmo*.