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THE BIOLOGY, REPRODUCTION AND DEVELOPMENT OF PACIFIC SALMON

By A.I. Smirnov

In memory of my dear teacher
Professor
Sergei Grigor'evich
Kryzhanovskii

Introduction

The Pacific salmon of the genus Oncorhynchus (family Salmonidae) inhabit the northern part of the Pacific Ocean and the adjacent regions of the Arctic Ocean. The genus includes such valuable commercial fishes as the chum, O.keta (Walbaum), sockeye, O.nerka (Walbaum), the pink, O.gorbusha (Walbaum), the chinook, O.tschawytscha (Walbaum), the coho, O.kisutch (Walbaum), and the masu, O.masou (Brevoort). Until mid-twentieth century, the salmon constituted the main object of the fishing industry in the Far East. With the development of active oceanic fishery, its part in the total catch became less prominent. For a number of reasons, the main of them being overfishing at sea, the absolute size of the catch also diminished. In the majority of the salmon-producing rivers the runs of salmon became very small, so that the stocks were no longer replenished in the normal way. The problem of protection 3*

* Numbers in the right-hand margin indicate the corresponding pages in the original.

and rational exploitation of this valuable biological resource assumed national importance.

The life cycle of the Pacific salmon is short, but complicated. Its species are anadromous and monocyclic, dying off after the first spawning. They deposit a small quantity of large eggs and the embryos develop for a long time, sustained by the food reserves which these eggs contain. Following fertilization, the females bury the eggs in the bed of sand and stones on the bottom of fresh waters. The progeny are protected from predators and the harmful influence of some abiotic factors in typical nests---spawning redds---but are able to develop normally only when these nests are sufficiently well ventilated with clean water. The disturbance of water circulation, drying, freezing, silting of spawning grounds and deterioration of water quality all greatly increase mortality of eggs and larvae.

Unfavourable conditions for reproduction and developement of 4
salmon arise under the influence of both natural and man-made factors, the latter including overexploitation, disturbance of hydrological regime and lowering of water quality in spawning and nursery grounds. The influence of the factors that harmfully affect the process of reproduction is aggravated by the low abundance of the spawning fish. All these circumstances increase the importance of the development of scientific measures for the management of the industry, protection and inprovement of the spawning and nursery grounds. It has become obvious that more intensive salmon husbandry is necessary.

Scientific data of many kinds are required for the development of measures that would permit us to achieve abundant enhancement of stocks and a high level of sustainable catches; the knowledge of the ecology of reproduction and of the adaptive characteristics of development is of fundamental importance. So far we do not possess a sufficient amount of this type of information on different species of Pacific salmon. Until recently, no research was conducted into the ecological aspects of embryology. The lack of knowledge began to be particularly acutely felt when salmon farming in the Far East assumed mass proportions.

There can be no doubt about the importance of the study of the ecology of development and characteristic features of ontogeny in all species, since each salmon species is a valuable object of fishery and husbandry. This information is indispensable for the precise definition of the place occupied by individual species in nature during separate stages of their life cycles, for the understanding of the process governing their distribution and for the appreciation of their interspecific and intraspecific relationships. It would allow more accurate predictions of abundance, more exact control of the fishery, better organization of protection for the spawners, spawning grounds and offspring, as well as the development of methods intended to increase the efficiency of natural reproduction. The detailed knowledge of embryogeny serves as an important foundation for the improvement in the biological supervision of the course of development of salmon in fish farms, on artificial spawning grounds and in nature. It is to be hoped that a comparative morphological and ecological study of the development of salmon will add to the scientific data important for our understanding of the evolution of this group, and expand and deepen our concepts in the field of ecological embryology of fishes.

The material was collected in various regions of the Soviet Union; we were able to study the development of all species present in our fauna. In the course of his study, the author was guided by the precepts of the theory of stage-by-stage development (Vasnetsov, 1946, 1948, 1953a) and the theory of the ecological grouping of fishes (Kryzhanovskii, 1949, 1956), which form an important basis for ecological embryology. They bear out the concept of the dialectic of organism and environment, of the adaptive nature of the process of development and the unity of ontogeny. The attention of the investigator is focussed on the importance of elucidating, and taking account of the special features of the environment, morphology, physiology and behaviour of the organism at different stages of its ontogeny, as well as on the qualitative differences in the systems of adaptations among representatives of different 5
ecological groups and species. These two theories have been widely recognized by biologists in various fields and have been successfully applied in the development of procedures used in the fishing industry.

This book contains short accounts of the modes of life, and ecology of ontogeny as well as step-by-step descriptions of the development of each species. It reviews the characteristics of the ecological group of lithophilic egg-burying fish, the processes governing the development of salmon, generic and specific characteristics and particular features of the ontogeny of individual intraspecific forms. Some problems of evolution of the salmon, their distribution, the ways of enhancing their stocks, movements in biological technology of salmon husbandry and the prospects of introduction and acclimatization of the Pacific salmon are also discussed.

The author was attracted to the study of the Pacific salmon by the corresponding member of the Academy of Sciences of the USSR, G.V. Nikol'skii, the leader of the expedition which studied Far East salmon, and by Professor P.A. Moiseev, who was the Director of TINRO. In his work he was invariably supported by them, as well as by the management of the Sakhalin and Kamchatka branches of TINRO*, Glavrybvod and its far-eastern enterprises, the collective fish farms which provided the base for this work. Dr. of Biological Sciences F.V. Krogius and Dr. of Geographical Sciences E.M. Krokhin provided facilities for work in their laboratories and provided interesting material, as well as their valuable advice. The author had the benefit of consultations with Professor B.I. Cherfas, Dr. V.Ya. Levanidov, Candidates of Biological Sciences I.B. Birman, I.I. Kurenkov, I.I. Lagunov and others. S.F. Zarubin and L.I. Khovrin kindly assisted with some references in Japanese.

The author considers it his pleasant debt to stress the special attention given to this work by his teacher, Professor S.G. Kryzhanovskii, whose recommendations were exceptionally valuable and who for a long period supervised it as the scientific supervisor. The interest shown by Dr. of Biological Sciences N.N. Disler is also acknowledged.

The work was carried out in the Department of Ichthyology of the Moscow State University. Significant input into it was provided by the members of our small team, including technicians and students at various stages in their curriculum, all of whom shared the hardships of field conditions during our expeditions.

To all who rendered assistance in his work, the author is deeply grateful.

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* Pacific Institute of Fisheries and Oceanography - Translator.

HISTORY OF THE STUDY OF FAR-EASTERN SALMONS, THEIR REPRODUCTION AND DEVELOPMENT.

Salmon fishery has been of great importance to the population of the far east since ancient times. Salmon attracted the attention of the very first explorers who reached the rivers of the Pacific drainage and the shores of that ocean.

The beginnings of the study of the Pacific salmon were laid by Russian scientists (Krasheninnikov, 1755; Steller, 1774, et al.). Information which they provided was subsequently widely used by foreign (Suckley, 1861; Gunther, 1866; Jordan and Evermann, 1896) and many Russian researchers. Their views on some aspects of salmon biology retain their value until the present time.

For a long period the investigations were directed towards development of fishing industry. Increase in population density, expansion of transport and marketing, all prompted vigorous growth in salmon catches. Poor management of the industry frequently resulted in overfishing; signs of stock depletion became manifest by the end of the nineteenth century. The question arose: What are the reasons for the fluctuating in the abundance of salmon and how should one care for their replenishing? First steps were taken towards finding ways of regulating fisheries, towards protection of spawning grounds. Construction of fish farms began (Brazhnikov, 1900; Schmidt, 1905, 1916; Chamberlain, 1907; Kuznetsov, 1912; Soldatov, 1912, 1914; Borodin, 1914; Gilbert, 1914, 1924).

With the establishment of the Soviet rule in the Far East the fish protective measures were intensified. Nature reserves [established for research in the natural sciences] and protected regions [concerned generally with only one or a few of the wildlife resources] were set up, and groups of specialists were directed to various regions to study salmon biology. Reports on the freshwater part of the life cycle of salmon were published by I.I. Kuznetsov (1928, 1937). The results of morphological (Chernavin, 1918, 1921) and physicochemical studies of the pre-spawning changes in salmon (Pentegov, Mentov and Kurnaev, 1928) were published, adding to the earlier work of Barret-Hamilton, 1900, 1902; and Greene, 1904, 1926). The hydrological and hydrochemical conditions of the spawning gounds were studied (Krokhin, 1935, 1936; Krokhin and Krogius, 1937a, 1937b). The accumulated data made it possibleto begin the work on the intraspecific differentiation (Pravdin, 1929, 1932; Taliev, 1931, 1932; Berg, 1934, fide Berg, 1953). The status of the knowledge of biology of the Pacific salmon of that time was summarized in known reviews (Schmidt, 1936, 1947; Davidson and Hutchinson, 1938; Pravdin, 1940).

The first symposium on the study of the Pacific salmon took 7
place in Vladivostok in 1938; the results of the investigations were summarized. The participants in the symposium agreed that fixed point observations on the spawning grounds are required to determine the productivity of spawning, find out the reasons for the fluctuations in stock abundance and to devise methods for forecasting permissible catch. Among those who organized and took part in this type of work in Kamchatka were F.V. Krogius, E.M. Krokhin, V.I. Gribanov, R.S. Semko, I.I. Lagunov, and V.V. Azbelev. In the basin of the river Amur the same parts were played by A.Ya. Taranets, A.G. Smirnov, I.B. Birman, V.Ya. Levanidov and I.M. Levanidova.

The difficulties of the war years restricted the possibilities of research. After World War II the studies on the far-eastern salmon resumed on a very broad scale. Their expansion was favoured by the organization of comprehensive expeditions, which brought together members of the staff of TINRO, MGU, IMZh AN SSSR*, Glavrybvod and later also of other instititions. Among the members of the expedition was a group of ichthyologists and ecological embryologists from Moscow.

A second symposium on the problems of the salmon industry of the Far East took place in Khabarovsk in May 1953. It reviewed the condition of stocks, the reasons for their fluctuations, the problems of fishery management, the work of husbandry institutions and of salmon enhancement stations, as well as the ways of improving salmon production. It has been pointed out that the ecological embryological studies led to discovery of shortcomings in the biological techniques of salmon husbandry and provided valuable recommendations for increase in the efficiency of artificial reproduction (Moiseev, 1954; Kaganovskii, 1954). Among the measures aimed at the improvements in the salmon industry, suggested by the participants in the symposium, prominent place was given to better methods of artificial reproduction, increase in extent of husbandry and more rational basis for it, as well as the development of the theoretical base for the transplantation of the Pacific salmon species.

At the beginning of the fifth decade of this century, the Japanese fishing industry engaged in unregulated marine fishery for salmon, which resulted in depletion of stocks. In a number of regions the density of

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*MGU = Moscow State University; IMZh AN SSSR = Institute of Animal Morphology, Academy of Sciences of the USSR.

spawners on the spawning grounds dropped to an insufficient level, so that the recruitment of the stocks was drastically reduced. The conditions called for scientifically based proposals aimed at introduction of strict control of marine fishery. In connection with it, studies of ichthyology, hydrobiology and oceanography were intensified in the regions of the wintering grounds, feeding grounds and along the migration paths of the salmons.

During the third symposium on the studies on the Far Eastern salmon, held in Petropavlovsk-Kamchatskii in December 1960, special attention was paid to the questions associated with the development of marine fishery and to marine research. The examination of the data provided by the fishery, results of tagging and of the marine studies conducted
by the specialists of various countries allowed identification of migrat- 3
ion routes of the salmon in the open sea, the relationship between the migrations and seasonal temperature changes, and the dynamics of water masses and movements in feeding grounds. The definition of the areas and conditions of wintering and feeding of salmon became gradually more precise for salmon reproducing in different regions and larger basins. Also dealt with were other problems of importance to the organization and regulation of fishery (Hirano, 1955; Moiseev, 1956, 1958, 1969; Bogorov and Vinogradov, 1958, 1960; Birman, 1958, 1967, 1968, 1969; Mednikov, 1958; Semko, 1958, 1962, 1964; Hart, 1962; Konovalov, 1971; et al.).

The depressed condition of the stocks obliged a shift in emphasis to the more intensive forms of production. The study of reproduction ecology and of adaptive characteristics in the development of salmon was in tune with the elaboration of correct approach to the solution of this problem. This study, undertaken by many specialists in various regions of the Far East, revealed features of specialization, which will be reviewed when individual species are discussed. It made it possible to form a clearer idea of the conditions favourable for the natural reproduction of salmon, as well as solving some problems of optimization of the regime in incubators and rearing ponds.

During the postwar years the work on transplantation of the Pacific salmon, with century-long history, was reactivated (Vibert, 1953a; Kuderskii et al., 1967). In spite of the conflicting assessment of the chances for acclimatization the work on this topic continued, and new possibilities began to emerge (Taliev, 1950; Kuznetsov, 1953; Ricker, 1954a; Smirnov, 1954c, 1956, 1962a, 1971, 1972a, 1972b; Krykhtin and Levanidov, 1962; Ricker and Loftus, 1968; Tokui, 1969; Christie, 1970). The results which were achieved will be discussed below.

The achievements of the reasearch on the Pacific salmon in the course of the last decade were reviewed in a symposium which took place in Moscow, in February 1972. The participants in that symposium heard and evaluated papers on the status of stocks, abundance fluctuations, population genetics, natural and artificial reproduction, as well as on acclimatization of the Pacific salmons. Special attention was paid to the improvement of reasearch methods. The symposium stressed, in particular, the importance of the investigation into the influence of the industrialization of the Far East on the natural reproduction of salmon and the development of methods of increasing production under the condition of scarcity of spawners (Lagunov, 1973).

In the development of fish husbandry one can observe a close relationship between the knowledge of the biology of reproduction and development on the one hand, and the efficiency of the biological technology of husbandry (Cherfas, 1956; Skatkin, 1962). However, the details of the ontogeny remained unknown for a long time for most of the Pacific salmon species. It was considered sufficient to depend on the knowledge based on related species, particularly of the Atlantic salmon. The objective value of such data is determined by the closeness of relationship between the species compared and by their membership of the same ecological group, which, in its turn, determines certain similarity of embryogenesis. One must not, however, forget about the special features 9
of each species as regards ecology and ontogeny, as has been repeatedly pointed out by the outstanding expert in fish embryology, S.G. Kryzhanovskii (1939, 1949, 1950, 1953).

Passing on to the review of the literature on development of salmon, one must stress that it is voluminous and cannot be dealt with exhaustively in a brief account. Necessary additions are being made with the description of the author's own material and its discussion.

The first studies of the development of the salmonid fishes were made by Lereboullet (1861), Gotte (1873), His (1878), Oellacher (1872) and Klein (1876). The information they provided was soon enlarged by the work of Ryder (1881, 1885), Ziegler (1882, 1902), Kupfer (1886), Henneguy (1888), Kopsch (1894, 1898, 1904) and Swaen and Brachet (1889, 1901). These authors studied the structure of eggs, formation of blastodisc, cleavage, formation of periblast, the process of gastrulation and organogenesis. Much later, embryogenesis of <u>Salmo salar</u> L. and of other representatives of that genus was studied by P.P. Ivanov (1937), Battle (1944), Stefanov and Dencheva (1964/65), Winnicki (1967), A.F. Turdakov (1968), O.A. Lebedeva and M.M. Meshkov (1969), etc.. Also studied was the mechanism of gastrulation (Pastells, 1936; Ballard, 1968; Ballard and Dodes, 1968).

The attention of the embryologists was attracted by the Pacific salmon much more recently. A description of the development of the chinnook, detailed for its time, is found in the monograph by Riddle (1917). Short reports on the development of masou and chum were published by the Japanese scientists Hata (1927) and Handa (1933). A number of developmental stages of the sockeye, coho, pink and chum were described (Ievleva, 1951). At a later date, data were published on the embryology of the chum and some information of the sockeye (Manon and Hoar, 1956; Shiraishi and Uchida, 1957; Olsen, 1964, 1968; Hiroi et al., 1973). All these investigations were conducted on a traditional plane of descriptive embryology.

A large volume of literature was devoted to more detailed problems, such as development of systems of organs and individual parts of the body. Studies were made on the activation and fertilization of salmon eggs. These processes were studied in particular in the chum, masou and sockeye (Kusa, 1950, 1953, 1956, 1958; Kanoh, 1952; Yamamoto, 1951, 1952; T. Yamamoto, 1957, 1966; Namano, 1957). It has been elucidated how long spermatozoids and eggs remain fertile in water (Smirnov, 1963c, 1964b; Foerster, 1968). The accumulated data on morphology, cytochemistry and physiology of spermatoziods and eggs of salmonid and other fishes, and on changes occurring in reproductive cells during fertilization were reviewed by Ginzburg (1963, 1968). The problems of physiology of water exchanges of eggs and embryos of fishes were elucidated by Zotin (1954, 1961). The rate of growth of the embryos during different stages of development was determined (Kronfeld and Scheminsky, 1926; Gray, 1928; Mannery and Irving, 1935; Hayes and Armstrong, 1942; etc.).

A long time ago, Baer (1835) observed in embryos a rich vascular system of the yolk sac and postulated its respiratory importance. Fol- 10
lowing the research of S.G. Kryzhanovskii (1933, 1949, 1956), who demonstrated the great diversity of the structure of embryonic and larval respiratory systems and their adaptive importance, there was a growth of interest in the study of the vascular system of fish embryos. For the Pacific Salmon, the ontogeny of the vascular system was first investigated in the chum (Disler, 1954, 1957).

As the results of the in vivo observations on the movements of the fish embryos, use of time-lapse photography, setting up of physiological experiments and study of rate of diffusion of oxygen across semipermeable membranes, it has been demonstrated that the embryonal mechanics of the salmon, just as that of other fishes, represents one of the mechanisms which serve to intensify external respiration of the embryos (Disler, 1953, 1957; Walker, 1953; Reznichenko, 1957, 1958a, 1958b; Reznichenko et al., 1968).

The attention of the researchers was attracted to the changes in egg membranes in the course of embryogenesis, to the structure and function of the eclosion glands. Information on this subject and lists of relevant literature are contained in many Russian sources (Privol'nev, 1943; Buznikov, 1955, 1961, 1964; Buznikov and Ignateva, 1958; Sakun and Chistova, 1960). The relationship between the function of the eclosion glands and the external factors, in particular the conditions of gaseous regime and of water flow. The defensive role of the external non-chitinized layer of the membranes was determined (Bell, Hoskins and Bagshaw, 1969).

The process of fin formation of salmon was described (Harrison, 1895; Faytelson, 1936; Francois, 1957; Szubinska-Kilarska, 1958), as well as the development of myotomes (Ryndzyunskii, 1939), ontogeny of alimentary canal (Greene, 1912, 1926; Kudinskii, 1966; Vernidub, 1967a, 1967b) and development of the kidneys (Ford, 1958; Ford and Newsstead, 1958). The process of the differentiation of gonads was examined (Robertson, 1953; Manon and Hoar, 1956; Persov, 1962, 1965, 1966, 1968).

In recent times great interest is shown in morphological and functional study of the receptors, in behaviour of fish and its changes during the ontogeny. The development of eyes and the reation to light of larvae and fry of salmon were studied (Woodhead, 1957; Brett and Ali, 1958; Ali, 1959, 1966). A comparative study was made of the development of the eyes of fishes, in relation to their ecology (Baburina, 1972). A lot has been done to acquire knowledge of the organ of olfaction and its role in food-gathering, defensive and spawning behaviour, school formation and orientation in space during migrations; the important role of chemoreception in search by salmon for its place of reproduction was demonstrated (Hasler and Wisby, 1951; Hasler, 1954, 1957; Flerov, 1962; Brett and Groot, 1963; Pfeifer, 1963; Groves et al., 1968; Malyukina et al., 1969, 1974). The development of the sense organs of the lateral line of chum and other fishes in relation to the change of their behaviour in the course of ontogeny were studied in detail by Disler (1960).

The sensitivity of the developing eggs to the influence of various abiotic factors was investigated (Hein, 1907; Hata, 1927; 11
Kikiforov, 1939, Privolhev, 1941a; Privolhev and Nikiforov, 1959; Vernodub, 1949, 1951; Hayes, 1949; Hayes et al., 1953; Smirnov, 1954b, 1955b, 1964b; Alderdice and Wickett, 1958; Combs, 1965; Brannon, 1965; Korovina, Lyubitskaya and Dorofeeva, 1965; Ievleva, 1967; etc.). The specific character [species specificity] of the reactions of the developing organism to the external influences was demonstrated; the reactions were uniform only to those external factors that influence the same physiological mechanisms (Kororvina, 1956, 1964).

Information on the changes of some morphological characteristics under the influence of the external factors is of great interest. It has been shown that the incubation of eggs at different temperatures and gaseous regimes leads to changes in the number of segments, vertebrae, scales and finrays (Lyubitskaya, 1952, 1961; Taning, 1952; Garside, 1966c). The existence of stages and periods of ontogeny stable or sensitive to temperature changes was discovered (Ivanov, 1949; Polyanskaya, 1949; Combs and Burrows, 1957; Orska, 1957; Combs, 1965; Gorordilov, 1969, 1970; etc.). The influence of the thermal factor on the rate of growth is well known. It also undergoes changes under the influence of radiation (Eisler, 1958, 1961; Leitritz, 1960; Hamdorf, 1961; Lyubitskaya, 1961; Dorovina, Lyubitskaya and Dorofeeva, 1965). During the period in the ontogeny when salmon develops in the gravel, the influence of insolation causes pathological changes, the character of which was investigated in chum salmon (Disler, 1954, 1957).

The gaseous regime of the environment significantly influences the embryos. Researchers working with different species of salmon have noted increased oxygen demand with the course of development, as well as the appearance of pathological changes, higher mortality of eggs and premature hatching in the presence of insufficient oxygen. High oxygen content of water brings about an increase in the rate of development (Vasil'ev, 1958, 1959b; Privol'nev and Nikiforov, 1959; Bishai, 1960, 1962a, 1962b; Shumwey et al., 1964; Winnicki, 1967; Kotlyarevskaya, 1968a; Ostroumova, 1969; Khodzher, 1973a, 1973b, 1973c). High saturation of water with carbon dioxide retards development (Levanidov, 1954a; Alderdice and Wickett, 1958). However, when the oxygen content of the water is sufficiently high, salmon is able to develop in the presence of substantial quantities of carbon dioxide (Townsend and Earnest, 1940; Townsend and Cheyne, 1944).

Changes in the mode of life during development and specific [species] characteristics of the behaviour of the fry of Pacific salmon were described from observations in nature, as well as on the basis of experimental data (Disler, 1951, 1954, 1960; Hoar, 1951, 1954, 1958; Ali, 1959, 1966; Chapman, 1962; Mason and Chapman, 1965; Kamyshnaya, 1967; Reimers, 1968; Ishida et al., 1973). Studies were made on the timing and conditions of migrations and the condition of the juveniles of various species on leaving rivers (Neave, 1943, 1955; Krogius, 1954, 1967; Krykhtin, 1955, 1962; Scud, 1955; Roppel, 1956; Gouley et al., 1958; McDonald, 1960; Smirnov and Kamyshnaya, 1965; Volovik, 1967a; Pushkareva, 1967;
Perova, 1968; etc.). Relationships were determined between cyclical 12
fluctuations in illumination, temperature and other abiotic factors on

the one hand, and changes in the activity of the neurohormonal complex, regulating the level of metabolism and determining the behaviour, in particular migratory behaviour of juvenile fish, on the other. A parallel existence was found in the migrants of the mechanisms of hyper- and hypotonic osmoregulation, ensuring survival under the conditions of changing salinity (Hoar, 1951, 1958; Fontaine, 1954, 1964; Evropeitseva, 1957; Houston, 1957; Baggerman, 1960, 1963; Barannikova, 1961, 1968; Bocharov, 1961, 1963; Natochin and Bocharov, 1962; Natochin et al., 1970; Zaks and Sokolova, 1965).

Crossings were made for most of the possible variants between species of the Pacific salmon. The experiments demonstrated the absence of physiological barriers that would prevent hybridization. Some first generation hybrids proved fully viable. There exist hybrids with accelerated rates of development, growth and maturation (Foerster, 1935; Inaba, 1953; Smirnov, 1953a, 1954a, 1969; Krykhtin, 1962; Ivankov, 1973). A valuable experiment was performed on the selection of the Pacific salmon (Donaldson, 1970; Donaldson et al., 1973; Kirpichnikov, 1973).

We shall deal in some detail with the ecological and embryological studies of animals which are of interest to us. The ecological direction in embryology of fishes was initiated in the Moscow school of comparative morphologists, led by the Academician A.N. Severtsov. It took shape under the influence of demands made by the fishing industry, most of all by the fish husbandry, which required exact knowledge of ecology and special features of development of various fishes. Natural reproduction of many valuable species was becoming difficult in consequence of the construction of hydroelectric stations, which damaged the migration routes and changed the conditions of the spawning rivers. It was necessary to develop methods of replenishing fish stocks under the conditions of increasing influence of human activity on the aquatic environment. Consequently, in many regions embryological studies were instigated, which brought to light extraordinary variation of conditions, methods of reproduction and characteristics of morphogenesis in fishes. The accumulating data did not fit into the framework of earlier concepts, which saw ontogeny as the "chronicle" of the phylogenetic processes and underestimated the specific nature and adaptive importance of variability at the earlier stages of the developing organism.

The comprehension of the huge empirical material was assisted by reference to the dialectical materialistic theory, which, as is well known , visualizes the process of development as a unity of contradictions, the unity of the quantitative and qualitative changes, both gradual and progressing in jumps. The materialist dialect bears out the unity of the old and the new, the general and specific, the form and function the external and internal, the organism and its environment. These concepts have opened the perspectives for the learning of the principles of 13
development of organisms and exerted great influence on the formation in embyology of a new direction--ecological embryology.

The comparative study of the research on development of fishes led to valuable generalizations, prominent among them being the theory of the step-by-step development and the theory of the ecological groups of fishes.

Thorough investigations of changes in various systems of organs and in the organism as a whole, carried out by V.V. Vasnetsov (1946, 1948, 1953a, 1953b) and his collaborators on various species, made it possible to elucidate qualitatively distinct stages of ontogeny, which received the name of "development stages". Within the period of each of these stages there occur no significant changes in the developing organism, in structure, physiology, behaviour and relationship with the environment; the system of adaptations remains relatively stable. The organism undergoes reconstruction, changes its system of adaptations, when passing from one stage to the next. This step-by-step theory of development reflects, therefore, the unity of the gradual development and the occuring in jumps during ontogenetic transformations. As an example, the stages of cleavage, gastrulation, mixed endogenous and exogenous feeding, and others can be named. The groups of stages, resembling one another in the general character of adaptations, were named "periods" of development. Strictly speaking, the periods of development have long been observed by the researchers, who distinguished embryonic, larval, juvenile and sexually mature periods in fishes. The step-by-step theory of development discovered significant principles of the ontogenetic development. It has been accepted by biologists in various fields (Arshavskii, 1948, 1955; Matveev, 1956; Shilov, 1965; Baburina, 1971; et al.). It has been called "one of the great general principles in ichthyology" (Gerbil'skii, 1959, p.34).

Examining the results of the morpho-ecological investigations of development of fishes, carried out in various watersheds, S.G. Kryzhanovskii (1949) established the existence of certain ecological groups, the representatives of which have in common their environment,

methods of reproduction and details of development. He identified the following groups: pelagophilic fishes, which deposit floating eggs; phytophilic fishes, depositing their eggs on bottom vegetation; psammophilic fishes, which reproduce on sandy bottoms; lithophilic, depositing their eggs on stones, ostracophilic fishes adapted to development within the mantle cavity of molluscs; groups of fishes building nests, carrying their offspring and some others. The names of the ecological groups point to the type of brood care, locality of egg deposition, i.e. to the type of living condition of the offspring, which determine the nature of the adaptations of the developing organism. The theory of the ecological groups played a significant role in the development of the step-by-step theory. In particular, it enabled recognition of the adaptive character of different stages in the ontogeny in various fishes. Literature pays close attention to the great importance of these two theories to the solution of problems associated with the organiz-
ation of rational fishing industry, intensification of the natural re- 14
production of fishes and improvements in biological techniques of fish husbandry. They allow the increase in depth of embryological studies and knowledge of the principles of evolution of ontogeny (Vasnetsov, 1953b, 1953d; Kryzhanovskii, 1950, 1953; Nikol'skii, 1954a, 1965; Matveev, 1956, 1964; Eremeeva, 1964, 1967; Disler, Reznichenko and Soin, 1965; Eremeeva and Smirnov, 1965).

S.G. Kryzhanovskii (1949, 1956) placed the salmon in the ecological group of lithophilic fishes burying their eggs. An accurate determination of the character of ecological specialization of these fish made it possible to plan further concrete investigations. As the result of detailed ecological and embryological study of the autumn Amur chum, qualitatively distinct periods and stages of its ontogeny were discovered and their specific characters determined (Disler, 1951, 1954, 1957). Other authors studied the pink salmon (Soin, 1954, 1964, Smirnov, 1954a, 1954b, 1964b; Vasil'ev, 1958, 1959b; Frolenko, 1959; Muntyan, 1963; Smirnov and Kamyshnaya 1965); masou (Soin, 1954; Krykhtin, 1955, 1962; Smirnov, 1962b; Kanidyev, 1964); chinook (Smirnov, 1958, 1960b); coho and sockeye (Smirnov, 1958, 1959a, 1960a, 1963b, 1964a, 1964b; Ievleva, 1967; Egorova, 1970). Comparison of the accumulated facts pointed to the significant ecological and functional morphological differences between species and some intraspecific forms. These data were of theoretical importance and expanded our possibilities to solve many problems that were troubling the practical fish culturists. We shall give some details below.

The information on the specificity of the spawning localities increased the accuracy of the regulation of the industry and, at the same time, the mode of rational utilization of the spawning reserves. The principle involves provision of the optimal density of spawners of all species and intraspecific groups on the spawning grounds. When the special characteristics of the mature spawners and of the micro-habitat of the spawning grounds were taken into account, it became possible to evolve the concept of the adaptive significance of the pre-spawning changes of the salmon and of the special features of the spawning stage (Smirnov, 1959b, 1964b, 1965; Eremeeva and Smirnov, 1965; Eremeeva, 1967).

Ecological and embryological study has revealed, characteristic for salmon, strong development of the embryonic and larval organs of respiration and, at the same time, the correspondence between the level of development of these organs and the gaseous regime of the spawning redds, which is specific in nature. Information was accumulating on the relatively low oxygen saturation of water washing the eggs, particularly in forms which reproduce in the localities where spring brooks originate (Disler, 1953, 1957; Levanidov, 1954b 1968; Smirnov, 1954a, 1963b, 1964b; Soin, 1954, 1964; Vasil'ev, 1957, 1958, 1959b; Krokhin, 1960; Kanid'ev, 1965; Kanid'ev and Levanidov, 1968). These data are at variance with the view of the salmon as oxyphilic fish (Schmidt, 1947; Tretyakov, 1949; Puchkov, 1954). In view of this a review is needed of the recommendation on the type of water supply of the fish rearing equipment, in rearing various species.

Morpho-ecological studies discovered details of structure, 15
behaviour and requirements of hatched embryos and larvae, determined by evolutionary adaptation of salmon to develop in mixed sand and stone ground. It became obvious that keeping free embryos and larvae in containers with smooth bottoms is contrary to the ecological requirements of salmon.

One of the measures of intensification of hatchery production of chum and pink was proved to be supplementary feeding of fry, a procedure not previously used in the far-eastern fish hatcheries and during acclimatization of these fish. The method of feeding was being gradually improved (Vasil'ev, 1954; Levanidov, 1954a, 1955, 1957, 1964c, 1969; Smirnov, 1954a, 1963b; Chernyavskaya and Tankov, 1959; Florenko, 1964, 1965; Kanid'ev, 1966; Kanid'ev and Levanidov, 1968; Kanid'ev et al., 1970). As the studies continued on this topic, attention was focussed on the differences between species and on the validity of restricting supplementary feeding of the pink in hatcheries to the period before the completion of the stage of mixed feeding (Smirnov and Kamyshnaya, 1965).

Observations on the development of fry showed profound changes in structure, changes in location, in character of feeding, in behaviour and interrelationship between individuals. Such observations make it possible to understand the rules governing the distribution of fry of various ages and species in their habitats, to define their needs better and ensure sufficient feeding, as well as to define more precisely the character of intraspecific and interspecific relationships. The study of the developmental stages serves as an important base for the knowledge of the principles of the dynamics of population abundance (Nikol'skii, 1954a, 1965; Eremeeva, 1964, 1967; Eremeeva and Smirnov, 1965; etc.). The need of the practical fish husbandry, faced with the important problem of producing physiologically normal fry, to take into account the distinguishing features of species and changes with age, is quite obvious. The knowledge of the age changes of the fry and of its needs at various stages, allows the selection of correct time and optimal conditions for release from hatcheries, which is of major importance for the increase in age coefficient, and consequently in efficiency and economic value of hatchery reproduction of fishes. Finally, one would wish to stress, that the theory of stage-by-stage development and of ecological groups of fishes gives significant help in the study of the material provided by physiological and biochemical studies of fish of various ages.

During recent years the development of the biological basis for

a rational salmon industry in the Far East and for improvement of the biological techniques to be used in salmon production made considerable progress. In some regions salmon rearing became the main method of maintaining the commercial stocks. However, the stocks of salmon remain at a low level and to increase them one needs much greater effort. Not only strict regulation of fishery is required, but also the change to
the most intensive possible way of enhancing stocks. As has been said 16
above, this problem can be successfully solved only in the presence of a deep knowledge of biology of each species during different stages of its life. The knowledge of this type, as far as the Pacific salmon are concerned, cannon as yet be considered sufficient. Missing so far is thorough description of such valuable species as the sockeye, chinook and coho. On the development of pink there exist only short publications. The study of the ontogenetic characteristic features of intraspecific biological forms has only just begun. All this points to the importance of the comparative ecologo-embryological study of the Pacific salmon.

THE REGION OF INVESTIGATIONS, MATERIAL AND METHODS. 17

Expeditionary work, carried out in various regions, made it possible to become acquainted with the specific and intraspecific variability of salmon. The autumn chum, the pink, masou and coho were studied in the Sakhalin during 1952-1954, 1959, 1960 and 1965. The fish rearing establishments Sokolovskii, Adotymovskii and Lesnoi, situated in the drainage of the rivers Naiba, Tym' and Lesnaya respectively (all draining into the Sea of Okhotsk), were used as the main bases for this work.

To become more broadly acquainted with the fish husbandry practices and to make material more complete, we travelled to the Kalininskii, Parusnyi, Poronaiskii, Pugachevskii and other fish establishments in Sakhalin, as well as to the Teplovskii fish farm, situated in the drainage of the river Bira, a tributary of the Amur (Fig. 1). In the Paratunskaya Experimental Laboratory of the Kamchatka branch of TINRO, which is situated on Lake Dal'noe in the drainage of the river Paratunka, opening in Avachinskaya Bay, the sockeye, chinook and coho were studied in 1956, 1957 and 1961. Data on the coastal strip masou were collected in August and September 1970 in the Khasan area of Primorskii Krai in the rivers Barabashevka and Kedrovka. In connection with the work on acclimatization of pink and chum, in 1961 we travelled to Umbskii (river Umba in the White Sea watershed) and Taibol'skii (river Kola in the Barents Sea watershed) fish farms. An expeditionary detachment was collecting material in the river Muchka, a tributary of the river Teriberka, opening into the Barents Sea, in 1965, 1967, 1968, 1969 and 1973.

The biological study of the fish, biochemical analysis of eggs and fry, collection of information on meteorological, hydrological and hydrochemical conditions of spawning grounds, redds, hatchery incubators and feeding ponds were accomplished with the use of commonly accepted methods. This allows us to limit this section to short explanations.

Current velocity was measured with a bathymetric tachometer. For collection of water samples from the bottom of spawning grounds, redds and fish rearing appliances we used apparatus similar to the pseudobathometer of G.Yu. Vereshchagin. Quantity of oxygen dissolved in water was determined with the aid of Winkler's method, free carbon dioxide by alkaline titration and the reaction of the environment with the aid of Michaelis' apparatus. Rate of filtration of water through the gravel of spawning grounds and redds was recorded with the aid of an electric measuring device which permitted registration of movement of the solution of an electrolyte (cooking salt), which was released into gravel at the level of deposited eggs. A similar method, known also to hydrogeologists, was also used in the study of the spawning grounds by Vasilyev (1958), who described the method of this work.

13

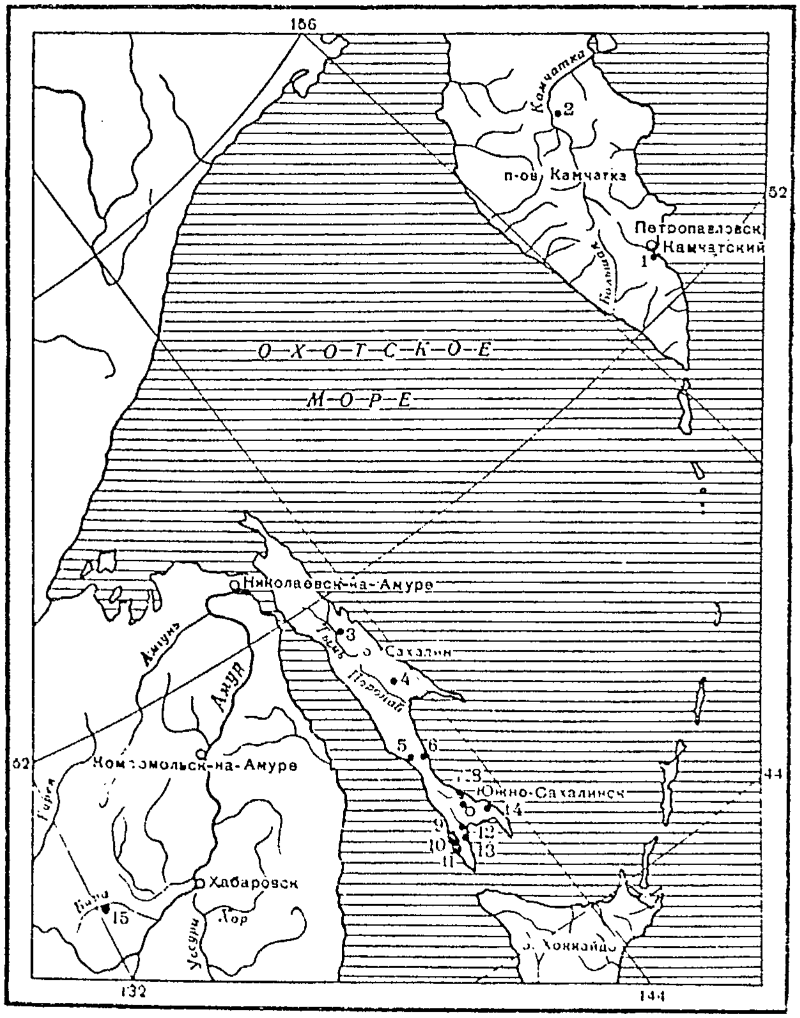


Fig. 1. Localities where material was collected.
1 - Paratunskaya Laboratory of the Kamchatka branch of TINRO; Fish husbandry establishments, 2 - Ushkovskii, 3 - Adotymovskii, 4 - Poronaiskii, 5 - Parusnyi, 6 - Pugachevskii, 7 - Sokolovskii, 8 - Bereznyakovskii, 9 - Kalininskii, 10 - Sokol'nikovskii, 11 - Yasnomorskii, 12 - Anivskii, 13 - Taranaiskii, 14 - Lesnoi, 15 - Teplovskii

To assess the amount of oxygen utilized by the eggs, larvae and fry, 19
the method of closed vessels was used.

Samples of 50 to 100 eggs were taken for biochemical analysis. After removal of inner fluid with filter paper, the eggs were weighed, dried in a thermostat at a temperature of 70° until constant weight was reached and then powdered. Fat was extracted with ethyl ether in Soxhlet apparatus. Total nitrogen was determined with the aid of Khjeldahl's method (with polymicrometer). Quantity of ash was determined after burning dry substance in a muffle furnace at a temperature of 300-350°. All determinations were made twice.

To collect information on sperm production, spawning males were kept in conditions resembling natural ones. During prolonged observations sperm was collected from live males which were then returned to their confined places. When single collections were made, males were killed. The number of spermatozoids was counted in Goryaev's chamber, in a manner similar to that used in counting blood cells.

The method of calculating time during which eggs and sperm retain in water their ability to participate in the process of fertilization (their fertility), was described earlier (Smirnov, 1963c). Water used in experiments was collected from spawning grounds. To determine the fertility of the eggs, separate batches (150-200 eggs) were fertilized with fresh sperm after they had been kept in water for the required time. To determine the period during which sperm retains its fertility, a sample of 1 ml. of sperm was taken from each of three males, diluted in 1 l. of water. Samples of 15 ml. of suspension were taken at intervals of 10 seconds and used to fertilize fresh eggs. Control eggs were fertilized with the aid of the "dry" method. The eggs were then incubated up to the stage of 8-64 blastomeres, fixed, and the number of the dividing eggs was counted.

The influence of the mechanical factors on the developing eggs was studied using a mechanical vibrator (Smirnov, 1954b, 1955b). The experimental sample of eggs was divided into portions of about 200 eggs, which were placed on hatching trays and incubated in a hatchery apparatus. Prior to fertilization, during the period of swelling and subsequent course of development, eggs with their trays were subjected to vibration. They were then returned to the incubator. The sensitivity of the eggs at the time of the application of vibration was judged by the number of non-surviving eggs. Observations on the course of development of the surviving eggs allowed also determination of less vital changes caused by the action to which they were subjected.

Eggs were fertilized with the aid of the "dry" or Russian method (Smirnov, 1963b). Fertilization was heterospermic. After swelling, the eggs were placed in standard hatchery trays, size 31 x 31 cm., from 1.5 to 3 thousand eggs per tray. Ten trays with eggs were placed in special stands and covered by protective lids. Stacks of trays were then placed in hatchery incubators.

The Far Eastern hatcheries are equipped with trough-type apparatus (Cherfas, 1956; Chernyavskaya and Tankov, 1959; Smirnov, 1963b). The bottom and the sides of the apparatus in the Sokolovskii hatchery are made of cement and contain four trays of eggs each. Each apparatus in turn is situated 5 cm. lower than its predecessor and the water which enters it over a dam beam is aerated. Similar apparatus in the Adotymovskii hatchery are made of wood and arranged in vertical series. The Paratunskii experimental incubator is equipped with Williamson's apparatus. In some of the Sakhalin establishments, troughs are made wide, and stacks of trays are places in them athwart the current, several in each stack. Free embryos and larvae are maintained both at the bottom of these troughs and in feeding containers of considerable area. The bottoms of most of these containers consist of several layers of coarse, rounded gravel. During the years covered by our work, the bottom of the feeding areas in Adotymovskii and Teplovskii hatcheries was sandy. To incubate eggs in the river we used small containers with wooden frames and side walls; front and back walls, the bottom and partitions between individual sections were made from brass netting and covered with asphalt varnish. Such "river" apparatus was placed near the bank in pure gravel. In all instances, both eggs and larvae were protected from solar radiation. To incubate eggs within the bottom on spawning grounds we used containers of net, with stiff wire frames, volume 1 dm^3. Experimental eggs were placed in them mixed with gravel, after which numbered containers were buried in the bottom on the spawning ground. All the far eastern fish hatcheries and experimental incubators are provided with naturally flowing water, which is filtered before entering them. Many establishments are supplied with ground water which is collected from springs that have passed through natural spawning grounds. In recent years some establishments were provided with pumping equipment to obtain auxiliary water supply from the rivers. The hatcheries producing pink salmon are supplied with river water. It is collected with the aid of special drainage apparatus from below the river bed (Koposov, 1959). Information on the quality of water in which experimental eggs were incubated is given with the description of development of the salmon. Each year some eggs from the Sakhalin, Kamchatka and Kola Peninsula were delivered by plane to Moscow. The incubation of these eggs and rearing of larvae were completed in the experimental apparatus of the department of ichthyology in Moscow University.

Microscopic examination of eggs and fry was conducted primarily in vivo. The embryos were first examined through the membrane. When these were insufficiently transparent, some details could be examined
through the micropyle field. After that, the embryos were carefully 21
removed from their membrane. When this was difficult (during the early stages), a part of membrane at the animal pole of the egg was removed and the study of the embryo continued through this artificial "window". Accurate drawings, which were made with the aid of the drawing apparatus RA-1 served as documents of the results of morphological studies. Mobile embryos, larvae and fry were anaesthetized with MS 222 (tricain-metasulphonate), urethane and diurethane. It must be noted that the latter two substances seriously weaken heart action, so that circulation is interrupted in small capillary vessels; when their action is prolonged, the embryo frequently dies.

To obtain more accurate details of some parts of the embryo, for example, the lateral line organs, live embryos were stained with an aqueous solution of methylene blue. To make microscopic preparations, samples were fixed in 5% isotonic solution of neutral formalin and in Bouin's fixative.

Development of each species was studied on several series of eggs, fertilized at different times and developing under different conditions. During all the years of this work, material consisting of many series was obtained and examined. To include it here in full would swell this book to excessive volume. For this reason, for each species, data were used mainly from observations gathered from two series, incubated under different conditions.

Oncorhynchus keta (Walbaum)

By volume of catches, the chum occupies the second place among the Pacific salmon. The the years when the runs of the pink are small, it moves to the first place. The mean length of the mature individuals is 60-70 c., weight 3-4.5 kg; the record individuals exceed more than 1 meter in length and weigh more than 14 kg. This species has long been reared in the Far East. In many respects it has been better studied than its relatives.

Distribution and life in the sea. During the summer the fish move to the high latitudes, reaching the northern shores of the Sea of Okhotsk and Bering Sea. A small quantity of chum migrates into the waters of the Arctic Ocean, in the west to the river Lena, in the east to the MacKenzie river (Berg, 1948). In the maturing specimens the feeding migration passes into spawning migration, while the fish of the younger ages, with the onset of the autumnal cold move into the area affected by the warm waters of the Kuroshio and the North Pacific Current, where they spend the winter. Information on the wintering grounds, feeding grounds, or migrations is contained in many sources (Hirano, 1953; Birman, 1958, 1967, 1968; Semko, 1958, 1964; Hartt, 1962; Sano, 1966). The southern limit of the distribution of the chum coincides more or less with the 10° isotherm, the northern, with that of 1.0-1.5° isotherm. The chum spawning in the rivers of Asia, winters and feeds in various areas. According to the existing information, from the area situated to the south of the western group of the Aleutian Islands, the migrations can be traced to the river Anadyr', the eastern and western shores of Kamchatka, and the northern shores of the Sea of Okhotsk. Autumn chum tagged in the Aleutian region were taken in the rivers of the Sakhalin, Hokkaido, Honshu and even in the Amur. From the area of the wintering grounds, situated to the south-east of the Southern Kruil' Islands and Hokkaido, the summer chum migrate to the Amur, the rivers of Sakhalin and Hokkaido. In the same area, some parts of the chum populations from Okhotsk, western and eastern Kamchatka spend their winters. In the Sea of Japan, to the east and south-east of the Korean Peninsula, the chum from Primore and a part of the summer chum population from the Amur, Sakhalin and Hokkaido overwinter and feed. The range of the chum is broader than those of the related species. The autumn-spawning chum travels particularly far from its native shores.

During the winter, the fish remains at a depth of up to 300-500m day and night Its vertical migrations are apparently small; they are limited by the concentration of the food plankton at those levels. With the onset of the warmer spring temperatures, the number of food organisms rises in 23
the surface layers, to which the chum also move. They remain close to the surface at night, during the spring at a depth of 0-50 m., during the summer, at 0-13 m. It is at the depths of 8-10 m. that drift net fishery takes place at that time. By day, following food organisms, the fish descend to several tens of metres. The vertical movements of the fish is observed within about the same temperature limits as its horizontal distribution. In the north, warming occurs in a narrower layer of surface water and the vertical migrations there are less extensive. The spring migrations of the chum from its wintering places

into the colder areas coincide with the rise in temperature of the surface water to 2.5-3°. During the period of the greatest warming of the ocean, in August and September, the distribution of the feeding chum is limited in the south to the surface isotherm about 14°. In the areas of the ocean with temperatures of 15-17°, one does not find the salmon during its feeding season (Birman, 1958, 1967, 1968). In the Sea of Okhotsk the salmon are taken at temperatures of up to 18.7°--higher than in the ocean. This discrepancy is explained by A.I. Frolov (1964) by the change in the physiological condition of the fish coinciding with the passing from the feeding to the spawning migration. Finding themselves in the zone of the influence of the river run-off, the mature spawners begin to react positively to the water of lower salinity and move into the estuaries and the mouths of the rivers.

Areas of Reproduction. To spawn, the chum enters almost all the rivers of the Asiatic continent from the northern border of its distribution to the rivers Tumen-Ula and Rakuto in the south. It occurs only rarely in the Commodore Islands. It spawns in great numbers in the rivers of the Sakhalin and the Kuril' Islands, and abundantly enters into the rivers of Hokkaido; the limits of its distribution are the northern rivers of Kyushu. In North America, chum spawns from the MacKenzie river to the rivers of Monterey Bay (Berg, 1948; Clemens and Wilby, 1961; Neave, 1966b, Sano, 1966).

Intraspecific Differentiation. Fishermen have long been distinguishing between the summer and autumn chum. Berg (1934, quoted after, Berg, 1953, 1948) referred to them as races, or ecotypes; it is in this sense that we are going to use these terms in this book. As a type form,

O.keta (Walbaum), Berg accepted the summer spawning chum, without differentiating between individuals from various regions. Contrasted with the type form was the autumn spawning Amur chum, *O.keta infraspecies autumnalis* Berg. Smirnov (1947) pointed out the ecological nature of the seasonal forms of the Amur chum. In the drainage of the Amur, the autumn chum spawns near the origin of the streams, whereas the summer chum reproduces further down the rivers and streams and its redds are washed mainly by ground water. The temperature and hydrochemical regime of these two types of spawning grounds is significantly different, as will be shown in detail below. The ecological differences are reflected in the entire biology. V.K. Soldatov (1912) noted the larger size, weight and fecundity of the autumn chum, which also grows faster. The data on the differences in size, weight and fecundity and other characteristics 24
of the seasonal races of the Amur chum are quoted by many authors (Kuznetsov, 1928, 1937; Lovetskaya, 1948; Birman, 1952, 1956; etc.). They also differ from each other in morphology and in karyotypes (Grigo, 1953; Kulikova, 1971, 1972).

In contrast with the summer chum, the autumn chum enters the Amur during the time of the autumn spate, its gonads still poorly developed. The large size and high fat content of the autumn chum is seen as an adaptation to a prolonged migration upstream (Nikol'skii, 1963). It moves up the Amur as far as 2,000 km. and more. The main bulk of the autumn chum spawns in the Amur drainage in areas with low snowfalls and severe winters, its progeny developing successfully only because the redds are supplied by ground water which does not drop greatly in temperature during the winter. This form occupies the southern part of the species range, corresponding with the borders of the ancient system of the Paleoamur (Birman, 1952, 1956).

The summer chum migrates up the Amur for a much shorter distance, arriving in commercial concentrations as far as the river Ulchi (about 600 km. from the mouth of the Amur). In the drainage areas of large rivers, the summer and the autumn chum prefer different tributaries. When they do enter the same tributary, the spawning grounds of the autumn chum are situated further upstream. The summer chum matures somewhat earlier and more uniformly than the autumn one: in the Amur, the maturing fish are mainly four years old, sometimes three years old, whereas the spawning population of the autumn chum is dominated by the five year old and four year old individuals; a small number of individuals mature as seven year olds, and in the southern part of the range as two year olds (Lovetskaya, 1948; Birman, 1951, 1956; Sano, 1959; Volovik and Landyshevskaya, 1968).

Being ecologically different, these two forms react differently to climatic changes. In the drainage of the Amur, the summer chum used to be quantitatively dominant. During the severe winters of 1911-1914 its numbers dropped catastrophically and its stocks remain in depressed condition to this day. The offspring of the autumn chum suffers smaller losses during severe winters with low snowfalls and its stocks are more stable (Nikol'skii, 1952, 1954a; Birman and Levanidov, 1955; etc.).

Kulikova (1972) writes of greater variability of characteristics in summer chum, when compared with those of the autumn one, and relates this to the large size of the range which encompasses several geographic zones. It is our view that the differences observed can be explained mainly by the fact that observations were made on all summer spawning chum. This fish comprises forms with significant differences in ecology, and consequently, in morphology and biology.

It should be pointed out that the summer spawning chum in Kamchatka, in contrast with the Amur summer chum, prefers for spawning quiet streams, springs, and limnocrenes, and builds its redds near the point of emergence of the ground water (Kuznetsov, 1928, 1937; Krokhin and Krogius, 1937b; personal observations). Consequently, summer spawning Kamchatka chum is an ecological analogue not of the summer, but of the autumn Amur chum. Of importance here is also the fact that these forms are reprod-
ucing in the drainage areas which have long been isolated from each 25
other in the systems of Paleoyukon and Paleoamur repectively (Lindberg, 1948, 1972); their feeding areas are also separate from one another. It is these differences in the ecology of development, as well as ancient isolation, that one whould consider as responsible for the morphological and biological differences between the summer spawning chum from Kamchatka and the Amur. There exist valid reasons for their taxonomic separation. It has been proposed to refer to the Amur summer chum as *O.keta infraspecies amurensis* (Smirnov, 1973).

Morphologically and biologically variable is also the Kamchatkan chum. Abramov (1948) pointed out the distinctive features of the Kamchatkan chum of the late run, referred to by the local inhabitants as "mánok" and separates it as an independant race. In his view, *O.keta infraspecies manok* Abramov, is distinguishable from the Kamchatkan summer chum by larger size (mean length 66.10 ± 0.23 cm.), low fecundity (2122 ± 36 eggs), larger number of vertebrae and by some other characteristics. This salmon enters the rivers with less mature gonads, spawns in October--November and even later. In the river Banna, a tributary of the Plotnikova, mánok reproduces in localities with rapid current, upstream from the summer chum. The spawning grounds are not associated with the point of emergence of ground water. The young, after their emergence from the ground leave the river almost immediately. Morphologically and biologically manok is different from the Amur autumn chum. The data obtained by Birman (1964) corroborate the special character of the summer and autumn chum from Kamchatka. For that author, only the question of the taxonomic rank of these forms remains open.

The above divisions do not exhaust the entire intraspecific variability of the chum. Berg (1948, p. 178) wrote: "It is possible that further investigation will force us to isolate the chum from Lena as a separate form." In connection with this, the morphological and biological characters of the chum from the Anadyr is of interest (Kulikova, 1971, 1972). In agreement with Pravdin (1940), Berg spoke also of the separate form of Kamchatkan small chum, distinguished by early runs, larger number of pyloric caeca and by other features.

Birman (1951, 1952, 1956) contributed much to the study of the differentiation of the seasonal races. He drew attention to the fact that the river Amgun is used by relatively small, autumn chum of low fecundity. Its mean characteristics are: length of males (AS) 64.4 cm., females 63.0 cm., fecundity 3258 eggs. Particularly large autumn chum spawns in the river Kur; here, mean length of males is 73.7 cm., females, 70.2 cm., and fecundity is 4293 eggs. Variations also occur in the size of the eggs, which are particularly small in the chum from the river Bira. Having taken into account also some morphological differences, Birman arrived at the conclusion that there exists biological specificity in the autumn chum of all larger tributaries of the Amur. He designated them as the local populations.

The same author postulated the existence of distinctive local 26
populations also in the summer Amur chum. Subsequent investigations confirmed the correctness of his postulate (Svetovidova, 1961). It has been found, for example, that small fish (mean size of males, 57.5 cm., females, 55.5 cm.) with low fecundity (2266 eggs) migrate into the river Beshenaya. The members of this stock are distinguished by large size of trunk; they have many vertebrae and gill rakers and a long dorsal fin. The summer chum of the rivers Ul and Dzhappi (mean length of males, 62.7 cm., females, 60.6 cm.) are distinguished by their large size. The fecundity is slowest in the summer chum from the river Amgun (2190 eggs) and it has a characteristically deep body. The summer chum from the river My has high fecundity, mean 2523 eggs. The fish from that river are distinguished by a slow rate of growth, particularly during the first year of their life in the sea. On the other hand, the fish from the river Ul grows slowly during its third year, but rapidly during its fourth, the year of maturation. There are also differences in the progress of the run. In the small river My the run has one peak, in the river Ul, two peaks, while in the river Beshenaya there are three periods of intensive spawning run of the chum. This suggests that it is not a single, qualitatively unique group of chum that spawns in the major tributaries. On the basis of the differences in the rate of growth of the summer chum from different rivers, Svetovidova postulated that their feeding grounds in the sea are also different.

We shall give a brief characteristic of the chum from Sakhalin, the area of our work. The stocks of the summer chum are in depressed condition in that area as well. At the present time, one meets chum only rarely south of the Terpenie Bay. Its mean length is 62.5 cm., mean fecundity 2366 eggs (range 1254 - 3528 eggs). The ecology of reproduction is similar to that of the Amur summer chum (Dvinin, 1952).

The autumn chum runs for spawning into practically all the rivers in Sakhalin. Particularly rich in this fish are the rivers Tym', Poronai, Naiba and Lyutoga. The mean length of females from the south-western rivers in Sakhalin varies from year to year between 63.9 and 68.5 cm., mean weight from 2.7 to 3.9 kg.. They deposit from 1712 to 3928 eggs, mean fecundity fluctuating from year to year between 2483 and 2542 eggs. Mean size of males in different years is between 64.1 and 70.7 cm., weight between 2.7 and 4.3 kg. (highest values: length 82 cm., weight, 6.8 kg.). The fish enters these small rivers at IV - V and V maturity stages and the bulk of the young leave the rivers before the appearance of the scale rudiments (Dvinin, 1952). The autumn chum in the river Tym' is particularly large and distinguished by its rapid growth. In some years the mean weight of the females reaches 69.6 cm., and the weight 3.65 kg; corresponding values for the males are 74.6 cm., and 4.69 kg. Mean fecundity is slightly higher than 3,000 eggs. The chum enters the rivers Tym' and Poronai without nuptial colouration, most of them during the fourth and fifth year of life. The autumn chum from the river Naiba, which is husbanded in the Sokolovskii and Bereznyakovskii hatcheries, matures a year earlier, and is intermediate in size. The mean weight of the females during different years varies within the limits 58.0 - 67.3 cm., weight 2.80 - 3.48 kg;

length of males 59.1 - 69.6 cm., weight 2.54 - 3.70 kg. Mean fecudity 27
exceeds 3,500 eggs. In the chum from different rivers, some differences were observed in morphometric indices (Volovik and Latishevskaya, 1968; Ivankov, 1972).

Our attention was attracted in 1952 to the entrance into the river Naiba of noticeably larger chum towards the end of the spawning season. For the individuals which approached the trap of the Sokolovskii hatchery on September 21, the mean length of the males was 61.8 cm., and for those approaching on December 2, it was 66.0 cm. The mean size of the females was, correspondingly, 63.5 and 65.0 cm., and their fecundity 2,772 and 3,952 eggs respectively. It is interesting that the fish which entered the river later were less mature. Among them we took a record female, which weighed 7 kg. and contained 7,865 eggs (Smirnov, 1954a). It is not impossible to suppose that this large, late running fish during its feeding period moves up to the Aleutian Islands and then approaches its spawning rivers not from the south but from the north. The lack of genetic uniformity of the chum from the river Naiba has been demonstrated (Altukhov, 1973).

The differentiation of the chum in the rivers of Sakhalin has an ecological basis. The significant climatic differences of various areas of the island, stretched latitudinally and washed by the waters of a cold and a warm current, are well known. The south-western rivers of the island are small, while the length of the river Tym' is 330 km., and the Poronai 350 km; the type of water supply [flood regime] and the role played by the ground water in it are also different (Fedorova, 1962; Zemtsova, 1968). In addition, the rivers are entered by fish from different areas of wintering and feeding, from the Sea of Japan and from the Pacific. It appears that the variability of the chum reproducing in the rivers of Hokkaido is determined by similar factors (Sano, 1959, 1966). Very large chum reproduces in the rivers of the South Kurile Islands (Ivankov, 1968, 1970).

This brief review shows how extensive is the ecological, morphological and biological variability of the Asian chum. It is far from being limited to the differences in the spawning seasons, which attract the greatest attention. In the course of its evolution, this species became adapted to reproduction both on the grounds [bottom] mainly washed by the underflow and in the localities, where subsoil waters emerge, the two differing significantly in their thermal and gaseous conditions and their salt composition. Moreover, in different areas - of large river systems - isolated from one another since geologically old times, ecologically different forms reproduce during the same season. In their turn, these forms are subdivided into local stocks, which also can be internally differentiated.

In the rivers of North America, the run of the chum is not as strictly delimited by seasons, as, for example, in the Amur. The spawning takes place mainly in the autumn, the spawning grounds are situated not far upstream, but in the lower tributaries and small streams, including the zones with tidal influences (Foerster, 1955; Clemens and Wilby, 1961; Neave, 1966c). The chum of the river Yukon presents a special case. The fish enter this river early, by the end of July the run is 28
over. The migration covers a long distance (Gilbert, 1924). The North American chum is not extensively variable as that in Asia. The catches of that fish are about half as large as off the shores of Asia (Levanidov et al., 1970)

Anadromous Migration, Maturation of Spawners. As has been quoted from the above sources, the spawning run of the chum is prolonged. The earliest runs occur in the East Kamchatka area, towards the end of the first half of June. The runs are later in the Anadyr area, from the middle of July to the end of August. In the West Kamchatka area chum appear in the last ten days of July. The spawners enter the rivers of Terpenie Bay from the end of July or beginning of August to the end of September. In the mouth of the Amur, the run of the summer chum begins with the first days of July and becomes heavy within a few days, remaining in that condition for about a month. The end comes in the middle or end of August. The females of the summer chum enter the rivers close to the time of the completion of vitellogenesis in their ovocytes(maturity stages III, III - IV). In the males at the time, the process of spermatogenesis is active. Spermatocytes and spermatids are found in the seminal ampullae, side by side with spermatogonia (Ievleva, 1964).

In the Amur, the first individuals of the autumn chum appear in July to the middle of August, the main run occurring at the end of August to the middle of September. At the time of entry into the Amur, the gonads of the autumn chum are less mature than those of the summer chum. Spawning takes place between the middle of September and December, inclusively. The spawning grounds of the autumn chum are situated in the small rivers of the Amur liman and lower tributaries of the Amur, but the main bulk of the fish migrates up to the tributaries of the middle reaches of the Amur, mainly into the rivers Gur, Tunguska, Anyui, Bira and Bidzhan. The most important spawning grounds are located in the tributaries of the river Ussuri (Khor, Bol'shaya Ussurka, Bikin).

Many individuals reach the river Kumari, and isolated ones move as high
as the rivers Argun and Onon. The autumn chum enters the rivers of
Sakhalin from the end of August, beginning of September, mainly from
the second half of September or beginning of October. The run contin-
ues up to the middle of November. The run and the spawning in the
drainage of the river Naiba is considerably spread out. The first
individuals begin to enter the trap of the Sokolovskii hatchery at the
end of August, with mean daily temperature of water about 15°. The run
then ceases for about 15 to 20 days, to resume in the second half of
September, when the water temperature drops to 12 - 13°. At the end of
September, daily catches reach up to several hundreds of fish. Massive
runs coincide with the rising in the level of the river, increase in
current velocity and cooling of water to about 10°. At the beginning
of October, the intensity of the run weakens somewhat, but it becomes
particularly high from the middle of October and remains so up to the
beginning of December. The movement of the chum towards its spawning
grounds is observed up to the middle of the second half of December.
Towards December the water temperature drops to 0.5 - 0.2°. The fish 29
moves to the localities of emergence of ground water, which at that
time has temperatures of 5 - 7°, in places even higher. In the rivers
of Hokkaido, the run of the chum continues throughout December, and has
been observed also in January (Sano, 1959, 1966).

In contrast with the Amur and other large rivers, chum spawners enter small rivers of Southern Primore, Sakhalin and Hokkaido during the main run either spent, or at IV - V and V maturity stages. Spawning takes place at a distance of a few kilometers from the sea.

At the beginning of maturation the scales lose their silvery shine. The body assumes a greyish-yellow tinge, the dorsum darkens. With the migration up the river and continuation of maturity, there appear on the sides of the fish 6 - 7 or more transverse pale lilac stripes, turning later into dark lilac or dark raspberry colour. On the abdomen these stripes fuse into a single longitudinal stripe. On the flanks, the pale, bright stripes alternate with dark ones. With time, the belly, head and dorsum turn almost black. Towards the end of the spawning, the palate, tongue, and the bases of the gill arches turn dark. Simultaneously with the change in colouration, the skin becomes thicker, the scales disappear within it, often becoming partially resorbed. Hook-like teeth, larger and stronger in the male, grow on the jaws, palate, vomer and tongue. The jaws become longer and, in males, curve up. The body of the males becomes laterally compressed, a small keel appears on the dorsum. The pre-spawning changes are more obvious in the males, particularly the large ones. It has been observed that the nuptial livery is particularly well developed in the specimens which spawn in sluggish streams, the water of which contains little oxygen. The bodily proportions change to a lesser extent (Fig. 2).

As is known, the spawners do not feed in fresh water; the development of the gonads and the movement of the fish upstream are achieved at the expense of the nutrient substances accumulated in the sea. During their migrations up the Amur, for 1,200 km., the females use up 8% and the males 5.8% of their fat (Pentegov, Mentov and Kurnaev, 1928).

<u>Spawning grounds and development conditions</u>. In investigating the ecology of the reproduction of the chum, it is interesting to compare

the spawning grounds of the summer chum and the pink in the Amur. These fish select for their reproduction similar, often neighbouring places and the periods of their spawning partly overlap. On this basis one might form the opinion that their requirements as to the conditions of reproduction are similar. A corresponding conclusion of the inter-specific relationship between them can be formed. It has been observed, however, that the summer chum in the drainage of the Amur and in the rivers of Sakhalin spawns as a rule in the lower and middle reaches of the rivers, while for the pink, it is usual to migrate into the upper reaches. When the runs are heavy, the spawning grounds come close together in the middle reaches and both species can build their redds close to each other. Even in such cases, however, certain selectivity is manifest. In contrast with the pink, the chum selects for its spawning deeper places (from 60 to 100 cm.) and mainly closer to the river bank, where there is shade or submerged logs (Kuznetsov, 1928). The summer chum spawns at a distance from the riffles, in deeper pools. In such places the current is slow: in the river My, a tributary of the Amur liman, the current velocity is from 10 - 20 to 60 - 80 cm/sec. The bottom of the grounds is subject to considerable silting which is deleterious to the water transport through the redds (Nikol'skii, 1952; Nikol'skii and Soin, 1954; Vasil'ev and Yurovitskii, 1958; Strekalova, 1963).

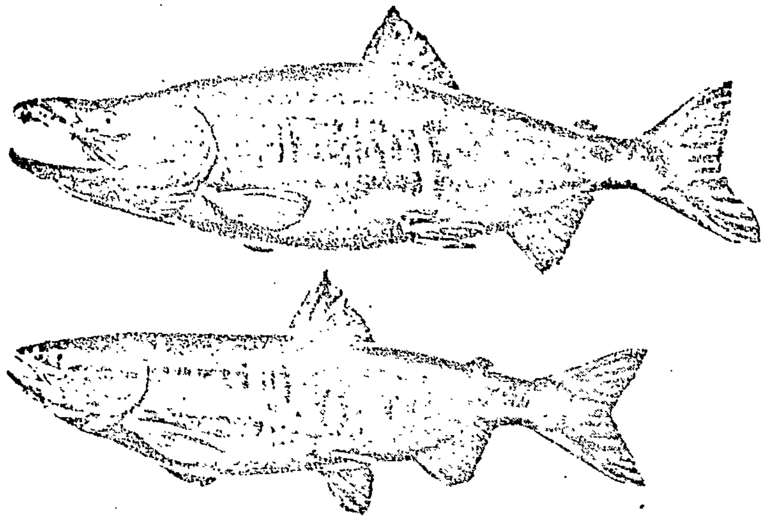


Fig. 2. Ripe (running) spawners of the autumn chum male (upper) and female.

The summer chum in the Amur spawns during the warmest time, when the water temperature in the river mouth fluctuates from 9.8 to 13.6° and in the upper regions of the spawning ground drops to 6 - 7° (Kuznetsov, 1937). The eggs deposited at the beginning of the spawning develop for a fairly long time at the temperature of 12 - 14° and their incubation takes about a month. At the end of the spawning season, in September, the temperature of 9 - 10° prevails for some time, to drop in October to 3° and then to approach zero (Soin, 1954).

The mating play of the salmon and the process of burying the eggs were described by many authors (Rutter, 1904; Chamberlain, 1907; Soldatov, 1912; Kuznetsov, 1928; Semko, 1954; Sano, 1959; Strekalova, 1963; Barsukov, 1964). The female positions herself in a selected place, head upstream, turns sideways and carries out vigorous, wave-like tail motions, moving forwards. Strong sweeps of the tail stir from the bottom silt, sand, and small stones. The current favours transport of the material stirred from the bottom downstream. However, excavation of hollows and building of spawning redds can be successfully accomplished by salmon also in the absence of current. When a sufficiently large hole has been excavated, the male, together with the female, enters it (sometimes two or three males). Several males keep close to each spawning female. The female and, most fequently, the largest male approach each other, and lower their tails to the bottom. Waves of convulsive motions pass along their bodies, facilitating expulsion of eggs and milt. Eggs, with milt poured over them, are immediately covered with the bottom material by the females, using the same method as in excavating the hole. The summer chum deposits its eggs in two, more often three batches, so arranged in the common redd that they are flushed with fresh water. The dispersion of the eggs increases the survival chances of the offspring. The eggs are buried rather deep; in friable bottom up to 30 - 40 cm and even 50 cm, in more solid ground nearer the surface.

The process of egg deposition involves clearing a surface up to 3 metres long and 2.5 metres wide. These dimensions are most commonly 1.2 and 1.0 metres respectively. The area of the spawning redds is not only cleared from silt and fine sand but becomes, in a way stratified. Deeper in, it is coarser, so that the eggs fall in the interstices between stones. Above it is fine gravel, followed by particles of medium size. Deposition of eggs takes place usually by night, less often at dawn or dusk, and by day. The process of deposition takes in 50% of cases 3 to 5 days, but can be completed in one day or extend for a whole week. The death of the females after spawning occurs most commonly within 9 to 14 days, but varies from 4 to 22 days (Kuznetsov, 1928, 1957). When one female has spawned, males move on to others and accompany several females in spawning. Mass spawning grounds are typical for the chum.

In the nests of the summer Amur and Sakhalin chum the eggs are mainly flushed by the so-called subterranean water, replenished by the infiltrating stream water. One observes also the small addition of subsurface stagnating ground water (Levanidov, 1969). The fragmentation and the cleaning of the material of which the redds are built makes it more permeable. Daily fluctuations of temperature within the redds are smaller than those on the surface and usually do not exceed 1.5 - 2°. During the winter, however, the difference of 0.2 - 0.5° suffices to protect the eggs from freezing.

The oxygen content of water taken from the redds is slightly higher than in that taken from the bottom nearby. The difference is due to the cleansing of the substance of the redds from silt which actively binds oxygen. In the redds of the summer chum in the river My during September we observed from 2 - 3 to 8 mg/l of oxygen; this was 3.5 - 4 mg/l less than in flowing water. The amount of carbonic acid varied from about 2 to 10 mg/l and pH from 6.2 to 6.3. The current velocity in the redds was 0.3 - 2.6 m/hour (mean 1.240). Due to the autumn cooling
of water and increase in solubility of gases in it, the oxygen content 52
increased. During the winter, the lowering of the water level in the river, silting and condensing of the bottom cause lowering of permeability and deterioration of the gaseous regime of the redds. Particularly dangerous is the feezing of the bottom, which brings about extreme

conditions. For the development of the summer Amur chum, favourable oxygen content is from 4.5 to 7 - 8 mg/l (Vasil'ev and Yurovitskii, 1954; Vasil'ev, 1957, 1958, 1959b).

The summer spawning chum from Kamchatka gravitates towards the places of emergence of ground water. Current velocity on its spawning grounds is 12 - 33 cm/sec. In the water of the river spawning grounds, oxygen content is 8 - 9 mg/l (about 70% saturation), free carbonic acid from 5.80 to 13.75 (mean 7 - 9) mg/l; pH varies from 6.4 to 6.9 (Krokhin and Krogius, 1937b).

In the Amur, the rivers of Primor'e, Kurile Islands, Sakhalin, Hokkaido and Honshu, the autumn chum reproduces in localities supplied with ground waters. In limnocrenes, or spring-fed spawning creeks on the basin of the Amur, the summer temperatures do not exceed 11 - 12°; in the winter they fluctuate within the limits 2.5 - 5° (on Hokkaido spawning grounds, sometimes higher). This salmon develops at a temperature of 1.0 to 11.5° (Levanidov, 1954b; Sano, 1959). In the rivers of British Columbia the temperature during the spawning of the chum sometimes reaches 16° (Neave, 1966c).

The autumn chum is larger than the summer one and its redds are also larger. On friable ground, where currents are weak, deep holes are dug, slightly exceeding the length of the female. Where stones are large and the currents rapid, the spawning redds assume an elongated oval shape. Their width is usually 1.5 m, length 2.5 m. Width of redds varies from 106 - 213 cm, and length from 125 to 320 cm. Eggs are deposited up to 30 - 40 cm. below ground level, sometimes deeper than 50 cm. (Kuznetsov, 1929, 1937). Average surface of redds in the Sakhalin rivers is 1.6 m^2 (Rukhlov, 1969).

In the riffles on the spawning grounds of the autumn chum, the current velocity is 10 - 30 cm/sec, and in the pools it is quite insignificant. The rate of filtration of the water in the nests on different grounds varies generally from 11 to 36.5 and mightreach 72 m/hour. The surface water on the spawning grounds in the river Khor and in Lake Teploe contains on the average 6.8 - 9.5 mg/l of oxygen in October, 5.8 - 8.8 mg/l in November, and 1.6 - 6.2 mg/l (12.6 - 48.4% saturation) at some spawning grounds in February. Beginning in April the aeration of the ground water improves. In some nests the water contained about 2 mg/l of oxygen (15% saturation); nevertheless, the eggs within them developed normally. The limits for successful development of autumn chum are established at 2-8 mg/l of oxygen content (15 - 60% saturation), 7 - 14 mg/l of carbonic acid during the beginning and 15 - 27 mg/l at the end of embryogenesis (Levanidov, 1954b, 1969).

The conditions of development of the same salmon in the Sakhalin
can be judged from the data obtained by analysis of the ground water,
which previously fed a spawning creek and now one of the branches of 33
Sokolovskii hatchery. According to 39 samples analysed by our unit in
1960, the water supplying the hatchery contained 4.38 - 6.52 mg/l oxygen
(saturation 39.3 - 53.3%, average 45.1%). The highest oxygen content,
7.3 mg/l, and of free carbonic acid, from 21.6 to 30.8 mg/l, was observed
in 1952. The water has a stable, slightly weak reaction; at times, pH
dropped to 6.4 - 6.2.

Spawning Efficiency, survival. Prolonged development under well protected conditions usually ensures high survival of salmon and good recruitment for the stocks. However, at times such fish are observed to drop in abundance, a drop sometimes assuming catastrophic character. The study of the reasons for mass mortality of offspring points to the dominating influence of the changes in living conditions in fresh water; sea water is more stable (Levanidov, 1968, 1969).

As a rule, few isolated eggs remain unshed within the bodies of spawned females; their number rarely exceeds 1 - 1.5% of fecundity. Beginning with the period of Kuznetsov's work, the high proportion of egg fertilization is also known. Losses at the time of spawning present a different picture. In the basin of the Amur they comprise 21 to 31% (Levanidov, 1954b); in Kamchatka they reach 68% (Semko, 1954), in Sakhalin 75% (Rukhlov, 1969) of average fecundity. The main reasons for mortality are freezing, dessication in dry years, silting and lowering of permeability of the redds. In the summer chum and pink in the Amur, as many as 25 - 50% of redds with total egg mortality were observed; in years with severe weather, in some rivers as many as 90 - 100% of the redds of pink salmon are destroyed by freezing (Birman and Levanidov, 1953). Since some ground water permeates the redds of the summer chum, the danger of their freezing is lower.

The developmental conditions of the autumn chum are more stable. From 10 to 20% of redds of this fish are subject to freezing and silting. Kuznetsov (1928) assessed survival up to the point of emergence from the redds as being up to 50% of the average fecundity. The same value in Ambanskie spawning grounds in the river Khor was 37 ± 5%, in Georgevskie 37 ± 3%, and average proportion of survival of deposited eggs was 58 and 51% respectively. According to the study of 150 redds in various rivers, 24 ± 4% of eggs of summer chum survived during the period of embryogenesis, while examination of 125 redds of the pink showed survival of 22 ± 5% of potential fecundity (Levanidov, 1969). In the river Memu on the island of Hokkaido, the loss of eggs of the autumn chum during the incubation was determined at 7.7% (Sano, 1959), which suggests very favourable conditions in the studied spawning ground.

In Karimanskii spring (basin of the river Bol'shaya on Kamchatka), the number of the offspring emerging from the redds, in different years varied from 1.2 to 4.8% of the eggs deposited. Predators, abundant in that locality, destroyed from 1.6 to 68% of fish emerging from the redds. To sum up, for one spawning spawning female, from 20.5 to 106 fish migrated from the spring, with a seven-year average of 52.8 (Semko, 1954). This number dropped subsequently even more, to produce a 19-year average 34
of 40 fish (Levanidov, 1969). From Hooknose River (British Columbia) for one spawning female, on the average, migrate 260 smolts (Parker, 1962) and from the river Ukhlan (north western coast of the Sea of Okhotsk) 400 smolts (Kostarev, 1964).

The number of migrants as a percentage of mean fecundity (downstream migration coefficient) is a very variable value. In the Karymaiskii Spring, the limits varied within the range of 0.68 - 4.2% (mean, 2.3%), in the river Ukhlan, 0.4 - 33.0% (mean, 13.9%) and in the Hooknose River 0.99 - 22.04% (mean, 11.6%). In Sakhalin, in the river Tym', the coefficient of downstream migration in 1962-1968 fluctuated from 2.0 to 24.3%, average value being 9.1% (Rukhlov, 1969; Kanidyev et al., 1970). For the summer chum the corresponding figure, calculated in five rivers in the basin of the Amur between 1953 and 1960 varied from 2.0 to 22.1%, mean figure being 9.7% (Levanidov, 1964b).

Judging from the results of tagging smolt in the Teplovskii hatchery, the return of spawners of the autumn chum was estimated at 1.5%. The return coefficient of the autumn chum, derived from smolts released by the Sakhalin hatcheries (disregarding catches of the fish in the sea), varies from 0.24 to 0.57% (Kanidyev et al., 1970). The survival of chum in the eastern part of its range is estimated to be 0.85 - 2.5% of the migrating smolts. It is believed that the juveniles perish mainly during feeding near the shore; in the open sea, elimination is low (Foerster, 1955; Parker, 1962; Ricker, 1967).

DEVELOPMENT OF THE CHUM.

It seems desirable to make some comments as regards the division of ontogeny into periods, and the terminology used in descriptions of development, because the literature contains discrepancies in this field.

In morphology it is customary to understand as a 'developmental stage' any arbitrarily selected condition of the organism (Vasnetsov, 1953a; Kryzhanovskii et al., 1953). As an exemple, one could name stages of 2 or 32 blastomeres, stages of 5 or 20 segments, an embryo of 6 mm length, the stage of the beginning of eye pigmentation, etc. The aggregate of the consecutive stages of a particular segment of ontogeny, during which the developing organism and its relationships with the environment undergo no significant changes, was named by Vasnetsov a '<u>stage of development</u>'. "Each stage is distinguished from others by its characteristic structure, physiology and biology, both the structure and physiology being adapted to the particular type of biology and environmental conditions" (Vasnetsov, 1953a, p.210). We shall adhere to this definition of the term. Various authors denote developmental stages by letters or numbers, or name them after characteristic features of functional morphology and ecology.

Kryzhanovskii pointed out that during each stage there occur
both qualitative and quantitative, both gradual and abrupt changes, 35

which within a certain range do not alter the main characteristic of the stage. Only having reached a certain level is quantity transformed into a new basic quality, and the organism moves to the new developmental stage. All essential preconditions to change into a new quality, to a new stage of development, arise during the preceding stage (Kryzhanovskii et al., 1953, p.72).

The groups of stages characterized by common adaptations are, in their turn, referred to as periods of development.

During the embryonic period of ontogeny, the embryos feed on maternal food stores, contained in the yolk. This type of endogenous feeding is characteristic not only of the embryos within egg membranes, or embryos proper, but persists for some time also after hatching in free embryos. For these reasons, this segment of ontogeny can also be referred to as the embryonic period, or period of endogenous feeding.

A most important biological distinction of larvae is their conversion to the active acquisition of food from the external environment and their possession of temporary larval organs. The morphological, physiological and ecological characteristics acquired by larvae and retained during the larval period of development serve the task of active acquisition of food. Salmon prepare for active feeding while still possessing large remnants of yolk, so that their larvae are characterized by a prolonged period of mixed endogenous-exogenous feeding. When there is no food available, the duration of mixed feeding is shorter.

Towards the juvenile period of life, the temporary larval organs disappear and some organs characteristic of the adult fish make their appearance (for example, unpaired and paired fins with their skeleton and musculature, or scales). There occurs a corresponding change in the habitat and behaviour.

The significant characteristic activity of adult fish is their intensive feeding, which ensures timely maturation of reproductive organs and successful reproduction. Salmon can feed in fresh water (permanently landlocked and residual forms) and in the sea (anadromous or diadromous forms).

The migration of the salmon to their places of spawning is preceded by major functional morphological transformations. During the spawning, changes take place in behaviour and in environment. Taken together, these many-sided changes indicate the biological specificity of this segment of ontogeny, which we have named the spawning stage. Together with the pre-spawning migration, this stage logically forms the reproductive period (Smirnov, 1959b, 1964c, 1965; Eremeeva and Smirnov, 1965; Eremeeva, 1967). After reproduction, the Pacific salmon die.

We shall describe now the reproductive products and development of the chum.

Reproductive Products. The spermatozoids of chum, as of its 35
related species and other teleosts, are of the flagellate type (Riddle, 1917; Lowman, 1953; Ginzburg, 1968). Salmon eject mature spermatozoids in separate portions over a prolonged time. To gain insight into the times and quantity of sperm deposition, mature males were kept in ponds (Smirnov, 1963a, 1964b). Sperm was collected[literally "strained off"] intravitam portion by portion,as it matured. The volume of individua portions of sperm (volume of ejaculate) was measured, as well as the concentration of spermatozoids and the sperm's ability to fertilize eggs.

Fig. 3. Retention of fertility by chum spermatozoids in water; 1 - at a temperature of 5.3°; 2 - at 11.0°.
Vertical: Quantity of Fertilized Eggs, percent.
Horizontal: Time spent by spermatozoids in water prior to fertilization, sec.

Some males produced sperm for almost a month. At intervals of 1 to 2 or 3 days, it was possible to obtain from one male up to 10 - 11 portions of sperm. The volume of ejaculate varied from 3.6 to 17.9 ml, averaging 9.2 ml. One expermental male produced more than 130 ml. of sperm. In the thickest sperm, the number of spermatozoids per mm^3 was 32.4 million; the corresponding number in the liquid sperm was 17.36 million; the average figure was 24.12 million per mm^3. Counts have shown that an average volume of ejaculate contains more than 220 billion spermatozoids. Sperm taken from different portions was used for artificial fertilization of eggs. Its good quality was demonstrated by checks.

At a temperature of 10 - 11°, energetic movements of spermatozoids of autumn chum and pink in water taken from the spawning grounds were observed for 30 - 55 seconds; weak oscillatory movements were observed every 90 and even 170 seconds. This is close to the time which was found for the lake trout (Ginzburg, 1968).

Having entered the water, the spermatozoids rapidly lose their fertility (Fig. 3). In our experiments at a temperature of 11°, diluted sperm after 10 seconds already fertilized 6% fewer eggs than it did in the "dry" fertilization method; after 30 seconds 22% fewer eggs were fertilized, and after 90 seconds, only isolated eggs were fertilized by water-diluted sperm. The spermatozoids retained their fertility for a longer period at a lower temperature.

The eggs of chum are very large. In 64 females of autumn chum examined from the river B. Takoy, the average weight of mature eggs varied from 183 to 300 mg ($M = 239.25 \pm 0.19$; $\delta = 29.8$). The diameter of swollen eggs of Sakhalin autumn chum varied from 6.7 to 9.0 mm, the modal size being 7 - 8 mm. The eggs are telolecithal, oligo- 37
plasmatic and contain very little protoplasm and huge quantities of yolk. The large store of nutrient substances ensures the development of large embryos and their prolonged existence at the expense of endogenous feeding.

Information on the biochemical composition of chum eggs and related species is given in Table 1.

Table 1: Biochemical composition of the eggs of salmon belonging to the genera Oncorhynchus and Salmo (after Smirnov, Kamyshnaya and Kalashnikova, 1968).

Species	No. females	Length females (cm)	Weight single egg, mg	Dry Weight %	Dry weight content fat %	protein %	ash %
Chum	7	63.2	195.4	44.28	9.73	66.28	3.72
Sockeye, diadromous	3	58.0	111.0	39.74	7.77	66.54	3.73
Sockeye, residual	3	24.3	59.6	38.63	5.50	67.14	3.81
Pink (Sakhalin)	4	55.0	166.0	41.72	12.84	69.11	3.44
[illegible] (Kola Peninsula)	6	47.5	115.0	43.49	8.02	69.82	3.56
[illegible]	1	103	(259.0)	(37.55)	8.74	66.07	2.45
[illegible]	4	65.7	176.0	40.07	4.65	73.52	4.07
Masu (1959)	11	49.1	171.6	45.64	12.93	63.70	3.55
Masu (1960)	5	49.9	173.7	45.21	8.53	65.04	3.48
Atlantic salmon	21	87.0	110.0	40.24	7.90	71.64	4.55
Baltic salmon	6	87.0	114.0	39.21	6.75	71.29	[illegible]

Note: Figures indicate mean values. Observations on swollen eggs of chinook shown in brackets.

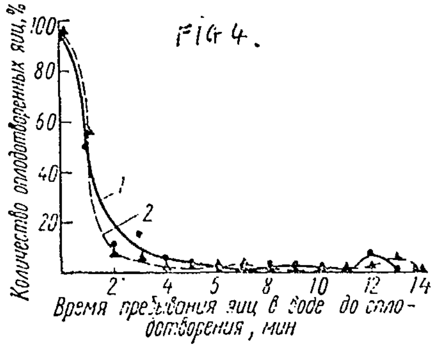
The egg membranes of salmonid fishes consist of a zona radiata and a thin external homogeneous layer. The thickness of the membranes of swollen eggs of autumn chum is about 55 microns (55.1 ± 0.38). The membrane is composed of ichthyokeratin*(Bell et al., 1969). In the chum, the zona radiata is differentiated into two layers (Yamamoto, 1951; Kanoh and Yamamoto, 1957; author's own data). The inner part of the zona radiata, about 5 microns thick, is distinguished by a looser/more porous structure. The homogeneous surface layer is 1 - 1.5 microns thick. In S. gairdneri (Rich.) the outer layer of the chorion contains neutral carbohydrates, protein and mucopolysaccharides of a non-sulphate type (Hagenmaier, 1973). It protects the egg from the influence of hatching enzymes acting from outside (Bell, Hoskins and Bagshaw, 1969).

The eggs of the autumn chum are bright orange. A comparison of the colours of the eggs of different females with the colour fields of the atlas of colours (Rabkin, 1956) identifies the colour shades as being in the range of 589-592 millimicrons wave length. Fertilized eggs of Kamchatkan chum contain 1.60 - 1.76% astaxanthin (Yarzhombek, 1970).

The time during which eggs of chum in water retain their ability to be fertilized (fertility) has been determined as being between 2 and 30 minutes (Kusa, 1950; K. Yamamoto, 1951). In connection with this, it must be stressed that the bulk of eggs after being activated by water lose their fertility rapidly. In our experiments at 10 - 11°, after 1 minute in water fertility was 38

* Revisor's note: Appeared in original text as ikhtulokeratin, literally "ichthulokeratin".

40% less than the "dry" method of insemination (control). After 3 minutes it was 80 - 90 % less and after 12 minutes only isolated eggs became fertilized (Fig. 4).



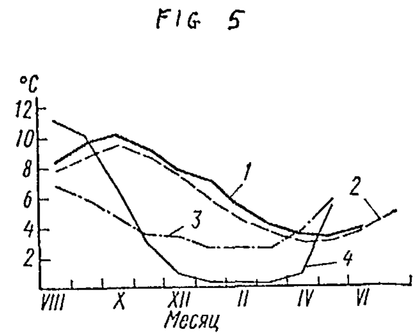


Fig. 4. Retention of fertility by eggs of chum in water. 1 - at temperature 11.0; 2 - at 10.3.
Vertical: Percentage of eggs fertilized
Horizontal: Time in water before fertilization, minutes.

Fig. 5. Temperature conditions in incubators in years when material was collected. 1 - Sokolovskii hatchery, season 1952-1953; 2 - Same, 1953-1954; 3 - Adotymovskii hatchery, season 1954-1955; 4 - Lesnoy hatchery, season 1964-1965.
Vertical: Temperature; Horozontal: Months.

Conditions of Development of Material Studied. The description is based on observations on eggs developing in incubators of the Sokolovskii hatchery. Incubators were supplied with pure spring water, containing 3.4 - 8.0 mg/l of oxygen, and 20 - 30, sometimes about 40 mg/l of free carbonic acid*; pH value varied within the range 6.2 - 6.6. Daily temperature fluctuations were not more than 0.1 - 0.2° (Fig 5).

*Revisor's note. "Carbonic acid" is an equivalent of the original Russian uglekislota, which also translates as "carbon dioxide".

The water was slowly warmed up during the summer and at the beginning of autumn, reaching 10 - 10.5° in the middle of October. Only after that date it began to cool off slowly; in December it was 7 - 8°; the minimum of 2.5 - 5° was reached in March - April. At the end of April the water began to be warmed again.

The rate of development of the chum at the Sokolovskii hatchery is here being compared with that of the Amur autumn chum at the Teplovskoe hatchery (Disler, 1957). In the latter place, the mean monthly temperature of the water in 1950 and 1951 was, correspondingly: in October 3.9 and 4.4°; in January it dropped to 2.7 and 3.3°, in April it warmed up to 5° and in May to 6.8°. Oxygen saturation of water in the hatchery apparatus was 40 - 60% of normal, the quantity of carbonic acid varying from 4.4 to 17.0 mg/l.

<u>Embryonic period of development.</u> 59

During the embryonic period, development continues at the expense of the stores contained in the yolk, for which reason we refer to it also as the period of endogenous feeding. This segment of development, which is passed by the embryos within the egg, is often referred to as the incubational interval.

The existence of the daughter individual begins with the fusion of the nuclei of the parental gametes and the formation of a zygote. This is preceded by complicated processes which have been quite well explored in chum.

<u>Insemination, Activation of Eggs and Formation of Zygotes.</u> According to Yamamoto (1952), mature eggs of chum are at the stage of metaphase of the second maturation division. This is typical for the

mature ovocytes of teleost fishes (Ginzburg, 1968).

The meiotic process progresses further after the contact between spermatozoid and egg and the activation of the latter with water. At a temperature of 7.5 - 9.0° the transformation of the nucleus of the egg cell is completed about 3 hours after insemination,and the female pronucleus begins to migrate towards the male one, which by this time has already reached the place of the future encounter. Within 3.5 - 4 hours after insemination, the pronuclei conjugate and form a zygote.

The transformation of the nuclear apparatus of the parental gametes coincides in time with the hydration of the egg, the formation of the perivitelline space and the hardening of the membrane (Zotin, 1954, 1961). The process of hydration begins after activation of the eggs by water and secretion under the membrane of osmotically active substances contained in the alveoli of the cortical layer of the cytoplasm. The cortical alveoli of the eggs of chum and sockeye have a diameter from 3 to 30 microns and contain osmotically active acid mucopolysaccharides, as well as a small quantity of protein and, presumably, amino-sugars (Kusa, 1949, 1956, 1958; Kanoh and K. Yamamoto,1957; K. Yamamoto 1951; T. Yamamoto, 1957; Hamano, 1957).

The body cavity fluid in salmon serves as a strong activator ,and spermatozoids in it retain their motility much longer than in water (Scheuring, 1925; Derier, 1951; Ginzburg, 1968). In the cavity fluid and in isotonic solutions, the salmon spermatozoids are capable of penetrating eggs (Privol'nev, 1941b). Experiments conducted on the eggs of chum (Kusa, 1950; K.Yamamoto, 1951) and other salmonid fishes (Ginzburg, 1963, 1968)

have shown that to involve the spermatozoid in further development, the eggs must be activated by water. It is on these characteristics of the reproductive products that the method of "dry" or Russian artifical fertilization of eggs is based, having been developed by V. P. Vrasskii. This method is currently used with some alterations (Smirnov, 1963b). The eggs are mixed with undiluted sperm, which is collected from several males. Then a small amount of water is added and the mixing is repeated. After a change of 40
water, the eggs are kept completely undisturbed to allow the swelling to occur. In our experiments, at a temperature of 6 - 7° and 5°, the hydration of eggs was completed in 40 - 50 to 60 minutes (Fig. 6). As a consequence of hydration, the weight of the chum eggs increases by 13.4 - 18% (Aski, 1939).

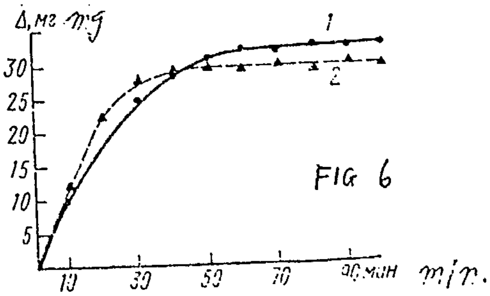


Fig. 6.

The experiments tabulated in Table 2 have shown that before their entry into water, the eggs readily withstand considerable mechanical impact. This ensures preservation of the eggs during the jerking motions of the female digging out spawning holes and while they are being buried. The same quality of the eggs allows successful transportation of mature and anaesthetized or killed females and unfertilized eggs placed in special isothermic packs.

Within 15 minutes after insemination the influence of a vibrator increased mortality, which was particularly high in an experiment performed after 30 minutes. The sensitivity of the eggs subsequently decreased. High sensitivity coincided with the time of hydration. One of the obvious reasons for this is the reduced toughness of the membranes; another is again the reduced toughness of the surface layer of the egg cell cytoplasm caused by the destruction of the cortical alveoli. During the process of hydration (swelling) the egg should remain completely undisturbed.

In hydrated (swollen) eggs, the fat drops aggregate at the animal pole, forming a dome-shaped protrusion on which develops a cytoplasmic tubercle or an embryonal disc. Due to the polarity of their structure, the eggs are always situated with their animal pole upwards.

It must be noted that in instances where mature females
have not spawned in time, some eggs can begin to hydrate while they are still
in the body cavity; their membranes turn hard, and the fat drops coalesce and 41
become larger. Such over-ripe eggs are referred to by fish
culturists as "peas". They cannot be fertilized and their presence
indicates general lowering in the quality of the eggs.

Table 2. Mortality of the eggs of autumn chum caused by the action of a vibrator at different stages of development (from Smirnov, 1955b).

Age after fertilization	Stage of Development	Mortality, % Series 1	Series 2
	Before placing eggs in water	0.9	0.5
15 min.	Intensive hydration	27.3	86.5
30 min.	Swelling continues	68.1	89.0
1 hour	Ditto	8.6	16.6
2 hours	Swelling completd	1.0	5.6
3 "	Formation of embryonic tubercle	6.9	18.2(?)
5 "	Ditto	1.0	3.3
8 "	Some eggs with 2 blastomeres	3.5	13.7
11 "	2-4 blastomeres	4.4	11.6
1 day	Up to 16 blastomeres and more	7.3	13.2
1.5 days	Large-celled morula	7.7	15.7
2 days	Medium-celled and in some eggs small-celled morula	7.8	17.4
3 "	Small-celled morula, in some eggs blastula	8.4	14.5
4 "	Gastrulation beginning in some eggs	7.0	16.3
5 "	"Cricoid" stage	11.8	15.4
6 "	Clearly defined "embryonic nodule"	18.5	32.5
8 "	Development of embryonic stria	5.2	9.4
10 "	6-8 segments, rudiments of eyes observable.	1.6	17.8
12 "	20 and more segments, about half of yolk sac covered by epibolic growth	3.7	7.8
15 "	In some embyos 47-48 segments, heart beats; in others, up to 52 segments, epiboly completed	20.5	24.7
18 "	60 and more myctomes, vascular network formed on yolk sac	0.8	1.2
22 "	Beginning of eye pigmentation	0.3	0.5
33 "	Rudiments of dorsal and anal fins appear	0.0	0.4
45 "	Black pigment appears on head	0.7	0.4
53 "	3 days before hatching begins	0.6	0.6

Note: Eggs were incubated at a temperature of 8.0 - 9.6°C. Eggs of series 1 were subjected to vibration for 70 seconds at different stages. The axis of the vibrator rotated 100 times during that time. Eggs of series 2 were exposed to vibration for 210 seconds in each experiment.

Stage 1. Formation of Cytoplasmic Tubercle and Embryonic Disc.

We accept the formation of the zygote as the beginning of the first stage of ontogeny. The stage lasts up to the beginning of cleavage.

In the Teplovskii hatchery, at a mean temperature of 3.4^{o}, this stage lasted about 20 hours. In the Sokolovskii hatchery at 9.6^{o}, in some eggs the beginning of cleavage was observed 8 hours, and in others 10 hours, after insemination. 42

During this stage at the animal pole of the eggs, in the place of accumulation of fat drops, the cytoplasmic tubercle is formed. In mature egg cells, only a small accumulation of cytoplasm at the animal pole can be seen. In the first hours after insemination, the process of concentration of cytoplasm progresses slowly. In our case, the cytoplasmic tubercle remained flat 6 hours after insemination, its diameter being 1.4 - 1.6 mm and its outlines ill-defined and interrupted. This indicated that the process of concentration of cytoplasm was incomplete. A fully formed embryonic tubercle assumes a shape close to semispherical. Its outlines are clearly drawn. The diameter of a fully formed embryonic disc in autumn chum varies from 0.9 to 1.3 mm.

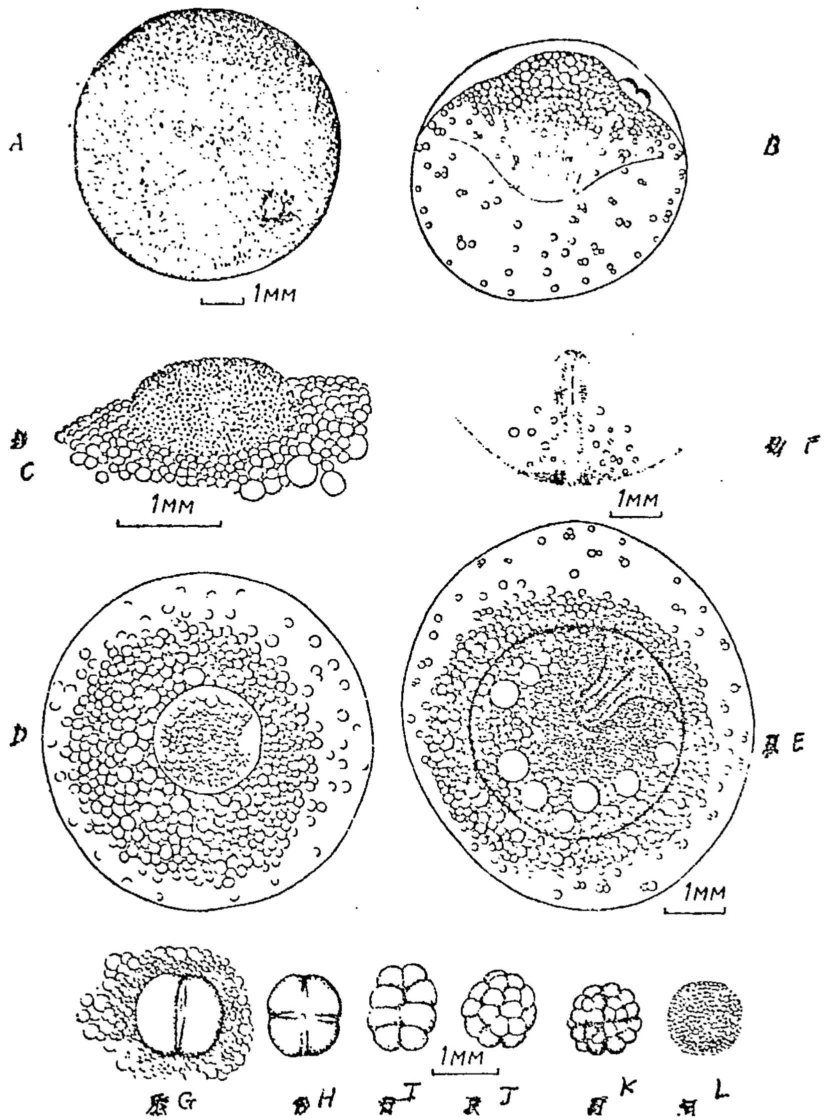
Towards the end of the stage, the lower surface of the yolk sac becomes able to adhere to the membrane (Disler, 1957). Between the surface of the animal pole of the egg cell and the membrane, a space is formed that reaches 0.4 - 0.8 mm (Fig. 7,B) in size.

During this stage, the susceptibility of the eggs to injuries is lowered. This favours transportation of the hydrated eggs from the collection points to incubators and their distribution on trays. On Sakhalin Island fish culturists transport wet eggs without water, packing them closely. Mortality of the eggs during transport comprises 1 - 2%.

Stage 2. Segmentation of the Embryonic Disc. This stage begins with the appearance of the first line of cleavage and ends with the formation of the blastomere blasula, which forms at 3.3° at the age of 8 days, and at 10.4° at the age of 3 days (about 31 degree-days. The two formed blastomeres resemble bean seeds in shape. The second cleavage line runs perpendicularly to the first, forming four closely adhering blastomeres. Two third cleavage lines run parallel with the first and form 8 blastomeres, arranged in two parallel rows (Fig. 7,G-I). At this stage, the embryonic disc becomes an elongated oval, and its surface area increases somewhat. According to Disler, in chum of the Teplovskii stock during this second stage, two, three or four blastomeres lie above others directly adjoining the yolk. The furrows (lines) of the fourth cleavage run in a horizontal (equatorial) plane and result in the formation of 16 blastomeres, arranged in two layers. The lower blastomeres are larger than the upper ones. Examining eggs in cleavage, one can see not only 4, 8, 16, 32, but also 3, 6, 12, about 30 and other numbers of blastomeres, which indicates that not all blastomeres necessarily undergo synchronous cleavage. After the 4-5th cleavage, the embryonic disc assumes a circular shape.

45

Fig. 7. Early stages of development of autumn chum.
A - egg after hydration, upper view; black micropylar field can be observed; to the left embryonic disc showing through the membrane.
B - Live egg, lateral view, at the stage of two blastomeres in transmitted light. C - Embryonic disc at the stage of blastomere blastula.
D - Egg at the stage of the appearance of the "marginal knob".
E - Stage of the "marginal tongue" (differentiation of the embryonic layers and the chord), upper view in transmitted light. F - A part of the embryonic disc at the stage of formation of the anterior end of the embryo. G - L -- stages of cleavage of the embryonic disc, upper view; preparations stained with methylene blue. Drawings A - F after Disler (1957); G - L original.



In the process of further segmentation, the upper blasto- 4
meres are more closely packed, they become somewhat smaller and are flattened. Lower blastomeres are larger, divide more slowly, and are more loosely packed. Those of them that are situated on the periphery of the blastodisc retain their connection with the

marginal cytoplasm. A part of the cytoplasm of the lower blastomeres pushes between particles of yolk, giving rise to the beginning of the central part of the periblast.

Under the embryonic disc and in immediate proximity with it are situated smaller fat drops. When one turns the egg rapidly over, they change their place together with the blastodisc. Larger fat drops, situated along the periphery, are easily moved in the yolk sac, independently of the blastodisc (Disler, 1957).

With the beginning of segmentation, the sensitivity of the eggs to mechanical impact increases (see Table 2). For this reason the eggs should be placed in the incubators before the beginning of the segmentation and should incubate in complete peace.

Stage 3. Blastula. Lasts from the formation of the blastomere blastula to the beginning of gastrulation. At a temperature of 3.3°, this stage takes 10 - 11 days, at 10.4° from 2.5 to 3 days. One of the external signs of the transition to the blastula stage is the beginning of enlargement of the blastodisc (Ivanov, 1937; Disler, 1957). In chum, the diameter of the blastodisc at this stage is 1.3 - 1.4 mm. It projects dome-like above the surface of the yolk sac and encloses the zone of small fat drops.

At the blastula stage the periblast is well developed, having formed as the result of cleavage of blastomeres next to the yolk. At the same time, one of the new nuclei forms a typical blastomere, while the other enters the intermediate layer of cytoplasm separating the blastodisc from the yolk. Further mitotic division of these nuclei below the blastodisc forms a polynuclear syncytial structure known as the periblast or parablast (Riddle, 1917, Ivanov, 1937; Manon and Hoar, 1956).

The surface of the blastula is covered by a layer of polygonal cells closely adhering to one another. Underthis layer there are loosely scattered larger calls. P.P. Ivanov termed the initial stage of the blastula of the Atlantic salmon the blastomere blastula. With time, the outer layer of cells becomes more solid, and the blastomeres situated below adhere to it, i.e., one observes the process of epithelization. A late blastula is known as an epithelial blastula. The diameter of a late blastula in the Amur autumn chum reaches 2.3 - 2.6 mm (Disler, 1957). The eggs of the Sakhalin autumn chum are larger, and the diameter of its blastula reaches 3.0 - 3.2 mm.

Stage 4. Formation of Embryonic Layers. During this stage the process of gastrulation takes place. Under the conditions existing in the Sokolovskii hatchery, at a mean temperature of 10.4°, the formation of the embryonic layers began at the end of the sixth day. The stage was completed within two days, when the first meso- 45
dermal segments were formed. In the Teplovskii hatchery at 3.4°, gastrulation begins at the age of 18 - 19 days and is completed within about 6 days from its beginning.

During gastrulation, the embryonic disc enlarges, flattens, and, in its central part, becomes thin. In one of the marginal parts of the blastodisc, the future caudal end of the developing embryo, a thickening forms, the "marginal knob" (fig. 7,D). With the aid of vital labelling of the parts of blastodiscs, it has been established that the surface cells of the blastoderm in salmonids and other teleosts are arranged on the surface of the yolk sac exclusively by epiboly. They do not turn under the embryonic disc and take no part in the formation of the hypoblast. The process of invagination, described earlier (Pasteels, 1936) is not observed in teleost fishes. At a certain time, the inner cells of the growing blastoderm, singly or in groups, become detached from it, migrate in the direction of the body rudiment and form the hypoblast. On the other hand, the cells situated directly under the epithelial surface of the blastoderm, becoming arranged in a single layer, form the epiblast (Ballard, 1966, 1968; Ballard and Dodes, 1968; Trinkaus, 1972).

When the diameter of the embryonic disc reaches about 3.5 mm., its margins extend beyond the zone in which the small fat drops are situated. The "marginal knob" extends in length and changes into the "marginal tongue". The embryonic layers become more clearly delineated. According to Manon and Hoar (1956), the epidermal layer of the embryo is formed of flattened cells. Below it are the larger cells of the ectoderm. Directly under the ectoderm, along the longitudonal axis of the embryo, the cells of the mesoderm are arranged in a solid string. Between them and the periblast are scattered the cells of the endoderm, which become flattened somewhat later. At the anterior end of the embryo, below the ectoderm, there is a conspicuous layer of cells of the prechordal plate. In the nuclei of the central periblast one does not yet observe mitosis; they divide amitotically. At the beginning of gastrulation, Manon and Hoar found a group of noticeably enlarged cells with outgrowths similar to the pseudopodia of the amoebae. These amoeboform cells were tentatively named primordial embryonic cells. Persov (1966, 1968) places the appearance of the primordial reproductive cells in chum at a somewhat later age.

When the diameter of the embryonic disc reaches 4 mm, the embryonic streak enlarges to 1.5 mm. In transverse sections of such an embryo, slightly anterior to its caudal outgrowth, in the central part there are concentrically arranged cells of the rudiments of the chord. Lateral to it there is an undifferentiated lateral mesoderm. Below and slightly to the side of the rudiment of the chord there forms a space surrounded by cylindrical cells, representing the rudiment of Kupfer's vesicle. Externally, on both sides of the longitudinal axis of the embryo, a thickened layer of ectodermal cells forms small longitudinal swellings, the neural plate.

Fish embryos at early stages of development have a proto- 46
plasmic motor system which has been observed by many investigators. In the Atlantic salmon, the embryonic motor system has been studied with the aid of time-lapse cinephotography (Wülker, 1953). Changes in the character of the motor system of embryos during the ontogeny of fishes belonging to various ecological groups and the relationship of the motor system to temperature and gaseous regime have been a subject of studies (Reznichenko, 1959a, 1959b; Reznichenko et al., 1968). Movements within the egg membranes are due to the contractile activity of the cytoplasm which covers the yolk sac. The waves of its contractions cause deformation and changes in the centre of gravity of the egg, which lead to a change in its position in space. In salmon at early stages of development, the animal pole executes a circular, either clockwise or anticlockwise movement. At a low temperature it is difficult to observe these movements by studying a live egg under the microscope. At a certain stage, the movements

become more easily observable. In the course of our observations at 14°, the blastodisc of chum described a complete circle in 4 minutes 40 seconds to 5 minutes. As a consequence of such movements of eggs, and later of the embryo, the perivitelline fluid moves and the internal respiration of the embryos is intensified.

With the beginning of gastrulation, the sensitivity of the egg to mechanical influences increases. An impact of equal magnitude causes about twice as high mortality at the stage of the well-developed "embryonic knob" as it does at the cleavage stage.

Stage 5: Formation of the Head and Trunk of the Embryo. This stage comprises the part of development from the beginning of segmentation of the trunk mesoderm to the formation of 46 - 47 segments. At a mean temperature of 3.2°, it began on the 24th or 25th day, and ended on the 35th or 36th. Under the conditions in the Sokolovskii hatchery, the beginning of segmentation was observed at the end of the 8th and the beginning of the 9th day (81 - 85 degree-days). Towards the end of the 10th day, the embryos had up to 18 - 20 segments, on the 12th day, 35 - 36 segments. The stage was completed at the age of 14 days (137 - 142 degree-days).

The first somites form in embryos 2 mm long, when the diameter of the embryonic disc increases to 4.5 mm (Hanon and Hoar, 1956). Disler observed the formation of three somites and the beginning of differentiation of the parts of the brain in embryos 2.5 mm long. When the length of 3mm had been reached, the number of somites had increased to seven (at 3.4° in 26 days). The blastodisc had by that time surrounded up to half of the circumference of the egg. In embryos about 3.5 mm long, the number of segments had increased to 13 (Fig. 8, A-C).

Manon and Hoar point out that at embryo length 3.0 - 3.5 mm, cavities form in the rudiments of the eyes and change into optic vesicles. Soon the distal part of their wall invaginates and forms optic cups. Above the anterior end of the chord, due to the invagination of the inner layers of ectoderm there appear the rudiments of the auditory capsules. At the moment of their appearance, they are 47
situated at a considerable distance from the anterior end of the embryo. At the base of the brain at the level of the posterior margins of the eyes there appears the infundibulum. Somewhat posterior to this area, the ectodermal rudiment bends inwards, giving rise to the pharyngeal pockets. The rudiment of the heart begins to form from the lower part of mesoderm. The lateral mesodermal plates divide into somatic and splanchnic layers, the narrow slit between them pointing to the formation of the pericardial coelome. A longitudinal group of endodermal cells in the middle part of the body of the embryo produces the rudiments of the intestine.

In embryos 4 mm long, the somites become differentiated into dermatomes, myotomes and sclerotomes. The pronephric fold is formed. The cells which give rise to the axial blood vessels and to blood cells are situated on the ventrolateral side of the sclerotome along the body.

In the Teplovskii hatchery, on the 31st day of development, when the embryos reached the length of about 4.0 - 4.5 mm, they had 30 - 31 segments (somites) and more than 3/4 of the yolk sac was covered by blastoderm. Microscopic observation in vivo clearly showed differentiation of the parts of the cerebrum and encephalomeres of the medulla oblongata, optic cups, placodes of lenses and otic capsules. The rudiment of the heart, tubular in shape, descended into a large pericardial cavity (Fig. 8,D).

According to our experimental findings, from the time when the blastoderm has covered more than a half of the surface of the yolk sac, the sensitivity of the eggs to mechanical disturbances diminishes for some time.

Stage 6. Separation of the Posterior End of the Embryo from the Surface of the Yolk Sac. According to Disler, this stage extends from the formation of 46 - 47 to 65 segments. In the Teplovskii hatchery, at a mean temperature of 3°, the stage took from 35 - 36 to 45 days. Within that time, the length of the embryos increased from 4.8 to 6.5 - 7.0 mm. In the Sokolovskii hatchery, at a mean temperature of 9.6°, the stage began at the age of 15 days, and at 10.1°, at the end of the 14th day, and continued for 4 - 4.5 days. The significant functional characteristic of this stage is expressed in the establishment of the neuromuscular motor system of the embryos.

The external appearance of the embryo at the beginning of this stage is shown in Fig. 8, E. By this time the process of epiboly, i.e., covering of the yolk sac with blastoderm, is nearing completion. The tail bud begins to differentiate. The olfactory placodes appear anterior to the eyes. The rudiments of the opercula become noticeable. The cardiac tube becomes folded over; infrequent, weak contractions of its wall can be observed. The frequency of pulsation of the heart rapidly increases, ensuring mixing of the cavity fluid. Hyotomes have acquired the ability of contracting. The consumption of oxygen by the egg increases considerably (see Table 3), corresponding to the greater requirements of the embryos, which have attained a large size.

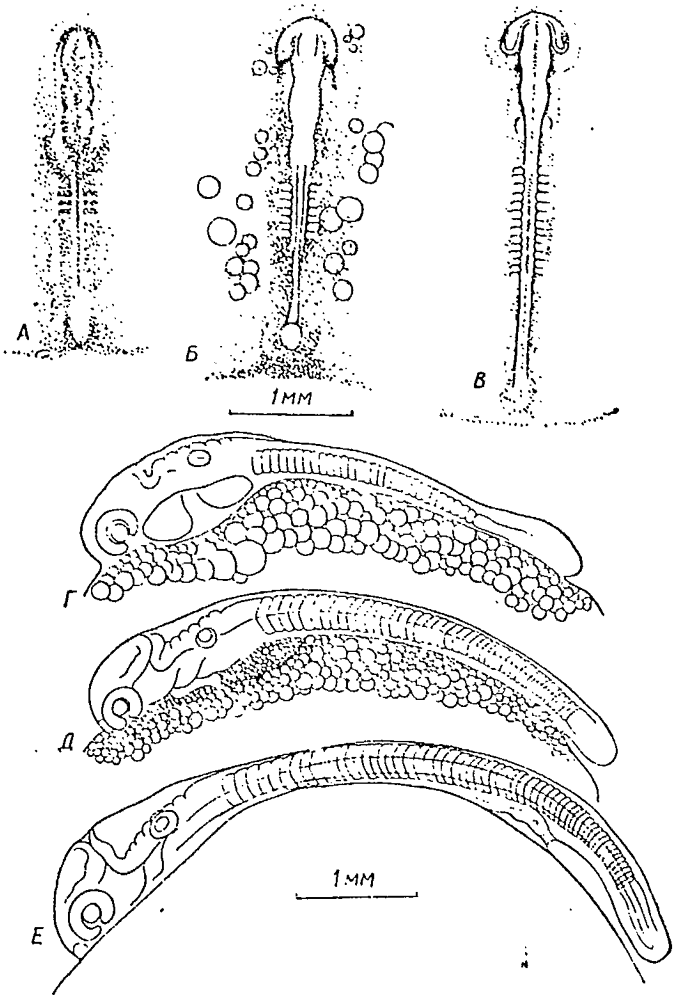


Fig. 8. Steps in the beginning of segmentation of mesoderm and of head and trunk formation in the embryo of the autumn chum. A - embryo at the 3-segmented stage, removed from a fixed egg; dorsal view. B - 7-segmented stage. C - 13-segmented stage. D - embryo at a stage of 30 - 31 segments; lateral view (as in following drawings). E - 46-47 segmented stage. F - 58-segmented stage. After Disler (1957).

Table 3. Oxygen consumption by embryos, larvae and fry of chum.

Temp. °C	Stage of Development	Oxygen consumption mg/hr/1000 eggs or individuals
	From Handa (1934)	
About 8	Beginning of development	0.10
	Pigmentation of eyes	1.00
	Two days before hatching	4.10
	At hatching	6.00
	3 days after hatching	8.30
	From Wickett (1954)	
3.7--5.2	Beginning of development	0.13
8.0--8.2	Before eyed stage	0.30
0.1--0.7	Ditto	0.20
0.1--0.7	Weak pigmentation of the eyes	0.20
3.6--4.9	Eyes dark	0.79
5.9--6.1	10 days before hatching	0.20
	From Lukina (1973)*	
3.5	Formation of embryonic disc	0.15
3.5	Cleavage of embryonic disc	0.17
3.5	Blastula	0.19
4.0	Gastrulation	0.28
4.0	Formation of head and trunk	0.49
4.0	separation of posterior end of body	0.76
4.0	Beginning of circulation	1.91
4.0	Subintestinal-yolk sac circulation	2.88
4.0	Liver-yolk sac circulation	3.39
4.5	Before hatching	4.91
4.5	During hatching	7.34
4.5--5.0	Embryos hatching later	9.51
5.0--6.0	Larvae	13.2
6.0--9.0	Fry	33.5

Note: Experiments were performed three times, at the following oxygen concentrations: before hatching, 6-8 mg/l, for free-living larvae and embryos, 7-8 mg/l, for fry, 8-10 mg/l.

Small fat drops are situated mainly under the cephalic part of the embryo. They and a few large drops adjacent to the embryo move together with it when the egg changes its position.

Fat droplets at greater distances from the embryo, on the turning of the egg alter their position in the yolk independently of its distribution.

In 5 mm long embryos, the rudiments of lenses are still not separated from the ectoderm. The retinal and the pigmented layers begin to differentiate in the eyes. The rudiment of the cerebellum makes its appearance. Three pairs of pharyngeal pockets are visible. Epimyocardium is formed. The axial blood vessels are laid down and 50
in the pericardial cavity there appear embryonic blood cells. Along the middle line, the rudiments of the lateral line organs begin to appear.

After the separation of the tail bud, the number of the caudal segments increases rapidly. The tail elongates and the rudiment of the unpaired fin fold begins to appear on it. With the beginning of the separation of the posterior part of the trunk from the yolk, the preanal fold begins to develop.

In the Teplovskii hatchery, at the age of 42 days (147 degree-days), the embryos had up to 58 segments, of which 16 - 17 were caudal. The length of embryos reached 5.5 - 6.0 mm. The posterior part of the intestine and the anal orifice had formed (Fig. 8,F). The same condition was reached by the embryos in the Sokolovskii hatchery at the end of 15 days (150 degree-days), when they had the length of 6.0 - 6.3 mm. Under conditions existing in the Teplovskii hatchery, the process of epiboly takes 45 days to complete (156 degree-days); in Sokolovskii it takes 18 (183 degree-days). At the time of the closing of the yolk plug, the eggs of chum and of other salmons are extremely sensitive to mechanical disturbance and perish even when lightly touched. Epiboly does not become completed in all embryos at the same time, and until this process is completed, the eggs must be kept free of any disturbance.

The embryos of chum have a very large yolk sac, and the process of its covering (overgrowth) extends to later stages of development. In the smallest eggs of chum epiboly is complete at the 52 - 53-segmented stage, while in the embryos of S.salar, in the presence of about 30 segments (Battle, 1944).

When the process of epiboly is completed, the sensitivity of the eggs to trauma is drastically reduced. Even in the chum, this takes place before the appearance of pigment in the eyes. This fact should be taken into account by fish culturists.

Before the disappearance of the yolk plug, the lenses detach themselves from the ectoderm and descend into the depth of the optic cups. The differentiation of the cerebrum makes considerable progress; its ventricles become enlarged, the olfactory lobes are laid down, the large cerebellum, epiphysis and hypophysis form. The differentiation of the first gill arches can be observed. The endoderm produces the the intestinal tract. A digitiform outgrowth of the mid-gut gives rise to the liver. Renal glomeruli and the pronephric duct begin to develop. Blood islands begin to appear on the yolk sac.

Towards the end of the stage, the posterior part of the trunk, up to the 29th segment separates from the yolk sac. During this stage the motility of the embryos increases. They flip their tails from side to side, and at times perform with it wave-like motions.

<u>Stage 7. Development of the Subintestinal and Vitelline Circulation.</u> This stage embraces the period from the beginning of blood circulation to the formation of the cardinal veins. At a mean temperature of 9.6°, it takes 1.5 - 2 days, at 3.5° about 5 days. 51
Towards the end of the stage, the embryos reach a length of 7.3 to 7.8 mm and develop up to 71 segments.

Under the conditions existing in the Sokolovskii hatchery, the beginning of circulation in some embryos was observed at 52 - 53 segments, when a small yolk plug was still present (15 days, 144 degree-days). In most embryos this took place on the 16th-17th day, when the number of segments increased to 58 - 60. At the beginning of circulation, the stream of blood in the vessels is weak, erythrocytes are few and their colour is pale. The presence of haemoglobin in salmon is demonstrable histochemically before the beginning of circulation (Ostroumova, 1962).

At the beginning of this stage, the blood flows from the heart along the paired mandibular arches of the aorta (arc mandibularis aortae). Above the gill region, vessels separate from them, along which the blood flows to the head and, along the dorsal aorta (aorta dorsalis) to the trunk. Posteriorly to the anus, the dorsal aorta passes into the caudal artery (a.caudalis). At the beginning of circulation, the caudal artery runs only along 2 - 3 caudal segments, bends downwards and passes into the caudal vein (v.caudalis). This vessel, having curved over the posterior intestine, passes directly into the subintestinal vein (v.subintestinalis) along which blood runs for a distance of 25 - 26 segments. Slightly in front of the preanal fin fold, the subintestinal vein comes out on the left side of the surface of the yolk sac, giving rise to the vitelline vein (v.vitellinae) which is also known as the subintestinal-vitelline vein (v.subintestinalis vitellinae) (Soin, 1968). On the left side of the yolk sac, the stream of blood describes a small arc, links with the blood flowing from the anterior cardinal vein (v.cardinalis anterior) and enters the atrium. In other salmon species, the primary course of circulation is formed in a similar manner.

Under the conditions existing in the Teplovskii hatchery, the beginning of circulation in the chum was observed at the age of 45 days, directly after the closing of the yolk plug. The embryos were 6.5 to 7.2 mm long, they had 65 segments, 41 of which were in the trunk. By this time, the pectoral fins have been established. The head has started to separate from the surface of the yolk sac. At the start of the stage, the blood flowed along the caudal vein to the 10th caudal segment and at the posterior sector of the subintestinal-vitelline vein there were two or three capillary vessels (Fig. 9, A,B). This is a later stage of differentiation. The delay in the beginning of blood circulation can be explained by a smaller number of eggs and better aeration of water in the incubator of the Teplovskii hatchery.

In the course of the stage, the caudal arteries and veins lengthen, the subintestinal vitelline vein drops lower, the number of capillaries in the yolk sac increases. The vitelline vein descends in the following manner. There is a gradual increase in the number of formed elements in the blood islands located near the outward side of the vein; these islands merge and are combined with the bloodstream, as the inner sector of the vessel gradually empties.

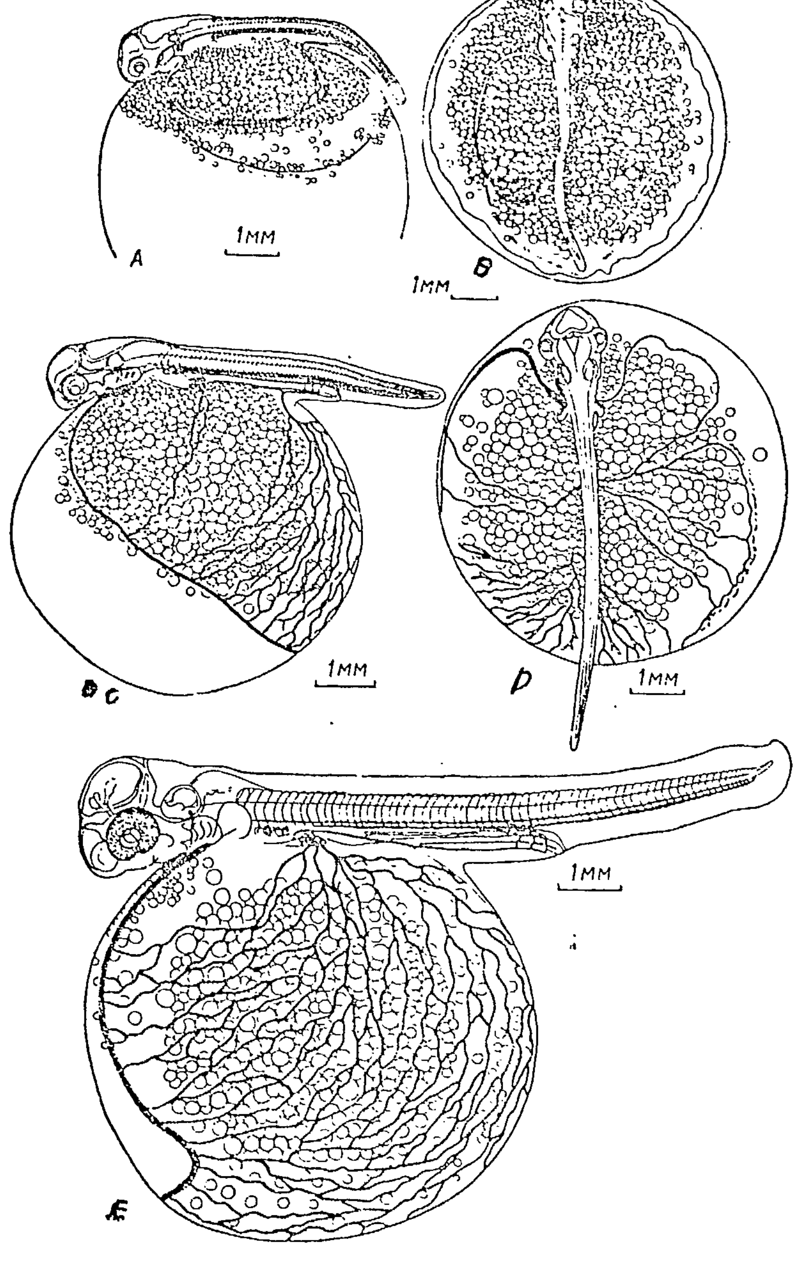


Fig. 9. Embryos of the autumn chum at various stages of the development of the subintestinal-vitelline circulation; sketches in vivo. A - embryo at a length of 7.2 mm, stage of 65 segments; the blood circulation has started. B - the same embryo, top view, the membrane partially removed. C - embryo at a length of 7.8 mm, at a stage of 73 segments; the hepatic-vitelline veins have appeared. D - the embryo at a length of 8.2 mm, 73 segments; top view. E - embryo at a length of 11 mm, the number of segments is reduced to 66 (according to N.N. Disler, 1957).

New capillaries are also formed by the consolidation of blood islands. (Disler, 1957). 53

Developing embryos move ever more energetically and often. With the start of circulation, the use of oxygen by the eggs is nearly double in comparison with the previous stage. The eggs constantly undergo mechanical disturbance(see Table 2).

Stage 8. The Origins of the Cardinal Veins and of the Mixed Subintestinal-vitelline and Hepatic-vitelline Circulation

During development in the incubator of the Teplovskii hatchery, substantial changes in the embryos are noted on the 50th day of development (about 160 degree-days), and at the Sokolovskii hatchery, at the age of 18 - 19 days (183 - 193 degree-days). In the first instance, the stage lasted about 14 days, in the second--5 days. Towards its completion, the embryos reached a length of 10.5 - 11.0 mm.

By the start of the stage, the vessels are filled abundantly with intensely coloured red corpuscles. The blood-flow to the eyes starts. From the head, the blood flows along the anterior cardinal veins (v.cardinalis anterior), which, anteriorly to the pectoral fins merge with the newly formed posterior cardinal veins (v. cardinalis posterior), and form the short Cuvieri canals (d.d. Cuvieri) (fig. 10). In the vessels of the two first pairs of gill arches there appear elements of blood, though there is as yet no blood-flow through them. On a considerable part of the rear half of the yolk sac, a net of capillary vessels is formed. They are now found not only on the left side, as previously, but also on the right. In living embryos, small balls of pronephros can be clearly seen posteriorly to the pectoral fins.

In the Teplovskii hatchery, 3 - 5 days after the start of the stage, or, in our case, 1 - 1.5 days, the segmentation of the cauda is complete, and the number of myotomes reaches the maximum--72 - 73, of which 30 - 31 are caudal. The length of the embryos is 8 - 8.2 mm. By this time, the pectoral fins are growing out noticeably. On the dorsum, the unpaired fin fold grows as far as the first myotomes. The head is now distinct from the yolk sac. Owing to the formation of the curves of the brain, the auditory vesicles are drawn close to the eyes and the length of the head decreases. In the auditory vesicles, the formation of the semi-circular canals is taking place along several small otoliths. In the eyes, granules of melanin are visible. The olfactory pits are formed. The blood-flow appears in the first pairs of gill arches. In the yolk sac, the blood vessels occupy a significantly large area. The marginal vitelline vein descends to the lower side of the yolk sac. The liver has become fairly large and is situated between 5 and 9 segments, having moved a little to the right. Blood circulation has started in the liver and yolk. Initially, the blood flows from the liver through a fine blood vessel to the left side of the yolk sac, and into the marginal vitelline vein. Two vessels lead from 54
the liver to the right side of the yolk sac. The first of these forms a short loop and flows into the right Cuvieri canal, while blood from the second flows towards the marginal vitelline vein. These vessels branch out shortly thereafter (Fig. 9, C,D).

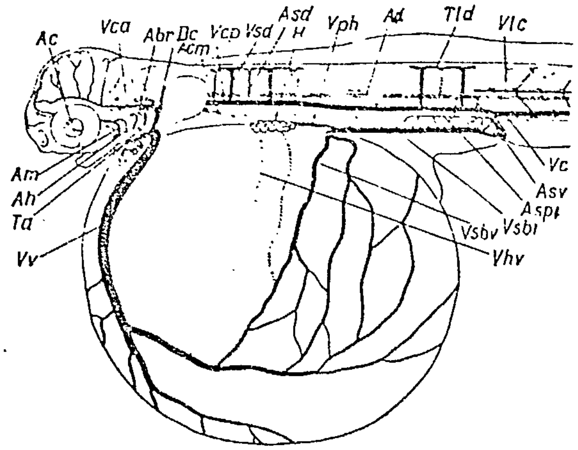


Fig. 10. A sketch of the location of the basic blood vessels of salmon embryos (vessels are shown which actually exist at various stages of development).

The subintestinal-vitelline vein which supplies the vessels of the caudal sector of the yolk sac with blood gradually empties after the formation of the rear cardinal veins and the blood circulation of the liver. At the same time, a number of vessels appear in the yolk sac, supplied with blood from the liver. In this way, the blood supply to the yolk sac is typically compound during this stage, in the presence of the gradually growing importance in the role of the blood supply from the liver.

In chum raised in the incubators of the Sokolovskii hatchery, at the age of 21 days (205 degree-days), granules of secretion. of a polysaccharide nature were present in the cytoplasm of certain 55
epithelial cells in the region of the still forming mouth and gill chambers. It is assumed that these cells secrete the enzyme hyaluronidase into the submembrane space (Sakun and Chistova, 1960). This enzyme

is found in the perivitelline cavity of the eggs of chum. Its function is held to be connected with the regulation of permeability of the egg membranes and embryo covers, and also plays some part in the act of hatching (Busnikov and Ignat'eva, 1958).

Stage 9. The Functioning of the Liver and Yolk Circulatory System. The stage lasts from the change of function of blood supply of the yolk sac fully to the hepatic veins, to the beginning of the differentiation of the cones of myotomes. In the Teplovskii hatchery it started on the 64th day (224th degree-day) and lasted about 19 days, and in the Sokolovskii hatchery at an age of 23 - 24 days (235 - 245 degree-days) and ended after 6 - 7 days.

By the start of the stage, the height of the heads of the embryos has increased (fig. 9,E). The auditory capsules draw close to the eyes. The eyes become dark. Numerous tiny otoliths consolidate into large formations. Having begun to show earlier on, the funnel of the mouth cavity now deepens. The growth of the lower jaw accelerates. The gill covers grow out noticeably. The bases of the pectoral fins form, with the longitudinal axis of the body an angle of about 30 degrees. The caudal section has lengthened and now exceeds 1/3 of the total length of the embryo. The rear extreme of the cord curves upwards and the caudal fin loses its symmetry. The supporting and muscular elements of the tail have started to form. (Fig. 11,A). The number of segments in the tail decreases to 27 - 28. An analogous process is also found in other teleost fishes. In the caudal section, the isolation of vertebrae is taking place. The contents of the intestines acquire a lemon-yellow colour, apparently caused by bilious pigments which have appeared.

The auricle and ventricle of the embryos are clearly discernable. In the hyoid arches, in the third, and a little later in the fourth pairs of gill arches, the movement of blood is visible. A net of capillaries develops on the covering of the sincipital region of the head, then over the cerebellum and the occipital region. Segmented vessels appear, the formation of which goes from head to tail. The caudal vein loses its connection with the subintestinal vein, and the latter, with the vascular system of the yolk sac. The rear section of the intestine is entwined by the branches of the supraintestinal artery (a.supraintestinalis), and the central section, by the capillaries of the intestinal artery (a.coeliaca). The blood flows from these capillaries to the subintestinal vein, along which it flows to the liver. A thick vascular net supplied with blood exclusively through the hepatic veins develops on the yolk sac. On embryos at a length of about 13 mm, at the bases of the anal and dorsal fins, an accumulation of mesenchyme and the rudiments of muscular gemmae are visible. Having lengthened, the caudal section occupies 37% of the overall length of the embryo. Loops of capillaries appear at the bases of the supporting and muscular elements of the caudal fin. The capillaries cover the entire surface of the yolk sac. Embryos extracted from the eggs have egg-shaped yolk sacs. The diameter of some fat drops reaches 1 mm.

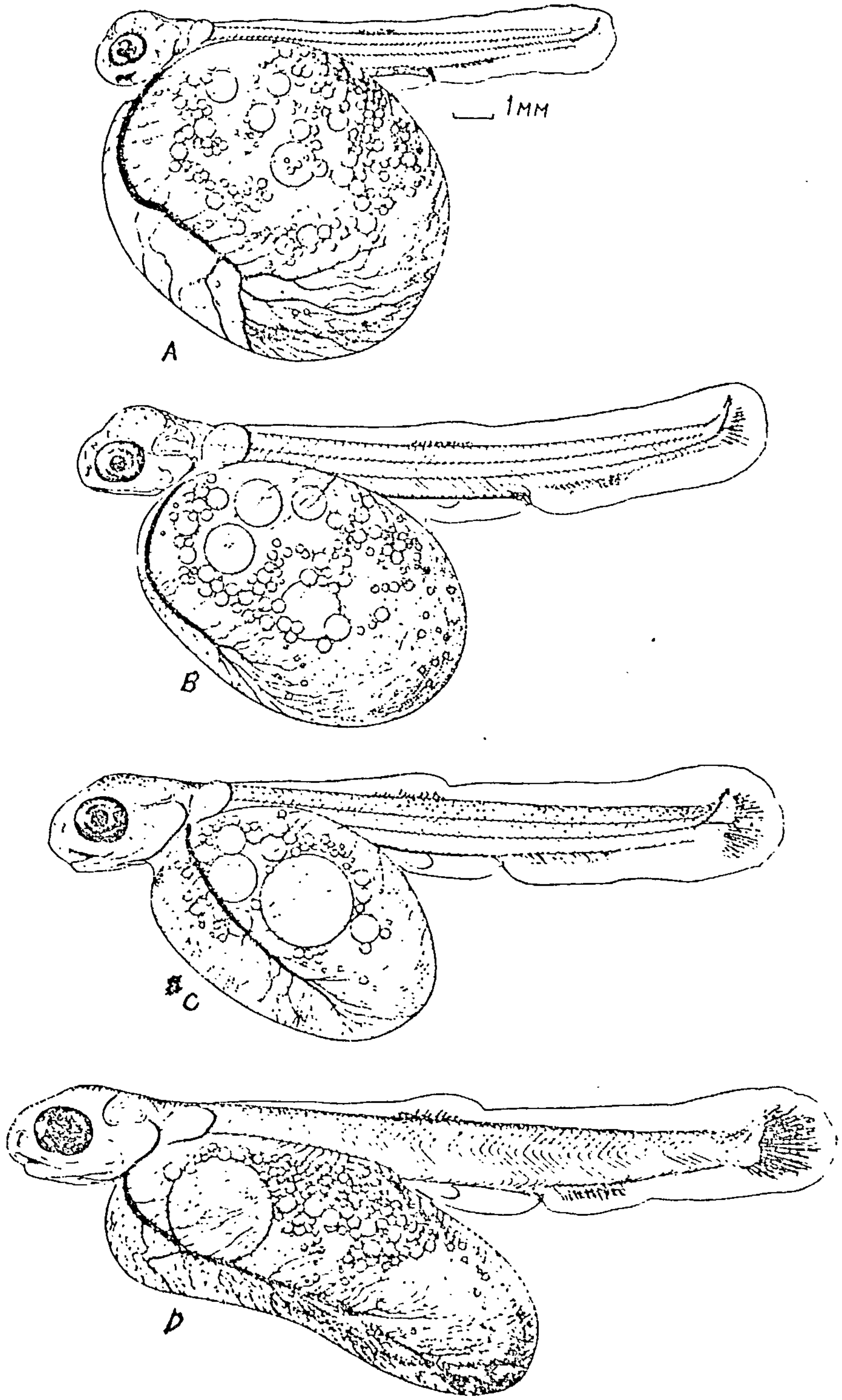


Fig. 11. Late embryos of the autumn chum. A - age of 30 days, length 13.1 mm. B - age 38 days, length 17.7 mm. C - age 48 days, length 21.5 mm. D - embryo at the moment of mass hatching, age - 51 days, length 23.5 mm. Development at a temperature of 9.2 - 10.5 degrees (in the Sokolovskii incubator). Sketch in vivo.

Stage 10. Differentiation of the upper and lower cones of myotomes. The upper and lower cones of myctomes at a mean temperature of 3.3 degrees started to form on the 83rd day (about 270 degree-days). In our series this took place on the 30th and 31st days (207 - 217 degree-days). At a temperature of 3.3 degrees, this stage lasted 12 - 17 days, and at 10 degrees, 5 - 6 days.

At the start of the stage, the embryos had a length of 14 mm and more (fig. 11,B). By this time the gill covers have started to cover the second pair of gills. On the 3rd, and then 4th and 1st pairs of gill arches, the rudiments of gill filaments appear. The bases of the pectoral fins assume an almost vertical position and acquire mobility. Under 25 - 30 mytomes of the torso, there appear the small, longitudinal folds, of the rudiments of the pelvic fins. Projections of cones of myotomes grow into the bases of these newly appeared unpaired fins, and the projections later form the muscles of the fin rays. The rudiments of the rays appear initially as rod-like clotting of mesenchymatous cells. The process of cartilage formation leads to the formation of the lepidotrichia, which are supported on the pterygiophores (Y. Francois, 1955, 1957). In chum, as in other Pacific salmons, the differentiation of the anal fin slightly precedes that of the dorsal fin. Gradually, the abdominal lobe of the caudal fin grows out. In it, up to 8 - 10 rays are formed. The lower aristate offshoots of the last vertebrae form the broad hypural discs. In the course of the stage, the thickness of the capillary net on the yolk sac continues to grow on account of the increasing number of anastomoses between vessels. The marginal vein descends to the ventral side of the

yolk sac. Capillary vessels develop on almost all of the upper surface of the head. Capillaries appear in the rudiments of the pseudobranchia. The subclavian artery (a.subclavia) forms the circular vessels of the pectoral fins. Segmented vessels appear in all of the caudal myotomes. From the segmented arteries of the frontal torso, vessels branch off to the spinal chord, deep into the muscular material and to the surface of the body. A net of capillaries with 58
a respiratory function forms on the integument of the body (Smirnov, 1953b). The branches of segmented vessels over the myotomes form the truncus longitudinalis dorsalis, and, at the surface of the body, along the centre line, the truncus longitudinalis lateralis, which feed blood to the capillaries passing at the surface of the body along the intersegmental myosepta. At the start of the stage, on the integument of the head, and then of the torso, melanophores appear.

The development of the upper and lower cones of myotomes proceeds from the tail to the head in an order contrary to that in which the myotomes appear. The vertebrae also differentiate in this sequence. A.G. Ryndzjunskii (1939) connects the earlier complication of the form of the tail myotomes with its importance in swimming, that is, with the function of the organ in later stages of development. One should note that the movements of the tail are important for the life of the embryo. They are favourable to the circulation of blood and facilitate the intermingling of perivitelline fluid.

By the end of the stage, the number of caudal segments is reduced to 22 - 23, and the overall number of segments decreases to 62 - 63.

The unpaired fin folds at the bases of the unpaired fins broaden and elements of support form in them. In the caudal lobe, a fairly thick net of capillaries grows. The frontal margin of the lower jaw reaches a vertical line dropped from the forward margin of the eyes. Contours of bone elements appear in the upper and lower jaws. The mouth acquires motility. The gill covers cover the 3rd pair of gills. The liver develops into a large organ, permeated by a thick net of blood vessels. The differentiation of the upper and lower cones of myotomes reaches completion. The olfactory pits take on a lengthened form. The auditory vesicles assume the appearance of irregular pyramids. On the integument of the head small orange-red lipophores appear. Along the sides of the head and under it on the forward part of the yolk sac hatching glandules begin to appear (Fig. 11, C). By the end of the stage, the length of the embryos has reached 16 - 18 mm.

Stage 11. Development of the Motility of the Jaws and Gill Covers, and the Completion of Incubation. During the present stage, the development of the embryos under the membrane is completed. The duration of incubation at different temperatures varies greatly. In the described series, the incubation of eggs lasted 51 - 55 days (521 - 530 degree-days). The great bulk of embryos at hatching had a length of 22 - 23 mm, while some even reached 24 mm. In the Teplovskii hatchery, N.N. Disler noted the hatching of chum at the age of 122 - 128 days (408 - 420 degree-days) and at a length of 20 - 22 mm. The smaller size of these embryos is connected with the fact that chum of the Teplovskii stock produce smaller eggs.

During the course of the stage, the formation of the oral

apparatus continues. The lower jaw grows past the vertical line of the forward margin of the eyes. The mouth assumes a somewhat lower position. The floor of the oral funnel breaks open. The gill covers now cover all the gills. The 59
formation of the septum dividing the aperture of the olfactory pit into anterior and posterior openings, begins to show (fig. 11,D). The mouth, gill covers and gills acquire motility. The movements of the jaws and the gill covers in the eggs are hampered because the large head of the embryo is pressed against the yolk sac.

By the time of hatching, the lobes of the pectoral fins are growing out, and their tips reach the 5th to the 6th myotomes. Rays become clearly visible in the dorsal and anal fins. Fins emerge from the unpaired fin fold which resorbs noticeably. At the base of the fatty fin, an accumulation of small melanophores and lipophores becomes noticeable. The tips of the pelvic fins, which have grown larger, draw close to the margin of the preanal fin fold. 15 - 19 lepidotrichia develop in the caudal fin.

The dorsal surface of the embryos darkens noticeably. Granules of pigment in the chromatophores acquire the ability of migrating, owing to which the embryos can change colour. In the trunk, the melanophores are numerous up to the centre line of the body, while lower down only isolated melanophores occur. They appear between the rays of the caudal fin. A row of pigmented cells forms over the spinal cord (neural row), along large blood vessels (haemal row), the lining of the body cavity becomes pigmented. Small red-orange lipophores cover the dorsal surface of the head and in a small number appear on the back of the embryo. Posterior to the rudiments of the dorsal and anal fins, lipophores penetrate the base of the unpaired fin fold.

By the end of the stage, the capillary net on the yolk sac reaches its maximum thickness. The length of the capillaries on 1 mm^2 of its surface reaches 7.5 - 8 mm. The net of capillaries becomes complicated close to the surface of the body. It must be noted that with narcotization of the embryos, the small capillaries of the body integument quickly empty, so it is necessary to study these vessels without the application of narcosis.

For several days before hatching, large embryonic cells with a diameter of 7.2 - 15.4 microns are distinguishable in the gonads. In their nuclei, mitotic figures are observed. The mitotic division of the primary sexual cells lasts even after hatching (Robertson, 1953).

Embryos are able to make energetic wavelike movements with the tail, and when stimulated, start to rotate under the membrane. Removed from the egg, such an embryo is able to rise into the main body of the water and move several centimeters ahead, but the locomotion of the tail weakens quickly and the embryo sinks to the bottom. Under favourable conditions of aeration, the embryos in the eggs move rarely, and this helps to conserve energy stores. Intermingling of the perivitelline liquid at this time is brought about by rythmic movements of the pectoral fins.
The movement of the mouth and gills serves the fulfillment of this aim. 60

By the end of incubation, the ureter and urinary bladder are filled with accumulated and crystalized products of nitrogen metabolism. As is known, at the time of incubation, the eggs excrete through the membrane only a small amount of ammonia (Svetlov, 1928; Hayes, 1949). For salmon burying their eggs closely grouped in the ground, where the current is weak, this peculiarity has a vitally important significance, since, thanks to it, the water in the spawning redds remains clean.

Immediately before hatching, the embryos become restless, turning energetically. Under the action of a proteolytic enzyme excreted by the hatching glands, the egg membranes disintegrate, and the embryos leave them. Experiments on the eggs of the European salmon have shown that the hatching enzyme is excreted into the submembrane space in a short time, and quickly breaks up the membrane. Accumulated hyaluronidase prepares the membrane for the action of the hatching enzyme. The significance of mechanical factors in the act of hatching is not great. In experiments, embryos treated with narcotic hatch with complete success, exclusively on account of the dissolution of the egg membranes by the hatching enzyme. The reduction of the partial pressure of oxygen in the perivitelline liquid is an adequate stimulus inducing secretory activity in the hatching glands. The process of secretion proceeds, possibly as a neurohumoral reflex (Buznikov, 1955, 1961, 1964; Buznikov and Ignat'eva, 1958). "Hatching can take place either earlier or later in relation to the development of the embryo itself, depending on the influence of environmental conditions" (Vasnetsov, 1953a, p. 210).

Since the hatching glands in salmon are grouped on the head and upper-anterior section of the yolk sac, secretion produced by them could function locally. This is prevented by the movements of the embryos, with the help of which the enzyme is distributed in the submembrane space and exerts influence on the entire membrane. If conditions turn out to be unfavourable, the embryos are inhibited and lose their mobility, the secretion of the hatching glands operates locally, dissolves only a small part of the membrane, and only the head protrudes; the hatching

of the embryos becomes difficult, and they may die. Under the conditions of a high saturation of water by oxygen, hatching may be delayed; this may also be caused by an unnecessarily strong water current. Fish culturists are interested in rapid hatching. "The embryos can achieve an easy exit from the membrane only when there is a weak water current, that is, under conditions approaching nature" (Disler, 1957, p.27). In fish hatcheries of various countries egg diseases have been observed that lead to premature weakening of the egg membranes, their deterioration and the emergence of weakened embryos in abnormally early stages of development. Such disease can be caused 61
by gram-negative bacteria, certain Protozoa and single-celled fungi of the class Archymyceteae. Sometimes the disease takes on extraordinarily large proportions and tens of millions of eggs perish (Handa, 1933, 1934; Lyaiman, 1957; Sakun and Chistova, 1960). It is possible to avert and liquidate the disease successfully by using as a preventative and treatment formalin, malachite green and other preparations as indicated by their use in the Sokolovskii and other Sakhalin hatcheries (Smirnov, 1963b, 1964b).

As far back as 1912, V.K. Soldatov noted that embryos left their eggs at different times, even where the eggs were taken from the same female, and connected this with individual peculiarities of the eggs. Under the conditions at the Sokolovskii hatchery, mass hatching lasts 2 - 3 days, but can extend as long as 7 - 10 days and more if the water temperature is low. In this hatchery, depending on the temperature, periods of incubation fluctuate from 49 to 80 days and more, but most often hatching lasts 53 - 60 days. In other hatcheries, adapted for chum rearing, periods of incubation vary from 45 - 196 days (223 - 610 degree-days). In some instances, hatching starts at the end of October (Sokolovskii hatchery), in others--during spring (Krasnopol'skii hatchery) and lasts accordingly to November or May. This comparison shows great differences in the rate of developement and periods of incubation of chum in the Sokolovskii and Teplovskii hatcheries; such differences are also observed in nature. It has been noted that with the lowering of water temperature the time of incubation of eggs becomes longer, whereas the number of degree-days gets less. Therefore the determination of the rate of development in degree-days has significance as a guide.

Stage 12. The Passive State of Free Embryos. The stage starts after the emergence of the embryos from the membranes and lasts at a temperature of 3.3° for 5-7 days, and at a temperature of 9° for 3 - 4 days. Newly hatched embryos react weakly to external stimuli and move little. Their length varies greatly. Their size depends on the size of the eggs and the stage of development. Thus from eggs with a mean diameter of 8.7 mm, embryos were hatched measuring 21.0 - 24.5 mm, with a modal length of 22.5 - 23.0 mm, whereas from eggs with a diameter of 7.9 mm, embryos were hatched measuring 19 - 23 mm, with a modal length of 20.5 to 20.7 mm. Small specimens from eggs of a similar size had 1 - 3 rays less in the tail than larger embryos. At the Poronaiskii hatchery, chum from mixed eggs hatched at a length of 21 - 25 mm ($M = 23.0 \pm 0.08$) and weighing from 149 to 240 mg, where $M = 199.6 \pm 2.1$ mg (Zhiteneva and Galkina, 1965). At the Teplovskii hatchery, embryos left their eggs at a length of 17.3 to 22.0 mm, with a mean of 19.0 mm, and a weight of 174 mg (Levanidov, 1954b; Disler, 1957). The differences are explained by the small size of the eggs of the chum from the Teplovskii stock.

When leaving the egg, the chum has a huge, egg-shaped yolk sac. The yolk contains many small fat drops and usually one large one, with a diameter of about 3 mm. When the embryo changes position, the fat drops in the yolk may move around as before. In figure 11 D, an embryo is shown in which during the time the drawing was made the fat drops moved to the left side. 62

The number of trunk segments remained as before; in the tail at the moment of hatching, it decreased to 22 - 21. The myotomes of the tail became broader, on account of which the length of the post-anal section comprised 36.5% of the entire length of the embryo. The shape of the tail lobe was asymmetrical.

The unpaired fin fold continued to resorb. The dorsal fin stood out from it, and the contours of the fatty fin became noticeable. The majority of the lepidotrichia was in the dorsal and anal fins. By the time of mass hatching, there were usually 17 - 19 lepidotrichia in the caudal fin. If at hatching, their number was less than 15, it indicated early hatching. In the embryos, a bony pectoral girdle was formed. The pectoral fins were large and curved. In the pelvic fins, support elements were still absent. By the time of hatching, the preanal fin fold had reached its maximum development.

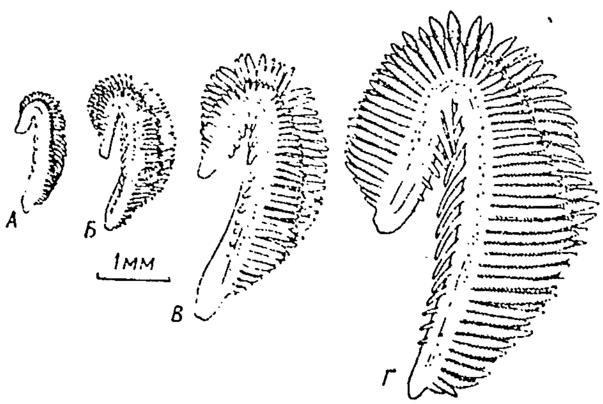


Fig. 12. The First Left Gill of the Chum.
A - At the moment of mass hatching, the length of the embryo is 23 mm. B - With the appearance of dark spots on the sides of the body, the length of the embryo is 29.2 mm. C - At the start of the accumulation of air in the swim bladder, the length of the larva is 34 mm. D - At the start of the fry period of life, the length of the fry is 44 mm.

The mouth of newly hatched embryos occupies a rather low position. In the auditory capsules, semi-circular canals and large otoliths are clearly discernible. The stato-acoustic organs have drawn as close to the eyes as possible. The gill covers now enclose the gills. On the first gill, the middle filaments are 0.25 mm long and become branched; 63
capillaries appear in the filaments. The gill rakers appear, looking like small protuberances (fig. 12, A).

At the start of the stage, the gastrointestinal tract has the form of an almost straight tube. The rudiment of the stomach, having a length of about 1 mm, is noted for its thickened walls and some contraction on the boundary with the intestine.

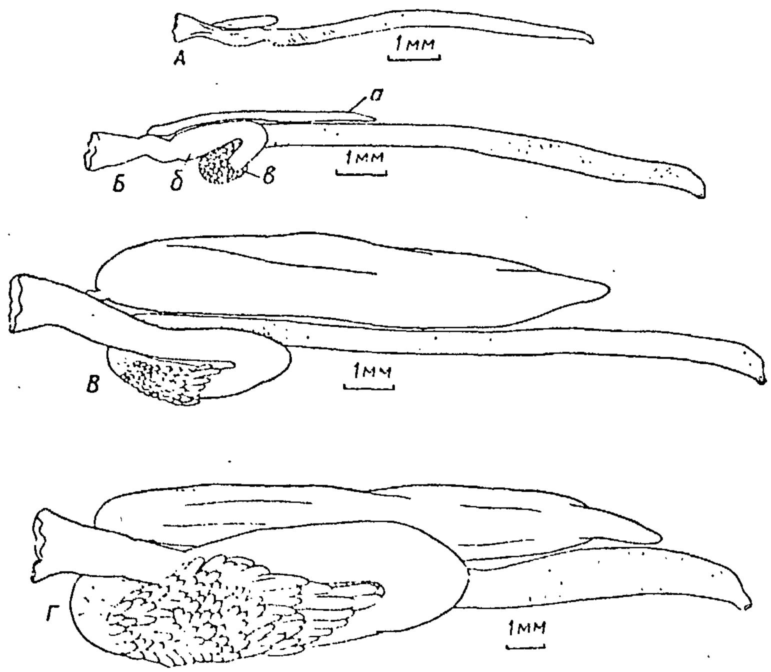


Figure 13. The gastrointestinal tract and swim-bladder of Chum. A - During mass hatching the length of the embryo is 23 mm. B - During the appearance of the dark spots on the sides of the body the length of the embryo is 29.2 mm. C - In a larva 36 mm long. D - In a fry 44 mm long: a) the rudiment of the swim bladder b) the anterior (glandular) section of the stomach c) rudiments of the pyloric caeca in the pyloric section of the stomach.

On its future pyloric section, kidney-shaped protrusions are noticeable--the rudiments of the first pyloric caeca. The length of the intestine is 7.5 - 8.0 mm--about 39% of the overall length of the embryo. The mucous [membrane of the] intestine has acquired folding. The rudiment of the swim bladder has grown to 1.1 - 1.2 mm (fig. 13, A).

The urinary bladder after hatching starts to empty periodically, and fill up again. At the same time, the number of crystals abundantly filling the ureter grows less. The embryos quickly free themselves from the accumulated products of metabolism, and if the water flow in the nurseries 54
is weak and the density of stocking is excessively high, the embryos' environment can deteriorate.

By the time hatching occurs, dark spots form over the eyes auditory capsules, melanophores uniformly cover the entire dorsal half of the body and are situated between the rays of the caudal fin. The lipophore pigmentation of the head becomes stronger. Lipophores appear on the entire dorsal side of the body and in the caudal section of the unpaired fin fold.

The organs of the lateral line--neuromasts--look like small protuberances. They form rows: the supraorbital, the infraorbital, the temporal and preopercular-mandibular; neuromasts appear also near the olfactory apertures. Along the centre line of the body, sensory protuberances have differentiated as far as the middle of the caudal section or a little further. The neuromasts of the supratemporal and jugal groups have not yet differentiated. The sensory protuberances in live embryos are painted with a water solution of methylene blue; if the nerves innervating them do not become coloured, this indicates an insufficient functional maturity (Disler, 1957, 1960).

Leaving the membranes, the embryos remain lying between the stones of the spawning redds. In nurseries with flat beds, they lie on their sides. The pectoral fins are in almost constant motion, which facilitates the circulation of water at the surface of the yolk sac and the body and also has a respiratory significance. Rythmic working of the mouth and gill covers provides good ventilation of the gills. After the embryos have left the membranes their oxygen consumption rises sharply.

From time to time in the nurseries the embryos start moving actively, turn over with their backs up, and swim quickly ahead. They move without leaving the bottom with their heads inclined down. When placed in open water, they quickly descend to the bottom. Their large yolk sac interferes with manoeuvrebility. Experiments have shown that such embryos do not yet react clearly to streams of water; they react indifferently to the touch of all objects; they do not react to noise. The embryos react weakly in a negative way to light, and when bright light is present, they gradually move away to shaded areas (Disler, 1957, 1960). Newly hatched embryos stay for some time in the nests where the eggs lay and then start to move away through slits between the stones. Depending on the water current regime of the nesting grounds they can move in different directions, but with time, draw close to the surface of the[river]bottom. In nurseries, newly hatched embryos slip through the mesh of the hatchery frames, and gather under the piles[of frames]. Owing to high congestion, they cover the surface of each other's yolk sacs, and can suffocate even in water highly saturated with oxygen. Such accumulations must be scattered without delay.

The described relatively calm state of the newly hatched embryos ("pro-larvae") of chum, peculiar also to other salmons, definitely resembles the limited mobility of newly hatched embryos of many lithophilous and phytophilous fishes (Kryzhanovskii, 1949; Kryzhanovskii, Smirnov and Soin, 1951). Thanks to such behaviour, the stores of nutrients available to the embryos are economized. 65

Stage 13. The Formation of the Unpaired and Pelvic Fins and the Swim Bladder. Transfer to the new stage is clearly shown by a change in behaviour. The embryos (fig. 14, A) start to seek shelter from the light and move actively against the current.

Figure 14. Fry of the autumn chum. A - 20 days after leaving the eggs; development at a mean temperature of 7.3 degrees, length 28 mm. B - larva 32 days after leaving the egg, length 31.7 mm. C - downstream migrating larva, length 36.5 mm. D - fry, length 52.5 mm.

A strongly pronounced positive reaction to the touch of foreign objects appears (positive tactile sense).

At the Teplovskii hatchery at the start of the stage the embryos had a length of 24 - 26 mm. At a temperature of 3.4°, the stage lasted 45 - 48 days. At the Sokolovskii hatchery at a temperature of 8.5 degrees, the stage lasted 25 - 27 days.

During the course of the stage, the unpaired and pelvic fins form. The swim bladder grows very quickly, and the digestive tract

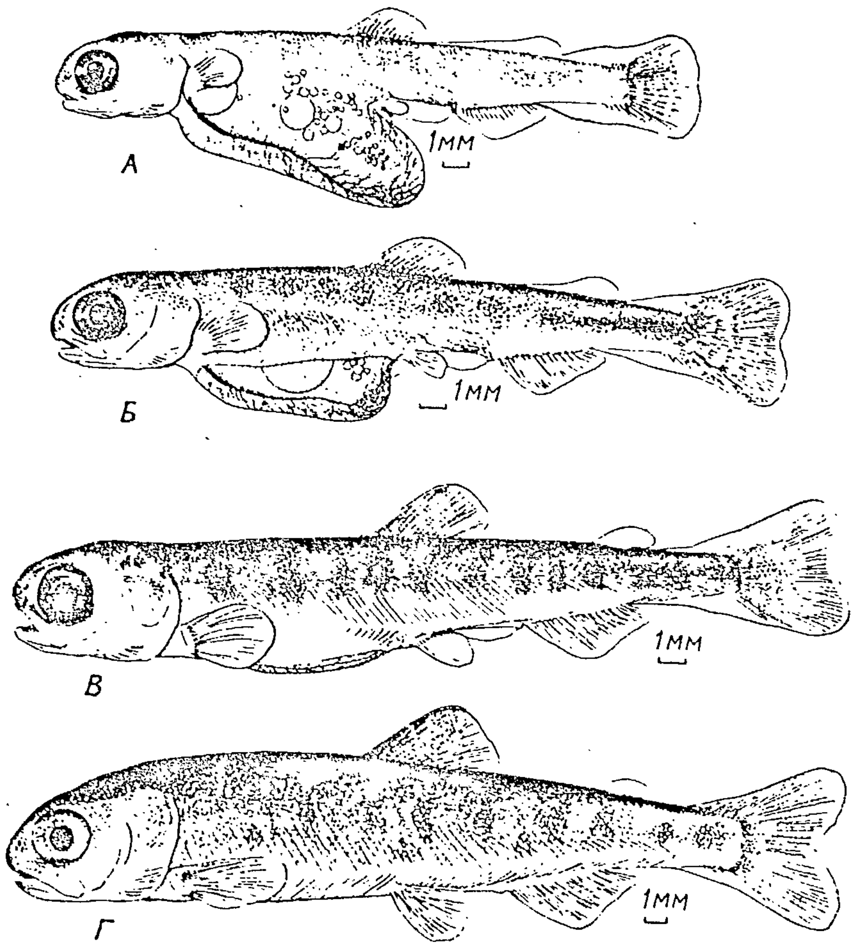


Figure 14.

lengthens and differentiates. By the end of the stage, the larvae have reached a length of 30 - 32 mm and start to consume external nourishment.

The caudal section grows at an accelerated rate, and 20 days after hatching, the length of the post-anal section exceeds 38.5% of the overall length. The resorption of the dorsal and ventral fin folds continues. The preanal fold preserves its previous dimensions. The height of the dorsal, anal and fatty fins increases. All rays have been established in the dorsal and anal fins. The caudum once again assumes a symmetrical form. The accelerated growth of the upper and lower [fin] rays leads to indentation of the lobe of the caudal fin. As many as 3 to 4 segments form in its large rays. Rays are established in the pectoral and pelvic fins.

On the jaws appear the rudiments of teeth which cut their way through by the end of the stage. Leathery folds grow on the edges of the gill covers and rays form in these folds. The leathery folds reach the pectoral girdle and cover the gills completely. The lower jaws and gill covers perform rythmic respiratory movements. The changing of water in the gill cavity is facilitated by the velum which has grown in the mouth. The lateral protuberances on the walls of the olfactory pits close in, isolating the anterior and posterior olfactory aperatures. The space between the eyes and the auditory capsules starts to increase slowly. The absolute and relative size of the head grows. After hatching, the embryos' resorption of the yolk accelerates. Study of chum and other salmons has shown that the periblast, which comes into close contact with the volk veins wherever endothelium is absent (Cordier, 1941; Yamada, 1959), plays an important role in this process. In time, an ever larger part of the yolk sac is covered with ventral protrusions of myotomes; small blood vessels on its surface become emptied,and the gills play an ever more important role in the provision of oxygen to the organism. Such capillaries, located in the blade of the caudal fin and on the surface of the body, carry out a respiratory function.

The gastrointestinal tract lengthens on account of the curves forming in it. The intestine fills with contents of a greenish-yellow colour, and peristaltic movements of its walls become noticeable. The number and size of pyloric appendages increases. The swim bladder grows quickly (fig 13, B). The centre region of the gonads becomes vascularized,and the reproduction of embryonic cells continues (Robertson, 1953).

The melanophores on the sides of the body spread to the lower cones of myotomes, appear at the base and along the anterior edge of the dorsal fin, and increase noticeably in quantity in the caudal fin. Pigmentation becomes stronger in the membranes of the brain and spinal cord, the lining of the body cavity and blood vessels. Small red-orange lipophores spread below the central line of the body.

The differentiation of the sensory protuberances of the lateral line organs on the head and the entire body terminates. A water solution of methylene blue taints not only the neuromasts, but also the innervating nerves in them, which indicates the functional maturity of this system of sensory organs. The embryos now react clearly to water current and move against it, being able to withstand a weak flow. They are sensitive to water currents, caused by the movement of other individuals, and when a few specimens have been stimulated , the entire mass of embryos starts moving. A positive reaction to touch is clearly expressed.

This reaction originated in connection with the peculiarity of stony and sandy stone nests and prevents free embryos from leaving the river bed prematurely. Finding themselves outside the nest for any reason, the embryos are stimulated and swim actively until they fall into crevices between the stones. The sensitivity to light of the larvae also tends to prevent their leaving the nest prematurely.

As is known, sunlight has a negative effect on the eggs and newly hatched embryos of salmon. According to the observations of N.N. Disler (1957), at a mean temperature of 4.1°, the fatal effect of sunlight is noted up to an age of one month after hatching. Sunlight brings about the discolouration of red corpuscles and decreases their number. Under its action, the black pigment develops more intensively, whereas the orange breaks down and is preserved only on the sincipital surface of the head. Off-white islets of dying tissue appear on the yolk sac. Planarians adhere to the decaying parts and devour the yolk, which hastens the mortality of the embryos. The change of colour of fish through the effects of light has been noted previously. Carotinoids were shown to play a part in the light-sensing reactions of fish (Sumner and Fox, 1933, 1935).

With the appearance of a positive reaction to current and the touch of foreign objects and sensitivity to light, the embryos in nurseries with flat bottoms start moving against the current and look for shelter. They gather at the entrance of the water, in depressions in the bottom and hide in cracks between the boards. As mentioned before, such accumulations are dangerous to the life of embryos, and fish culturists are obliged to expend a great deal of effort to keep them dispersed. When embryos move about nurseries , they damage the tender covering of the yolk sac on the rough bottom, and this can be fatal. An arched curvature of the trunk, a change in the shape of the yolk sac, and a shift of the fat drop to the rear, where it can press on the intestine, sometimes occur in nurseries. Such changes are connected with the keeping of free chum embryos on flat bottoms, that is, under conditions unnatural to them. It is true that a levelling out of such aberrations in subsequent development is indicated. Under illumination in the nurseries the development of objective vision is accelerated; the chum start swimming a little sooner and can abandon the nursery prematurely (Disler, 1954, 1957, 1960). The natural requirements of free embryos are met by having nurseries covered with several layers of large smooth pebbles, which must be washed with water from below. 68

This stage completes the embryonic period of the development of chum. At the Teplovskii hatchery it ends at the age of 177 - 180 days (601 - 612 degree-days), and at the Sokolovskii hatchery at the age of 80 - 83 days (the number of degree days turned out to be extremely large--760 - 788).

The Larval Period of Development.

At the start of the larval period of development, the embryos become able to obtain and digest external food. In the presence of available food and suitable temperature: chum start to consume external food even though the yolk is still large, almost half its size at the time of hatching. Larvae therefore continue combined endogenous and exogenous feeding for an extended period of time. The unpaired fin folds continue to serve the larvae as organs of locomotion; they reduce by the beginning of the fry period. The remnants of embryonic respiratory organs are also larval characteristics; their significance gradually decreases, and the role of the gill apparatus grows. At the start of the period, dark specks appear on the sides of the larval body, becoming more pronounced with development. N.N. Disler allotted one stage to the larval period of life of the chum and related species--the stage of combined feeding.

The Stage of Combined Feeding. Under conditions at the Teplovskii hatchery, at a temperature of 3.5 degrees, the larval stage of development started 50 - 55 days after the embryos left the membranes. At a mean temperature of 5°, the stage of combined feeding lasted 30 - 40 days. During that time, the larvae grew from 30 - 32--38 - 40 mm (Disler, 1957; Kol'gaev, 1963). At the Sokolovskii hatchery, chum converted to combined feeding at a length of 29 - 32 mm and a weight of 230 - 255 mg; the remnants of the yolk at that time weighed 70 - 83 mg and made up from 27.5 to 35% of the total weight of the larvae. At a mean temperature of 7.5°, the stage lasted 24 - 26 days.

In early larvae, the lower jaw reaches almost to the tip of the snout. The maxillary teeth cut through. The larvae perform snatching motions with the mouth. The yolk sac loses its rear section which has been trailing behind, and its lower outline appears almost parallel with the longitudinal axis of the body. The shape of the body becomes streamlined (fig. 14, B). The mobility of the young fish increases.

By the start of the larval stage of development, the majority of the fat drops in the yolk flow together, and form one very large drop, which soon assumes a stretched egg-shaped and sometimes pear-shaped form. The yolk becomes viscous, which hinders the shifting of the fat drop. If prior to this the larvae have held their heads up, the fat drop in them is found at the front. Since the fat drop has the function of a hydrostatic organ, its frontal position allows the larvae to maneuver well. In nurseries with a flat bottom, the larvae, when they move, hold their heads down, and the fat drop moves to the rear section of the yolk sac. In such a position, it presses against the intestines, and hampers the passage of food; when the larvae ascend into the main body of the water, it restricts their movements.

At the start of the stage, the lower cones of the torso myotomes cover roughly half of the yolk sac, and at the end, its entire remnant (fig. 14, C), and finally, the yolk is fully resorbed. With the loss of the respiratory surfacesof the yolk sac, the basic role in providing the larvae with oxygen goes to the gills.

During the course of the stage, the fatty fin completes its emergence from the fin fold, the pre-anal fin fold resorbs, and the cleft in the blade of the caudal fin develops. The lepidotrichia of the caudal fin branch out, and the number of their segments increases. Above and below the long rays appear short ones, the so-called reduced rays of the caudal fin. The segmentation of lepidotrichia of the other fins takes place.

In early larvae, the swim bladder fills with air, the anterior (glandular) and pyloric sections of the stomach differentiate, and many pyloric appendages are formed (Fig. 13,B). The level of differentiation of these organs is higher than in the Atlantic and Baltic salmons (Vernidub, 1967b). Under the conditions in the Sokolovskii hatchery, 55 days after hatching, there appear signs of the conversion from oogonia to oocytes, the start of the protoplasmic growth of the latter, and the differentiation of the sexes (Persov, 1966, 1968). The eyes become mobile. The number of neuromasts increases on the head and trunk.

With age, the pigmentation of the larvae grows stronger, especially on the dorsal surface. On the sides, dark oval transverse spots form (parr marks) of which the chum usually have 10 - 12, and now and then as many as 14. Melanophores abundantly cover the lining of the body cavity, the brain and spinal cord, and large vessels. The lipophore pigment of the body becomes stronger. The orange-red colour of 70
the fins is already discernable with the naked eye. Accumulations of guanine appear on the surface of the gill covers and on the sides of the body. The term "parr" characterizes the colouration peculiar to such larvae.

In nature, the chum start to use food--detritus, diatoms, Cyclopodia, and now and then, small larvae of Chironomidae--while they are still in the[river]bed. This food is found with the help of the organs of touch and taste. This food was shown to be in more than 60% of larvae 30 - 33 mm long obtained from the spawning grounds of Teplovskii Lake. The larvae convert to external feeding before the swim bladder fills with air (Disler, 1954, 1957). In early chum larvae extracted from spawning redds of other bodies of water food was not in evidence, or was present only in a small number of individuals (Levanidov, 1957). Probably the possibility of feeding starting in the nests is connected with the abundance of food organisms in the[lake]bed.

By the end of their stay in the nests, the larvae's sensitivity to light and positive tactile reaction weaken. They gradually draw closer to the surface. The first journeys out of the nests are made at night; during the day, the larvae hide again under the stones (Woodhead, 1957; Heard, 1964; Dill, 1969, 1970; McNeil, 1969). They still shy away from bright light. The larvae are already prepared for dwelling in the body of water and still survive if the nests are destroyed by spring floods. However, a significantly large yolk still hampers some larvae, and impedes their movements, and such larvae become easy prey for predators. Development of salmon in the bottom up to late stages increases their survival rate. The possibility of prolonged use of the protective characteristics of the nest by the chum combines with the option of external feeding at the start of the larval period of development.

Leaving the bottom, the larvae rise to the surface of the water, swallow air bubbles and fill the swim bladder with air. After that, they are able to remain steadily in the main body of the water. For the first while, the larvae remain in the region of the nesting grounds, and accumulate in shallow places near the shore with a weak current, and often overgrown with higher vegetation. Their food consists of specimens of fauna in the weeds, overgrowth on stones and organisms in the [lake] bed; plankton is rarely consumed.

The larvae stay in a group. According to data from Disler, (1954, 1957, 1960), in schools they coordinate their movements, mainly by visual means. Eyesight also plays a vital role in the procuring of food and orientation in space. In the current, the larvae keep

steadily to a selected section. Drift caused by the current is controlled by eyesight and touch i.e.,by means of periodic touching of the pelvic surface on the bottom. It is important to note that the tactile 71
reaction is specially important for larvae staying in a selected area of a water body at night, when visual orientation in space is not possible. Early larvae do not react to the movement of objects above the water, and react weakly to vibrating objects. When touched, they swim away from irritating objects. By the end of the stage, the upper field of vision appears. The larvae start catching small insects which have fallen into the water. The rudiments of the tubules of organs in the lateral line now appear on the head. The chum swim out into more open, deeper areas, where they form large gatherings. In such groups, characteristic movement in a circle is often observed (Hoar, 1954, 1958).

At the end of the stage, the remnant of the yolk and the fat drop are quickly resorbed, but the storage products in them do not disperse fully, being redistributed within the organism, and deposits of fat appear in the body cavity. The yolk sac that has impeded the movements of the larvae disappears, but part of the food matter contained in it is preserved in the form of fatty tissue, and offers an energy reserve for the time of downstream migration when the fry uses a great deal of energy and can find itself in a low food area of the water body.

In chum larvae, as in the pink,special large sodium-excreting Keis-Wilmer cells soon appear at the base of the gill filaments which protect the larvae from an excess of sodium upon entering sea water. In these same fish,whose young live in the river for an extended time, these cells do not develop for a long time (Black, 1951, 1957). The larvae soon begin to show a preference for salt water. They withstand frequent transfer from fresh water to salt and back again. This indicates the simultaneous existence of mechanisms of hypotonic and hypertonic osmoregulation (Natochin and Bocharov, 1962; Bocharov, 1963). This quality allows juveniles to remain for a long time near a river mouth or near the sea shore, where the degree of salinity is variable.

The young of chum from small rivers migrate en masse to the sea during the stage of mixed feeding, still carrying the remnant of the yolk sac. On the 25th of May 1954 in the river Pugachevka, the smallest downstream migrants caught had a length of 35 mm and a weight of 276 mg; their mean length was 38 mm, and their mean weight, 335 mg. Notwithstanding the continuous cloudiness, rain and turbid water, the first downstream migrants were caught at 8:40 p.m., and the mass migration started only when it was fully dark. From the other Sakhalin rivers, the chum migrate en masse at a length of 35 - 45 mm and weight of 333 to 600 mg; from time to time, specimens are found up to 56 mm in length and weighing up to 1400 mg (Esaulov and Fedotova, 1963). However, V.K. Soldatov (1912) noted that the chum in rivers can remain there for up to 3-4 months and reach significant proportions. As a rule, catadromous migration takes place intensively during the night, with the maximum occurring 2-3 hours after sunset. When there is bright moonlight, the migration rate lessens. Migration of chum is also observed during the day. 72
This happens usually in large rivers, especially where the water is muddy. Sometimes, the day migration can be larger than at night. The migration is active in character (Neave, 1955; Roppel, 1956; Vasilenko-Lakina, 1962; McDonald, 1960; Landyshevskaya, 1967).

While swimming down large rivers, the chum stay in good feeding areas, going into creeks and lakes situated along the route of migration; during flooding they settle in flooded areas. They feed actively and grow rapidly. The[long]sojourn in rivers and increasing size are considered to be a factor favourable to the maximum survival of the chum (Levanidov, 1964a, c; Sakano, 1964; Kanid'ev, 1966).

With the early migration of chum, as with pink, progress in the ratio of body proportions , in weight and intensive silvering are not noted, as before the migration into the sea of other salmons. Some authors consider the morphological, physiological and ethological differences in downstream migrants of chum and pink to be evidence of an absence in them of the so-called "smolt" stage and the process of smoltification (Hoar, 1951, 1958; Houston, 1957). When guanine starts to settle in the integument of the chum larvae, signs of the activation of the thyroid gland begin to show. On this basis, the above state analogizes with the process of smoltification (Zueva, 1965). Meanwhile, in spring, the activity of the thyroid gland in chum downstream migrants is low. In summer,when the fish are compelled to stay in fresh water, signs of the activation of this organ begin to show (Baggerman, 1960; Eales, 1963).

The Fry Period of Development.

By the start of the fry stage of development, the temporary larval organs and the preanal fin fold disappear, and some organs and functions characteristic of the adult fish appear. The scales are established. The fry change in their bodily proportions, the shape of the fins, and colour. The chum may spend this period both in the rivers and in the sea near the river mouth.

First Fry Stage. N.N. Disler allotted two stages in the fry period of the development of chum. According to his data, the larvae of chum turn into fry at a length of 38 - 40 mm. During the course of the first stage, the fry reach a length of 50 - 55 mm. At a mean temperature of 6.5°, the stage lasts about a month. Under varying conditions, initial establishment of the scales becomes noticeable at a length of 27 to 40 mm (Sano, 1959).

At the start of the stage, the gill rakers number 18 - 20, which gradually increases; the gill filaments lengthen and become branched, abundantly supplied with blood (fig. 12, D). In fry from the river Naiba, when the body lengthened from 36 to 48 mm, the length of the 75
trunk in comparison with the length of the body increased from 65.4 to 66.6%; the depth of the body, from 16.7 to 17.1%; the preanal distance (from the end of the snout to the insertion of the anal fin), from 62.6 to 63.2%; the distance from the pectoral to the pelvic fins, from 26.8 to 27.4%; from the pelvic fins to the anal fin, from 13.4 to 14.7%, whereas the predorsal distance decreased from 46.3 to 44.7%. The size of the fins increased; the length of the pectoral fins increased from 13.9 to 14.3% of the length of the body, the height of the dorsal fin, from 11.3 to 11.7%. The blades of the caudal fin increased insize, while the relative length of its central rays decreased. The snout lengthened from 2.9 to 4.1%. The relative diameter of the eyes decreased by approximately 0.5%. The branching of the segmented lepidotrichia continued in the fins. The exterior changes which took place corresponded to the more mobile made of life of the fry. Clark's condition factor rose from 0.52 to 0.61.

Shiraishi and Uchida (1957), using a method of graphic comparison of the changes in the proportions of the body and individual organs of chum, showed that the turning point in the changes in the relative size of the head, and eyes and of the dorsal, anal and pectoral fins is at the end of the absorption of the yolk, that is, during conversion from the larval to the fry period. The condition of the large fry improves, which is considered to be a preparation for downstream migration (Kizevetter, 1948; Levanidov and Levanidova, 1957).

On the sides of the body of the fry, above and below the large transverse dark spots, small additional spots appear, approximately equal in diameter to the pupils. In colour and exterior appearance, the fry of chum (fig. 14, D) are similar to the fry of sockeye, and it is difficult to tell them apart on the basis of existing keys (Lagunov, 1939. A number of features that we have found simplify the diagnostics. For example, there are melanophores on the anal fin of chum, where on the sockeye, they are absent; in the chum gills, the central filaments are noticeably longer than the rakers, and in sockeye, on the contrary, the gill rakers are longer than the filaments. Also, the scales of these species differ.

According to Disler's data (1957, 1960), at the start of the fry period, the neuromasts of the trunk and caudum remain open. Accessory sensory protuberances budding off from the main row appear on the trunk. The supraorbital, infraorbital and temporal canals of the lateral line organs start to form, and also the canals on the preopercle and the lower jaw. The fry become more mobile, and very sensitive to agitation of the water. Their eyes catch the movement of objects, not only in the water, but also above it. Fry, like larvae, stay in groups.

The feeding of fry has been studied in different bodies of water (Konstantinov, 1951; Synkova, 1951; Levanidov, 1954a, 1955, 1957; 1964a 1969; Levanodov and Levanidova, 1957; Bolovik, 1964; Frolenko 1965; Nikolaeva, 1968, 1972; Shershnev, 1971). The spectrum of feeding is quite wide. The basic and preferred food items are larvae and pupae of chironomids, chiefly from the sub-families Ortocladiinae and Diamesinae. 74
They also use a great deal of nymphs of ephemera of the genera Ephemerella, Siphlonurus and stonefly, larvae, pupae and adult individuals of midge of the genus Simulium, some mosquitoes, and also Oligochaeta. In individual bodies of water chum feed on many small water sowbugs, fly larvae and other organisms. Such small plankton as cyclopida and Daphnia are rarely found in the stomach, and are only used as food incidentally. The feeding spectrum of larger fry broadens to include terrestrial invertebrates. In fry in the river Naiba, 30 different food components have been discerned. At the same time, identification down to the species level could by no means in all cases be made from preserved remains. Large fry feed less frequently than small ones (morning and early evening maximums have been noted), but more intensively.

It has been established that chironomid larvae are not only the preferred, but the most efficient food; their food value coefficient is 2.6, whereas that of the mayfly is 3.6. With change in food, growth slows down, and the consumption of the new food per unit of weight gain increases sharply (Nikolaeva, 1972). According to the data of V.Ya Levanidov (1954a, 1969), the daily ration of food at a water temperature of 7 - 10° is 10 - 12% of the body weight of the fry, and 17 - 20% at a temperature of 12 - 16°. The daily weight increase in the first case is 3.5 - 3.9% of body weight. The breathing rate changes accordingly. If at a temperature of 10° for every gram of the live weight of the fry 0.325 mg of oxygen are used per hour, at 20° this will increase to 0.636. Fry prefer a temperature of $8 - 14^{\circ}$. In the river Amur, they feed actively at temperatures reaching $25 - 26^{\circ}$ and under experimental conditions, large individuals endured a temperature of $28 - 30^{\circ}$. V.Ya. Levanidov (1955) encountered chum fry in bodies of water containing from 5-6 to 12 - 14 mg/l oxygen. According to his data, the rate of feeding and degree of assimilation and growth do not change with fluctuation of oxygen content from 5 to 11 mg/l. At 10°, asphyxiation takes place when the oxygen content decreases to 1.5 mg/l. For chum fry, the threshold oxygen content at 17° is 1.99mg/l, and at 25° increases to 3.36 mg/l (Privol'nev, 1963).

Second Fry Stage. At a length of 5 - 5.5 cm, the fry leave the shallow water and enter deeper parts of rivers, limnocrenes and lakes, while those that have migrated from rivers earlier, live near the mouths of rivers, estuaries and areas of the sea near the shore. In the area of the Teplovskii hatchery the fry do not remain past a length of 6 - 7 cm, while in the Amur, they are found measuring up to 9 cm (Levanidov, 1964a). Since chum can spend the first and a significant part of the second fry stage of development in the rivers, it can be raised in hatcheries for quite an extended time.

The overall trend in the changes in exterior of the fry was described above. By the time the fry have reached a length of 6 - 7 cm, the process of differentiation of fin rays is complete. Fry remain- 75
ing in fresh water acquire a certain bulk (fig. 15).

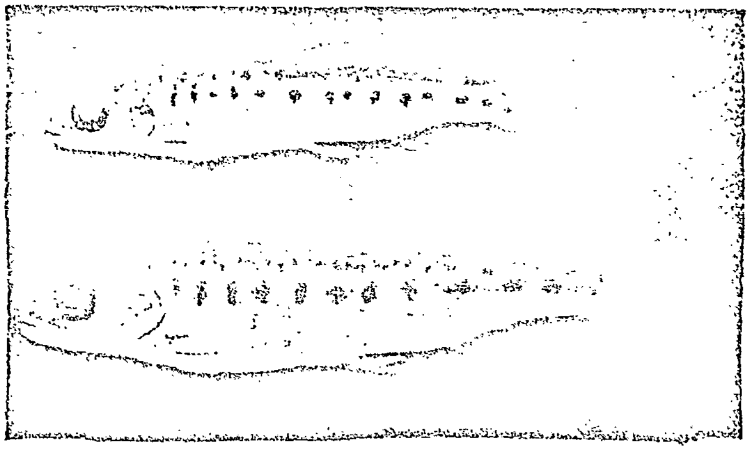


Fig. 15. Chum fry at lengths of 56 and 69 mm, weight 1.5 and 3.5 g respectively.

The number of their pyloric caeca reaches a practically definitive amount. At this size, the formation of canals of lateral line organs is complete on the head, trunk and caudum (Disler, 1957, 1960).

A fry entering the sea at the start of the migrating season remains for 3 - 4 months close to the shores. The shallow waters warm up early, and at the end of April--beginning of May, many edible zooplankton develop here. Fry in the shallows feed intensively and grow quickly. In spring, various small forms of Harpacticoida serve as basic food. In June and July, the role of large forms of Gammaridea and Musidacea gradually increases. In the food of larger fry, which go out into deeper areas, adult insects, large Mysidae, decapods and fish larvae are found ever more rarely (Frolenko, 1969; Shershnev, 1971).

Migration to the sea in various stages of development and a period of growth near the shore where the salinity is changeable shows the continuing existence of the chum's mechanism of hypertonic and hypotonic osmoregulation. The disappearance of the fry from areas near the shore after reaching a length of 10 - 12 cm is probably connected with the reorientation of this mechanism and adaption to life in the conditions of oceanic salinity.

Characteristic Features of the Reproduction and Development of Chum. In common with other species of the genus Oncorhynchus, chum is a monocyclic fish. It matures at an age of 2 to 8 years. Usually the spawning populations are dominated by two age groups: most commonly they are 3 and 4-year-olds, or 4- and 5-year-olds. The species is represented only by the migratory form and is the second most abundant (after the pink) one, its distribution being wider than that of other members of the genus Oncorhynchus. 76

The chum occupies spawning grounds of two drastically different types. Some of them are situated in the rivers and are washed by the subriver bed water with some addition of the upper ground waters. Under these conditions, the thermal and hydrochemical regimes of the redds closely depend on the main channel water regime of the river. This explains why the spawning ceases with the onset of the autumn cooling, and why there is a high mortality of the offspring during severe winters. Spawning grounds of the other type are scattered in localities of various types at the points of emergence of ground waters. These waters, poorer in oxygen, contain a large quantity of free carbonic acid and their reaction is weakly acid. Their regime is more stable, and has no direct relationship with the fluctuations in the temperature of air and river water. Consequently, spawning on grounds of this type can take place during different seasons, including late autumn and winter. Spawning grounds of the first type are typical for the summer chum and those of the second for the autumn chum in the Amur and the rivers of Primore [Soviet Maritime Territory] Sakhalin and Hokkaido. The summer and autumn races, reproducing within the borders of the ancient basin of Paleoamur, differ from each other in morphology, karyotypes, size, rate of growth, fecundity and life span of the young stages in the rivers; they prefer different regions, waters and localities. These racial differences are stable from the hereditary point of view.

It should be stressed that chum reproducing in the same season, produce qualitatively distinctive forms in different regions. For example, the summer-spawning Kamchatkan chum (probably, within the borders of the Paleoyukon) selects spawning grounds provided with ground waters and, consequently resembles in its developmental ecology not the summer, but the autumn chum from the Amur. These forms also feed and grow in different regions and differ morphologically and biologically, the differences between them reaching the subspecific rank.

The subspecies, in their turn, form populations associated with large rivers or rivers of a particular region, the populations consisting of generatively isolated local stocks (subpopulations). Comparison of the biology of reproduction draws attention to differences associated with the length of the anadromic migrations. The distance of the spawning ground from the sea is reflected in the size, fatness, stage of maturity of the spawners at the time of their entry into the rivers, length of life of the young fish in fresh water and in other features. Chum entering the same spawning rivers, for example, the rivers of Sakhalin, come from different feeding grounds and differ qualitatively.

The males of the chum produce sperm for a long time and extrude it in large portions with a high concentration of spermatozoids. The absolute fecundity is relatively low, the eggs are very large: their weight reaches 300 mg, exceeding that of the eggs of the pink by 1.5 times and that of the sockeye by more than twice. The eggs contain a large quantity of astaxanthin and are orange, deeper shades of this color occurring in forms reproducing at the point of emergence of ground waters.

There are some noteworthy characteristics of morphogenesis. In contrast with the Atlantic salmon and the sockeye, in the chum the fourth cleavage line runs in the equatorial plane and forms two layers of cells. The tendency to distribution of the blastomeres in two layers is sometimes noticeable at the eight blastomere stage. As the result of large amounts of yolk, the process of epiboly is prolonged to the formation of 56 - 58 segments. Consequently, the eggs retain for a long time a high sensitivity to mechanical impact. When oxygen content is low, blood circulation may begin at the stage of 52 - 53 segments, though it is usually somewhat later. Embryonic and larval organs of respiration are more strongly developed in forms which spawn at the points of emergence of ground waters. The species has become adapted to development under the conditions of low saturation of water with oxygen. The melanophores appear in the body integument at the beginning of the 10th, and lipophores at the end of the 10th, stage of development. At a temperature of about 10°, incubation takes 50 - 60 days (up to 600 degree-days and more), and at lower temperatures it extends up to 130 days, though the number of degree-days decreases (to about 420). Hatching is typically simultaneous.

As in other fishes of this ecological group, the eggs of the chum withstand considerable pressure, but are very sensitive to tactile stimuli, vibration and rotation; they are adapted to development under conditions of complete peace and darkness. Hatched embryos acquire a positive reaction to current and contact with foreign objects, and photophobia. Positive tactile reaction and photophobia disappear in larvae before their emergence from the redds. The period of endogenous feeding of the embryos and the stage of mixed feeding of the larvae of this species are particularly prolonged. The chum reaches in its redds a high level of differentiation and a large size--up to 30 mm and more.

The larvae feed on various relatively large benthic and other organisms, not on small zooplankton like larvae of the majority of teleosts. The larvae and fry of the chum lead a gregarious life. They have streamlined bodies, relatively short paired and low unpaired fins. Their spotted colouration resembles that of the young sockeye. The young of chum differ sharply from the latter by a large number of melanophores in the anal fin, as well as by short gill rakers
(in comparison with gill filaments), their smaller number and other 78
features.

The freshwater part of the life cycle of juvenile chum is shorter than that of other salmons, with the exception of pink. The catadromous migration occurs mainly in the spring. The chum leave the rivers at the end of the stage of mixed feeding, and during the first and, less frequently, second stage of the fry period. The young of the summer spawning form remain in the rivers somewhat longer than those of the autumn spawning form.

In the process of evolution, the chum has become adapted to development in redds supplied (mainly) by subchannel, as well as by ground, waters, both kinds differing significantly in their thermal properties, gaseous regime and other characteristics. The reproductive seasons of similar forms, distinguished from one another by the ecology of their ontogeny as well as by their morpho-functional characteristics, differ from one region to another. This is related to the hydrological and hydrobiological characteristics of the watersheds and to their geological history, as well as to the fact that the fish feed in different regions of the sea. Broad morpho-biological diversity reflects the adaptive plasticity of the species. The chum was able to colonize a huge area, including different climatic zones,

to reproduce in habitats of different types, beginning in the summer and ending in deep winter, to utilize for feeding extensive spaces of the seas and oceans and thus to maintain high abundance. The chum is more abundant in those regions which are inhabited by ecologically distinct intraspecific forms.

THE SOCKEYE--ONCORHYNCHUS NERKA (WALBAUM). 78

At the end of the second and the beginning of the third decade of this century, the annual catch of the sockeye in the USSR was on the average 250,000 centners (25,000 metric tons, Translator's note). In view of its great value for the canning industry, the value of the sockeye was about 25% of that of the entire catch of Kamchatkan salmon. Between 1931 and 1942 the average catch of sockeye was 7.6 million fish annually, whereas between 1955 and 1966 it was only 1.4 million. The catches of this species are smaller than those of the chum and pink, though in the eastern part of its range, only smaller than those of the pink (Kuznetsov, 1937; Krogius and Krokhin, 1956; Levanidov et al., 1970).

Distribution, Life in the Sea and Age at Maturity. The distribution range of the sockeye is markedly smaller than those of the chum and pink. The species is most abundant off the shores of Alaska and in the Kamchatkan fisheries district: it is absent from the Sea of Japan. The most important wintering and feeding grounds of our stocks are situated to the south of the western islands of the Aleutian ridge . Western Kamchatkan stocks overwinter more closely to the northern Kurile Islands and migrate to spawn through gaps between them. The fish migrating into the rivers in the spring remains in the sea farther north than that which moves to spawn 79
in the summer. The beginning of the migration of the spring sockeye is noted when the surface water reaches a temperature of of 2 - 4°, that of summer sockeye is noted at a higher temperature (Berg, 1948; Birman, 1967).

Maturation occurs most commonly at the age of 4 - 5 years, less often at 3 or 6 - 7, in rare instances at 8. The period of feeding at sea takes usually 2 - 3 years; for a small proportion of individuals, 1 or 4 years.

The young begin their migration from springs several weeks after their emergence from the redds; they live in the lakes from 1 to 3 or even 4 years. A certain number of individuals does not migrate into the sea, and matures in the lakes as small residual forms. The kokanee sockeye is widely distributed.

Intraspecific differentiation. Suvorov (1948) distinguished six races in the stocks of Asian sockeye. Berg (1948) recognized, in addition to the typical Kamchatkan sockeye, also O.nerka infraspecies asabatsch Berg, which he considered a form parallel to the autumn chum. "Azabatch" is distinguished by larger size, fecundity and late spawning. As one of the autumn races, Berg recognized "ovetch", O.nerka infraspecies ovetsch Taliev. Berg also spoke of "arabach", a race known to the natives of Kamchatka, distinguished from the typical nerka by smaller size, small eggs, red flesh during spawning and paler nuptial livery. According to Ostroumov (1965), O.nerka infraspecies arabatsch occupies in the basin of the river Kamchatka a separate spawning region, the southern part of the Central Kamchatkan Depression. This salmon reproduces from the end of July to the first half of September. "Arabach" is distinguished by some morphological features, by low fecundity (average 2750 eggs) and by shorter fresh-water cycle.

The kokanee sockeye exists in both continents. The form from the Japanese lakes is known as O.nerka adonis, Jordan and McGregor. In our territory, kokanee lives in Lake Kronotskoe in Kamchatka and in Lake Sorochnoe on the island of Iturup. The landlocked sockeye of the North American waters, where it is distributed much more broadly, is known as kokanee, or Kennerley's sockeye, O.nerka kennerlyi (Suckley). The land-locked form grows slowly, and matures at an age of 2 - 7 years, when it has a length of 23 - 35 cm and a weight of 200 - 300 g, less often 750g. It has considerably fewer pyloric caeca than the migratory form, shorter caudal peduncle, relatively shorter length of snout and a higher head. There are some differences also in other morphological features. The nuptial livery is less pronounced. Fecundity is low (Krokhin and Krogius, 1936; Ricker, 1940; Berg, 1948; Vernon, 1957; Tokui, 1959, 1961; Nelson, 1968; Kurenkov, 1972). In Lake Sorochnoe the kokanee feeds on large gammarids and smelt, it grows more rapidly, and matures mainly at the age of 3+ and 4+, at a mean length of 40cm and weight of more than 900g. Some individuals grow to 47 cm and weigh over 1400 g (Ivankov, 1968).

The age composition of the spawning populations of anadromous sockeye is very complicated. However, each year they are dominated by some 2 or 3 age groups. Most of the stock migrate into the river Kamchatka during their fifth year, having lived in the fresh water 1 year; a con- 80
siderable part of the young live in the lakes of this basin for 2 years and return to spawn as five- and six-year-olds. In the spawning population of the river Ozernaya one can distinguish 7 age groups, dominant among which are five- and six-year-olds, fish that have spent 2 - 3 years in Lake Kurilskoe. In Lake Dal'nee stock of the basin of the river Paratunka, one can observe up to 15 age groups, among which predominate four- and five-year-olds* that have spent 1 or 2 years in the lake.

Significant differences exist in size, weight and fecundity. The sockeye of the river Kamchatka reaches a length of 80 cm and weight of over 4 kg; average length of the females is 58 cm, weight 2.5 kg. In the river Ozernaya in 1940 - 1959 the average size of 5-year-old females* was 50.6 - 53.2, males 51.8 - 53.2 cm; average weight of females varied

*According to W.E. Ricker, dvukhletka, trekhletka, chetyrekhletka, pyatletka, shestiletka,etc., here translated two-,three-,four-,five-year-old, refer to fish 1+,2+,3+,4+, i.e. in their 2nd,3rd,4th,5th year of life. Tr.

from 1.66 to 2.35 kg, males from 1.70 to 2.56 kg. At the age 6_2+* during individual years average length of females reached 63.8, males 66.1 cm, while weight was 3.88 and 3.91 respectively. Five-year-old females from Lake Dal'nee, at an average length of 53.9 cm, weigh 1.87 kg, while males have and average length of 57.6 cm and weight of 2.28 kg. In the river Kamchatka fluctuations of absolute fecundity were observed from 1570 to 6448 eggs, average about 3760 eggs. Annual averages of fecundity of females belonging to the modal age groups in the river Ozernaya vary from 2100 to 4100 eggs. In Lake Nachikinski the average fecundity of the spring run sockeye is 2330, that of summer run 3640. The fecundity of the sockeye of Paratunskie lakes is even lower: In Lake Blizhnee it constitutes 2,000 to 2,400 eggs, in Lake Dalnee 2,500 - 2,600, in kokanee sockeye about 500; at the same time the average fecundity of the sockeye reproducing in the springs in the basin of Paratunka is near to 5,000 eggs (Kuznetsov, 1928; Krogius and Krokhin, 1948, 1956; Egorova et al, 1961). In the Karymaysh spring during individual years, the mean fecundity varied from 4,500 to 5,165 eggs (Semko, 1954). Average fecundity of the sockeye of the Canadian Lake Cultus in 1932-1938 varied within the limits 3,796 ± 42 - 4,310 ± 69 eggs (Foerster and Pritchard, 1941). The fecundity of the kokanee is about 450 - 480 eggs (Rounsefell, 1957). The fecundity of the fish from the river Icha proved to be particularly high: the five- and six-year-olds that had spent one year in fresh water contained on the average 5,555 and 6,387 eggs repectively (Grachev, 1968).

*First figure indicates the total number of years, second (lower) the number of years spent in fresh water, plus the presence of growth on the scale after the formation of the last annual ring.

A wide variation in the absolute fecundity points indirectly to the variation in the conditions of husbandry.

The sockeye form separate stocks, groupings confined to individual rivers, lakes, their tributaries and individual spawning grounds. In the basin of the small river Paratunka, for example, morphological dif- 31
ferences exist between the sockeye of the Lake Blizhnee, Lake Dal'nee and those reproducing in the spring-fed streams. Lake Dal'nee is visited by ecologically variable fish of spring and summer runs. The former enters the lake and spawns earlier, at greater depth (Krogius, 1949, 1954; Krogius and Krokhin, 1956; Krogius, Krokhin and Menshutkin, 1969). Several local groupings can be observed also in other basins (Thomsen, 1945; Berg, 1948; Schaefer, 1951; Semko, 1954; Hartman and Raleigh, 1964; Mathisen, 1966). Groups distinguishable morphologically and biologically and with separate localities of reproduction and feeding are known also in landlocked sockeye (Vernon, 1957; Kurenkov, 1972). The anadromous sockeye originating in different basins also show some differences in their feeding areas, although their stocks also mix with one another in the sea (Birman, 1958, 1967; Konovalov, 1966, 1971). Separate identities of groups which occupy small parts spawning sections have been noted recently (Konovalov, 1972). Fine differentiation and complicated composition of population are particularly characteristic of this species. The fish of reproductively isolated groups can be distinguished by its times of migration and spawning; there are differences in the size of smolts, quality of food of the young, rate of growth, number of vertebrae, bodily proportions, scale structure, fecundity, fat and protein content at the beginning of migration, in coloration of mature individuals and other features (Krogius and Krokhin, 1956; Krogius, 1958, 1970; Ricker, 1956; Foerster, 1968; Konovalov, 1972).

Reproductive Regions.

The sockeye moves north for reproduction to the river Anadyr, migrates in large numbers into the rivers of the Olyutorsk Region and Kamchatka, along the continental shores in a southerly direction, reaches the river Okhota, enters the rivers of the Commodore and Kurile Islands and the northern part of Hokkaido. It does not frequent the rivers of the Sakhalin, the basin of the Amur and Primorye. The most abundant populations in our country live in the basins of the river Kamchatka and Ozernaya. The spawning region of the North American stocks extends from the Bering Strait to the southern California river Klamath (Berg, 1948; Nikita, 1962, Foerster, 1968).

Anadromous Migration, Maturation of Spawners and Times of Spawning. Migration into the rivers begins soon after they are opened. At the mouth of the river Kamchatka the run is observed from the end of May and continues for more than three months; the main run of the early-spawning form takes place in June, the run of the summer sockeye "azabatch" continues up to the end of August. Sockeye move up the river Ozernaya from the middle of July to the middle and in some years to the end of September. In Lake Dal'nee, the spring sockeye runs from May to the end of June, and the summer one from the middle of July to the end of August (Kuznetsov, 1928; Krogius and Krokhin, 1956; Semko, 1954).

The periods of reproduction of the sockeye, like those of its spawning migration, are very prolonged. In the lower reaches of the river Kamchatka, the spawning extends from the middle of July to the end of October. In the river Bol'shaya the spring sockeye spawns during July 82
and the first days of August, while the summer sockeye reproduces up to the beginning of October. In the basin of the river Ozernaya, spawning

continues from the end of July to the end of January and even into February. In the spring-fed streams of the middle and upper reaches of the river Paratunka spawning has been observed from 10 - 15 of August to the end of September. In Lake Blizhnee it takes place from the middle of August to the 2nd third of November, being most intensive from the 20's of August to the beginning of October. In 1961 the run was poor and the beginning of spawning was later by about 10 days. Lake Dal'nee, situated in the basin of the same river, is frequented by two "seasonal" stocks. The spawning grounds of the sockeye of the spring run are situated in deep water and are not accessible to direct observation. Judging from indirect data (capture of running individuals, finds of eggs in the stomachs of predatory fishes, occurrence of carcasses), reproduction took place from the 20's of July to the end of August. Spawning of the sockeye of the summer run takes place from 25 - 28th of August to the end of October; September is the month of massive oviposition. Some males of the residual (dwarf) form mature by the end of the 1st third of September and take part in the spawning of migratory form of the salmon. However, the first running residual females appeared not earlier than 5 - 10th of October; they spawn to the second half of November.

The spawning grounds are situated from the lower reaches to the high mountain sections of the rivers. In the basin of the river Kamchatka, the spawning lake Azabache is only 35 km from Ust-Kamchatsk, Lake Ushki more than 200 km, while some fish ascend to the upper reaches of the river. Along the river Yukon this species travels a distance of more than 3,000 km. By the time 1,100km have been transversed, the percentage of fat in males drops from 9.34 to 3.23 and in females from 10.55 to 2.7 (Idler and Bitners, 1958). Covering an average distance of 56 km per day, the sockeye utilises each day about 15 kilocalories (Atkinson, 1963). An excessive use of energy to overcome obstacles to migration may lower the effectiveness of spawning.

The sockeye enters the rivers while its gonads are poorly developed and reaches the spawning lakes as a grilse at III-IV stage of maturity. In the rivers the fish matures during the time it spends in the pools where the current velocity is low; in the lakes it spends 1 - 2, sometimes 3 - 4 months in a pelagic zone (Krogius, 1954; Ievleva, 1964, Foerster, 1968). The spawning grounds are reached by the salmon in nuptial livery with running or almost ripe sex products (the latter applies to a small proportion of females). Silvery individuals do not occur there. This points to the ecological character of the spawning grounds, unsuitable for the life of the immature salmon.

The onset of maturation is manifest in the dulling of the silvery shine on the scales. The fish becomes darker. Later on, in the integument appears red pigment, imparting at first a brownish, then increasingly intensive red colour. With maturation, the fish becomes intensively red, with a raspberry-like tinge. The head of mature individuals has a green colour with a yellowish tinge, but the opercula assume red hues of 33
differing intensity. The dorsal, adipose and anal fins, and the base of the caudal fin become red, less so the ventral fins; the pectoral fins and the tip of the caudal fin become olive green. The tips of the first rays of the pectoral, ventral and anal fins develop whitish borders. Between the rays of the dorsal and caudal fins there appear elongated dark spots. The males are coloured more strongly than the females but the differences are not great (good colour illustrations of the silver and mature sockeye are shown in the atlas "Commercial fishes of the USSR"

(1949) and in the monograph of Foerster (1968). The changes in colouration are accompanied by thickening of skin. The scales sink into it, and their outer regions are resorbed. The bodies of the maturing males become thicker. On their dorsum, as in the pink salmon, a large keel grows. The jaws lengthen, the tip of the upper jaw curves downwards. The teeth grow to a large size (fig. 16). The form of the body, the skeleton of the head and the teeth of the females undergo less profound changes.

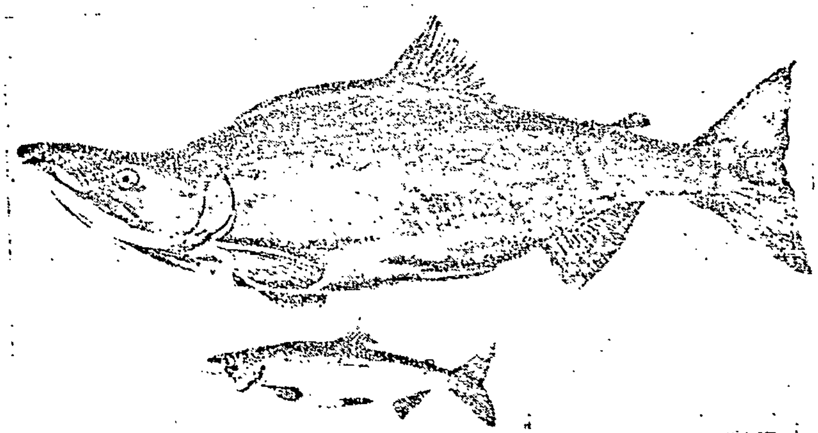


Fig. 16. Running anadromous (upper) and residual males of sockeye.

In some adult individuals, the belly retains its pale colour and traces of the transverse dark spots remain on the body. When the changes in coloration are slight, the shape of the body and of the skeletal elements are also less modified. This is characteristic to fishes of smaller sizes and those which reproduce on well oxygenated spawning grounds of the rivers and fast-running streams (Smirnov, 1956b).

Judging from specimens kindly provided by E.M. Krokhin, the landlocked sockeye of Lake Kronotskoe in Kamchatka changes less than the anadromous one during the period of maturation. Its colour is paler, the keel on the dorsum of the male is barely noticeable, the teeth are only slightly enlarged. The prespawning changes of the landlocked 84 sockeye in other waters are also not very extensive (Tokui, 1959, 1961).

Spawning Grounds, Spawning, Conditions of Development. Information on the spawning grounds and spawning of sockeye are contained in the work of many authors. Of particular interest to us is the work of Krokhin (1960), which reviews data on the spawning grounds of the Kamchatkan sockeye, including those localities where we have worked.

The spawning grounds are situated in shallow parts of the rivers, spring-fed streams, limnocrenes and littoral parts of lakes. Redds are built from the very margin of the water (Fig. 17), most commonly at the depth from 30 to 70 cm and up to 1.5 to 2 m. Less commonly one finds spawning at a depth of 4 - 6 m and much deeper (Ricker, 1966; Ostroumov, 1970b).

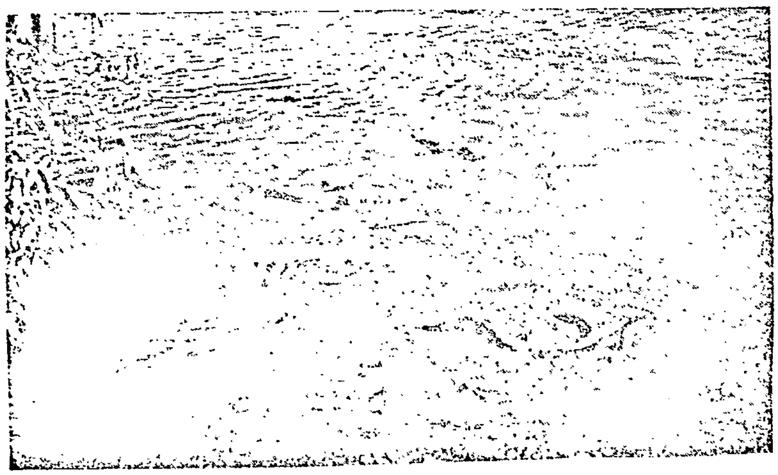


Fig. 17. Mass spawning of sockeye in Lake Blizhnee [illegible].

In the spawning grounds in the rivers, the velocity of the upper layer as a rule does not exceed 10 - 20 cm/sec; in the lakes it drops to zero. Eggs deposited in the ground are washed by the spring water; the spawning grounds are situated close to the points of their emergence. Localities are selected, where the ground is easily disturbed. The sockeye often spawns in the localities with considerable deposits of sand and silt (Kuznetsov, 1928; Krogius, 1951; Burner, 1951; Semko, 1954; Krokhin, 1960; Foerster, 1968).

The size of the redds dug during oviposition varies, depending on the size of the stones, density of the bottom, current velocity and the size of the fish. The width of the redds varies from 0.9 to 1.7 m (average 1.25), length from 1.5 to 4.5 m (average 2.45 m). The eggs are deposited in individual batches and buried at a depth from 10 - 15 to 30 cm and even to 40 cm. When the ground is easy to move, one ob- 85
serves most commonly 4 - 5 separate groups of eggs (nests), linked in one general redd (Kuznetsov, 1928; Semko, 1954; Mathisen, 1966).

The females play the active part in the construction of the redds. Around each female hover several males. Males play a less important part in clearing the spawning ground. There are some reports on their participation in the construction of the nests (Hartman and Releigh, 1964). The abundance of the males ensures fertilization of the deposited eggs. The proportion of the fertilized egg reaches 98% or a value close to this figure (Kuznetsov, 1928).

According to the observation by various authors, up to 4 - 6 groups of spawners follow one another on the spawning ground during the season. When there is a lot of fish, the females of the later runs may destroy some earlier nests. When the occupation of the spawning grounds is of normal density, they dig the ground away from the existing nests. Kuznetsov (1928) considered this destruction of nests as one of the most serious deficiencies in reproduction of salmon. Describing his observation on sequence of spawners in Lake Ushki, he noted, however: "Usually, when possible, the new fish occupied a space between redds." This, of course, lowers the danger of nest destruction. Under the condition of low stock abundance, the loss of eggs due to the destruction of nests in this manner can hardly be significant. We must also take into account the positive role of the close filling of the spawning grounds and sequential runs of spawners. Massive and extended spawning ensure good frontal cleaning of the ground, which has beneficial influence on the water supply of the nests and development of the eggs.

The investigators stress disposition of the spawning grounds of the sockeye at the points of emergence of the ground waters on the bottoms of the spawning localities. According to Krokhin (1960), spawning grounds are disposed in correspondence with the accumulation of ground waters. Temperature of water washing the spawning grounds is stable, both in daily and annual cycles, and is characteristically low in absolute figures (for the grounds investigated it was in the order of 3 - 5°). At the same time, the water in the lakes, particularly along the banks, undergoes intensive heating during the summer (in shallow spawning grounds of Lake Dal'nee, and Lake Blizhnee we observed heating up to 15 - 16°, while the ground water emerging in the area of the spawning ground was 5 - 7°). Judging from many years of observations in one of the streams near Lake Dal'nee temperature of ground water during the coldest months was only slightly less than 3°, in August and September it is about 4.2°, its maximum is slightly more than 4.5° and the annual average is 3.4°; annual fluctuations of temperature are small, 1.5 - 2°. Permanently low temperature is characteristic of the Karymayski spawning stream. Its surface water is well oxygenated, and the subsoil waters washing the nests are poorly aerated (Semko, 1954).

Comparing the quality of the ground water of the spawning grounds, 86
Krokhin notes their characteristic low oxygen content, increased free carbonic acid and silicic acid and low pH. As the result of studies on a number of habitats in Kamchatka, the following conclusion is made: "The waters on the spawning grounds of sockeye have properties which are contrary to the widespread beliefs that they are rich in oxygen and poor in carbonic acid" (Krokhin, 1960, p.99). Based on the data of the same author, the characteristics of the ground waters of the spawning grounds of the sockeye in Lake Dal'nee Paratunskoe are given below.

Index	Littoral of central part	Littoral of western part
Dissolved oxygen content		
in mg/l average	~4.5	~7.0
fluctuation	1.46-9.41	3.03-11.37
in % average	>50	~55
fluctuation	13.4-75.6	24.9-85.7
Free carbonic acid content		
in mg/l average	~5.5	12.0-13.0
fluctuations	0.83-18.2	6.76-22.0
Carbonic acid bicarbonate content in mg/l		
fluctuations	29.6-44.2	10.6-24.7
pH, fluctuations	7.1-8.2	6.4-6.9

The data of the hydrochemical studies suggest that even in a small spawning aquatory, individual spawning grounds can be supplied with water of distinctly different properties. This is due to the lack of uniformity of the geological structure of the shores of the spawning habitat.

Effectiveness of Reproduction. In the river Kamchatka on the average 18.2% of sockeye eggs do not find their way into the nests during reproduction. 16.2% of the eggs in the nests perish. Out of 75 redds examined, all or almost all eggs died in 9 nests and larvae, in 2 nests (Kuznetsov, 1928). In the spawning grounds of Lake Dal'nee from 20 to 80 (average 50%) of the eggs perish, and in Lake Kurilskoe, 25 - 30%. In only one unfavourable year up to 65% of the eggs did not survive (Krogius and Krokhin, 1956).

The differences in the effectiveness of reproduction are shown also by the following data. The females deposit practically all the eggs, but in some areas 1.5 - 2.8% of the eggs remain in their bodies after spawning (Foerster, 1968). In the Karymayski stream (basin of the river Bol'shaya, Western Kamchatka), when the run of the spawners was good, this figure was 6.6% of their fecundity (while in chum it was 12%). In the same waters, 36.5% of the eggs were lost during deposition. 87
The quantity of young migrating from the stream, varied from 2.5 to 18.7% of eggs deposited in the nests, constituting an 8 years' average of 12.1% (Semko, 1954). During 21 years of observations, from 1 to 824 (average 263) young per one spawning female migrated from the stream (Levanidov, 1969). In a small Canadian stream Tally in 1949 - 1959 the number of fingerlings constituted from 1.3 to 19.3% of potential fecundity (average 8.4%), in Scully, a 6 years' average was 12.1% (Foerster, 1968).

The young sockeye live in lakes for a prolonged period and many of them perish, mainly by predation. The number of young migrating out of Lake Dal'nee in 1935 - 1962 was between 0.04 and 1.22% of the number of eggs contained in the females (Krogius, Krokhin and Menshutkin, 1969). This figure is slightly higher for the lakes of North America: in Lake Cultus it is 1.13-3.16%, in Lake Babine 0.48-2.0%, in Lake Lakelse 0.4 -

8.5% (Foerster, 1955). In the Karymayskiy stream, the larvae and small fingerlings are preyed upon by the char (Salvelinus) as well as by larger salmon fingerlings, including sockeye. The loss constitutes from 13 - 91% of the nest output (Semko, 1954). Total mortality of the young during their life in the Canadian lakes fluctuates from 10 to 60% (Ricker, 1966). Destruction of predatory fishes and food competitors allows the survival of the young salmon to increase significantly (Foerster and Ricker, 1941, after Foerster, 1968; Krogius and Krokhin, 1956).

The survival of the young in the sea varies, due to the fact that they migrate there at different sizes and ages. The sea survival of the young of various broods, migrating from the Canadian Lake Babine varies from 1.03 to 6.43%, for Lake Chilko this figure is 6.03 - 20.8% (7 years' average 12.73%); the return coefficient for Lake Cultus is 7.16-7.46% (Ricker, 1966). The young migrating from Lake Dal'nee are particularly large and the return of adults varies from 10 to 36%, average being about 20% of the number of the downstream migrants. A relative stability of this figure made it possible to use the count of those migrants for prognostication of the quantity of the returning spawners and of the possible catch (Krogius, 1949, 1951; Krogius and Krokhin, 1956).

DEVELOPMENT OF MIGRATORY SOCKEYE

Observations were carried out in the basin of the river Paratunka, lakes Dal'nee and Blizhnee, River Dal'naya, stream Tundrovoy and other spring-fed streams.

Reproductive Products. By holding males in the pounds of the counting fence on the river Dal'nee we were able to obtain from one of them sperm 8 times, in all, 41.8 mg; samples were collected over two days. In various specimens and at various times the volume of ejaculate varied from 2.3 to 8.5 ml. From 6.36 to 15.41 million spermatozoids (average 10 - 11 million) were counted in 1 mm^3 of ejaculate.

In 1961 on the spawning grounds 11 males 52 - 66 cm long (average 61.2 cm) and weighing 1.7 - 3.15 kg (average 2.46 kg) were taken. Sperm obtained from them was from 3 to 28 ml; from 4.02 to 18.22 million sperma- 38
tozoids, an average 10.27 million being present in $1mm^3$. These samples proved to be copious because the males were killed and their sperm strained after death. Judging from generalized data, in each ejaculate per 1 g of live weight of the male there are slightly more than 47 million spermatozoids. This figure is higher in other species. In the process of spermatogenesis in sockeye, one observes the death of part of the spermatozoids (Weisel, 1943). Perhaps this explains the small quantity of sperm produced by the sockeye.

Sperm diluted in water rapidly loses its fertility. At a temperature of 11°, 10 seconds after dilution, the quantity of fertilised eggs decreased by 24%; 30 seconds after activation, only isolated eggs were fertilized. The spermatozoids retain their fertility in water slightly longer at a temperature of 8.0° (Fig. 18).

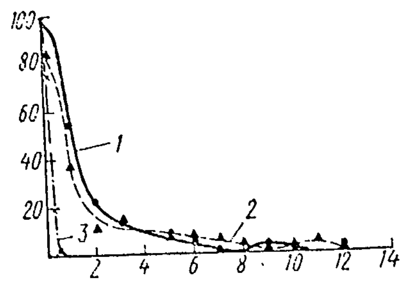


Fig. 18. Retention of fertility by eggs and spermatozoids of sockeye in water.
Vertical: Proportion of fertilized eggs, %.
Horizontal: Time spent by eggs and sperms in water before fertilization, minutes.

1 - changes in proportion of fertilised eggs (in %) kept in water at a temperature of 11°;
2 - same at 8.0°.
3 - changes in proportion of fertilized eggs (in %), fertilized by spermatozoids kept in water for various times at 11°.

In females of the summer run, taken in the spawning grounds of the Paratunskie lakes, the weight of the mature oocytes varied from 84 to 132 mg ($M = 109.2 \pm 2.02$, $\sigma = 13.4$, $n = 44$). The weight of eggs of the females from Tundrovoy stream varied from 85.5 to 121.2 mg (average for 8 females 108.2 mg). The differences in the weight of the eggs were insignificant, in spite of the fact that the fecundity of the sockeye reproducing in the streams is about twice as high. We had at our disposal only one mature female of the spring run, taken in Lake Dal'nee. Its eggs proved to be very small (weight 77.5 mg) and had unusually intense colour.

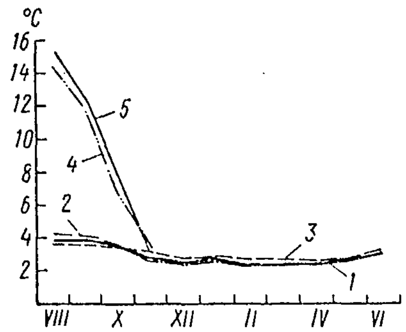
The mature eggs of the sockeye of Lake Dal'nee contained on the average 39.74% dry substances, which included 7.77% fat, 66.54% protein and 3.73% ash.

The eggs have a red-orange colour, with a raspberry tinge. Comparison of the eggs with the atlas of colours (Rabkin, 1956) allows one to determine roughly the variations in their colour as being within the wavelengths 591 - 604 nm. The eggs of sockeye contain more astaxanthin than those of other salmons (Yarzhombek, 1970).

Having been activated by water, a considerable proportion of the eggs loses its fertility, even after one minute. At a temperature of 89
11° after 2 minutes, 75% of the eggs lose their ability to be fertilized, after 6 minutes 92%; after 11 minutes 100%. At 8°, individual eggs retained their fertility in water for 12 minutes (see Fig. 18).

<u>Conditions of Development of Investigated Eggs.</u> A large part of the eggs was kept in the incubator of the Paratunskaya laboratory, equipped with apparatus of Williamson's system. Water temperature at

the beginning of development was about 4.5°, at the end of incubation it dropped to 2.5°; daily fluctuations did not exceed 0.2° (Fig. 19). According to Krokhin (1960), the water of the stream supplying the incubator had a stable gaseous regime. It contained 12.2 - 12.9 mg/l oxygen, and 4.8 - 5.7 mg/l free carbonic acid; its pH was 6.9 - 7.0. A part of the eggs of the same batch were incubated in experimental apparatus, supplied with river water (we shall refer to this apparatus below as river apparatus). At the beginning of incubation, the average daily temperature in it was 15 - 16° with maximum at midday of 18 - 19°. Towards the middle of November, water temperature gradually dropped to 3.5°. Daily fluctuations reached 2.5 - 3.1°. Oxygen saturation of water approached 100%, and sometimes exceeded this figure; the reaction of the environment was close to neutral.



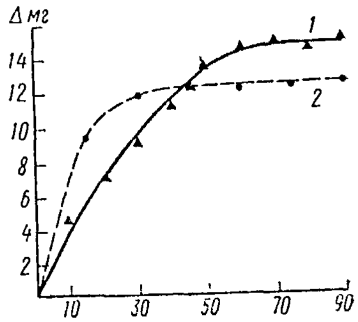


Fig. 19. Horizontal: months. Temperature regime in Paratunskii experimental incubator (1 - in 1956 - 1957; 2 - in 1957 - 1958; 3 - in 1961 - 1962) and in the river apparatus (4 - in 1956; 5 - in 1957).

Fig. 20. Vertical: mg, horizontal: minutes. Water utilization by inseminated eggs of sockeye. 1 - at 4.0 - 5.6°, average weight of egg before swelling 127.4 mg, 2 - at 13.7 - 14.1°, average weight of egg before swelling 96.6 mg.

Embryonal Period of Development.

The description is based mainly on the observations on eggs, fertilized on the 20th and 27th of August 1956 and 28th of August 1957. Additional information is supplied from some observations on the eggs from other batches (series). In particular, examinations were made on fixed samples of eggs of migratory and residual sockeye, collected in 1955--1956 by F.V. Krogius and kindly placed at our disposal.

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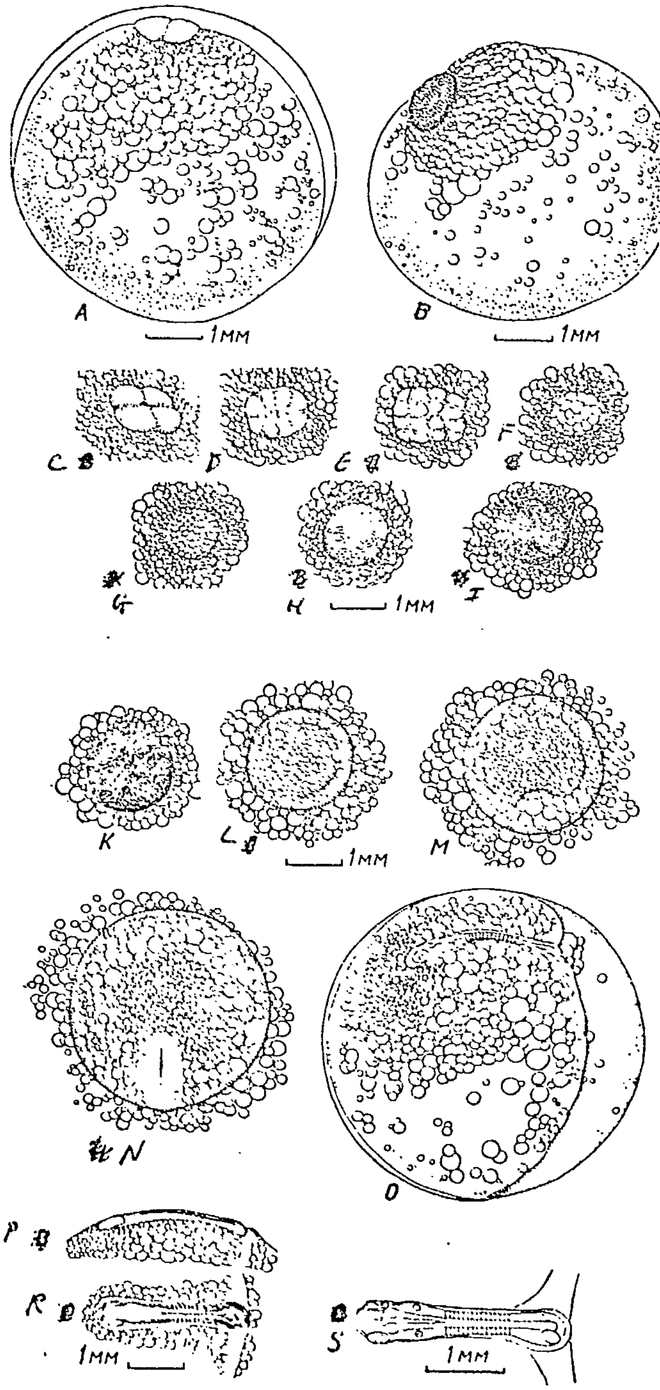


Fig 21.

Fig. 21. Cleavage, blastula, gastrulation and later stages of development of the sockeye. A - live egg, drawn in transmitted light, lateral view. Visible two blastomeres, situated at the points of accumulation of fat droplets. B - fixed egg without membrane, at morula stage, lateral view. C - N - Embryonic discs, removed from fixed eggs with small portions of yolk. C - 4 blastomeres; D - 8 blastomeres; E - 16 blastomeres; F - formation of 32 blastomeres; G - I - Morula of large, medium-sized and small cells; K - blastomere blastula; L - beginning of gastrulation; M - stage of appearance of "marginal knot"; N - stage of appearance of "embryonic streak". P,R - Embryo with 6 segments, upper and size views; S - embryo with 13 somites; O - drawing of live egg in transmitted light at the same stage of development.

Observations on hydration of eggs were conducted at temperatures of 4.0 - 5.6 and 13.7 - 14.1° (Fig. 20). In the former instance the eggs, before being placed in water, weighed 127.4 mg, in the latter, 96.6 mg. At a higher temperature, the utilisation of water proceeded intensively up to 20 min. and swelling was completed 30 - 40 minutes after activation. At a lower temperature the increase in weight of the egg continued for about 60 min. Checks have shown that the eggs of different females as the result of hydration increase their weight by 10.8 - 16.1% (an average based on 12 females - 13.3%), and their volume increases by 12.9 - 17.9% (average 15.3%). The diameter of hydrated eggs, taken from various females, varied from 5.6 to 6.5 mm. The shape of the eggs is not strictly spherical, but rather oviform. The weight of the hydrated eggs fluctuated from 96.4 to 151.2 mg (average 119.3 mg); the weight of their yolk and cytoplasm was 78.6 - 120.2 mg (about 80% of the weight of the eggs) and the weight of the membranes, 4.4 - 6.7 mg (average 5.2 mg); weight of the intramembrane fluid was 13.4 - 25.2 mg (average 18.5 mg). The thickness of the membranes of the hydrated eggs fluctuated from 23 to 42 mk (33.0 ± 0.60). External appearance of the eggs taken from different females varies. In about 20% of the females, the eggs assumed a dull, whitish coating after swelling. According to Ievleva (1967), whose data are quoted also below, mature oocytes are resistant to mechanical influences. The sensitivity increases with the beginning of hydration of the eggs and becomes low after it has been completed.

Stage 1. Formation of the Embryonic Disc. In its development, sockeye passes through basically the same stages as the chum. This allows us to give here a brief description of this process. The description is based mainly on the observations made on eggs developing in Williamson's apparatus, which was supplied with stream water. Used for comparison are data on development of eggs in apparatus provided with river water.

During the initial time after insemination the cytoplasm in the 92
eggs becomes slowly concentrated. Two hours before the beginning of cleavage, the cytoplasmic mass remained flat, had a diameter of 2 mm and an uneven outline, suggesting that the formation of the embryonic disc was not completed. Reports on the diameter of the embryonic disc in sockeye equal to 1.96 - 2.07 mm (Ievleva, 1951), refer to this condition.

Fully formed embryonic discs have an almost regularly round, less often slightly elliptical outline. Its diameter is 1.0 - 1.3 mm; when elliptical, its larger diameter reaches 1.4 mm. The surface of the embryonic disc has few differences from those of other related species, but in the sockeye it is flat and contains less cytoplasm.

Stage 2. Cleavage of the Embryonic Disc. At a temperature of 3.8 - 4.0° the first cleavage furrow in different eggs appeared within 22 - 25 hours after insemination (Fig. 21, A). After 12 hours four blastomeres were formed, after another 10 hours 8 blastomeres. At this stage, the blastodisc becomes somewhat elongated. One and a half days after first cleavage 12, 14 and 16 blastomeres were found distributed in a single layer and more free than in the chum. The furrows of the fifth cleavage pass in the equatorial plane and form the second layer of blastomeres.

At an average temperature of 13.7° the first and subsequent cleavages were observed in 5 hrs 40 minutes, 6 hrs, 8.5 - 9 hrs, 12 - 12.5 hrs, 15 - 15.5 hrs and 18.5 - 19 hrs. hours after insemination. At an age of 22 hrs, from 60 to 90 blastomeres were counted, at the end of the first day a morula of large cells was formed. At low temperatures, the eggs reached this condition at the beginning of the second day (about 13 degree-days). The outlines of the morula are sharp; seen from above it has the shape of a circle with a diameter of 1.0 - 1.2 mm, its height reaches 0.3 - 0.4 mm. The cells of the surface layer are smaller and are more densely packed than the lower cells.

At a temperature of 5.8°, the stage of 28 blastomeres was observed at the age of 72 hrs. The lower threshold temperature for these stages of development is within 4.4 - 5.8°, upper 12.8 - 14.2°. One day later, further development can proceed at a temperature decreased to 1.7° (Combs, 1965). In Ushkov fish farm, the beginning of development was observed at 3.8 - 4°. Probably, the eggs of the Kamchatkan sockeye are more resistant to cold. Sensitivity of eggs during cleavage to mechanical stimuli becomes greater. We give below the timing of the subsequent stages by those embryos that developed in apparatus equipped with river water (Table 4).

Stage 3. Blastula. At a temperature of 4°, the transition to blastomere blastula stage takes place at the beginning or the end of the 6th day, at 13.4°, at the end of the second day (25 - 27 degree-days). At the early blastula stage, the diameter of the blastodisc is 1.3 - 1.4 mm (Fig. 21, K). In the first instance the diameter of the blastula increased to 2 mm within 3 - 4 days, it became more flat, its surface blastomeres had a diameter of 20 - 25 mk. Towards the end of the stage, the blastodisc covered the zone of small fat droplets. 93

Table 4

Rate of Development of Sockeye in Apparatus Supplied with River Water.*

Stage	Average daily temp., C°	Age of Embryo, days	No. of degree-days
1	13.7	0.25	3.5
2	14.3	~2	25--27
3	14.4	~3.5	46--52
4	14.0	6.5--7	79--86
5	13.6	10.5	150
6	13.5	11.5--12	163--169
7	13.6	about 13	about 183
8	12.6	about 18	about 250
9	10.8	28--29	367--378
10	8.3	36--37	460--470
11A	6.5	50	593
Start of mass hatching	6.0	62	674

* Data refers to the time at the end of each stage.

Stage 4. Formation of the Embryonic Layers. In embryos from Williamson's apparatus, the beginning of gastrulation was observed on the 11 - 12th day, in those from the "river" apparatus, at the age of 3 days 7 hours to 3 days 16 hours (46 - 52 degree-days). By that time the diameter of the embryonic disc exceeded 2 mm, and the disc became flat. The cells of the ectoblast were reduced to the size of 20 - 18 mk. The "marginal knot" was formed, the embryonic layers were differentiated (Fig. 21, L,M). On the 17th day, the diameter of the blastodisc reached 3 mm, the "marginal tongue" was formed. At the age of 19 days (74 degree-days) the blastodisc had a diameter of 3.5 - 3.7 mm and covered the entire zone of accumulation of fat droplets. The embryo reached the length of 1.3 - 1.5 mm (Fig. 21, N). Similar conditions in the "river" apparatus were reached by the embryos towards the end of the fifth and the beginning of the sixth day. With the onset of the process of gastrulation the sensitivity of the eggs to mechanical stimuli increased.

Stage 5. Formation of the Head and Trunk of the Embryo. The first segments and the signs of the differentiation of the brain appeared on the 20 - 21st day (78 - 82 degree-days). By that time, the diameter of the embryonic disc reached 4 mm and the length of the embryo rudiment increased to 1.7 - 1.9 mm. This stage was reached by the sockeye slightly earlier than by the chum.

Towards the end of the 23rd day, the embryos reached the size 94
of 2.5 - 2.7 mm, they developed 5 - 6 segments and optic buds (Fig. 21, P, R). At the age 26 days (101 degree-days) the margins of the blastoderm reached the equatorial zone of the egg. The body of the embryos grew to 2.6 - 3.0 mm and they had 10 - 14 somites (Fig. 21, S, O). Definitive parts of the brain were formed, the cerebellum appeared, the encephalomeres and crystalline lens placodes were clearly observable. Pronounced otic capsules were almost 0.3 mm away from the eyes. The cephalic section constituted more than 32% of the total length of the embryo. Posteriorly, Kupfer's vesicle is well visible below the caudal kidney. Rudiments of the heart appeared, as well as those of pharyngeal pockets and the mid-gut. The body of such embryos is flat, pressed into the yolk mass, and barely rises above the surface of the egg.

Month-old embryos were 3.7 - 4.0 mm long and had 15 - 17 segments.

The blastoderm enclosed a large part of the yolk sac. Sensitivity of the eggs to mechanical stimuli was slightly lower.

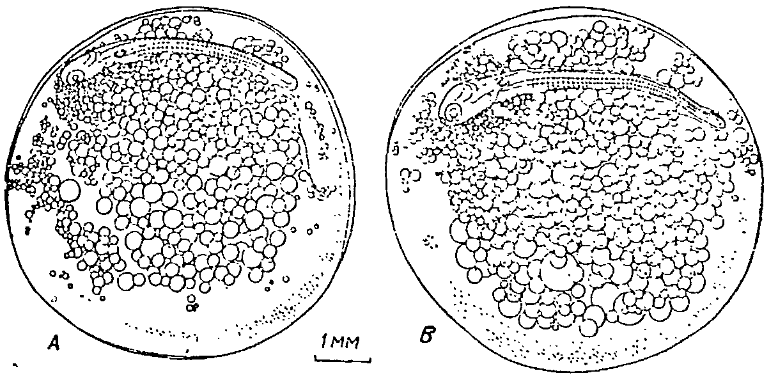


Fig. 22. The Egg of Sockeye. A - before the completion of the process of epiboly, the length of the embryo was 4.6 mm; B - the stage of the beginning of differentiation of the posterior part of the body from the yolk sac; the length of the embryo = 5.6 mm. In vivo drawing through the membrane by transmitted light.

Fig. 22,A shows an egg before the completion of the process of epiboly. The length of the embryo is 4.6 mm, number of segments is 31. The embryos have developed crystalline lenses, clearly noticeable olfactory placodes, the cardiac tube has descended into the cavity developed below the head. The caudal kidney reached the length of 0.4 mm.

Under the conditions of the apparatus being supplied with stream water the process of epiboly is completed at the age of 30 - 33 days (up to 130 degree-days). With the incubation of eggs in the river apparatus, the yolk plug was closed at the age of 8 - 10 days (113 - 120 degree-days). At that time, the majority of embryos had 27 - 30 segments and a length of 95
2.6 - 4.1 mm.

It is interesting that in the same apparatus, embryos of the same age (113.3 degree-days) in small eggs (weight 84 mg) reached a length of

3.2 mm and had from 23 to 30 segments. Epiboly was completed in all individuals with 27 segments, and in some eggs already at 23 segments. In larger eggs (weight 99 mg) embryos had a length of [illegible].7 - 4.1 mm and 26 - 29 segments. In most embryos with 26 and 27 segments, a small yolk plug still remained. At the time of the completion of epiboly, the eggs are particularly sensitive to traumatisation. Resistance is acquired after the disappearance of the traces of the yolk plug.

At a temperature of about 4° pulsation of the cardiac tube and "twitching" of the embryos was observed at an age of [illegible] - 34 days. Such embryos were 4.2 - 4.7 mm long and had from 42 to [illegible] segments. In development in the river apparatus, the heart began pulsating, when embryos had 1 - 2 segments less. Embryonal movements began slightly earlier than in chum. At a temperature of 11.5 - [illegible] the heart contracted 27 - 28 times per minute.

<u>Stage 6. Separation of the Posterior Part of the Trunk from the Surface of the Yolk Sac.</u> At an average temperature of 3.9°, different embryos passed to the new stage at the age of 36 - [illegible] days. They were 5.0 - 5.5 mm long and had 45 - 47 segments (Fig. [illegible]). The head section of the embryos was relatively large. Otic capsules in which otoliths began to develop were separated from the eyes by a distance of about 8 trunk myotomes. Rudiments of opercula and the gill arches were well noticeable. The tail section was noticeably lengthened. The rudiments of the unpaired and preanal fin folds became defined. The posterior end of the gut, anus and urinary bladder were formed. At that time, the digestive tract had the shape of a straight tube, at the end of the first third of which the stomach section was marked by [illegible] dilation and some thickening of the walls. In live embryos, buds of [illegible]nephron were seen,

in which were lodged small crystals, suggesting the beginning of the functioning of that organ. The atrium cordis and ventricle were formed. At the end of the stage at 15° the heart contracted 60 - 62 times per minute. Embryos carried out energetic, sometimes spasmodic movements.

Stage 7. Development of the Subintestinal-Vitteline Circulation System. The beginning of the blood circulation in some embryos developing in Williamson's apparatus was observed at the age of 41 days; within 3 days after that, it became established in the overwhelming majority. Embryos were 5.5 - 6.3 mm long, and had 60 - 63 myotomes. At first the flow of blood was weak. The caudal artery passed into the vein on the second or third caudal myotome. The subintestinal vein passed to the left side of the yolk sac opposite the 23 - 25th trunk myotome. Along the sub- 96
intestinal-vitteline vein, which has the shape of a small arch, the blood moved towards the heart. In the outer side of that vessel, one could see reddish islands of blood corpuscles. In comparison with the chum, this stage is brief. Under incubator conditions, it takes about 3 days (10 - 12 degree-days).

In embryos from the river apparatus, the seventh stage began at the age of 11.5 - 12 days, at 54 - 56 myotomes, i.e. at the earlier stage of morphogenesis, and continued for about half a day.

Stage 8. Laying Down of the Cardinal Veins and Development of the Subintestinal-vitteline and Hepatic-Vitteline Circulation. At the age of 44 - 46 days (174 - 182 degree-days) the embryos were 6.8 - 7.5 mm long and had 70 - 72 segments. The vessels were abundantly filled with erythrocytes.

The frequency of heartbeat and the velocity of blood movement increased. Blood began to penetrate the tail up to 10 segments and more. Posterior cardinal veins were formed. On the yolk sac there appeared sinuous capillaries of the subintestinal-vitelline vein and the first hepatic-vitelline vessels. Otic capsules moved closer to the eyes. Olfactory pits made their appearance. The head began to separate from the surface of the yolk sac. The tail became twice its previous size. Behind 21 - 22nd myotome, the unpaired fin fold appeared and widened on the dorsal side. At the base of the 3 - 4th trunk myotome the rudiments of the pectoral fins appeared. The rudiment of the swim bladder was laid down. From time to time, the embryos tilt to one side or the other and make swimming movements with their tails (Fig. 23,A; development from the 28th of August to the 10th of September, length of embryo 7.1 mm). In the river apparatus the 8th stage began at the age of 13 days.

In 48 - 53 days in the incubator and in 15 days in the river apparatus, pigment appeared in the eyes of the embryos, which by that time reach the length of 7.8 - 8.9 mm. Segmentation was completed, the tail consisting of 31 - 32 segments (Fig. 23, B). Embryos had a well marked buccal pit. Opercula became somewhat larger, but did not yet cover the first gill. The first unpaired fin fold continued to grow. The lobes of the pectoral fins grew and their bases formed an angle of about 20° with the longitudinal axis of the body. Gill circulation has begun. The caudal artery provides 18 - 20 segments with blood. Capillaries appear on the upper surface of the head and in the occipital area. In embryos from river apparatus, segmental vessels have formed along the entire trunk section. During this stage, the density of the vessels on the yolk sac rapidly increases. A continuously larger role in the blood supply of this organ is played by the vessels emerging from the liver, while the importance of the subintestinal vein decreases. In comparison with the chum, this process has a more rapid course.

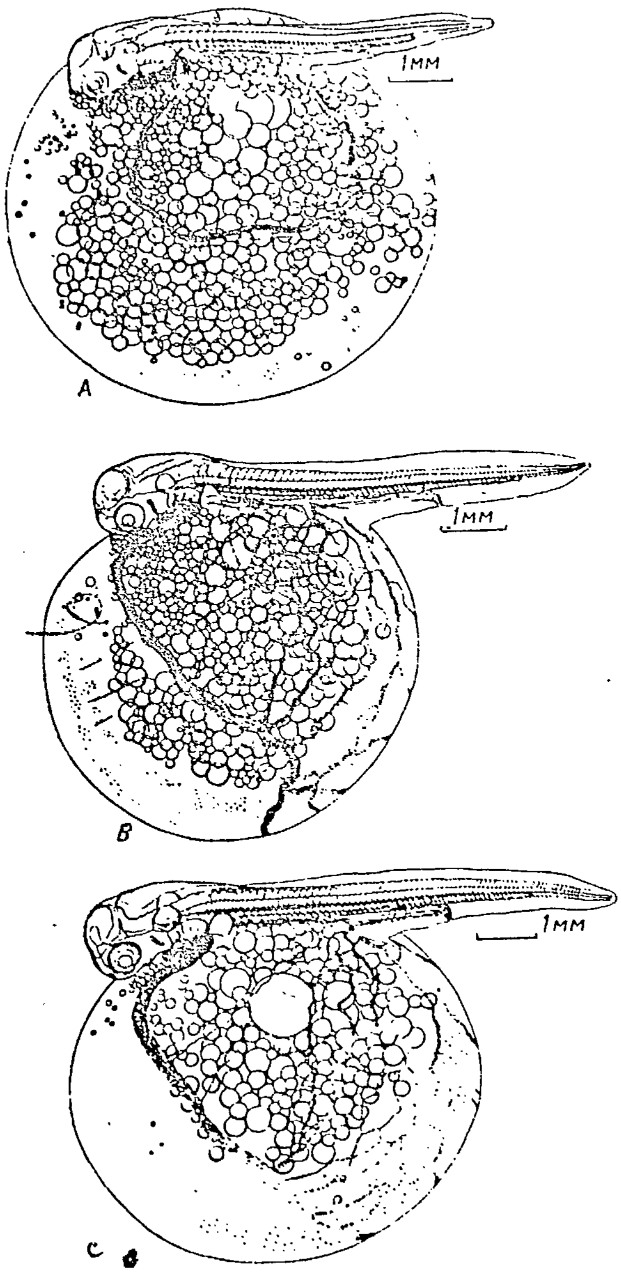


Fig 23

Fig. 23. Embryos of Sockeye, removed from the egg and drawn in vivo. A - Stage of the beginning of formation of the capillary net on the yolk sac, length of the embryo is 7.1 mm. B - Stage of the appearance of pigment in the eyes, length of the embryo is 8.3 mm. Development proceeded in the apparatus supplied with river water. C - Stage close to the preceding one, length of the embryo is 8.9 mm. Development proceeded in the apparatus supplied with stream water.

<u>Stage 9. Functioning of the Hepatic-Vitelline System of Circulation.</u> The connection of the subintestinal vein with the vessels of the yolk sac was lost at the age of 61 - 63 days (239 - 246 degree-days); from that time on , they are supplied with blood only from the liver. The embryos have reached the length of 9.0 - 9.8 mm (Fig.24,A). They had 75 - 76 myotomes. The distance between the otic capsules and the eyes became shorter than the width of a trunk myotome. Semicircular canals were formed. Numerous small otoliths began to combine into large ones. Eyes were grey, crystals of guaninebegan to appear in them. The caudal section increased to 33 - 34% of total length. The tip of the chorda twisted upwards and the tail lost its symmetry. The enlarged pectoral fins began to move (in the chum this occurs somewhat later), their bases forming an angle of about 45° with the longitudinal axis of the body. The intestinal content assumed a yellow-greenish colour. When the anatomy of the live embryos was studied, it was observed that the yolk became more viscous. 98

In the majority of the embryos, three pairs of gill arches, and in some, all of them were supplied with blood. Subclavicular arteries were formed. Segmental vessels developed up to 17 - 20th caudal myotomes.

Posterior mesenteric and intestinal arteries formed a capillary network on the intestine.

The embryos began to move in the eggs less frequently. This is due to the increased mobility of the pectoral fins, which ensure mixing of the perivitelline fluid.

In river apparatus, embryos at the beginning of this stage (18 days) had 73 - 74 myotomes. On the 22nd day (about 300 degree-days), when they had reached the length of 10 - 11 mm, there appeared the first hatching glands (Fig. 24,B). At the same age, the hyoid vessels began functioning. The entire surface of the yolk sac became covered with the thick network of capillary vessels. In the cerebral cavity fluid there appeared diffuse pinkish pigment, which was not found in the chum. At an average temperature of 3.8° the embryos reached a similar condition at the age of 77 - 80 days. However, their hatching glands appeared later, on the 84th day.

Stage 10. Differentiation of Upper and Lower Cones of Myotomes. The appearance of the rudiments of the upper and lower cones of myotomes in embryos, developing in an average temperature of 3.6°, was observed at the age of 96 - 100 days. The relative size of the head by that time decreased to about 16% of the total length of embryos, while the postanal section, which began to increase rapidly, reached 36%. Large otoliths were formed. Growing lower jaws pushed forwards of the vertical line drawn through the centre of the eye. Opercula covered two pairs of gills. At the point of origin of the anal and dorsal fins, the unpaired fin fold widened to 0.3 - 0.4 mm and muscular buds made their appearance. The place of the rudiment of the adipose fins became clear. There were

26 - 29 caudal segments; their number began to decrease. At the base of the lobe of the caudal fin, the hypurals made their appearance. The first rays were laid down in the caudal fin, the capillaries formed several loops. The idea of the changes which took place is given by Fig. 24,C, which shows an embryo slightly later than the stage described above.

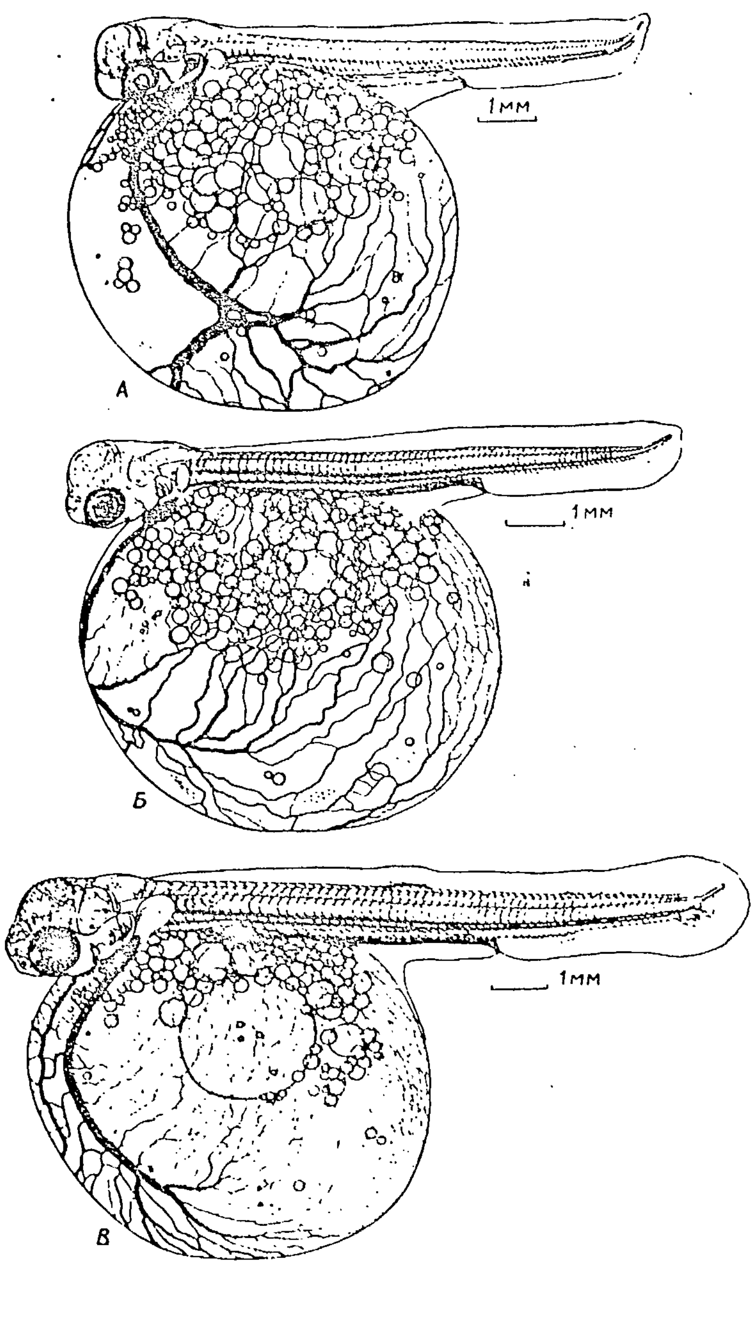


Fig 24

Fig. 24. Embryos of sockeye at various stages of development of the hepatic-vitelline circulation. 99
A - stage of the appearance of capillaries above the brain, length of embryo--9.8 mm.
B - stage of the appearance of guaninein the eyes, length of the embryos--10.8 mm.
C - stage of the appearance of rudiments of unpaired fins, length of embryos--13.2 mm.

In the yolk sac, due to the coalescense of small droplets, one 100
or two large fat drops were formed. The sac was covered by a thick network of capillaries. The network of vessels was particularly well developed in the embryos provided with river water. Whereas at the age of 25 days the total length of capillaries per 1 mm^2 of yolk sac surface was slightly more than 5 mm, four days later it increased to 7.6 mm (average of 5 measurements). At the beginning of this stage, the segmental arteries began to branch. They sent vessels to the spinal chord and to the surface of the body. The subepidermal capillary network, with respiratory importance, began to form in the integument. In live embryos one could see well the capillaries surrounding the kidneys, as well as small crystals in the renal glomeruli and the ureter The cardiac activity was noticeably stepped up: at a temperature of 12°, 68 - 71 beats per minute were carried out.

The eyes of the embryos became dark and irridescent. On the upper surface of the head, occipital region and behind the rudiment of the adipose fin there appeared small, pale-gray melanophores.

At the beginning of the stage, the lower jaws became mobile. The embryos infrequently moved their tails, and waved their pectoral fins at short intervals.

Developing in the river apparatus, the embryos reached the length of 14.5 - 15.5 mm in 34 days (438 degree-days) (Fig. 25,A). By that time the opercula covered three pairs of gills. Rudiments of the filaments appeared on the second and third gills. The upper and lower cones of myotomes became markedly larger. The tail section reached 37 - 38% of the body length. From 5 to 7 lepidotrichia were formed in the caudal fin. Below the 25 - 27th trunk myotome, sickle-shaped folds were observed, the rudiments of the ventral fins. The length of the capillaries per 1 mm^2 of yolk sac approached 10 mm. In individual embryos from river apparatus the first red lipophores appeared in the integument of the dorsal part of the head. The yolk sac in embryos removed from the eggs began to assume oviform shape. Increase in viscosity of the submembrane fluid was observed.

Stage 11 A. Development of Mobility of the Jaws and Gill Covers and the Attainment of the Greatest Density of Vessels on the Yolk Sac. Changes similar to those which were observed in the autumn chum at the beginning of the terminal stage of incubation of the eggs occurred in the sockeye at an average temperature of 3.5° at an age of 125 - 130 days, and at 12.8°--at 36 - 37 days. By that time, the height of the head became much greater. The unpaired fin fold became broad. The length of the pectoral fins exceeded 1 mm. The rudiments of skeletal elements appeared in the anal and dorsal fins. From 15 to 17 rays formed in the caudal fin, the network of capillaries became more extensive. At the base of the caudal lobe, a large lacuna was formed, filled with blood. The rudiments of the upper and lower arches of vertebrae became well marked (Fig. 25,B).

Fig. 25. Embryos of nerka, removed from the eggs at the end of incubation. A - stage of the deposition of ventral fins, length of embryo, 15.5 mm. B - stage of the beginning of intensive pigmentation of integument and internal organs, length of embryo 18.5 mm; C - embryo at the beginning of reduction of capillary network on yolk sac, length 19.1 mm. 101

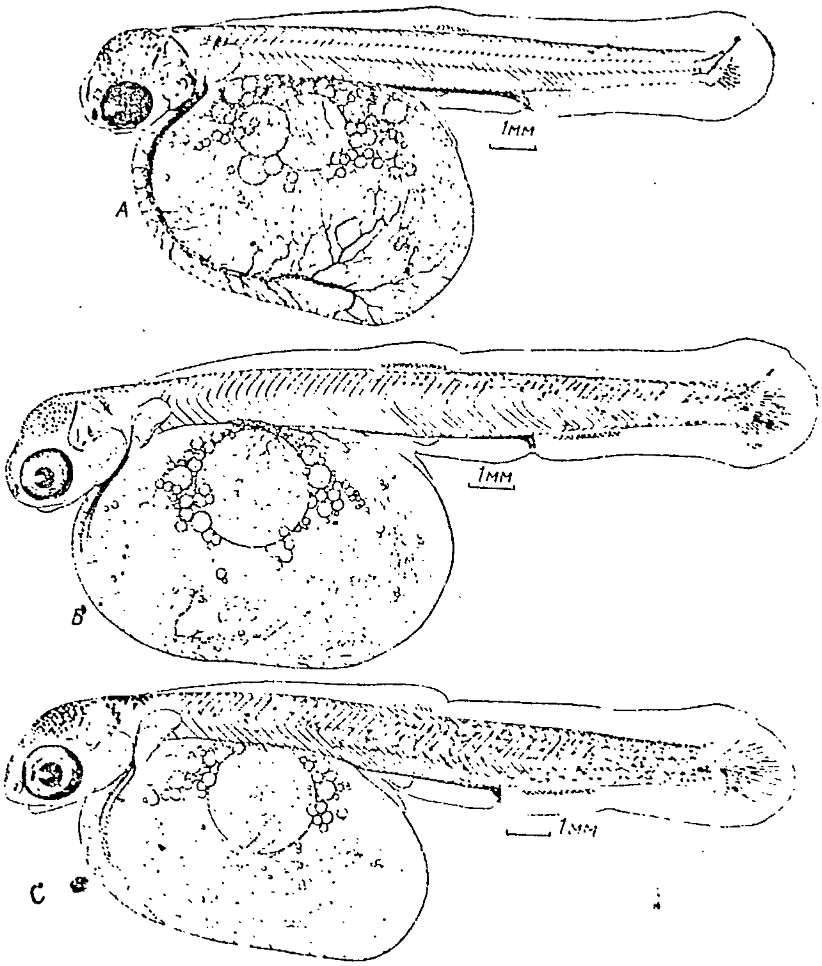


Fig 25.

During this stage, the lower jaws continue to elongate. At the end of the stage, connection is established between the buccal and the branchial cavities. Olfactory pits become oval and subdivisions appear in them. Opercula have grown and cover the gills. Filaments appear on all gills. A capillary network develops in the gills and pseudobranchs. The density of the capillaries on the yolk sac by the end of this stage reaches its maximum: it constitutes 10.0 - 10.5 mm per 1 mm^2. 102

At the same time, the process of pigmentation proceeds intensively. Melanophores appear above the spinal chord, along the large blood vessels, on the inner lining of the body cavity. The number of lipophores increases on the head, dorsum and in the lobe of the caudal fin. The latter, like melanophores, at first appeared on the head, then at the tip of the tail and gradually spread to the trunk.

The heart beats energetically, at a temperature of 15°, contracting 94 - 96 times per minute. Grown embryos surround the yolk sac. Their large heads are submerged in it and press against the heart. The heart beat, as the movements of the mouth, cause oscillations of the yolk mass and, apparently, facilitate blood movements in the capillaries covering the yolk sac.

The embryos rarely move in the eggs. The mixing of the perivitelline fluid is caused mainly by the movements of the pectoral fins, as well as the jaws and the opercula. If the egg is disturbed, the embryos are stimulated and begin to turn under the membrane. After being removed from the eggs, the irritated embryos are capable of rising and swimming for a short while in water. They begin to empty their urinary bladders, which points to the functional maturity of the excretory apparatus. In the chum and other salmon species, hatching takes place at this stage of differentiation.

<u>Stage 11 B. Beginning of the Reduction of Vessel Network on the Yolk Sac and the Completion of Incubation.</u> A long time before hatching--in apparatus supplied with stream water at the age of 140 - 145 days (450 - 463 degree-days), and at about 50 days in the river apparatus--some fine capillaries of the yolk sac begin to empty, the density of the vessel network and the size of the sac itself are reduced. The decreased importance of the role of this embryonic organ

of respiration is compensated for by the development of the capillary network in the gills, the integument and the caudal fin. The reduction of the capillary network on the yolk sac in other salmon species takes place after the hatching of the embryos. This particular characteristic of the embryo is due to the prolonged period of incubation in the course of which a high level of morphological differentiation is attained (Smirnov, 1964, a,b). This special character of the concluding period of development of anadromous sockeye under the membrane gives grounds for its isolation into a separate stage. For convenience of comparison we do not assign to it a new number, but designate this preceding part of development as stage 11 A, followed by stage 11 B.

Fig. 25 C shows a 52-day-old embryo, removed from the egg, incubated in river apparatus. At this age, the embryos were 18 - 19 mm long. The length of capillaries per 1 mm^2 of the yolk sac was reduced on the average 103
to 8.7 mm. A large part of its surface was covered by the intestinal wall and its size was diminished. As the result of resorbtion of the embryonic fin fold, the rudiments of the unpaired fins became well delimited. From 16 to 18 fin rays were laid down in the caudal fin, in the larger of them three segments were formed. The rudiments of paired fins became larger. Up to 30 branching filaments were formed on the first gill arch.

Fig. 26. Sockeye embryo at hatching and later.
A - At the beginning of group hatching, length of embryo is 22.2 mm. B - at the end of hatching, length of embryo is 24.5 mm. C - topography of the hatching glands of sockeye; D - embryo on emerging from egg, obtained from landlocked female, length 14.3 mm. E - early larva, 21.7 mm long, reared from the eggs of landlocked female.

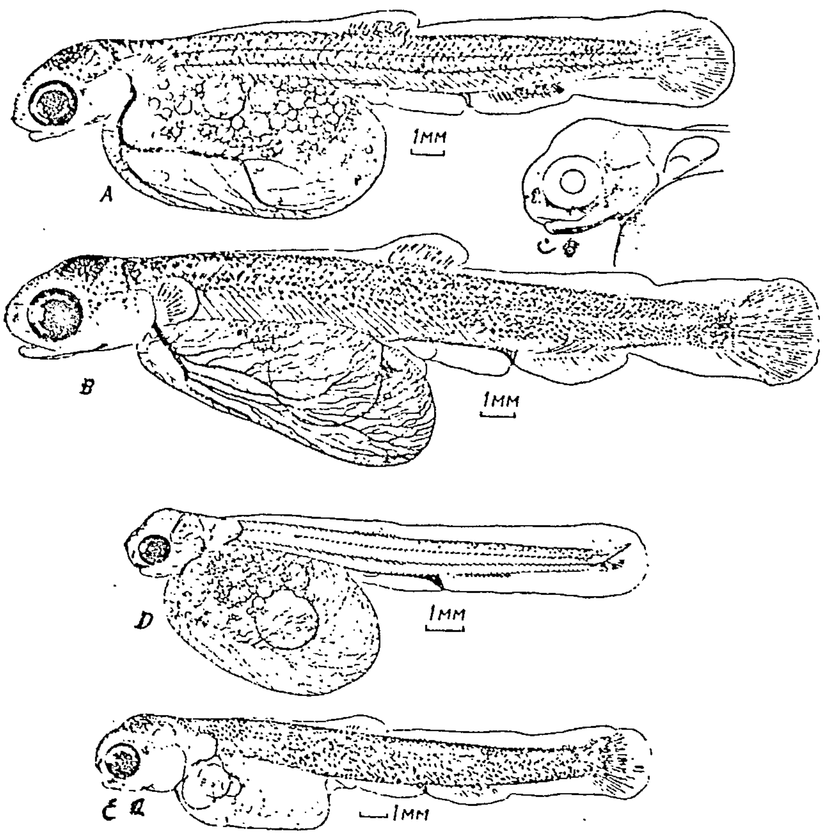


Fig 26

Large melanophores are present over all the body, but are scattered widely. An accumulation of melanophores forms a dark spot on the
head. It covers the brain and spinal cord, the area of the otic capsules,
and large blood vessels; the inner lining of the abdominal cavity is heavily 104
pigmented. Lipophores are concentrated on the dorsal surface of the head,
the dorsum of the embryos and between the rays of the caudal fin.

Numerous hatching glands have developed, their disposition being shown in Fig. 26, C.

Still within the membrane, the embryos energetically move their pectoral fins, at 13.5° executing up to 175 - 180 movements per minute. At the same temperature, the heart contracts 80 - 85 times per minute. The sensitivity to stimuli and locomotory activity of the embryos increases before hatching. Membranes become thinner, the size of eggs increases and their shape becomes oviform.

Table 5.

Length of Incubation of Eggs of Kamchatha Sockeye

Locality	Changes of Temperature during incubation C°	Hatching					
		Single		Onset of mass hatching		End	
		days	degree-days	days	degree-days	days	degree-days
Paratunski incubator	4.2--2.5	170	about 545	177	563	185	585
River apparatus	15.3--7.5	55	628	62	674	89	783
Ushkovski	4.4--4.2	116-148	570-674	--	--	151-172	638-748*
farm	4.3--4.2	138	583	154	662	168	772**
Karymayski incubator	6.8--2.5	150	592	--	--	--	--**

* Personal communication from N.A. Andreeva.
**According to N.Ya. Ievleva (1951, 1967).

Depending on conditions, the length of incubation of eggs varies within a wide range (Table 5). The influence of temperature is particularly significant. In our experiments, at an average temperature of 10.5°, emergence from the eggs began on the 54th day, at 8.1° on the 71st, at 3° after 170 days of incubation. At higher temperatures, the length of incubation was shortened, but the number of degree-days increased. On the spawning grounds of Lake Kurilskoe, the temperature of the ground water during incubation drops from 6 to 2° and the development of the egg takes about 5 months (Kuznetsov, 1928; Krogius and Krokhin, 1956). In Cultus Lake, the incubation of the eggs takes more than 170 days, while in Lake Babine, hatching begins after 50 days (Foerster, 1968).

Stage 12. Passive Condition of Free Embryos. This stage begins after hatching. On hatching, the sockeye has a small remnant of the yolk and a considerably higher level of differentiation in comparison with other species (Fig. 26,A). The mouth in emergent embryos is subventral. 105

Their huge eyes are mobile. The olfactory pits are almost completely divided by a bar of tissue into anterior and posterior halves. Skinny folds of opercula have grown up to the bases of pectoral fins and first rays appear in them. Lobes of pseudobranchs have appeared. On the first gill can be seen rudiments of rakers (Fig. 27, A). A small remnant of the embryonal fin fold has remained. Non segmented rays are well formed in the dorsal, anal and pectoral fins. Up to 20 rays can be found in the caudal fin. Central rays have up to 3-4 segments. The tips of the ventral fins project beyond the margin of the preanal fold, but still have no rays. The adipose fin has become observable. The ureter duct is packed with a large number of crystals.

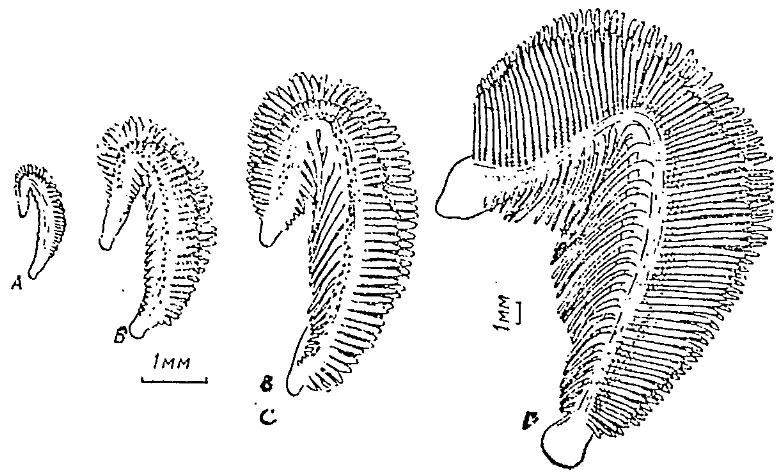


Fig. 27. First left gill of sockeye. A - at the beginning of group hatching, the length of the embryo is 22 mm. B - at the appearance of dark spots on the sides of the body, the length of the larva is 25.2 mm; C - in fry 36 mm long. D - in 2-year-old smolt 16.5 cm long.

The body of the embryo is covered by large melanophores, but they are widely scattered: in the middle part of the trunk above the lateral line there are 5 - 7 cells per myotome, and below it 2 - 3 cells. Lipophores are sparse, up to 10 - 15 per myotome. They are present in the base of the fin fold, in the dorsal and adipose fins, but are more abundant between the lepidotrichia of the caudal fin. Carmine coloured and recently emergent smaller lemon-yellow chromatophores are more numberous at the tip of the snout and in the interorbital space. Chromatophores are absent from the pectoral, ventral, and anal fins and from the preanal fin fold.

The lateral line organs are represented by sensory swellings (protuberances), well shown by in vivo stain with methylene blue. In spite of the morphological stage of differentiation being higher than in chum hatching, the nerves approaching neuromasts also do not yet stain in vivo.

At the beginning of the group hatching in the river apparatus, the embryos reached the length of 19 - 22 mm and weighed 111.5 - 146 mg, the remnant of the yolk weighing about 80 mg. Depending on the time of hatching, the weight of the yolk decreased during incubation by 20 - 25%, and on one series, the embryos which hatched in the last phase had their yolk decreased by 30%. In the incubator supplied with cold, well aerated water, hatching began at the condition similar to the one described above, but the embryos were less strongly pigmented.

By the completion of incubation of the main mass of eggs, the embryos reached a length of 23 - 24.5 mm and were at a higher level of differentiation (Fig. 26,B). Judging by the material collected by F.V. Krogius during his examination of the nests, in nature, sockeye hatches at the stage close to the one shown in Fig. 26 A,B.

Having hatched from the membranes, the embryos become quiescent and only rarely make attempts to move. They work their pectoral fins energetically, at 10^{o} performing up to 160 - 165 movements per minute. At the same temperature the jaws and opercula move up to 90 times, while the heart beats 75 - 76 times per minute.

The urinary bladder of hatched embryos begins to empty and rapidly fills again and again, clearing from the body the accumulated metabolic wastes. At a temperature of 6.6 - 7.2° a thousand embryos of the same age utilised in one hour the following quantities of oxygen: below membranes 3.76 mg; after hatching 11.01 mg.

In rearing containers with smooth bottoms the embryos lie on one side; when the bottom is of gravel, they crawl into spaces between pebbles. When on even surfaces, they are able to move forward by crawling with the yolk sac along the bottom, and if they swim up (when disturbed), then only for a brief moment.

As is the case with the chum, the reaction of the hatched embryos to currents is not very definite. They are indifferent to slight touch and to diffuse light. When touched strongly, they move away from the disturbing object. They are disturbed by bright sunlight. Even those embryos that have hatched last are characterised by similar reactions and weak activity. At a temperature of 2.4 - 2.8°, the embryos remained passive from 7 to 10 days. This allows us to suppose that under the protection of the egg membranes, the sense organs of the embryos can reach only a certain level of perfection and for their further development and establishment of their functions, adequate external influences are necessary.

<u>Stage 13. Formation of the Unpaired and Ventral Fins and of</u> 107
<u>the Swim Bladder.</u> Transition to the new stage is clearly marked in the change of behaviour. The embryos begin to react positively to the water current and swim towards the point where it enters the apparatus. A positive reaction to touch and photophobia begin to develop .

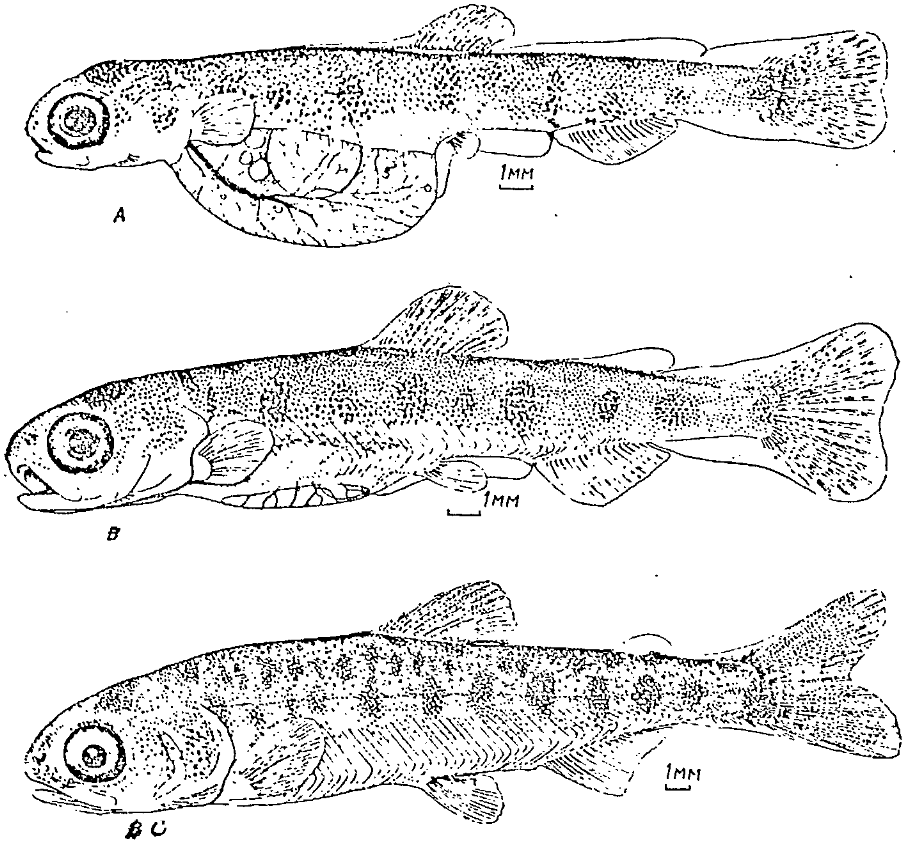


Fig. 28. Free embryo of sockeye, length 25.6 mm (A); larva 26.2 mm long (B); sockeye fry 39.7 mm long (C).

This stage began in the incubator at an age of about 245 days (690 degree-days), when the embryos were 25.5 - 27.8 mm long. They weighed 130 - 145 mg, with the weight of the yolk remnant being 23 - 44 mg (average 35 mg, or about 1/3 of the original weight). In Fig. 28,A is shown a sockeye 25.6 mm long, developing for 78 days in a river apparatus and following 12 days in an aquarium (in all, about 830 degree-days).

The yolk sac in free embryos assumed an elongate-oviform shape, and its posterior upper part had the shape of a small cone. Abdominal 108
walls covered its major part. The number of capillaries on the yolk sac was greatly reduced. The role of the branchial respiration became more important. The gill filaments became long, branching. The number and the size of the gill rakers have increased (see Fig. 27,B).

The length of the head increases to 17% of the total weight and more. The mouth becomes almost terminal. Teeth appear on the jaws. The embryos carry out grasping movements with their jaws.

The dorsal and anal fins are fully separated, their rays begin to branch. The adipose fin becomes outlined. The lobe of the caudal fin and the pectoral fins grow conspicuously. Fin rays appear in the ventral fins. The resorbtion of the fin fold has not yet begun.

Dark spots begin to form on the flanks of the body. Melanophores acquire the ability to expand. Deposition of guanine forms on the gill covers, lateral surfaces of the body and the peritoneum (the appearance of guanin on the opercula was first observed 60 degree-days after hatching).

In the gastro-intestinal tract a characteristic loop was observed. The pyloric part of the stomach was formed and the rudiments of the pyloric caeca appeared. Folds were formed in the intestinal mucosa. Observing live embryos, one can see weak peristaltic movements of the intestinal walls. The rudiment of the swim bladder has reached the length of 2.5 - 3.0 mm and continues to grow rapidly (Fig. 29,B).

The sockeye has acquired the ability to maintain a stable position with its dorsum upwards. When out of the ground, it is able to rise into the water from time to time, but can swim only for a short time. The embryos perform snapping movements and are able to ingest small particles of nutrients.

In the bottom of the spawning ground in Lake Dal'nee the embryos from artificially fertilized eggs (experiment performed on the 19th of November, 1955 by F.V. Krogius and the fixed samples were kindly placed at our disposal) reached the level of development similar to that described for the age 226 days; they continued to remain in their nests in this condition.

Larval Period of Development.

The Mixed Feeding Stage. Under the conditions of the incubator, the transfer to the mixed feeding is observed at the age of 250 days (720 degree-days) and more; in the river apparatus after 95 days (about 880 degree-days).

Fig. 28, B shows a free swimming and actively feeding larva, age 295 days (about 860 degree-days). Other larvae of that sample were 26.0 - 28.5 mm long and weighed from 123.5 to 135.5 mg, with the weight of the yolk remnant 22.5 - 37.5 mg. By that age almost all the fat droplets coalesced into one large one, which assumed pyriform shape. The stomach
became anatomically distinct. A considerable number of pyloric caeca 109
were laid down. Adipose tissue developed on the intestine and the stomach. The swim bladder grew almost to the posterior end of the body cavity and filled with air (Fig. 29, C). Large, branching filaments grew on the gills; 24 - 26 gill rakers were laid down (Fig. 27,B).

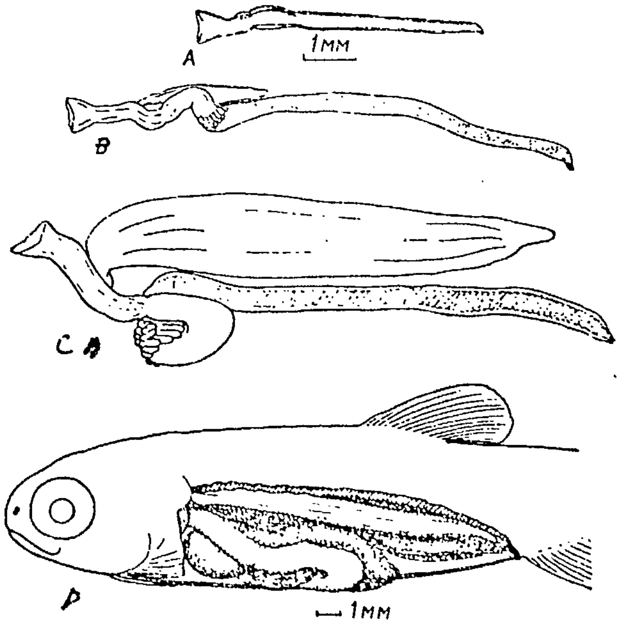


Fig 29

Fig. 29. Development of the Gastro-Intestinal Tract and Swim Bladder. A - appearance of the rudiment of the swim bladder, length of the embryo--12.2 mm. B - appearance of pyloric caeca, length of the free swimming embryo, 25.6 mm. C - stage of filling of the swim bladder with air, length of the larva 26.2 mm. D - sockeye 36 mm long with dissected abdominal cavity. Fat depositions can be seen on the stomach and intestine.

The height of the dorsal fin has increased, in percent of the body length, according to Smith, up to 8.34 ± 0.19, anal up to 5.91 ± 0.09, length of pectoral up to 10.74 ± 0.24 and ventral up to 6.17 ± 0.16. During this stage, the preanal fin fold is gradually resorbed and the adipose fin becomes quite definite. Ventral fins become mobile.

The dark lateral spots become more clearly outlined in larvae, above and between them, small spots make their appearance. Fins become more intensively coloured, but the anal and ventral, as before, are devoid 110
of melanophores, which is a diagnostic character of the species.

Before leaving their nests, the larvae remain near the surface for some time, in the zone of penetration of daylight and here they become used to the daily cycle of illumination (Heard, 1964; Bams, 1969). Already at that time, the larvae apparently begin to feed more regularly. The emergence from the ground is preceded by the loss of photophobia and of positive tactile reaction. This occurs directly before the covering of the yolk sac remnants by the abdominal walls. In the Paratunski incubator, a similar condition was attained 2.5 - 3 months after hatching.

The time of emergence of larvae from the ground in nature is prolonged. This is due to the extensive period of the spawning and the differences in the thermal conditions of the spawning grounds. In the basin of the river Kamchatka, the earliest emergence of the sockeye from the redds has been observed in January - February. In the basin of the river Ozernaya, the early larvae are observed in water from April to the beginning of September (Krogius and Krokhin, 1956). In the waters of British Columbia, the sockeye emerges from the ground from April to June-July, and in the cold rivers of Alaska some larvae remain in the ground until September (Burgner, 1964; Foerster, 1968).

An overwhelming number of larvae leave their nests by night and only few by day. For some time they prefer to remain in poorly illuminated parts of the habitat. In Lake Dal'nee the fry lives for about 1 - 2 months in the littoral zone, and feeds on small crustaceans, chironomid larvae and aerial insects. Later, it wanders off into the pelagic zone where it feeds on plankton (Krogius and Krokhin, 1956). On the stream spawning grounds prior to the descent to Lake Azabache of the basin of the river Kamchatka, the sockeye occurs from April to the end of June. At that time, the fry are 2.5 - 3.7 mm long and weigh 119 - 447 mg (average 190 mg). Intensity of feeding is low. The fry prefer small chironomid larvae and microbenthos (Simonova, 1972b). When the fry remain in the stream for a long time, benthic organisms retain their importance in the feeding throughout the year (Semko, 1954).

At the end of the mixed feeding stage, as in the chum, the remainder of the yolk and the fat drop are rapidly resorbed. At the same time, adipose tissue is deposited in the abdominal cavity.

The sex is differentiated before the disappearance of the yolk sac. The appearance of the oocytes at their synaptic stage was observed by Persov (1968) after hatching (728 degree-days after fertilization).

From the larval age onwards, sockeye lives gregariously, but it

forms schools less actively that the chum and pink (Hoar, 1958). Larvae prefer shaded localities with slow current. During the day, they retreat to deep layers of water or hide under stones, or roots among the inshore vegetation. At the end of the stage of mixed feeding the larvae leave the areas of the spawning grounds. From the stream spawning grounds, the fry migrate into quiet parts of rivers near the banks, or into lakes; from 111
the lake bank spawning grounds, they move to the pelagic zone. The young move to the feeding (fattening) areas both with the current and against it, if these areas are situated upstream from the spawning grounds. Migrations take place mainly during the dark time of the night. From the streams which have no connections with the lakes the young can move into the sea as young-of-the-year, and even with small yolk remnants present (Krogius, 1954, 1970; Semko, 1954; Krogius and Krokhin, 1956; Clemens and Wilby, 1961; Ricker, 1966; Hartman et al. 1967).

The Fry Stage of Development.

In the experimental containers (literally, ponds - Tr) of the Paratunskaya laboratory, where the larvae were placed in the spring, transition to the fry condition took place at the end of August. In a sample taken on the 31st of August 1957, fry 34 - 35 mm long and weighing 290 - 310 mg had scales with one sclerite (samples were taken above the lateral line, slightly in front of the adipose fin). They completed resorbtion of the preanal fin fold. In specimens 36 mm long, 25 - 29 gill rakers were counted. The middle rakers became longer than gill filaments, which is typical for the species (Fig. 27,c).

The fry are characterized by intensive linear growth and particularly by increase in weight. The fry in the containers on the 15th of August 1957 were 27.0 ± 1.02 mm long, with an average weight of 145.2 mg and with a small remnant of yolk present. By August 31 the length rose to 36.5 ± 4.59 mm, and weight to 385.6 mg, i.e. it increased more than 2.5 times. The condition coefficient, according to Clark, was 0.47 in larvae and 0.57 in fry. The sex of fry could be distinguished with the naked eye, on dissection. The ovaries were 5 - 6 mm long and, in the cephalic part, 0.4 - 0.5 mm wide; diameter of oocytes reached 57 - 67 mk. Testes were present as fine thread-like structures.

Fig. 28B and 28C show a later larva and an early fry respectively, shown as being of the same size. This comparison clearly illustrates changes that have taken place. In fry the head and trunk are higher, the mouth longer. The maxillary bone has almost reached the posterior margin of the eye. The height of the dorsal and anal fin and the length of the pectoral and ventral fins have increased. The rays of the anal fin had up to four segments , those of the dorsal - up to 6. The caudal peduncle became stouter, the lobe of the caudal fin developed a deep notch, "reduced" rays made their appearance.

Fry which were reared in the shallow small ponds with gravel-sand bottoms and with vegetation near their banks retained spots characteristic to larvae and assumed a golden shine. Along the flanks of their bodies were 7 - 12 oval spots with diameters almost equalling that of the eyes. Above them were paler spots, about the size of pupils and on the dorsum quite tiny spots. Below the large lateral spots in a 112
few specimens there were also several small spots. The belly was free of melanophores. From the ventral and the anal fins , melanophores were absent as before. The melanophore and lipophore pigmentation of the

remaining fins in the sockeye was weaker than that of other salmon species, except for the pink. The same is true of the lipophore pigmentation of the integument. At a temperature of 3.8 - 4.7°, the fry with an average weight of 1,867 mg eat in one day chironomid larvae equalling 1.19% of their body weight, and at 11.2 - 19.5° this figure in fry weighing 1,755 rose to 9.37% (Simonova, 1972b).

In contrast with fry reared in these ponds, the fry in the pelagic zone of the lake assume coloration of typical pelagic fishes. They have silvery bellies and sides, on which spots are almost invisible, and a dark-blue dorsum.

During spring and summer, the young inhabit epilimnion. Their distribution in depth is limited by the thermocline layer. With the onset of colder temperatures in the autumn the sockeye migrates into deeper layers. The young in the lake feed on plankton. The daily ration of the young-of-the-year weighing 4-9 g reaches in the summer 11.7% and in the winter 1.4 - 1.7% of their body weight, and in yearlings weighing up to 30 g, in the summer up to 7.7% and in the winter 1.4 - 1.7% of the body weight (Krogius, 1949; Krogius and Krokhin, 1956; Krokhin, 1957). Active feeding is observed at a temperature of 5 - 17°, optimal temperature about 15° (Brett et al., 1969).

In the pelagic zone of the lakes the character of the environment and the feeding of the young are sufficiently stable. This, apparently, is one of the reasons for the slight morphological changes with age in the young sockeye (Fig. 50). A comparison of the yearlings 101.4 mm long and weighing 8.95 g, migrating from Lake Dal'nee with the young-of-the-year shows the following changes. With age, the relative (in percentage of AC) length of the trunk increases from 63.5? ± 0.18 to 69.59 ± 0.45, and the length of the caudal peduncle from 13.03 ± 0.17 to 17.88 ± 0.17; the length of the head decreases (from 25.9 ± 0.14 to 24.44 ± 0.18), as does its height. The relative height of the dorsal fin and anal fin continue to increase (reaching 13.45 ± 0.27 and 10.58 ± 0.17 respectively. Pectoral and ventral fins become relatively shorter, to 15.1 ± 0.14 and 11.74 ± 0.11% of the body length respectively.

The large fry of sockeye are distinguished by a large number (30 - 40) of closely spaced gill rakers with denticles at their tips (Fig 27, D). They form a device which allows them to catch plankton (Cyclops, Daphnia), on which the young feed in the pelagic zone of the lakes. In the streams, rivers and littoral zone of the lakes, the sockeye feeds mainly on the small microbenthos, larvae and pupae of chironomids and other insects (Synkova, 1951; Krokhin, 1957; Simonova, 1972b).

In different lakes, the size of the yearlings varies from 5 to 12 cm, their weight from 5 to 20 g. Lake Dal'nee is distinguished by high feeding potential. There, the young grow rapidly, yearlings reach the weight of 14-41 g, the average weight of two-year-olds being about 37 g. In contrast, Lake Kurilskoe is 1'3
poor in food, and in it, the sockeye grows slowly, one-year-olds weighing 4 - 11 g. In different years, the weight of the two-year-old migrants varies from 5.9 to 10.1 g, length from 8.5 to 10.7 cm, and of the three-year olds, correspondingly within 8.3 - 15.1 g and 9.8 - 13.5 cm (Krogius and Krokhin, 1956; Selifonov, 1970).

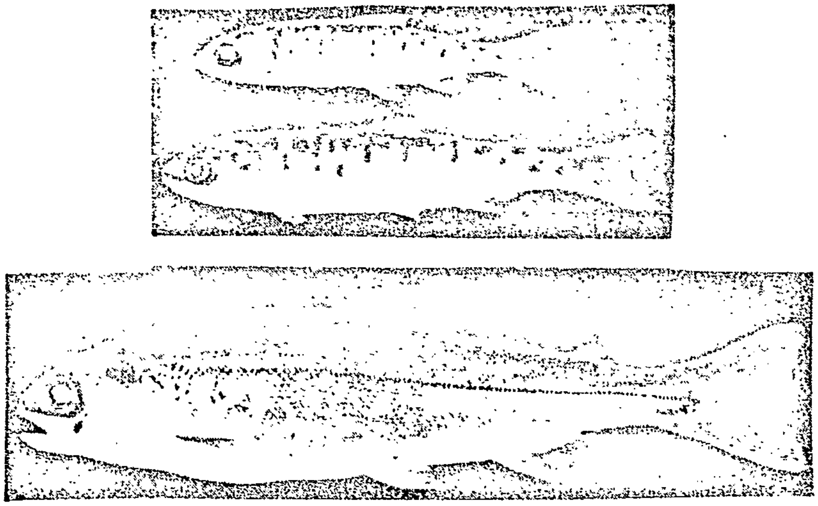


Fig. 30. Young sockeye. Upper: young-of-the-year, 52 and 67 mm long; Lower: two-year-Old migrant, 156 mm long.

In the spring, with the increase in the length of the day, intensification of solar radiation and warming of water, the young undergo the process of smoltification, changing from the parr condition to the smolt(silvery fry) condition. This process is regulated by a complex neurohormonal mechanism. Before their seaward migration, the young become more active and show preference to brackish water. Changes in the mechanism of osmoregulation were studied on the sockeye in Lake Dal'nee. Before seaward migration, sodium-excreting cells become activated in the gills. The kidneys become able to function similarly to the nephrons of marine fish (Zaks and Sokolova, 1965; Natochin et al., 1970). The mechanisms of hyper- and hypotonic osmoregulation, which permit them to live under the conditions of variable salinity are active in migrating fish. When migration is for any reason delayed, the mechanism of hypotonic osmoregulation begins to work more intensively. As was demonstrated on the sockeye and other salmon species (Hoar, 1959; Wagerman, 1960), after the migration season passes, the earlier preference to the brackish waters is lost. The organism is adjusted and the young fish lives in fresh water until the next spring.

The young fish of Lake Dal'nee migrates as one- and two-year- 114
olds, with small numbers of three-year-olds. The descent begins during the first days after the opening of the lake and warming of the water to above 4° (being particularly active at a temperature of 14 - 15°). It continues during June, and the first half of July, rarely extending to the beginning of August. First to migrate are predominantly fish of older age groups. Three of four peaks of descent are observed during the season. Exit from the lake occurs mainly between 8 pm. and 2 am., with the maximum at midnight. At first, the descent begins at later evening hours, but at its height it begins about 3 to 5 pm. Towards the end of the season, small numbers of fish migrate also by day. The diurnal migration is more active from Lake Blizhnee. Large numbers of fish migrate during high temperature periods. However, strong warming of water, just like other unfavourable factors, can interrupt migration and hold up in the lake young fish physiologically ready to migrate into the sea (Krogius, 1954, 1967; Krogius and Krokhin, 1956).

Characteristic Features of Life and Development of the Residual or Landlocked Form of Sockeye.

Some proportion of sockeye in Lake Dal'nee matures without migrating into the sea. The study of the offspring of such residual, dwarf forms, was of great interest. Observations were conducted in 1956 and 1957 and were briefly described (Smirnov, 1959 a, 1964 a,b). Males predominate among dwarfs while in the young which do migrate into the sea, the sex ratio is opposite. There are more dwarfs when the population is more subdivided and the food supply to the young is abundant (Krokhin, 1967). This conclusion concurs with the observed decrease in the descent of the young Black Sea salmon and its change into trout, when the feeding conditions in the river become better (Barach, 1957).

The dwarf sockeye mature at different ages. Almost always the two-year-olds predominate. They spawn also at the age of 3+ and 4+. Males mature at the age of 2+. Among the three-year-olds, females constitute about 5%; the percentage of females is somewhat higher among the four-year-old fish, but one must remember that the absolute number of fish of that age is small (Krokhin, 1967). The proportion of males is also very high in the residual sockeye in Cultus Lake (Ricker, 1938, 1940).

Before spawning, the dwarf spawners undergo small changes (see Fig. 16). Among males, the growth of the jaws and the formation of the hump is almost never noted. Scales are only slightly submerged in the skin, come off easily, and bear almost no traces of damage. Coloration becomes dull but a slight metallic sheen is retained (more often in females). The spawners become dark. Typical for the running males is an olive-green tinge and a slightly pink, narrow band along the middle line of the body. The females assume a bluish-purple tinge, but in some of them coloration develops similar 115
to that of the males. On the head and the dorsum of males and females appear small dark spots; spots are also more definite on the dorsal and caudal fins.

The dwarfs spawn locally in the lake. It is also noteworthy that they do not cease to feed before spawning; consequently, their metabolism does not change as drastically as in anadromous individuals.

In our material, dwarf males of 1956 were 20.3 - 25.8 cm long and weighed 111 - 220 grams. The length of the females varied from 23.5 to 27.8 cm, weight from 129 to 199 g.

The majority of the males which were at our disposal were running, and had probably already deposited part of their sperm, which should be taken into account, when assessing data on the weight of their tests. It varied from 3.6 to 6.6% of body weight. In one of the immature males the gonads weighed 11.7g, with body weight 178 g. The weight of the ovaries varied from 25.0 to 40.2 g and constituted from 10.0 to 23.3% (average of 14 specimens - 15.7%) of body weight of the females. These figures are higher than in the migratory sockeye, the weight of the gonads of which varies in the males from 2 to 6%, and in the females from 7 to 12% of the body weight (Kizevetter, 1958).

Fecundity of investigated females varied from 411 to 593 eggs (average 482). In a Japanese lake, Tovada, the females of the landlocked sockeye 28.5 - 34.5 cm long had from 442 to 879 eggs, average 644 (Kikita, 1962). The comparison of egg production per unit of weight is of interest. In the migratory sockeye from Lake Dal'nee, average weight 1.5 kg, about 1550 eggs were produced per 1 kg of weight, while at the weight of 2 kg, there were 1290 eggs per 1 kg. Dwarf females, on the other hand, produced up to 2,800 eggs per 1 kg of body weight, i.e. twice as many.

Running dwarf males from Lake Dal'nee begin to appear during the second five days of September. They take part in the spawning of the migratory sockeye. The first running dwarf males , were caught in 1956 only on the 6th of October, and in 1957 on the 10th of October. Specimens with eggs approaching maturity occured up to the middle of November and spawned, apparently, in the second half of that month. The displacement of the maturation season leads to the attainment of maturity by the eggs and the oviposition at lower temperatures. The beginning of the reproduction of the anadromous sockeye coincides with the maximum warming of the surface and ground waters. During that time the average daily temperature of water flowing out of the lake is higher than 14°. The dwarf females begin spawning when the water temperature in the lake drops to 5 - 6° and the ground waters begin to cool. In contrast with the anadromous sockeye of the summer run, which spawns in the shallow areas near the banks, the residual sockeye, judging from the catches of fixed gill nets, deposits its eggs at the depths not less than 2 - 3 meters.

Passing now to the special features of the development of the egg of dwarf sockeye, we must first of all note the small size of the eggs, the 116 weight of which varied from 51 to 69 mg (average 58.5 mg), while in the migratory individuals mature eggs weighed from 84 to 134 mg. The eggs of the residual females contain rather less drymatter and fat (2.3% less) and similar proportions of protein and ash (see table 1). The absolute quantity of the nutrient substances and the calorific value, in comparison with the eggs of the migratory sockeye, is about a half. No differences in the coloration of the eggs were observed. The diameter of the embryonic disc varies from 0.8 to 1.15 mm. It is insignificantly smaller. The reduction in the size of the egg is almost entirely at the expense of the yolk. The perivitelline fluid weighed from 15.7 to 23.2% of the weight of the hydrated eggs; by comparison with the eggs of migratory females, these eggs take in more water.

The development of the residual and the anadromous forms has, of course, features in common. The following description of the development would call for many repetitions. We considered it satisfactory to restrict it to the data on the rates of growth (table 6) and to pointing out demonstrable differences.

Table 6.
Rates of Development of Dwarf Sockeye Females.

Stage of Development	Length of Embryo in mm.	age	
		days	degree-days
Beginning of cleavage	--	about 1.0	3.8
16 blastomeres	--	2.0	7.5
Blastula	--	7.0	26.5
Beginning of Gastrulation	--	11-12	41-45
Appearance of first somites	1.6-1.8	19-20	74-78
Stage of 22-24 somites	2.8-3.3	31	110.4
Beginning of circulation	5.3-6.0	39-41	138-144
Appearance of melanine in eyes	7.5-8.0	54-56	177-182
First movements of pectoral fins	9.0-9.3	60-62	192-197
Appearance of muscle bundles in unpaired fins	9.5-10.0	72-74	223-228
Formation of guanine tail becomes heterocercal	10.8-11.3	87-89	261-266
Laying down of ventral fins	11.5-12.0	104-107	308-315
Beginning of hatching	13.3-15.3	138	405
Mass hatching	--	about 150	about 430

Some differences become clear in the rate of development, more noticeable during the second half of incubation. For example, in the eggs of the residual sockeye the first segments were formed about one day earlier. The process of epiboly was completed considerably earlier and at a smaller number of segments, which is related to the small size of the yolk sac. The beginning of circulation in both instances was observed at a similar number of degree days, but the embryos in the eggs of the dwarf sockeye at that time had 3 - 5 segments more. Some retardation (in stages of development) could be associated with the better conditions 117
of oxygen supply for embryos in small eggs with a relatively large diffusion surface,

as well as with the lower oxygen requirements of the small embryos. The eye pigmentation in the embryos of the eggs from dwarf females began about 20 degree-days earlier. Comparison of the times of the beginning of differentiation of the upper and lower cones of myotomes and laying down of the unpaired fins shows a gap of about 120 degree days.

At the moment of hatching, the embryos are distinguished not only by their small size, but also by the low level of differentiation (Fig. 26, D). Their head is short (about 15% of the total length), mouth is abbreviated. The bisection of the olfactory pits has only just begun. The opercula do not fully cover poorly developed filaments of the last gill. No teeth rudiments are visible. Otic capsules are very close to the eyes. No traces of reduction of the unpaired fin fold can be seen. In the dorsal and anal fins, the muscle rudiments are barely noticeable. In the caudal fin only 6.8, rarely 10 ray rudiments are present. Ventral fins are minute. Upper and lower cones of myotomes are short. The yolk sac is relatively large and a thick network of blood vessels is developed on its surface. Pigmentation is poorly developed. Few pale melanophores are present on the head and on the caudal section; they are almost absent from the integument of the trunk. On the head, the first lipophores made their appearance. Vital stain with methylene blue one day after hatching revealed a lower level of differentiation of the lateral line organs, when compared with the embryos hatched from the eggs of migratory individuals. By their morphological condition, these embryos resemble those of the migratory sockeye at the end of the 10th stage of development. The hatching took place within a shorter time and was more synchronised.

Having emerged from the eggs, the embryos became quiescent and moved only rarely. At first they reacted poorly, only to bright light, showing no reaction to the weak water currents and touching with external objects.

After their liberation from the membranes, the respiratory conditions of the embryos and the evacuation of the metabolic wastes improve. This favourably affects the rate of morphogenesis. From 7 to 10 days after hatching, i.e. in about the same period as in the chum and migratory sockeye, the embryos become photophobic, positively react to current and develop positive tactile sense. All this happens at a considerably earlier stage of morphogenesis than in the embryos of the chum, anadromous sockeye and other salmon species. It might be concluded that the emergence from the membrane stimulates the development of the corresponding sense organs.

Fig. 26,E shows a larva of the residual sockeye, 21.7 mm long. Its swim bladder has begun to fill with air and the larva is capable of maintaining itself upright in the water. Comparison of this drawing with the figures 26A and B indicates the similarity of other morphological features of this stage with the embryos of the migratory sockeye on hatch- 118
ing, although the differences in size are considerable. At the same time, these larvae are distinguished by higher mobility; they begin to hunt for external food. The offspring of the dwarfs pass on to live in open water and to external feeding at a much earlier stage of morphogenesis than those of the anadromous individuals, at small sizes. Such acceleration compensates to some extent for the small store of yolk in the eggs of the dwarf females.

The embryos from the eggs of the dwarf and anadromous females at similar stages of morphogenesis also differ from one another in size. At the stage of the appearance of melanin in the eyes, they are smaller by about 0.8 mm; at the beginning of the development of rays in the caudal fin they reach 2 mm; at the laying down of ventral fins, about 3 mm. Also significant are differences of size at hatching, which can be seen in the drawings. After hatching, the rate of growth and development of the dwarf embryos increases, particularly with the transition to external feeding. This creates conditions for the disappearance with time of the difference in size of the offspring of residual and anadromous females.

The importance of the increased rate of development of the embryos hatching from the eggs of the dwarf females is easy to imagine, when one takes into account the later oviposition of the latter. Accelerated development allows them to pass on to external feeding during more or less the same calendar time as the offspring of the anadromous females. Were it not the case, the earlier transition to active feeding of the larvae of the anadromous females--the numbers of which are huge--would place the offspring of the dwarf individuals in unfavourable conditions.

Thus, the residual individuals are distinguished by the small size, low absolute and increased relative fecundity, feeding of spawners right up to the spawning time, later maturation of females and autumn spawning, absence of spawning migrations and, at the same time, of drastic change in environment before spawning, as well as a weak and characteristic manifestation of prespawning changes. The eggs of the dwarf females are about twice as small, which affects the sizes of the embryos and the larvae. The process of epiboly is concluded more rapidly. Hatching occurs at an earlier stage. After it, one observes acceleration of development. The filling of the swim bladder with air and transition to active feeding occur at much earlier stages of morphogenesis, and at a smaller size. Consequently, with the loss of anadromic migration, the fish undergoes complicated changes, which affect very diverse stages of ontogeny.

Characteristic Features of Ecology, Reproduction and Development of Sockeye.

The sockeye gravitates towards northern regions. In Asia it reproduces mainly in the waters of Kamchatka and the northern shores of the Sea of Okhotsk; it is distributed up to the South Kurile Islands and Hokkaido, but does not move up the Amur, nor the rivers of Primorye and 119
Sakhalin. In the waters of North America, the species is more widely distributed and is about 2.5 times more abundant. This can be explained by the abundance of river basins, including lakes, in which the sockeye finds favourable reproductive conditions.

Migratory sockeye matures at the age from 3 to 8 years. The marine cycle of life extends for 1 - 4 years, the freshwater from several weeks to three, even four years. Some individuals mature without going to sea. All this makes for a very complicated age structure of spawning populations. The species is more associated with fresh waters than related salmon species.

The sockeye is the only Pacific salmon which has formed a generative-limnophilic form, reproducing in typical lakes. Another form, a generative-rheophilic form, reproduces in streams, limnocrenes and rivers. Spawning grounds of the sockeye are confined to the localities of emergence of ground waters. The formation of the two forms, named above, reflects in our view, leading directions in the evolution of the species. Generative-limnophilic sockeye is of low fecundity, its young feed mainly on plankton and live in the lakes from one to several years. Generative-rheophilic sockeye is much more fecund, the food spectrum of its young is much broader (main food being benthos), and the freshwater cycle shorter. High fecundity, apparently, compensates for the higher elimination in the sea, where the young go when small. Differences between these two forms are very significant and reach subspecific rank. The forms, in their turn, are represented by populations reproducing in different seasons. The landlocked sockeye which, as noted above, is distinguished by many features, is widespread. Both landlocked and anadromous sockeye form local groupings (subpopulations or micropopulations), confined to certain, sometimes small spawning sections. Sockeye is characterised by particularly complicated specific and intrapopulation structures.

The run of spawners into the rivers continues for more than three months. Spring, summer, and in some rivers also autumn migrations can be distinguished. The spawners enter the lakes as silver salmon and until their exit to the spawning grounds, live for a long time in the pelagic zone. The times of spawning are widely staggered, to correspond with the different seasons of the runs into rivers.

In the spawning localities, currents are either absent or do not exceed 10 - 20 cm/sec. Nests are situated up to 1.5 - 2 m from the water's edge, in some places deeper, on friable, frequently much silted

ground, where ground waters emerge. The temperature regime of these waters is stable both in daily and annual cycles; absolute values for temperatures are low (in Kamchatka). Also stable is the hydrochemical regime of the waters washing the spawning redds. These regimes are characterised by low oxygen content in comparison with mainstream water, increase in free carbonic acid and weakly acid reaction. The waters 120
washing individual spawning grounds differ, even in small aquatories. This, in particular, explains the accurate return of the spawners to their place of birth and the reproductive isolation of small groups. The sockeye has very well developed homing behaviour. Characteristic for the species is the considerable number of males in nest grouping, high concentration of spawners and their frequent replacement on the spawning grounds in the course of the season.

The males extrude their sperm in the course of a short time, in small batches; the concentration of spermatozoids is low (average 10 - 11 million per 1 mm^3). The eggs are more often deposited in 4-5 batches. They are smaller than in other related species (average weight about 110 mg), covered by a thin membrane (23 - 42 mk), contain particularly abundant astaxanthin and have intensely red coloration, with a pinkish hue.

The characteristic features of embryogenesis are as follows. The embryonic knoll in the sockeye is flat, blastomeres up to the stage of 16 cells inclusive are situated in one layer. The embryos are of relatively small size. The process of epiboly is concluded early, most commonly at 27 - 30 segments, in small eggs even at 23 segments. In connection with this, the eggs easily become insensitive to mechanical stimuli and vibration, but in general the eggs of the sockeye are more sensitive to these stimuli than the eggs of other salmon species.

Blood circulation begins most commonly at the stage of 58 - 60 segments, somewhat later than in the chum. This is related to the small size of the eggs and thin egg membranes. Blood rapidly assumes an intensive colour. The subintestinal-vitelline vein functions for a short time. Hepatic-vitelline circulation develops rapidly. The embryonic-larval organs of respiration attain high development. The sockeye is distinguished by the fact that in its embryos, the network of capillaries on the yolk sac is makedly reduced before hatching. The eggs incubate for a longer time than in other salmon species, and the embryos reach a particularly high level of differentiation before hatching.

Chromatophores appear on the body late, embryos and larvae are less strongly pigmented than in other species, excluding the pink, and melanophores are absent from the ventral and anal fins.

The young lead a gregarious life. The larvae live for a short time in the littoral zone of the lakes. Having migrated into the pelagic zone, the young become streamlined (tall and thin), assume silver coloration of the belly and flanks and a dark dorsum. They develop numerous long gill rakers with terminal denticles, enabling them to feed successfully on plankton. When living in the shallow waters of the streams and other localities, the young retain for a long time spotted coloration. Catadromous migration begins after the waters have become free of ice and warmed above 4°. It continues for a long time, due to the differences in the age of the migrants, and the belonging of the latter to different seasonal forms.

The prespawning changes of the anadromous and dwarf forms, as 121
well as the development of their offspring differ significantly from one

another. Migrating from the sea up rivers, the sockeye ceases to feed and assumes intensely red colouration before spawning. Males grow a hump, large teeth and their jaws elongate and become crooked. The individuals which do not leave the lakes, mature somewhat earlier. Retaining dwarf size, they do not undergo significant prespawning changes and continue to feed right up to the spawning. Dwarf females have low fecundity, and mature later, in the autumn. Their eggs are half the size, the incubation period is shorter; their embryos hatch at an earler stage of morphogenesis. Such embryos also pass to living in open water and to utilisation of external food at a lower level of differentiation. Thus, the loss of the migrating habit leads to profound changes at different stages of ontogeny.

THE PINK SALMON - O. GORBUSCHA (WALBAUM)

The pink salmon is a small but rapidly growing and most abundant salmon, so that the pink fishery is of great economic importance. During the period of the highest catches, 1931 - 1942, in the western part of its range, the average annual catch was about 146.5 millon fish, while in 1955 - 1966, only 82.9 million (Levanidov et al., 1970). A sharp drop in stock size was caused mainly by the rapidly developing unregulated Japanese fishery during the fifties.

Distribution and Life in the Sea. The range of the pink is slightly narrower than that of the chum. In comparison with the latter, the common regions of reproduction are slightly displaced to the north. During the summer, the fish in the west reach the river Lena, in the east, the rivers Colville and Mackenzie. North American stocks in the south reach slightly further than the river Sacramento, the Asian reach the southern rivers of the Korean Peninsula and the island of Honshu. Abundant populations reproduce in the rivers of the Sea of Okhotsk and the basin of the Amur.

Three regions of wintering and feeding can be distingusihed: the Sea of Japan, the Pacific-Kurile and the Aleutian-Bering Sea. The relative productivity of the stocks feeding in these regions has been calculated as being 10, 81 and 9% respectively (Semko, 1962). The pink that reproduces in the rivers of East Kamchatka and Olyutorski Bay overwinters and feeds mainly to the south of the western islands of the Aleutian ridge. The main bulk of the West-Kamchatkan pink overwinters closer to the South-Kuriles. From here the fish migrates to the rivers of Southern Kurile, East Sakhalin and the Sea of Okhotsk shores
of the continent. The Amur pink of the late run lives also in this region. 122
The main bulk of the Amur pink, as well as the fish that reproduces in the rivers of Primorye, Bay of Aniva and slightly more northern rivers of the Sakhalin, overwinter and feed in the Sea of Japan. The northern border of the wintering grounds coincides, apparently, with the surface isotherm about 3.5°, and the southern, with the isotherm about 10°. With the spring warming, the pink moves north. During the spring and beginning of summer, the groupings of the fish are restricted by the surface isotherms 6 - 12°, the main bulk being concentrated within the isotherms 7 - 9°. In the open sea, the pink moves on a broad front, feeds intensively and grows very rapidly (Birman, 1958; 1967; Semko, 1958, 1962; Hartt, 1962; Ishida, 1966).

Age and Fluctuations of Abundance. The mainly one-age group composition of the spawning populations and the maturation of the pink at the age of two years have been noted long ago (Schmidt, 1905; Gilbert, 1914; Tikhyi, 1926). Hypotheses were made of the four-year age of the pink and of the maturation of some of them at the age of three years. These were assessed by various authors (Kaganovski, 1949; Vedenski, 1954; Ricker, 1962; Lapin, 1964, 1971). Tagging experiments confirmed its return and the maturation of the overwhelming bulk of the individuals at the age of two years (Pritchard, 1939; Parker, 1964; Bilton and Ricker, 1965, etc.). A small number of individuals with signs of tagging (without appropriate fins) were taken during the third summer of life. This was attributed to the loss of fins due to natural causes (traumas, destruction of fins by predatory larvae of some species of Copepoda). The study of the material published on the results of tagging and the return allow us to assign such individuals, at least a part of them, to fishes maturing at the age of three years (Lapin, 1964, 1971).

The alternation in even and odd years of abundant and poor runs of the pink is characteristic of many regions. The two year cycle and single-age composition of spawning populations are considered a specific (species) characteristic. The origin of a population dynamics of this type is connected with the stability of the conditions of reproduction, ensuring a necessary minimum of recruitment (Nikolski, 195[illegible]). In some regions, in addition to the two-year periodicity of catches, a four-year one is also observed (Kuznetsov, [illegible]; Smirnov, 1947; Kaganovski, 1949; Vedenski, 1954). Even longer term fluctuations in the abundance of the pink and other salmon species are associated by [illegible] with the periodicity of solar activity; [illegible] the period of [illegible] radiation. This relationship has been particularly clearly observed in the Amur.

The length, weight and fecundity of fish of abundant generations, as a rule is lower. From time to time, the relationship of abundance of consecutive generations changes, the poor brood becoming abundant and vice versa. These changes do not occur at the same times in different regions. In the Sakhalin pink during past years, abundance and biological 123
characteristics of the fish of consecutive generation were sharply different (Dvinin, 1952). According to Landyshevskaya (1964), in 1958, an abundant year, the main bulk of the pink in different regions of the island was 43 - 45 cm long and weighed 1.1 - 1.3 kg. In 1959, the run of pink was poor, its average length was 49 - 50 cm and weight 1.5 - 1.6 kg. In 1960, instead of the expected increase, a sharp drop in catches occurred and the incoming fish was again large, highly fecund, with an average length of 46.6 - 49.0 cm and weight 1.4 - 1.5 kg; the previously abundant generations became poor.

Several hypotheses were postulated to explain the phenomenon of dominance of certain broods. They were reviewed by Ricker (1962). In his view, the most acceptable explanation in the difference between catches of the even and odd years was given by Neave Fevris, who worked out a hypothesis of depensatory influence of predators. Its essence is in the fact that the off generation suffers during its downward migration a large proportion of individuals and this retards increase in abundance of subsequent generation. Accepting Neave's theory as better formulated, Ricker, however continues to regard the "phenomenon of dominant" as remaining to be a puzzle, still unsolved by science. The recognition of the fact that the spawners mature at different times allows the building of a mathematical model, explaining the characteristics of the dynamics of the stocks of this salmon species (Lapin, 1964, 1971).

Intraspecific Differentiation. As has been shown by Pravdin (1932), the Amur pink in comparison with the West Kamchatkan is smaller, has a smaller head, briefer snout, smaller scales, slightly higher number of branching rays in the anal fin, and can be distinguished by some other features. A comparison made between them served as a basis for separating the Amur pink into a distinct form, O. gorbuscha natio amurensis. Kaganovski (1949) viewed the different abundance of the pink in on and off years in large regions, and differences in time in the change of abundance of the runs, as indications of separate identity of the stocks inhabiting more or less extensive areas. Taking into account other biological features, he postulated the existence of East Kamchatkan, West Kamchatkan, Okhotsk and Sea of Japan races or stocks. In his view, these races were divided into populations, the number of which depends on the characteristics of the spawning rivers.

Dvinin (1952) found morpho-biological differences between West Kamchatkan and East Kamchatkan pink and associated these differences with the feeding of the fish in the Sea of Japan and the Pacific. Subsequently, several local stocks of the Sakhalin pink were discovered and it was demonstrated that biologically distinct pink runs into different rivers at different times of the spawning season (Volovik, [illegible]). A proposal was made to distinguish between the Okhotsk, Amur and Primorye stocks, and their characteristics were shown by Enyutina ([illegible]).

The pink that reproduces in the rivers of the South Kurile islands 124
is distinguished by its large size. According to data collected in 1953 - 1965, its average length was 51.1 cm, weight 1,650 g and the absolute

fecundity about 1,600 eggs. While in other pink populations the males are larger than the females, here the females are larger than the males. An early run is observed in the Kuriles, from the 2nd third of June to the beginning or middle of August, and the late run which begins subsequently continues up to the middle or end of October. The size, rate of growth and fecundity of the pink of the late run are all greater. Moreover, it approaches the shores from the north and spawns in the lower reaches of the rivers, while the summer pink approaches the rivers from a sourtherly direction and spawns higher up (Ivankov, 1967, 1971).

Kaganovski (1949) once suggested that the pink that spawns late should be referred to as the autumn pink. This form is distributed fairly widely. The reproduction of the pink during October was observed in the basin of the river Bol'shaya (Kuznestov, 1928). There is also autumn spawning pink in the Sakhalin. In Hokkaido it is the autumn spawning that is more common (Sano, 1959). In the rivers of South-East Alaska the run of the pink is prolonged. The fish of the earlier run (July-August) migrates to the upper reaches and that of the later (September-October) spawns in the lower reaches of the rivers (Merrel, 1962; Wells and McNeil,1970). Summer and abundant autumn runs occur in the rivers of British Columbia (Foerster, 1955; Neave, 1966a). A relative reproductive isolation of the individuals of different runs is considered by Vernon (1962) as a leading reason for the divergence of the species. An attempt was made to introduce early-spawning pink into a river which is visited by the late-spawning form. The introduced individuals after maturation came to spawn two weeks earlier; this fact is seen as the proof of the genetic nature of the maturation time (Ricker, 1959, 1972).

According to our observations, in the basin of the Sakhalin river Naiba, the pink at the end of September and in October builds its nests near the places of the emergence of ground waters. This ensures productive spawning after the cooling of the river. The adaptation of the autumn-spawning form to build nests in places washed by ground water which is warmer during that time, i.e. special features of the ecology of spawning and development, basically differentiates it from the summer-spawning form and is at the basis of the ecological and morphological divergence of the species.

Thus, there are indications of the qualitative differences between the pink of large regions. The relationship between establishments of such groups and the lack of contact between large river systems during the geological past, and occupation of different sea areas for feeding is not excluded. Populations reproducing in individual rivers or groups of small adjacent rivers (tributaries of large rivers) could have differentiated later. The spawners migrate from various feeding 126
regions into some spawning rivers, for example, in the Sakhalin, and such groups are distinct in their biological characteristics. In the basins of different regions there are both summer and autumn spawning forms, differing from one another in the ecology of development and morphological and biological features.

Low absolute fecundity is characteristic for the species. As can be seen in Table 7, the individual variations of this character are large, but average values can be very similar even in fishes of regions so distant from each other as Kamchatka and Primorye. As has already been said, the pink has different fecundity in even and odd, poor and abundant years.

Table 7
Fecundity of the Pink from different regions. 125

Region, river	Year	Length of female cm	Absolute fecundity, no. of eggs: range	Absolute fecundity, no. of eggs: Average	Reference
Kamchatka					
river Bol'shaya	1933, 1935	48.5	1000--2350	1636	Semko, 1939
	1934, 1936	44; 55	800--2000	1169	
Karymaiski stream	1942--1950			from 1286 to 1600	Semko, 1954
rivers of the Okhotski littoral			500--2700	from 1162 to 1785	Kostarev, 1965
river Amur	1925, 1927	51.8	1083--2926	1813	Kuznetsov, 1928
	1926	48.6	662--1598	1192	
river Iski	1951	49.3	628--3203	1978	Enyutina, 1954
river Argun'	1951	44.3	675--2475	1528	
river My	1951	49.3	1306--3080	1879	Strekalova, 1966
	1952	50.3	1149--3215	1716	
river Tumnin	1947, 1948		374--2732	1354	Johansen, 1955
Sakhalin Island, south-western rivers	1946, 1947	44.9; 53.6		1525; 1576	Dvinin, 1952
south-eastern rivers	1947, 1949			1230; 1306	"
river B. Takaya	1953	48.71±0.68	1204--2028	1579±48	personal
	1954	55.15±0.54	1300--2256	1831±61	data
Iturup Island	1965				Ivankov, 1971
river Slavnaya					
summer race		47.9±0.34		1354±35	
autumn race		52.2±0.32		1545±39	
Island Hokkaido		42.5--49.6	1517--2916		Hikita, 1962
river Yubetsu				1956	
river Shibetsu		50--53	1668--2099	1891	"
Alaska		44--48	1330--1775	1564	"
Sashin stream	1951	50--54	1928--2461	2152	Rounsefell, 1957
British Columbia	1930--1940			from 1535 to 1899	
MacClinton stream	(even years)			(1599)	
Fort John stream	1947			1520	
	1950			1593	

Attention is attracted to the high fecundity of the pink from the river B. 126
Takaya of the basin of the river Naiba, where it spawns at a late date. Individual fish there reach the length of 68 cm and weight of more than 4.5 kg. High fecundity is characteristic also of the autumn spawning pink of the river Slavnaya, Iturup Island, and some rivers of Hokkaido. The same can be said of the late spawning form from the stream Sashin in Alaska and MacClinton in British Columbia. An analogy exists here with the autumn chum, reproducing in localities washed by the ground waters, a form also more fecund than the summer spawning one.

Anadromous Migration, Maturation, and Times of Reproduction.

Within its range, the pink visits almost all the rivers, though it exhibits a certain selectivity. Some of them, typical "pink rivers", have abundant runs, others are visited by small numbers of fish. For example, only a few pink migrate into a large river like Kamchatka, its catch there constituting only 2-4% of the total salmon catch (Ostroumov, 1964). In contrast, the river Amgun', a left tributary of the Amur, is visited by large pink runs. The pink enters by preference into the Sakhalin river Lesnaya. There are many such examples.

The pink runs into the rivers of Primorye from the end of May or the first days of June, until the end of July. Somewhat further North (in the river Tumin) the run ends in the last third of August. Spawning continues from the end of July to the middle of September (Vasilenko, 1959; Vasilenko-Lukina, 1962). The pink begins to enter the Amur during the first days of June; from the 20's of the month the run becomes abundant and so it remains until the middle or end of July, to end in different years in the 20's of July or in the middle of August; isolated fish are also observed in September. When stock abundance is low, the feeding conditions improve, and the fish matures more rapidly and migrates to spawn earlier. Entry into the spawning rivers of the Amur system is observed at temperatures from 5.5 to 22.1°. Spawning in the river Ny, opening into the south-western part of the Amur liman, continues from the 2nd or last third of July; it becomes abundant in August for 10 - 15 days and ends about the middle or towards the end of September. Oviposition in the river Iski begins in the 1st third of August and ends in a shorter period. Spawning in the river Amgun' is usually observed from the last third of July and continues for about a month (Kuznetsov, 1928; Strekalova, 1963; Enyutina, 1972). In the Okhotsk region, the run of the pink is observed in June-July, in the bays Gizhiginskaya and Penzhinskaya, in June-August. The pink migrates into the river Bol'shaya in western Kamchatka from the first days of July, the run becomes more conspicuous from the 2nd third of the month, while the approach to the spawning grounds continues to the beginning of October. Spawning continues from the middle of August to the end of October (Kuznetsov, 1928). The pink runs into the rivers of the eastern shore of the peninsula somewhat earlier.

The pink approaches the rivers of the Sakhalin from different feeding regions, a fact which is reflected in the times of the run. According to Dvinin (1952), the pink runs into the rivers of the south-western shore from 15 - 20th of June to the end of August. Further north the run is delayed by 10 - 15 days. Spawning continues from the second half of July to the end of August or beginning of September. The entry into the rivers of the Bay of Terpenie is observed from 20 - 25th of June until the middle of September. Spawning in the rivers of the eastern shores of the Sakhalin continues from the end of July to the end of September or beginning of October. According to our observations, it extends to the 20's or the end of October.

Entry of the pink into the rivers of the South Kuriles extends for more than 3.5 months. The run of the summer form begins in the 2nd third of June, and of the autumn one, in the middle of August, and continues to the middle or the end of October (Ivankov, 1967). In various rivers of Hokkaido the migrations appear at the end of July and the middle of August and are observed up to the beginning or the end of October; the fish of the late run is quantitatively dominant (Sano, 1959, 1966).

On its approach to the rivers, the fish enters fresh waters. The estuarine and river species significantly differ from the marine ones by many characteristics, and the migrants must become adapted to the environmental changes. For example, in the liman of the river Bol'shaya at the time of the peak run is observed a large oxygen deficit, an accumulation of free carbonic acid and a lowering of pH. The water temperature in the lower reaches of the rivers is higher than in the sea. On moving up the river, the fish enter comparatively cool water (Semko, 1939). During the hot, dry summer of 1965 during the run of the pink, the temperature in the lower reaches of the southern Sakhalin rivers exceeded 25°. It is not excluded that the high temperatures serves as one of the stimuli for the movement of the fish to the upper reaches, where the water is colder. It is also hastened with the increase of the water level in the rivers (Pravdin, 1929). The pink in most instances arrives earlier on the spawning grounds and begins to spawn earlier with colder water (Sheridan, 1962).

As a rule, the fish of the early runs has less mature sex products and moves further up the rivers. Individuals which migrate later and are more mature spawn in the lower reaches. During the years of [illegible] runs the spawning grounds situated lower down are also filled early.

In the river mouths of the south-western coast of Sakhalin, the majority of individuals are at the II - III stage of maturity ([illegible]irin, 1952?). This situation is not, however, prevalent everywhere. The pink enter the river Bol'shaya in the Kamchatka at a maturity stage near to IV, with the weight of the ovaries being from 7.5 to [illegible].5% of the weight of the females. Most individuals lose silver coloration already in the liman (Semko, 1939).

During the movement up the rivers, the pink favours sections with a current velocity of about 20 - 30 cm/sec (Krykhtin, 1962). When the water level is high and the current swift, as well as during the abundant runs, the fish moves particularly high up. Not infrequently it occupies areas which dry up during a drop in water level. In such places there is high mortality of both the fish and the deposited eggs. The duration of the catadromous migration varies. In the Amur, the pink used to cover about 700 km (Kuznetsov, 1928); in the river Bol'shaya 250 km (Krokhin and Krogius, 1937b). In the large rivers of Sakhalin the migration route exceeds 300 km and in the small rivers the spawning grounds might be situated near the mouth, in the flood and ebb zone.

Before moving to the places where the nests are made, the spawners dwell for some time in shaded, deep places with weak currents; there they mature. The prespawning changes of the pink were described by many authors. They are as follows. In the male pink, the snout and large teeth grow more than in those of other species. The body becomes laterally compressed, a keel-like hump grows on the back, particularly conspicuous in large individuals. The back assumes a dark-brown colour, the flanks become lilac-coloured, sometimes reddish, and the belly remains pale. There are no transverse spots on the body. Small, irregular spots, outlined in wavy, blurred contours on the back and sides appear. Almost black, oval spots are situated between the rays of the dorsal and caudal fin. The shape of the head and body of the female changes but little. The back becomes darker than in the males, and the belly remains pale (Fig. 31).

It has been suggested that the hump of the males is important to create circulation of water within the nest hollow that would favour fertilization of the eggs (Semko, 1954). Aleev (1963, 1964) links the changes in the body form with the great degree of manoevrability, required during life in shallow rivers, when the nests are being constructed. The flat and high body of the pink males also answers these requirements. It remains unclear, why similar structural changes do not occur in the males of other salmon species, except for the sockeye, and in females. After all, it is the females that carry out the main work on nest construction.

Spawning Grounds and Spawning; Conditions of Development. The main bulk of the pink choose for their reproduction the river beds, brook and streams, the bottoms of which are washed by the subsoil alluvial current. The spawning grounds are concentrated in the foothills and upper reaches. The pink usually moves higher upstream than the summer chum, but during abundant runs these salmon species might reproduce close to each other.

The spawning grounds are situated on the borders between pools 129
and riffles and on the riffles themselves. The ground of the spawning localities is coarse gravel with a large admixture of sand; the 4 - 8 cm component predominates, here and there large cobble stones are found; the admixture of loess and silt is small. Gravitation to places which are shaded by trees or high banks is observable. The pink avoids very silted pools, or mud and overgrown places.

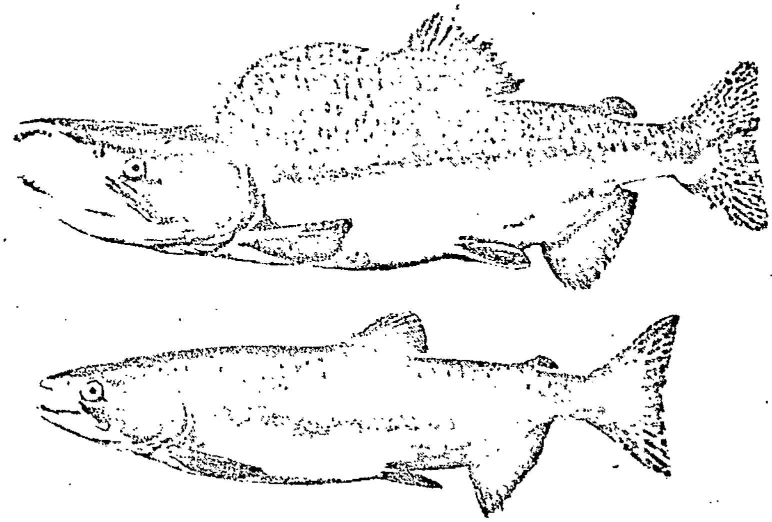


Fig. 31. Running individuals of the pink, male (upper) and female.

The well populated spawning grounds are mainly at depths of 20 - 25 cm, less often they reach the depth of 100, sometimes 150 cm. In dry years and when the spawning grounds are overcrowded, the nests can be found at a depth of 10 - 15 cm. The current in localities of the nests varies from 30 to 100 m/sec, sometimes reaching 140 m/sec. Directly over the redds, about 5 - 7 cm from the surface, the velocity is lower and rarely exceeds 60 - 70 cm/sec.

The temperatures during the spawning differ widely. In the river Bol'shaya in Kamchatka it varies from 5 to 14° (Semko, 1939), in the Amur from 6.0 - 15.5°, and the mass spawning occurs at 9.2 - 13.7° (Soldatov, 1912; Kuznetsov, 1928). In the Kurile Islands spawning is observed in the autumn at a temperature of 5 - 6°, and during the summer up to 14° (Ivankov, 1967). During the spawning period of the Sakhalin pink, fluctuations observed in water temperatures were from 7 to 19° (Dvinin, 1952). In the river Lesnaya during 1967, the temperature at the peak of spawning reached 24.5°. However, already at water temperatures 17° the activity of the spawners dropped, nuptial behaviour and cleaning of the ground were

discontinued. Maturation of the females was retarded; the males ceased 130
to extrude sperm. During that time spawning was observed only near the point of emergence of the colder ground waters. About 12 hours after slight rain which caused a drop in water temperature to 16 - 15.5°, the picture changed drastically. The fish became active, the nuptial plays were resumed, as well as cleaning of the ground and oviposition. Obviously, in this southern region, the upper spawning temperature lies within the limit of 16 - 17°.

Typical of the spawning grounds of pink in the river Bol'shaya are current velocity 30 - 60 m/sec, oxygen content 8.35 - 12.8 mg/1 (85-90% saturation), free carbonic acid approximately 3-4 mg/1 and pH greater than 7 (Krokhin and Krogius, 1937b). It has been observed that the spawning pink has significant effect on the hydrochemcial regime of the river, particularly during abundant runs. During the spawning and postspawning period, the quality of oxygen in the water drops, the content of free carbonic acid, nitrogenous substances and phosphates increases and pH drops (Semko, 1939).

Many rivers of Sakhalin, in which the pink spawns have clean, stony-sandy bottoms, well aerated water, sufficiently high winter water which is protected from freezing by profuse snowfalls. Our unit studied the spawning grounds on the river Belaya, a small second order tributary of the river Naiba (hydrochemical analyses were performed by A.N. Kanydyev). The bottom of the river is clean, stone and sand. The pink spawns there in the middle reaches, with the autumn chum reproducing below it and the masou above it. The nests are at depths of 20 - 40 cm, where average current velocities are about 40 - 50 cm/sec. Between the 1st of September and the 9th of October in 1960 the water contained up to 12 mg/1 of dissolved oxygen (saturation 93.5 - 104.7%). The quantity of free carbonic acid was from 3.8 to 5.0 mg/1, pH was from 6.5 to 7.0.

In another "pink" southern Sakhalin river, Lesnaya, with a clean stone and sand bottom, in many places rock bed, current velocities on spawning grounds were from 15 to 82 cm/sec. Between September and December the quantity of oxygen increased from 8.87 to 14.04 mg/1 (saturation from 79.9 to 96.1%), remained high until February, and gradually decreased to May, when it reached 10.94 mg/1. The quantity of free carbonic acid varied within 2.6 to 9.8 mg/1 and pH from 6.3 to 6.5 (Kandyev, 1967a).

During abundant runs in some localities up to 4 - 8, sometime up to 16 females were spawning per $1m^2$ (Kuznetsov, 1928; Vasilenko, 1959). Around each spawning female were several males; their number towards the end of the season might rise up to 8 - 10 (Soin, 1954; Strekalov, 1963). We counted in the Sakhalin up to 5 - 6 males around spawning females.

Cleaning the ground, digging holes and building of redds continues round the clock. Oviposition occurs at dusk and during the night. When illumination is low, oviposition can sometimes be observed at midday 131
(Wickett, 1959; Sheridan, 1960). As in other salmon species, the females after oviposition intensify digging movements, which favours rapid covering of the deposited eggs (Barsukov, 1964).

Spawning continues from 1 - 3 to 8 days. During cloudy weather, the redds are constructed more rapidly. Under those conditions the females which have deposited their eggs remain near the redds up to 10 - 13 days. The pink deposits its eggs commonly in 2 - 3 batches, sometimes one finds up to 4 groups of eggs in the redds. The eggs are rarely found on the ground surface, they are more often at a depth of 25 - 40 cm, sometimes deeper than 50 cm. Individual batches of eggs are placed inside the redd at distances 30 - 50 cm from each other, diagonally to the current and at different depths. Depending on the size of the females, solidity of the ground and current velocity, the width of the spawning redds varies from 60 to 150 and the length from 107 to 250 cm; when the ground is friable, the eggs are deposited more deeply (Kuznetsov, 1928; Semko, 1939; Taranets, 1939; Strekalova, 1963; Kanid'ev, 1967a).

When the runs are abundant, digging through earlier constructed nests has been observed. In view of this, the problem of the permissible density of filling the spawning grounds has long been considered. Calculation of the numbers of fish allowed to pass through to spawn was based on the size of the redds; it was considered necessary to assign to each female 1.5 - 2 m^2 of spawning surface (Kuznetsov, 1937; Semko, 1939). Taranets (1939) postulated that the maximum allowable filling is such that each female would be assured of 0.45 m^2 of spawning surface; such surface is required to distribute the eggs in the redds.

While admitting negative influence of the overcrowding on spawning grounds, one must not underestimate the fact that during mass runs the spawners prepare the ground better, and that this helps to utilise new spawning surfaces, while the fish that perishes after the spawning serves as fertiliser (Smirnov, 1947; Semko, 1954). For the pink, the eggs of which are washed by the subsoil current, the dense, frontal cleaning of large surfaces is very important. It improves permeability of the ground so that the eggs are well aerated. The necessary "natural melioration" of the spawning grounds is ensured precisely during abundant and repeated visits of the spawners in the reproductive localities.

The developing eggs of the pink are washed by the water which is in a continued process of exchange from the mainstream, as a result of which its quality is similar to that of the mainstream water. The physical and chemical regime of the spawning redds is somewhat more stable than that of the surface current (Vasiliev and Yurovitski, 1954; Wickett, 1958, 1962; Kanidyev, 1967a). According to Vasiliev (1956b), the average filtration rate of water in the redds of the river My in the autumn was 3.6 m/hr. Before the middle of September the water contained on the average 8.1 mg/l oxygen (from 6.24 to 10.0 mg), 2.8 mg/l of carbonic acid (from 1.2 to 5.6 mg/l). Later, before formation of the ice cover, the permeability of the ground was lowered, but the oxygen content in the sub-soil water rose to 9.9 mg/l (from 6.8 to 11.6), and carbonic acid 4.7 mg/l (from 2 to 10.2 mg/l); pH varied from 6.2 to 6.5. In the winter, before the freezing of the ground, the water in the nests contained 7.5 - 10.0 mg/l of oxygen, 8 - 10 mg/l of carbonic acid; pH dropped to 6.2 - 5.9. Freezing of the river right down to the bottom caused a catastrophic drop in oxygen content and abundant saturation of the water with carbonic acid. Observation on the development of eggs showed that at 3 - 4 mg/l of oxygen, more than 50% of the eggs died, while among the hatching embryos, half showed all kinds of deformities: anophthalmia, microphthalmia, cyclopism, microcephaly. In water containing 6.3 mg/l of oxygen, embryos had retarded growth, and at 7 - 8 mg/l of oxygen, development proceeded normally. Observing development in water containing more than 9 mg/l or oxygen, Vasiliev noted retarded development of respiratory organs and more rapid uptake of the yolk. Studies in that river allowed the conclusion that at a temperature not higher than 8 - 9°, the optimum oxygen content for the development is within 7 - 9 mg/l (Vasiliev and Yurovitski, 1954; Vasiliev, 1959b).

In the Sakhalin rivers the conditions of the development of the pink are slightly different. In the river Belaya at the depth of egg deposition during the hot period, the average daily temperature reached 18.2° (highest 19.2°). Current velocity in the nests varied from 0.45 to 1.63 cm/sec. In the water washing the eggs the quantity of dissolved oxygen in the autumn increased gradually from 9.23 to 11.09 mg/l; most frequent content of free carbonic acid was 3.73 - 5.89 mg/l (in some samples up to 14.51 mg/l); pH value varied from 6.4 to 7.2. In the river Lesnaya the water in the nests filtered with the speed of 0.2 - 1.6 cm/sec. From the beginning of incubation to the hatching, permeability becomes lower, and before the emergence of the young from the redds it increases again. During September-April the water contained 0.5 - 1.7 mg/l oxygen less than above the bottom (during incubation period, average 11.08 mg/l, during development of free embryos and larvae 12.17 mg/l). Better oxygen saturation of water was observed at the beginning of winter. The average quantity of carbonic acid during the period of incubation was 5.8 mg/l, and during the life of the larvae in the ground, 6.8 mg/l. The pH value from 6.25 to 6.42. In the redds in the river Thamerka, a tributary of the Lesnaya, a drop was observed in the oxygen content up to 5.41 mg/l (49.2% saturation). Judging from the data on the regime of the redds in the Lesnaya and in the incubator of the farm, which is provided with the water from that river, [illegible] ([illegible]) accepted as the optimal oxygen content in water for the development of pink 9 - 11 mg/l, but he observed normal development also at 8 mg/l. Probably, the population of that river has become adapted to development at a higher oxygen content than the pink of the river My or the river Iski (see below). It appears, however, that even in the basin of 133 the river Lesnaya, the pink is not uniform in this respect, if one takes into account poorer aeration of spawning grounds in its tributary, the river Znamenka.

There are other reports on successful development of the pink at fairly low saturation of water with oxygen. Such a picture was observed by Taranets in the river Iski, where the water in the spawning grounds contained from 4.7 to 8.8 mg/l of oxygen, at saturation 30 - 65% (Levanidov, 1968). Under experimental conditions, the Primore pink was able to develop at 3 - 4 mg/l of oxygen, while the eggs of the pink in the northern river of Tauy (district Magadan) develcped at an oxygen content from 5.5 to 8.0 mg/l (Lukina, 1966). In 1959 in a small tributary of the river Belaya, the water on one of the redds which I studied contained on the average 6.1 mg/l of oxygen and 14.2 mg/l of carbonic acid, the pH value varied from 6.4 to 6.8. In the autumn, average saturation of water with oxygen was 56.4%, and the lowest was 51.8%. The embryogeny of the pink had a normal course. In the subsoil stream of the pink spawning grounds of the rivers of British Columbia and South East Alaska, low oxygen content has also been observed. In one of the streams in the lower course, the water usually contained 4.8 - 6.1 mg/l, in the middle reaches, 6.3 - 7.4 mg/l and only in November the quantity of oxygen rose to 8.0 - 9.6 mg/l (McNeil, 1962, 1966).

The huge distribution range of the pink includes rivers with different hydrological and hydrochemical regimes, so that the fish becomes adapted to development under different, sometimes relatively harsh conditions. The autumn form is less demanding as regards water aeration. The ability of the pink to develop under different conditions is borne out by the practices of husbandry not only in the farms provided with well aerated river water, but also in incubators supplied with stream water poor in oxygen. Studying the development of the pink in the [illegible] farm, supplied with stream water, we found no abnormalities. On the basis of the study of the regime of redds in different rivers and incubators of Sakhalin farms, the following recommendations were made for the incubation of the pink eggs: oxygen saturation 65 - [illegible]%; it should not drop below 50% in the water flowing out of the incubators (Smirnov, [illegible]). When the incubators are situated in the basins of the rivers with particularly good gaseous regimes of spawning grounds, this value can be increased by about 10%.

Depending on the climatic conditions of the spawning regions and the times of oviposition, the duration of development varies in a wide range. In the river Karchatka the eggs incubate for 110 - [illegible] days ([illegible], 1939). In the river [illegible] at early spawning, the incubation takes about 30 days, at late spawning it is prolonged to 110 - 120 days and the period spent by the pink in the ground reaches 240 - 280 days ([illegible], [illegible]). In the southern rivers of Sakhalin, the eggs deposited at the beginning of the spawning incubated for 1.5 - 2 months, spawned in the middle of September, incubated for about 3 months, after which about another 5 months pass until the emergence from the ground. In the rivers of Alaska, the development of the eggs and larvae in the ground takes 5 - [illegible] and even [illegible] months ([illegible], [illegible]; McNeil, 1962).

The pink emerges from the nests at a length of 28 - 32 mm. The seaward migration can begin after the emergence from the ground or after a few weeks stay in the area of the spawning grounds. The fry lead a gregarious life (Hoar, 1954, 1958; Kamyshnaya, 1967). The mass descent is confined to the period of spring spate and takes about a month, but its duration is extensive. For example, from the southern Sakhalin rivers the pink migrates from the end of April to the middle of July; in the rivers, the young can be found also in August. The main bulk of the migrants are 30 - 35 mm long and weigh 200 - 250 g (Kuznetsov, 1928).

Spawning Productivity. Under favourable climatic conditions and optimal water levels on spawning grounds, the mortality of eggs in the nests of the Amur pink was estimated by Kuznetsov (1928) at 6.7%. Under less favourable conditions this value fluctuated from 12.8 to 67.5% (Taranets, 1939). In the Kamchatkan river Bol'shaya, the mortality in the nests was observed at 2 - 3% of the eggs (Semko, 1939). In the river Lesnaya, in Sakhalin, this value is on the average 9.2% (Kanidyev, 1967b), in the Naiba and Tym it varied from 18 to 25% (Rukhlov, 1968). The results of comparative observations are of interest. In the river My about 1.7% dead eggs were found in the pink redds, while in the nests of the summer chum, situated nearby, there were 2.8% (Strekalova, 1963). In comparison with the summer chum, the lower mortality of eggs of the pink can be attributed to the stability of the water supply of the redds and favourable gaseous regime (Nikol'skii, 1952, 1954a).

Also considerable are the fluctuations of the migration, and the downstream migration coefficient, the percentage of migrants from the deposited eggs. This coefficient in the Karymayskii stream varies from 0.? to 5.7% (Semko, 1954). The migration coefficient of the pink in

1950 - 1960 from the five rivers of the Amur basin (common percentage) varied from 0.8 - 19.8%; average value for the even years (disregarding a catastrophically low figure for one of the seasons) was 9.1% and in the odd years 9.3% (Levanidov, 1964b). In the river Lesnaya during 9 years of observation, fluctuations were found to be about tenfold, from 2.7 to 26.3%, average figure being 15.5% (Kanidyev, Kostyunin and Salmin, 1970). The migration coefficient of the pink in the Canadian streams of MacClinton varied from 6.9 to 23.8% (average of 6 cycles 14.5%), and in Port John from 0.88 to 16.47%, average for 10 years being 5.63% (Pritchard, 1948; Hunter, 1948, 1951, 1959). In Alaska, in the stream Sashin between 1940 and 1959 the migration coefficient varied from 0.1 to 22.8%, the small average figure being 5.16% (Merrel, 1962). However, in other streams of south-eastern Alaska, the mortality before the emergence of the larvae from the ground proved high; during five season it varied from 75 and 99% (McNeil, 1966).

Mortality is caused by a variety of reasons. One of them is the incomplete deposition of eggs. Under favourable conditions, several eggs 135
remain in the body of the female. In the river Lesnaya even when the spawning grounds are obviously overcrowded, the unspawned eggs constituded about [illegible] (Kanidyev, 1967b). However, this figure in some waters during the years of abundant runs, reaches [illegible] (Semko, 1954). Ofcourse, all the eggs which do not get into the nests perish. These losses vary in broad limits from 15 to [illegible] and even more (Taranets, 1939; Semko, 1954; [illegible], 1958; Kanidyev, [illegible]; [illegible], 1972). During hot, dry years many spawners die before spawning.

To the reasons sharply lowering the effectiveness of spawning belong also silting of the redds, and especially, freezing of the spawning grounds (Kuznetsov, 1928; Smirnov, 1947; Nikol'skii, 1952, 1954a). When the level of the rivers is high during spawning, the pink deposits its eggs in places which dry up after the lowering of the water level; such spawning is ineffective. Autumn spates, during which a part of the utilized spawning grounds are washed away or silted up, lead to large-scale mortalities.

In individual water systems large numbers of the young are destroyed by the predatory fishes, including large fingerlings of salmon. The pink are subject to considerable destruction also near the river mouth and in the inshore regions of the sea (Semko, 1954; Bakshtanski, 1968).

The return coefficient of the spawners, a percentage of the migrating smolts, in the Amur pink during even years 1952 - 1960 varied from 0.9 to 12.5% (average figure being 5.04%; commercial catches disregarded), and during the odd years from 0.5 to 10.0%, average 4.4% (Levanidov, 1964b). The return in the Lesnaya during 8 cycles varied from 0.4 to 4.7%, average 1.62% Kanidyev, et al., 1970). Into the Canadian streams MacClinton and Port John the percentage of the returning fish was on the average 1.02 and 2.67% (Foerstera 1955).

The Development of the Pink.

The Development of the pink was studied in 1952, 1953 and 1959 in the Sokolovskii farm, in 1954 in Adotymovskii and in 1965 in Lesnaya. Some material was collected in other fish farms of Sakhalin. Observations on the development in the nests were carried out in the river Belaya, a tributary of the Naiba. Work was carried out also in the Umbskii farm and on the river Teriberka (basins of the White and Barents Sea), where the pink had been introduced.

The Reproductive Products. The males of the pink produce milt in small batches with a low concentration of Spermatozoids. An average volume of the ejaculate was 6.5 ml, but in one case it exceeded 20 ml. An average spermatozoid content per 1 mm^3 of the pink sperm is about 18 million and in each individual ejaculate, about 64 million spermatozoids occur per gram of live weight of the male (Smirnov, 1963a, 1964b).

At a temperature of 10 - 11°, spermatozoids actively move in 136
water for 50 - 55 seconds, and weaker side-to-side movements were observed up to 1 - 2 minutes. The sperms rapidly lose in water their ability to fertilise eggs. At a temperature of 9.8 - 10.1°, 10 seconds after the sperm has been diluted with water, 15 - 18% fewer eggs were fertilized than the control eggs, which were inseminated with the fresh sperm; 30 seconds after dilution only a half or even 30% of the eggs were fertilised, and after 60 - 90 seconds, only isolated eggs. In some experiments the spermatozoids retained their ability to fertilize isolated eggs for 2 - 3 minutes (Smirnov, 1963c). At low temperatures, the sperm retains its fertility in water for a longer time.

Table 8.
Size and Weight of the Sakhalin Pink.

River	Length of females, after Smith, cm.	Diameter of eggs, mm	Weight of eggs, mg.			
			Range	M	±m	σ
R. Takoi	45--60 (51.0)	5.2--6.4	118--198	154.95	1.85	16.0
Lesnaya	49.5--57.2 (51.0)	5.5--6.7	120--212	157.35	2.13	1.78

Note: Data on the pink of the river Lesnaya are collected at our request by A.I. Kanidyev, to whom we take this opportunity of expressing our gratitude.

The pink deposits fairly large eggs. Of the studied females, 68% had eggs weighing from 141 to 170 mg. There is a tendency to an increase in the weight of eggs with the increase in the size of the females, but there are also large females with small eggs and vice versa. It is interesting that in the pink introduced into the Barents and White Seas, the fecundity increased and the size of the eggs decreased (Persov, 1963; Galkina, 1965; Smirnov and Kamyshnaya, 1965). According to our data, the weight of the mature eggs in the Kola pink varies from 83 to 138 mg (M = 119, 85±5.25). Their proportion of dry weight and protein is somewhat higher and the fat content lower (See Table 1). The calorific value of these small eggs is almost 35% lower (Smirnov et al., 1968). The egg has a pale-orange colour. Comparison with the samples of the colour Atlas shows that the colour of the mature eggs varies within the limits of wavelength 584.4 to 589 nm.

Within 1 minute after placing the eggs in water at a temperature of 9.8 and 9.9° fresh milt fertilized 27 and 37% fewer eggs than in the control. Within 2 minutes, in the first series, 30% were fertilized and in the second, 15% of the eggs. Fertility of the eggs was diminishing and soon proved to be negligible, but in samples of corresponding series, 137
inseminated after 10 and 12 minutes, the percentage of fertilized eggs approached 10. Isolated eggs retain fertility to 15 minutes and more (Smirnov, 1963c).

The Embryonic Period of Development.

In 1952 and 1953, observations were conducted on the development of the eggs of pink, at the same time as on the fertilized eggs of autumn chum and of hybrids between these two species (Smirnov, 1953a, 1954a, 1964a,b).

In 1959 it proved possible on two occasions to inseminate at the same time eggs of the pink and masou and to obtain hybrids between them. The eggs were incubated in a single rearing apparatus, which allowed comparison of the rate of development of these species and their hybrids. Observations were conducted in the Sokolovskii farm; reports on the regime of its incubator are given on p.38. The description contains some observations also on other batches of eggs, some of them developing in the Lesnaya farm. The incubator in the latter locality is supplied by well aerated river water and has a regime close to that existing in the river Lesnaya, the characteristic of which was given above.

Stage 1. Hydration of Inseminated Egg; The Stage of Embryonic Disc Formation. Observations on weight changes of the hydrating eggs were conducted at a temperature of 10.2°. Eggs were collected from two females. The eggs from the first female, before being placed in water, had an average weight of 154.2 mg, those of the second 127.3 mg. Intensive hydration occurred between 10 and 30 minutes and was completed after 40 - 50 minutes after placing the eggs in water. Hydrated eggs weighed 166.5 and 138.1 mg; weight increase was 8.0 and 8.5%. Hydrated eggs are not strictly spherical. We encountered eggs with diameters from 5.6 to 7.9 mm. The dimensions of developing eggs of the Sakhalin pink vary from 5.5 to 8.3 mm, with M = 6.9 ± 0.004 (Galkina, 1965). The diameter of the eggs of the Amur pink is 6.0 mm (Vasiliev, 1959b).

During the process of hydration, the egg membrane becomes solid and loses its transparency. Its surface is covered by a dull, white coating. The micropyle field, situated near the animal pole of the egg and with a diameter of 1.6 - 1.9 mm, is devoid of the white coating. Here lies a funnel-like depression leading to the micropyle opening.

In developing eggs, fixed in an isotonic formalin solution, the thickness of the membranes varied from 55 to 80 mk ($M=69.9 \pm 0.60$). The egg membranes of the pink are thicker than those of the other salmon species and its live eggs withstand pressure up to 8 - 9 kg (Nikol'skii and Soin, 1954).

Special experiments revealed significant changes in the sensitivity of the hydrated eggs to mechanical stimuli (Smirnov, 1954b). The design of the experiments is similar to that which was used in the study of sensitivity of the eggs of chum. In the first series, each consecutive batch of developing eggs was subject to the action of a vibrator, until 138
its axis performed 100 rotations; those of the other series were exposed to 300 rotations. Experimental and control eggs were incubated in the same apparatus at a temperature of 7.8 - 9.6°. The results of the mechanical influences were determined by the number of dead eggs (Table 9). Mature eggs before entry into water are resistant to tactile stimuli.

Table 9.
Mortality of the Eggs of Pink caused by Mechanical Influences at Different Stages of Development (after Smirnov, 1954b).

Age after fertilization	Stage of Development	Egg Mortality, %	
		First Series	Second Series
0	Before placing eggs in water	0.5	19.1
15 min.	Beginning of water uptake	--	72.8
30 min.	Continued hydration of eggs	21.0	95.4
1 hour	Embryonic swelling is formed	3.1	84.4
1.5 hours		--	33.3
2 hours		6.3	15.7
3 hours		4.4	4.8
5 hours		4.9	6.9
8 hours		2.8	--
10 hours	Beginning of Cleavage	--	20.0
12 hours	2 - 4 blastomeres	0.9	32.0
18 hours	8 blastomeres	3.4	--
1 day	16 blastomeres and more	4.0	24.3
1.5 days	Large cell morula	1.3	25.8
2 days	Large and small cell morula	15.5	25.9
3 days	Small cell morula, in some cells blastula	6.8	55.6

Table 9 cont.

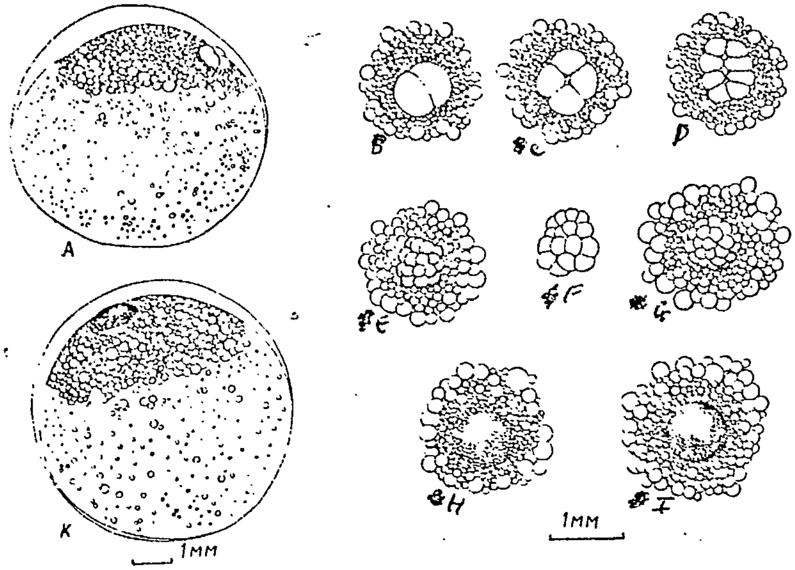
Age after fertilisation	Stage of Development	Egg Mortality, %	
		First Series	Second Series
4 days	Blastula	15.5	44.0
5 days	Beginning of Gastrulation	--	17.2
6 days	Stage of "Embryonic knot"	24.4	--
7 days	Stage of "Embryonic streak"	--	52.0
9 days	Embryos about 2 mm	35.3	74.8
12 days	Stage of 15 - 18 segments	--	77.6
13 days	Stage of 25 - 30 segments	16.5	--
15 days	Stage of 40 - 45 segments, caudal bud formed	--	36.9
16 days	Beginning of circulation	1.4	--
18-19 days	Epiboly completed in some embryos	4.9	29.5
22-24 days	Appearance of pigment in eyes	0.5	1.9
28-30 days	Eyes are gray	0.5	0.0
39-40 days	Laying down of ventral fins	1.8	0.0
51 days	Onset of formation of gill filaments	0.5	0.0
63 days	Before hatching	0.0	0.0

Soon after the beginning of hydration, the sensitivity of the eggs rises sharply, reaches its maximum in about 30 minutes and then gradually drops and in about 2 hours the eggs become insensitive. During that time the eggs remains completely at rest. 139

Stage 2. Cleavage of the Embryonic Disc. Towards the beginning of cleavage the embryonic disc assumes a shape close to a hemisphere, slightly narrower at the base. Its diameter in the eggs of the pink from the river [illegible] was 0.7 - 0.9 mm (Vasil'ev, 1959b), and in those of the pink from the river Kalininka 0.9 - 1.0 mm (Frolenko, 1959). My data on measurements of the blastodisc up to the stage of 4 blastomeres are close to those of Vasil'ev. After the third and fourth division, the blastomeres occupy slightly lower surfaces. As in the chum, the blastodisc is situated above the accumulation of small fat droplets (Fig. 39).

Fig. 39. Different stages of cleavage in the eggs of the pink. A,K - live cells, drawn in transmitted light at stages of 4 blastomeres and blastula respectively. B - I - embryonic discs, removed from fixed eggs with adjacent part of yolk and drawn after staining with methylene blue.

B - F - stages of 2,4,8 and 16 blastomeres. G - Formation of 32 blastomeres. H - large cell morula. I - Small cell morula.



At a temperature of 9.0 - 9.5° the first cleavage furrow appeared 11 - 12 hours after insemination, the second cleavage occurred between 17 and 18 hours, third after 21 hours and fourth after 26 hours. At the age of 30 hours, 32 blastomeres were formed and in the middle of the second day, 64 blastomeres. The eggs were not dividing at the same times; in some of them the onset of the consecutive stage was retarded by 2 - 2.5 hours. In the Lesnaya farm at a temperature of 13.0 - 14.7° the first division occurred 8.5 hours after insemination, and up to 128 blastomeres were formed towards the end of the first day.

At early stages of cleavage, the embryonic discs are 0.4 - 0.5 mm high. Up to the stage of four blastomeres, these discs are round. During 140
the next cleavage they become somewhat elongated; the oval shape is retained by the discs also at the stage of 16 blastomeres, but later it assumes

a round form. During the fourth division the furrows run in the equatorial plane and two layers of cells are formed. In the middle of the second day of development a large cell morula is formed, and towards its end a small cell morula (Fig. 32, I). At that age, the diameter of the surface blastomeres decreases to 60 - 65 mk.

The sensitivity of the eggs to mechanical stimuli increases with the onset of cleavage. In the second series of experiments, the mortality of such eggs after exposure to vibration increases to 20% and with the beginning of the second division up to 32%. This effect was, however not observed when the action of the vibrator was of short duration.

Stage 3. The Blastula. At a temperature of 8.4 - 8.6°, the embryonic discs of individual eggs began to grow towards the end of the third day, and their diameters increased to 1.2 - 1.3 mm. With temperature fluctuations from 12.6 to 14.7°, a similar condition was reached in 42 hours. The cells of the upper layer of the blastula had a diameter of 30 - 35 mk, but in some of them, they had already decreased to 25 - 23 mk. The growth of the blastodisc serves as an indication of the formation of the blastomere blastula. The superficial blastomeres became more compact with time and form a layer of microscopic polygonal cells, different from the loosely assembled and larger, lower cells. Towards the end of the stage the diameter of the blastodisc reached 1.8 - 2.0 mm and covered the zone of the small fat droplets (Fig. 33,A). The sensitivity of the eggs to mechanical stimuli continued to rise.

Stage 4. Formation of the Embryonic Layers. Towards the end of the seventh day (about [illegible] degree days) the diameter of the blastodisc reached 2 mm. The diameter of the cells of the ectoblast decreased by that time to 10 - 1[illegible] mk. The disc in its central part became so much thinner that one could see through it the small fat droplets situated below. The margins of the blastodisc covered a part of the large fat drops; the diameter of the latter continued to increase. In the caudal part of the embryonic disc the "embryonic knot" was formed (Fig 33, B). With the growth of the embryonic shield and "embryonic streak" was formed. The differentiation of the embryonic layers and of the chord began. At the age of 9 days, the diameter of the embryonic disc was 2.5 - 3.0 mm, and the length of the embryo 1.2 - 1.3 mm (Fig. 33,C). In the Lesnaya farm at a temperature of 11.0 - 14.7^{o}, gastrulation began at the age of 3.5 days; by the end of the fifth day, the diameter of the blastodisc reached 2.2 - 2.5 mm, and the length of the embryo 0.8 - 1.1 mm. Sensitivity of the eggs at the beginning of gastrulation increases and they should be protected at that time from all possible mechanical disturbance.

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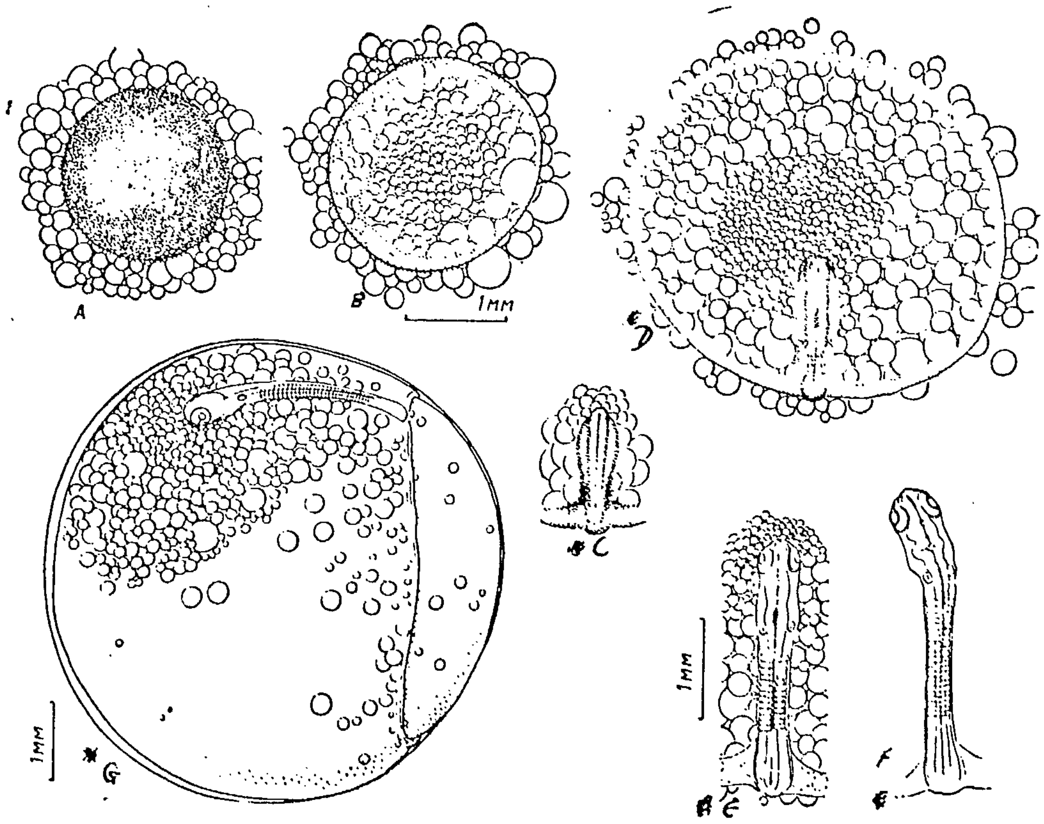


Fig. 33. Development of the Pink from the Blastula stage to the beginning of the formation of the head and trunk. A - late blastula. B - beginning of formation of "embryonic knot". C - part of embryonic disc with "embryonic plate" 1.3 mm long. D - beginning of formation of trunk segments, length of embryos 1.5 mm. E - embryo 2.6 mm long, with 13 segments. F - embryo 3.1 mm long with 22 segments. G - live egg with embryo at 30 segments stage; blastoderm surrounds more than 2/3 of yolk sac.

<u>Stage 5. Formation of Head and Trunk of the Embryo.</u> At the end 142
of the 10th day (82 - 86 degree-days) the first somites developed in the embryos and the brain vesicles began to form. The diameter of the embryonic disc towards that time increased to 3.5 - 4 mm, embryos reaching the length of 1.5 mm or slightly more (Fig. 33,D). Under the conditions in the Lesnaya farm, the first somites appeared at the end of the 6th day.

In the Sokolovskii farm during the 12th day (113.6 degree-days) the embryos' length was 2.4 - 2.7 mm. The smaller among them had 5 - 7 somites. The rudiments of the optic cups were clearly visible by that time. At the tail end, Kupfer's vesicle could be clearly seen. The blastoderm surrounded a part of the surface of the yolk sac with a diameter of 4.5 - 4.7 mm. In embryos with 13 somites crystalline lenses were clearly visible in the eyes, the otic capsules were laid down, the rudiments of the head and trunk were differentiated (Fig. 33,E).

Ford and Newstead (1958) noted the origin of nephrotome and of the pronephric folds and the embryos 3.33 mm long, with 18 somites. Nephrotome was situated in the region of the 6 - 7th somite. At the same time, an elongate, dense cell mass, which represented the rudiment of the main blood vessels, was found below the chord.

In our series, the embryos 3 mm long had 22 somites (Fig. 33,F).

The differentiation of the section of the brain continued, encephalomeres were observed. Otic capsules at that time were at a large distance from the eyes, the caphalic section was large.

At the age of 13 days (122.7 degree-days) the embryos reached 3.5 - 4.0 mm. They had up to 33 - 35 somites (Fig. 33,G). The tail bud began to form (slightly earliėr than in the chum). Under the anterior section of the head the pericardial cavity began to form. The growing blastoderm covered more than a half of the yolk sac. From that time onwards, the sensitivity of the egg to mechanical disturbance decreases.

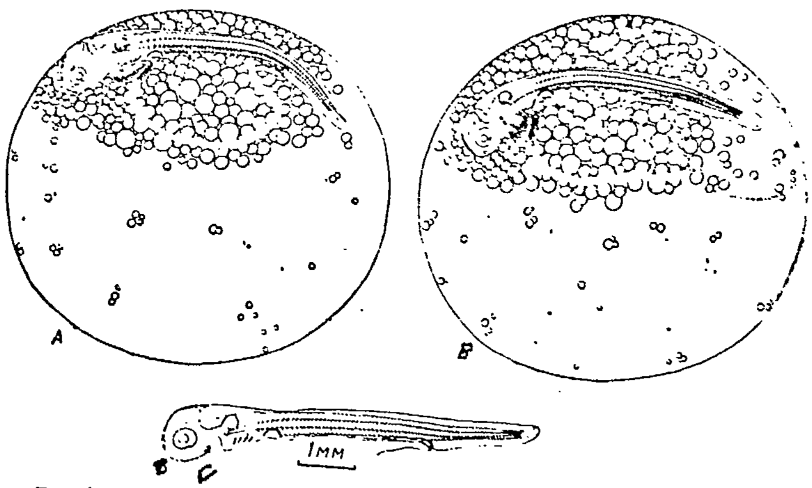
Stage 6. Separation of the Posterior Trunk from the Surface of the Yolk Sac. In eggs developing in the Sokolovskii incubator, this next stage began at the age of about 17 days (155 - 160 degree-days), and in the Lesnaya, at the beginning of the 13th day. The embryos were 4.2 - 4.5 mm long.

After the formation of the posterior section of the intestine and anus and the first appearance of the caudal section, the posterior part of the trunk began gradually to detach from the yolk sac. This process was accompanied by the development of the preanal fin fold. In the pink, the anus formed at the level of 40 - 43 segments. At the beginning of this stage, the rudiments of the opercula appeared, the olfactory placodes were distinguishable. At the length of embryos 4.75 mm the beginning of the histological differentiation of the components of the pronephros was observed. In the embryos 5.24 mm long the pronephric glomeruli were observed, and the maximum development of the pronephros was reached at the length of 16.66 mm (Ford and Newstead, 1952).

At the age of 17 days in a few embryos, weak contractions of myotomes and of the cardiac tube were observed. In such embryos, the epiboly was not yet completed and the small oval yolk plug was still present. Under the conditions of the Lesnaya farm, however, the embryos began to move after the completion of epiboly. It is possible that in the former case, the development of mobility was stimulated by the lower oxygen content of the water.

Before the closure of the yolk plug, the sensitivity of the eggs to mechanical disturbances sharply increased.

Stage 7. Development of the Subintestinal-Vitelline Circulation System. The appearance of the blood stream was observed at the end of the 19th and the middle of the 20th day of development (178-183 degree-days). Such embryos were 5.5-6.0 mm long. At the age of 19 days they had up to 58, and at 19.5 up to 61-62 myotomes (Fig. 34,A). Under the conditions of the Lesnaya farm, circulation began at the age of 14 - 15 days. At that time, the temperature of the water during the morning hours dropped to 10°.



tem i ys- 5.7 mm. B - Beginning of the formation of the capillary net on the yolk sac, length of embryo 5.? mm. C - appearance of pigment in the eyes, length of embryo 6.7 mm. A and B, drawing of embryos removed from eggs, in vivo. C - embryo drawn directly after separation from the yolk sac.

Circulation in the pink began 1 - 2 days later than in the masous, incubated in the same apparatus in the Sokolovskii farm. The heads of such embryos began to separate from the yolk sacs. Otic capsules were separated from the eyes by the distance equal to the width of about 9 trunk myotomes. The volume of the brain became much larger. The buccal funnel was noticeable. The rudiments of the opercula appeared. The form-
ation of the olfactory pits began. At the bases of the first three myo- 144
tomes, slightly to the side of the trunk, appeared the rudiments of the pectoral fins. Viewing under the microscope live embryos in transmitted light, slightly above and behind the pectoral fins one could see the first glomeruli of the pronephros. The unpaired fin fold was formed, best developed below. The preanal fold extends along 16 - 17 myotomes.

At this stage, blood had a pale colour. The blood stream in the dorsal aorta reached the first caudal segments, moved downwards, skirted around the posterior intestine and along the subintestinal vein moved to the left side of the yolk sac. There the subintestinal-vitelline vein ascribed a small arc and carried the blood to the heart.

In the pink, the blood circulation might begin also at a slightly earlier stage of development. At the same Sokolovskii farm in 1953, the movement of the blood was first observed at the age of 16 - 17 days (150 - 160 degree-days). Such embryos were 5.4 - 5.6 mm long and had 58 - 60 myotomes, 42 - 43 of them trunk myotomes. In some embryos of this series the movement of blood began before the completion of epiboly. Speeding up in the functioning of the circulatory system is related by us with the slightly poorer conditions of aeration of the eggs.

Subsequently, the blood supply extends to the continuously larger part of the caudal section. The subintestinal-vitelline vein descends lower and fine capillaries appear on the yolk sac (Fig. 34,B). The embryos move their tails from one side to the other. Under the conditions in the Sokolovskii farm, this stage lasted 2.5 - 3 days, slightly longer than in the masou. After the completion of epiboly the eggs become highly resistant to tactile stimuli and vibration.

<u>Stage 8. Origin of the Cardinal Veins and of the Mixed Subintestinal-Vitelline and Hepatic-Vitelline Circulation.</u> Towards the end of the 22nd and beginning of the 23rd day (206 - 211 degree-days) the length of the embryos reached 6.4 - [illegible] mm; the number of myotomes rose to 67 - 68, of which 23 - 24 were situated behind the anus. The numbers of erythrocytes increased and the blood assumed a bright red colour. Blood was supplied at the beginning of the stage to 10 - 12 segments. From the caudal vein, blood began to flow not only into the subintestinal vein but also into the newly-developed posterior cardinal vein. On the yolk sac behind the trunk of the embryo appeared more than 10 wavy capillaries, between which existed anastomoses. The subintestinal-vitelline vein descended, became longer, collected blood from the vessels of the left and right sides of the yolk sac and carried it to the heart.

The appearance of melanine in the eyes of embryos of various series was noted at the age of 22 and 23 days (213 and 215 degree-days), when they were 6.5 - 6.9 mm long and had 73 - 75 myotomes (Fig. 34,C). The report on the beginning of pigmentation of eyes at [illegible] degree-days and length of [illegible] mm is erroneous (Tevlova, 1951).

At the stage described here, the tip of the chord is slightly bent upwards. The unpaired fin fold has become longer. The pectoral fins have grown markedly and their bases assumed slanted positions. In the stato-acoustic organs, semicircular canals have begun to form; the distance between them and the eyes has diminished. The head has begun to straighten out quite noticeably.

Two pairs of gills are supplied with blood. Capillaries have formed on the upper surface of the head. The caudal artery has come closer to the germinal segments. The first segmental vessels have made their appearance. From the liver, to the left and right side of the yolk sac run hepatic veins, along which blood flows to vessels formed by the sub-intestinal-vitelline vein. The capillary network supplied by the hepatic veins grows rapidly, while the supply of blood to the yolk sac through the subintestinal vein continues to diminish. With the increase in the size of the embryos and the development of the capillary network, oxygen utilisation rapidly increases. Whereas thousands of 26-day-old embryos at the stage of poor eye pigmentation at a temperature of 6.2 - 6.9° utilised in an hour 0.3 mg of oxygen, a week later, at 7.9 - 8.3° this figure increased to 0.6 mg (Wickett, 1954).

Stage 9. Formation of the Hepatic-Vitelline Circulation System. The subintestinal-vitelline vein became empty by the 28 - 29th day (264 - 273 degree-days), when the embryos reached the length of 7.5 - 8.2 mm. From that time, the yolk sac is provided with blood only by the hepatic veins. In such embryos, the caudal section is markedly longer. The number of myotomes in it dropped by 2 - 3. The unpaired fin fold on the dorsum reached the first segments and became much broader. The bases of the pectoral fins assumed semi-vertical positions. The head became higher, the eyes grey. In the otic capsules, semicircular canals continued to develop; numerous small otoliths fused into large ones.

At the beginning of this stage, 3 pairs of gills were supplied with blood. The vessels of the occipital regions developed. Segmental vessels appeared in almost all trunk myotomes. Almost the entire surface of the yolk sac, with the exception of a small part below the head was covered by capillaries. From the right side, blood started to flow to the heart along the right branch of the marginal vitelline vein. The posterior section of the intestine was covered with the capillaries of the posterior mesenteric artery, along which blood flowed to the subintestinal vein. Fig. 35, A (31 days, 293 degree days) gives an idea of the level of differentiation of embryos towards the end of this stage. Such embryos from time to time tilt their bodies to the left, or the right side and begin to smoothly execute swimming movements from side to side.

Stage 10. Differentiation of the Upper and Lower Cones of Myotomes.

Upper and lower cones of myotomes in the tails of most embryos appeared at the age of 32 days (303 degree-days), at a length of 10.6 - 11.5 mm. In some embryos they were observed a day earlier, in other, later. In the Lesnaya farm, the 10th stage began at the 29th - 30th day. Such embryos had large, black, irridescent eyes. The opercula covered the first gill. In the olfactory pits, subdivisions were observed. At the place of the future anal fin, muscle bundles (rudiments) appeared. The place of the laying down of the dorsal fin was marked by a slight broadening of the fin fold and by an accumulation of mesenchymal tissue. The bases of the pectoral fins assumed almost vertical positions and the fins began to receive a supply of blood. Four pairs of gill arteries became functional. Segmental vessels developed in all the caudal myotomes. The marginal vein descended to the ventral side of the yolk sac. Yellow-greenish pigment appeared in the lumen of the intestine.

On the 34th day (323 degree-days) the rudiments of the upper and lower cones were present in all myotomes (Fig. 35,B). From that time on, in embryos removed from the egg, the yolk sac assumed an oviform shape. The entire yolk sac is covered by capillaries. The length of the capillaries per 1 mm^2 of its surface reached 3.5 mm. More rapid fusion of the small, and formation of the large fat drops was observed.

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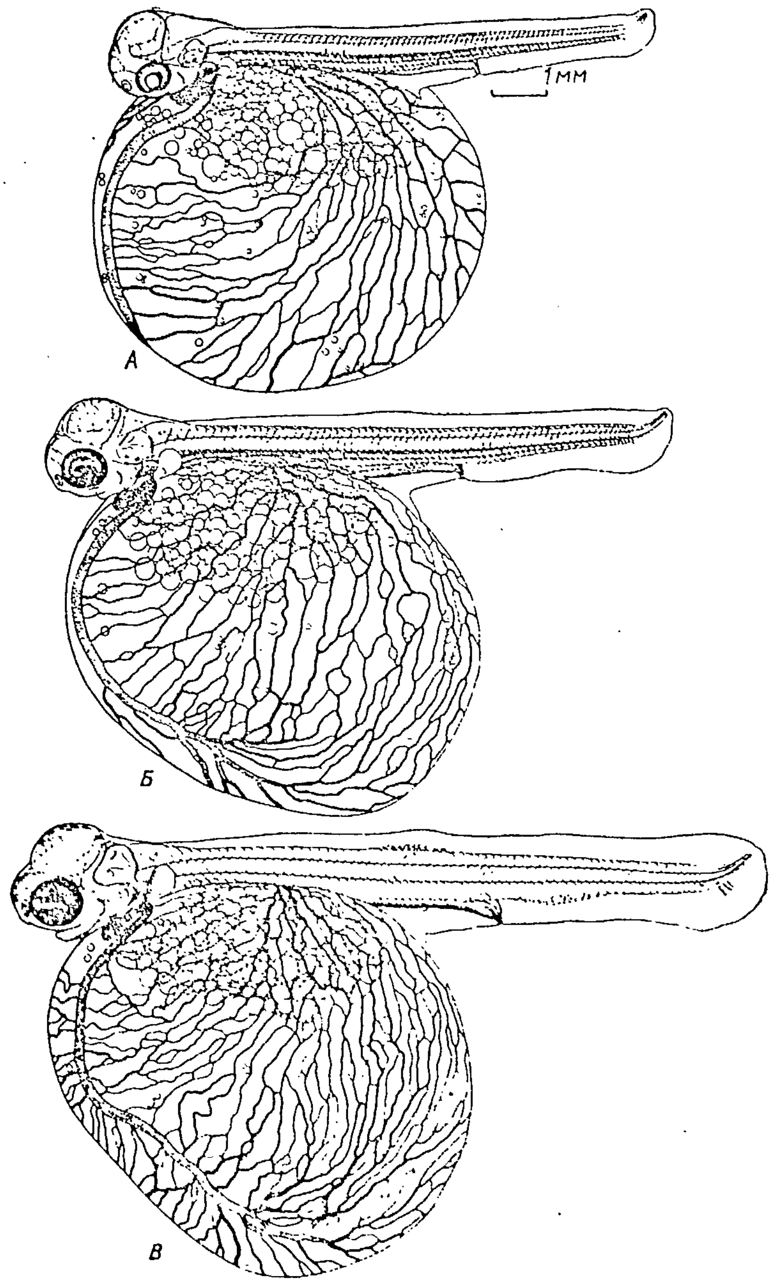


Fig. 35. The pink at various stages of the formation of the vitelline circulation and development of the upper and lower cones of myotomes. A - age 31 days (293 degree-days), length of embryo 10.4 mm. B - age 34 days (323 degree-days), length of embryo 11.4 mm. C - age 40 days (392 degree-days), length of embryo 14.1 mm.

At 38 days (370 degree-days) the embryos were 12.6 - 13.3 mm long. Their pectoral fins became capable of movement. The process of the formation of the hypurals began. At the base of the lobe of the caudal fin, the first capillary loops began to form. They appeared also along the myosepta of the first trunk myotomes.

By 40 days (392 degree-days) the embryos grew to 13.5 - 14.5 mm. The heads of the embryos began to elongate. The lower jaw reached the vertical line drawn through the centre of the eye. The opercula covered two pairs of gills. The hyoid vessels become functional. On the upper surface of the head developed a close capillary network. The length of the capillaries per 1 mm^2 of the surface of the yolk sac increased to 5 mm. The volume of the urinary bladder became larger. In live embryos under the microscope, newly developed hatching glands could be seen. Muscle bundles were clearly observable in the dorsal fin. From 3 to 4 lepidotrichs appeared in the caudal fin and the dorsal part of the lobe grew larger. During this stage, a rapid growth of the caudal section was observed, in which formation of vertebrae took place. The unpaired fin fold continued to broaden. The ventral fins were laid down. The first melanophores appeared on the surface of the head (Fig. 35,B). In the pink, the chromatophores appear later than in all other Pacific salmon species.

In embryos 14.7 mm long, the formation of the cartilaginous base 143
of the skull is completed, its lateral walls are formed, the development

of cartilage takes place in the gill arches and in the rudiments of the pectoral fin girdle (Ievleva, 1951).

During this stage, the embryos do not move much within the membranes, only rarely performing a few movements with their pectoral fins. Now and again they become agitated and carry out a few sinuous movements. At the end of the stage some individuals begin to move their jaws weakly.

Stage 11. Development of the Jaw Mobility and of Opercula; End of Incubation. At the beginning of this stage, the visceral apparatus becomes mobile. In a large part of the embryos, this occured at the stage of 45 - 47 days (445-466 degree-days), when they reach the length of 15 mm or over. By that age, otic capsules move maximally close to the eyes. Opercula cover three pairs of gills, on which there appeared rudiments of filaments. The growing lower jaw almost reaches the level of the anterior margin of the eye (Fig. 36,A).

The expanded caudal section constitutes about 35 - 36% of the total length. The formation begins of the skeletal elements of the dorsal and anal fins. The pectoral fin lobes become large, their bases narrow. The ossification of the parts of the dorsal girdle continues. The embryonic fin fold on the back begins to contract in length.

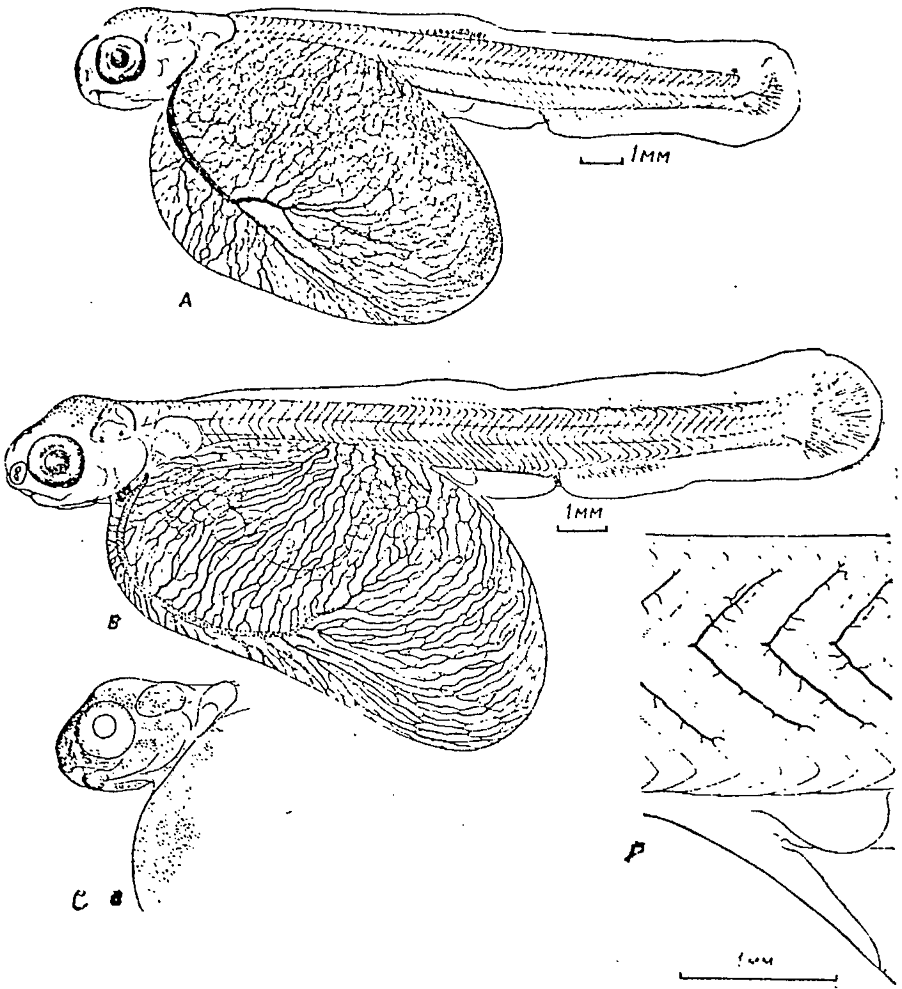
The density of the vascular network on the yolk sac continues to increase; the net of capillaries on the head, in the integument and caudal lobe enlarges. Intersegmental capillaries have developed along the entire trunk and on the first caudal myotomes. The melanophores in the integument of the head became more abundant, and turned dark; small orange-red lipophores appear.

At the age of 56 days (560 degree-days) the embryos reached the length of 18 mm and over. They became able to move their eyes. Opercula grew up to the last pair of gills. Contact was established between the buccal and branchial cavities. Gill filaments grew to 0.15 - 0.17 mm and capillaries appeared in them, as well as in pseudobranchs. The caudal section now constituted up to 36.5 - 37.25% of the total length. In the tail, 13 - 14 lepidotrichs appeared. The contour of the adipose fin was drawn. At that time, the hatching glands, which are particularly abundant in the pink, are well visible (Fig. 36,C).

By the time of hatching, the capillary network on the yolk sac reaches its highest development. There are up to 6.5 mm of capillaries per 1 mm^2 of its surface; this is less than in related species. The vessels branching off from segmental arteries form a fairly dense net along the spinal cord and near the body surface (Fig. 36, D). The upper surface of the head was covered by melanophores; they are smaller on the back, paler 150
and sparse. Small reddish lipophores are also more abundant on the head, sparse on the back; behind the dorsal fin they appeared at the base of the fin fold; they are somewhat more abundant at the place of the developing adipose fin.

At 10.4 - 10.7° the stage took 20 - 23 days.

Fig.36. The pink at the end of incubation of egg. 149
A - age 49 days (455 degree days), length of embryo 17.9 mm.
B - age 64 days (645 degree days), length of hatched embryo 18.9 mm. C - topography of hatching glands. D - net of capillary vessels in the integument above ventral fins during hatching.



<u>Stage 12. Passive Condition of Free Embryos</u>. The first embryos 150
hatched during the 64th day; after 2 days, hatching became abundant and ended during the 70th day (from 645 to 708 degree-days); temperature during incubation varied from 10.7 - 8.4°. Under the same conditions the eggs of the pink incubated longer than those of the chum (according to the number of days about 20% longer, according to degree-days 12% longer).

As in the rivers, where depending on on the time of spawning and water temperature the eggs incubate for 1 - 1.5 to 4 - 5 months; in fish farms, these periods are also subject to considerable fluctuations. In the Sakhalin farms, mass hatching takes place at the age of 50 - 150 days, and the number of degree-days varies from 300 to 740. The changes in the period of incubation, depending on the time of the collection of eggs, under conditions existing in the Lesnaya farm--which is provided with river water--are given in Table 10. The egg collected in the autumn develops at a low temperature for a very long time, but the number of degree-days is smaller; the pericd of hatching is also much extended.

Table 10.
Duration of the Incubation period of Pink eggs collected at various times in the Lesnaya fish farm during the 1964/65 season.

Date of Collection	Beginning of hatching: days	Beginning of hatching: degree-days	Duration of Hatching, days
25--31/VIII	55--59	536.0--523.9	up to 21
7--9/IX	70--75	508.4--504.7	up to 24
16--19/IX	80--84	446.4--433.9	up to 34
25--29/IX	88--92	386.5--346.5	up to 50
5/X	104	300.4	39

The embryos of the batch described here were from 18.2 to 21.7 mm long on hatching (the size of their absolute majority was 19 - 21 mm; measurements were made on live fish). The weight of the embryos was 119.5 - 174.0 mg (M - 143.2 ± 17.1), the weight of the yolk constituting from 74 to 84.3% of the total. In one batch of small eggs, the embryos hatched at a length from 16 to 18.5 mm (17.49 ± 0.7). In eggs with a diameter of about 6.7 mm at about the time of hatching, the embryos reached the length of 18.3 - 19.9 mm, and in the eggs with the diameter 7.4 mm they were 20.4 - 21.7 mm (measurements in vivo).

The hatched embryos have large heads with large mobile eyes. 131
Their gills with well developed filaments and rudiments of the first rakers

are covered by opercula. Branchiostegal rays are present. The maxillary bones are well developed. The formation of the partition in the olfactory pits has been completed. The yolk sac elongates after hatching, its posterior end extends to the anal orifice and drops a little lower (Fig. 36, B). By the time of hatching, the main bulk of fat drops merges into one large drop, the diameter of which reaches 2.5 mm and over. The upper part of the yolk sac is beginning to be covered by the growing myotomes.

In the hatched embryos, 66 - 68 myotomes were counted, of which 25 - 27 were caudal.

The postanal section constituted about 36 - 37% of the total length. In the tail, 20 - 22 bone rays formed, the middle of which had up to 3 and even 4 parts (segments). In early hatching, there are fewer than 18 rays in the tail and they have fewer parts. Near the end of incubation, the unpaired fin fold is much reduced, so that the contours of the unpaired fins are much more easily noticeable. The rudiments of lepidotrichs and of pterygophores in those fins are well marked. The preanal fin fold, in contrast, continues to grow. The pectoral fins become large, and the rudiments of ventral fins, elongated. In the time of hatching, the pink resembles the chum as regards the level of development of the organs of the lateral line canal. It is more poorly pigmented than in other species.

The gastro-intestinal tract at the time of hatching is an almost straight tube, in which a slight thickening of walls and visible flexion demarcate the place of formation of the stomach. The rudiment of the swim bladder is represented by a digitiform outgrowth, slightly longer than 1 mm.

After hatching the embryos become quiescent. According to the level of differentiation of the receptor organs, responses to external stimuli and behaviour are no different from other salmon species. Having emerged from the eggs, the embryos at a temperature of 8 - 9^{o} remain in a relatively passive condition for about a week. At a temperature of 3 - 4^{o} this period is almost twice as long.

Stage 13. Formation of the Unpaired and Ventral Fins, and of the Swim Bladder. At the beginning of this stage, the free embryos begin to react positively to current and contacts with external objects, their reaction to light becoming negative. In rearing ponds with even bottoms, as we have observed in the Adotymovskii farm, they try to move to the places of entry of water, and there, as well as in hollows in the bottom, they form groupings. In rearing ponds with gravel bottoms, and with a moderate current they become more evenly distributed. The embryos are excited by bright light, noise, and mechanical disturbances, and can rise in the water. However, being burdened with a huge egg sac, they do not remain swimming for long and soon descend to the bottom. It should be noted that 152
at a low temperature, behavioural changes are rare.

Near the beginning of the stage, the mouth becomes subterminal (Fig. 37, A). The unpaired fin fold in front of the dorsal fin is resorbed; the preanal fold remains large as before. The upper and lower rays begin to grow vigorously in the tail, due to which an indentation forms in its lobe. Rays develop in pectoral and ventral fins.

After hatching, the resorbtion of the yolk becomes more rapid. During this stage, the number of the gill rakers increases, as well as their size; the branching gill filaments continue to grow. The sections of the gastro-intestinal tract become differentiated, the pyloric caeca are laid down.

The rudiment of the swim bladder grows rapidly. The melanophores continue to remain small, are scattered, and situated only on the dorsal side of the body. At the end of the stage in the skin, besides orange-red lipophores, smaller chromatophores of a lemon-yellow colour also form. The peritoneum is intensely pigmented with melanophores; they cover the brain and the cord and spread along the main blood vessels.

The pink is distinguished by earlier appearance of the reproductive cells and a rapid development of the gonads which in all individuals form at first as ovaries (Robertson, 1953; Persov, 1965, 1966, 1968). According to Persov, 7 - 10 days after hatching one finds in the gonads oocytes of the period of protoplasmic growth. In different conditions of temperature the differentiation of sex and formation of testes takes place during the period from 30 to 123 days after hatching (5?? - 906 degree-days), when larvae are from 24 to 30 mm long.

The Larval Period of Development.

The Mixed Feeding Stage. In the rearing ponds, the larvae of the pink remain lying on the bottom and do not rise up in the water if the temperature is below 2.5 - 3° (Chernyavskaya and Tankov, 1959). The transition to active swimming and feeding is also delayed by darkness. When conditions are created favourable for feeding--required temperature, sufficient illumination, appropriate food--the larvae are capable of ingesting and digesting food, while they still have large remains of yolk. One of such larvae is shown in Fig. 37,B. Its length is 27.3 mm, total weight 188 mg, weight of yolk 68 mg (about 36% of total).

By beginning of active feeding, teeth appear on the jaws, and the prehensile function of the mouth is developed. The greater part of the yolk sac is covered by growing myotomes; they become streamlined. The yolk becomes more viscous and fat drops in it are unable to move as before. The large fat drop becomes elongated. The stomach and the intestinal loop become immersed in the remains of the yolk. Peristalsis of the gut becomes observable.

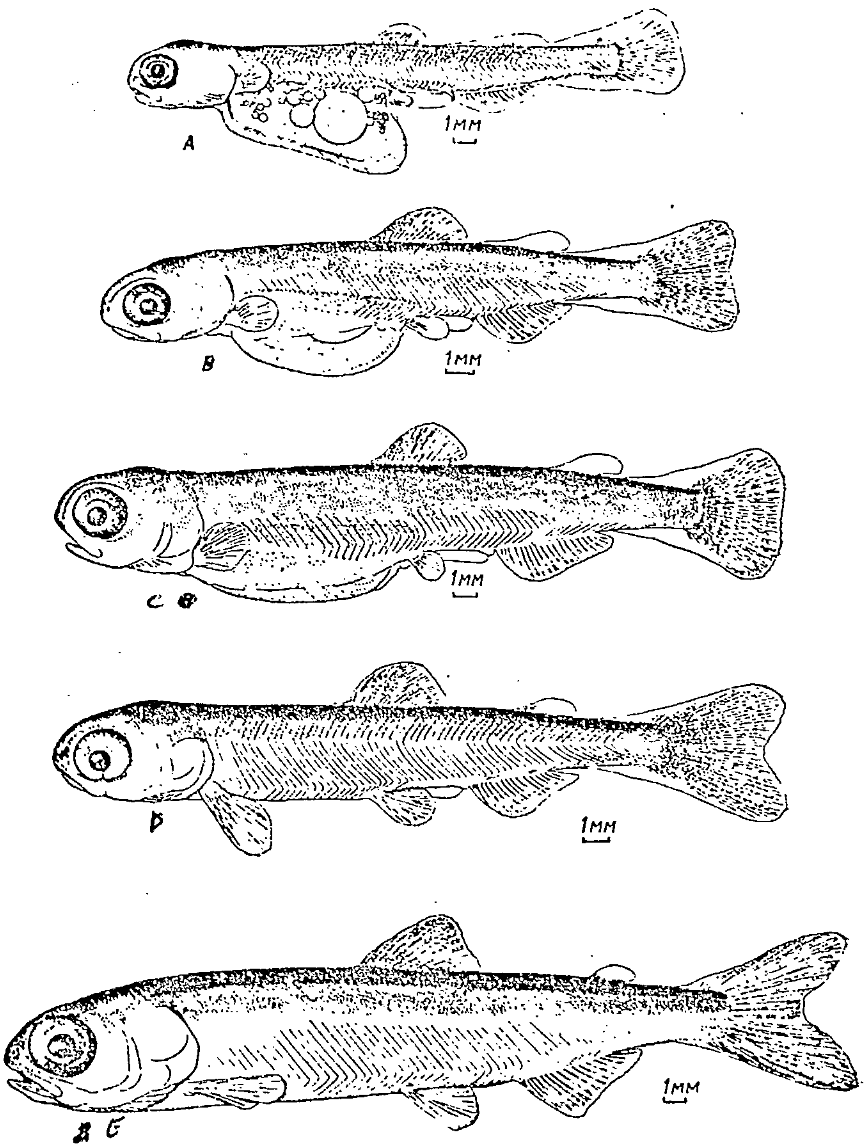


Fig. 37. Young pink at different stages of development. A - free embryo 26.2 mm long; B - larva 27.3 mm long. C - migrating larva 30.2 mm long. D - migrating larva 31.3 mm long. E - fry 46.3 mm long.

Adipose tissue accumulates in the body cavity. Behind the dorsal and 154 anal fins, a small remnant of the embryonic fin fold still remains. The pre-anal fold remains large as before. Lepidotrichs begin to develop in the newly-delimited anal and dorsal fins. The top of the head and the dorsum of the larvae assume a dark colour. Melanophores spread below the middle line, but do not reach the lower ends of the myotomes, as in the other salmon species, and do not form spots. In the dorsal and caudal fins the number of melanophores increases slightly, but in the anal and paired fins they are absent as before. The body cavity becomes strongly pigmented. Deposits of guanine appear in the integument. The opercula and the flanks of the body become silvery. The larvae lose their photophobia and their positive tactile sense.

At a temperature above 3 - 4°, the pink is active. The fry often rise to the surface of the water, and remain in mid-water for an increasingly longer time, continuing to move actively their tails and pectoral fins. After the swim bladder has been filled with air they find it easier to maintain midwater positions. In aquaria, such larvae catch small plankton and particles of egg yolk.

Under the conditions in the Sokolovskii farm at a temperature of 8.0 - 9.6° the pink changes to free swimming in 50 - 55 days (450 - 490 degree-days) after hatching. When the incubators are provided with river water, hatching and development of free embryos takes place during the period of low temperature, so that the corresponding period of development extends to 3 - 5 months. For example, in the Lesnaya farm, the fry which hatched from the eggs in December, rises into the water in April and even in May.

Fig. 37,C shows a larva caught on the 20th of May, 1959, in the river Belaya. It is 30.2 mm long and weighs 228 mg, the weight of the yolk remains being 58 mg. Only a few individuals migrate with such large yolk remnants. Strong spring spates might wash out the nests and then the number of migrating larvae with large yolk remnants increases. The larva is silvery. The tail is bilobed. A small vestige of the unpaired fin fold is preserved and the preanal fold has become narrow.

At a low temperature the pink might remain in the nests almost to the stage of full resorption of the yolk. It survives the periods unfavourable for active feeding and migration in the well protected nests. As soon as the water becomes warmer, the larvae emerge from the ground. They soon form into schools, the size of which gradually increases. The larvae are very timid. In the case of danger, the schools rapidly disperse, the larvae hiding at the bottom among stones, snags and vegetation (Hoar, 1951, 1958; Smirnov and Kamyshnaya, 1965; Kamyshnaya, 1967). In most cases the fry do not remain in the area of the spawning ground and begin to migrate before the transition to active feeding.

Migration takes place during the dark hours, being most intense 156
in the depth of the night (Taranets, 1939; Boppel, 1956; McDonald, 1960; Smirnov and Kamyshnaya, 1965; Volovik, 1967; Pushkareva, 1967). Migration during the twilight and night hours protects the migrants from predators. Under certain conditions the pink migrates into the sea also during the day (Kaganovskii, 1949; Vasilenko, 1959; McDonald, 1960; Esaulov and Fedotova, 1963; Smirnov and Kamyshnaya, 1965). This is more often observed in the lower reaches of large rivers, when water turbidity is high. In the Arctic the seaward migration takes place under the condition of the round-the-clock light, during the polar day.

Table 11

Morphological Characteristics of the young pink from the rivers Pugachevo and Mychka and those grown in Umbskii fish farm.

(from Smirnov and Kamyshnaya, 1965, abbreviated)

Character	River Pugachevo		River Mychka		Umbskii Fish Farm: from 35 to 40 mm		Umbskii Fish Farm: more than 40 mm	
	M±m	σ	M±m	σ	M±m	σ	M±m	σ
Body length, according to Smitt, mm	32.30±0.02	0.11	32.79±0.14	0.64	38.45±0.01	0.07	42.30±0.02	1.11
In % of body length								
body length to end of scales	88.45±0.28	1.18	88.61±1.24	0.80	89.24±0.15	0.75	89.53±0.20	0.11
length of trunk	67.01±0.28	1.21	68.08±0.35	1.11	65.92±0.25	1.22	66.79±0.21	1.15
length of snout	3.07±0.03	0.07	3.47±0.15	0.49	4.93±0.06	0.28	4.84±0.04	0.24
length of head	21.82±0.23	0.97	23.38±0.19	0.65	24.44±0.12	0.59	23.51±0.14	0.75
horizontal diameter of eye	7.92±0.08	0.31	8.00±0.07	0.23	7.63±0.05	0.27	7.16±0.04	0.24
height of head through occiput	13.43±0.14	0.60	13.56±0.22	0.73	15.30±0.11	0.56	14.71±0.15	0.79
greatest body height	13.45±0.22	0.79	12.75±0.35	1.10	15.86±0.14	0.70	16.0[illegible]±0.14	0.77
length of caudal peduncle	14.52±0.16	0.45	14.63±0.21	0.66	14.65±0.15	0.76	14.7[illegible]	[illegible]
distance:								
predorsal	44.85±0.15	0.63	46.23±0.44	1.40	45.04±0.19	0.96	44.59±0.16	0.87
postdorsal	34.86±0.27	1.10	34.08±0.16	0.50	34.70±0.18	0.88	35.[illegible]	1.31
preventral	47.51±0.21	0.82	49.03±0.37	1.18	48.57±0.20	1.01	49.31±0.23	1.25
preanal	60.84±0.30	1.30	61.34±0.40	1.26	62.49±0.24	1.20	62.07±0.22	1.17
postventral	25.91±0.29	1.08	26.82±0.47	1.50	26.61±0.18	0.90	27.00±0.22	1.18
ventroanal	12.92±0.20	0.85	13.45	--	13.42±0.14	0.67	13.05±0.12	0.64
No. of rays in dorsal fin	II--III, 11--13	--	III, 11--12	--	II--IV, 10--13	--	III-IV, 10--12	--
No. of rays in anal fin	II--IV, 14--16	--	III, 14--16	--	II--IV, 13--15	--	II--IV, 13--15	--
No. of gill rakers on first arch	17 (15--18)	--	17 (16--18)	--	23 (22--24)	--	23 (22--[illegible])	--
Length of intestine, % of body length	40.90	--	43.56	--	42.32	--	42.84	--
Condition coefficient, after Clark	0.43	--	0.42	--	0.58	--	0.57	--

Descent to the sea sometimes begins before the thaw, but massive descent takes place with the spring and with the warming up of water to 4-5° (Wickett, 1962).

The highest temperature at which migrants are still found in the Amur reaches 18.6° (Enyutina, 1972).

During the mass descent from the river Pugachevka (25th of May 1954), the weight of the migrants varied from 129.5 to 230.0 mg (average 186.0 mg), length from 30.0 to 34.5 mm. The vestige of yolk was on the average 5.76% of body weight. Various authors reported fluctuations in length of the migrants within limits of 27 - 42 mm and in weight from 80 to 500 mg (Enyutina, 1972).

Table 11 shows results of morphometric study of migrants and fry which were fed for some time in the farm. The migrating pink is characterised by a long head (21.82% of body length) and a streamlined body (Fig. 37, D). It has large eyes, a blunt snout, almost terminal mouth, and no scales. Larval characters have been retained in the shape of the vestige of the preanal fin fold. The caudal fin is large and bilobed, the lower lobe being somewhat longer than the upper. The lepidotrichs of the caudal fin have up to 7 sclerites and more; those of the other fins have 3 - 4 sclerites. The larvae have a fully developed stomach, characteristic loops of the intestine, and up to 15 - 18 pyloric caeca. There are considerable deposits of adipose tissue in the body cavity. On dissection, sex can be distinguished by the naked eye. In the yellow-orange, ribbon-like ovaries about 0.4 - 0.6 mm wide, forming oocytes can be seen, with a diameter from 53 to 96 mk, while the testes appear as thin, thread-like whitish streaks.

The back of the migrants is dark, with a blue-green tinge, the sides and the belly are pale, and silvery. The dorsal and the caudal fins are poorly pigmented, melanophores are absent from the pectoral, ventral and anal fins. Lipophores are also scarce in them, fewer than in the larvae of the same age in other species. On the shallow spawning grounds this coloration clearly reveals the fry, but this appears to have no dangerous consequences. This conclusion is arrived at when the details of behaviour are taken into account: the larvae are very timid and hide at the slightest danger, and migrate mainly at night.

In the Sakhalin rivers, in the intestine of the migrating pink, 157
food is rarely found. Active feeding of Kamchatka pink fry in the rivers was observed (Semko, 1939). In different tributaries of the Amur from 8.3 to 33.7% of migrants contained food or food remains; during the warm period the number of the feeding individuals increased to 70% (Levanidov and Levanidova, 1957). In the rivers of the Kola Peninsula, where the pink has been introduced, the fry feed actively in the region of the spawning grounds. The migrants caught by S.P. Mutyan on the 8 - 10th of July of 1962 and kindly given to us for examination had in the digestive tract larvae of chironomids, stone-flies, blackflies and small quantities of planktonic organisms (Table 12). A study of the ecological characteristics of the chironomid larvae found, has shown that they inhabit overgrown stone surfaces and macrophytes of the marginal zones of rivers.

Table 12.
Food Composition of the Pink from the River Muchka
(after Smirnov and Kamyshnaya, 1965)

Component	Frequency of occurrence	Mean no. per stomach	Component	Frequency of occurrence	Mean no. per stomach
Corynoneura sp.	72.7	2.27	Orthocladius semivirens	9.1	0.09
Cricotopus from group algarum	45.5	0.72	Ablabesmyia sp.	9.1	0.09
Cricotopus biformis	9.1	0.09	Limnophyes sp.	9.1	0.09
Eukiefferiella bicolor	9.1	0.09	Simuliidae sp.	18.2	0.18
E. quadridentata	18.2	0.18	Larvae of Mayfly	18.2	0.18
Eukiefferiella sp.	36.4	0.54	Diaptomus sp.	100.0	14.81
Procladius sp.	18.2	0.18	Cyclops sp.	54.5	2.36
Psectrocladius from group psilopterus	36.4	0.27	Bosmina sp.	45.5	1.18
Psectrocladius sp.	18.2	0.18	Sand	9.1	0.09
Tanytarsus from group gregarius	18.2	0.18			

The migrants from the river Muchka were slightly longer in comparison with those from the Sakhalin river Pugachevka and were more variable in this regard (Table 11). However, they weighed rather less (178 mg) and the weight of the yolk remnant constituted only 3.14% of the total body weight. They are distinguished by the more elongated "filiform" body. The relative size of the head is smaller, snout marginally longer. The dorsal fin is displaced backwards. The vestige of the preanal fin fold is retained, the scales absent. It was noticed that the length of the intestine of these individuals was slightly greater than that of the migrants from the river Pugachevka, a fact which might be related to active feeding.

In the same river in 1966 and 1968 the active feeding of the pink fry was observed by us during a prolonged period. The prolonged stay of the fry in the river can be explained by intensive round-the-clock illumination. The spring of 19[illegible] in the Kola Peninsula was late and cold. The emergence of the pink from its nest was delayed. The migration was observed from the second half of June to the end of the first five days of July. During all that time one could see in quiet near-shore parts of the river and in shallow pools near the spawning grounds actively feeding larvae. The migrating young of the later samples reached the length of 40 mm and weight of 400 - 420 mg. No yolk remains were found in such large pink fry but they had abundant fat deposits in the body cavity. Larger among the individuals caught had retained the vestige of the preanal fold (larval organ) and had no scales, i.e. they left the spawning region at the very end of the stage of mixed feeding. The fact that the pink migrates out of the rivers even under such peculiar circumstances, with vestiges of larval organs, points to the stable hereditary nature of this specific characteristic. In the lower reaches of the river, in the zone of tidal influence, the young remain for some time, just as it has been observed in the Far East.

The transition of the larval pink to active feeding in the river is observed, as we have seen, under various conditions. Those facts bear out the value of the organisation of supplementary feeding of these larvae in the rearing ponds. It allows for an increase in the size of the released fish and for carrying out the release under conditions most favourable for the migration and subsequent feeding. We must warn at the same time, however, that the pink should not be retained in the rearing ponds too long, since it has become adapted to leaving the rivers before the transition to the fry period of life. It would be counterproductive to shorten artificially the marine period of life of this species, which is short anyway, and during which there is rapid growth and formation of the gonads.

The Fry Period of Life.

The changes of the pink during its transition to the fry stage are less marked by comparison with those occuring in related species. The direction these changes take is shown by comparison of individuals 35 - 40 mm long with larger ones (see Table 11). In large fry reared in the Unbshii farm, where the eggs are transported from Sakhalin, the body is higher, the length of the head and the postdosal distance become larger, while the diameter of the eye and the predorsal distance become shorter. With age, the number of the gill rakers and of pyloric caeca approach the definitive. The young fish 42 - 43 mm long and over had scales. In large individuals intensive silver colour was observed. They had high a condition coefficient. All this points to the change in morphological and physiological condition and transition of the pink to intensive feeding.

According to our observations, some large specimens cease to attempt exit from the rearing pond and do not undertake catadromous migration. Among them are those which began the fry period of development in the rearing pond. A small number of the pink remain for not less than a month in the Sakhalin rivers after their emergence from the ground. In the river Bolaya on the 30th of July 1959 we took young fish with an average height of 39.4 mm and weight of 356.5 mg. Individuals longer than 42 mm had scales; they lost the vestige of the preanal fold. They were typical fry (Fig. 57, D). On the 3rd of August a specimen 4[illegible].3 mm long was taken, weighing [illegible] mg. Such prolonged stay of the pink in the Far-eastern rivers is an exception. It is known that mass examinations of the scales of the adult pink coming in to spawn revealed no signs of scales being laid down in the rivers, scales with the so-called "river annulus". This fact should be kept in mind when one determines the stage of the fry released from the fish farms.

Taking into account that the descent of the fish occurs mainly at night, the favourable time for the release of the young from the rearing ponds is dusk. The pink moves downstream fast and does not scatter in the shallow water like the chum. The increase in water level and in current velocity stimulates the migration, turbid water lowers the impact of the predators. Obviously the high water levels favour successful migration of the pink into the sea. The release of the fry from the rearing ponds should coincide with the beginning of the spring temperature rise in the water at the river mouth and the spring bloom of the food organisms. This will also ensure rapid growth of the fish. They will reach large size before the marine fish, feeding on the pink, approach the shores.

The fry feeds for some time in the estuarine space and in near-shore areas, growing very rapidly. From the middle of August, the fry move off into the open sea. At about the beginning of September the young-of-the-year in the Sea of Okhotsk reach the size of 15.2 - 21.5 cm and occur there until late into the autumn (Andrievskaya, 1968; Birman, 1968). Along the south-western shore of the Sakhalin and in the Aniv Bay the pink occurs at the end of October - beginning of November. By that time it reaches the length of over 23 cm and weight 153 mg. The migration of the fish from there to the wintering grounds is delayed (Dvinin, 1952). This is most likely due to the influence of warm current on that region.

Characteristic Features of Reproduction and Development of the Pink. The pink is a small, but rapidly growing, most rapidly maturing and most abundant salmon species. The age and size composition of its populations is more uniform than those of other salmon species. The spawning grounds are situated mainly in the beds of the rivers, in their foothill and mountain reaches. 160

In Asia, the dominant and the most widespread is the summer spawning form. In the summer, the spawning takes place in a broad range of temperature. The current in the spawning grounds is fairly rapid, the ground is friable, pebble-sand, washed by the waters of the subsoil stream which, as a rule, are well oxygenated. Since the physical and chemical regime of the subsoil stream is closely dependent upon the changes in the regime of the river water, the reproduction ceases when they cool down. In the autumn, the pink spawns in those sectors where the subsoil stream is mixed with the ground water and where the spawning temperatures are retained for a longer time, as well as in the areas with a warmer climate. The autumn spawning form is less abundant, less widespread, as distinguished by somewhat higher absolute fecundity, develops at a lower oxygen content of the water. The summer and the autumn spawning forms of the pink are ecologically and morphologically less distinct than the corresponding forms in the chum.

The reproduction clearly shows a feature characteristic for the species: high abundance and density of populations. The pink occupies the largest spawning surfaces. The redds are situated close to one another, each female is accompanied by many males; several groups of spawners follow one another in the course of one season.

As the result of mass spawning the ground is frontally cleared in large areas, becomes highly permeable which ensures good ventilation of the nests. At the same time, clearing of large surfaces leads to the impoverishment of the initially poor fauna of the spawning grounds, which makes the feeding of the numerous offspring difficult.

The species has become adapted to development under conditions of sufficiently stable water supply to the redds. The fluctuations in the river levels, spates during the time of reproduction, silting of the spawning grounds, and freezing during severe winters with low snowfalls lower the effectiveness of spawning and can cause a sharp drop in abundance that will affect a number of generations. In the majority of basins the strength of broods of consecutive years is different, which is reflected in the quality of the spawners.

The characteristic features of the pink in large regions and local stocks has been described. In some rivers there are qualitative differences in the spawners of different runs, which overwinter, feed in different regions (for example, the Sakhalin pink both in the ocean and the Sea of Japan) and occupy more or less distinct spawning grounds.

The males produce less sperm than those of other species, excluding the sockeye. The absolute fecundity is low and abundant recruitment is ensured by the spawning of a large number of fish. The eggs are relatively large, have a pale-orange colour, and contain less astaxanthin than the eggs of the related species. Egg membranes are thicker than in other salmon species, the eggs are capable of withstanding particularly great pressures.

The embryogeny of the pink is characterized by the later completion of the process of epiboly. Since the species is adapted to development under conditions of good aeration, the embryonic and larval organ form less rapidly and do not reach as high a level of development as those of related species. Circulation begins after the 58-segment stage, the subintestinal-vitelline vein functions for a relatively long time, the hepatic-vitelline circulation is established near the end of the process of segmentation. The chromatophores appear later than in other salmon species (melanophores at the end of the 10th stage, lipophores at the 11th stage of development) and are few in number. Under comparable conditions, the eggs are incubated for a longer time than those of related species, except for the sockeye.

The reproductive cells appear in the pink particularly early, the gonads develop rapidly and in all individuals at first as ovaries (protogyny is observed); differentiation of the male sex occurs before the larvae emerge from the nests. Larvae and fry are gregarious, have streamlined bodies, relatively short paired and low unpaired fins. The young do not have spotty colouration, characteristic of the salmon and other fish of the same ecological group.

The pink migrates to the sea directly or soon after the emergence from the nests. The overwhelming majority of the young do not feed in the area of the spawning grounds and when migrating down small rivers. The catadromous migration is accomplished before the attainment of the fingerling stage of development. There are no dwarf males. The freshwater part of the life cycle is limited to a minimum. A strict fixation of the moment of seaward migration and the rapid development of the gonads are associated with the short lifespan. Since the species is adapted to exist almost entirely at the expense of the abundant marine food resources and reproduces in the most widely spread spawning grounds, with large spaces, it is able to form populations of characteristically huge abundance.

CHINOOK SALMON - O. TSCHAWYTSCHA (WALBAUM)

The chinook is the largest of the Pacific Salmon species, provides a high quality product and is an important object of the salmon industry.

Distribution. In Asia, the chinook reaches in the North the river Anadyr (isolated individuals), is most abundant along the eastern shores of Kamchatka, and enters the rivers of the northern coast of the Sea of Okhotsk, right to the liman of the Amur and the Commodore and Kurile Islands. A small population reproduces in Hokkaido. The rivers of Primore and Sakhalin are not visited by this species. Our fishery is concentrated mainly in the region of the river Kamchatka, where more than 90% of the total catch is taken. Average annual catches in 1965 - 1970 were about 10 thousand centners (1,000 metric tons, translator's note), and in 1954 exceeded 16 thousand centners (1,600 metric tons). The main bulk of chinook inhabits the eastern part of the range. In North America, this species 162
is distributed from Point Barrow on the Arctic Ocean coast to the Ventura river in California. The most abundant are the populations of the rivers Columbia, Sacramento and Fraser (Berg, 1948; Smirnov, 1960b; Ostroumov, 1964; Mason, 1965; Vronskii, 1972).

In the ocean the chinook occurs at least from 41°N (near Japan from 40°N) to 60°N. The temperature limits of winter distribution are not altogether clear. It is suggested that this rapidly growing salmon species cannot winter in very cold waters. In April the chinook, having begun its movements towards the spawning rivers, was found at a temperature of 6.6° south of the Aleutian Ridge. In May significant concentrations are noted to the south of the Commodore Islands and in June the salmon concentrates in the central part of the Bering Sea; in the eastern region of the latter, with the warmest winter temperature, lives the immature American chinook (Mason, 1965; Birman, 1967).

<u>Size, Weight, Fecundity and Age at Maturation</u>. In the river Kamchatka, the average weight of the commercial-size chinook is 8.3 - 8.5 kg; there are specimens weighing 20 - 25 kg. In the sea, this salmon species grows very rapidly, the rate of growth increasing with years. Males migrating to spawn at the age 5_1+ in different years average from 87.3 to 100.7 cm in length, the females from 88.7 to 95.9 cm. The individual fecundity of the Kamchatkan chinook varies from 4,200 to 20,000, the average being 9,350 eggs (Kuznetsov, 1928; Grachev, 1967, 1971; Vronskii, 1972). According to Canadian data, record weight is 57 kg (Clemens and Wilby, 1961). In the river Sacramento in different years the average size of the chinook was from 72.9 to 94.4 cm, the weight 4.58 - 6.4 kg, fecundity 3,423 - 7,222 eggs. In the Fraser river, with the females being on the average 87.1 cm long, fecundity was 4,944 eggs, and in the Klamath river, at a length of 89.8 cm, it was 4,364 eggs (Roundsefell, 1957; Mason, 1965).

The females mature at the age of 3 to 7 years, more commonly 4 - 5 years; the males, mainly a year earlier. Dwarf males mature during the first year of river life at a length of 75 - 175 mm. A small number of individuals matures during the second year, such males (grilse) are 22 - 47 cm long. Some young migrate from the rivers with the remnant of yolk and without scales, while others, after having lived in fresh water for about 3 months or having spent 1-2 winters in the rivers. The variation of the life span in the rivers and the sea creates very complicated age structures of populations.

Intraspecific Differentiation. The possible existence of differences in the time of run and spawning of the chinook in the river Kamchatka and the Bol'shaya has been suggested (Pravdin, 1940). The chinook which reproduces in the river Kamchatka near the villages Milkovo and Dolinovka, is assumed to represent a separate seasonal race (Vronskii, 1972). However, there are no records of conclusive data, which would confirm the presence of seasonal races in the Asian chinook. In contrast, in the rivers of North America the seasonal forms are clearly delimited. By the transfer of eggs and by tagging the population produced in that way, the heritable stability of the racial characters was established. When the eggs were introduced into rivers visited by fish with a different ecology, the fry of the spring form produced spawners which came to spawn in the spring, and from the fry of the summer form those that came to spawn in the summer (Rich and Holmes, 1929; Berg, 1948; Ricker, 1972). There is a certain regularity in the distribution of races. In the North, in the river Yukon, the chinook is ecologically uniform, has a spring run and summer spawning; all its young winter in fresh water. Further to the south live different races. For example, the river Columbian is entered in the spring by small chinook, with an average weight of 6.8 kg, and in the summer by large chinook weighing on the average 13.6 kg; the chinook of the autumn run weighs from 9.1 to 11.3 kg. The species is also ecologically variable in the river Sacramento. The autumn chinook enters the rivers more mature and does not migrate as far upstream as the spring fish. It is also distinguished by the fact that the main bulk of its young moves out into the sea during the first summer of life, while the young of the spring chinook winter in the rivers. In the catches of the fishermen of British Columbia 78% of the individuals were recorded with scales of the ocean type, and in the population of the river Sacramento this percentage is up to 80 - 90% (Gilbert, 1924; Pritchard, 1940; Burner, 1951; Mason, 1965).

Anadromous migration, maturation and times of spawning. The chinook begins to move up the rivers immediatedly after the ice breaks; possibly some do so even under the ice. In the river Kamchatka some speciments begin to move up by the middle of May; the peak of the run is in June, most commonly in its second half, but isolated specimens are taken up to September. The migration into the rivers of Avachinskaya Bay, including the river Paratunka where we studied this species, also begins early, but ends in July. In the region of Olyutorsk the commercial run lasts from the second half of June to the second half of July. On the west of the peninsula, in the river Bolshaya, the run takes from the first half of May to the end of July (Kuznetsov, 1928; Pravdin, 1940; Smirnov, 1960b; Vronskii, 1972).

The chinook enters the mouths of the rivers at maturity stage III. The individuals which migrate later, have more highly developed gonads, and in some of them the prespawning changes can be found already in the lower reaches of the rivers. The autumn chinook does not migrate high up. On the other hand, the anadromous migration of the spring form covers hundreds and thousands of kilometers. In the river Kamchatka the chinook reaches the upper tributaries, having travelled more than 700 km (Kuznetsov, 1928; Ostroumov, 1964), and in the Yukon it migrates more than 3 thousand km, (Gilbert, 1924). In the river Columbia during the time of migration to the spawning grounds the chinook loses from 15 to 20% of its weight. The fat content drops by more than 13%, that of protein by 3% (Greene, 1926).

The prespawning changes in appearance are slight. The body of the males becomes somewhat flattened from side to side, but the hump hardly develops at all. The snout becomes longer and the teeth larger. The females become markedly fuller, since they carry a lot of large eggs. The head and the back of mature females become almost black. The flanks assume a wine- 164
red colour, paler towards the tail; the belly is dark violet, with an admixture of grey tinge. Along the dorsum down to the middle line of the body there are scattered numerous black spots, diameter 4 - 5 mm, singly, in pairs or in groups of 3 - 4, in various arrangements. The colouration of the males is similar, but brighter; their sides become raspberry-red. The black spots in the males are smaller, but more numerous, on the anterior part of the trunk they are found below the middle line, and are clearly marked on the dorsal, adipose and caudal fins.

In the upper part of the basin of the river Kamchatka, chinook spawns from the end of June to the beginning of August, in the region of the villages Milkovo and Dolinovka from the end of July-beginning of August to the beginning of September. In the river Bol'shaya, spawning takes place from the middle of July to the middle of August (Kuznetsov, 1928; Berg, 1948; Vronskii, 1972).

Judging from personal observations (in 1956, 1957 and 1961), and information given by the fishery protection personnel and by local fishermen and hunters, one can conclude that in the river Paratunka, spawning takes place from the 20's in July to the end of August. Massive spawning takes place during August 1-20. It is interesting to note, that when we visited this river on the 16 - 19th of August 1961, we found no spawners on the mass spawning grounds of 1956 - 1957 and we saw only isolated individuals which had spawned higher up. The summer was rainy, the river high, the current in lower spawning grounds very rapid. The change in hydrological conditions forced the fish to migrate higher up, where it found conditions suitable for spawning in the existing situation. Since high summer waters are common in the Kamchatkan rivers, the sectors which fulfill the requirements of the reproducing fish change, and the summer spawning chinook had become adapted to such changes.

Tagging of the running fish, carried out in 1956 and 1957 in the Columbia river has shown that the chinook of the spring run move higher up than others, it spawns in small tributaries from the 10 - 15th of June to the end of August. The salmon of the summer run spawns from the 5th to the 15th of September in lower, large streams. The autumn chinook reproduces from the 5th to the 20th of October on the limited sector of the lower reaches of the main river bed (French and Wahle, 1960). In the river Sacramento the spring run, with its peak in May and June, spawns in September and October; the spawners of the autumn run, most abundant in October, spawn from October to March. Also observed was a winter run, extending until early spring; this fish spawns from the 20's of April or from May to July (Putter, 1904; Fry, 1961; Mason, 1965). The return of the spawners mainly to the places of their birth was corroborated experimentally (Groves, Collins and Threfethen, 1968).

Conditions of Reproduction and Development. Chinook enters for reproduction mainly into large and middle-sized rivers, less often into small ones, such as Paratunka, the length of which is about 85 km. 165
The most abundant Asian population reproduces in the river Kamchatka, but even in that basin only 17 - 20 rivers are used out of hundreds of tributaries (Kuznetsov, 1928; Ostroumov, 1964). This is due to the ecological uniformity of the population (Smirnov, 1971, 1972a).

The Kamchatkan chinook use spawning grounds of the river bed type. They are situated in the main river bed and in the side channels. "Chinook never spawns in the streams. This is mainly due to the shallowness of the latter: it is also possible that chinook, like the pink, avoids localities supplied with ground water" (Krokhin and Krogius, 1937b, p.52). In 1956 we have studied the spawning ground in the side channel of Aleshka, river Paratunka. It was situated several tens of metres below the entry of the stream Tundrovoi. During the spawning it was 1.5 - 2.0 m deep. The surface current reached 150 cm/sec. At noon, when the air temperature rose to 17°, the temperatures of the upper layers of water did not exceed 7°, and in the bottom layers it was about 0.5° lower. The influence of the cold water of the nearby Tundrovoi stream ($5.5 - 6.5^{\circ}$) was obvious. In the localities where reproduction took place the ground was very solid, consisting of large gravel, pebbles and cobbles, among which was fine sand. To dig a hole in such a ground, while maintaining position in rapid current is possible only for a very strong fish. Both during the period of oviposition and 1½ months later, when the water level drops to 0.5 m and the current velocity markedly decreases, we saw no other salmon. They spawned above and below the sector selected by chinook.

A mass spawning ground in the river Paratunka was studied in 1957. It was much higher up than the first, in a rapid riffle with a large stone bottom (Fig. 38). A part of the nests were situated near the bank at depths of 20 - 25 cm. The majority of the fish reproduced at depths of 0.5 - 1.5 m, some even deeper. The current velocity above the nests varied from 65 - 110 cm/sec. Directly at the bottom, the current was weaker. During the time of reproduction and subsequently other salmon were also not seen in that sector.

Before oviposition the chinook digs in the ground an oval hole, from 20 - 25 to 50 cm deep. The depth of the excavation is usually limited by large stones, near which the main bulk of the eggs is placed. In these excavations the current is weaker and vertical circulation is observed, which can be seen by adding stain to the water. Water eddies increase the chance of meeting between eggs and sperm. The females deposit their eggs in two or three batches. The eggs are placed at a distance of 10 - 15 to 40 - 45 cm from the surface, and in the sectors with weaker current, where the redds are raised higher above the bottom level, the layer of earth above the eggs might reach up to 80 cm thickness (Kuznetsov, 1928, Smirnov, 1960b; Vronskii, 1972).

According to Vronskii, in the basin of the river Kamchatka one finds both dense accumulations of spawners, where the surfaces of individual excavations overlap, and scattered distributions of nests. In the 166
tributaries of the upper reaches of the rivers, depths on spawning grounds are small, while in the main river bed they are up to 2 m and over; current velocities from 0.3 to 1.5 m/sec. In the main river bed in the bottom of

the spawning grounds dominated fractions with diameters of more than 10 cm, while in some subsidiary channels the ground in places of spawning consisted of sand and fine gravel. A large part of the nests was situated in the places where the pools pass into riffles. Not infrequently they were also found below obstructions and individual sunken logs. The dimensions of the redds varied in a wide range. In different places their width reached 3 - 3.5 m, and length 3.7 - 4.3 m.

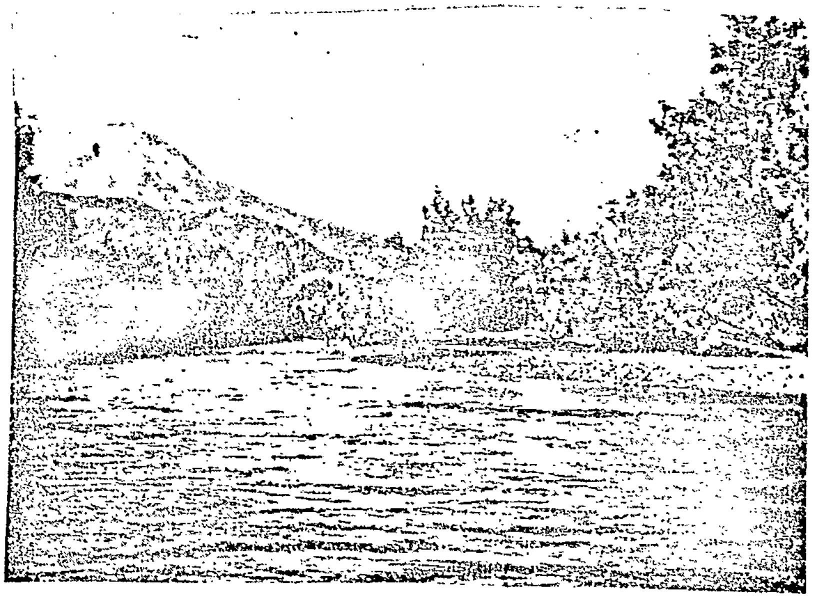


Fig. 38. Mass spawning ground of chinook in the river Paratunka, Kamchatka.

Interesting observations were conducted in the river Columbia. In its upper tributaries reproduces small chinook of the spring run. The nests are built in small stone bottoms, where the depth in places reaches only 5 cm. In large tributaries and in the main river bed, the fish of the later run spawn. Here the depth of the spawning grounds reaches 122 cm, but the majority of redds are located at a depth of 20 - 40 cm. In the sectors with the greater current velocity the redds consist mainly of coarse gravel, pebbles and cobble stones. The redds of this large salmon

are particularly large. The average surface of the redds of chinook in the Columbia river is about 5.1 m^2, about twice as much as that of the chum's redds. As a rule, one redd is far from another. In rare cases, when they 167
are in close proximity, one is slightly higher upstream and to the side from the other (Burner, 1951).

During the reproduction period on the spawning grounds of the Paratunka river, the temperature fluctuated from 6 to 10°; it was 0.5 - 1.5° lower in the nests. In the middle of September the water in the river dropped to 3.0 - 3.5° in the mornings and in the nests was 1.2 - 2.0° higher. In the rivers of North America, chinook of different stocks spawn at water temperature in the river from 4.5 to 17.9°. Summer spawning in the Columbia river takes place at a temperature of 8.3 - 11.7° (Burner, 1951). The eggs were successfully incubated at 16.1°, but its mortality began to rise when the initial temperature rose to 18.4° (Olson and Foster, 1957). During the winter in the water in some redds, oxygen content was 6.7 mg/l, and in others it dropped to 3.2 - 3.6 mg/l. It is interesting that the survival of the eggs at such low oxygen content was 60.2 - 89.6%, if water circulation was satisfactory. Filtration rate proved to be sufficient at about 1.0 - 1.5 cm/min. In some redds the water contained more oxygen than 6.0 - 6.5 mg/l, but because of low circulation rate the survival of the eggs dropped to 30 and 22.5% (Gangmark and Bakkala, 1958).

In Kamchatka, chinook reproduces at the period of highest air and river water temperature, and the water remains warm in the redds up to the middle of September. For this reason the development proceeds rapidly. On the 14th and 15th of September 1957 we opened previously tagged nests. In one of them the eggs were deposited on the 15th of August, and the embryos during one month had reached the beginning of the 9th stage (see below). In the level of their development they corresponded with the embryos reared in incubators for 220 - 240 degree-days. Consequently, development in the river took place at average daily temperatures of about 7 - 8°. The embryos of the latest stages, the age of which was about 50 days, were completing the 10th stage of development. In the incubator this took 370 degree-days. Taking into account the incubation period of chinook one can presume that these embryos hatched as late as November.

In the river Kamchatka the emergence of the larvae from the redds was noted at the end of March. At the beginning they remain near the banks, in shallow areas with slow current (Kuznetsov, 1928). The young fish gradually disperse.

Effectiveness of spawning. There exist limited reports on the effectiveness of spawning of the Kamchatkan chinook. According to Vronskii (1972), after spawning about 0.6% of the eggs remain in the body of the female, and the quantity of eggs in the redds constitutes about 12% and does not exceed 30% of the absolute fecundity. Kuznetsov (1928) observed more significant losses of eggs during the period of spawning; they are due to the high current velocity on the spawning grounds. In the nests examined he found no more than 6% of dead eggs; the average mortality taken from the examination of 10 redds was about 2%

Development of Chinook. 168

Reproductive products. The spermatozoa of chinook are 19.6 mk long, the head with its sharp point is 2.6 mk long, the diameter of its middle part about 2 mk (Riddle, 1917). Males produce large quantities of seminal fluid. There are about 30 million spermatozoids in 1 mm^3 of thick sperm.

In 1957 we took 5 mature females from 87 to 104 cm long and weighing 8.5 - 14. 3 kg. The eggs of various individuals before hydration (swelling) had diameters from 7.2 to 7.5 mm, their average weight was 209.3 - 245.2 mg and volume 200 - 220 mm^3. The weight of the individual eggs varied from 199 to 247 mg. Weight of large and small eggs taken from the same female differed by about 10%. Biochemical analysis showed high fat and protein content (see Table 1). It should be noted that the Paratunka chinook deposits relatively small eggs. The average weight of the eggs of Californian chinook from the Klamath River is 327 mg, the largest weight 387 mg (Leitritz, 1960). The diameter of the eggs might come near to 10 mm (Ricker, 1972). The eggs have an intensive orange-red colour with a pink hue (slightly paler than the eggs of the sockeye). The colour of the eggs corresponds to the wavelength order 592 - 600 nm.

<u>Development Conditions of Examined Eggs</u>. The eggs were incubated in the same apparatus in which were placed also the eggs of sockeye. In 1956 the first batch incubated in spring water with a temperature of 3.8 - 4.1°, the second in apparatus supplied with river water with an average daily temperature at the beginning of incubation 14 - 16°, with the high in individual days up to 17 and 19°. Near the end of incubation the water cooled down to 12°. Daily fluctuations reached 2.5 - 3°.

<u>The Embryonic Development Period.</u>

<u>Stage 1. Hydration of Eggs, Formation of the Embryonic Disc.</u>

Collection and artificial fertilisation of eggs were conducted in the area of the spawning ground. Eggs were transported in an isothermic box. It was delivered to the laboratory and placed in the incubator within 31 and 52 hours after insemination. When transport was more rapid, the eggs prior to being placed in the incubator had reached the 32 blastomere stage.

According to Riddle (1917), the developing eggs of chinook have diameters of 7 - 9 mm (average 7.5 mm) and weight 260 - 330 mg. Prescott (1955) reports that the weight of the eggs as the result of hydration increases by 15.5% and the volume by 16.5%. In the experiments with heavy water (D_2O) he convincingly demonstrated that the perivitelline fluid is formed from the external water which has penetrated the egg. The weight of the eggs of different females from the river Paratunka after hydration increased from 4.7 to 13.6%, their diameter was 7.5 - 7.7 mm, average weight 227 - 258 mg (weight of individual eggs reached 267 mg). It was observed that the eggs which have been longer retained in the body of the female took up less water. 169

During the time of hydration the egg membrane becomes semi-translucent, dense and elastic. Its thickness, according to Riddle, is 64.7 mk. In hydrated eggs of the Kamchatkan chinook the thickness of the membranes varied from 38.0 to 57.0 mk (53.75 ± 0.78). Hydrated eggs were covered with the whitish shine coat which in reflected light had the characteristic mother-of-pearl sheen. The micropyle field, with a diameter slightly more than 1 mm, had no such coating.

Stage 2. Cleavage of the Embryonic Disc. The first cleavage furrow formed about 4.5 degree-days after insemination. The subsequent divisions ensued after 5.2 - 5.5, 6.3 - 6.6, 7.4 - 7.7, 8.5 - 8.8, 9.7 - 10.0

and 10.8 - 11.2 degree-days. The cleavage furrows were situated as in other salmon species. According to Riddle (1917), the furrows of the fifth division pass in equatorial plane and form the rudiment of two layers of cells. Up to the stage of 64 blastomeres, the embryonic disc retains a slightly elongated shape, and with the 128 blastomere stage becomes round. At that stage, between the lower blastomeres form intercellular spaces, which subsequently, according to Riddle, constitute the space between the blastoderm and periblast (Fig. 39). In our material the furrow of the fourth division was in equatorial plane, forming 2 layers of cells (Fig. 40). The first furrow was deeper than the others and its position could be detected up to the formation of 64 blastomeres. After the 128 cell stage (in the incubator after 1 day and 22 hours) the blastodisc assumed a round shape with a diameter of about 1 mm. Up to the stage of 128 blastomeres the chinook develops at a temperature not less than 4.4 - 5.8°. The upper threshold of temperature lies within limits 14.2 - 15.5° (Combs and Burrows, 1957; Combs, 1965).

Fig. 39. Stages of cleavage (A and B) and blastula (C) of chinook (according to Riddle, 1917).

At the age of 3 days (21 degree-days) the blastodisc had a diameter of 1.0 - 1.2 mm and height of 0.45 - 0.49 mm. The diameter of the cells of the upper layer was 72 - 80 mk. Later, small and densely crowded cells covered a mass of freely dispersed cells. The blastodisc was situated above the periblast; at a temperature of 7.5 - 12° the beginning of its formation was observed 44 hours after insemination. 170

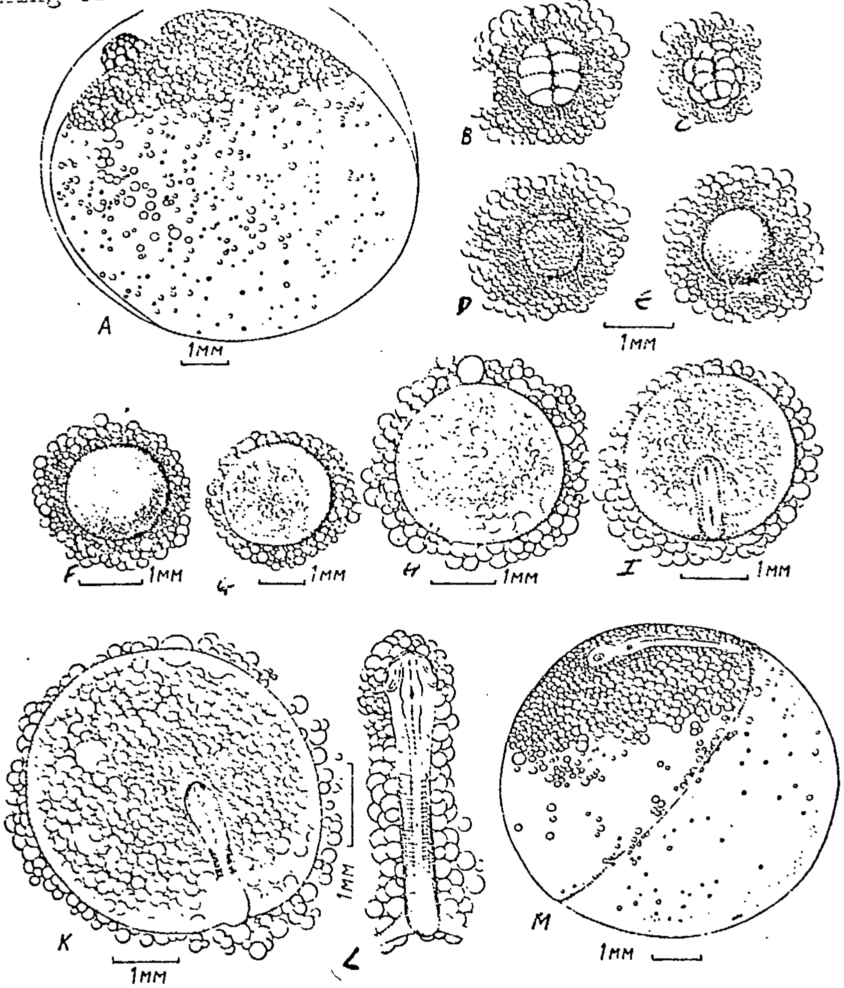


Fig 40. Development of chinook from the cleavage stage to formation of the head and trunk of the embryo.
A - Lateral view of living egg in transmitted light at the beginning of cleavage. B - L blastodiscs and embryos with part of the yolk sac at different stages of development. B - 8 blastomeres. C - 16 blastomeres. D - large cell morula. E - small cell morula. F - blastula. G - beginning of gastrulation. K - beginning of segmentation of trunk mesoderm, length of embryo 2.4 mm. L - embryo 3.3 mm long with 21 somites. M - fixed egg without membrane with 25 - 26 somite embryo. H - "embryonic knot" stage. I - stage of embryo streak

At 4° one thousand embryos age 4 days took up in 1 hour 1.41 mg of oxygen (average of two measurements). This figure is smaller in comparison with the oxygen uptake during hydration of eggs. Later on, the metabolic intensity gradually increases (Table 13).

Table 13
Oxygen uptake by embryos and larvae of Chinook.

Age	Stage of Development	Temp °C	Oxygen uptake, mg/hour per 1,000 eggs	per 100 g of eggs
up to 2 hrs.	Hydration of eggs	11.2	2.23	0.96
4 days	Morula	4.0	1.41	0.59
6 days	Blastula	4.6	1.45	0.60
14 days	"Embryonic knot"	6.5	1.65	0.68
22 days	Beginning of segmentation	3.5	1.92	0.80
27 days	Blastoderm covered half of yolk sac surface	4.4	1.80	0.75
56 days	Appearance of hepatic veins on yolk sac	3.5	1.46	0.54
70 days	Beginning of formation of upper and lower cones of myotomes	3.5	1.90	0.73
78 days	Beginning of melanin pigmentation	3.2	2.07	0.83
87 days	Deposition of first rays in caudal fin.	3.2	2.04	0.77
107 days	From 6 - 8 rays appeared in the caudal fin	2.7	2.67	1.01
35 days	Before hatching	11.7	5.47	2.28
35 days	Hatched embryos	11.7	25.60	11.63
65 days	Transition of larvae to free swimming	8.5	42.68	14.93
72 days	Actively feeding larvae	6.9	43.55	14.23

Note: Experiments with embryos age 56 days and more were conducted in 1956, others in 1957, when the determinations were completed by L.E. Gracher.

Stage 3. Blastula. At the age 5 days 9 hours the embryonic disc resembled the condition described by Riddle for 101 hours after fertilization (Fig. 39, C). Its diameter increased up to 1.35 - 1.5 mm. The diameter of the cells of the covering layer of blastula diminished to 40 mk (Fig. 40, F; 26 - 28 degree-days). The blastodisc becomes wider and denser with time. During the first phase the stage took about 5.5 days, during the second slightly more than a day.

Stage 4. Gastrulation. At a temperature of 3.7 - 4.1° the signs of gastrulation were observed at the beginning of the 11th days, at 15.5-16.5° in the middle of the 4th day. The embryonic disc had a diameter of 1.7-2.1 mm. The diameter of the cells of the surface layer decreased to 20-25 mk. Through the now-thinned 172
central part of the disc could be seen small fat drops below. From the caudal side of the forming embryo the marginal part of the disc began to grow thicker (Fig. 40G)

When the diameter of the blastodisc increased to 2.5-3.2 mm (68 degree-days), the "marginal knot" developed (Fig. 40, H). The borders of the embryonic shield moved beyond the zone of accumulation of the small fat droplets. In the river apparatus, at an age of 5 days 5 hours (about 75 degree-days) the embryonic streak was formed, 1.3-1.4 mm long (Fig. 40, I). With the beginning of gastrulation the eggs became very sensitive to tactile stimuli.

Stage 5. Formation of the Head and Trunk of the Embryo. In the eggs of the first batch the segments appeared at the age of 19 - 20 days (80 - 84 degree-days), in those of the second at the beginning of the 6th day. By that time the diameter of the blastodisc reached 3.5 - 4 mm, and the length of the embryos 2 - 2.2 mm. Some embryos in the river apparatus at the age of 5 days 17 hours had 3 - 4 segments; the differentiation of the parts of the brain became observable in them (Fig. 40,K).

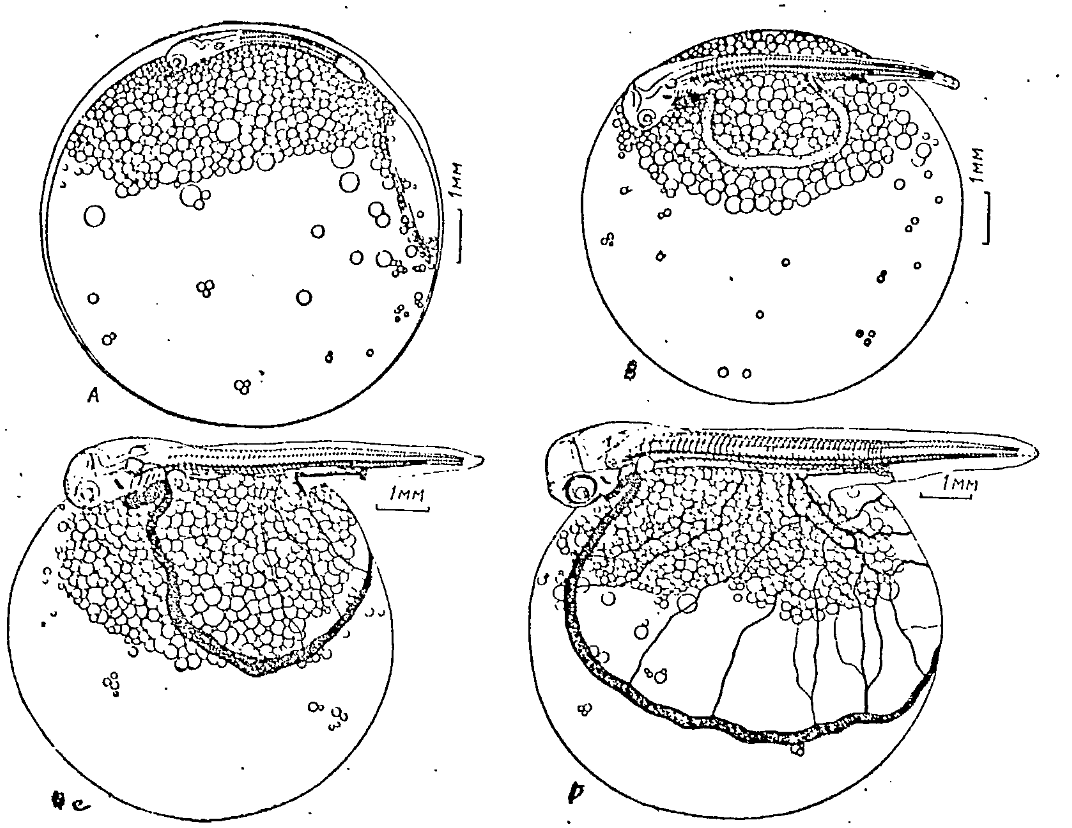
In the incubator, 2 days after the beginning of segmentation the embryos reached 3.2 mm long. They formed 7 - 8 segments each, and the rudiments of the eyes became visible. One day later, at the stage of 12 - 13 somites, the rudiments of the crystalline lenses and otic capsules appeared. When the embryos had 20 - 22 segments (about 100 degree-days), the head section constituted 34.5% of their total length (Fig. 40,L).

At the age of 25 days (104 degree-days) blastoderm enclosed up to a half of the yolk sac. Embryos reached a length of 3.3 - 3.6 mm; they had 25 - 26 segments. The pericardial cavity was formed, in it the rudiment of the heart. The main bulk of the fat droplets concentrated near the body of the embryo and only a few smaller ones were outside the zone of epiboly (Fig. 40, M).

By 34 days (138 degree-days) blastoderm covered 2/3 of the surface of the yolk sac or somewhat more. In the eggs from the river apparatus a similar stage was observed at the age of 8 days (115 degree-days). Embryos were 4.1-4.4 mm long and had 35 - 37 segments (Fig. 41, A). A small tail bud was formed. The size of the head section was reduced to 28% of the length of the embryo. Otic capsules were separated from the eyes by a distance almost equal to the width of 10 segments. Relatively small eyes had a diameter of about 0.4 mm. Olfactory placodes became visible. The parts of the brain and encephalomeres became clearly distinguishable. When the blastoderm covered more than a half of the yolk sac, the sensitivity of the eggs to tactile stimuli was for some time reduced.

Stage 6. Separation of the Posterior Part of the Embryo from the Surface of the Yolk Sac. By the end of the 36th-beginning of the 37th day (145-150 degree-days) the embryos reached a length of 4.9 - 5.2 mm, and developed 45 - 48 segments. Only a small yolk plug remained. The tail bud continued to differentiate.

Fig. 41. Chinook at stages of completion of epiboly and beginning of development of the circulatory system. A - stage near to completion of epiboly, length of embryo 4.1 mm. B - beginning of circulation, length of embryo 6.6 mm. C - stage of appearance of posterior cardinal veins, length of embryo 8.5 mm. D - stage of appearance of melanin in eyes, length of embryo, 9.8 mm. 173



The rudiments of opercula appeared. At this stage weak contractions of myotomes were observed. The cardiac tube became flexed and in embryos with a larger number of myotomes carried out wave-like contractions. When developing in river apparatus, the pulsation of the heart was observed at the age of 9 days, after the period of only 129 degree-days. At that age the sensitivity to tactile stimuli rose sharply. 174

In the small eggs of the first batch, the process of epiboly was completed in embryos 5.5 - 6.0 mm long, at the stage of 48 - 49 segments (development from the 5th of August to the 14th of September 1956, about 160 degree-days). By that time the length of the head constituted 23% of the total length of the embryos. The tail bud became separate from the yolk sac, its length being equal to the width of seven trunk myotomes. The anal opening was formed below the 43-44th segments. The rudiment of the unpaired fin fold appeared. In the main bulk of embryos epiboly was completed at 53 - 56 segments, and in large eggs after the formation of 58 and 59 segments. At a higher temperature in individual eggs the covering of the yolk sac by blastoderm extended to the stage of 63 - 64 segments. Thus, depending on the quality of the egg (their size) and on the conditions of incubation, the process of epiboly is completed at different stages of morphological differentiation. There are indications that the process might be completed in embryos of North American chinook 4mm long having 38 segments (Riddle 1917). Such acceleration of epiboly, perhaps, indicates genetic properties of the material which Riddle had at his disposal. During the time of completion of epiboly the egg is very sensitive to disturbance.

Stage 7. Development of the Subintestinal-vitelline Circulation System. Under conditons of low temperature, circulation in different embryos was discovered 43 - 47 days after fertilisation (172 - 187 degree-days), when they reached a length of 7 - 7.5 mm and had 64 - 66 segments. By that time the tail, in which 21 - 22 segments could be counted, and posterior section of the body were separate from the yolk sac. The head, as before, continued to adhere closely to the yolk sac and its length continued to become reduced. Rudiments of the opercula appeared. The olfactory pits began to form. Otic capsules increased noticeably; semicircular canals in them began to differentiate and numerous small otoliths were visible. From the 15th or 17th myotome along the back runs the narrow fin fold. Considerable length was reached by the preanal fold.

Pectoral fins were laid down. Behind them could be seen glomeruli of the pronephros. The separation of the stomach could be seen.*

At the beginning of this stage there are few formed elements in 175
the vessels, the erythrocytes are poorly pigmented, the blood flows slowly and washes only two segments of the tail section. The diagram of the circulation is similar to that described for the chum. (Fig. 41, B).

In embryos reared in the river apparatus circulation began at 63 - 64 segments (10¼ days, 147 degree-days). In some of them a small yolk plug was left. Embryos were tilting from time to time, either to the left or to the right side and moved their tails slowly. At a temperature of about 14.5° this stage took less than a day, at 3.5 - 3.7° about 4 days.

Stage 8. Origin of the Cardinal Veins and of the Mixed Subintestinal-vitelline and Hepatic-vitelline Circulation. In the first batch between 49 and 52 days (195 - 207 degree-days) the blood vessels of the embryos were abundantly filled with formed elements. The embryos reached the length of 7.8 - 8.5 mm (Fig. 41,C). The number of segments in the tail increased to 35. The head of the embryos began to detach itself from the yolk sac. The distance between the eyes and the otic capsules contracted to the width of 5 trunk myotomes. The buccal funnel becamse deeper. The rudiments of the lower jaws made their appearance. The increasingly broader unpaired fin fold reached the 4 - 5th trunk segment. From 18 - 20 caudal segments were supplied with blood. The posterior cardinal veins and Cuvierian ducts were formed. The Subintestinal

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The author had no opportunity to include drawings which he prepared on development of gastro-intestinal tract, swimbladder and gills of chinook and coho.

vitelline vein descended below the accumulation of fat droplets. From 5 to 6 fine capillaries appeared on the yolk sac.

With development in river apparatus, a similar condition of the circulatory system was observed at the end of the 11th day or beginning of the 12th (160 - 165 degree-days), when the embryos were 7 - 7.3 mm long.

The following experiment was conducted. A part of the eggs were placed in Petri dishes with a water layer barely covering the eggs, and were then placed in river apparatus. It was discovered that in absence of running water the beginning of circulation was delayed by more than a day. The vessels developed abnormally. Along the dorsal aorta blood flowed only to the middle of the trunk, then the vessel crossed to the yolk sac, ascribed a short arc and ran towards the heart. Later on, the blood penetrated the posterior end of the trunk and the tail, but the vessel of that section did not develop fully. The tail formed slowly and abnormally. After some time the eggs begin to die. Transfer of the surviving eggs into running water prolonged the life of the embryos, but their development was already disturbed and these eggs produced freaks. The experiment shows that the reduction of circulation during incubation might be one of the reasons for egg mortality and the appearance of monstrosities.

In embryos of the first batch, age 55 days (218 degree-days) and in those of the second at the age of 14 days (209 degree-days) the hepatic circulation began (slightly later than in the sockeye and coho), bloodstream appeared in the first pair of gill arteries; the first segmental vessels were formed. At that age, melanin appeared in the eyes. Fig. 41,D 176 shows an embryo 2 days after the appearance of melanin in its eyes. Such embryos were 9.5 - 9.9 mm long and had 77 - 78 myotomes. Their caudal section constituted 30 - 30.5% of the total length. In the renal glomeruli and ureters appeared crystals, which indicates the beginning of the function of that organ. Segmental vessels were formed along the entire trunk and in the first segments of the tail. About a half of the surface of the yolk sac became covered with a capillary network.

In the river apparatus, at the beginning of pigmentation of the eyes, the embryos were 8.6 - 9.1 mm long. They had 80 - 81 myotomes, i.e. their segmentation was completed. Two pairs of gills were supplied with blood. The capillary network on the dorsal surface of the head began to develop . At a temperature of 13.5 - 14° the heart contacted 50 - 51 times per minute.

Stage 9. Formation of the Hepatic-vitelline Circulation System.

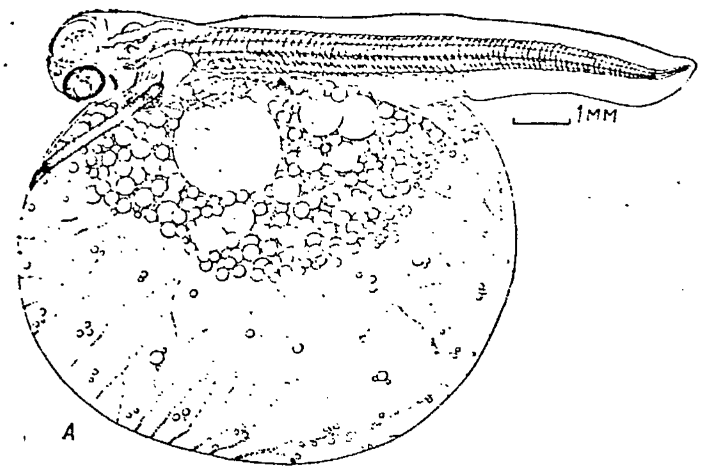
At a temperature of about 4°, the blood flow from the liver was observed on the 62-63rd day. The embryos reached the length 10.3 - 11.8 mm and had 78 - 80 myotomes (37 - 38 caudal ones); segmentation was conpleted. The head became very large. Otic capsules were enlarged, their bases became broader, the semicircualr canals and large otoliths were formed. The tip of the chord began to twist upwards and the tail showed the beginning of the loss of symmetry. The bases of the pectoral fins assumed an oblique position. One or two pairs of gill arteries filled with blood. Only 6 - 8 posterior caudal myotomes were not supplied with blood. The entire yolk sac was covered with capillaries, except for a small part below the head. The length of the tail increased rapidly during that stage.

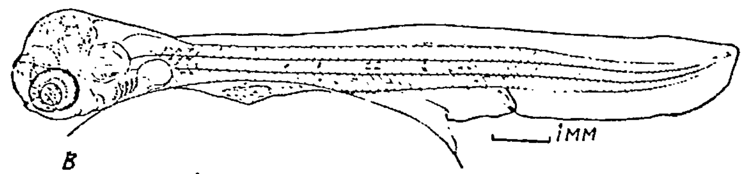
The embryos from river apparatus showed the transition to hepatic-vitelline circulation of the 18th day (260 degree-days), when they were 10 - 11.5 mm long (Fig. 42,A). Already three pairs of gill arches were supplied with blood, a sluggish flow of blood was observable in the hyoid vessel. Capillaries appeared on the upper surface of the head. In most caudal myotomes, segmental vessels were formed. The network of capillaries on the yolk sac became denser (length of capillaries per 1 mm^2 reached about 4 mm).

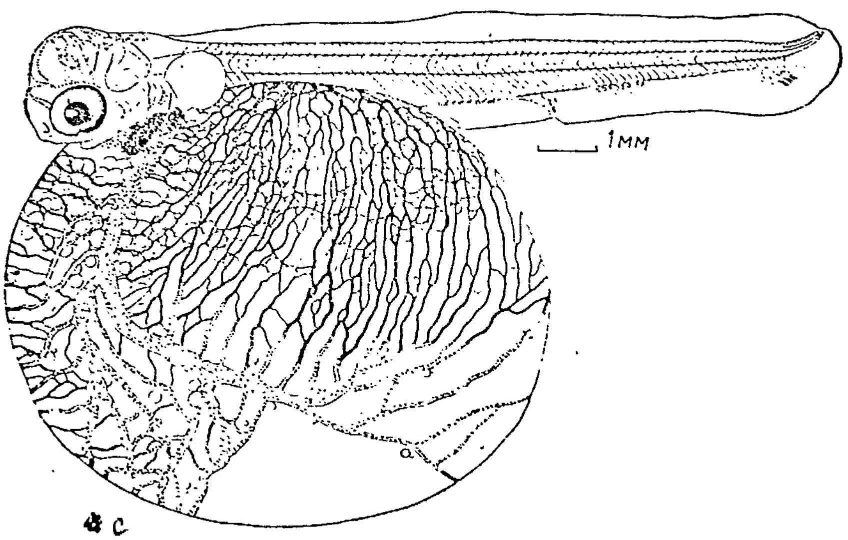
<u>Stage 10. Formation of the Upper and Lower Cones of Myotomes.</u>

The rudiments of the upper and lower cones of myotomes in the embryos of the first batch appeared on the 68th - 70th day (270 - 276 degree-days), when the embryos were 12 - 13 mm long. Their heads became higher but were still relatively short. The caudal section constituted 32 - 33% of the total length. The unpaired fin fold reached its greatest length and became much broader. The rudiments of the unpaired fins became visible. Three paires of gills were supplied with blood. On the dorsal side of the head there developed a thick network of capillaries. The entire surface of the yolk sac was covered with vessels. The lower afferent vitelline
vein was formed. The first hatching glands became observable. On the 178
surface of the head, near the large vessels and on the mesentery, the first melanophores appeared. In Fig. 42,B is shown the embryo several days after the beginning of this stage, having developed in an incubator for 75 days.

Fig 42. Chinook at the stage of transition to hepatic-vitelline 177
circulation and differentiation of myotomes. A - stage of completion of segmentation of caudal mesoderm and appearance of blood stream in hyoid arches, length of embryo 11.4 mm. B - beginning of formation of upper and lower cones of myotomes--laying down of unpaired fins and appearance of melanophores, length of embryo 12.9 mm. C - appearance of first lepidotrichs in the caudal fin and lipophores in the integument of the head, length of embryo, 14.5 mm.







In embryos of the second batch this stage began at the age of 21 days (302 degree-days). They were about 13.5 mm long and were distinguished by longer tails (up to 37% of the total length). Pectoral fins became mobile. Guanine appeared in the eyes, but melanophores on the head and body were still absent. Segmental vessels were formed in all myotomes and in the first myotomes, began to branch. 178

Three days later these embryos reached the length of 14 - 15 mm (Fig. 42,C; 344 degree-days). Their otic camsules were at their closest to the eyes, which became black. Opercula covered the first pair of gills. Lower jaws became longer and, like opercula, mobile. Upper and lower cones developed in all myotomes. The caudal section exceeded 38% of the total length of the embryos. The last caudal myotomes were breaking up and their number was reduced to 34 - 35. Three hypurals were formed. First rays were laid down in the caudal fin. Ossification of the components of the dorsal skeleton began. Pectoral fins were supplied with blood. The upper surface of the head was covered by a thick network of capillaries. Blood vessels appeared at the base of the lobe of the caudal fin. The length of capillaries per 1 mm^2 of the yolk sac exceeded 7 mm. At this stage raspberry-red lipophores appear in the integument of the head (in Fig. 42,C they are shown as small black dots).

The embryos remain motionless for most of the time, only wobbling slightly from side to side. Occasionally they performed 10 - 15 movements of fins per minute. Along the intestine waves of weak peristaltic movements were passing now and again.

In embryos reared in the incubator, muscle bundles at the base of the dorsal fin appeared on the 76 - 79th day (300 - 310 degree-days). In comparison with the embryos developing in apparatus with river water, they had relatively short tails, the length of which constituted about 35% of their total length. These embryos were distinguished also by less developed network of vessels, and had more melanophores. At the age of 83 days 326 degree-days) the embryos reached the length of 13.5 - 14.7 mm. The ventral fins were laid down. The pectoral fins became mobile. In the lumen of the intestine yellow-greenish pigment was visible. The yolk became more viscous.

Stage 11. Development of the Jaw Movements and those of Opercula, Completion of Incubation. In the first batch in various individuals, this stage began on the 90 - 95th day, and in those of the second batch on the 26th day (corresponding to 347 - 364 and 372 degree-days respectively). The former embryos had a length of 14.8 - 16.3 mm. The relative size of their head started to increase. Opercula almost covered the second pair 179
of gills. The rudiments of gill filaments have appeared. Formation of subdivisions in the olfactory pits was observed. The caudal section comprised 36% of the total length of the embryos. Hypurals were formed and rays of the tail fin became more numerous. Differentiation of skeletal structures in anal and dorsal fins became noticeable. Ventral fins were laid down. Segmental vessels develop in the entire body. In the head section of the trunk, capillaries appeared above the chord and near the body surface. The length of the capillaries per 1 mm^2 of surface of the yolk sac reached 6 mm. The vessel network in these individuals was not as dense as in the embryos of the same size developing in the river apparatus (see Fig. 43,A,B). The tail of the latter was longer, more than 38% of the total length, and its lobe was better developed. The stronger pigmentation should be noted, there being more melanophores on the head and tail than in the trunk region. It is interesting to note that in the embryos from an incubator first lipophores were found only 70 degree-days after the appearance of melanophores in the integument of the head. In the embryos which developed in the river apparatus, in contrast, lipophores

were observed first and only 40 degree-days later, at the age of 26 days (Fig. 43,A), appeared melanophores. Since the material of the batches compared was genetically homogenous, these differences indicate the relationship between the process of pigmentation and the condition of incubation of eggs.

On the 31st day the embryos in the river apparatus reached the length of about 19 mm (Fig.43,C; 440 degree-days). Their opercula covered three pairs of gills. Capillaries began to grow into the gill filaments. At this age the tail section consitituted up to 40% of the total length. In the caudal fin formed 12 - 14 rays; the largest of them had 2 sclerites each. A thick network of capillaries developed between the rays. Vertebrae began to form in the tail. The differentiation of the anal and dorsal fins continued. The signs of reduction of the unpaired fin fold appeared. The network of vessels on the yolk sac reached maximum development. The length of capillaries per 1 mm^2 of its surface exceeded 9 mm.

While under the membrane, these embryos almost unceasingly moved their pectoral fins, at 14.5° performing 180 - 200 movements per minute. Heartbeat was 90 - 95 per minute. From time to time, when disturbed, they carried out wave-like, thrashing movements with their tails. When removed from the egg, such embryos were able to swim for a short distance.

By the 38th day (527 degree-days) the embryos of this batch reached the length of 20 - 21 mm. The head constituted 15% of the body length. Lower jaws grew to the vertical line drawn from the anterior margin of the eye. Velum developed in the buccal cavity. The embryos moved rythmically their jaws, opercula and gills. A network of capillaries developed in the rudiments of the pseudobranchs. Well developed bars almost completely divided the olfactory orifices.

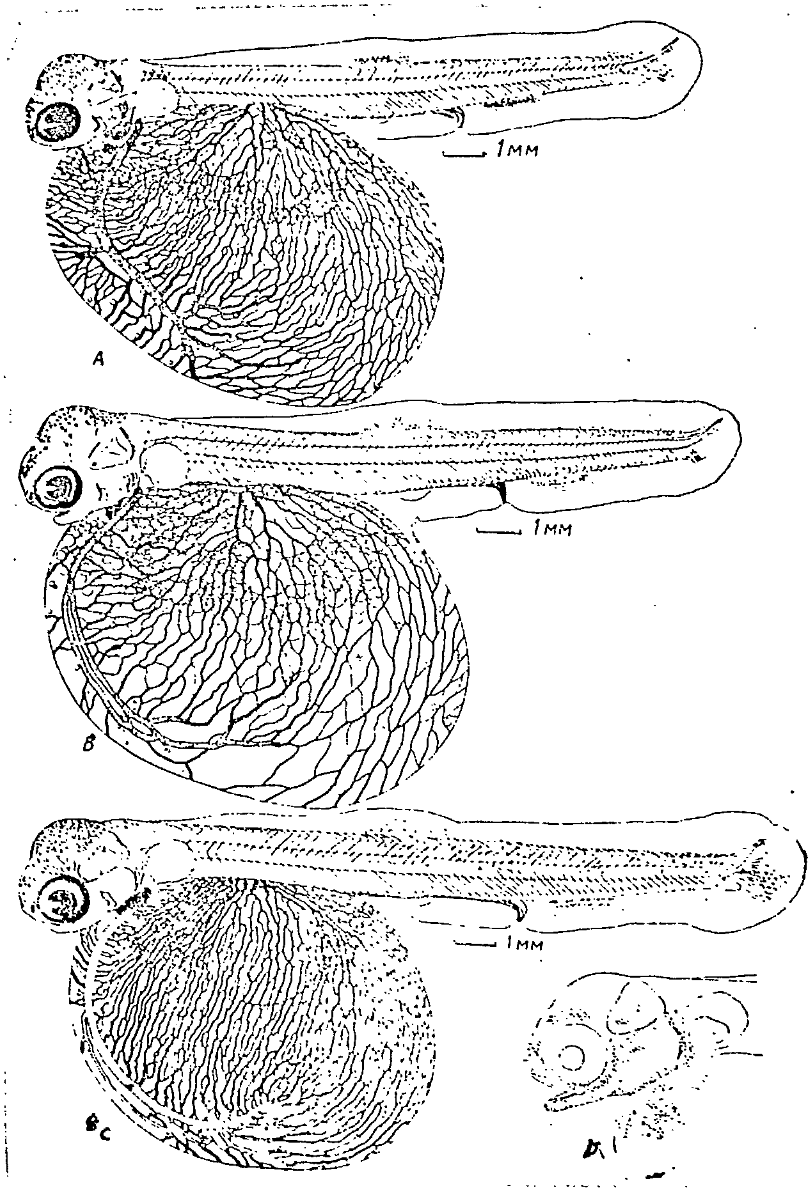


Fig. 43. Chinook at the end of incubation. A - stage of formation of the ventral fins, length of embryo 16.5 mm, development in river apparatus. B - embryo 16.5 mm long, reared in incubator with spring water. C - embryo 19.1 mm long, reared in river apparatus. D - distribution of hatching glands.

From 15 to 17 lepidotrichs developed in the tail; the largest of them had 3 - 4 sclerites each. The contours of the unpaired fins were clearly drawn. The surface of the head of the embryos turned dark. Melanophores were scattered over the entire body, but they were markedly less abundant in the anterior third of the trunk. A mass of pigment cells covered the spaces between the rays of the caudal fin. Chromatophores appeared in the lobes of the anal and at the base of the adopose fins. Numerous hatching glands became clearly visible (Fig. 43, D). In comparison with the sockeye, the chinook has more glands on the snout, lower jaws and pectoral glands, but fewer on the opercula. 181

When the apparatus is well supplied with water, these embryos rarely move inside the membranes. They pervormed up to 190- 200 movements per minute with their pectoral fins at 13 - 13.5°. Before hatching the embryos were excited and began to turn round within their membranes. The intensity of their respiration increased.

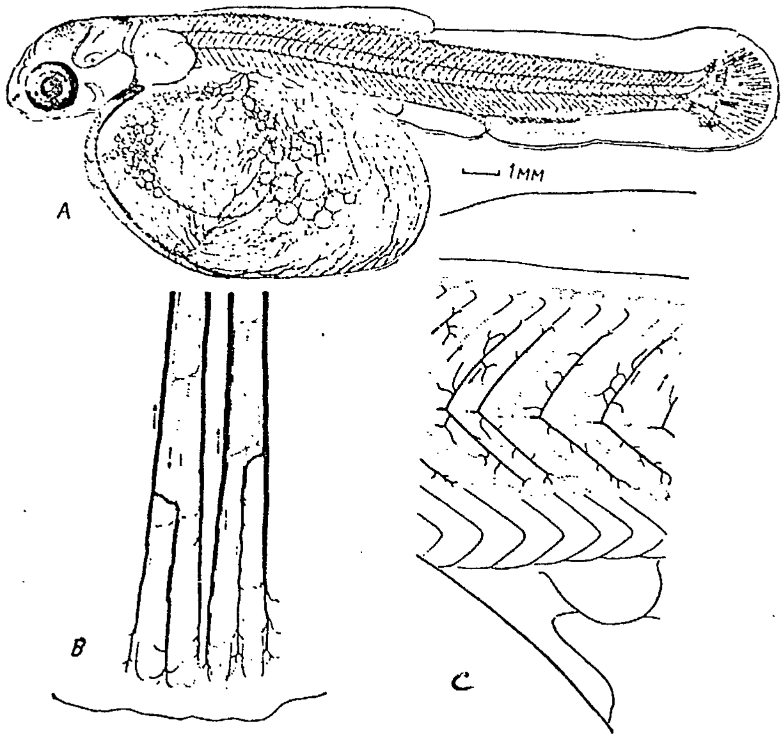
Stage 12. The Passive Condition of free Embryos. The Hatching of embryos in river apparatus in 1956 began on the 39th day (537 degree-days), became massive on the 41st day (563 degree-days) and was completed in three days. In the following year, hatching began on the 34th day (470 degree-days) and became massive on the 36th. More or less simultaneous hatching is characteristic for chinook. In 1956, mass hatching in the incubator took place at the age of 145 - 150 days (500 - 513 degree-days) and ended at the age of about 160 days (540 degree-days). In 1957 hatching was earlier, having begun on the 101st day (397 degree-days). In the Ushkovskii farm in 1934 - 1939 mass hatching of chinook occurs on the average 95 days after fertilization (about 576 degree-days).

In 1957 during mass hatching in the incubator larvae were 18 - 20.3 mm long (average 19.4 mm) and weighed 212 - 214 mg (average 228.4 mg). The weight of the yolk was 165 - 189 mg, average 180 mg, and average weight of the body of the embryo 49 mg, or slightly more than 21% of the total weight. In river apparatus the embryos hatched at a length of 19 - 21 mm (average 19.9 mm) and weight 216 - 251 mg (average 233 mg). The weight of the embryo itself varied from 42 to 74 mg and was on the average about 60 mg (slightly more than 25% of the total weight). During the incubation period under the conditions of higher temperature the weight of the yolk dropped by 12.5%.

The appearance of the embryo during the period of mass hatching is illustrated in Fig 44,A. In 1956 the eggs were large and embryos on hatching measured 22 - 23 mm. The yolk sac was oviform. The majority of fat droplets coalesced, only one huge drop was formed. The drawing shows their position in an embryo placed on one side. When the embryos are in the position with their dorsum up the fat droplets occupy a dorsal position.

During the time of hatching, the count of myotomes was 72 - 75, 182
the tail had 29 - 31 myotomes and constituted about 41% of the total length. The mouth of the embryos is semiventral. Eyes are large, immobile. Well-grown skin outgrowths of opercula left uncovered only the tips of some gill filaments. Large lobes developed in pseudobranchs.

Fig. 44. Chinook during mass hatching. A - general view, length of embryo, 22.4 mm. Development in river apparatus from the 5th of August to the 15th of September 1956. B - section of the caudal fin lobe with two rays and blood vessels. C - capillary network running towards the body surface in the ventral fin region.



Differentiation of rays continued in the unpaired fins, melanophores and lipophores appeared, their outlines became sharp; the contour of the adipose fin was also clearly drawn. In the caudal fin one could see up to 20 - 22 rays (when hatching is early there are only 13 - 15 rays). The tips of the ventral fins almost reached the margin of the preanal fin fold. The rudiments of rays appeared in the pectoral fins. The bodies of the hatching embryos were more intensively pigmented than those of the pink, chum and sockeye.

After hatching, the fine capillaries of the yolk sac begin to empty. This loss is partly compensated for by the development of capillaries between the rays of the caudal fin (Fig. 44,B) and near the body surface (Fig. 44,C). The role of branchial respiration is considerably increased.

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The embryos did not react to a light touch or to a weak illumination. Bright light disturbed them, but they remain indifferent to dim light. Hatched embryos lie motionless in one place, energetically waving their pectoral fins. At 14 - 15° the heart beats 92 - 95 times per minute. Lifted up by a stream of water, the embryos can actively maintain their position for a short time. After their emergence from the eggs, the oxygen uptake by the embryos rises sharply (see Table 13).

Stage 13. Formation of the Unpaired and Ventral Fins and of the Swimbladder. After a certain time, like in other species, the behaviour of the embryos changes. In 1957 in the river apparatus this change was observed on the 46th day (617 degree-days), when the embryos had the length of 22 - 24 mm (average 22.9 mm). They began to move against the current, and reacted positively to the touch of external objects; they appeared strongly disturbed in illuminated areas and hid in the darkness. At a temperature of 2.5 - 2.6° similar changes occurred approximately 15 days after hatching, the modified behaviour being less definite under those circumstances.

In river apparatus 18 days after hatching, the embryos reached 28.2 - 29.7 mm (during that time the temperature dropped from 12 to 9.5°). Spots appeared on their bodies (Fig. 45,A; development from the 5th of August to the 3rd of September 1956, 755 degree-days). The unpaired fin fold was strongly reduced. The rays of the dorsal fin began to subdivide into sclerites. The tail assumed a symmetrical form. The so-called reduced caudal rays made their appearance. Rays formed in the pectoral and ventral fins. Almost a third of the yolk sac was covered by growing myotomes. During this stage was observed rapid growth of the rudiment of the swimbladder. In the apparatus, the chinook now and again rose into open water, but remained swimming only for a short time. Under the condition of low temperature the spots on the sides of the body of chinook appeared at the age of 185 days (610 degree-days).

Larval Development Period.

The stage of mixed feeding. Reared in the river apparatus and then in aquaria, the chinook began to ingest food on the 70 - 73rd day (843 - 863 degree-days). A similarly morpho-functional state was reached by it in the incubator at the age of about 220 - 230 days (690 - 700 degree-days). These larvae were 29.3 - 30.5 mm long and weighed more than 345 mg (Fig. 45,B). There bodies became streamlined. On the jaws, teeth cut through; the mouth acquired its prehensile function. By that time only a small part of the vascularized surface of the yolk sac with sparse capillaries
on it remained uncovered. A small vestige of the unpaired fin fold re- 184
mained behind the adipose and anal fins. The signs of resorbtion of the preanal fin fold were barely noticeable. The anterior, branching rays of the unpaired fins began to enlarge. The lobe of the caudal fin became large and intensely pigmented. At the tips of 4 - 6 of the first rays of the pectoral fins, black and cherry-red pigment cells began to form. Lipophores appeared on the ventral fins.

Fig. 45. Young stages of Chinook.. A - Free embryo, 29.7 mm long. B - larva 33.3 mm long. C - larva 37.5 mm long. D - fry 44.5 mm long.

Up to 10 - 12 large, oval, dark spots formed along the middle 185
line, above them were small, round spots, about half their size. The body acquired a slight silvery sheen. Guanine deposits were particularly abundant on the gill covers, flanks and the mesentery.

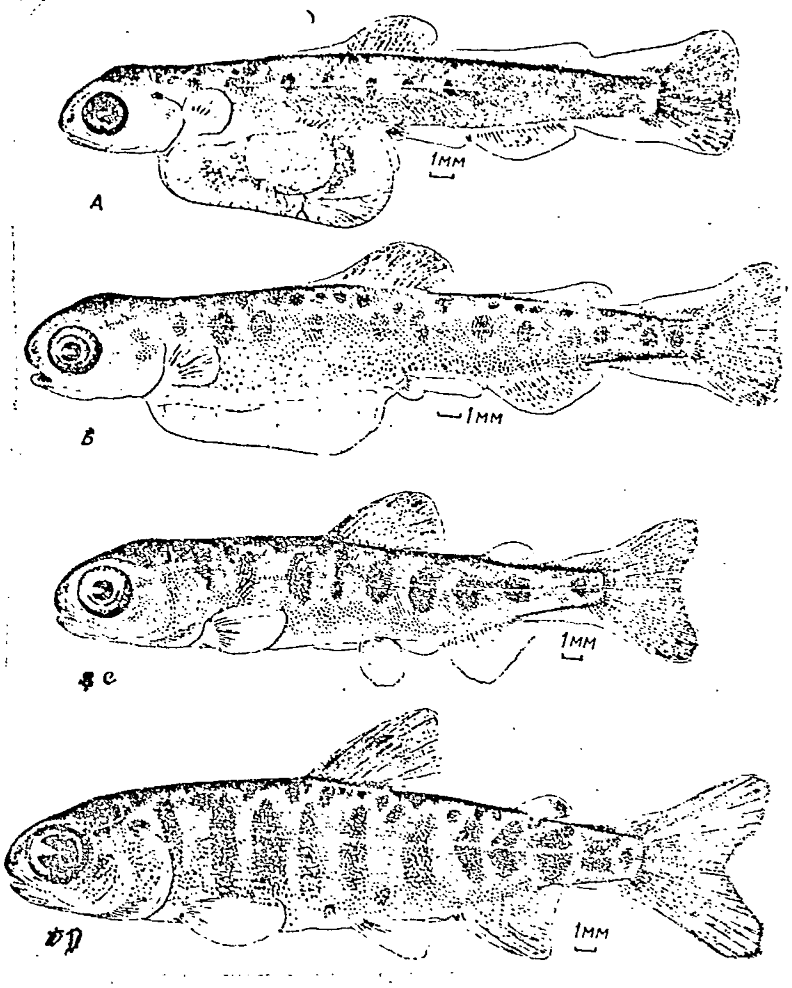

Fig. 45.

Large, branching gill filaments developed. Up to 7 - 8 gill rakers were laid down. Both parts of the stomach underwent anatomic differentiation. Rudiments of the pyloric caeca became visible. The swimbladder was filled with air.

At the age of 84 days (873 degree-days) the larvae, transferred after the onset of cooling from the river apparatus into aquaria, were 28 - 31 mm long (average of 25 specimens 29.8 mm) and weighed 237 - 329 mg (average about 300 mg). The remnant of yolk weighed 63 - 83 mg and constituted from 20 to 28% (average about 23%) of the total weight. In the aquaria, such larvae actively hunted <u>Cyclops</u> and <u>Daphnia</u>.

Under the conditions of poor lighting the larvae had dark colouration, but as soon as the light increased they turned pale. Changes in colouration could be repeatedly provoked by altering illumination. Under natural conditions, apparently, most larvae at this stage are still in the nests, but some individuals already begin to emerge from the ground. Having left the nests, the young move to the shallows near the banks, where the current is slow.

Soon after transition to life in water, the remainder of the yolk is covered by the abdominal walls and is rapidly resorbed. At the same time adipose tissue develops in the cavity. Towards the end of this stage the resorption of the preanal fin fold becomes more rapid (Fig. 45, C).

In nature, the young chinook 34 - 39 mm long already keeps itself in isolation. Each individual occupies a space of about 0.11 m^2 and defends it actively. By night the fry are passive, stay near the shallow at the banks, sometimes in the areas with water depth less than 5 cm. In running water they are found only at the bottom; when there is no current, they can be found both at the bottom and near the surface. In the winter they conceal themselves among the stones and, since they have protective colouration, they are diffecult to find without careful searching (Edmundson, Everest and Chapman, 1968).

Mass migration of the young from the North American rivers occurs before the deposition of the scales and completion of the resorption of the yolk, i.e. in the presence of the larval characteristics. This is typical for the stocks with late run and spawning. Rutter (1904) reported on the migration of chinook with remnants of yolk and at an average length of 3.8 cm from the Sacramento river. Many larvae and fingerlings up to 55 mm long also migrate into the sea from the Columbia River. From the northern rivers the young migrate later. Chinook spends not less than a year in the rivers of Alaska, from the river Taku 94% of all individuals migrate during the second year and 6% during the third year of life (Mason, 1965). There are no reports on catches of the Asian chinook from the oceanic type of scale centre. In our rivers the young spend at the most one winter.

The Fry and Fingerling Stage of Development. 186

In the young reared in river apparatus and with the onset of cold transferred to aquaria, the scales began to develop at a length of 34 - 35 mm. In the last days of August 1956 in the middle course of the Paratunka river we caught fry with 1 to 3 sclerites on their scales (Fig. 45,D). In some specimens a small remnant of the preanal fin fold was retained. The age of these specimens, counting from oviposition, was one year.

By the time of scale formation the chinook practically loses its larval characteristics. One can find in them only traces of yolk and preanal fold. Large fry become progressively high-bodied, as can be seen from the figures below.

Length of fry, mm	Weight, mg	Greatest body height in % of length, after Smith
37	440	16.2
44	900	19.3
59	2100	20.1

In chinook fry, the snout is short and blunt. Eyes are large. Attention is attracted to a large number of rays in the skin fold of opercula (branchiostegal rays), which in chinook is up to 16 - 19, while in the related species not more than 14 - 15. Pectoral fins are long, their tips almost reach the vertical line drawn through the anterior margin of the base of the dorsal fin. The anterior branching rays of the dorsal and anal fins become longer and form sharp tips. The long rays of the caudal fin are almost twice as long as the middle rays.

The flanks of the fry are silvery with a greenish-blue tinge. Above the middle line, the body is dark pistachio-coloured, the back brown with a blue-green tinge. The outline of the elongated, elliptical large lateral dark spots is very sharp. Between their upper ends are situated oviform spots the size of the pupils, and higher up, on the back, there are even smaller ones. In some specimens individual small spots appear also below the large lateral ones. In the anterior part of the dorsal fin, at the level of the middle of the fin rays, a dark streak was formed. Melanophores outline the margins of the adipose and caudal fins. A small number of melanophores is present between the first rays of the pectoral fins, they are very few on the anal fin and absent from the ventral. All fins are bordered with numerous lipophores of bright cherry-red colour. Towards the proximal part of the fins the number of these pigment cells decreases and that of the yellow-orange lipophores increases. The sharp tips of the dorsal, anal and also tips of the ventral fins assumed a whitish colour. A bright red streak appeared on the lower jaw at the base of the teeth. In the integument of the head and body dominate 187
orange lipophores which are progressively masked by the deposits of guanine.

The colouration of the chinook fry resembles that of coho fry. Differences are in the fact that the general intensity of the colouration is brighter in chinook, its lateral spots are longer and narrower with sharper outlines, the small spots on the dorsum are better visible and the dark spot near the distal end of the anal fin, clearly visible in the coho, is absent from the chinook; in its anal fin there are few melanophores.

By the time of transition to the fry stage, a large number of pyloric caeca has developed (as is well know, they are particularly numerous in the chinook). The number of rudimentary gill rakers approaches the definitive.

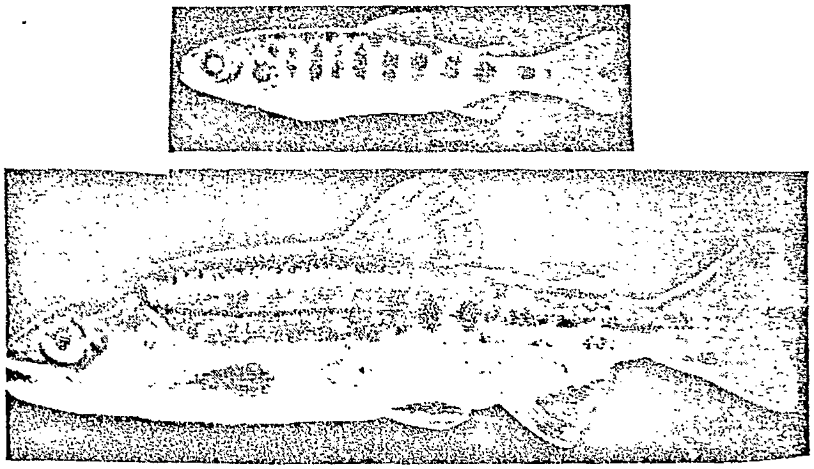

Fig. 46. Chinook fry, 59 mm long (upper) and yearling 143 mm long.

On dissection of fry, sex can be distinguished with the unaided eye; ovaries are stouter than testes and contain fairly large orange-coloured oocytes. In the specimen shown in Fig. 45,D the cephalic, broader part of the ovaries was about 5 mm long and 0.5 mm wide; the diameter of oocytes reached 60 - 65 mk.

At the beginning of August, the fry appeared in the lower reaches of the river Paratunka. They could be found in quiet, deeper parts, usually behind the projections of the banks or behind some submerged objects. The young were scattering throughout the basin.

Fig. 46 shows the external appearance of the young 59 and 143 mm long. The body of the chinook becomes wider and more stout with age. The head becomes somewhat longer, mainly because of the growth of the snout. The postanal section becomes relatively shorter. The size of the eyes in the compared specimens consitituted 32.4 and 20.8% of the head length. The relative length of the paired fins changed only 188
little during subsequent growth. The shape of the unpaired fins changes significantly. The sharpness of the anterior margin is lost; it becomes rounded. The relative height of the dorsal fin is reduced from 20.8 to 15.4% and that of the anal from 14.8 to 10.7% of the body length. With the transition to the second fry stage colouration also changes. Lateral spots become shorter. On the back there appear numerous small black dots, about half of the diameter of the pupil. Several such dots appear at the base of the dorsal fin and at the upper margin near the base of the lobe of the caudal fin.

Observations in nature and in the laboratory have shown that the fry of chinook occupy separate localities on the riffles and defend them. Rivalry is observed among individuals and a hierarchical dependence is established. In an experimental aquarium with running water, imitating natural conditions, the dominant individuals grew more rapidly. Gathering of fry in schools was observed in the ponds. The young fish school also in the estuaries. In the tidal zone, when the water level rises, they remain in midwater, changing from a solitary mode of life and rivalry to a gregarious mode of life. When the water level drops, their behaviour changes and they again occupy individual territories. It is not clear whether the aggressive behaviour of the large fingerlings leads to the seaward migration of the weak individuals.

Those that begin to descend from the spawning grounds earlier do not appear to be in unfavourable condition and grow rapidly. The young fish early abandon small rivers, stay for several months in the stream of large rivers and in August move towards the mouth. Until October, a small number of young fish remain in the spawning tributaries; they reach the length of 50 - 90 mm, and migrate into the sea during the autumn spate (Reimers, 1968). The young of the Kamchatkan chinook remain in the rivers for the winter.

Special features of Reproduction and Development of Chinook.

Chinook is the largest salmon species. In spawning populations of the Kamchatkan chinook predominate five- and six-year-old individuals, which have spent one winter in the river. Some of them reach the age of 7, rarely 8 years. Generally, however, the young of this species leaves for the sea at the end of the stage of mixed feeding, as fingerlings (young-of-the-year), yearlings and two-year-olds. Small numbers of males mature at the two-year-old stage. The dwarf males mature during the first year of their lives, and show the process of repeated spermatogenesis. The age structure of the population can, thus, be very complicated. Landlocked form is unknown, but can be produced artificially.

The races with summer spawning and those that spawn later differ from one another significantly in the ecology of development. Asia is inhabited by the summer spawning chinook. It selects spawning grounds of
the river bed type, the bottom of which is washed by the subsoil current 189
with some admixture of ground water of shallow origin. Its young pass one or two winters in the rivers. The spawning region of chinook in Asia is narrow, discontinuous; the species is not abundant. This is due to the ecological uniformity of populations.

In North America, the species is distributed more widely and is represented by different ecological forms. In the northern rivers, the run occurs in the spring and the spawning in the summer. In the rivers of the central region, in addition to the spring run there is also a summer run and autumn spawning, and further south the period of run and spawning is even more extended. The summer spawning form resembles the Kamchatkan chinook. Individuals with late spawning enter the rivers in more mature condition and spawn in lower reaches, in other tributaries and the main river beds. The basic ecological difference of the autumn and winter spawning chinook is in the fact that it builds its nests in the localities at the emergence of ground waters, which long retain spawning temperatures; these waters are poor in oxygen. The young of the autumn spawning form migrates to the sea as young-of-the-year, in the southern rivers many individuals descending before the development of scales. The characteristic of the seasonal races are genetically stable. Due to the ecological heterogeneity, the North American chinook utilises its spawning and food resources more widely, and builds up abundance many times greater than that occurring in the western part of its range.

Males produce milt in large batches with a high concentration of spermatozoids. During the time of reproduction this large fish clears particularly large surfaces. Eggs in the redds are arranged most commonly in two or three groups. Absolute fecundity of the chinook is considerably higher than that of other Pacific salmon species. In Kamchatka the average fecundity is 8 - 10 thousand eggs, the highest figure exceeding 20 thousand. The fecundity of the autumn spawning form is lower (which indicates greater viability and stability of the conditions of development), and its eggs are particularly large (weight of mature oocytes reaches 380 mg). The eggs are intensely orange-red with a pink tinge and are rich in astaxanthin. Egg membranes are slightly thinner than in the chum (53.75 ± 0.78 mk).

The large size of the eggs and the abundance of yolk are responsible for the prolonged process of epiboly, which in the Kamchatkan chinook is completed at the stage of 53 to 59 segments and can be prolonged to the stage of 63 - 64 segments. According to available data, epiboly in the North American chinook is completed at an earlier stage, which indicates that the representatives of various races have distinct morphogenesis. There are more segments formed than in other species; their number reaches 80 - 81.

Blood circulation begins after the formation of 63 - 66 segments. The embryonic organs of respiration are highly developed.

In embryos reared in apparatus with river water lipophores appear earlier (about 340 degree-days, i.e. earlier than in the sockeye), and melanophores later. In contrast, when incubated in cold spring water, the 190
eggs first acquired melanophores (about 270 degree-days) and considerably later the lipophores. In comparison with the sockeye the unpaired fins are laid down later, in larger embryos.

The development in the egg takes shorter than in the sockeye and pink but longer than in masu and coho. Hatching occurs simultaneously. In the level of its differentiation the hatching chinook resembles the chum, but its embryos are more intensely pigmented.

The development in the ground continues almost to the end of the resorption of the yolk. The larvae are characteristically spotted. Their bodies, dorsal and caudal fins are intensely pigmented, while the anal fin, in contrast, is weakly pigmented. The unpaired fins are high (but lower than those of coho and masou), the pectoral long; the caudal lobe is large and the preanal fold long retained. On emergence from their nests the young fish desperse in shallow water along the banks with slow current and keep close to the bottom

The bahaviour of the young chinook differs significantly from that of the chum, sockeye and pink. The young chinook occupy individual territories and defend them aggressively. When catching food, they perform short darting movements and return to the original place. With the onset of darkness their activity diminishes, they no longer rise in the water. The fish are high bodied, have long pectoral and high unpaired fins with elongated first branching rays. The spotted coloration is markedly expressed, and changes rapidly depending on the intensity of the illumination and colour of the bottom. The fish larger than 50 mm lose their aggressiveness and develop a tendency to schooling. The last-named characteristic is evident at the first fry stage when the level of the river is high, or when the fish finds itself in a deep area with slow current. The process of smoltification is very definite.

COHO - ONCORHYNCUS KISUTCH (WALBAUM).

The coho is a middle-sized salmon. When entering Kamchatkan rivers it is about 60 cm long and weighs 3.0 - 3.5 kg. Some individuals reach the length of 88 cm and weight 6.8 kg. The record weight is about 14 kg. This valuable fish is cultured in Kamchatka, Sakhalin and North America.

According to catches, the coho occupies fourth place in our salmon fisheries. In 1936 101.5 thousand centners (10.15 thousand metric tons; Translator's note) of coho were caught (Pravdin, 1940). The average yearly catch in 1954 - 1957 was 57 thousand centners (5.7 thousand metric tons), in 1965 - 1967 catches approximated the long-term average. In the east of its range the abundance of the species is about twice as large (Levanidov et al., 1970; Zobrin, 1970b). 191

Distribution, life in the sea, age composition. In Asia, coho is distributed from the river Anadyr to the rivers debouching into the southern part of the Amur liman. In the rivers of Primore it occurs only rarely. Coho moves to spawn in the rivers of the Commodore, Aleutian and Kurile Islands, Sakhalin and the northern rivers of Hokkaido. An abundant population reproduces in the basin of the river Tym in Sakhalin; further south it is not abundant. The main bulk of this salmon species is taken in the Kamchatkan fisheries district. In North America the species is distributed from Norton Bay in Alaska to Monterey Bay in California (Berg, 1948; Gribanov, 1948; Hikita, 1962; Godfrey, 1965).

The northern border of the winter grounds of coho in the ocean is limited by the surface isotherm of 5°, southern by 10.5°. The coho occupies a narrower area than the chum, pink or sockeye. In the Bering Sea, catches of this salmon are small. In the ocean it is scattered. Marine fishery is pursued at temperatures from 4 to 15.2°, the catches rise at a temperature of 8 - 12° (Birman, 1958, 1967; Semko, 1958; Godfrey, 1965).

According to Gribanov (1948) more than 2/3 of the individuals live in the river for one year, the remainder for two years, and a few fish of the Lake Ushkov, three years. A small number of young leave for the sea while still young-of-the-year and even before the appearance of scales.

There are more such migrants in the southern part of the range in North America. Dwarf males mature in the river for about a year. Some males spend in the sea only one summer and return to the river to spawn, having a length of 27 - 33 cm. Feeding in the sea usually extends over two summer seasons and rarely for a longer period. In the waters of British Columbia, in the population of coho up to 8 age groups are distinguished (Pritchard, 1940; Berg, 1948). The age compostition of the spawning populations is more uniform than in the sockeye and chinook. In the sea, coho grows more rapidly than related species, except for the chinook.

Intraspecific Differentiation. Coho is represented by migratory and landlocked forms. In many rivers, relatively early and later runs of spawners are fairly clearly distinguishable; these spawners reproduce at different times and in separate spawning grounds (see below). This points out ecological differentiation of the migratory coho, though it is not as pronounced as in the chum or chinook. Gribanov's (1948) investigation of the coho in the river Paratunka did not reveal morphological differences between fish of different runs.

Geographic differences in age composition of spawning populations are known. In the northern rivers dominate fish of older ages with two-year and longer life spans in the river, whereas in the southern regions maturation occurs earlier, mainly in three-year-olds, and the young migrate from the rivers during the first summer of their lives (Gilbert, 1914; Shapovalov and Tait, 1954, etc.). The age composition of the fish moving 192
into the rivers of the western shores of Kamchatka differs from that of the fish of the eastern shores. Judging from many years of data, in the river Kamchatka, the age group 3_2+ dominates and each year in the catches,

one finds a small proportion of fish, age 4_3+. In the river Bol'shaya the main age group is 2_1+ and individuals age 4_3+ are almost absent from catches. Fish age 3_1+ and 4_2+ are very rare (Zobrin, 1970b). Gribanov (1948) described differences of age and size compostition of fish reproductin in individual parts of the basin of the river Kamchatka. For example, 94% of coho entered the large left tributary, the river Kyrganik, at the age of 2_1+, while less than 10% of individuals of that age entered Lake Ushkovskoe in 1926 and 1927 and none at all in 1928. In the spawning population of the lake Ushka predominated fish age 3_2+, distinguished by their large size; average length of males was 76 cm, females 74 cm, while in the river Kyrganik the corresponding figures were 70 and 67.5 cm. These examples indicate qualitative differences of local groups of coho in that large basin.

Attention was attracted by the characteristic features of development of the nuptial livery. In the rivers of Kamchatka, and northern Sakhalin river Tym, the spawners before spawning undergo deep morphological changes and assume and intense red-brownish colouration. In the south of Sakhalin, in the river Naiba, the coho suffers little change before spawning. Running males retain their torpedo-like form, have shallowly embedded scales and pale coloration, with a weakly pink belly, while the females resemble those of the autumn chum in their colour (Smirnov, 1959b). Spawners in the rivers of Hokkaido have a similar appearance (Miyadi et al., 1965). In the river Naiba, the fish are small and of low fecundity and in the river Tym large and more fecund (Table 14). All this indicates morphological and biological distinctness of the populations reproducing at the southern border of the range of the species.

Variability in size and fecundity of the Asian coho are shown in Table 14. The table should be supplemented by information about high fecundity of the coho of one of the nothern populations; in the river Av'yavayam the average fecundity of individuals age 2_1+ was 6,922, and 3_2+ - 7,079 eggs (Grachev, 1971). The low fecundity of the North American coho attracts attention. The average absolute fecundity of females, 65.3 cm long, in Scott stream was 2,500 eggs, in the Frases river 3,152 eggs and in the river Namu, in females with an average length 69.3 cm, the count is 3,002 eggs (Foerster and Pritchard, 1936; Shapovalov and Taft, 1954; Rounsefell, 1957). Such differences suggest greater viability in the waters of North America.

A landlocked coho was described in the Lake Maloe Sarannoe, which is separated by a narrow strip from Avachinskaya Bay (Dvinin, 1949). Like migratory coho, the landlocked fish matures in the 3rd- 4th year. During the first and second years of life, its young grow more rapidly than those of the migratory form, and then the rate of growth slows down; during the third year the fish reaches only 27 and during the fourth about 194
36 cm. Mean fecundity of that form is 1,600 eggs. It is interesting that the fecundity of the lake coho on the North American continent is, like that of the anadromous one, considerably lower; in females 34 cm long and weighing 0.5 kg it is 567 eggs (Beal, 1955; after Rounsefell, 1957). The landlocked coho from the Lake Maloe Sarannoe has fewer vertebrae and pyloric caeca in comparison with the migratory one, but has more gill rakers. Its snout is shorter, forehead narrower, eyes larger. The dorsal and the anal fins of the lake coho are higher, the paired fins longer. The mature individuals assume intense colouration, characteristic for the Kamchatkan coho. The nests are built near the shore, on the gravel in the

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Table 14.

Length, weight and fecundity of coho from different areas.

Area	Length (AC), cm		Weight, kg		Absolute fecundity	Reference
	males	females	males	females	no. of eggs	
R. Kamchatka	--	51.5--65.5 (59.5)	--	1.81--4.32 (3.27)	2881--5974 (4883)	Kuznetsov, 1928
R. Kamchatka	--	--	--	(2.2--3.4) (2.95)	(3671--5132)[1] (4535)	Zorbidi, 1970
R. Bol'shaya	(56.8--68.0)	(54.2--65.8)	(2.2--5.2)	(2.0--3.8)	(3715--4800)[2] (4394)	
Karymaiskii stream	--	--	--	--	(4300--5343)[3]	Semko, 1954
R. Paratunka	(42.0--70.0) (58.32)	56.0--66.0 (58.80)	1.5--4.5 (2.9)	2.0--4.5 (2.9)	2800--7600 (4350)	Fribanov, 1948
R. Tym'	59.0--83.0 (70.1--75.3)	61.0--78.0 (71.0--75.3)	2.0--7.0 (4.22--4.85)	2.15--6.0 (4.33--4.87)	1756--9011 (4460--5370)[4]	Gritsenko, 1973
R. Naiba	51.0--68.0 (63.1)	60.5--71.0 (64.0)	1.4--4.3 (2.99)	3.1--4.6 (3.59)	2380--5810 (4320)[5]	personal data
Lake Maloe Sarannoe	(36.3)	(36.1)	--	--	1228--3066 (1600)	Dvinin, 1949

Note: Average figures quoted in brackets: 1 - for 1940 - 1967; 2 - for 1952 - 1967; 3 - for 1943 - 1950; 4 - for 1961-1963 and 1966; 5 - for 1953.

places of emergence of ground water. Spawning begins in the middle of October, for a long time continues under the ice and ends in the last days of March. 194

Anadromous Migration, Prespawning Changes and Times of Spawning.

Along both shores of the ocean, the coho approaches rivers later than other species of salmon, except for the autumn chum and chinook of the late run. The times of the run and spawning are prolonged. Into the river Kamchatka the coho enters from the middle of July, mass run is observed from the 20's of that month, and the most intenstive one during the second half of August; the spawners can be found in the river mouth until December. In the upper reaches of the river Kamchatka, the early run occurs from August to the middle of October. Spawning takes place from the 20's of September, becomes massive in the beginning of October and ends on the 20 - 25th of October. During the second half of October, the second run of coho begins and continues to the middle of December, and even to a later date. This fish reproduces from the end of November to January, and in some streams until March. In the region of the village Verkhne-Kamchatsk the summer coho spawns mainly in the tributaries--the rivers Andrianovka and Poperechnaya; on the other hand, the winter coho does not migrate up the river Andrianovka further than 2 - 3 km and spawns in the main bed of the river Kamchatka. In the region of Bol'sheretsk of the western coast of Kamchatka, coho appears in the last five days of July, the main part of the run is observed in the second half of August; entry into the river takes place until the end of October. Further North, in the region of Kikhchinsk, in the rivers of the Okhotsk shore, the mass run is observed in the second half of August and in the first days of September (Gribanov, 1948).

In the region of the Avachinskaya Bay and in the river Paratunka, a summer and an autumn run can be distinguished. The summer run begins in the last days of June, reaches its maximum at the end of August - beginning of September and ends in the middle or in the 20's of September. In the river Dal'nyaya in 1956 I observed spawning during the 20's of August, but it begins more commonly during the first days of September and assumes a mass character in October. According to Gribanov (1948) in summer, coho does not enter the Nikolaevskie streams, situated near the mouth of the river Paratunka. In the lower reaches, the autumn run continues all through October and later. This coho spawns in November and December in the upper reaches of the basin and in the Nikolaevskie streams.

In the Sakhalin rivers also two runs of spawners were identified. 195

In the river Tym' coho spawns in the tributaries Nysh, Pilenga, Kun'va, Irkir, Vos', Krasnaya, Chernaya, Belaya, Tykovskii and other streams. Near the spawning grounds before the middle of August, no spawners appear; few individuals arrive during September, and then, after a break of about half a month's duration, the late run begins, which continues long into the winter. Spawning continues to the beginning of January. Further south, in the rivers Poronai and Pugachevka the run lasts from the middle of October, and in the south of the island, in the river Taranaika, during the last 10 days of October. In the river B. Takaya in 1953 the arrival of the fish was observed from the 6th through the 24th of October and then ceased, to reappear agian in the beginning of December and continue through the first 10 days of January. Thus, here we have an autumn and winter run (Smirnov, 1960a). Coho moves up the river of Hokkaido from the end of September to the beginning of October (Sano, 1959).

Off the coasts of South East Alaska and British Columbia, coho appears at the beginning of July, the run continues until the end of August and beginning of September. In North America mass spawning occurs in November-January, but, as in Kamchatka, oviposition extends until March (Shapovalov and Taft, 1954; Godfrey, 1965).

Thus, the early and the late (autumn and winter) run and spawning of this fish can be distinguished almost everywhere. The quantitative relationships are different: in the basin of the river Kamchatka, for example, coho of the early run is more abundant (Ostroumov, 1964), and in the more southern region later runs are more abundant. The localities of reproduction of fish with different times of migration do not coincide.

It has been observed that the entry of fish into the rivers and its move to the spawning grounds coincides with the beginning of the flood tide, temperature drop below 10° and stormy weather, either rain or snow. The main bulk of fish enters the rivers in a silvery condition, at maturity stage III-IV (Gribanov, 1948). Silvery individuals occur in the river also in later periods of the year, hence the name of the fish is white salmon or silver salmon. Coho moves along the rivers slowly, mainly by night tarrying for lengthy periods in deep places and hollows.

Shapovalov and Taft (1954) do not relate the entry of coho into rivers with a definite maturity stage. They record the migration of both silver and of almost mature individuals with well developed nuptial livery. The more mature fish spawns close to the river mouths. In the North American rivers, coho spawns mainly in small streams and rarely migrated further than 270 km. In our country migrations of considerable distance are known: in the river Kamchatka they are more than 700 km (Kuznetsov, 1928).

During its upward movement and stay in the hollows the fish gradually assumes nuptial livery. Prespawning changes of coho have been described by many authors (Chamberlain, 1907; Chernavin, 1918,1921; Shapovalov and Taft, 1954; Smirnov, 1959b). In the initial phase of maturation the silvery sheen of the scales becomes dull, the fish turns dark, pink colour 196
appears on its belly and sides. With time, the reddish hue begins to prevail. The body of maturing males becomes flatter at the sides, a small hump develops on the back, teeth grow to a large size, jaws become strongly elongate, particularly the upper jaw which assumes a hooked downward bend (Fig. 47). Scales are embedded deep in the skin and become partly resorbed. The top of the head and the back of the spawners remain dark olive.

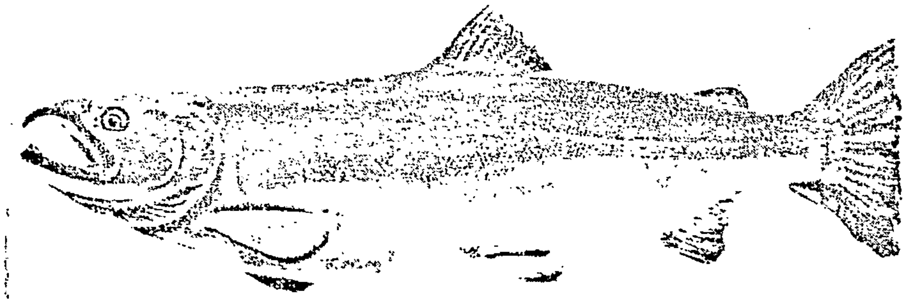


Fig. 47. Mature male coho.

Reddish spots, with underlying olive colour appear on the preopercular and opercular bones. Body flanks assume an even brick -red or dark-raspberry colouration. In some individuals more or less distinct transverse dark spots appear on the flanks, and the belly also becomes dark. On the dorsal side of the body are scattered numerous small, dark spots. There are larger spots between the rays of the dorsal fin, on the adipose fin, between the rays of the upper part of the lobe of the caudal fin. Pectoral fins darken. At the base of the unpaired and caudal fins, red pigment appears. Distal ends of the ventral and anal fins become white. (See "Commercial fishes of the USSR", 1948, Plate 43; Clemens and Wilby, 1961, Pl.2). The hump does not develop in females. Their jaws elongate only slightly and curve slightly; red pigment is less distinct, the dark-olive colour with reddish tinge being dominant. There occur, however, females with intense carotinoid pigmentation, typical of males. In the course of oviposition the spawners progressively darken. The body shape and colouration change less in small individuals.

Spawning grounds and Conditions of Development. Krokhin and Krogius (1936b) recorded in the basin of the river Bol'shaya spawning of coho in the same localities which are selected by the chum and sockeye (with the exception of lakes). In comparison with the sockeye, its spawning takes place in places with greater current velocities. In the stream spawning grounds of the upper reaches of rivers in the basin of 197 the river Bol'shaya the characteristic current velocities are 0.2 - 0.3 m/sec, alkaline reaction of water and low content of free CO_2.

Coho spawns both in the main river beds, preferring its upper regions, and in the side channels, streams, pothole and limnocrenes (for example, in Lake Ushki in the basin of the Kamchatka river). Typical lakes are avoided. Spawning grounds coincide with the points of emergence of ground water. Nests are often built near the banks with more rapid currents, but they occur also in the shallows with slow currents, or where current is absent, with the bottom covered by a thick layer of silt (Kuznetsov, 1928; Smirnov, 1960a).

In the basin of the river Bolshaya, coho spawns at depths from 6 to 40 cm, as reported by Kuznetsov (1928). The length of the redds varied from 157 to 266 cm, width from 67 to 96 cm. Eggs are buried to the depth of 9 - 23 cm with 3 - 4 groups (nests). There are from 203 to 448 eggs in individual nests, with the total number in a redd from 157 to 3,628. These figures are much lower than absolute fecundity, which indicates serious losses of eggs during oviposition in rapid current. It is also possible that some females build several redds. According to the same author, there are rivers in Kamchatka, which are visited by coho only. The following regular feature was also observed: where many "summer" coho come, there fewer "winter" coho reproduce and vice versa. The relationship between coho and other species was commented upon in the following terms: "Arriving as the latest fish on the same spawning grounds, coho, quite naturally, becomes a pest for the previously deposited eggs of chinook, chum and sockeye, digging them out while building its nests" (Kuznetsov, 1928, p.174). This categorical conclusion denies the specific features of ecology of the species, and is without sufficient factual basis.

Of course, in isolated instances, burying of eggs can cause losses in the closely situated redds of other species. In some nests of coho one finds eggs of the chum (Gritsenko, 1973). Such instances, however, are rare. In the basin of the river Paratunka we observed the closeness of the spawning grounds of coho and sockeye. The females of these two species selected different microhabitats. Coho is stronger and kept to places where current is more rapid and ground with larger stones. Building its nests, it not infrequently deepens the bed of the river and the current becomes more rapid above the nests. The neighbouring nests of the sockeye were situated in quieter spots, protruded from untouched ground and retarded the stream. In some streams, for example Tykovskii in the basin of the river Tym', coho spawns close to chum, but in that case we did not observe topographical overlap of their redds. It has been reported that in the basin of the Columbia river there is a partial overlap between regions and period of spawning of coho and autumn spawning chinook. Coho prefers places with slower current, and direct neighbourhood of spawning redds of the two species was observed only in one region. The nests 198
of coho were often situated between logs and fallen trees and varied in shape. The ground of the redds contains up to 10% silt (more than in other species). The mean depth of spawning grounds was about 20 cm and the greatest, 66 cm. The depth of the nest holes varied from 7.5 to 50 cm (average about 20.3 cm). The area of the redds was about 2.8 m^2, i.e. greater than in sockeye and chum. Their size is influenced by the size of the fish,

character of the bottom and current velocity (Burner, 1951).

On the spawning grounds of coho in the river Paratunka, Gribanov (1948) observed oxygen content from 9.9 to 15 mg/l, with average saturation near 100%. CO_2 content varied from 15 mg/l to complete absence (average 6.61 mg/l). The investigator concluded that coho selects places with lower oxygen content. There are facts contradicting this view. This salmon species often spawns in places with abundant deposits of silt and slow current. In the river Dal'nyaya we recorded in the spawning grounds of coho current velocity at the surface up to 32 cm/sec (mean of 20 measurements 19 cm/sec). Five centimeters from the bottom the velocity of current did not exceed 18 cm/sec, being on the average 14 cm/sec. Over some nests the apparatus registered no current. In the second half of October and beginning of November 1957 the surface layers of water contained from 10.8 to 12.8 mg/l oxygen (88.5 - 98.7% saturation). Water taken from the nests as a rule contained less oxygen. Fluctuation from 6 to 14.2 mg/l were observed (saturation 46 to 109.6%). In the nests with lowest oxygen saturation of water the eggs developed quite normally. In one of them the water was more highly saturated than the river water. With time, some drop in oxygen content in the nests was observed which can be related to the silting of the ground.

Semko (1954) describes a case of disturbance in water supply into the incubator. Within one day, as the result of metabolism of the eggs and larvae, the quantity of oxygen in water dropped to 2.7 mg/l (19.1% saturation), content of free carbonic acid reached 43.8 mg/l, temperature was 1.5°. The larvae of coho and sockeye perished, while the eggs survived. In our experiments, coho developed normally in the incubator of the

Sokolovskii fish farm, supplied with water with about 50% oxygen saturation. In coho larvae with small yolk remnants the signs of asphyxia were observed when the oxygen content dropped to 2.58 mg/l, improvement in water flow restoring these larvae to their normal condition (Chapman, 1940). With the necessary minimum of oxygen (about 4 mg/l) the young fish withstand the presence of considerable quantities of free carbonic acid and weak acid reaction of the environment (Townsend and Cheyne, 1944).

Since the spawning is prolonged, it takes place in a sufficiently wide range of temperature of the river water. Spawning streams of the river Bol'shaya in October have temperatures of 5.3 - 4.5°, in November 4.3 - 2.3°. Gribanov observed on the spawning grounds of the river Paratunka temperature fluctuations from 0.8 to 7.7°. In 1957 in the river Dal'nyaya was observed scattered spawning of coho during the second half of August. During that time, the average daily temperature in the river on the spawning grounds of coho varied from 15.5 to 17.7°, in some days rising to 18.5 - 19°. Spawners during hot periods kept close to the places of emergence of colder ground water. In the middle of October, water temperature above the nests dropped to 9 and 6.5°, at the end of October to 4.0 - 3.5°; later on it did not diminish below 3 - 2.5°. In October, water temperature in the nests varied from 4.8 to 6.5°, and in the beginning of November from 3.6 to 4.8°. In the spawning grounds of coho in the basin of the Columbia river the temperature varied from 5.6 to 14.4° (Burner, 1951).

<u>The Effectiveness of Spawning</u>. When the nests were open in the rivers Bol'shaya and Kamchatka, only a few dead eggs were found, 2.3 - 14.5%, average about 6.5%; nests with all eggs dead were rarely encountered

(Kuznetsov, 1928). Gribanov (1948) usually found in the nests not more than 4 - 5% of dead eggs and only in rare instances did this figure reach 30 - 60%.

According to Semko (1954), in the Karymaiskii stream after spawning, during the year of the greatest mass run, 0.3% of the eggs were left in the bodies of the females; this figure was even lower in other years. A great quantity of eggs is lost during oviposition. In 1947, 72.2% of the eggs were deposited in the nests. This figure is higher than for other species. Survival of eggs in the nests is from 0.8 to 21.4, average 10.6%. Calculated for each spawning female from the stream, from 16.6 (in 1948) to 760 young fish migrated (in 1947), the average figure for 8 years being over 300 migrants. From the fertilized egg to fry, 3.6 - 21.4% survived. From the original number of eggs about 0.15% of individuals survived until the time of descent from the river (age 1+ and 2+). Corresponding figures in this river were higher only for the sockeye. In two streams of Vancouver Island, from the number of eggs contained in migrant females, in different years, from 11.8 to 40% of the larvae developed, the average of 12 measurements being 22.8%. This is higher than the survival of pink and chum. The high effectiveness of spawning is related to the more stable conditions of water supply to nests and with lesser danger of the nests being dug up (Neave, 1949). Godfrey (1965), who reviewed the accumulated data, calculates the survival of coho from the egg to smolt stage within the limits of 0.7 - 9.65%. From smolt to adult fish in the sea, an average from 3.55 to 35.6% survive and only in one of the streams the return, in relation to the smolts, was 56.9%. From the egg to the mature adults 0.02 to 0.91% survive, average about 0.13 to 0.15%.

Development of Coho.

Reproductive Products. Spermatozoa of coho have an asymmetrical oviform head about 2 mk long and 1.5 mk wide. Below and slightly to one side of the head is the middle part with a diameter of 0.4 - 0.7 mk. The length of the tail with different fixation varies from 28 - 35 mk (Fig. 48). 200
Electron microscopic studies revealed in the tail an axial thread consisting of 11 fibrils, which except for its terminal part, is covered by a spiral of fine strands (Lowman, 1935).

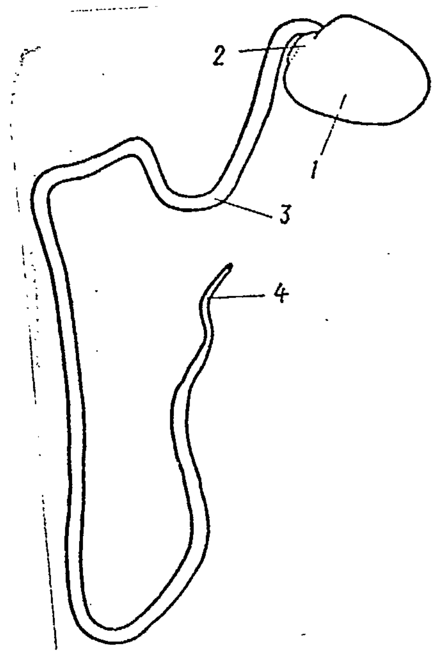


Fig. 48. Spermatozoon of Coho. 1 - head; 2 - middle part; 3 - tail section; 4 - terminal part of tail (drawn from photomicrograph of Lowman, 1953).

Males caught while in running condition could be kept in ponds and sperm could be obtained up to 19 days. During that time from the male 61 cm long were obtained 14 samples of sperm, total volume 116.6 ml; maximum quantity of sperm exceeded 190 ml. In experimental males, the volume of ejaculate varied from 4.3 to 46.0 ml (average figure about 20.0 ml).

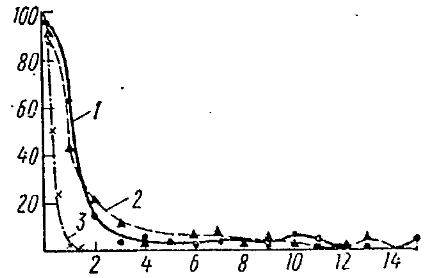
The number of spermatozoids in 1 mm^3 of sperm varied from 11.74 to 32.75 million; the average figure of 13 counts was 20.27 million. In 1961 sperm was taken from seven males taken at the spawning grounds (length 60.5 - 70 cm, weight 2.2 - 4 kg). Average volume of ejaculate was 40 ml and the greatest 90.5 ml, but sperm was more liquid, thinner. As a mean of 32 samples, concentration of spermatozoids was 17.34 million. Counts have shown that for one gram of live weight of males more than 115 million spermatozoa are ejaculated on a batch of sperm. This abundance can be related with spawning in rapid current and with widely scattered distribution of nests. As in other salmon species, spermatozoa of coho are activated in the ovarial fluid and become capable of penetrating the egg (Rucker et al, 1960). Activated by water, spermatozoa rapidly lose their biological qualities (Fig. 49).

The eggs of coho are only slightly larger than those of the sockeye. The size variablility of the eggs is substantial. In 19 running females from the river Tym', 61 - 79 cm long, weight of eggs varied from 76 to 173 mg (M=131.8±4.45). In the river Paratunka in 5 running females, 61-66.5 cm long, eggs weighed from 126.7 to 196.1 mg (average 169.7 mg). Fluctuations in absolute fecundity are to some extent connected with the variability of the size of eggs. An impression is created that 201
in the eastern part of the range, the eggs of coho are larger. Eggs are bright, orange-red (colour corresponding with the wave-length 592-594 nm). The intensive colouration indicates the abundance of astaxanthin (Yarzhombek and Grachev, 1964). The composition of the eggs is shown in Table 1. Individual eggs in water at 11° retain their ability to fertilize eggs up to 13 minutes and at 6.5° up to 15 minutes. The majority of eggs, however, loses fertility very rapidly; in 1 minute almost 50%, and in 2 minutes about 80% of eggs (Fig. 49).

Embryonic Period of Development.

Stage 1. Hydration of Eggs and Formation of the Embryonic Disc.

Within about 10 minutes, inseminated eggs become slightly adhesive, the character being washed away by water. At 6°, the process of hydration of eggs takes 70 - 75 minutes (Fig. 50). In our experiments the eggs of different females as the result of hydration increased in weight by 12.6 to 15.8% (average weight increase in eggs of seven females was 13.5%). Small eggs after hydration had a diameter of 5.8 mm, large 7.3 - 7.5 mm. The thickness of the membranes varies from 36 to 57 mk ($M=47.3\pm0.55$). The surface of the hydrated eggs becomes off-white and dull.



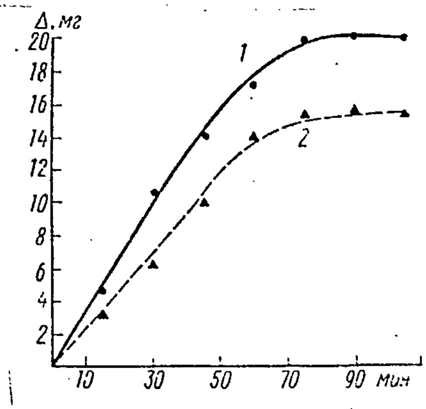


Fig. 49. Retention of fertility in water by eggs and spermatozoa of coho. 1 - changes in the proportion of fertilized eggs kept in water at 6.5°. 2 - same at 10.0°; 3 - changes in the numbers of fertilized eggs by sperms which were kept for different lengths of time in water at a temperature of 11.0°. Vertical: Quantity of fertilized eggs, %; Horizontal: Time spent in water, by eggs and sperm, min.

Fig. 50. Water take up by inseminated eggs of coho at a temperature of 6.0 - 6.5°. Mean weight of eggs before hydration 147.4 mg (1) and 118.0 mg (2).

As in other species, prior to the entry into water the eggs are 202
resistent to mechanical influences. With the beginning of hydration their sensitivity to touch and vibration rises sharply and drops for a short time after hydration (Table 15). During hydration the majority

of fat droplets gather near the animal pole of the eggs and the concentration of cytoplasm begins. The formed embryonic disc has a diameter from 1.05 to 1.2 mm and height 0.4-0.5 mm.

Table 15.
Mortality of Eggs of Coho, caused by action of a vibrator at various stages of development.

Age after fertilization	Stage of Development	Mortality of eggs, %
15 min.	Hydration of eggs	98.6
45 min.		84.4
1 hr.		31.3
2 hrs.	Formation of embryonic disc	24.4
5 hrs.		23.8
8 hrs. 50 min.	First cleavage	30.0
1 day	Up to 16 blastomeres and more	40.1
2 days	Small cell morula	23.0
4 days	beginning of gastrulation	50.3
6 days	"Embryonic knot"	59.9
8 days	Formation of first segments	18.8
12 days	Appearance of caudal bud	23.9
15 days	Beginning of circulation	5.1
23 days	Beginning of pigmentation of eyes	9.4
35 days	Laying down of ventral fins	4.2
45 days	Up to 14 rays in the tail	0.6
51 days	Before hatching	2.1

Note: Eggs were incubated at a temperature of 9.6 - 8°. Eggs at different stages were exposed to vibration for 210 seconds.

Stage 2. Cleavage of the Embryonic Disc. In the Sokolovskii farm eggs, fertilized on the 19th of October 1953 (first batch) and developing at first at a temperature of 9.5°, began the process of cleavage 8 hours 50 minutes after insemination. At the age 12 hours, most eggs had 4 blastomeres, at 18 hours 8 and towards the end of the first day from 12 to 28 blastomeres. At the age 1½ days their number exceeded 100. In 2 days, the morula was formed, its surface cells with a diameter of 30 - 45 mk. The eggs of the second batch were fertilized on the 22nd of October 1954 and were incubated in the Adotymovskii farm. At the beginning of development the average daily temperature was 4.6°. The course of temperature changes is shown in Fig. 5. In these eggs, cleavage began at the age of 20 hours and by the end of the second day 64 blastomeres were formed.

After the first division the base of the embryonic disc assumes an oval shape; its long axis reaches 1.3 - 1.4 mm and at the stage of 8 203
blastomeres 1.55 mm. After the fourth and fifth division, the base of the embryonic disc becomes round, blastomeres are crowded closely together, the diameter of the blastodisc decreases. The dividing embryonic disc becomes slightly immersed in the mass of yolk (Fig. 51,A,B). With the beginning of cleavage, the sensitivity of the eggs to vibration increases. The eggs of coho are more sensitive to this influence than those of the chum and pink.

At the end of the stage of cleavage at a temperature of 3.2 - 3.5°, 1,000 eggs took up in one hour 0.139 mg of oxygen (calculating per 1 kg of eggs, 0.9 mg of oxygen).

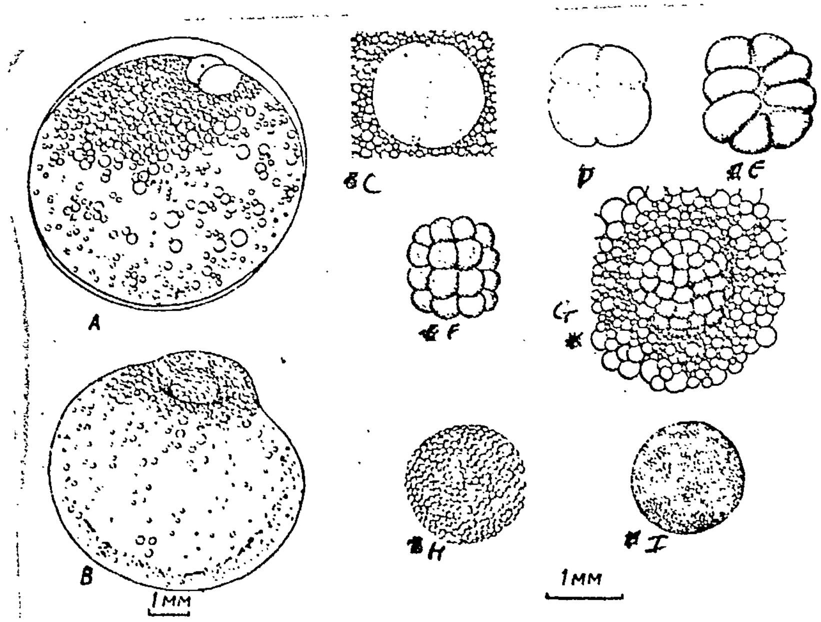


Fig. 51. Early stages of development of coho. A - live egg with two blastomeres; drawn in vivo in transmitted light. B - fixed egg without membrane at stage of large-cell morula. C - I - blastodiscs at different stages of cleavage. Fig. C and G show small parts of yolk sac with fat droplets.

Stage 3. Blastula. At a temperature of 9.6°, the blastula stage is reached by the end of the 3rd day. Blastodisc at that time became flat and slightly larger. At the age 3 days 4 hours, its diameter reached 1.6 - 1.7 mm and it covered the zone of the small fat droplets completely (Fig. 52,A). The surface of the blastula consisted of crowded polygonal cells about 25-30 mk in diameter. Below them were loosely arranged larger cells. In larvae of the second batch, the blastula stage was reached at the age of 6 days and continued for about 2 days.

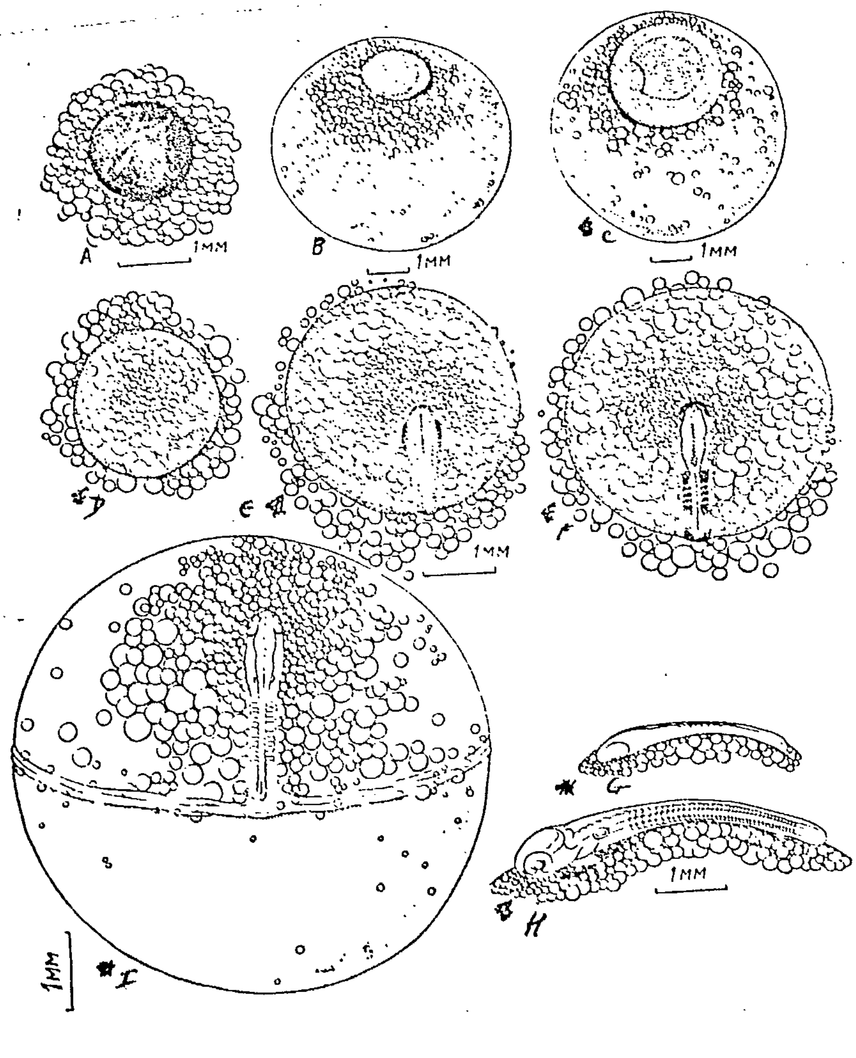


Fig. 52. Development of coho from the blastula stage to the beginning of the formation of the head and trunk. 204
B, C, I - egg without membranes; remaining figures show embryos without yolk sac. A - blastula. B - beginning of gastrulation. C,D - formation of "marginal knot". E - stage of "marginal streak". F - embryos at the beginning of segmentation of trunk mesoderm. G - embryo 2.7 mm long, with 6 segments, lateral view. H - embryo length 4.7 mm with 37 segments, lateral view. I - embryo 3.1 mm long; blastoderm covers about half of the surface of the yolk sac.

Stage 4.--Gastrulation. In the first batch by the age of 4 days the diameter of the blastodiscs increased to 2.2 - 2.4 mm and they began to cover the larger fat drops (Fig. 52,B). At the age of 6 days (57.5 degree-days), when the diameter of the blastodisc reached 3 - 3.3 mm, the "marginal knot" was formed (Fig. 52,C,D), soon to be transformed into the "marginal streak" (Fig. 52,E). In the second batch gastrulation began towards the end of the 8 days (38.8 degree-days). During the 14th day the embryonic shield had a diameter of 5 - 5.3 mm and "marginal streak" increased to 2 mm. With the beginning of gastrulation the sensitivity of the eggs significantly increased.

Stage 5. Formation of the head and trunk. In the first batch segmentation of the trunk mesoderm began at the end of the 8th day (72 - 76 degree-days), in the second at the end of the 16th- beginning of the 17th day. Embryos with 3 - 4 segments were 2.2 - 2.6 mm long. They developed primary brain vesicles. The diameter of the embryonic shield by that time reached 4 mm (Fig. 52,F). In embryos with 5 - 7 segments, the rudiments of optic cups formed (Fig. 52,G). Soon, otic vesicles appeared, removed from the eyes by the distance about equal to the width of 10 segments (Fig. 52,I).

The growth of the embryo was accompanied by a rapid covering of the yolk sac with the blastoderm. With an average temperature of 4.3° during the 20th day, blastoderm covered about a half of the sphere of the yolk sac, the embryos formed 13 - 14 segments. Below and slightly to the left of the posterior end of the chord, Kupfer's vesicle was visible.

In the two batches compared at the age of 11 days (115 degree-days) and during the 25th day (105 degree-days) the process of epiboly was completed. A stage close to this is shown in Fig. 53,A. By that time, in eggs with a diameter of 7.1 mm, embryos reached 4.5-4.7 mm in length and had 30-30 segments. In eggs with a diameter of 6.5 mm the process of epiboly was completed slightly earlier, at 29-31 segments and embryo length 4.3-4.5 mm. This took place earlier than in other salmon species, except for the sockeye. At about the same time, the caudal bud becomes differentiated, which at 37 segments reached a length of 0.7 mm.

At the end of the stage at a temperature of 4.8°,1,000 eggs in 1 hour took up 0.63 and 1.07 mg of oxygen (1 kg of eggs 3.79 and 5.26 mg respectively). Large eggs take up more oxygen (second of the figures quoted).

Stage 6. Separation of the posterior part of the trunk from the surface of the yolk sac. Under conditions in the Sokolovskii farm, this stage began at the age of 12- 12.5 days (115 - 120 degree-days), when the embryos reached a length of 4.6 - 4.8 mm and had 37 - 40 segments. Segmentation of the trunk section by that time was completed; it consisted of 38 - 40 segments. The posterior part of the intestine and the anal orifice were formed. Differentiation of the stomach was observed. In the apparatus of the Adotymovskii incubator, coho reached this stage at the age of 27 - 28 206
days (114 - 118 degree-days).

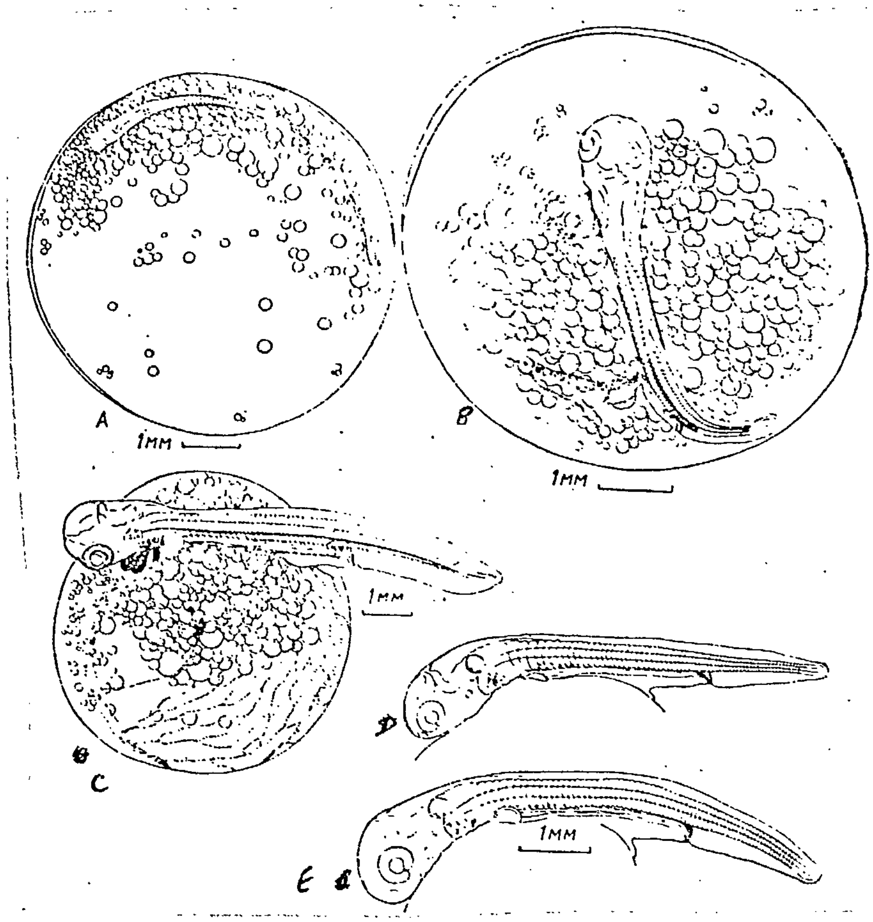


Fig. 53. Development of coho from the completion of epiboly to the appearance of melanin in the eyes.
A - stage close to the completion of epiboly, length of embryo 4.2 mm. B - beginning of development of circulatory system. Drawing in vivo, upper view, transmitted light. D - embryo, length 6.8 mm without yolk sac, at the beginning of circulation. E - embryo 7.2 mm long without yolk sac. C - stage of appearance of pigment in the eyes; embryo 8.5 mm long, removed from egg (A,B,C--drawings in vivo).

The head section of embryos remained large; otic vesicles were separated from the eyes by a distance almost equal to the width of 7 trunk segments. Diameter of the eyes was about 0.4 mm. Olfactory placodes were sharply marked. The convolutions of the brain were formed. 207
The cerebellum began to grow, encaphalomeres became well visible. The rudiments of the opercula became evident. The pericardial cavity was formed, the rudiment of the heart visible in it.

During this stage, the otic capsules become enlarged, groups of small otoliths appear in them. The length of the head section becomes smaller, and the height of the head increases. The length and the number of segments of the caudal section increase rapidly; the unpaired fin fold develops. The posterior part of the trunk section gradually separates from the yolk sac. At the same time the preanal fin fold grows. The embryo rises above the yolk sac.

In some embryos in the Sokolovskii incubator, the heart muscle contracted at the stage of 39 - 41 segments, more often at 43 - 45 segments, when the contractions of the trunk myotomes became noticeable (14 days, 134 degree-days). At a lower temperature, in the Adotymovskii incubator, the establishment of the nerve-muscle motor function was delayed to the stage of the formation of 47 - 49 myotomes. At that stage the length of embryos reached 6 - 6.3 mm (35 - 38 days, about 145 - 155 degree-days). At a temperature of $3.2 - 3.5^{\circ}$, 1,000 such eggs take up in 1 hour 0.556 mg of oxygen (2.5 mg per 1 kg of eggs).

Stage 7. Development of the subintestinal-vitelline system of circulation. The appearance of the bloodstream in various embryos of the first batch was observed on the 15th and 16th days (144- 153 degree-days), in those of the second on the 38th - 40th day (155 - 162 degree-days). These embryos were mainly 6.5 - 6.8 mm long and had 59 - 61 myotomes (in some 63), of which 39 - 40 were trunk myotomes (Fig. 53,B,C). In the Adotymovskii incubator, supplied with river water well aerated and with low temperature, circulation began at a slightly later stage of differentiation.

By the beginning of the stage, the absolute length of the head increased slightly, but its relative length decreased and constituted less than 25% of the total length of the embryos. The height of the head continued to increase. The head began to detach from the yolk sac. The rudiments of the pectoral fins became visible. In live embryos, the first glomeruli of the pronephros could be seen through the ventral ends of the 4 - 7th myotomes. The unpaired fin fold on the back grew to the level of the first segments.

At the beginning of this stage, blood supplied the trunk segments and only the first one or two caudal segments. The vessels filled rapidly and abundantly with cells. The caudal artery and vein soon enlarge, as well as the subintestinal-vitelline vein; fine capillaries appear on the yolk sac. The mobility of the embryos progressively increases.

Stage 8. Appearance of the Cardinal Veins and Mixed Heptic-Vitelline and Subintestinal-Vitelline Circulation. In the Sokolovskii incubator within less than a day, and in the Adotymovskii in 1.5 - 2 208
days after the beginning of circulation, blood supply extended to the 10-12 caudal myotomes. Posterior cardinal veins and the Cuvierian ducts are formed, and the first vessels of the hepatic-vitelline vein make their appearance. At the beginning of this stage the embryos were 6.3-7.7 mm long; in the first batch they had 66 - 68 myotomes, in the second 68 - 70.

In the course of this stage the first and the second pairs of the branchial arteries began to function. The numbers of the capillaries of the yolk sac increase rapidly. In the two batches in the 21 - 22nd day (100 - 210 degree-days) and 44 - 46th day (175 - 182 degree-days) the embryos increased in length to 8.2 - 8.6 mm and melanin appeared in their eyes (Fig. 53,C). In the Sokolovskii incubator pigment in the eyes of coho appeared one day earlier that in those of the pink, and the embryos were somewhat larger. By the end of the stage the segmentation of the caudal mesoderm was completed.

Stage 9. Formation of the Hepatic-Vitolline Circulation System. Blood supply to the yolk sac from the subintestinal vein was discontinued in embryos 8.6 - 9 mm long; this took place in the first batch at the age of 23 - 24 days (218 - 227 degree-days), in the second batch at 52 - 56 days (202 - 217 degree-days). The embryos had 67 - 69 and 75 - 77 segments respectively, of which trunk segments counted 37 - 38 and 42 - 43. The head of embryos removed from the membranes straightened out. Its height markedly increased. The eyes became large. The oval olfactory pits formed. The stato-acoustic organs were situated at the distance equal to the width of approximately two myotomes from the eyes. In them there developed semicircular canals, and the otoliths became large. A small buccal depression was formed. The rudiments of the opercula partly covered the first pair of gills. The tip of the chord twisted upwards. The fin fold on the back grew to the level of the first myotome. The preanal fold noticeably increased, its anterior end was situated on the caudal surface of the yolk sac. The bases of the pectoral fins assumed oblique position (Fig. 53,C).

At the beginning of the stage, the blood flows in three paire of branchial arteries. Capillaries appeared on the upper surface of the head. Only 3-5 terminal segments were not supplied with blood. In all trunk, and the first 10 caudal myotomes, segmental arteries and veins were present. The posterior mesenteric artery was formed, its capillaries surrounding the posterior part of the intestine; the middle part of the intestine was covered by the capillaries of the anterior mesenteric artery. Blood flowed into the vessel network of the yolk sac only from the large hepatic veins. Throughout this stage the embryos remained motionless for most of the time, only rarely inclining to the left or right side and smoothly moving their tails to right or left, reaching their heads with the tips of their tails.

By the end of the stage, in spite of the drop in temperature to 2.7°, the respiratory intensity rose, and in 1 hour 100 embryos took up 0.71 mg of oxygen, and 1 kg of eggs, 3.26 mg.

Stage 10. Differentiation of the Upper and Lower Cones of Myotomes. The beginning of the formation of the upper and lower cones of myotomes was observed on the 31 - 33rd day (289 - 306 degree-days) and on the 67 - 71st day (254 - 267 degree-days). By that time the embryos grew to 10 - 11.3 mm. A well-grown lower jaw protruded in front of the vertical line drawn through the pupil. The eyes darkened, crystals of guanine appeared in them. Otic capsules were situated directly near the eyes and the length of the head was relatively shorter. Pinkish, diffuse pigment appeared in the limen of the brain. Opercula became enlarged and covered two pairs of gills. The terminal caudal myotomes began to disintegrate and the number of segments diminished. Further lengthening of the tail was due to the increase in the width of the myotomes. Hypurals began to form, the first rays of the caudal fins were laid down, capillaries appeared among them. In the place where the anal and dorsal fin were laid down, the fin fold began to broaden, muscle bundles were formed. Signs of ossification of the dorsal skeleton were found. The bases of the well-grown pectoral fins assumed an almost vertical position; the fins began to be supplied with blood and became mobile. The embryos from that time onwards began to move only rarely.

During this stage, the blood stream appears in the 4th pair of gill arches and in the hyoid arches. On the upper surface of the head a dense network of capillaries develops. Segmental arteries and veins form in all myotomes. In the anterior part of the trunk, capillaries run from the segmental vessels to the brain and the body surface. The number of capillaries on the yolk sac continues to increase. The lumen of the intestinal tube assumes a yellowish-greenish colour. Melanophores and small cherry-red lipophores appear on the head and upper side of the trunk.

In the embryos of the first batch at the age of 35 days (324 degree-days) and in those of the second at the 74th day (216 degree-days) the ventral fins were laid down. At the same time the rudiments of the upper jaw appeared. In the olfactory cups bars began to form. After in vivo staining with methylene blue, the rudiments of the gill filaments could be seen. A small number of the hatching glands could be distinguished. With the increased complication in the shape of the myotomes, the embryos began to be able to carry out wave-like movements of the tail and trunk.

<u>Stage 11. Development of Mobility of the Jaws and the completion of Incubation.</u> In the Sokolovskii incubator, the 11th stage began at the age 40 - 43 days (372 - 379 degree-days), in Adotymovskii at the age 86 - 91 days (309 - 321 degree-days). The stage ends with hatching. At its beginning the embryos were 14-15.5 mm long. In embryos removed from the membranes, the yolk sac assumed an oviform shape. Its posterior end drooped. The diameter of some fat droplets increased to 1 - 1.5 mm.

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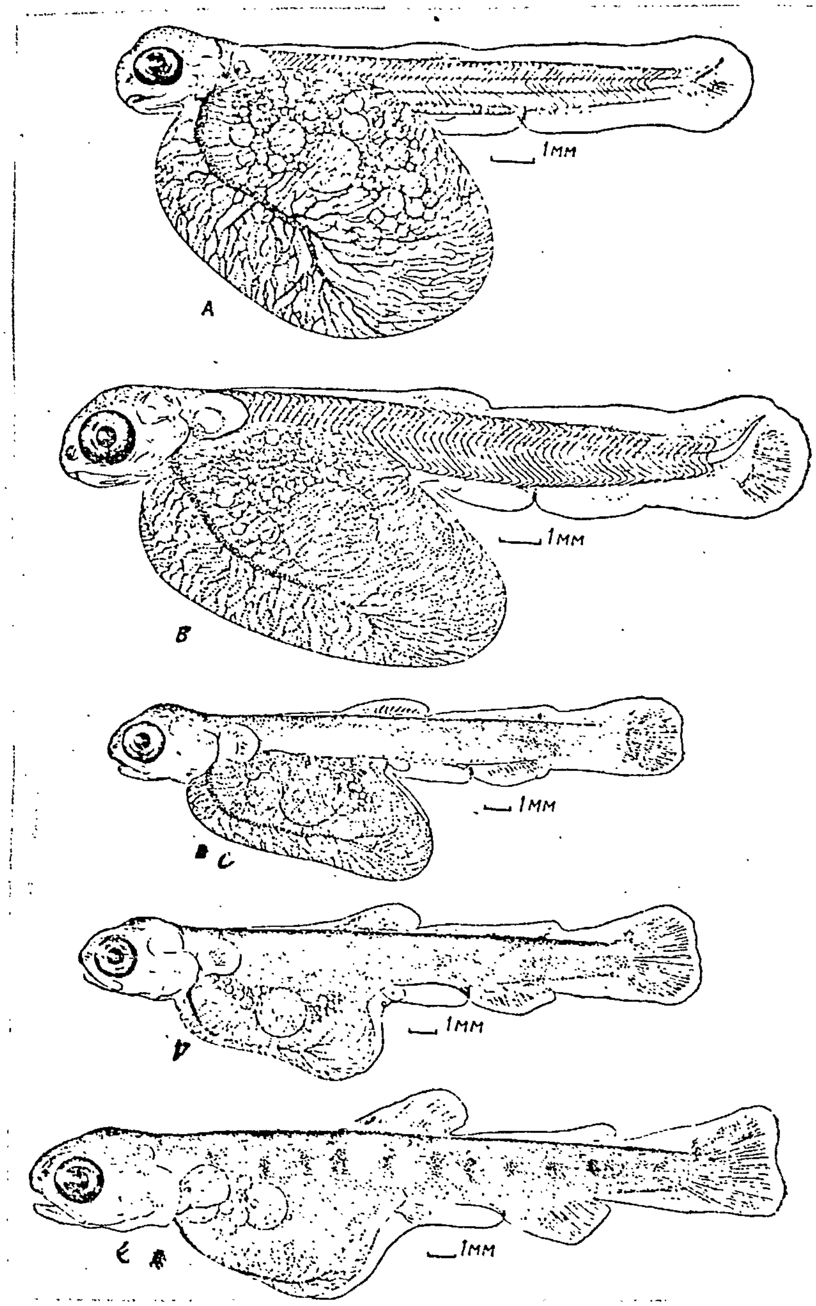

Fig. 54. Embryos of coho. A - at end of incubation, length 15.8 mm; at average temperature 9.3° developed for 40 days. B - at the beginning of hatching, length 18.8 mm. C - free embryo 23.8 mm long. D - free embryo 26.0 mm long. E - larva 30.4 mm long.

Of the changes that have taken place, we shall note first of all 211
the relative shortening of the head, which now constitutes about 17% of the length of the embryo. Opercula covered the gills. The tip of the

lower jaw reached the vertical line drawn from the anterior margin of the eye. During this stage the buccal funnel breaks through. By the end of the stage the branchial and buccal apparatus becomes weakly mobile. The eyes are black, irridescent; their diameter is more than 1.2 mm.

As a result of the resorption of the embryonic fin fold, the contours of the anal and the dorsal fins are more definite, at their bases of which large muscle bundles have developed. The rudiment of the adipose fin was formed. The ventral fins became well visible. Up to 5 - 6 lepidotrichs were laid down in the tail. Vertebrae began to be formed in the caudal section.

The density of the vascular network on the yolk sac continued to increase. In Fig. 54,A one can well see the big lower vitelline vein and the right branch of the marginal vitelline vein entering it, but already markedly reduced.

The pigmentation increased on the dorsal surface of the head and body. Isolated melanophores appeared in the dorsal and caudal fins, as well as above the brain. The density in the distribution of the lipophores also increased. Beside the dorsal surface, they spread in the unpaired fin fold and caudal fin. The hatching glands are well visible.

Until near the hatching time the embryos are quiescent within the membrane and only rarely tip their bodies to right or left, waving their tails at the same time, or performing with them wave-like movements. Continuous mixing of the perivitelline fluid is ensured by rythmical movements of the pectoral fins. The same task is served by the movements of the mouth and strong pulsation of the heart, the movements of which cause displacement in the mass of yolk. Before hatching the embryos become agitated and begin to move energetically within their membranes.

Stage 12. The Passive Condition of Free Embryos. From the eggs fertilized at various times between the 14th of October and the 23rd of October 1953 and reared in the Sokolovskii incubator, hatching began at the age of 50 and 54 days (445 - 486 degree-days) and continued for 3 - 5 days. In the Adotymovskii incubator, where by that time the water was cooled down to 2.5 - 2.2°, hatching continued for almost a month. The periods of incubation of coho under various conditions is shown in Table 16.

Judging from the existing data, coho develops in temperatures of narrower range than its related species. At an average temperature of 11.4° a rise in the mortality of eggs was observed (Allen, 1958). According to our observations, at the beginning of incubation, short exposure to temperatures of 12 - 13.5° did not disturb development and caused no increase in mortality. The lower limit can be judged from the experimental data obtained in the farm incuabors. In the Paratunski incubator the development began at 3.7 - 4° and ended at 2.3°. In the Ushkovskii farm, ebmryogeny takes place at a constant temperature about 4.5 - 4.1°. In the Adotymovskii farm during the period of incubation of eggs, the water cooled from 5 - 4.5° to 2.5 - 2°. In the Karymaiskii incubator, coho developed while the temperature changed from 3.5 to 0.8°. Semko (1954) calls this species the most cold-loving one.

Table 16. Duration of Incubation of Coho under Different Conditions.

Average temp. during incubation, °C	Age at hatching days	Age at hatching degree-days	Locality	Reference.
2.9	136	397	Kamchatka, Karymaiskii incubator	Ievleva, 1951
2.17	137--158	300--346		Semko, 1954
4.5	86--101	~378	Kamchatka, Ushkovskii farm	Gribanov, 1948
4.1	124	371	Sakhalin, Adotymovskii farm	Smirnov, 1960a
8.8--9.0	40--54	445--486	Sakhalin, Sokolovskii farm	Smirnov, 1960a
~8.9	48	427	California	Shapovalov,
~10.7	38	407		Taft, 1954
~10.7	from 34 to 37	363.8--395.9		Shaw, Mage 1943

Fig. 54,B shows an embryo at the beginning of mass hatching. The size of the embryos depends on the size of the eggs. From the eggs with diameters of 6.3 mm they hatched at an average length of 20.2 mm, the longest reaching 21 mm. In a small egg, prior to hatching, the embryo reaches 16-19 mm. After hatching, the yolk sac assumes an oviform shape. Its posterior end almost reaches the beginning of the tail and droops slightly. The duration of incubation of coho is relatively short and during that time not much yolk is utilized. In the Sokolovskii farm during the incubation, the weight of the yolk was reduced by about 13.5%. In hatching embryos there is usually one large fat drop, with a diameter of 2-2.4 mm, surrounded by small droplets.

The head by the time of hatching becomes high, but constitutes only 16 - 17% of the length of the embryos. The otic capsules draw close to the eyes, the diameter of which reaches 1.4 mm. Three or four rudiments of gill rakers become visible. Opercula--in the skin of which rays have appeared--cover gills with well developed filaments. The post-anal section becomes markedly elongated and consitutes more than 38% of the total length of the embryos. The number of myotomes in the tail is reduced to 25-27.

In the caudal lobe develop hypurals and 15 - 17 lepidotrichs (when hatching is earlier only up to 10 lepidotrichs were counted, while in the embryos that hatched late their number rose to 20). By the time of hatching the rudiments of the lepidotrichs appear in the dorsal and anal fins. Slight projection in the outline of the fin fold, accumulation of the pigment cells and of mesenchyma mark the rudiment of the adipose fin. The lobes of the pectoral fins become large, more than the width of 5 trunk myotomes. The changes in the vascular system are as follows. The capillary vessels appear in the gill filaments and in the pseudobranchs. Capillaries entwine oculomotor muscles. An abundant capillary network developed on the dorsal surface of the head. The vessels branching off from the segmental arteries formed branches above the brain and in the integument of embryos. The network of capillaries between the rays of the caudal fins became denser. By the time of hatching the capillary net on the surface of the yolk sac became very dense, length of capillaries per 1 mm^2 reached 9.5 mm and more. 213

By the time of hatching the separate existence of the stomach was more distinct. Transverse wrinkling of the internal wall of the gut was poorly marked. The rudiment of the swimbladder appeared as a small digitiform outgrowth, about 1.5 mm long.

At the time of emergence from the membrane, coho is intensely pigmented. Melanophores have covered the anterior and dorsal surface of the head, individual cells appeared on the opercula. On the body the melanophores spread up to the lower cones of myotomes. They were present in unpaired fins and at the base of the unpaired fin fold behind the dorsal fin. The perineural, perivascular and peritoneal pigment series were well distinguishable. On the surface of the head and the body between the melanophores, small cherry-red lipophores were scattered. In the unpaired fin fold and in the tail the lipophores occupied a larger area than the melanophores, but they were still absent from the anal fin.

As in other salmon species, the embryos after hatching became quiescent. Their eyes were still motionless (mobility appears at the end of this stage). The movements of the buccal and branchial apparatus are less vigorous. Frequent rythmical movements of pectoral fins create a current of water along the body and the yolk sac. Reactions to external stimuli are similar to those described for the chum. Also similar is the condition of the sense organs of the lateral line system.

I.S. Vasil'ev compared the intensity of respiration of the embryos which were in the eggs and those that were just hatched; comparison was made in the laboratory at the time of hatching. Measurements were made in the laboratory at the time of hatching. Measurements were made in a vessel with circulating water at a temperature of 5 - 5.5°. One thousand eggs in 1 hour took up from 45.7 to 76.7 mg of oxygen (average 56.5) and embryos that hatched from the eggs took up from 81.2 to 114.5 mg (average 101.8 mg).

Individuals which were the last to emerge from the eggs reached the length of 21 - 23 mm. Among those that stayed longer under the membrane were also small embryos with lengths 17 and even 16 mm. They were found to have various defects: reduced eyes, poorly developed unpaired fin folds, 214
underdeveloped opercula or weak vascular network. The heart of these embryos worked more slowly. In some of them, hatching glands were poorly developed.

<u>Stage 13. Formation of Unpaired and Ventral Fins and of the Swimbladder.</u> At a temperature of 4 - 6° within a week after hatching the behaviour of the embryos underwent a change. They began to react to water current and to move against it, they were agitated by illumination, reacted positively to the touch of external objects. In weak current and darkness the embryos lay quietly. When agitated, they swam up, but with difficulty and for a short time. Apparently, from that time onwards they were able to spread out within the redds, gradually moving towards the surface.

By the beginning of this stage the mouth assumed a subterminal position (Fig. 54,C). The skinny margin of the opercula grew up to the bases of the pectoral fins. The unpaired fin fold in front of the dorsal fin became recuced. The preanal fold grew almost to the posterior end of the yolk sac. In the lobe of the caudal fin a notch could be seen; in its rays up to 5 sclerites were formed. The lepidotrichs of the anal, dorsal and pectoral fins became well visible. The density of the capillary network on the yolk sac noticeably diminished. The embryos turned dark. The numbers of lipophores also increased, particularly on the top of the head and on the back. Lipophores appeared in the anal fin, at the base of the preanal fold, on the pectoral and ventral fins.

With the increase of length up to 24.5 - 26 mm the anal and the dorsal fins became high and well distinct (Fig. 54,D). In the anal fin appeared the so-called reduced rays. The first rays were laid down in the ventral fins. Teeth appeared in the jaws. Bars were formed in the olfactory pits. The skin folds of the opercula continued to grow.

In contrast with the other species, the preanal fold in coho does not cease to grow and reaches the lower side of the yolk sac. The yolk becomes viscous and the fat droplets in it move when the embryos change their position. Deposition of fat in the body cavity was observed.

During this stage the bodily proportions do not change much. By the end of the stage, dark spots appeared on the sides of the body (Fig. 54,E). By that time the yolk sac becomes small, assumes a streamlined shape and its weight becomes reduced to 55 - 70 mg. At the same time the stores of fat in the body cavity become larger. In front of the adipose fin a small vestige of the unpaired fin fold is retained. The tail becomes symmetrical, its rays branching. The tips of the ventral fins reach the margin of the preanal fold. The latter continue to grow in length and in width. At the level of the ventral fins its width reach-
es or exceeds 1 mm, and its anterior margin is nearer to the head than 215
the dorsal fin. The preanal fin reaches this size only in coho.

At that age in cerato- and epibranchial elements of the gill arches up to 12 rakers were counted. Large gill filaments become branched. The stomach continues to develop , the inner wall of the intestine becomes markedly folded, peristaltic movements are observed. The rapidly growing rudiment of the swimbladder in small coho 25mm long reached 4.2 - 4.5 mm.

Free embryos from time to time swim up to the surface and perform grasping movements. In aquaria they begin to catch small planktonic organisms and other food. Within 2 - 3 days feeding activity increases and individuals with well filled intestinal tracts appear. In the rearing pond of the Adotymovskii farm at an average temperature of 3.1° coho began to swim 33 - 38 days after mass hatching. At temperatures below 3.5°, activity of larvae was low.

F.V. Krogius, when opening nests in the Danilovskii stream (basin of the river Paratunka), fixed samples of eggs and larvae which were kindly given to us for examination. Judging from that material, spots on the bodies of isolated coho individuals appeared at the end of February. It is interesting that, in contrast to the embryos reared in the incubators, in those from the nests the yolk sacs did not droop and the larvae had more streamlined forms.

The Larval Period of Development.

Stage of Mixed Feeding. In the presence of accessible food and, other favourable circumstances, coho begins to ingest and digest food, while possessing a substantial remnant of yolk and before the swimbladder is filled with air. In rearing ponds with even bottoms, the transition to active feeding occurs at slightly earlier stages of development than in nature. In the Adotymovskii rearing pond with a progressive increase in temperature up to 5 - 6°, coho changed to live in midwater within about 2.5 months after mass hatching. Eggs fertilized on the 27th of October 1954 hatched in bulk about the 8 - 10th of March and larvae changed to free swimming on the 20 - 25th of May 1955, when water in the rearing pond warmed up to 5.7 - 6.0° (age 206 - 211 days, 670 - 710 degree-days). Mass hatching of eggs fertilized on the 4th of November 1954 began on the 20 - 25th of March and the transition to active swimming on the 28 - 31st of May 1955 (205 - 208 days; 700 - 725 degree-days). In the Sokolovskii farm, the young reared from eggs collected in the middle of October changed to life in midwater in the first days of February, at the age 110 days and later (850 degree-days and more). This occurred shortly before the 216
completion of covering of the vestiges of the yolk sac by the abdominal walls. The swimbladders of these larvae were filled with air.

Gribanov (1948), digging up redds, found no larvae larger than 25 - 27 mm, and the smallest individuals which he caught in the farms and streams were 27 - 30 mm. Small coho of this size occured between March and the middle of the summer. The emergence of larvae from the nests continued about 5 months. This is related to the very staggered spawning and differences in the temperature regime of the water washing the eggs in the ground. According to Shapovalov and Taft (1954) in the Californian rivers coho abandons its nests with a small yolk remnant. Emergence from the ground is spread over 7 weeks. It is accelerated when the rivers become shallower, when the stones are moved, spawning grounds are silted and in the cases of increase in water temperature. Larvae emerge from the spawning redds mainly by night.

Fig. 55,A shows a coho in which the ventral walls have completely covered the remnant of the yolk sac. Its length is 26.2, or less than that of the individual shown in Fig. 54,E, but its level of differentiation is higher. In addition to resorption of yolk the following changes took place. The height of the head and the body and the diameter of the eye all increased. The skin membranes of the opercula grew and covered the bases of the pectoral fins. These individuals are often found in strongly silted localities and large skin membranes serve as a good protection of the gills from silting. The postanal sector became enlarged and now constitutes about 38% of the total length. Only a small vestige of the unpaired fin folds can be seen behind the anal and adipose fins. The preanal fold has grown to the tips of the pectoral fins; a considerable number of lipophores is present along its margins. In this condition one can observe elongation of the first branching rays of the dorsal and anal fins.

The young fish have typically mottled bright coloration. Its general hue is olive-green, shot with golden hues. The back is dark, brownish, the belly pale with an orange tinge. The entire body, apart from a narrow ventral part, is covered with numerous melanophores. On the opercula and below the lateral line, melanophores are more scarce but larger. In the integument of the head and body are present numerous small cherry-red erythrophores and pale-orange xanthophores. Lipophores, concentrated at the tip of the lower jaw, impart to it a bright orange-red colour. Along the sides of the body form 8 to 12 dark, transverse spots. They are broader than in similar specimens of chinook, which little coho resemble in many respects. Above the large spots there form small oval or triangular spots, about the size of the pupil. The pectoral fins are pale-orange. Ventral fins have the same, though slightly brighter colour. Lipophores cover the entire surface of the paired fins; melanophores are scarce and only present at the bases of the fins. The pale orange dorsal fin took on the intense colour of the tips of the branching rays and membranes between them, 217
and acquired a reddish streak at the anterior end of its base. The margin of the membrane of the dorsal fin between the second and the sixth ray became whitish. The developed white stripe is highlighted by the accumulation of melanophores. The anal fin is even more brightly coloured. The white edge along its anterior margin is more distinct, the melanophores situated behind it together with lipophores are more numerous. Lipophores and melanophores abundantly cover the entire lobe of the caudal fin, concentrating along its margins. A narrow stripe of lipophores extends along the external margin of the preanal fold. It has been observed that in the sluggish, silted places, the young fish assume more intense lipophore colouration. In cold streams and on dark bottoms the melanin pigmentation becomes more intensive.

Having emerged from their nests, the larvae live on the littoral gravel and sand shallows, often greatly silted, with a weak current. Close to the banks they find shelter under the overhanging branches of bushes and grass. Immediately after their emergence from the ground, the larvae keep together in schools and feed actively. The most common food are chironomid larvae (Zorbidi, 1970). Some of these larvae soon begin to migrate out of the area of spawning grounds, scatter along the river and occupy individual territories. The larvae of coho are rightly called "the nomads" and the larger young fish "settlers" (Chapman, 1962).

The Juvenile Period of Development.

Stage of Feeding in Shallow Waters. The coho changes to juvenile condition at the length of about 34 - 35 mm. The juveniles have higher bodies, which at average length of about 47 mm and weight 1.1 g reaches almost 32% of trunk length. Diameter of the eyes approaches 40% of head length. The mouth assumes terminal position, which points to the change in the method of feeding. The skin membrane of the opercula becomes much reduced. The pectoral and ventral fins reach their greatest relative length (27 and 22% of trunk length respectively). The height of the dorsal and anal fins exceeds 28 and 24% of trunk length. Their long anterior branching rays form sharp tips. The lobe of the caudal fin continues to become wider, its ventral half becomes longer. The typical morphological characteristic of the juveniles is that the vestige of the preanal fold in the coho is retained longer than in other salmon species (Fig. 55,D).

By the beginning of this stage the young fish have rakers on all parts of gill arches, including the lower ones (hypobranchialia), but

they are rudimentary and their total number has not yet reached the definitive. The intestinal loops and stomach with long pyloric caeca, typical of salmon, are formed. The vestige of the yolk is resorbed. The intestine and the stomach are covered by abundant deposits of fat. 218
The young fish develop rudimentary scales. The specimen shown in the drawing had below the dorsal fin small scales with one, and below the adipose fin two sclerites. The character of colouration undergoes no significant changes, but becomes brighter. The number of the dark spots has increased. Small spots has increased. Small spots appeared on the dorsal surface of the body.

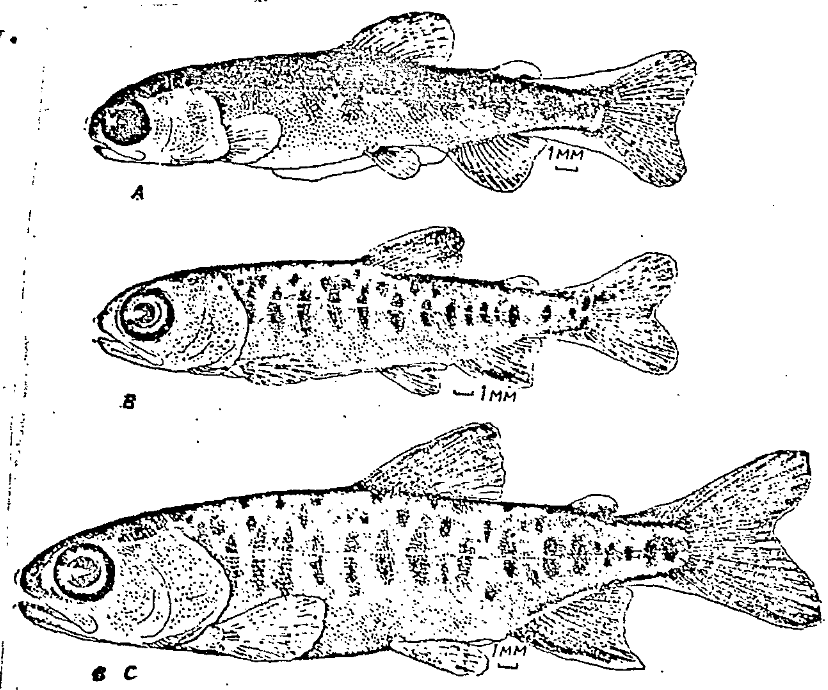

Fig. 55. Juvenile coho. A - Larva 26.2 mm long. B - juvenile 36.5 mm long. C - Juvenile 42.3 mm long.

The juveniles are characterized by so-called territorial behaviour. They occupy individual territories, which they aggressively defend. The young fish stay near the bottom behind some shelter which weakens the current: stones, ridges of sand or sunken branches. From there they dart out after small objects carried by the current or dropping into the water—potential food particles. The young fish also dart towards other fish, swimming into protected terrotory, and chase the intruders away. The signs of the aggressive behaviour can be observed already in a week after emergence from the gravel. Within 10 days there begins dispersal of the fish to individual microhabitats. The individuals that have emerged from the nests earlier, occupy territories situated nearer to the spawning 219 grounds and grow more rapidly, while those that emerge from the ground later are forced to move further downstream (Mason and Chapman, 1965).

With the onset of darkness the movement and feeding activities decrease, the young fish remain near the bottom. The change of behaviour is related to the loss of visual orientation in space, which stimulates corresponding behavioural reactions. The question arises, how can the small fish maintain their position in running water during the night, without losing their selected territories? It appears that in the event of increase in current velocity and displacement by the stream, the wave-like movements of the preanal fold and of the elongate tip of the anal fin, which touch the bottom, increase in frequency and serve as a kind of signal to increase the intensity of the locomotor apparatus to compensate for the more rapid current. This can be seen as one of the functional reasons for the strong development and long retention of the preanal fold, as well as for the elongation at the appropriate age of the first rays of the anal fin (its characteristic form is related also with the type of movement of the young fish). When the fish change to life in deeper water, these morphological features are lost.

At the beginning of the juvenile period of life the coho feeds mainly on the larvae of the amphibian insects, the chironomids, stoneflies and mayflies. Beginning in May the proportion of the pupae increases, and then that of the imagos of Chironomidae. With the end of the mass fly-out of the chironomids, the importance of their larvae increases again. The food spectrum of the coho is very broad; in its stomach occur almost all forms found in the sample of benthos collected from the places where the young fish feed. Crustaceans, rotifers, diatoms and other planktonic organisms occur rarely, mainly in larvae and small juveniles. In the food of individuals larger than 40 mm during the summer months predominate adult insects, including terrestrial ones (Synkova, 1951; Gribanov, 1948: Mundie, 1969; Zorbidi, 1970a).

The Stage of Feeding of Juveniles in Deep Localities. Large juveniles move to deep waters. The migration is directed not only downstream from the spawning grounds, but not infrequently also against the current. For example, large numbers of coho feed in the Paratunskie Lakes, Dal'nee and Blizhnee, although this salmon does not reproduce either in lakes or in their tributaries. The juveniles migrate into the lakes from the rivers by moving against the current. In the shallow parts of the lakes the juveniles find abundant food, grow rapidly and remain there for the winter.

With the increase in size, the agressiveness of juveniles, which is sometimes given undue importance in the dispersal of the coho, becomes weaker (Chapman, 1962). According to observations in nature and in experimental impoundments the behaviour changes when the juveniles reach the length of about 45 - 48 mm (Mason and Chapman, 1965).

The external changes with age in pigmentation are illustrated in

Fig. 55,C and 56. The study of large juveniles revealed the direction of the occuring changes; we shall mention the more important among them. During the second juvenile stage, the differentiation of the parts of the gastro-intestinal tract and of the branchial apparatus are completed. The relative size of the head and proportion of its parts change slowly. The eyes become relatively smaller with age. In the yearling fish the horizontal diameter of the eyes is slightly less than 39%, in two-year-olds less than 37% of the length of the head, while in the adult fish this figure is only 15% (Gribanov, 1948). During the entire freshwater period of life the eyes remain much larger by comparison with the adults, which indirectly indicates the importance of vision in obtaining food by the juveniles. Further, while in the young-of-the-year fish 47 mm long the length of the trunk was 65.65±0.31%, in yearlings about 73 mm long and weighing 4.64 g it increased to 68.8±0.23% of body length, after Smitt At the same time the back became wider, i.e. the growth in volume became greater. The greatest body weight gradually decreased. The fins became markedly smaller; their shape changed. In the yearling fish the height of the dorsal fin was 24.25±0.38%, that of the anal 21.11±0.41%, length of the pectoral 24.63±0.28% and of the ventral 19.87±0.23% of trunk length. Anterior branching rays of unpaired fins by now projected less beyond the other rays. Condition factor (after Clark) in young-of-the-year was 0.91, in yearlings 0.96.

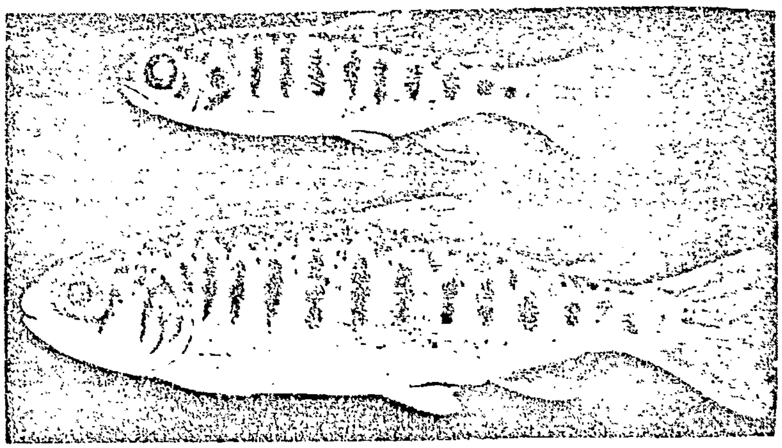

Fig. 56. Coho 53 mm long and weighing 2.6 g (upper) and coho migrating to the sea, 89 mm long and weighing 10.2 g.

The number of the large transverse spots on the sides of the body increases to 12 - 14. On the top of the head and on the back, up to the middle line, there appear many small spots with irregular outlines, their size 3 times smaller than that of the pupil. Orange-red lipophores on the body and fins are more distinctly visible. The sides of the body and 221
the belly become silvery, i.e. the colouration becomes typical of the inhabitants of the pelagic zone. The proportions of the body, however, remain greatly different from those of the adults.

In the deep parts of the habitat with slow current, more commonly in the second half of summer, one can see groups of individuals of different sizes, from 47 - 50 mm to much larger. In such groups occur also juveniles of other salmon species. In the upper reaches of the river Tym', in quiet, deep places, in immediate proximity to coho, we observed juveniles of masou. Usually the little coho stayed at slightly greater depths. In the river Paratunka, in places of accumulation of juvenile coho occurred also juveniles of chinook, which stayed closer to the bottom. Formation of common schools by coho and sockeye was observed (Gribanov, 1948). These facts also point out to the loss of agressiveness on transition at the appropriate age to life in deep water.

Investigators who studied the feeding of coho noticed huge numbers of ingested adult insects. The hunting method is very characteristic. During quiet evenings in shallow water and river pools one can see how a great number of juveniles jump out of the water in pursuit of insects swarming above. Numerous splashes create the illusion of large raindrops falling in the water. Mass ingestion of insects remains throughout their entire flight period both during the life of the juveniles in fresh water and after their migration into the brackish water.

In connection with the migration of large coho juveniles into the lakes inhabited by the sockeye, the question arises whether this creates competition between them. In judging this, one must take into account firstly, that the juveniles of these species are as a rule territorially separate from each other: coho stays in shallow water near the banks, while the sockeye is the inhabitant of the pelagic zone. Moreover, we must keep in mind that in the planktonophagous sockeye there develop numerous long gill rakers, which make catching of plankton possible. Coho has few gill rakers, 19 - 23, they are short, wide apart, and cannot fulfill this function. In the stomachs of large coho juveniles plankton is virtually absent not only in the rivers, were it is scarce, but also in the lakes, rich in plankton (Gribanov, 1948). Obviously, coho cannot compete for food with a plankton-eater.

Large juveniles feed on salmon eggs, which are carried during oviposition from the nest hollows and are doomed to perish. From the age of 1 coho in some water feeds on the juveniles of chinook, chum, sockeye, char and small individuals of its own species. In the Karymaiskii stream, for example, it changes to feeding on other organisms only during the period of absence or extreme scarcity of fish (Semko, 1954). The predatory nature of coho has been pointed out also by other authors (Synkova, 1951; Hunter, 1959). When sharing the same stream during the spring, and when abundant, coho might supress the juveniles of chinook (Stein, Reimers and Hall, 1972). There are also other assessments of the 222
role of this species in ichthyocoenoses. Gribanov (1948) spoke only of

partial change of the yearling to predatory feeding. Zorbidi (1970a) did not find small salmon in the stomach of the coho either in the spawning river or in the lake with abundant juvenile sockeye. She believed that coho causes practically no damage to their stock maintenance. In the lakes it eats a lot of fish, but they are stickleback and smelt, both trophic competitors of the juvenile sockeye. As can be seen, the relationship of coho with its related species differs from one area to another and from season to season; they should be judged separately in each concrete case. It should also be taken into account that the transition to predatory feeding of the large coho juveniles, as that of other salmon species, is favoured by high concentration of juveniles, which is often artificially created (Hunter, 1959; Ricker, 1962; Levanidov, 1969).

Smoltification is very distinct in coho. Before its descent to the sea the reaction of preference for sea water begins to be manifest. It lasts throughout the duration of the migratory season. This reaction can be caused by the artificial extension of the daylight period and can be suppressed by making the day shorter (Baggerman, 1960). In nature, transition to pre-migratory condition coincides with the spring lengthening of the day and increase in intensity of solar radiation. The juveniles undergo deep morphological and physiological changes, which are characteristic of the complicated process of smoltification. When the young fish are physiologically prepared, the transition to migration and change of environment is stimulated by external factors: changes in current velocity, water level in the river, temperature, gaseous regime, oxygen content, illumination, abundance of food (Neave, 1943; Hoar, 1951, 1954, 1958;

Shapovalov and Taft, 1954; Baggerman, 1960; etc). Coho smolts gather in schools. Their sensitivity to light increases and the smolts hide in shaded and deeper places. During the night, on the other hand, one observes a rise to the surface and an increase in movement activity, leading to the descent downriver. The behaviour of the juvenile coho is seen as closest to the original river form of the salmon, while the most specialized is believed to be the behaviour of the juvenile pink and chum (Hoar, 1958).

Along the river Dal'nyaya the juveniles migrate from the lake from the end of May to the end of August, mass migration being in July. Accumulations of coho in the lower reaches of the river Paratunka are observed up to the middle of September. From the beginning of June the young fish appear in flood-plane lake and remain in Avachinskaya Bay up to December, when they reach 17 - 22 mm (Gribanov, 1948).

According to the observations of the staff of the Paratunskaya experimental laboratory, coho begin to swim downstream from Lake Dal'nee when the average daily temperature in the river reaches 3.8 - 4.0° and the water level progressively rises. Mass migration takes place at the end of June, beginning of July, accompanied by progressive rise in the temperature from 8 to 13°. Abundant exit from the lake coincides with 223
overcast, rainy weather and dense fog. Migration continues until the beginning of August. By that time the level in the river drops to its lowest and the water warms up to more than 15 - 16°. Mass migration down the river begins usually in the evening, and is most intensive by night. However, when clouds are heavy, during foggy and rainy weather at the peak of the migration, mass descent is observed almost round the clock.

From the spawning streams juveniles migrate also mainly by night. During 4 years of observations in the Karymaiskii stream, 8% of the larvae migrated during the daylight hours, 28% of yearling fish and about 40% of two-year-olds (Semko, 1954). Mass exit from the rivers of North America takes place in April-August, but a small number of migrants in the southern rivers can be found at all tires of the year (Godfrey, 1965). The extended period of migration of juvenile coho from the rivers is caused by the prolonged periods of spawning and emergence of larvae from their nests, as well as by the differences in the rate of growth of juveniles and differences in the age composition of the migrants.

Characteristic Features of Reproduction and Development of Coho.

Coho is a salmon of middle size, distinguished by short lifespan and rapid rate of growth. In the sea an overwhelming number of individuals live one winter and feed only slightly longer than the pink. Some males spend several summer months in the sea, and the dwarf males mature in the rivers. From the rivers the juveniles migrate at the stage of mixed feeding, either as young-of-the-year or after one or two winter seasons. The age composition of the spawning populations is more complicated in the northern regions. There exists a landlocked form.

Migration into the rivers takes place from the end of the summer until the winter. In most rivers two peaks of run are observed, as well as relatively early and late spawning, which drags on deep into the winter and takes place in separate places. No morphological differences were found among spawners running at different times.

Coho reproduction in the southern rivers of Sakhalin and the rivers of Hokkaido is small. Coho has low fecundity, is distinguished by a low degree of development of nuptial livery, which indirectly points to the special character of reproductive ecology. Local stocks can be distinguished by age composition, size, fecundity, time of run and spawning. The differences between the fecundity of fish from different continents are significant. Average absolute fecundity of the Asian coho approaches 4,000 eggs, while that of the North American is 2,500 to 3,000 eggs.

The spawners enter large rivers at maturity stage III-IV; they remain silvery for a long time and migrate over large distances (in the river Kamchatka about 700 km). In many North American rivers this fish 224
enters while more mature and reproduces not far from the sea.

Spawning begins at the end of August, but assumes mass character in the autumn and winter. Among the representatives of the genus Oncorhyncus, coho matures and begins to develope at lowest temperatures. Spawning grounds are situated from the tidal zones to the sources of the rivers, in streams, potholes , limnocrenes and rivers at places where the ground waters emerge. Redds are built both in places with fairly rapid current and in those where the current is slow and there are considerable silt deposits.

Males eject sperm in large batches (average volume of ejaculate is about 20 ml), in 1 mm^3 of which are about 17 - 20 millions of spermatozoa . Eggs are deposited in 3 - 4 batches. They are relatively small (mature oocytes of Asian coho weigh 76 - 196 mg), have membranes 36 - 54 mk thick and an intensive orange colour.

Eggs can be incubated at low oxygen content; it has been observed to survive in a short-term drop of oxygen to 2.7 mg/l. As in other salmons, after the beginning of circulation the oxygen uptake increases. One of the special features of morphogenesis is rapid completion of the process of epiboly, which is finished at 29 - 33 somites. The embryos become more mobile after the formation of 43 - 45 somites, and in good aeration at the stage of 47 - 49 somites. The branchial and buccal apparatus becomes mobile earlier than in the pink, but somewhat later than in the sockeye. Circulation is established at the stage of 59 - 61 somites. Transition to the hepatic-vitelline circulation occurs often before the completion of segmentation. Embryonic-larval organs of respiration reach a high degree of development. Melanophores and lipophores appear between 254 and 306 degree-days, the embryos are more pigmented than those of all other salmon species, except for masou. Among salmon species, coho belongs to one with a relatively short period of egg incubation.

In larvae, opercula grow very broad, the skin membranes protecting the gills from silting. The preanal fin fold grows for a longer time than in other salmon species, reaches greater length, becomes pigmented by lipophores, of which there are few, and is retained for a long time. Emergence from the nests is spread from the early spring to the middle of the summer. The larvae keep in groups for a short time. The juveniles develop bright, spotted colouration.

The young fish have high bodies, long paired and high unpaired fins with elongated branching first rays, and a broad caudal fin with a deep notch. Coho is characterized by territorial behaviour. The fish occupy individual territories and defend them aggressively. They are able to jump out of the water and catch insects flying above it.

Having reached the length 45 - 47 mm, juveniles move into the deep regions of the river, migrate into lakes, sometimes against the current. 225

They lose their aggressiveness and group in schools. The height of the body, the height of the unpaired and length of the paired fins becomes diminished with age. The food spectrum of coho is very broad. This salmon feeds on huge quantities of aerial insects.

The process of smoltification is very definitely expressed in coho. Migration of juveniles from the rivers begins in the spring, takes place through the summer, and in the south also in the autumn. The lengthy period of downstream migration is due to the staggered spawning, emergence of the larvae from the nests, differences in the rate of growth, and morphologically variable conditions and differences in the age of the migrants.

MASOU-OMCORHYNCHUS MASU (BREEVOORT).

Masou is a relatively scarce salmon, the flesh of which is distinguished by its high quality. Masou is reared in the USSR and Japan, where it is used as the object of acclimation. In our waters this species is more abundant in Primore, where in some years they catch up to 12,000 centners (1.2 thousand metric tons, Translator's note). Soviet fishermen catch annually about 800 - 1,000 tons, the catch of Japanese fishermen varies from 2,000 to 5,000 tons, being on the average about 3,000 tons (Senko, 1956; Krykhtin, 1962; Tanaka, 1965; Birman, 1972).

Distribution and Life in the Sea. Masou lives only in the northwestern part of the Pacific. It is at its most abundant in the Sea of Japan and in Tatar Strait. The migratory form goes to spawn from the southern rivers of the Korean Peninsula and the rivers of Kyushu to the rivers of Kamchatka. The landlocked form has been described from the river of Daikokei in the north of Taiwan. There are abundant runs of spawners in the rivers of Honshu, and the most abundant ones are in those of Hokkaido. The populations in the rivers of Primore reach considerable abundance, as well as those in the Sakhalin, and the basin of the Amur. Further north the abundance sharply decreases. The southern border of distribution in the Sea of Japan lies near 38°, in the Pacific between 37 and 38°. Distribution in the sea is limited by the surface isotherms 8 - 12°. Masou feeds in the sea on planktonic crustaceans and young fish, among which are particularly common greenling, and occur also herring, saury, anchovy, icefish, sand launce, cottids and smelt (Pravdin, 1940; Dvinin, 1959; Krykhtin, 1962; Tanaka, 1965).

Intraspecific Differentiation. Masou has evolved both migratory and landlocked forms. In anadromous populations a high proportion of males mature at an early age, without going to sea; it differs from year to year, which is reflected in the sex ratio in migrating schools. Fish of different regions differ in the size of migrants and in lifespan, in rate of growth, sizes of mature individuals, fecundity, scale structure, 226
character of prespawning modification and times of spawning.

In the rivers of Sakhalin the young of masou live mainly for one year, a certain number for two years, and some, less than a year. In the last instance one observes migration of young-of-the-year fish (Volovik, 1963). In the sea the fish passes most commonly one, less often two winters and matures as a three-year-old, more rarely as a four-year-old. In different rivers and in different years the age composition differs. According to Krykhtin (1962), into the south-western rivers of Sakhalin in 1953 and 1954 ran 69% of three-year-olds and 31% four-year-olds. Among them about 70% were females; the number of males in various rivers varied from 27 - 54%. In fish caught in the rivers and coastal waters of this region no differences were found in the size and weight of males and females of the same age, and these figures are shown together for both sexes. The masou which enters the river Naiba on the south eastern coast of the Sakhalin has similar size and fecundity (Table 17). Further north, in the basin of the river Tym', larger and more fecund masou migrates upstream. In its tributary, the river Pilenga in 1954, among fish migrating to spawn, 38.2% were males. According to the observations of fish culturists, during preceding years males constituted about 30.4% and in 1949, when the spawners were abundant, there were more females (52.7%). Size-weight indices and fecundity of masou reproducing in the rivers of the South Kuriles, are similar to those of the Sakhalin masou (Ivankov, 1968).

In the tributaries of the Amur and in the rivers of Primorskii Krai there reproduces a large and fecund masou. In the rivers and in the sea it lives longer and spawns later. According to Vorob'ev (1926) in the river Tumnyn masou is particularly abundant; some males reach the length 71 cm and weigh 9 kg. The fecundity of the fish in that river varies from 1,702 to 5,347 eggs, being on the average 3,444 eggs (Yoganzen, 1955). In the Amur in 1926, masou was somewhat smaller and was less fecund, (Kuznetsov, 1928). In 1970 in the river Barabashevka (which flows into the Amur Bay within the Bay of Peter the Great), masou migrated upstream from the end of August to the beginning of September; the fish was large and twice as fecund as the Sakhalin fish (Table 17). According to the Primor'e fish husbandry establishment, in 1967, the males there were 47 - 65.7 cm long ($M=55.4 \pm 0.2$), females 49-66.2 cm

(M=55.8±0.2); the weight was respectively 1,600 - 4,700 g (M=2756±68.6) and 1,820-4,150 (M=2,960±34.4); fecundity varies from 1933 to 5945 eggs (M=3531±84). Among the fish of this region one finds a certain number of five-year-olds and a considerable number of individuals which live in the rivers for two years (Nikol'skii and Soin, 1954; Semko, 1956). Birman (1972) arrived at the conclusion that the Primor'e-Amur masou is older than previous calculations would have it. According to his data, an overwhelming number of individuals live in the rivers for two years, fewer for three years, and some, probably one year; the marine period of life takes from one to three years. He recognized seven age groups:

Table 17.

Length, weight and Fecundity of Masou of Different Regions.

Region, river age of masou	Length, cm male	Length, cm female	Weight, g male	Weight, g female	Absolute fecundity, No. of eggs	Reference
Kamchatka						
r. Kolpakovka	(44)		(1300)		(2025)	Semko, 1956
r. Utka	(46.2)		(1480)		(3700)	
R. Amur	46--67 (56.8)	47--62 (54.4)	1800--3200 (2309)	1600--3100 (2337)	1386--5228 (3216)	Kuznetsov, 1928
Primor'e						
r. Tumnin	up to 71 (63)	to 67 (60.5)	to 9020 (5490)	to 6050 (3977)		Vorob'ev, 1926
r. Barabashevka	50.5--66.0 (57.7)	56.8--62.8 (59.5)	1750--3900 (2532)	1650--3550 (2807)	2994--5385 (4030)	Personal data
Sakhalin						
south-western rivers	34--55 (44.6)	34--54 (45.5)	600--2700 (1350)	600--2400 (1400)	739--2683 (1900)	Dvinin, 1959
3-year-olds		37--57 (47.2)		500--2900 (1940)	860--2460 (1514)	Krykhtin, 1962
4-year-olds		47--60 (53.4)		1300--3000 (2058)	1325--3059 (2237)	Krykhtin, 1962
r. Tym'						
3-year-olds	(49.3--53.8)	(51.3--54.3)	(1510--2070)	(1933--2050)	1832--4262 (2268--2861)	Gritsenko, 1973
4-year-olds	(52.5--55.9)	(52.7--56.1)	(1930--2420)	(1860--2218)	1170--4950) (2342--3076)	
r. Naiba	36--53 (42.7)	44.5--53.5 (49.0)	447--1360 (820)	1500--1750 (1330)	1120--2340 (1688)	Personal data
South Kuriles	(47.3)	(47.9)	(1570)	(1570)	(1656)	Ivankov, 1968
Is. Hokkaido						
r. [illegible]okusibetsu	--	44.6--49.8	--	--	1987--2698 (2402)	Hikita, 1962
r. Sibetsu	--	44.0--49.5	--	--	1932--2879 (2549)	
r. Chitoze	50.0--71.0 (62.7)		1500--5100 (3400)		1968--5362 (3822)	Tanaka, 1965

Note: Average values are shown in brackets.

among them four-year olds constituted 46%, five-year-olds 31.8% and six-year-olds 4.8%. 228

Kamchatkan rivers are visited by fish of different types. The size of masou from the river Utka and those of Sakhalin are similar, but the former is more fecund. Smaller and not highly fecund fish migrates up the river Kolpakovka. From the Kamchatkan rivers the young migrate mainly as yearlings or two-year-olds; the marine life cycle takes mainly two years, but for some it is only one year (Semko, 1956). Birman (1972) calls the Kamchatkan masou the most slow growing one. He recognizes stocks from different regions as separate races.

Also in the rivers of Hokkaido, masou of a different quality reproduces. The rivers Tokusibetsu and Sibetsu, for example, are inhabited by fish similar to the Sakhalin one, while in the river Chitoze reproduces a large, highly fecund fish (Table 17). Representatives of different stocks differ from one another in scale structure (Sano, 1959; Hikita, 1962; Tanaka, 1965).

Masou is characterized by widespread neoteny. Dwarf males mature during their first year of life at a length of more than 90 - 100 mm. In Sakhalin, at the age of two years, they have an average length of 12.8 cm, weight 29 g, and at three years, length 16cm and weight 65.5 g (Krykhtin, 1962). After maturation, dwarf males do not perish and take part in subsequent spawning (Ohno, 1934; Smirnov, 1959b, 1965; Volovik, 1963). Before their first maturation they do not migrate, or change drastically their environment and continue to feed; their body shape and colouration changes only slightly. During the second maturation the nuptial livery is more definite.

Berg (1948) called masou living in the fresh water O.masou morpha formosanus (Jordan et Oshima). It is widespread in Japan and in the rivers of the eastern regions of the Korean peninsula. The relict landlocked form survived in the high mountain lakes in the north of Taiwan. Isolated dwarf males are caught in the rivers of Sakhalin and Kamchatka (Semko, 1956; Krykhtin, 1962). After the construction of a dam on the river Sedanka near Vladivostok masou lived for some time in the reservoir (Moiseev, 1957). Berg placed also O.rhodurus Jordan and McGregor in this taxon. This rare salmon is distributed to the south of O.masu and is represented by both anadromous and landlocked forms (Oshima, 1934; Hikita, 1962). Its young are distinguished by the presence of round red spots on the flanks, not encountered in the young of other species of Oncorhynchus. There are different views on the taxonomic position of this species. Some authors consider it an independant species (Oshima, 1934; Hikita, 1962), others see it as a subspecies of masou, O.masu rhodurus. It is here, perhaps that O. iwame and Kimura and Nakamura, described in 1961 (Benko, Koh and Needham, 1962 after Christie, 1970), belongs.

Masou grows slowly in the rivers and streams. The males mature during their first year of life, at lengths of about 100 mm and more; the females at the age of 3 to 6 years. At the age of three years, mature females are 19.6 - 24.1 cm long. Fecundity varies from 50 to 400 eggs. Diameter of ripe eggs is about 5 mm. In the lakes the rate of growth is higher. In Lake Biva, masou reaches the size of the anadromous form. Intensive feeding ensures rapid growth of masou also in artificial freshwater basins. The landlocked form is more slender than the migratory one. 229

Its prospawning changes are less extensive, bright red colouration does not appear. In large males the height of the body increases and they become darker, retaining traces of spots typical to young individuals (Tanaka, 1965). In the ponds, second maturation was observed not only of the male, but also of the female landlocked masou. This is seen as the evidence of the phylogenetic old age of the species (Christie, 1970; etc.).

Anadromous migration, Maturation. Masou migrates up the rivers soon after the breaking of the ice cover. In the river Tumin and in the Amur the run occurs from May to the middle of July, mass run being in the middle of June (Vorob'ev, 1926; Navozov-Lavrov, 1927). In the southern rivers of Sakhalin, the run takes from the middle or end of May to the end of July, mass run occurring during the second half of June. In the central part of the island and further north these dates are about 10 - 15 days later (Dvinin, 1952; Krykhtin, 1962; Smirnov, 1962b). The migration of masou into the rivers of the western coast of Kamchatka is observed from the middle of June till the 10 - 15th of July, with the peak during the first five days of July (Semko, 1956). In the southern rivers of Primor'e the migration and spawning occur later. For example, in 1967 the spawners migrated up the river Barabashevka from the middle of June to the middle of September, the peak of the run was during the first twenty days of July. During the dry, hot summer of 1970 the water in the river was low and the spawning migration was delayed. Mass run occured in the middle of August, after heavy rains, the run continued at least to the 20's of September. According to reports of the local fishermen, in some years masou runs up the river until the beginning of October. In 1970, the fish moved into the lower reaches of the river from the evening until dawn. This can be related to the considerable warming of water during the day, up to 22° and over, while during the night it cooled down to 13 - 14°. In the middle of September the males run up the river Barabashevka at the IIIrd and IVth maturity stages and females at the IIIrd-IVth and close to the Vth stage, with signs of prespawning changes. The weight of testes reached 7.4%, of ovaries 13.7 - 29.6% and on the average was 20.5% of body weight. In the mouth and lower reaches of the river some spawners continued to feed (mainly on anchovy).

Masou moves up the spawning tributaries of the Amur at the III-IVth stage of maturity (Kuznetsov, 1928). The spawners run up the rivers of the Sakhalin at less mature stages. At the beginning of the run the testes constitute 0.4 - 1.5% of body weight. In the river they change to running condition slightly earlier than the females (Dvinin, 1952). Migration into rivers begins at water temperatures from 4 to 12°. The run is more intensive during the first half of the day, becomes weaker from about 15 to 18 hours, at dusk intensifies and by night weakens again. At low water masou 230
migrates mainly during the daylight hours. With the rise in water level in the river the run increases (Krykhtin, 1962). The fish runs into the lower reaches of West Kamchatka at maturity stage III-IV. In the river Kolpakovka the weight of the ovaries on entry constituted 7.1 - 8.6% of the weight of females, in the river Utka it was 16.3 - 20.9% (Semko, 1956).

From the time of entry into the rivers to the beginning of spawning, a lot of time elapses. In Sakhalin it is about two months. Ascending to the places of reproduction, the fish must overcome barriers, log jams, rapids, small waterfalls. After overcoming each successive obstruction the spawners hide in deep places under overhanging banks, behind large boulders, rocks and tree stumps. The salmon chooses as its resting places shaded localities with slow current. The movement of the fish towards its spawning grounds increases with the approaching maturity.

By the time of the mass migration the level of the Sakhalin rivers drops. Spates after rains activate movement and help the fish to overcome obstacles in the upper parts of the rivers. Migration towards the spawning grounds proceeds particularly actively with the rise in water temperature to 14 - 15°. During the period of mass run the average daily temperature in the river B. Takaya in 1959 rose to 16 - 17°, water sometimes warming up to 19°. When the water in the river cooled down to 11° (and by night to 10°) the movements of the fish ceased. During the time spent by masou in the rivers of Hokkaido water temperature reached 20° (Tanaka, 1965). In the spawning tributaries and upper courses of the rivers, water temperature is lower in comparison with that in the main channel. It cannot be ruled out that it is precisely the rise in temperature in the lower part of the river that prompts the fish to move higher up.

Ascending along the river the fish gradually matures. Its integument begins to lose silvery colour, the back darkens, along the sides of the body appear up to 17 - 18 pinkish transverse stripes, alternating with dark olive-greenish stripes. In the males the hump grows, the jaws lengthen and the teeth grow. According to Krykhtin (1958, 1962), by the time of maturity the weight of the testes reaches 7.8 and of the ovaries 28% of body weight. Stripes along the sides of the body become bright red with a raspberry tinge, they become larger and on the belly fuse into a general pink band of paler colour. The back becomes dark brownish. The fins darken and at the same time red colour appears on them. The tips of unpaired fins and the lower margin of the caudal fin become white. On the back and the fins, bright oval spots are clearly delineated (Fig. 57). In the colouration of the mature females dark colour predominates. The uro-genital papilla swells and assumes a red colour. Under unfavourable conditions, for example at temperatures lower than that of spawning, colouration of spawners becomes dull.

It is interesting that the prespawning changes of the dwarf males are small and appear only with the IVth maturity stage. 231
Their bodies only become flat and higher; there is no formation of hump and the jaws and teeth undergo few changes. In larger specimens pre-spawning changes are more defined. They develop huge testes, the weight of which reaches 17 - 24% of the body weight. Dominant in coloration is an olive-greenish hue, the back darkens, dark oval spots typical to the young fish are retained on the flanks. Along the lateral line runs a narrow reddish band, present also in immature yearlings. It is not always possible to distinguish by external appearance between the mature small dwarf males and the young fish of similar size.

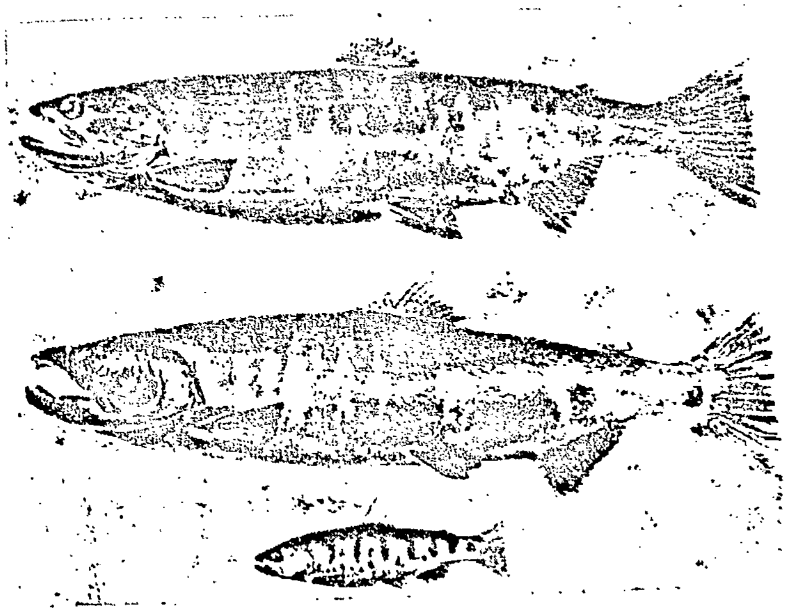

Fig. 57. Running individuals of Masou. Female 44.7 cm long (upper); male 45.7 cm long (middle); Dwarf male 15.2 cm long (Lower).

Spawning grounds, Spawning and Conditions of Development. For reproduction, masou ascends into the upper reaches of spawning rivers or enters small tributaries. In places of mass spawning, as a rule, there is no reproduction of related species. At the end of the season, isolated individuals build nests lower down, in the regions of mass spawning of chum and pink. However, they select different microhabitats. For example, in one of the lower stream tributaries of the river Belaya, masou built nests in places with more rapid current than the chum; and pink, in contrast with them, spawned far from the places of emergence of subsoil waters.

In the places of reproduction of masou the river banks are abund- 232
antly covered with tall grasses, bush and trees, often closing their crown above. The bottom of the spawning grounds is stone and sand, often with a rocky base and steep slope. Small spawning streams, running down steep slopes of the hills are full of rapids and only in isolated places have small horizontal surfaces, covered with stone chips, gravel and coarse sand, which are used for the construction of nests (Fig. 58). In broader places, resembling shoals of rivers running over plains, several females spawn. Even in grounds of this type, however, the nests are broadly scattered. Around the females there are usually one (rarely two) migratory male and several dwarf males.

Examination of samples of eggs taken from fresh nests bear out the view that masou usually spawns in the morning and during the evening hours. It was possible to observe directly deposition of eggs at about 19 hours. The weather was clear, but thick canopies of trees prevented penetration of sun rays into the place of oviposition.

In 1959 in the river Belaya and its tributaries current velocity above the nests was observed to be from 38 to 114 cm/sec, most commonly 50 - 60 cm/sec. In the dry year 1960, according to estimates made by a member of our unit, A.N. Kanid'ev, the average velocity in front of the nests was about 40 cm/sec. Rapid current allows this small salmon to move a large quantity of ground substrate during the process of oviposition. Redds have usually an oval shape (in plane), elongated in the direction of the current for about 1 - 3.5 m and with a transverse diameter of 0.5 - 2 m. Most of the material of which redds are built consists of gravel less than 6 cm in diameter and coarse sand, with the remainder being large stones. In new redds there is no silt or fine sand. During rains the redds are being silted up. Masou most commonly spawns at depths of 10 - 20 cm and the tips of the redds are exposed even after a slight drop in water level. At a depth of 30 - 45 cm redds are found only rarely. In Hokkaido the redds are situated at depths reaching 60 cm (Sano, 1959). Eggs are commonly found at 15 - 25 cm (in some cases, in friable gravel, at 40 - 45 cm) from the tops of newly-built redds.

Masou most commonly deposits two, less often three batches of eggs. In the redds separate batches of eggs consisted of 60 - 440 eggs. The total number of eggs in a single redd was from 190 to 680 eggs, and average of 28 counts being 563 eggs, which is about 32% of the average of absolute fecundity (Kanid'ev, 1964). It is possible that the females build more than one redd each.

The eggs of early depositions develop at a high temperature and with good water supply. Incubation takes a little more than a month. In

1959 in the river Belaya incubation proceeded at an average temperature in various nests from 10 - 14°. The water collected from the redds contained from 7.46 to 11.45 mg/l of oxygen (average of 12 samples 10.7 mg/l); saturation was from 71 to 104.7%. In the redds situated in a small stream tributary of that river, there were 7.35 - 9.35 mg/l of oxygen (65.5 - 87.1% saturation), while the saturation of the surface layers of water was 86.6 - 91.2%. 233

Fig. 58. Narrow stream with abrupt fall, on the small horizontal stretches of which scattered redds of masou are situated.

The regime of the redds in the same river was studied in 1960 by Kanid'ev (1964). Temperature in the redds during the period of incubation varied from 17.2 to 8.4%, with daily fluctuation of 2 - 3°. In the river water at the same time, temperature varied from 19 to 7.9°. Current velocity within the redds was 0.7 - 1.6, average 1.21 cm/sec. At the beginning of incubation the eggs were washed by water with the average oxygen content 9.8 mg/l. With the cooling of water its contents increased and in October reached 10.25 mg/l. Aeration of water increased also during the rains. Carbonic acid in water taken from the redds soon after the deposition of eggs was about 4.54 mg/l; by the end of incubation its content rose to 5.41 mg/l. Water in the redds contained 0.5 - 2 mg/l of oxygen less and of carbonic acid 0.3 - 0.5 mg/l more than river water. Daily fluctuation of oxygen content were 0.3 - 0.4 mg/l; there was less of it at 6 - 11 a.m. and more than other times at 4 - 7 p.m.. The water of the river Belaya has a weakly acid reaction, less often neutral. In 1959 in the redds of the river spawning grounds the pH value fluctuated from 6 to 6.7 (average 6.4); in a stream spawning ground this value was about 0.1 lower. In 1960 the reaction was near to neutral. 234

The spawning of the dwarf form in the Hitotsuze, in Miyadzaki Prefecture, was observed at the end of October - beginning of November at temperatures of 13.5 - 15.5° (Kimura, 1972).

Development of Masou.

Reproductive Products. In the impoundments, the males produced sperm for up to 19 days, giving 8 - 9 batches, from 1.4 to 53 ml in volume (average 12.8 ml); the total volume of sperm reached 81 ml. The numbers of spermatozoa in 1 mm^3 varied from 16.8 to 36.8 millions (average 21.23 million).

The ejaculate contained per 1 kg of live weight of the male up to 307 million spermaltozoa, i.e. almost 5 times more than in the pink.

At 9.3°, 20 seconds after the dilution of sperm in water, it fertilized 90% of the eggs, in 1 minute 60%, and in 2.5 minutes only isolated eggs were fertilized (Fig. 59). The same graph shows rapid loss of fertility by eggs in water.

Ripe eggs weigh from 126 to 226 mg ($M=174, 79 \pm 3.22, \sigma=25.2$). Four-year-old females more often produced large eggs than the three-year-olds. The eggs are orange-pink or red-orange colour with a raspberry hue (variation in the colour of the eggs is within the wavelength range 592 - 594 nm). Composition of the eggs is given in Table 1.

In 1959 the eggs of masou and of the pink were twice fertilized at the same time and the species were crossed. The eggs were reared in the
Sokolovskii incubator, the regime of which was described above. Simultaneous 235
insemination and identical conditions of development of the material make it of great value for comparison. When describing the eggs fertilized on the 10th of August 1959, we will refer to it as the first batch, and that fertilized on the 13th of August as the second batch. In 1954 the development of masou was studied in the Adotymovskii farm. Reports on the development of masou are given in the work of Krykhtin (1962), so our description will be brief.

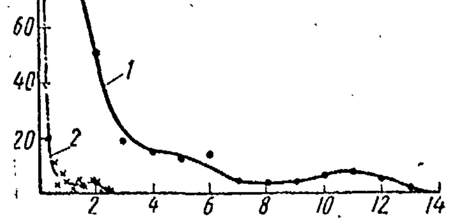

Fig. 59. Retention of Fertility by Eggs and Sperm of Masou in water. Horizontal: time in water before fertilization, min. Vertical: Quantity of fertilized eggs, % 1 - changes in the proportion of fertilized eggs after holding in water at a temperature of 9.5°; 2 - change in the proportion of fertilized eggs, inseminated by sperm kept for various lengths of time at a temperature of 9.3°.

Embryonic Period of Development.

Stage 1. Hydration of Inseminated Eggs, Formation of the Embryonic Disc. The process of hydration of eggs at 9.2° takes 45 to 50 minutes. Eggs of different females during the period of swelling increased in weight from 6.3 to 15% (average 11.5%). The diameter of the swollen eggs varies from 6.1 to 7.5, most commonly 6.8 mm. Diameter in some eggs reaches 8 mm. The thickness of the membranes of eggs that have begun to divide varies from 32.4 to 50.1 mk ($M=39.6\pm0.49$). Egg membranes are more transparent than those of the chum and pink. In the inseminated eggs the intensity of repiration increases. At 14° 1 kg of eggs takes up 52 - 55 mg of oxygen per hour. This figure then drops to 10 - 12 mg/hr, remaining at that level until the beginning of circulation.*

At a temperature of 8.4°, embryonic swelling was formed 12 hours after insemination. Its diameter was 0.9 - 1.1 mm, height 0.45 - 0.50 mm. 236

Stage 2. Cleavage of the Embryonic Disc. At the same temperature, cleavage began in 13 - 14 hours and one more hour was needed for two blastomeres to be formed in all eggs. The second to fouth division occurred at intervals of about 4 hours. After the third division, the outline of the embryonic disc assumed the shape of an oval with a small diameter 0.73-0.98

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*Here and below, data on oxygen uptake and rate of development of masou in Krasnopol'skii farm is given after Krykhtin (1962). Data on change in sensitivity of eggs to mechanical stimuli are taken from the same author and from Hata (1927).

and greater, 0.82-1.15 mm (Fig.60,A-G). The fourth furrow of cleavage runs in equatorial plane. In 30 hours 28 - 32 blastomeres could be found, and in 34 - 35 hours the number of blastomeres in eggs which developed more rapidly reached 64 (Fig.60,G). Towards the end of the second day the diameter of the surface blastomeres decreased to 80 - 70 mk, and at the age of 3 days to 30 mk.

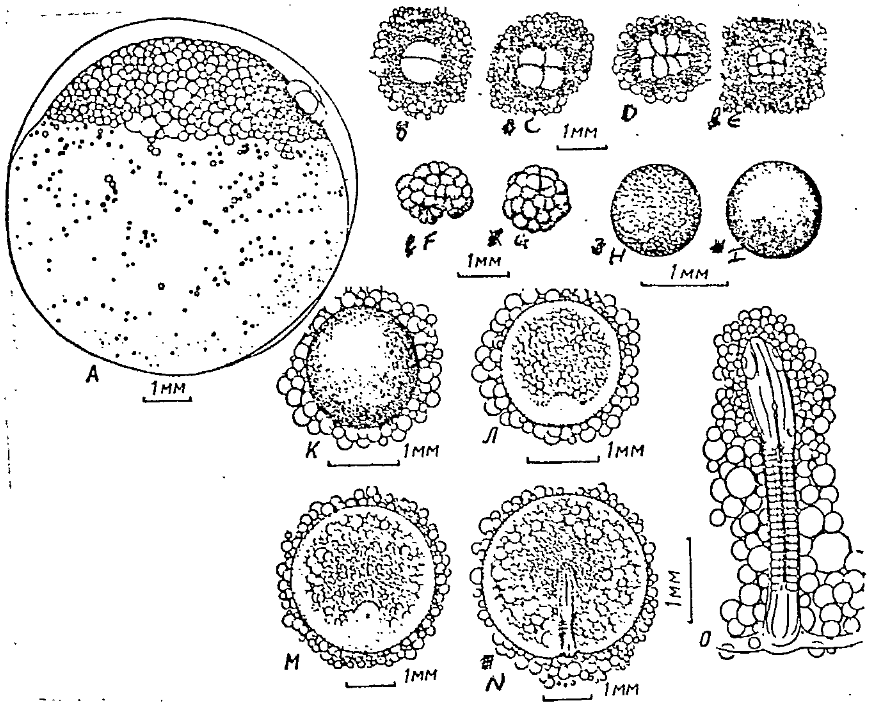


Fig. 60. Development of masou from first stages of cleavage to beginning of formation of the head and trunk. A - live egg with 4 blastomeres, drawn in transmitted light. B -E blastodiscs with adjacent sections of the yolk in stages of 2 to 16 blastomeres. F -I blastodiscs of later stages of cleavage to small-celled morula, inclusive, removed from the yolk. K - blastula. L - stage of "marginal knot". M - stage of "marginal streak". N - formation of first mesodermal segments, length of embryo 1.9 mm. O - embryo 3.3 mm long, stage of 20 segments.

Stage 3. Blastula. A few hours before the end of the fifth day /237
the embryonic discs began to enlarge; by the end of the day (42.5 degree-days) the diameter of the blastodisc reached 1.3 - 1.6 mm, and the blastula was formed (Fig. 60,K). At the age 5 days 6 hours blastodiscs had diameters of 1.6 - 1.8 mm. The cells of the surface layer decreased to

19 - 20 mk and those below them to 22 - 23 mk. This stage takes slightly more than a day.

Stage 4. Gastrulation. At the age of 6 days (51.5 degree-days) the diameter of the blastodiscs was 2 - 2.3 mm. They became flat, on their surfaces were cells with diameters of 16 - 18 mk. The differentiation of the embryonic layers began (Fig. 60, L). By the end of the 8th day the diameter of the embryonic shield reached 2.5 - 3 mm. The "marginal streak" was formed, 0.8 - 1.2 mm long (Fig. 60,M). By the end of the 10th day the diameter of the embryonic shield reached 3.5 mm. At an average temperature of 8.7^{0} this stage took about 4 days; in the eggs with a retarded rate of development it took about half a day longer. At temperatures of 10 - 16^{0} this stage was completed in 2 - 3 days.

Stage 5. Formation of the head and trunk of the embryo. At age 10 days 2 hours (86 degree-days) the blastodisc had a diameter 3.4 - 4 mm and covered about one third of the yolk sac. The embryo grew up to 2 - 2.2 mm. The first somites appeared, the parts of the brain began to differentiate, the rudiments of the eyes became visible (Fig. 60,N). On day 11, at 11 - 12 somites, the rudiments of the otic capsules were visible, the lenses began to form.

At the age of 12 days blastoderm surrounded about half of the sphere of the yolk sac. In embryos 3.3 mm long up to 20 somites were counted. The olfactory placodes were visible (Fig. 60,O). In embryos 4.2 mm long up to 30 somites were counted and the tail bud was formed. After the covering of more than half of the yolk sac by blastoderm, sensitivity of the eggs to mechanical agitations dropped considerably. In the Sokolovskii incubator this stage took about 6 days, in Krasnopol'skii 4 days.

Stage 6. Separation of the Posterior Part of the Embryo from the Surface of the Yolk Sac. The 16 day old embryos (150 degree-days) were 4.6 - 5 mm long and had 43 - 44 somites. Caudal myotomes appeared and the posterior section of the trunk began to separate from the yolk sac. At this stage, i.e. somewhat earlier than in the chum, chinook and pink, the walls of the cardiac tube began wave-like contractions (Fig. 61,A). By the beginning of this stage lenses were formed, small otoliths appeared, the rudiments of the opercula became noticeable. Blastoderm covered almost the entire yolk sac. During this stage the process of epiboly was completed. The yolk plug closed either in the middle or at the end of the 17th day (155 - 160 degree-days), at 52 - 53 somites, and more often at 54 - 56 somites. In individual cases the epiboly continued to the 18th day and the formation of 59 somites. As in other salmon species, the sensitivity of the eggs during that period is high. /238

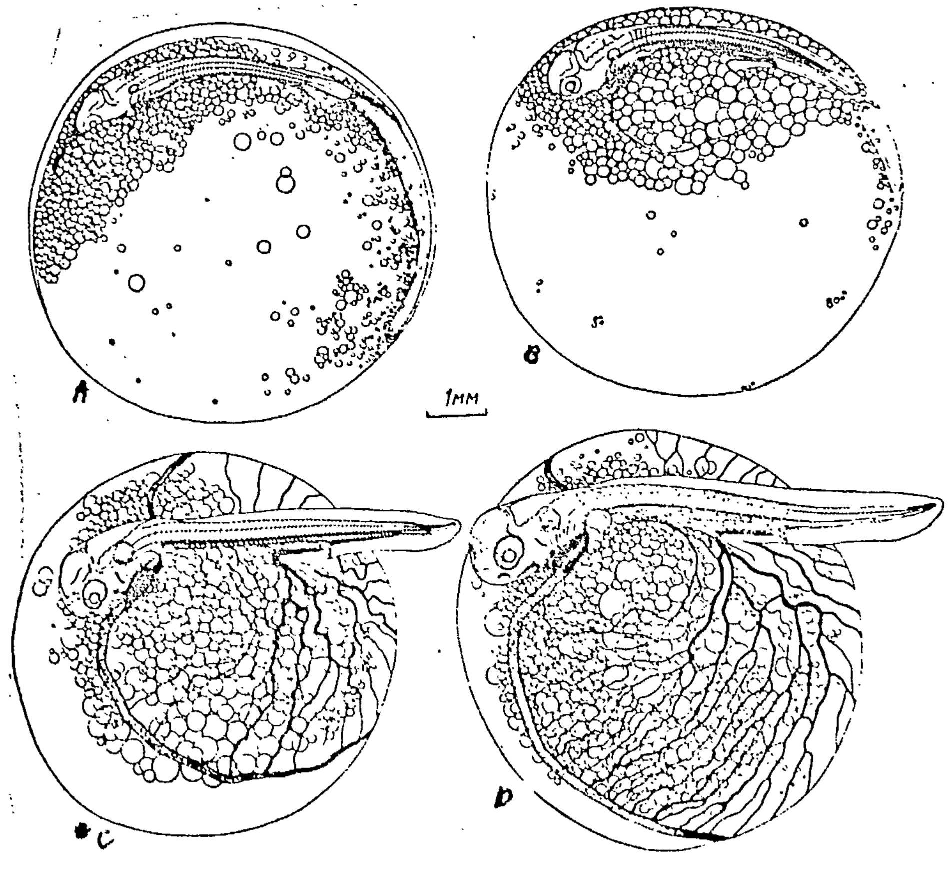


Fig. 61. Development of Masou after the formation of the tail bud and before separation of the head of the embryo from the yolk sac. A - embryo 5.0 mm long, with 43 segments. B - stage of beginning of circulation, length of embryo 5.6 mm. C - stage of the appearance of pigment in eyes, length of embryo, 7.2 mm, 79 segments. D - embryo 8.2 mm long, with 71 segments. Drawn in vivo; figs. B - D drawn from embryos removed from the eggs.

Stage 7. Development of the Subintestinal vitelline circulation.

Blood circulation was observed at the age of 17 days, in embryos 5.2 - 5.6 mm long, with 52 to 55 myotomes. In some of them at that time a small yolk plug was still present (Fig. 61,B). Embryos in which circulation began later had not more than 59 myotomes and length 5.8 mm. At first blood flowed along the dorsal aorta only to the 1 - 2nd caudal myotome and contained few cells. At the beginning of the stage one observes the buccal 239
funnel, the rudiments of the lower jaws appear, the head begins to separate from the yolk sac. Behind the rudiments of the pectoral fins in live embryos the glomeruli of the pronephros can be seen. At the same level on the right side appears the rudiment of the liver. Embryos energetically move their tails and now and again move their bodies from one side to the other.

Krykhtin (1962) observed the beginning of circulation in masou after the formation of 65 segments and attainment by the embryos of a length of 7.8 - 8.3 mm. His report on the blood flow at that time almost up to the last segments of the tail suggests that the described stage was later than the beginning of circulation.

Soon after the beginning of circulation the vessels become abundantly filled with erythrocytes, the length of the caudal artery and vein increases, more and more fine capillaries keep appearing on the yolk sac.

After the beginning of circulation the intensity of metabolism significanly increases. At the temperature of water 14° and oxygen content 10.6 mg/l, 1 kg of eggs takes up 15 mg of oxygen per hour. In the Sokolovskii incubator at 9.2° this stage continued for about 12 hours.

Stage 8. Formation of the Cardinal Veins and of Mixed Subintestinal-Vitelline and Hepatic-Vitelline Circulation. Cardinal veins were formed at the age 18 - 19 days, when the embryos reached the length 5.5 - 6 mm. In such embryos blood flowed along the caudal artery for more than 20 myotomes. From the caudal vein part of it flowed into into the posterior cardinal veins and the remainder into the subintestinal vein. There was a right and left branch of the marginal vein of the yolk sac. The surface covered by capillaries on the sac noticeably increased, as well as did their density. Hepatic circulation was established.

During this stage the absolute length of the head increased only a little and the relative length somewhat decreased. Acceleration of the absolute and of the relative growth of the tail section was observed, the unpaired fin folds grew in size. In some embryos at the age of 21 days (197 degree-days) melanin appeared in the eyes.

By the end of the 22nd day the embryos reached the length of 6.8 - 7.2 mm (Fig. 61,C). The head was separated from the yolk sac. The length of the tail comprised up to 30% of the total length and contained 30 - 32 myotomes. The bases of pectoral fins assumed an oblique position. The posterior mesenteric artery appeared.

By the end of the stage the segmentation of the tail was completed. The eyes turned gray. In stato-acoustic organs semi-circular canals became definitely formed and large otoliths developed. More than a half of the yolk sac surface was covered by capillaries. Two pairs of branchial arteries were formed. Segmental vessels were formed along the entire trunk (Fig.61,D). At a temperature of 9.5 - 9.7° this stage took about 7 days.

Stage 9. Formation of the Hepatic-Vitelline Circulation System. 240
At the age 25 - 26 days (235 - 245 degree-days) the subintestinal-vitelline vein became empty and from that time on the yolk sac was supplied with blood only through the liver. Embryos were 8 - 8.5 mm long. By that time the dorsal fin fold grew to the first myotomes and subsequently only increased in width. The rudiments of the unpaired fins were observed.

In embryos about 12 mm long (development from 13th of August to the 14th of September 1959) the head became high, but its relative length decreased to 17.3% of the total length. The eyes became black. Opercula covered the first pair of gills. The tail section exceeded 37% of the total length, the number of its myotomes from 32 - 34, present in the preceeding stage, decreased to 28 - 29. Three hypurals were formed, the first rays were laid down in the lobe of the fin, the capillary network began to develop , the caudal fin lost its symmetry. The pectoral fins lengthened perceptibly (Fig. 62,A).

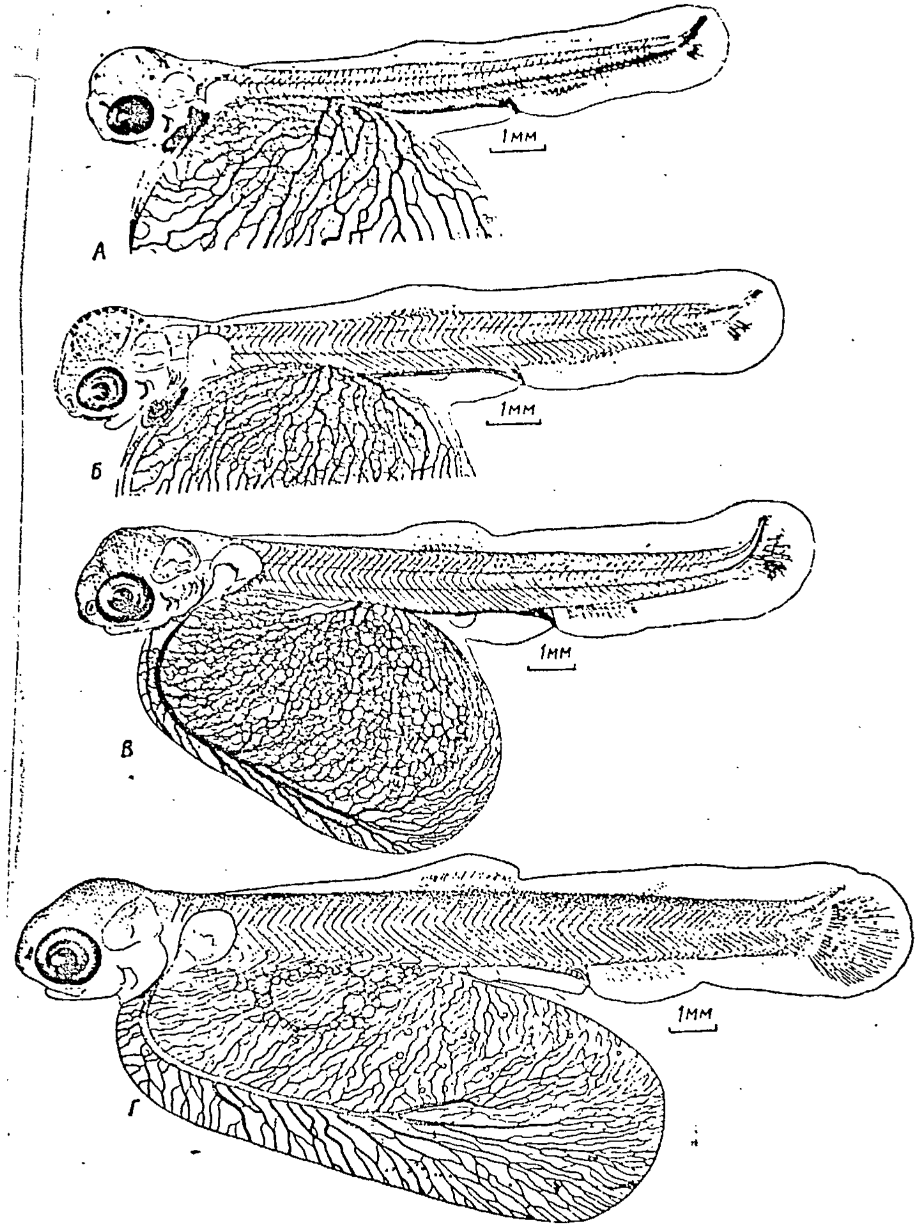
On the 28th day the blood supply commenced to the third and a day later to the fourth pair of gills. Hyoid arches of the aorta appeared. The capillary network on the upper surface of the head increased in density. The segmental vessels developed in the larger part of the caudal myotomes. The entire yolk sac was covered by the capillaries. The vitelline vein assumed a ventral position. At the age 29 days, i.e. slightly earlier than in the pink and chum, on the upper surface of the head appeared numerous small lipophores, bright red in colour. At a temperature of $9.6 - 9.9^{o}$ this stage took 4.5 - 6 days.

Stage 10. Differentiation of the Upper and Lower Cones of Myotomes. In some embryos age 36 days (343 degree-days) in the tail appeared rudiments of the upper and lower cones of myotomes (Fig. 62,B). Embryos reached the length 12.7 - 14 mm. The rudiments of the upper jaws became visible. On the 2nd and 3rd gill arch the rudiments of gill rakers appeared. Pseudobranchs became observable. The number of the caudal segments decreased to 25 - 26. Ventral fins were laid down. Pectoral fins became mobile. Segmental vessels formed the capillary network above the spinal cord and under the body surface. The length of capillaries per 1 mm^2 of the left side of the yolk sac reached 6.7 - 7.0 mm. At that age, i.e. much later than the lipophores, the first melanophores appeared on the head. The hatching glands became visible.

The embryos became able to perform wavy motions with their tails. At short intervals they waved their pectoral fins rhythmically. The intensity of respiration increased. In 1 hour at a temperature of $10 - 11^{o}$, 1 kg of eggs took up 17 - 18.8 mg of oxygen.

In the Sokolovskii farm at an average temperature of 10^{o} this stage takes 8 - 9 days; in the Adotymovskii farm by that time the temperature dropped to 4.2^{o} and the stage continued for more than half a month.

Fig. 62. Embryos of Masou Removed from the Eggs. 241
A - stage of deposition of unpaired fins, length of embryo 11.8 mm; B - stage of the appearance of ventral fins, length of embryo 13.5 mm; C - beginning of differentiation of adipose fin, length of embryo 15.9 mm. D - embryo before the time of mass hatching, length 20.0 mm; its development proceeded at a temperature of 9.9^{o}, age 53 days.



Stage 11. Development of Mobility of the Jaws and Opercula; Completion of Incubation. By the beginning of the last stage of incubation of the eggs, the embryos increased to about 15 mm. In the Sokolovskii incubator this stage began on the 38 - 40th day. By that time the enlarging lower jaws fully covered the buccal orifice. The jaws and opercula were moved energetically. Otic capsules were at their maximum closeness to the eyes. The caudal fin continued to differentiate. In the dorsal and anal fins, skeletal elements were laid down. Pigmentation of the body increased; melanophores of the neural and haemal series made their appearance.

By the 42nd day (405 degree-days) the embryos reached the length of 15.5 - 16 mm. In the Adotymovskii farm, when in the autumn the temperature drops sharply, the same condition was observed at the age of 70 days (Fig. 62,C).

At the temperature 10.3 - 10.7° this stage takes 10 - 14 days, and at the average temperature 4.3° it takes 24 - 27 days.

Stage 12. Passive Condition of Free Embryos. In the first batch during the incubation, temperatures changed within the range 8.4 - 10.7°; the first embryos emerged from the eggs on the 48th day, mass hatching took place during the 52 - 53rd day (518 - 528 degree-days), and the last embryos hatched during the 56th day (560 degree-days). In the eggs of other series, the earliest hatching was at the age of 45 days (452 degree-days). Masou hatches more or less simultaneously. The embryos from the small eggs hatched first. In the Adotyrovskii farm, where the temperature varied within the limits 8.3 - 4.5°, hatching began on the 68th day (423 degree-days) and assumed mass character at the age of 80 - 83 days (up to 494 degree-days). In the Krasnopol'skii farm eggs were incubated for 35 - 48 days (450 - 550 degree-days).

At a constant temperature of 16.2°, incubation of eggs of landlocked masou took 28.5 days, and at 5.8°--84 days. The highest rate of emergence of normal embryos was observed at temperatures from 8 to 11°; under those conditions incubation was completed in 505 - 508 degree-days (Kawajiri, 1927).

In small eggs embryos reach a length of 16 - 18 mm, and in large eggs 20 - 21 mm. Individuals hatched at different times, have 11 - 13 lepidotrichs in their tails, their division into separate components has begun.

During the period of mass hatching there are up to 17 - 20 rays, and in the middle rays, **three sclerites each.**

In our first batch mass hatching took place at lengths from 18.7 to 20.3 mm (Fig. 62, D). Embryos had 37 - 39 trunk myotomes and 23 - 25 caudal myotomes. A tail section, measured from the anterior projection of the first caudal myotome, reached 39% of the total length of the embryo, and measured from the anal orifice it comprised 35 - 36% of the total length. The anal and dorsal fins separated from the unpaired fin fold and the contour of the adipose fin became distinguishable. In the pectoral fins, rays began to form.

By the time of hatching the eyes of the embryos became mobile. 243
Opercula covered the gills fully. In the gills and pseudobranchs the capillary network became fully developed. The formation of the bars in the olfactory orifices was almost completed. The lateral line organs reached during the incubation the same level as they do in the chum (Fig. 63,A). There is a small rudiment of swimbladder, and the separate identity of the stomach was observable. From 3 to 5 rakers were laid down on the first gill (Fig.64,A). In the level of development, masou during hatching resembles coho. Among all salmon species its embryos are distinguishable by their intense pigmentation.

As in other salmon species, embryos after hatching behave passively and their reactions to external stimuli are not sharp. The embryos of masou remain in this inactive condition for 8 - 11 days at the temperature 10.6°, and 18 - 25 days at 3.8°.

Fig. 63. Lateral line organs in masou at the time of hatching of embryos (A) and in larva 32.2 mm long (B). Grooves of the developing canals marked by stippled line, large dots mark neuromasts. f.b.-organs of the jugular group of cheek region; f.d.-dorsal series of neuromasts; f.lat.-lateral series of neuromasts; f.ior-suborbital organs; f.om.-preoperculo-mandibular organs; f.sor.-supraorbital organs; f.sp.-supratemporal organs; f.t.-temporal papillae.

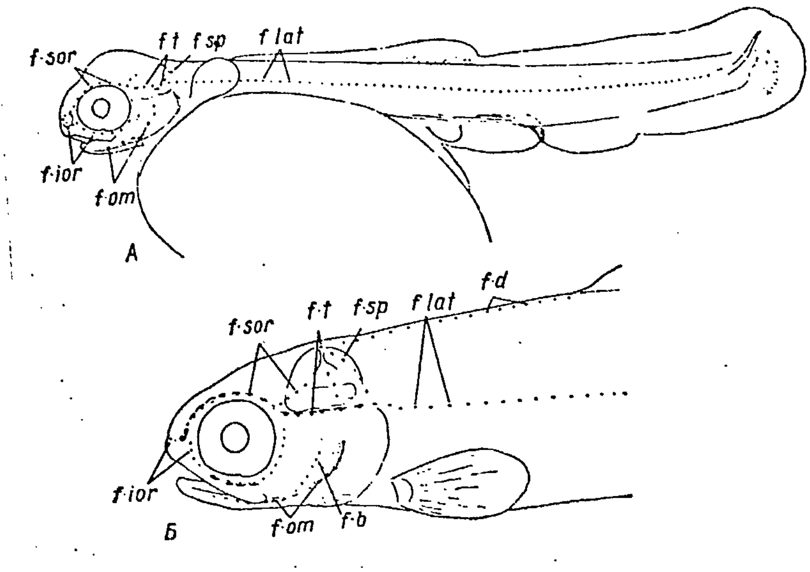


Fig 65

Stage 13. Formation of Unpaired and Ventral Fins, Development of the Swimbladder. At the age 60 - 64 days, when masou reached 23 - 25 mm, it began to move against the current, positively react to contact with external objects and negatively to light.

The mouth of embryos assumed a subterminal posititiom (Fig.65,A). 244
In skin membranes of opercula rays appeared. Rays were well visible in the dorsal, anal and pectoral fins and began to form in the ventral fins. The density of the vascular network of the yolk sac was reduced, its volume and the surface not covered by myotomes became smaller.

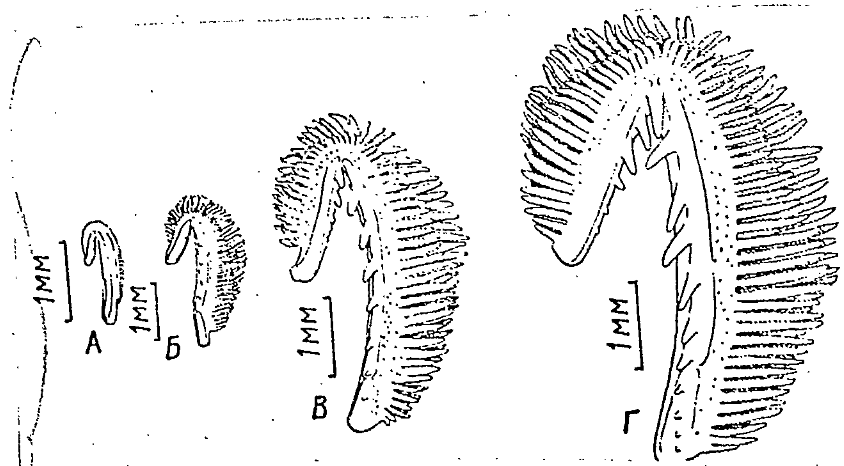


Fig. 64. First Left Gill of Masou. A - during period of mass hatching, length of embryo 18.5 mm. B - at the beginning of the formation of dark spots on the flanks of the body, length of free embryo 23.7 mm. C - in larva 33.0 mm long; D - in juvenile 38.5 mm long.

The embryos assumes a dark colour, many chromatophores appeared on the unpaired fin fold. In contrast to the related species, the chromatophores are present also on the preanal fin fold near the anus. In the skin, together with red lipophores appeared smaller chromatophores of orange colour.

At a temperature of 9.4 - 9.6°, 25 - 30 days after hatching, dark spots appeared on the flanks of the body (Fig. 65,B). By that time teeth have cut through on the jaws. The tails became symmetrical and developed a noticeable notch. Its rays began to branch, several reduced rays were laid down. The ventral fins became mobile. The preanal fold continued to grow. The body of the free embryos became more streamlined. Viscosity of the yolk increased and the fat drops in it ceased to change their positions. The first pyloric caeca appeared; intestinal tube loops began to form; weak peristalsis was observed. The rudiment of the swimbladder reached the length 3 - 3.5 mm; it began to grow rapidly. In rearing ponds these embryos from time

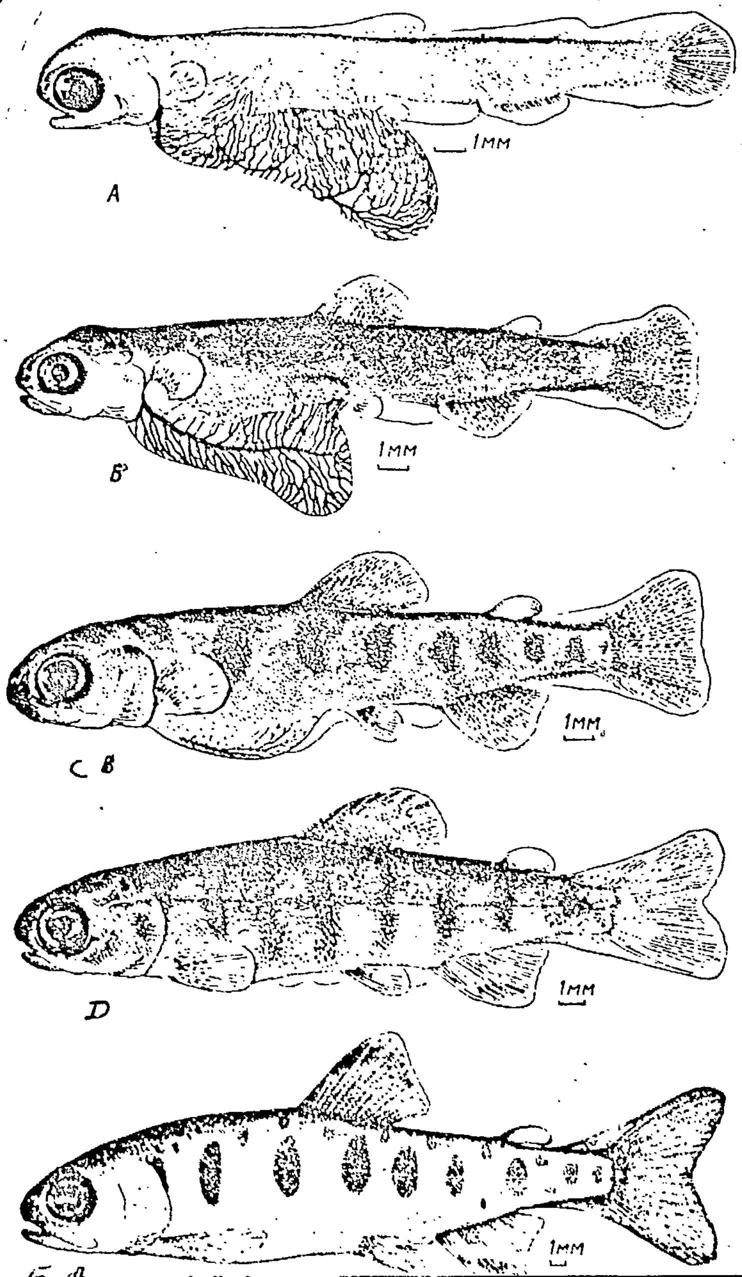


Fig. 65. Masou of different ages. A - free embryo 25.1 mm long. B - free embryos 24.6 mm long. C - larva 28.3 mm long. D - larva migrating downstream from spawning grounds, 32.5 mm long. E - juvenile 48.7 mm long.

to time rose in the water, but were still unable to swim for a long time and soon moved down to the bottom.

In the Sokolovskii rearing ponds at a temperature of 9.2°, this stage took 25 - 30 days, and in Adotymovskii at 2.7° - 2.5 - 3 months.

Larval Period of Development.

Stage of Mixed Feeding. With a drop in temperature from 9.6 to 8.6° in 35 - 40 days after hatching masou reached the length 25 - 29 mm and changed to life in midwater. The swimbladder was filled with air. Fins of the larvae became large. The tips of lepidotrichs branched. The preanal fin fold elongated to 5.5 - 6 mm. Transverse dark spots on the flanks of the body became large. The remnant of the yolk weighed 35 - 55 mg and was not yet completely covered from below by abdominal walls. (Fig. 65,C). The glandular and the pyloric parts of the stomach became differentiated from each other. On dissection the sex of larvae could be detected with the unaided eye.

Larvae have good orientation in space, move in midwater in all directions, actively grasp small live and artificial food. In the aquarium they fed on particles of egg powder, hunted small Daphnia, picked up from the bottom small or finely cut oligochaetes and chironomid larvae, while still having a considerable remnant of yolk left.

Transition to life in midwater is accompanied by a loss of photophobia and of positive reaction to contact. However, the larvae avoid direct sunlight. In nature, a similar change in behaviour occurs prior to the emergence of masou from the ground.

The juveniles do not remain long in the vicinity of their nests. In the south of Sakhalin, in the river Kalininka, the migration of juveniles from the region of spawning grounds down the river in 1954 was observed at the end of April. Further north, in the river Pugachevka, mass descent of larvae occurs during May and ends in the first days of June. This migration resembles the pattern of descent of the pink and chum. During rain and under overcast skies on the 25th and 26th of May 1954, the first specimens entered the trap erected in the river Pugachevka at 20 hrs 45 minutes. The largest catch was at 21 hours 40 minutes and at midnight. Later it declined and ceased at dawn.

Larvae migrating from the spawning grounds were from 27.9 to 35.0 mm long, most commonly 30 - 31 mm, and weighed from 130 to 280 mg, modal weight being 180 - 220 mg. The overwhelming majority of larvae had traces of yolk; only in few its weight reached 3 - 5 mg.

In relation to the body length, the length of the head of migrating masou (after Smitt) was 21.8 - 25% (23.71±0.27), height of head 13.1 - 16% (15.2±0.18), greatest body height 14.8 - 18.7% (16.4±0.25), length of 247
pectoral fins 13.1 - 18.7% (16.45±0.34), of ventral from 9.8 to 14.6% (11.45±0.26), height of dorsal fin 13.7 - 18.2% (15.82±0.35) and height of anal fin 12.1 - 15.2% (13.45±0.25). On the flanks of small individuals there were 4 and on those of large ones, 8 bright transverse stripes. In the dorsal and anal fins developed white and dark stripes (see below). The preanal fold protruded forwards in front of the vertical line drawn through the anterior margin of the base of the dorsal fin. Present on it were lipophores and melanophores, though not in all specimens (Fig. 65,D). By the level of

differentiation of the lateral line organs (Fig. 63,B), these larvae resembled those of the chum 35 mm long (Disler, 1960).

The stomachs of the majority of migrating little masou were empty, while the intestine, especially its posterior part, was filled with indigestible remnants of food organisms. This indicates that larvae feed actively in the region of spawning grounds. In 55% of migrating larvae were found remnants of larval Chironomidae, and in 44% of individuals, the remains of larval Ephemeroptera; their weight was 24.4 and 61% of that of the food bolus respectively. Already at that age 33% of larvae contained remains of terrestrial and aerial invertebrates, the weight of which reached 14.6% of that of the food bolus (identification of food remains was carried out by a member of our unit, S.P. Volovik, 1963).

Migrating larvae of masou, in contrast with those of the pink and chum, do not move out to sea. The purpose of their migration is different; it is dispersal in the river and colonization of extensive food bases. Further feeding progresses in well heated shallow littoral habitats of the upper and middle courses of the rivers, side channels and pools, sometimes seriously silted. We found larvae in places with water temperature up to 21°. At first they kept together in schools from 3 - 5 to several tens of individuals. Larval masou can often be seen among the juvenile chum. At the end of the larval period of development the preanal fold is rapidly resorbed. The larval period in the river continues for 2 - 2.5 months.

The Juvenile Period of Development.

Studying juveniles of different ages, Krykhtin (1962) distinguished the stage of feeding in shallow waters and that of feeding in the mainstream of the river. The latter continued until smoltification.

<u>Stage of Feeding of Juveniles in Shallow Water</u>. At the end of the stage of mixed feeding change occurs in the habitat, behaviour, appearance and colouration of the juveniles (see Fig. 65,E). By the beginning of the juvenile period of development the flanks of the body and the belly become silvery and the back dark, olive-greenish with a blue tinge. On the silvery background appear large, black, oval lateral spots. Between their upper ends are situated smaller black oval dots with less definite margins, and later there appear round, even smaller spots 248
below large lateral ones. Fins assume a bright colour. The membrane of the dorsal fin becomes orange, brighter at the base; distal tips of the anterior branching rays are covered with white pigment, behind which, nearer to the bases of the rays, runs a band of black pigment, while the remainder of the fin is bordered with a narrow red-orange band. The anal fin, the end of which is pointed, has a similar colour. The base, anterior part and tip of the adipose fin become covered with black and brightly orange chromatophores, and its centre with yellow ones. The membrane of the caudal fin is yellow-orange with a bright orange margin and numerous melanophores, grouped at the base of the lobe and close to the tips of the rays. On ventral fins there are much fewer melanophores and lipophores, their tips are whitish. Pectoral fins are coloured yellow-orange and only at the base have few melanophores. Juveniles living on dark bottoms assume darker colouration.

At an average length of 43.8 mm the height of the body of the juveniles reaches $22.55 \pm 0.26\%$ of their length. In relation to the body length the height of the dorsal fin is $18.75 \pm 0.33\%$, of the anal $16.3 \pm 0.32\%$, length of pectoral fins 18.97±0.28% and of ventral fins 13.8±0.2%. By the beginning of the juvenile period of life the number of the rudiments of gill rakers reaches 17 - 18 (Fig. 64,D). There are 33 - 36 pyloric caeca, while in adult specimens they number from 35 - 68 (Hikita, 1962).

In the river Belaya at the end of July 1959 among the juveniles caught were specimens 38.5 - 40 mm long, with single sclerites on scales below the adipose fin. In the river Lesnaya on the south of the east coast of the island we took juveniles 45 - 46 mm long, with only the central areaof the forming scales. Only further investigations will show what the reason is for the difference in tha time of scale formation.

Juveniles scatter over the shallow water, keep singly behind small sand ridges, stones and submerged branches. From those positions they dash out after small possible food objects, carried past by the stream, to return to the previous places. Their miniature hunting territory is aggressively defended by the juveniles. In experimental schools juveniles did not leave previously occupied deep and quiet places when additional juveniles were added, while from the places close to the fast flowing water some specimens swam downstream (Tanaka, 1973).

However, the young fish were not always solitary. Inspecting the rivers after rains, we repeatedly saw schools of juveniles in small pools which had deep as well as shallow places, weak current and sand and silt bottoms. In some schools 25 - 30 fish were counted, in others much more. In one of the schools, fished on the 23rd of July 1959 in the river Belaya, the juveniles were from 36 - 48 mm long. In small specimens scales were 249
missing, in larger they had from one to six sclerites. Such groups occurred usually during spates caused by rains. When the water level dropped

and current grew weaker the juveniles again dispersed along the shallows of the river course.

Feeding of the juvenile masou was studied in the rivers of the south-western shores of Sakhalin (Krykhtin, 1962). Our unit collected material mainly in the rivers of the south-eastern shores of the island (rivers Pugachevka, Naiba and Lesnaya). The main data were published (Volovik, 1963, 1964) and are used below. In 1970 we conducted observations in the rivers Barabashevka and Kedrovka, flowing into the Amur bay of the Bay of Peter the Great. We shall briefly review more significant features of the species' feeding.

While the variability in the food components of the larvae was small and the average stomach filling index was 360‰o, in juveniles feeding in shallow water the number of components exceeded 50 and the average stomach filling index increased to 450‰o. The frequency of occurrence of Chironomidae dropped to 23.6% (9.72% of weight of the food) and that of Ephemeroptera increased to 68% and they constituted 23.62% of the weight of the food bolus. The frequency of occurrence of Trichoptera was 13.2%, Plecoptera 12.2%, and the weight of various other organisms reached 41.8% of the total weight of food. Aerial insects occurred in 66% of specimens examined. Juveniles fed round the clock, but most actively early in the morning, in afternoon hours and during the dusk.

<u>The Stage of Feeding of Juveniles in the Mainstream of the River.</u> With the increase in size, juveniles become capable of resisting stronger currents and move to the main bed of the rivers. In the river Belaya this took place after reaching a length of 45 mm and weight of about 2 g. According to Krykhtin (1962), juveniles moved to the mainstream at a length

of 50 - 60 mm and weight about 3 g. The differences might be due to the special characteristics of the stocks examined and to the regime of the rivers, and condition of the food base during the years of study.

This species during its entire ontogeny is distinguished by the marked height of the body. In juveniles it increases gradually. Large juveniles which moved to the mainstream of the rivers, differ only little from the adult individuals as regards their meristic characters. The little fish have bright, varicoloured colouration (Fig. 66). On the flanks of their bodies are distinguishable rows of dark spots of various sizes. Along the middle line there runs a narrow raspberry-coloured band. Intensity of the lipophore pigmentation of fins, in comparison with the preceding stage, is weaker.

The young masou begins to feed on terrestrial and aerial invertebrates already in the spring. The relative importance of this food increases with age. During the first summer, terrestrial and aerial invertebrates constitute more than 65% of the weight of the food bolus, and during
the following summer more than 90%. The variety of organisms ingested by 250
the masou is very great. Among them occur both small and very large ones, reaching half the length and 10 - 13% of the weight of the juvenile fish. During the second half of the summer in the stomachs of the juveniles were found more than 150 different food components. It must be taken into account that with the aid of undigested remains one can in many cases identify only large systematic taxa, and, consequently the species composition of the animals eaten by masou is much greater than this figure. The stomachs of the juveniles in the summer are well filled with food and are very rarely empty. Obviously, greater variety does not suggest low availability of food,

but reflects the specific character of the food niche occupied by masou. For the life of its juveniles of great importance are invertebrates which reproduce and grow outside the water habitat. Thanks to this fact masou was able to colonise upper reaches of mountain rivers and small streams poor in food, and to live in fresh water the year round.

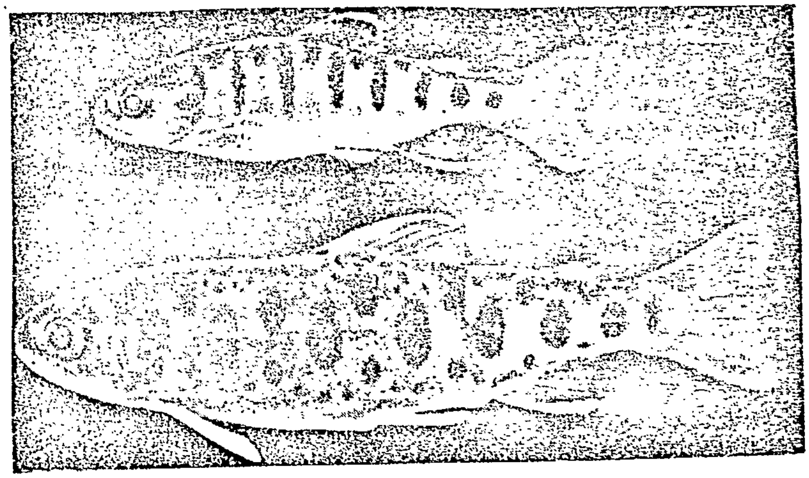


Fig 66. Juvenile Masou. A - juvenile 5.9 cm long, weighing 2.72 g (upper). B - yearling 9.2 cm long, weighing 9.97 g.

During the time of spawning of the chum and pink, their eggs occupy an important part in feeding of the juvenile masou, and during the spring in the stomachs of the yearlings there occur larval salmon and eggs of the spring-spawning fish. In connection with this, the question arises whether yearling masou is not an enemy of the juvenile chum, pink and other salmon species. Our observations, as well as data of other authors indicate that under natural conditions juvenile salmon in the stomachs of masou occurs for a brief period, not often, and in small numbers (Kalmykova, 1957; Krykhtin, 1962; Volovik, 1963, 1964). This is due, in particular, to mass downstream migration of the pink and chum by night, while the juveniles of masou feed intensively by daylight. he possibility of predation increases in the places of concentration of the young of different species and ages. Such a situation might arise, for example, below a rearing pond during the release of juveniles from them, near counting fences and other barriers. It would be incorrect to judge the role of an animal in biocoenosis from such arfificial situations. Also, concern about the feeding of juvenile masou on the eggs of salmon is not well founded. It is known that during the time of oviposition a considerable proportion of eggs do not get into nests, and outside the nests they are destined to perish. When the spawning grounds are abundantly filled, a lot of eggs are lost. They are fed upon by the juveniles of masou, coho, chinook and char. The removal of these eggs has a favourable effect on the sanitary condition of spawning grounds.

Late in the spring groups of parrs occur in deep, quiet parts of rivers and in pools, where the water is slightly warmer than in the mainstream. Juveniles change to feeding mainly on benthic organisms. Masou also spends the winter in similar habitats.

While studying the character of the growth of masou, it was observed that from the beginning of August the linear growth begins to dominate over the volume growth and the young-of-the-year become more streamlined (Krykhtin, 1962). Since some masou migrates to the sea as young-of-the-year, such change in the character of their growth and shape can be related to the reconstruction of the organism prior to catadromous migration.

The body of the yearlings before the migration becomes streamlined. Guanine is abundantly deposited in the integument, almost completely covering the lateral dark spots. Fat deposits in the abdominal cavity become smaller. During the remainder of the life in the river a tendency exists for reduction in the blood of smolts of chlorides, urea, aminoacids and for the increase in total nitrogen, fats containing phosphorus, as well as of water (Kubo, 1955). Smolts migrate downstream and form large schools in the deep, quiet places where the water is slightly warmer than in the mainstream of the river. Hence under favourable external conditions juveniles actively migrate into the sea.

Characteristic Features of Reproduction and Development of Masou.

The distribution of masou is limited to the southwestern part of the range of the Pacific salmons. The species includes both the migratory and landlocked form. Spawning populations in the rivers of Sakhalin are represented by three-year-olds with a small number of four-year-olds; rarely one finds five-year-olds. A considerable proportion of males matures at one year of age and such dwarf individuals spawn a second time.

The Sakhalin masou is small and of low fecundity; the average 252
length of females is less than 50 cm, average fecundity 1,700 - 2,000 eggs. The males are mainly smaller than the females. In the rivers of the southern Kuriles and in some rivers of Kamchatka the reproducing fish have similar qualities. Large fish of high fecundity reproduce in the Amur, in the rivers of Primor'e, of the Korean Peninsula and Hokkaido. In Primor'e the average size of females reaches 60 cm, and fecundity 4,000 eggs. The hump of the mature males is more distinct. Many individuals among the masou of Primor'e live a year longer than those of Sakhalin.

In the southern part of the range is distributed the landlocked form, the female of which matures at the age 3 - 6 years, is small and deposits from 50 - 400 eggs. In some lakes the landlocked masou reaches the length of 50 cm.

The run into rivers begins after the break-up of the ice cover, at early stages of maturity. The spawners move slowly into the upper reaches of the rivers. Spawning in the Sakhalin continues from the second half of July to the beginning of September, mainly in August. Masou moves into the southern rivers of Primor'e and some rivers of Hokkaido at a later date and spawns there in September-October. Mass spawning grounds of masou occur in the upper reaches of mountain rivers, as well as in small tributaries, where places suitable for reproduction are scarce; spawning redds are distributed far apart. This explains why the populations are relatively small.

Spawning takes place in shallow water with a current velocity of 40 - 60 cm/sec, in some places over 100 cm/sec. Spawning females usually are accompanied by one migratory male and some dwarf males. Eggs are deposited in two, less often three batches and are buried at a depth of 15 - 25 cm.

In river spawning grounds, in water taken from the redds, oxygen content was from 7.5 to 11.5 mg/l (71.0 - 104.7% saturation), and in redds situated near the point of emergence of ground water 7.4 - 9.4 mg/l (65.5 - 87.1% saturation). The value for pH fluctuated from 6.0 to 6.7. During the period of incubation of eggs deposited at the beginning of the spawning season, temperature in the nests varies within the limits 17.2 - 8.4° and incubation is completed in 33 - 40 days. Under farm conditions masou normally develops at water oxygen content 2.5 - 7.0 mg/l (35 - 70% saturation) and current velocity in the apparatus about 2 - 2.5 cm/sec. In experiments with eggs of landlocked masou better results were obtained at temperatures from 7 to 11°.

In correspondence with rapid current on spawning grounds, males of masou produce much sperm with a high concentration of spermatozoids. On the average, more than 300 million spermatozoids occur in ejaculate per 1 g of live weight, which is more than in other species of Pacific salmon. The weight of the eggs in Sakhalin masou varies from 126 to 226 mg ($M=174.79 \pm 3.22$). Hydrated eggs have a diameter of 6 - 8 mm. The egg membrane is relatively thin, 32 - 50 mk. Eggs are rich in astaxanthin and have an intensely orange-red colour with a pinkish tinge.

Because the egg cells contain a large amount of yolk, the process 253
of epiboly in masou takes longer than in sockeye and coho and is completed after the formation of 52 - 57 somites. Pulsation of the cardiac tube and contraction of myotomes were observed at the stage of 43 - 44 somites (earlier than in pink, chum and chinook). Circulation is established after the formation of 52 - 55 somites, earlier than in most related species. Embryonic organs of respiration form rapidly and reach a high level of development. Pectoral fins and buccal and branchial apparatus become mobile earlier than those of the pink (about 340 degree-days), and the gill filaments are also laid down earlier than in that species. These characters are evidence of the adaptation of masou to development under the condition of relatively low oxygen content. In comparison with other species of salmon, pigment in the eyes of masou appears earlier (about 200 degree-days), and the body of the embryo is more intensely pigmented.

The embryos of masou hatch at a lower level of differentiation by comparison with that of sockeye and pink. The period of endogenous feeding of hatched embryos, on the other hand, is longer.

The body of the larva of masou is as if encircled by transverse dark belts. The preanal fin fold grows and is retained almost as long as in the coho. After emergence from the nests, the larvae live in groups for some time, not infrequently joining schools of chum. They feed mainly on benthos.

The juveniles have high bodies. Their unpaired fins are high, with elongated first branching rays and characteristic colouration. Pectoral fins are long. Transverse bands on the sides of the body change into large, black, oval spots. Above and below these spots, with time, appear rows of smaller spots. Juveniles lead a solitary life, occupy individual territories and defend them aggressively. They dart from there after food objects carried past by the water flow. The diet is extremely varied; in the summer, food is dominated by terrestrial and aerial invertebrates, carried into river by wind and rain.

Having reached a length of 45 - 50 mm, juveniles from the littoral shallows move to deeper parts of the rivers with a rapid current. Spotty patterns on their bodies continue to grow more complicated. Along the middle line appears a narrow pinkish band. The height of the body increases. Unpaired fins become relatively shorter with age. In the autumn, juveniles migrate to deep, quiet parts of rivers and pools, where they gather in schools and spend the winter.

Large juveniles eat eggs of other salmon species, falling out of the nests, and destroy some young pink and chum. Special investigations have shown that masou does not cause great harm to stocks of other salmon species. Its juveniles feed mainly on food poorly utilized by other commercial fishes, and for this reason masou is a valuable component in the fish biocoenoses of the mountain rivers and lakes.

A small proportion of the juvenile masou migrate into the sea as young-of-the-year, the overwhelming majority spends one winter in the rivers, some two winters. In the rivers of Primor'e three winter seasons are observed. Descent from the rivers into the sea continues from April-May to September-October. Prolonged life cycle in fresh water, the presence of a landlocked form, second maturation of dwarf males, and also second maturation of some females reared in ponds, all suggest philogenetical old age of the species.

COMPARITIVE STUDY OF BIOLOGY OF REPRODUCTION AND SPECIAL FEATURES OF DEVELOPMENT OF THE PACIFIC SALMON SPECIES

CHARACTERISTIC FEATURES OF THE REPRODUCTIVE ECOLOGY OF SALMON.

The author of the theory of ecological groups of fishes wrote: "Adaptations of fishes to conditions of reproduction and development reflect not only significant ecological points of the embryonic period, but also significant points of all other periods of life. They imprint a seal on the biology of adult fishes, determine the character of migration, possibility of habitat changes and limits of distribution of fishes" (Kryzhanovskii, 1949, p.237). Study on the salmon provides abundant material which convinces one of a deep sense of correctness of this general statement.

Salmon belong to lithophilic fish that bury their eggs. In the gravel and sand ground the eggs can develop only in the presence of constant water change. In view of this the spawners select for egg deposition, localities with ground which is well washed by water. During the spawning, the ground is cleaned of silt and fine sand and becomes, to a certain extent, stratified, so that the permeability of the redds is improved. These fish are also characterized by the fact that their eggs are kept in complete darkness and are subject to mechanical influences caused by gravel and sand. Development in the nests is prolonged, and larvae reach a high level of differentiation, which increases their chances of survival after the emergence from the nest. High survival rate of the buried eggs allowed the fish of this ecological group to go along the path of lowering fecundity and increasing the size of the eggs, i.e. securing large stores of nutrient substances for their embryos, without which prolonged utilization of protective features of the nests would be unthinkable. Of significance is the fact that eggs and larvae in the ground experience less influence of seasonal and daily fluctuations in temperature, which are considerable in the waters of the middle and upper latitudes. This allowed the salmon and fishes ecologically close to it to colonize waters of different climatic zones. These fish cannot, however, reproduce in the sea.

Depending on the climate, type of spawning waters and localities selected, abiotic conditions of development fluctuate within a wide range. Since the abundance and density of the spawning populations, dynamic properties of the spawners and fecundity of fish vary, the spawning substrate 256 in the process of oviposition is cleaned in a different manner, the eggs are deposited at different depths and the density of their distribution is also different. Moreover, the numbers of fish dying and decomposing after spawning affects the hydrochemical regime and food base of the spawning areas. All this creates great variability in the conditions of reproduction and development, wide possibilities of adaptive radiation of lithophilic fish which bury their eggs. It also becomes manifest in the characteristic features of the ecology of the species and intraspecific forms.

A selective attitude of some Pacific salmon species towards their spawning habitats was noted long ago by Krasheninnikov (1755). Since that time many similar observations have been made. To this day, however, one encounters overestimation of the similarities between the spawning grounds of various species and particularly often with insufficient emphasis on the special features of ecology of intraspecific groups. This important problem is worth reviewing in detail.

Comparison of the ecology of various species draws attention to the fact that only generative-limnophilous sockeye reproduces in typical lakes of the Pacific salmon species. The juveniles of sockeye live in schools. In the lake they find a sufficiently stable food base in the form of plankton and they stay there for a long time. The migratory form, reproducing in the lakes, is distinguished by the most prolonged freshwater life cycle and is trophically closely linked with the fresh water. The landlocked sockeye, on the other hand, exists completely at the expense of the food resources of fresh water habitats. Considerably different from these forms is the generative-rheophilous sockeye, which colonizes stream and river spawning grounds with slow current. The food resources of the running water habitats are poorer, the juveniles that live in them feed on more varied food, particularly benthos, and are forced to abandon their spawning grounds early. If these young fish do not find lakes or limnocrenes which are rich in food, they move to the sea while still small and are subjected to extensive elimination. High mortality of the young fish is compensated for by higher fecundity. These ecotypes reflect main directions of the intraspecific evolution of sockeye.

Sockeye reproduces in places of emergence of ground waters and developes in low oxygen content. Because of the differences in the thermal regime of these water, affecting the rate of development and time suitable for spawning, formation of seasonal races is inevitable. As in other salmon species, they are subdivided into local stocks. Krokhin (1960) showed clear differences in the quality of water washing individual spawning grounds of summer sockeye even in a small lake, and attributed them to the geological variability in the geological structure of the banks. This qualitative difference in water of different spawning localities, whose narrow localization is related to the distinctive distribution of the pools of 257 ground waters, can be seen as one of the bases for accurate return of the spawners to the places of their birth and of the reproductive isolation of small groups. A multiplicity of such population components, forming complicated population systems, and ecological in their nature, is typical for sockeye. These characteristic features of specific and population structure of sockeye long ago attracted attention of investigators. With the aid of various methods, morphological, biological and genetic characteristics of groups of different levels and their ties with their spawning grounds and localities have been convincingly demonstrated (Gilbert, 1924; Thompson, 1945; Krogius, 1949; Schaefer, 1951; Krogius and Krokhin, 1956; Hartman and Releigh, 1964; Mathisen, 1966; Foerster, 1968; Konovalov, 1972; Ricker, 1972; etc.).

The chum occupies a different ecological niche and diverged in other directions. This species uses spawning grounds which are fed by both ground and subsoil (underflow) waters. Within the limits of the basin of Paleo amur, chum reproduces in the autumn and winter at places of the emergence of ground waters. The autumn-spawning form develops in low oxygen saturation of water, high carbonic acid tension, and weakly acidic environment. The summer-spawning chum of the same region occupies river spawning grounds, washed by the subsoil (underflow) waters with small admixture of ground water drawn from near the surface of the deposits. Such waters, as a rule, are more saturated with oxygen, but the water and gaseous regime of the spawning grounds of the summer chum is less stable. Not infrequent are cases of mass drying and freezing of nests, causing catastrophic decline of stocks. For a long time the abundance of the summer chum in the Amur has been in a depressed condition, and yet its spawning grounds are not colonized by the autumn chum, which supports the view that these two forms are ecologically clearly specialized.

In contrast with the Amur chum, the Kamchatkan summer-spawning chum reproduces in streams, limnocrenes and rivers at places of the emergence of ground waters. Consequently, with regards to the water supply of the redds and conditions of development it corresponds not to the summer but to the autumn Amur chum. Obviously, the Kamchatkan and the Amur summer-spawning forms of chum are not identical ecologically, morphologically and biologically; they should, therefore, be separated taxonomically (Smirnov, 1973). In Kamchatka there exists also autumn-spawning chum, regarded as a separate race (Abramov, 1948). Its spawning grounds are different from those of the autumn chum in the Amur. The chum of the river Anadyr is distinguishable by a number of morphological characters, the differences apparently reaching the level of the subspecific rank (Kulikova, 1971, 1972).

Within its large range, chum reproduces in basins, which were formed in remote epochs and which differ from one another in hydrological regime and composition of fauna. The stocks feed also in different regions. This could not but become reflected in morphological and biological characters of the so-called seasonal races of the different regions and should be kept in mind in research and practical activities. 258

The study of the autumn and summer chum in the Amur revealed qualitative variability of local stocks (Birman, 1951, 1956; Svetovidova, 1961). We shall quote one example. The autumn-spawning chum migrates into the Amur at low maturity and travels 2,000 km and more on its way to the spawning grounds. This fact affects the quality of spawners and the biology of the juveniles, which reach considerable size in the river. On the other hand, chum moves into the smaller rivers of the islands while almost mature. It spawns, beginning with the first kilometers away from the sea, and its juveniles leave the river in mass before the development of scales. The trophic links of this chum with the freshwater habitat are much weaker than those of the Amur chum. Due to the ecological plasticity the species came to occupy waters of different types and within them different localities. It has become widespread and has reached high abundance.

The pink reproduces mainly in the summer on river spawning grounds, the bottom of which is washed by subsoil (underflow) water. This type of spawning grounds remains uniform in regime over large distances and accomodates very abundant populations. Several runs of spawners of different character occur in the course of a spawning season. In the autumn this species reproduces near the points of emergence of ground waters (in some places in the streams), as well as in regions with a mild climate. The autumn spawning race is less abundant and the conditions of its reproduction are more stable.

In rivers with steep slopes and with clean stone-sand bottoms, redds are well aerated and the eggs of the pink develop in the presence of higher oxygen content, when compared with other species. However, within the limits of the huge area hydrological and gaseous regimes of the rivers and the climate are not uniform, and the conditions of development vary. A study of the summer-spawning pink in different regions resulted in establishment of groups reproducing in large rivers or groups of rivers (Pravdin, 1932, 1940; Kaganovskii, 1949; Dvinin, 1952; Enyutina, 1954, 1972; Volovik, 1967b).

This species is characterised by the numerous groups of nests and high density of filling of the spawning grounds by spawners. During reproduction they clean continuous large spaces. This ensures good aeration of the deposited eggs. On the other hand, cleaning of spawning substrate impoverishes even more the scanty benthic fauna of the mountain rivers. Feeding of numerous offspring under such conditions is impossible and juvenile pink leave the rivers, as a rule, before they change to active feeding. Thus, the species exists practically exclusively at the expense of the food resources of the seas and the ocean.

The riverbed spawning grounds of mountain rivers are systematically influenced by strong freshets, which change their topography. The adaptation to so changing a situation is the pink's slight attachment to the "native home". Insufficiently accurate homing of the pink has the same adaptive 259
importance as the strong homing of the sockeye.

Not infrequently observed is the closeness of the spawning grounds of the pink and those of the summer chum. Special studies revealed their characteristic features. The conditions of development of the pink are more stable, its nests are better aerated. It has been shown that due to selection of different places these species of salmon are not in conflict due to their spawning areas (Nikol'skii, 1952, 1954a; Vasil'ev and Yurovitskii, 1954; Soin, 1954; Vasil'ev, 1958; Strekalova, 1963).

The chinook of Kamchatka reproduces in the main beds of rivers and in secondary beds. It occupies places with rapid current and a coarse stone solid bottom. To maintain positions and to build nests in those places is beyond the possibilities of less strong salmon species. Spawning redds are supplied with subsoid water with some admixture of superficial groundwater. In the autumn they cool rapidly, therefore the reproduction of the Kamchatkan chinook is restricted to summer. In the river Kamchatka occur also shallow water spawning grounds with fairly friable ground (Vronskii, 1972). The food base in the region of the spawning grounds is limited. For this reason the juveniles disperse throughout the river soon after their emergence from the nests. They occupy individual territories and defend them. Migration to the sea follows after one or two winter seasons.

In the rivers of North America, in addition to the similar summer-spawning form, occupying northern regions, there lives also chinook with autumn and winter spawning. These fish reproduce at the places of the emergence of ground water which preserve spawning temperatures for a long time. From the southern rivers a large proportion or even all juveniles of the autumn-spawning chinook migrate during their first summer. The characters of races are genetically fixed (Rich and Holmes, 1929; Ricker, 1972).

Coho spawns in various waters, exclusive of typical lakes. It is distinguished by a late and staggered run and by reproduction which continues deep into winter. The possibility of spawning during the cold time of the year, as in related species, is associated with building of nests near the places of emergence of ground waters. Two peaks of the run are observed with spawning in different seasons, its places being separated from one another, but so far no morphological differences have been found between these spawners. It has been observed that coho prefers littoral places in the rivers with rapid current, but it spawns also in quiet, silted places. In the nests on river spawning grounds one observes both high and fairly low content of oxygen. The water washing eggs on the stream spawning grounds is usually poor in oxygen. Sometimes coho reproduces near sockeye, chum and chinook. With these facts in view and having to judge the interspecific relationships, one must take into account that the microhabitats and the regime of the nests of different species differ from one another in some features (Krokhin and Krogius, 1937b; Burner, 1951; personal observations). Juvenile coho,
like the young stages of chinook and masou, soon after emerging from the 260
ground loses its tendency to formation of schools, disperses throughout the habitat and occupies individual territories. Large juveniles go to feed in lakes. The food of the young fish is very varied. Of great importance in the diet are aerial insects. Before the descent to the sea, schools are formed. The populations of coho contain fairly many dwarf males. In some lakes a landlocked form has developed.

Masou is distinguished from related species by reproduction in the sources of mountain rivers and in small tributaries, where places suitable for spawning are scarce. Nests are built in shallow water with rapid current and are spread wide apart. This, as well as the poverty of the spawning grounds as regards food, are the reasons why the populations are not abundant. There exist summer- and autumn-spawning forms. Their spawning and feeding grounds are separate from one another. They differ from each other in age composition of spawning populations, the size of spawners, fecundity, type of prespawning changes and other features. Several local stocks have been identified. In the south of the range is situated the landlocked form. In this species, a particularly large proportion of males mature at an early age, as dwarfs, and this affects the sex ratio of the migrating populations and the composition of nest groupings. Juveniles occupy individual territories, eat great numbers of most diverse invertebrates which fall into the river from the land, from the bank vegetation and from the air. Masou in the rivers to a great extent exists at the expense of the organisms which reproduce outside its aquatic habitat.

Comparison of the living conditions of salmon species bears out the specific nature of the places of reproduction and feeding, characteristic not only of each species but also to intraspecific groups of various ranks. In connection with this it is worthwhile to stress the deep sense of the view of those physiological ecologists, who believe that "specificity of the environment is determined by the mechanisms of behaviour of the animal which limit its range of conditions much more narrowly than that within which the animal is capable of surviving" (Biment, 1964, p.92).

When discussing the problem of the selectivity of the habitats and species interrelationships during the time of reproduction, it would be

useful to mention even briefly, the hybrids of the Pacific salmon species. Both our studies and those of other authors revealed a high proportion of fertilization of the eggs in different crossing variants. Consequently, the physiological barrier, which would prevent the union of the reproductive cells of various species, is absent. Many hybrids develop successfully in the first generation and reach sexual maturity; the return of the hybrids from the sea into their native rivers has been demonstrated (Oshima, 1934; Foerster, 1935, 1968; Andreeva, 1953, 1954; Inaba, 1953; Smirnov, 1953a, 1954a, 1969; Kamyshnaya, 1963; Krykhtin, 1962; Ivankov, 1973; etc.). Taking into account high efficiency of contact between eggs and sperms of different species, abundance of populations, partial coincidence between the period of maturation and observed close proximity between spawning grounds of different Pacific salmon species, 261
one could expect natural hybridization of large proportions and widespread occurrence of hybrids. However, the natural hybrids of the Pacific salmon species occur only rarely. This fact indirectly confirms reproductive segregation of the species, at the basis of which might lie specificity in requirements as regards conditions of reproduction.

RELATIONSHIP BETWEEN SALMON AND SOME ABIOTIC FACTORS.

Seasons of Reproduction. Indications of the reproductive season contain a certain amount of information as regards the conditions of spawning and subsequent development. They allow in some measure judgement about the ecological requirements of fishes. Salmon is traditionally often included among the autumn-spawning fishes. However, all Pacific salmon species reproduce in the summer, autumn and, with the exception of the pink and masou, in the winter. Chinook has also spring spawning. Other fishes of this ecological group, for example representatives of the genera Salmo and Salvelinus, also reproduce in various seasons and the latter can be experimentally modified (Vladimirov, 1948; Savvaitova, 1969, 1973; Rounsefell, 1962; Vladykov, 1963; Dorofeeva, 1967). Only in certain races (ecotypes) and local groupings are the times of reproduction limited by narrow seasonal boundaries.

Temperature Conditions of Reproduction and Development. Taking into account the large size of the occupied range, reproduction in different seasons and considerable duration of the embryonic-larval development, one can assume a priori that the Pacific salmon is capable of reproduction and development within a broad range of temperature. This assumption is borne out by facts. We shall cite some of them. In South Sakhalin in the nests of masou was recorded a temperature of 17.2° (Kanid'ev, 1964). During hot, dry years in the rivers of Sakhalin in the region of mass spawning of the pink, water becomes heated to 24° and more. Spawning during that time ceases and resumes after the water has cooled down to 17 - 16°, but, as investigations have shown, the eggs that were deposited earlier continued to develop normally even at temperatures about 20°. Spawning at 21° has been recorded (Davidson and Hutchinson, 1938). Under stable temperature conditions, some eggs of landlocked masou developed to the hatching stage at a temperature of 16.2° (Kawajiri, 1927). When the temperature of the water was changed in the incubator during experiments in parallel with the natural seasonal cyclic changes, at initial temperatures slightly higher than 16°, the results of incubation of chinook eggs and their subsequent development were fully satisfactory (Olson and Foster, 1957). In our experiments, a short rise in water temperature in the apparatus to 19 - 20° did not disturb the development of this and of other Kamchatkan salmon species. 262

A high degree of resistance to temperature, as is known, is characteristic of the eggs of rainbow trout and has been observed in embryos of S. salar (Gorodilov, 1969, 1970). The detailed upper temperature limit for juvenile chum and pink of the American coast is 23.8 - 23.9°, and for chinook 25.1° (Brett, 1952). In the mainstream of the Amur and Ussuri rivers towards the end of the seaward migration of the pink and the chum, water was warmed up to 25°; in experiments, juveniles of the Amur chum withstood temperatures up to 28° (Levanidov, 1946a,b). During the winter, on the other hand, on the spawning grounds fed by the subsoil flow, the temperature approaches zero. Thus, during the period of embryonic-larval development of the Pacific salmon, fluctuations of temperature might approach 20°, and if the juvenile period of life is taken into account, this range becomes even wider. The above examples make it obvious that one must not place salmon among fish of embryostenothermal character (Gerbil'skii, 1965).

The regime of the nests washed by the ground water is more stable. On many spawning grounds the limits of fluctuations are 3 - 6°, at the most reaching 10°, and daily fluctuations are not infrequently limited to fractions of a degree (Kuznetsov, 1928, 1937; Disler, 1954, 1957; Levanidov, 1954b, 1968; Sano, 1959; Krokhin, 1960; personal observations).

Reports on the changes of relationship of the salmon with temperature (and other factors of external environment) during the process of development have been published by many authors (Vernidub, 1949, 1951; Cherfas, 1956; Privol'nev and Nikiforov, 1959; Gorodilov, 1969). It is interesting that, depending on the temperature in which eggs are incubated and its changes in certain stages, one observes morphological changes: there forms a different number of segments, vertebrae, scales, fin rays, etc.

(Ivanov, 1949; Lyubitskaya, 1952, 1961; Taning, 1952; Orska, 1957, 1963; Garside, 1966a,b). Very instructive is the change in adaptations at the initial stages of development. For example, subsequent embryogeny can continue at a temperature of 1.7°C, if the eggs of chinook were incubated at a temperature 5.8°C up to the formation of 128 blastomeres and of sockeye to a slightly later stage. In comparison with the eggs of chinook, those of sockeye are more resistant to lower and less resistant to high temperature. The eggs of pink withstood for a long time very low temperatures, if it developed at 5.6°C during the first month (Combs and Burrows, 1957; Combs, 1965). The work on S.salar revealed increased sensitivity of embryos to high temperature from the stage of middle blastula to pigmentation of the eyes (Gordilov, 1969). It is also known that the emergence of larvae from the redds and change to external feeding are dependent on the beginning of the warmer temperatures in the spring. Indicative is the example of the pink, the larvae of which change to external feeding in rearing ponds not earlier than the time of rise in water temperature to above 3°. As has been noted in the example of chum, there exist differences in the temperature adaptation of the juveniles in different rivers. The resistance of the eggs of salmon to low temperature 263
in the North has been observed (Lukina, 1966). The evidence available suggests that specific and population differences in relationship with temperature factors were formed in salmon in the course of history. Resistance to temperature changes during the course of ontogeny, these changes being coordinated with the seasonally cyclical changes in nature.

Gaseous Regime of Environment. Reviewing abiotic factors which determine the nature of adaptations of fish development, Kryzhanovskii

(1948, 1949) and other ecological embryologists stress the important role of oxygen regime. It should be stated that, as regards the problem of relationships between salmon and this particular factor, opposite views are expressed. Tret'yakov (1949) characterizing salmon, said that their eggs and juveniles require for development cold water, rich in oxygen. "Salmon species deposit eggs in running water very rich in oxygen", wrote Puchkov (1954, p.98). The same description of salmon is encountered in the work of Schmidt (1947). These statements reflect the view, dominant in recent times. This view took insufficient account of the characteristic features of the regime of the redds, as well as not paying enough attention to the morphological and functional characteristics of the eggs, embryos and larvae.

The results of studies in ecological embryology and of the conditions of development in nature and in incubators led to a different assessment of the adaptive characteristics of salmon. Having studied development of the autumn chum in the Amur, Disler (1954) arrived at the conclusion that at early stages, embryos are adapted to low oxygen content in water. According to Levanidov (1954b), in the basin of the river Khor this salmon develops at a concentration of oxygen within limits 2 - 7.7 mg/l (18 - 55% saturation). In individual localities, the entire development proceeds in the presence of 2 - 3 mg/l of oxygen (18 - 25% saturation). At all stages of development the intensity of respiration at an oxygen content from 2 to 8 mg/l remains constant. The autumn chum is successfully reared in the Sakhalin farms supplied with ground water, saturated with oxygen to about 50%, and sometimes even less. In the same farms not infrequently are incubated also eggs of the pink, which is more demanding as regards oxygen. One might mention here the view of the Japanese salmon husbandry expert Handa (1934), on which Sano (1959) based his opinion that it is permissible to lower the oxygen content in water to 4.5 mg/l, when working with large quantities of the eggs of chum. Krokhin (1960, p. 109) wrote the following as regards the conditions of development of sockeye: "The low quantity of oxygen and high quantity of free carbonic acid often encountered in ground water of the spawning grounds indicates that the eggs of sockeye are far less sensitive to these conditions than has commonly been supposed." High survival of the eggs of chinook in water containing 3.2 mg/l of oxygen has been observed (Gangmark and Bakkala, 1958). The embryogeny of masou takes its normal course at oxygen concentration within limits 2.7 - 7 mg/l (35 - 70% saturation) and current velocity 3 - 5 cm/sec (Krykhtin, 1962). Davison (1954, after Brown, 1957) concluded that incubation of the eggs of coho should proceed in water containing slightly more oxygen than 3 mg/l. When working with the same material in different conditions, it was observed that the duration of incubation is extended, size and weight of the juveniles diminished when oxygen content in water drops to 6.6 mg/l (Shumway et al., 1964).

It is shown that the oxygen requirements of salmon, and of other fishes, as well as the critical tension increase in the process of development, particularly after the beginning of circulation. When oxygen content is low or quantity of inhibitors of cytochromoxydase is above normal, the development is retarded, but its rate increases after improvement in aeration (Lindroth, 1942; Levanidov, 1954b; Wickett, 1954; Hamdorf, 1961; Brett, 1962; Gottwald, 1965; Yurovitskii, 1965; etc.). For example, during the first 9 days it proved possible to incubate the eggs of the chum at oxygen content dropping below 2.5 mg/l, but the requirements were increased later. At a temperature of 10°, the lethal level of the oxygen content at the beginning of incubation was 0.4 mg/l, to increase by its end to 1.0 - 1.4 mg/l. The critical value for oxygen concentration during the course of development varied within the limits from 1 to 7 mg/l (Alderdice and Wickett, 1958; Alderdice et al., 1958). At a temperature of 8 - 9°, the initial stages of cleavage of rainbow trout occur at 3.5 mg/l of oxygen, although at a retarded pace. After formation of 32 blastomeres it proceeds at a low oxygen content, but to pass gastrulation 5 - 7 mg/l of oxygen are required, and later, higher saturation (Ostroumova, 1969). Among the Pacific salmon species, the most demanding as regards oxygen is the pink. Under the conditions in the river My, at temperatures up to 9° this species develops normally in 7 - 9 mg/l of oxygen (Vasil'ev, 1959b), and in the river Lesnaya, with better aerated water, optimal oxygen content for development of the pink was determined at 8 - 13 mg/l or 70 - 90% saturation (Kanid'ev, 1967a). In the northern regions more oxygen is needed for the development of the pink than in the south (Lukina, 1966). Thus, the requirement as regards oxygen saturation of water differs in different species and among the representatives of the same species under different conditions.

In the redds and in incubators one frequently encounters fairly high tension of free carbonic acid. The facts prove that when adequate oxygen is present in water, salmon can develop also in considerable carbonic acid tension. However, in such situations, as also with the increase of concentration of other inhibitors of cytochoromoxydase, the rate of development is retarded (Levanidov, 1954b; Vinberg, 1956; Alderdice and Wickett, 1958; Basu, 1959; Brett, 1962; etc.).

The water of the redds situated in the spring has a typically weakly acid reaction; pH value in most instances fluctuated within the limits 6.2 - 6.8. On river spawning grounds the reaction of the environment within redds is usually weakly acid, neutral and, less commonly, weakly alkaline. Sensitivity of the salmon to the increase in hydrogen ion concentration increases, when oxygen saturation of water is low (Townsend and Cheyne, 1944). 265

The material accumulated indicates the wide adaptive potential of the Pacific salmon, which increases significantly due to ecotypical variability. Summing up the reports on the regime of the salmon redds, one should not forget to mention a frequently expressed view, according to which the development of salmon in nature is usually limited not by low oxygen content, but by slow percolation; it is very important that normal rate of percolation be ensured also in incubation apparatus (Krogius, 1951; Gangmark and Bakkala, 1958; Smirnov, 1954a, 1963b; Krokhin, 1960; Krykhtin, 1962; McNeil, 1962, 1966; Shumway et al., 1964; Levanidov, 1954b).

SPECIAL FEATURES OF FUNCTIONAL MORPHOLOGY OF SALMON.

Close relationships to one another and membership in the same ecological group resulted in close similarity between the fish studied. At the same time we noted fairly distinctly expressed specificity of abiotic and biotic conditions of spawning of different salmon species, as well as of the regime of their redds and mode of life of their young, which change in the process of ontogeny. Since the process of adaptive radiation and colonization of different environment is associated with specialization in functional morphology, it becomes obvious that it is of great importance to gain knowledge of the type of systems of **species** adaptations in all the multiplicity of their manifestations.

Production of Sperm and Length of its Retention of Fertility.

Under conditions of our experiments, males produced sperms from half a month (sockeye) to a month (chum). In isolated males of the chum and coho, normal sperm could be obtained more than 10 times and its total volume reached, correspondingly, more than 130 and 190 ml, while that of the sockeye was less than 50 ml (Table 18). Prolonged production of sperm is related to the deposition of eggs in small batches and with partici- ation of the males in spawning with several females. On impounded parts of the spawning ground of the sockeye, the eggs were successfully fertilised also when up to 15 females were served by one male (Mathisen, 1962; Matisen, 1963). In nature, however, a different picture is obser- ved; several males swim around each spawning female. Their large numbers increase probability that eggs will be fertilised (Soldatov, 1912; Shuman, 1950). Attention is drawn to ecological relationships. Typical for the sockeye is the large number of males in the nest groupings, high concentration of spawners and low rate of water flow on the spawning grounds. On the other hand, masou spawns in rapid current, the nests are 266 widely scattered and around the female swims often one migratory and several dwarf males. Its males produced a lot of thick sperm, while the sockeye produces a little sperm, which is liquid. In the ejaculate of the sockeye there are twice fewer spermatozoids than in masou and chum, six times fewer per each gram of live weight of the male than in masou (Table 18). The example of the pink is interesting. It spawns in currents more rapid than the chum, but produces fewer spermatozoids. As is the case with the

Table 18
Some Data on the Reproduction of Sperm by Pacific Salmon Species (after Smirnov, 1963,a).

Index	Chum	Pink	Masou	Sockeye	Coho
Longest time of sperm production under experimental conditions, days	26	14	19	16	19
Greatest number of sperm batches obtained from one male	11	6	9	8	14
Average volume of ejaculate, ml	9.2	6.5	12.8	9.9	19.9
Greatest quantity of sperm, obtained from one male during experiment, ml	133.6	68.8	81.5	41.8	192.8
Number of Spermatozoids in 1 mm³ of sperm, millions					
average	24.12	17.94	21.23	10.56	17.34
greatest	32.40	29.04	36.80	18.22	32.75
Number of spermatoziods in ejaculate, billions (round figure)	220	117	271	104	346
Number of Spermatozoids in ejaculate per 1 g of live weight of male, millions (round figure)	93	63	307	47	115

sockeye, this is compensated for by the larger number of males in nest groupings and by the high density of filling of the spawning grounds. Thus, for successful fertilization of the eggs, both abundant ejaculation of sperm and high concentration of spawners are important.

Spermatozoids survive in water for different lengths of time: in salmonid and cyprinid fishes this period is tens of seconds or several minutes, in acipenserids it is several hours, in herring and some other marine fishes it is measured in days (Ginzburg, 1968). No great differences were found in the species examined, but none the less they exist. In our experiments, 20 seconds after dilution of chum sperm with water 75 and 90% of eggs were fertilized in different batches; the corresponding value for masou was up to 90%, for pink 60 and 70%, coho about 50% and sockeye only about 20% of eggs. After sixty seconds in water, the chum sperm fertilised up to 70% of eggs, masou 60, pink about 30% and coho isolated eggs, while the sperm of the sockeye completely lost its fertility. In individual experiments the spermatozoids of pink and masou fertilized isolated eggs after 2.5 - 3 minutes in water. The sperm of chinook, diluted in water, retains fertility up to 5 minutes (Rutter, 1904). In some experiments of Foerster (1968) some eggs of sockeye were fertilised after spermatozoids were kept in water, at temperatures changing from 2 to 8^{o}, for one and even for 8 hours. In other experiments diluted sperm ceased to fertilise eggs already after several minutes. What are the reasons for such fluctuating results is not altogether clear. Since the temperature in experiments dropped to 2^{o}, one could suppose that cooling exerted a preserving influence. 267

Special Features of the Eggs of Pacific Salmon. Among the teleosts of our fauna, Pacific salmon species produce the largest eggs. This fact was stressed by Gunther (1866) and used as a taxonomic character in the establishment of the separate genus *Oncorhynchus*, the members of which were previously included in the genus *Salmo*. Significant specific differences must, however, be noted. The eggs of chinook, chum and masou are, indeed, distinguished by their large size. In other species they are smaller, while sockeye in this repect stands together with the members of the genus *Salmo*.

The eggs of the salmon are oligoplasmatic. The quantity of cytoplasm slightly varies from species to species. The differences in the size of the eggs are determined by the amount of deutoplasm. This leads to significant differences in the ratio of cytoplasm and yolk. For example, in the eggs about 6 mm in diameter, occurring in sockeye, coho and pink, there is about 400 - 500 times more yolk than cytoplasm, and in the eggs 8 mm in diameter, characteristic to chum and chinook, this figure rises to 1,000.

The obvious advantage of deposition of eggs with abundant store of nutrient substances, as has already been stated, is in the fact that the offspring are able to utilise for a long time the protective cover of the redds, to reach in them large size and a high level of differentiation and activity. Thanks to all these, the chances of the larvae of escaping from predators are subsequently enhanced. Moreover, large fish larvae have relatively smaller food requirements and greater swimming energy. As a result the area searched for food can be extended (Marshall, 1963). This is particularly favourable under the conditions of poor food supply in spawning and rearing areas.

A positive relationship has been observed between the length of the females and the size of eggs in the autumn chum in the Amur (Birman, 1952). A general tendency to larger eggs with increase in the size of salmon has been reported (Rounsefell, 1957). However, the picture is fairly variegated. The smallest eggs among the Pacific salmon species is produced by sockeye and coho, which exceed in size the pink and the Sakhalin 268
masou. The eggs of the pink and smallest salmon, are fairly large. A salmon average in size, the chum deposits very large eggs which are similar in size to those of chinook, the largest salmon. It should be mentioned here that the eggs of <u>Salmo solar</u>, which reach great length and weight, are relatively small.

There are literature reports on increase in size of eggs with displacement of fish to the north (Rass, 1947, 1953; Marshall, 1953). On comparison between species and intraspecific forms, we encounter facts of a different nature. Masou, for example, occupies the southern part of the range of the genus, but produces much larger eggs than sockeye and coho, both reproducing farther north. The autumn chum of the South Sakhalin river Naiba is distinguished by large size of its eggs. Chinook of the Kamchatkan river Paratunka produces eggs weighing about 240 mg, while the weight of the eggs of chinook in the Klamath river, situated in the south of the species range, is one and a half times greater (Leitritz) 1960). Attention is drawn to the very interesting fact that the eggs of the pink transferred from the southern rivers of Sakhalin and the South Kuriles to the northern rivers of the Barents Sea and White Sea become smaller (Persov, 1963; Galkina, 1965; Sakun, 1965; Smirnov et al., 1968). A similar fact stimulated a search for the ecological basis of the size of salmon eggs. It was logical to compare the season, the conditions of spawning and development with the size of eggs. Doing so established a fairly definite link between the size of the eggs and the thermic conditions of spawning and development (Smirnov et al., 1968). It has been found that the eggs are larger and contain more nutrient substances in salmon that spawn and develop at higher temperatures. This ensures a rapid rate of development of embryos and their increased activity as expressed in movements.

Let us review the data on the composition of eggs. The eggs of the Pacific salmon species are large and richer in food stores than those of the Atlantic salmon (Table 1). Among the representatives of the genus Oncorhynchus the eggs of the chum and masou are distinguished by large size and high content of dry substance (more than 44%); taking into account the data of Greene (1926) the same can be said about the eggs of chinook. The eggs of these species and of the pink contain more fat. In comparison with them the eggs of coho have only half the amount of fat. The eggs of the sockeye are distinguished by slightly lower protein content. A rough estimate of the of the energy resources available to the embryos was made by calculating the physiological caloric equivalents of protein and fat. The values obtained are somewhat lower than they should be, because carbohydrates, which are scarce in the eggs, were disregarded. However, they fully retain their comparative value (Table, 19). By this indicator, as well as by some others, the sockeye is near to the Atlantic salmon. All species with large stores of calorific energy in eggs, except for the autumn chum, spawn in the summer at a relatively high temperature. However, the autumn form of the chum, studied by us, and autumn-spawning chinook,

Table 19.
Data on Eggs of the Pacific Salmon Species

Index	Sockeye	Coho	Pink	Masou	Chum	Chinook
Weight of mature oocytes, mg: range	84--132	76--173	118--198	126--226	183--300	209--330*
M±m	109.20±2.02	131.80±4.45	154.85±1.85	174.79±3.22	239.25±0.19	--
variation coefficient	12.27	14.49	10.33	14.42	12.46	--
No. of females the eggs of which were weighed	44	19	75	61	64	5
Diameter of hydrated eggs, mm	5.6--6.5	5.8--7.5	5.6--7.9	6.1--8.0	6.7--8.0	7.0--9.0*
Thickness of membrane of dividing eggs, mk. range	23.0--41.8	36.3--57.0	55.4--79.8	32.4--50.1	49.4--66.5	38.0--57.
M±m	33.0±0.60	47.3±0.55	69.9±0.60	39.6±0.49	55.1±0.38	53.75±0.
variation coefficient	13.42	9.68	8.17	6.50	6.41	10.23
Average calorific value of egg, calculated from calorific equivalent of protein and fat, calories **	152	243	280	283	312	353

* Highest values from Riddle (1917) ** From Smirnov, Karyshnaya and Kalashnikova (1968); data on masou average of 2 years.

deposit eggs in places of the emergence of warm ground waters and develop for a long time at a temperature of 8 - 10^{o}. It is noteworthy that on the spawning grounds of Lake Teploe in the basin of the Amur the water is cooler (about 3 - 5^{o}) and the chum that spawns there produces smaller eggs.

The question arises, does the fact that the sockeye deposits small eggs, poor in food stores, and yet spawns in August during the warm time of the year, not contradict our supposition? It would appear that it does not. The fact is that this fish builds its nests in places of emergence of ground waters, retaining low temperatures in the summer. By its size and food stores the eggs of coho are similar to those of the sockeye. This species spawns in the autumn and winter. Salmon from the river Kola and the Baltic salmon spawn late and develop also at low temperatures (Novikov, 1953). Since some species and races of salmon spawn in places of emergence of ground waters, the temperature of which is not dependent on the latitude of the locality, there is no geographic parallelism in the changes in size of the eggs of these fishes.

The eggs of the salmon have bright colour, caused by high concentration of the carotenoid pigments. The eggs and muscles of the species of the genus Oncorhynchus contain the only carotenoid xanthophyll, astaxanthin. The representatives of the genus Salmo possess astaxanthin as well as lutein and zeaxanthin (Glover, Morton and Rosen, 1952; Gudvin, 1953; Kanemitsu and Aoe, 1958; Yarzhombek, 1964, 1970, 1972; Yarzhombek and Grachev, 1964; Borovik, 1966; Iriskina, 1968; Prikhodskaya, 1972). Carotenoids are extremely widely distributed in various organs and tissues of plants and animals. A large number of these pigments has been identified and various functions were attributed to them (Dunaevskii, 1947; Budnitskaya, 1952; Lebedev, 1953; Gudvin, 1954; Balakhovskii and Drozdova, 1956; Eremeev, 1957; Yarzhombek, 1970; Karnaukhov, 1971, 1973).

Since salmon develops under the cover of the ground, the colour of the egg and embryos cannot have cryptic or signal importance. Moreover, being concentrated in the internal organs, carotenoids cannot fulfill the photoreceptive or photosynthetic function which is being ascribed to them. Views were expressed that carotenoid takes part in the process of fertilisation, but they were not corroborated (Gudvin, 1954). At the same time it is difficult to agree to the rejection of the functional importance of these biologically active substances during the period of embryonic development of salmon and other fishes, or to the belief that the pigment of eggs is important primarily for the formation of chromatophores in future juveniles (Steven, 1948). Wide distribution of carotenoids in nature and indications of their varied role in the organism leads to the suggestion, as correctly observed by Gudvin (1954), that some common factor or property "by means of which all these functions are linked together" could be assumed to exist.

In search for an answer to the question on the significance of 271
differences in colour of eggs and embryos of fishes, we turned our attention to the relationship between the intensity of pigmentation and oxygen conditions in the environment. A comparative ecological embryological study showed that the eggs, integument and some internal organs of the embryo are more intensively pigmented in phytophilic, ostracophilic, oviparous and some viviparous species, as well as in fishes which hide their eggs under stones, shells and in the ground (Smirnov, 1945, 1950;

Kryzhanovskii, 1948, 1949). The representatives of these ecological groups develop in the environment poor in oxygen. In contrast, species which develop in better aerated water (pelagophilic, psammophilic), have poorly pigmented eggs and embryos. The following parallelism is observed: in species with intensively coloured eggs and embryos the embryonic organs of respiration develop earlier and more strongly, while in cases of poor pigmentation they are formed later and the reduction of the vascular system is observed. The establishment of ecologo-morphological relationships and the currently held views on the possible participation of carotenoids in oxydation-reduction processes allow us to postulate that carotenoid pigments augment functionally the vascular respiratory system of fishes. The concept of the ecological reasons for the carotenoid pigmentation extended to an explanation of the differences in coloration of adult fishes, including salmon during the nuptial season (Smirnov, 1950, 1954a, 1959b).

The relationship between the intensity of pigmentation of eggs and embryos, as well as the development of the embryonic and larval organs of respiration, on the one hand, with the conditions of aeration of environment on the other, was subsequently corroborated by the ecologo-embryological study of fishes of the families Gasterosteidae, Cottidae, Cottocomephoridae, Clupeidae, Percoidei and salmon of the genus Salmo and Oncorhynchus (Kryzhanovskii et al., 1953; Smirnov, 1953b, 1954a, 1955a, 1958, 1959b, 1960a, 1960b, 1964a, 1964b; Soin, 1954, 1956, 1964, 1968; Kryzhanovskii, 1956).

Comparison of pigmentation of the eggs of Pacific salmon, and development of embryonic organs of respiration with the conditions of aeration of the nests give a sufficiently clear picture. Thus, the eggs of the pink are distinguished by the pale orange colour, a small quantity of astaxanthin; embryonic organs of respiration are in this fish developed less than in related species and it develops at a high oxygen saturation of water. The eggs of the chum are bright-orange, contain more carotenoids, its embryonic organs of respiration are developed more strongly than those of the pink. Embryogeny of the pink takes place under conditions of lesser oxygen content. In other species the eggs are more intensively coloured and on the yolk sac there develops a particularly dense vascular network. The eggs of the sockeye are the richest in astaxanthin (Yarzhombek, 1970), the vascular network of its embryos develops rapidly and strongly, the spawning of this species is restricted to places of the emergence of ground waters, which are poor in oxygen (Krokhin, 1960).

Worthy of note are the data of physiological experiments, in which 272
was observed an increased resistance to high temperature of the more intensely coloured eggs of the Svir whitefish, when compared with the less strongly pigmented eggs. In the same eggs in some experiments was observed higher oxydative exchange, which was due to the presence in them of vitamin A (Barancheev and Razumovskii, 1937). The higher resistance of the intensely pigmented eggs to unfavourable external factors was observed in salmon and other species (Hubs and Stevenhagen, 1958; Loginova, 1966, 1969; Shvarevitch and Sakhnenko, 1968; Yarzhombek, 1970; Prikhodskaya, 1972). It is interesting that during incubation of rainbow trout eggs in water with low oxygen content a straight relationship was observed between the quantity of carotenoids in the eggs and the intensity of respiration of the embryos. No such correlation was found when water was normally saturated with oxygen

(Brovik, 1966). It has been reported that carotenoids have a positive influence on growth, development and survival of embryos of birds (Ermeev, 1957).

The problem of the relation of carotenoids to the oxydative metabolism has been worked on since the publications of Merezhkovskii (1883) and Arnould (1886, after Budnitskaya, 1952). The known hypothesis of Bakh (1912) that these compounds act as oxygenases in fermentative oxydation has been corroborated in model experiments (Borodina, 1939). It has been demonstrated that carotenoids and compounds similar to them are able to activat molecular and peroxide oxygen; it is established that one cannot understand the role of carotenoids in the activities of an organism without taking into account their participation in oxydative processes (Balakhovskii and Kuznetsova, 1955; Balakhovskii and Drozdova, 1956). There are reports on the participation of these substances in the oxydation-reduction reactions and their important role in adaptation of plants to unfavourable living conditions (Lebedev, 1953). Investigation is being made into the fuction of carotenoids in the mechanism of transfer of oxygen in the process of photosyntheses (Saakov, 1964; Saposhnikov et al., 1964). The concept of the role of carotenoids in the oxydative metabolism is based on the presence of a large quantity of unsaturated conjugate double bonds and of good electron donor and electron acceptor properties of these substances. As the result of the study of materials, obtained by the study of carotenoids in nervous and muscle tissue and from literature data, Karnaukhov (1971, 1973) arrived at the conclusion that they are probably involved together with haemoproteins in the processes of intracellular deposition of oxygen, allowing compensation for the slow rate of its penetration under conditions of hypoxia.

Evaluating the importance of carotenoids in the adaptations of salmon associated with the processes of reproduction and development, one must not disregard their role in the formation of the nuptial livery. One must have in view here not only assumption of bright colouration and optical effect, but also probable participation of these substances in oxydative metabolism. It has also been reported that carotenoids and substances close to them can retard keratinisation of integument, favour the establishment of epithelium, in tussue cultures modify integument tissues to make it resemble mucous epithelium, increase the organism's resistence to infection, etc. (Balakhovskii and Kuznetsova, 1955; etc.). In such many-sided influences of carotenoids one can see their important role played in structural modification of the skin of salmon in the process of maturation. These modifications favour intensification of the skin respiration and allow the salmon during spawning to stay in turbid, oxygen-poor water and carry out their work of clearing the ground and building their redds (Smirnov, 1959b). 273

As has been said, the functions of the carotenoids in the process of development and metabolism of organisms, fishes included, are varied. One can note with satisfaction that this complicated problem attracted the attention not only of embryologists but also physiologists, biochemists and biophysicists. This allows us to hope that it will be successfully solved in the future.

Among other special features of eggs, attention is drawn to differences in the structure and properties of membranes which play the part of an intermediary between the embryo and the external environment, as well as having a defensive function. After deposition, the surface of the eggs for a short time acquires slight adhesiveness. The external homogeneous layer defends the egg membranes from destruction by the preteo-lytic bacteria and, probably, from the action of the enzyme excreted during the time of hatching from the neighbouring eggs (Bell et al., 1969). The eggs of salmon are very strong. The developing eggs of trout and of Atlantic salmon are able to withstand pressure 3 - 3.5 kg, those of summer chum 4 - 5 kg, those of the pink 8 - 9 kg. Especially high strength of the eggs of the pink is associated with its spawning in rapid current, which increases the surface transport of the ground material, dangerous for the offspring (Nikol'skii and Soin, 1954; Soin, 1954). As can be seen in Table 19, in this species the membrances are thicker than in other species. The thickness decreases in the following order: chum, chinook, coho, masou. The thinnest membranes are those of the sockeye. The latter spawns in localities with weak current or in absence of current, and the thin membranes of sockeye eggs underline the view that there is a relationship between the thickness of membranes and the current velocity on spawning grounds. This relationship, however, is not of general character. Thus, both masou and coho spawn in rapid current, but their egg membranes are fairly thin. The fact is that the embryos of salmon can also be protected from damage due to the surface movement of ground by being deeply buried. Of course, only stronger fish are able to bury their eggs deep, such as chinook and coho. It is in these fish that we see membranes thinner than in the pink and chum. It should also be assumed that species developing in water poor in oxygen or in unstable gaseous regime cannot have particularly thick membranes. This assumption is born out by the example of the sockeye, coho and masou. On the other hand, the pink developes under the condition of higher oxygen saturation of water and for this reason was able to evolve along the path of development with particularly thick egg membranes.

The structural differences between membranes have been elucidated. The inner layer of the radiate zone of egg membranes in the chum and pink is more definite, its sturcture is more delicate, while in the sockeye it can be distinguished in histological preparations only by its intensive colour. The outer amorphous layer of membranes also shows differences. The eggs of the chinook, for example, have a whitish surface, which in reflected light gives off a distinctive pearl-like sheen. The egg membranes of the pink are opaque and in the eggs of the sockeye and masou they are more transparent than in those of other salmon species.

The eggs retain their ability to be fertilised for different lengths of time after having been placed in water. It has been reported that this period in the eggs of the chum reaches 15 - 30 minutes (K. Yamamoto, 1951). Only a few eggs under special conditions can retain their fertility for so long. In our experiments, 1 minute after being placed in water, 50% of the eggs of chum lost their fertility, 44% of those of the pink, and 15% of the masou. Almost all eggs of chum lost their fertility in 6 minutes, of pink in 7 - 8 minutes, of masou in 10 minutes. The extreme time of retention for isolated eggs was 12 - 15 minutes. These data point out the necessity for observation in salmon husbandry of the "dry method" of insemination of eggs, which would guarantee rapid contact between eggs and spermatozoids.

<u>Division into Periods of Ontogeny of Pacific Salmon and some Special Features of Individual Periods and Stages of Development.</u> Disler (1954, 1957) recognized 12 stages in the embryonic period of development of the autumn chum, a period which is prolonged in salmon. In the larval period he recognized one stage and in the juvenile period two. His division

of the ontogeny of Pacific salmon into periods was adopted by many authors (Krykhtin, 1955, 1962; Smirnov, 1958, 1963b; Vasil'ev, 1959b; Frolenko, 1966; Lukina, 1966, 1973). In this work his scheme has been accepted as a basis, with some modifications.

We accept as the beginning of the individual life the formation of the zygote. Many different changes are associated with the hatching. The embryo is freed of membranes and perivitelline fluid. It enters into direct contact with the stream, particles of ground and its relationships with the external environment are radically altered, as the result of which, the functional activity of the organs of respiration, locomotion, excretion and sensory organs also changes. In other words the entire biology is changed. For this reason we deem it correct to see the act of hatching as a border between two stages. Furthermore, in describing development, attention was drawn to the differences in the level of morphological defferentiation, at which juveniles migrate into the sea. Specific differences in the duration of the freshwater life cycle of salmon will be discussed in detail below. In this case we wish to stress 275
wide intraspecific and intra-population variability of this character. A good example is offered by the sockeye. This salmon can go to sea as larva, young-of-the-year, after one or several winters in fresh water and, finally, it can mature without going to sea. Similar examples indicate that the moment of catadromous migration is not related to the attainment of a strictly definite level of differentiation. This makes it difficult to recognize a special stage of downward migration. In connection with the division of ontogeny into periods, special features of the nuptial period of salmon's life were also reviewed. All observers are struck by the deep

prespawning changes in morphology, physiology and behaviour of the Pacific salmon, as well as the special features of ecological conditions in places of reproduction and the type of brood care. The adaptive value of some of these changes has been discovered and there is no doubt that they are of extreme importance both in the life of the individual and in the evolution of the species. The study of these changes and of the characteristic features of biology of reproduction from the point of view of the theory of stage-by-stage development led us to the conclusion that a spawning stage must be recognized as an entity (Smirnov, 1959b, 1964b, 1965; Eremeeva and Smirnov, 1965; Eremeeva, 1967). The Pacific salmon is monocyclic and its ontogeny is completed with the spawning stage. In this it is significantly different from the species of the genus Salmo, polycyclic fishes. As the result of complicated morpho-functional prespawning changes the spawners change their requirements of external environment, so that they move to appropriate parts of aquatories and deposit eggs under conditions which favour development of their offspring. By the same fact a hereditary link is established between generations and the continuation of the genus. In various species and intraspecific, ecologically distinct forms, prespawning changes and spawning occur in a specific environment. The knowledge of this specific character is necessary to develop an ecological method of maturity stimulation of spawners.

Passing to the comparative study of the details of development, it is necessary to stress the following. The results of a morpho-ecological study of the Pacific salmon and literature data convince us that each species during the different stages and periods of life, beside generalized features common to all representatives of the genus Oncorhynchus and other

fishes of the corresponding ecological group, posesses also certain specialized features. Within species there are also groups which significantly differ from one another in their reproduction ecology, the differences also being reflected in morphogenesis. A good example of modification in spawners and that of the course of development of their offspring is shown by the dwarf form of the sockeye (Smirnov, 1959a, 1964b). This fish is smaller than the anadromous form, has low fecundity and undergoes few changes before spawning. The embryos hatch from the small eggs of dwarf individuals at a much lower level of differentiation and subsequent devel- 276
opment is accelerated. Another example of deep changes in the course of ontogeny is the displacement of the maturation period in the dwarf males of masou, chinook and coho to the juvenile period of life (phenomenon of neoteny). Because of maturation at an early age, before migration to the sea, without significant change in environment, the dwarf males do not undergo considerable prespawning changes and, what is particularly remarkable, become able to participate in reproduction a second time, become polycyclic. The examples of plasticity in the process of development are far from being exhausted by the two quoted above. By pointing out some of them we wanted to underline the broad range of variability. In the comparative review below we do not propose to discuss all the variability of the specific and intraspecific variability of morphogenesis of salmon. This would result in undue expansion to the volume of this work. We will discuss only some material, which was presented in the descriptive part of this study.

Differences between Early Stages of Morphogenesis and the Process of Epiboly. Comparisons between stages of cleavage revealed differences in size, shape and position of blastomeres. In most species of the Pacific salmon blastomeres are relatively large and arrange themselves in two layers during the formation of 16 cells. In chum there is a tendency to two-layered arrangements even at the stage of 8 blastomeres (Disler, 1957). A different picture is characteristic of the sockeye. Its blastomeres have similar diameters but lie more freely and become arranged in two layers after the fifth division, at the stage of 32 blastomeres (see Fig.21E,F and Fig. 32E, 51, F, 60,D). A similar picture is observed in some representatives of the genus Salmo (Ivanov, 1937; Stefanov and Dencheva, 1964/1965; Vernidub, 1967a). These differences can be explained by the small quantity of cytoplasm, which, however, occupies the same area as in other species. This ensures formation of a sufficiently large embryo, typical to salmon.

There are also differences in the rate of morphogenesis. For example, division in sockeye proceeds more rapidly than in chinook (Combs, 1965). According to Ievleva (1951) the embryonic streak in coho and chum appears earlier than in the pink and sockeye. These differences become greater at a later stage. Ventral fins are laid down in chum 78 degree-days later than those of coho; in sockeye this difference is 198 degree-days. In the descriptive part there is a lot of material for similar comparisons. There are significant differences in the time of appearance of primary reproductive cells, laying down and differentiation of gonads. Among salmon, only the pink is characterized by protogyny. The gonads of this species form particularly rapidly, which is related to its short life cycle (Persov, 1965, 1966, 1968).

Differences in the quantity of yolk, and cytoplasm and their proportions in the eggs of salmon are reflected in the duration of the process of epiboly. Earlier than in other species, the yolk sac is covered by blastoderm in sockeye, as a rule at the stage of 23 - 26 somites. In coho the process of epiboly is completed at 29 to 33 somites, in large eggs of chinook, chum and masou only after formation of 52 - 58 somites, in pink it is sometimes delayed to the formation of 63 - 64 somites. In correspondence with these differences, other processes of development take place in situations which are not uniform. For example, blood circulation in sockeye is established much later than the completion of epiboly, while in the chum, chinook, masou and pink immediately after the disappearance of the yolk plug, and sometimes even in its presence. With the duration of the process of epiboly are associated periods of retention by the eggs of higher sensitivity to mechanical disturbances, since resistance appears after the completion of that process. The degree of sensitivity of eggs to mechanical irritation is also different. Similar stimulus causes highest mortality in the eggs of sockeye, somewhat lesser in coho, masou and lowest in the eggs of chum and pink (Smirnov, 1954b, 1955b, 1964b; Krykhtin, 1962; Ievleva, 1967). The eggs with thinner membrane are more susceptible to trauma.

Special Features of Development of the Vascular System and Embryonic Motor System. In connection with development within an environment poor in oxygen and in view of the large size of the eggs, the embryonic-larval organs of respiration reach a very high level of development in salmon. The respiratory function is fulfilled in embryos and larvae by the vascular network covering the surface of the yolk sac, those developing in the subepidermal layer of the integument on the upper surface of the head and on the trunk, as well as the mandibular and hyoid arches of the aorta, the capillaries of the paired, unpaired and caudal fins. The pseudobranchs reach a fairly high level of development. The gill filaments are laid down at the end of the incubation of the eggs. Gill respiration is established after hatching; its role increases in larvae and particularly in juveniles after the development of the scale cover. In parallel with the development in intensification of the function of the gills, the embryonic-larval organs of respiration undergo reduction.

The development of the vascular system shows specific differences and modifications associated with the special features of the regime of egg incubation. For example, in coho in the Sokolovskii incubator the heart starts pulsating at the stage of 43 - 45 somites, and in Adotymovskii at 47 - 49 somites. In the sockeye developing in river water the same condition occurred before development of 44 somites and at incubation in the stream water with lower temperature at the stage of 44 - 46 somites. In autumn chum, masou and sockeye circulation begins, as a rule, after the formation of 52 - 54 somites, but under conditions of good aeration it can be delayed for a period sufficient for the formation of another 10 somites. In the pink developing under good oxygen conditions, blood flow appears not earlier than the formation of 58 somites. In those salmon that develop under conditions of low water saturation with oxygen, blood 278
assumes intensive colour earlier, the cardinal veins are formed more rapidly, the hepatic circulation develops and the subintestinal-vitelline vascular system is replaced by the hepatic-vitelline. The network of capillaries on the yolk sac reaches greatest density by the time of hatching. The anadromous sockeye is an exception. In its eggs the embryos develope longer than in other species, and small vessels on the yolk sac begin to

undergo reduction before hatching. In our experiments the length of the capillaries per 1 mm^2 of yolk sac surface reached in the pink 6.5 mm, in autumn chum and chinook 7.5 - 8.0 mm, and in sockeye 10 mm (by the time of the hatching of sockeye this value dropped to 1.5 - 2.0 mm). These differences are shown in Fig. 67. Of great importance to the normal development of salmon is permeability of the ground. Its absence, as was described in the example of chinook can lead to anomalies in formation of the circulatory system, most extensive in the caudal region. This leads subsequently to retardation of growth and deformation of the tail section, to birth of monsters or death of the embryos.

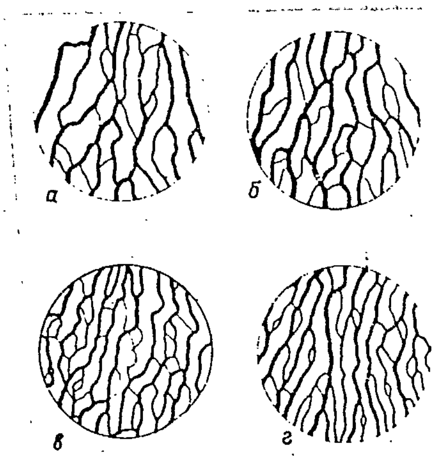


Fig. 67. Capillary network on the yolk sac at time of hatching of sockeye (a), chum (b), masou (c), and coho (d). Fields shown are of 1 mm radius, taken from the centre of the left side of the yolk sac.

The component part of the mechanism of external respiration of the fish embryos is the protoplasmic and neuro-muscular motor function. Its development in salmon has been described in sufficient detail (Disler, 1953, 1954, 1957, 1960; Wülker, 1953; Smirnov, 1958, 1960a, 1964; Reznichenko, 1959a, 1959b; Kotlyarevskaya, 1968a, 1968b). Specific differences in

motor function are well evident in the development of the function of the pectoral fins. In most species of salmon they become mobile during the course of the 9th stage of development (in chum after 215 degree-days, in sockeye 240, in masou and chinook after about 340 degree-days), but in the pink only at the end of the 10th stage of development (at 370 degree-days). It is noteworthy that with the beginning of the functioning of the pectoral fins the activity of the axial musculature becomes weaker for a considerable period. It is obvious that the functioning of the pectoral fins ensure sufficient movement of the perivitelline fluid and, as regards energy utilisation, it is more economic than the motions of the fairly large embryo. The mobility of the jaws and opercula develops later.
Functional activity of axial musculature increases again before hatching, 279
when the embryos begin to turn energetically under the membrane. Like hatching itself, this occurs in different species at different levels of differentiation. After hatching, the embryos again become quiescent for some time, while the frequency of the movements of the pectoral fins increases. Their energetic motions ensure constant change of water near respiratory surfaces. From that time onwards the importance of the gill respiration continues to increase steadily. Variability in the size of eggs, thickness of membranes, level of development of embryonic respiration organs, as well as the conditions of aeration of the nests, should be reflected in the intensity of the locomotory activity of the embryo. Unfortunately, so far no comparative studies on salmon in this respect have been made.

Some Special Features of Pigmentation of Embryos. There exist specific differences in the time, and order of appearance of chromatophores, their distribution and abundance. Chromatophores appear in masou earlier than in other species. Its first lipophores were observed at the beginning of the 9th stage of development, at embryo length about 10 mm, and melanophores at the beginning of the 10th stage. By that time, the length of embryos increased by about 3 mm. In coho the lipophores and melanophores on the head become visible at the beginning of the 10th stage, when the length of the embryos is slightly greater than 10 mm. In chinook, as in masou, the first to appear are the lipophores, but they are later, at embryo length 14 - 15 mm, while melanophores become noticeable when embryos reach a length of 16 mm. In remaining species melanophores are found first. In the chum and sockeye this takes place at the beginning of the 10th stage (at a length of about 14 and 13 mm respectively), and in the pink in the middle of the same stage. The first lipophores were observed in sockeye in the middle of stage 10, in the chum at its end, and in the pink only at the beginning of stage 11, when embryos were reaching a length of 15 - 16 mm. The embryos, larvae and juveniles of the pink are less strongly pigmented than those of other species. More rapidly and abundantly pigmented are the embryos of the chinook, coho, and particularly of masou.

In the offspring of the same female of chinook under conditions of low temperature and good aeration, first to appear were melanophores (see Fig. 42,B), while at a higher temperature and unstable gaseous regime, first to appear were lipophores, at a higher level of differentiation (Fig. 42,C). Changes in the development of pigmentation under different regimes of incubation of eggs are present also in other species.

Duration of Incubation and Level of the Development of Embryos on Hatching. Before embarking on comparisons it is necessary to note that the times of incubation in salmon are difficult to compare. This is due to the fact that depending on the conditions of development, hatching takes place at different ages, after a different number of degree-days. Moreover, in the same species, the hatching is desplaced to different levels of morpho genesis and even to different contiguous stages (Smirnov, 1959a, 1964a, 1964b; Kotlyarevskaya, 1968a, 1968b). The process of hatching it- 280
self in some species takes a relatively short time (masou, chum, chinook), while in others it is quite prolonged (pink, and particularly sockeye). Consequently, for the purpose of comparison, observations should be used made on the eggs of different species, developing under similar circumstances, which at the same time meet natural requirements of each species. Comparisons made with account being taken of these conditions (Smirnov, 1964b) showed that mass hatching began earlier in coho and masou (at 445 and 476 degree-days respectively), while the incubation of the eggs in pink and sockeye was longer than in other species (601 and 628 degree-days respectively). The level of development of embryos by the time of mass hatching rises in about the same order. Coho and masou hatch from their eggs at the beginning of differentiation of rays of the unpaired fins (see Fig. 54, B, 62,D); in chum and pink this process occurs at later stages (see Fig. 26, A,B) are distinguished by a particularly high level of development. On the other hand, the embryos hatch from the eggs of dwarf females of sockeye at a very early stage (see Fig. 26,D).

It appears that the assumption of the longer duration of incubation of eggs in early spawning salmon and contraction of incubation periods in forms with late autumn and winter spawning are in accordance with the truth. The examples of the pink and, in contrast, of coho bear out this supposition. However, the short incubation period of the summer-spawning masou cannot be understood in this light. Apparently the ecological relationships are more complex; to understand them one must take into account special features of morphogenesis and of the regime of spawning grounds. An impression is created that the hatching occurs earlier in those salmon species, whose water supply to the nests becomes poorer towards the end of incubation for one reason or another; embryos under membranes begin to experience oxygen insufficiency at earlier stages. Hatching improves conditions of metabolism and secures for the embryos the possibility to move to places which are better washed by the water. On the other hand, a prolonged incubation period could evolve under conditions of more stable water supply regime. As has been shown, this is typical to diadromous sockeye. Certain stability of water supply occurs also in the mainstream spawning grounds of pink (Nikol'skii, 1952, as well as those of the Kamchatkan chinook; as regards the duration of incubation they are on the second and third place after the sockeye.

Morphological and Biological Special Characters of Juveniles. Due to the large food stores, the embryos develop in the redds for a long time, reaching a considerable size, high level of differentiation and the ability to swim vigorously. Such juveniles after emerging from their nests are more successful in avoiding predators. Moreover, they are able to feed on relatively large invertebrates. Mainly benthic organisms serve as food for larvae. This is related to the characteristic features of the mountain and near-mountain rivers, poor in plankton.

As we have seen, all salmon can change to external feeding while still in posession of a considerable remnant of yolk. The stage of mixed feeding in these fish includes the entire larval period of life. However, in nature the time when the embryos become able to grasp and digest exogenous food often occurs much earlier than the actual change to active feeding. The reason for this might be absence of food or unfavourable external conditions such as low temperature, or poor illumination. The question arises, what are the consequences of the delay of change to active feeding by salmon, or of "relative hunger" as this condition has been named by Kronfeld and Scheminskii (1926). These authors observed retardation of growth of trout larvae if these larvae did not obtain exogenous food after resorption of more than half their yolk. A suggestion was made that these individuals begin to experience insufficiency of some substances, necessary for normal development. Obviously, larvae should be provided with food at the right time. In Sakhalin fish farms the cases of emaciation among juveniles used to occur. After preliminary experiments, additional feeding of the larvae of chum and pink was introduced; the need of juveniles of these species for additional feeding was included in the instruction on artificial reproduction of Pacific salmon.

Absence or poor quality food disturbs development and leads to rapid death of larvae of many fishes (Kostomarova, 1962). The larvae of salmon withstand insufficiency of food with less trauma. As has been demonstrated on the Atlantic salmon and on the chum, this is due to the fact that on completion of yolk resorption, nutrient substances are not fully used up, but are partially deposited in the body cavity of the larvae in the form of adipose tissue (Hein, 1906; Disler, 1954, 1957).

We were able to establish that this character occurs in all Pacific salmon species, as it probably does in all other fishes of the same ecological group. The deposits of reserve fat allow juveniles to survive temporary shortage of food, to find it more successfully in fresh waters or to reach the estuarine and marine areas rich in feed.

Comparison of juveniles of Pacific salmon species draws attention to the abbreviated freshwater cycle of the chum and pink. These species in their bulk migrate to the sea, while still possessing a small remnant of yolk. Some numbers of the chum remain in the rivers for a longer time, but these two species do not spend winter in fresh waters. It is precisely these two species, in contrast with other salmon species, that lack dwarf males and landlocked forms. The ecological reason for the early exit into the sea has been sufficiently well determined. It is due to the fact that the extremely numerous offspring of pink and chum do not find in spawning areas sufficient food for prolonged feeding. Juveniles of these species lead a gregarious life, a fact of defensive significance. The eliminating action of the predators in the rivers is further reduced moreover, due to the catadromous migration being carried out in huge numbers and mainly during the night. 282

The pink differs from the chum by particularly early seaward migration. Its juveniles in overwhelming majority abandon the rivers before the beginning of active feeding, and do not remain later than the completion of the stage of mixed feeding. This uniformity lowers adaptive possibilities. In comparison with other species of salmon, the larvae and juveniles of the pink have less high bodies, shorter fins, are less pigmented and devoid of spots on the flanks (see Fig. 37, C-E). The nectonic type of colouration can be attributed to the fact that the juveniles change early to feeding in midwater.

The chum lives in the rivers slightly longer than the pink. The bulk of its juveniles exit from the short southern rivers soon after transition to exogenous feeding. In large rivers a part of the population passes through the entire first, and a few individuals through a large part of the second juvenile stage of development. The point of transition to catadromous migration is not fixed as strictly in chum as it is in the pink. In the Amur the juveniles of the summer chum remained for a longer time (Soldatov, 1912). Characteristic to the larvae and juveniles of this species is spotted colouration, which is of critical importance. (see Fig. 14, B - D; 15). The juveniles disperse with age throughout the river and tributary waters, which allows utilisation of larger feeding areas.

The juveniles of sockeye (see Fig. 28B,C and Fig. 30, upper), as those of the two species mentioned above, remain all the time in schools. The external appearance and colouration of its larvae and juveniles resemble those of the chum (detailed diagnostic features given in species description). The sockeye is distinguished from other Pacific salmon species by a particularly prolonged freshwater phase of life. In its spawning and feeding areas there are always individuals at different stages of development, a fact which favours more complete utilisation of food resources. By comparison with related species, the sockeye satisfies its nutritional needs more fully than others in the freshwater habitat.

In the lakes, sockeye feeds mainly on plankton. The development of long and numerous rakers of special shape is related to the character of food (see Fig. 27). Following their migration from the littoral into the pelagic zone, the juveniles assume silvery nektonic colouration. Spotty colouration is retained for a prolonged time, when the fish lives in shallow water streams and is reared in ponds. In rivers and streams benthos and aerial insects assume great importance in the feeding of sockeye (Gribanov, 1948; Krogius, 1951; Semko, 1954; Simonova, 1972b). The juveniles can migrate from these feeding areas into lakes or large limnocrenes, where they remain for some time. However, a considerable number of sockeye migrates from the stream and river spawning grounds into the sea as young-of-the-year and even as larvae. Small juveniles are subject to greater elimination in the sea than the large ones. This explains higher fecundity of the individuals reproducing in streams and 283 rivers.

Juveniles of coho, chinook and masou lose their tendency to formation of schools, disperse throughout the habitat, occupy individual territories in shallow waters and defend them. A hierarchical relationship is established among juveniles of equal size. There are many common features both in the appearance and behaviour of juveniles of these species. From the territories they occupy, juveniles dart after food objects swimming by. The food spectrum of juveniles is very broad. The representatives of the aerial fauna constitute a major component of their food. Since juveniles feed on varied food and do not form dense groups, they are able to live for a prolonged time in the waters relatively poor in food organisms. To reflect the demersal mode of life and the characteristic mode of hunting, the juveniles are high-bodied, have long paired fins, high dorsal and anal fins with elongated branching rays and a large caudal lobe. The preanal fin of these species grows for a long time, reaches a large size and is retained for a long period. They are also distinguished by bright, spotted colouration. A large number of juveniles of this group of species live in fresh water not less than a year. They all show the phenomenon of neoteny and their dwarf males take part in spawning for a second time. Masou and coho have landlocked forms.

In addition to the similarities described, the juveniles of each species are distinguished by structure, behaviour and preferred habitat, all of which are reflected in the composition of their diet. Coho retains its preanal fold for a particularly long time; this indirectly indicates prolonged life in demersal habitats. Its juveniles select quiet, often strongly silted side channels and oxbow lakes, as well as places near banks with vegetation hanging down into the water. They move for feeding into lakes and avoid places with rapid current. The diet of the juvenile coho is distinguished by a particularly high proportion of aerial insects, which they successfully catch from the surface by jumping out of water. The shape of the body and the structure of the fin is suitable for this type of behaviour (see Fig. 55,C; 56). Comparing special features of ecology, colouration and migratory behaviour of juvenile Pacific salmon, Hoar (1958) considered it possible to take the behaviour of juvenile coho as being closest to the ancestral river form, and the mode of life, character of colouration and migratory behaviour of juvenile pink as the most specialized. In these species we saw clearly expressed relationships between structure, colouration, mode of life, particularly migratory behaviour, and the ecological niche they occupy. The same is true of other species.

The external appearance and behaviour of juvenile chinook resemble those of coho. They are distinguished by a slightly lesser height of unpaired fins, relatively weak pigmentation, particularly of the anal fin, and a different distribution of chromatophores (see Fig. 45,D; 46). Juvenile chinook are able to change their colour surprisingly rapidly, in accordance with the background of the bottom; they are very difficult to find among stones near the banks, where they hide (Edmunson et al., 1968; Reimers, 1968; personal observations). It is interesting that the juveniles of the autumn-spawning chinook, in contrast with those of the summer-spawning, migrate in their bulk to the sea as young-of-the-year, even before the appearance of scales (Rutter, 1904; Mason, 1965). 284

The juveniles of masou are particularly high-bodied and are distinguishable by their appearance (see Fig. 65,D,E; 66). Larvae feed mainly on benthos and live in schools for some time. Juveniles occupy individual territories, catch their food in a manner similar to that of coho, but do not jump out of the water after insects. The food spectrum grows with age. The euryphagy of masou is particularly strongly evident. The main characteristic of the diet is the abundance of various invertebrates originating outside the aquatic habitat. For this reason juveniles and dwarf individuals of masou are able to live in mountain rivers and small tributaries with very poor fauna. Masou is more rheophilic than coho, emerges from the ground earlier and utilizes shallows near the banks; its juveniles live in the rivers further upstream.

The examination of the interspecific and intraspecific relationships brings the attention of the investigators to distribution of predatory habits among juvenile salmon. Indeed, in the stomachs of yearlings and two-year-olds of coho, masou, chinook, sockeye, char and other species, small juveniles of salmon, conspecific included, are sometimes found in large numbers. In each such instance it is important that the reaseons for the predatory habit be examined. In this examination, account must be taken of the characteristics of the regime of the habitat, its populations, availability of food to fish, circumstances of fishing, reasons for concentration of juveniles and potential predators. Should this be neglected, erroneous ideas can be formed as to the extent of predatory and cannibalistic habitats. These errors are then reflected in fishery recommendations, in decisions as to further directions of scientific utilization of spawning resources, selection of species for husbandry and type of work on biotic improvement of the spawning and rearing grounds. A careful study of the biocoenotic relationships shows that in nature one does not often find conditions leading to grouping of juveniles of one or several species and of different ages. Such situations, however, not infrequently arise near barriers, fences for counting of migrants, or at places where juveniles are released from hatcheries, etc. This favours development of predation and cannibalism (Hunter, 1959; Ricker, 1962; Levanidov, 1969; personal observations). Studies on feeding and distribution of juveniles of different ages in several aquatories of Sakhalin gave no reason to speak of significant influence of large juveniles of masou and coho on abundance of other salmon species (Krykhtin, 1955, 1962; Kalmykova, 1957; Volovik, 1963, 1964; personal observations). In Kamchatkan lakes studied, coho eats a considerable quantity of fish, but they are young nine-spine and three-spine stickleback and smelt, all of which are trophic competitors of sockeye (Zorbidi, 1970a). In the same way, chars of the 285 genus Salvelinus cannot be considered as definitely harmful species for the salmon industry. In some water they consume few fish or destroy food competitors of young sockeve and in doing so are more useful than harmful (Krogius and Krokhin, 1948, 1956; Savvaitova, 1961, 1973).

We have discussed above specific and intraspecific differences between various spawners and places of reproduction, as well as adaptive features of embryogeny. Juveniles possess also features of morph-functional and ecological specialization, and characteristic behaviour. Under natural conditions larvae and juveniles of each salmon species occupy to some extent a different habitat, food nich. Like the entire system of adaptations, they vary with age, with transition from one stage to another. This must be carefully taken into account when one examines biocoenotic relationships and works out schemes for rational exploitation of the basins of spawning rivers. It is important to keep in mind that species and population differences of stocks allow more full utilization of potential possibilities of spawning and rearing grounds and the food resources of the seas and the ocean.

WAYS TO INCREASE PRODUCTION OF PACIFIC SALMON. 286

High technical development of marine fishing industry greatly indreased its impact on fish populations. At the same time there is an increase in the impact of the anthropogenic factors on the hydrological regime and water quality in spawning and rearing habitats, as the result of which productivity of salmon spawning is diminished. Under those conditions, the importance of regulatory and protective measures increases. More acutely than ever before, the necessity is felt for enhancement of the effectiveness of natural productivity of the stocks, improvement in the quality of composition of salmon populations and transplantation of valuable fish, as well as for increase in the scale of artificial production and improvement in biological techniques of salmon husbandry. There is obvious need for large-scale adoption of various fish husbandry measures, in the broadest sense, each of which should be introduced with account being taken of the characteristics of biology of the species, their structure and special features of intraspecies groupings.

Intraspecific Variation, Origin of Races, Possibilities of Restoration of the Salmon Fauna. The accumulated data on Pacific salmon show the complicated and characteristic structure of each species. These fish are polytypic and ecologically heterogenous. The study of the conditions of reproduction and development of the Pacific salmon makes one inclined to think that in the process of establishment of species and intraspecific differentiations (microevolution) an important role was played by colonization of different spawning grounds and feeding-growing areas. In particular, use by intraspecific forms of spawning areas, the ground of which is washed by waters of different origin, which have different thermal and hydrochemical regime, allowed the salmon to expand its areas and seasons of reproduction. This, in its turn, expanded food rescurces available for colonization and created conditions for food specialization. In consequence, existence was secured for a greater number of species. It is also known, that populations which are ecologically varied are better protected from the possible fluctuations in external conditions (Mayr, 1968, 1974). As Nikol'skii (1973) writes, the more complex structure allows the species to exist under changing living conditions. Hence one can understand the practical sense of extension in the intraspecific and intrapopulation differences in salmon.

The study of the ranges shows the unevenness of distribution of species and intraspecific forms, allows one to detect some general principles in distribution of salmon and the possibility for enriching the composition of fauna. From this point of view the example of chinook is instructive. In the western part of the range its stocks are small and concentrated in the region of Kamchatka, mainly in the basin of the Kamchatka river. However, in that river chinook uses only a small part of the tributaries. Its spawning area is discontinuous. We explained uneven distribution and low abundance by the ecological uniformity of chinook, which in our waters is represented by the summer-spawning form. In North America this species is common throughout a large territory and is taken in tens of times larger quantities. This is due to the fact that there, in addition to summer-spawning, there are also autumn- and winter-spawning forms, occupying spawning grounds of a different type. Due to ecological variability the available spawning resources become greater. Moreover, the offspring of the autumn-spawning chinook lives in the rivers for a short time, which also promotes increase in abundance. Comparison of the qualitative composition of populations of different regions shows that acclimation of autumn-spawning form is useful. It would allow us to distribute more widely and to increase the stocks of this valuable salmon species (Smirnov, 1972a). 287

In contrast with chinook, there is much more chum in the western part of its range and it is precisely there that the species is very diverse in its morpho-biological characteristics. Chum has developed summer- and autumn-spawning forms, the ecology of which varies significantly in different regions. In their turn, seasonal races are subdivided into local stocks (Birman, 1951, 1956; Svetovidova, 1961). Morpho-biological and genetic heterogeneity was demonstrated also for populations, reproducing even in small rivers of Sakhalin (Smirnov, 1954a; Altukhov, 1973). One of the distinguishing features of local populations (or local stocks) is the difference in duration of their river migrations. Associated with it are many characteristic features of spawners and the length of time the young spend in the rivers. The special features of the local populations and subpopulations, as well as differences in ecology of reproduction of seasonal races of the chum from different regions, must be carefully taken into account in salmon husbandry and in acclimation. For example, one cannot consider as biologically well founded transport of eggs from the farm situated on a small river to one distant from the river mouth by thousands of kilometers; there is no basis to look for success in acclimation of the chum adapted to reproduction in places of emergence of ground water, in those areas where supply of rivers with ground water is limited.

The study of reproduction and development of the intraspecifies forms of chum and other salmon species gives valuable material for evaluation of the problem of origin of seasonal races. Some authors (Schmidt, 1947; Abakumov, 1961) took into account mainly the differences in the length of the migratory routes, time spent by salmon in fresh water and associated with it some characteristics of spawners of various races. According to Abakumov (1961, p.188), fishes, spawning on distant spawning grounds (winter forms) should have greater energy stores and be stronger... Fishes spawning in nearby spawning grounds (spring forms), require smaller 288
energy stores. "These differences, apparently, provided the basis for the formation of seasonal races of migratory fishes."

Indeed, the autumn chum travels along the Amur for up to 2,000 km and more, but it reproduces also in small rivers of the lower reaches, and in the Amur liman. In short rivers its spawning grounds might be situated beginning with the tidal zone. The length of anadromous migration of this ecological form is strongly variable, the size and condition factor of its spawners are not uniform, as is also the level of maturity of gonads at entry into the river and other characteristics. In all instances, however, the autumn chum of the Amur builds its nests where the stone and sand bottom is supplied with ground waters that have, as has been said, special hydrochemical and thermal properties. It is these properties that ensure effectiveness of the autumn and winter spawning. The places of reproduction of the autumn chum are determined by the topography of this type of section; other characteristics are incidental. Adaptation to reproduction and development under conditions of ground water supplies to spawning grounds is characteristic to this race as a whole. It basically distinguishes the autumn chum of the Amur from the summer form, the spawning grounds of which are mainly washed by subsoil streams. The autumn and winter spawning of chinook, as well as of other species, is observed also in places washed with ground water, which retains spawning temperatures for a long time. Colonization of such places with a specific water regime is related to the origin of the appropriate characteristics in development. This process of adaptation encompasses the entire ontogeny. In our view, it was this process that constituted the basis for the formation of ecologically (hence also morphologically) distinct intraspecific groups of salmon, often referred to as seasonal races.

Masou is a scarce salmon, its low abundance being related to the ecology of development. It is more plentiful in the basin of the Sea of Japan, and it is there that it is most varied qualitatively. There are forms with summer and autumn spawning, which inhabit different rivers or even regions. Spawning is displaced to autumn in regions with a milder climate, in our territories to the southern regions of Primorskii Krai. The masou of Primor'e is distinguished by its large size and high fecundity; an attempt might be useful to introduce it into the southern rivers of Sakhalin and some other waters, of which we shall speak below. The landlocked form is recommended for introduction to hydro-electric reservoirs (Krykhtin and Levanidov, 1962). Experiments have begun to acclimate masou in North American waters (Tokui, 1969; Christie, 1970).

Coho migrates into rivers later than other salmon species and spawns mainly during the autumn and winter. In contrast with masou, spawning in different seasons occurs in the same rivers but in different localities. This indicates ecological differentiation of the species. So far no morphological differences between such seasonal forms are known. This salmon species lives in the sea only slightly longer than the pink and 289
grows very rapidly. It has been established that coho is able to fulfill its high growth potential also in large lakes (Ricker and Loftus, 1968), which increases the chances for its distribution.

In the north-western basin of the Pacific Ocean the stocks of sockeye are concentrated in the region of Kamchatka. Its spawning area is discontinuous like that of the chinook. The characteristic features of distribution of this species are largely due to its preference of rivers, in the basins of which are lakes. There are many such rivers in North America and this is the reason for high abundance of the species in the eastern part of its range.

Berg (1948) and other investigators recognized several races of sockeye, which is characterized by a very complex specifies and population structure. It must be stressed that only in this species evolved generative limnophilic and generative-rheophilic forms. The representatives of these ecotypes, in addition to other features, are distinguished by the duration of freshwater cycle and food specialization of juveniles. This should be taken into account more fully in salmon husbandry and in acclimation. In the basin of the Amur and in the rivers of Sakhalin, where eggs of the sockeye reproducing in lakes were transported, the species did not "take". The failure can be attributed most of all to the fact that the juveniles of this form did not find suitable and stable food bases. We believe that success can be achieved by working with the generative-rheophilic form, which in these regions would find more favourable conditions for completion of the freshwater part of their life cycle.

The populations of the pink are more uniform than those of other salmon species and are practically homogenous in age structure. The differentiation is also poor as regards ecology of reproduction and development. In the western part of the range the summer-spawning form is more widespread; its stocks are subject to sharp fluctuations. It appears that the conditions of productivity for the autumn-spawning form are more stable. The pink has the shortest cycle, grows most rapidly and is the most abundant among salmon. For this reason it attracts the attention of the experts on acclimation. The idea of introducing this species into the basins of the Atlantic ocean poor in salmon stocks is tempting; it is worthwhile to devote attention to its realisation. The pink was introduced into the rivers of the Gulf of Maine, where it reproduced for several years (Huntsman and Dymond, 1940; Bigelow and Schroeder, 1953). Kuznetsov (1953) suggested an attempt to introduce the pink into the White Sea. His proposal caused some criticism in view of its insufficient theoretical validity (Kuderskii et al., 1967).

In 1955, M.S. Lazarev and A.I. Smirnov worked out a biological basis for acclimation of the pink in the basins of the Barents and White Seas, which was approved by scientific and industrial circles. Beginning with 1956, Glavrybvod (Central Office for Fish Productivity, Translator's note) commenced implementation of this work. The eggs were taken to the fish farms of the Murman and Arkhangelsk districts mainly from the southern Sakhalin and South Kurile farms. A small quantity of eggs was taken from 290
the west Kamchatka and Magadan districts, climatically closer with the region of introduction. Voluminous literature illustrates the course of the work and the results of introduction. A sufficiently full list of literature is contained in the paper by Kuderskii et al., (1967); it should be augmented by reference to some sources of recent years (Kamyshnaya and Smirnov, 1968; Smirnov, 1971, 1972b; Kamyshnaya, 1972; Surkov, 1972; Surkova, 1972). Mass return of spawners from the sea into rivers was first observed in 1960, when the staff of Glavrybvod recorded more than 80,000 fish and the total number of fish approaching our shores were roughly calculated at 300 thousand (Mileiko, 1961). The pink spread very widely. In the west it was found in the rivers of Scotland, Iceland, Norway, in the east up to the rivers Pechora and Korotaikha (Berg, 1961; Mileiko, 1961; etc). To check on the productivity of natural spawning, no eggs were transported over from the Far East for several years. Observations showed that in the region of acclimation, except for years with early autumn cold, the

pink find conditions for effective spawning and completion of a full biological cycle. Particularly abundant was the return of spawners into the river in 1973. For the first time in that year it proved possible to expand the commercial catch and to produce a considerable economic effect. The largest run was into the river Umba in the White Sea. This was quite natural, since it was only in that river that the fish husbandry personnel released juveniles in 1972. In view of that fact, mass run of the fish into the rivers of the Barents Sea indicates their importance for the procuctivity of the introduced species. We have observed effective spawning during previous years in the Barents Sea river Muchka, a tributary of the river Teriberka. In 1973 it received many pink; spawning took place in favourable conditions; in the winter the eggs developed normally. Increased effort on the part of fish husbandry is necessary to produce more stable runs and a higher abundance of the pink. It is best to transport there the eggs of the early-maturing pink from the northern regions of the Far East. It is desirable that a qualitatively varied population be created in the European North. Since in the region of introduction the areas of spawning grounds is small, care should be taken to increase their surface and to build artificial spawning channels. Specialized fish farms should be placed on those rivers that are preferred by the pink. To increase the effectiveness of a culture it is important to start in time feeding of larvae and to release them from the rearing ponds, when abundant food appears near the mouth of rivers; prolonged retention of juveniles in rearing ponds has negative effects (Smirnov and Kamyshnaya, 1965). Experiments in introducing the pink into the basin of the Baltic has begun recently. Attention is drawn to the achievment of the return of the pink into the rivers of Newfoundland (Ricker and Loftus, 1968). Also interesting is the report of the reproduction of the pink that accidentally appeared in one of the Great Lakes (Schumacher and Eddy, 1960).

Discussing the problem of selection of fishes for aquaculture and acclimation, Karpevich (1970) points out the exceptional value of the salmonid fishes, distinguished by huge growth potential and relatively short period required for maturation. The Pacific salmon have particularly short cycles and form abundant populations. Specialists in fish acclimation have worked with these fish now for about a hundred years. The experience accumulated as the result of this work is reviewed by many authors (Davidson and Hutchinson, 1938; Vibert, 1953a; Smirnov, 1962a, 1971, 1972b; Krokhin, 1963; Kuderskii et al., 1967; Ricker, 1972). It shows that greater success is achieved in dealing with landlocked forms. Many positive results were achieved by fish culturists in transplants of anadromous forms within the range of distribution of the genus. Considerable difficulties were encountered in the work with anadromous forms beyond the natural boundaries of the genus, especially in transoceanic acclimation. However, interesting and hopeful results have been achieved in this direction also. 291

Among various measures which should be undertaken in the Far East the importance should be pointed out of the distribution of chinook and sockeye, and of expanding their spawning area. For the successful accomplishment of this task the most useful, as has been said, are the autumn-spawning chinook and the generative-rheophilic form of sockeye. The acclimation of the Pacific salmon in the basins of the Arctic seas should be, of course, in harmony with the measures undertaken for intensification of the productivity of the Atlantic salmon.

The assessment of the future of the salmon industry in the basins of European seas should take into account real complications caused by the hydroelectric contruction, changes in the hydrological regime of the spawning rivers and water quality. The natural productivity of the Atlantic salmon becomes continuously more difficult under the influence of anthropogenic factors. The role of salmoniculture becomes correspondingly more important. However, artifical production of the Atlantic salmon is labour-consuming and expensive. This is due to the prolonged freshwater life cycle of the species of the genus Salmo and the necessity for long maintainance of spawners and rearing of the young. There are various ways to solve this problem: more intensive rearing of the young, development of a form with a short freshwater phase of life, selection of such forms in nature. It has been shown above that among the Pacific salmon there are species, as well as intraspecific forms with very short periods of freshwater life. Farm production of such salmon is much cheaper, has been well established and can be carried out on a commercial scale in the lower reaches of the rivers.

The possibility of intensive salmon husbandry under the conditions of regulation of the river runoff has been dealt with by experiments conducted in the Caspian Sea. Derzhavin (1936) proposed acclimation of Pacific salmon in the Caspian Sea. He visualised it as natural reproduction of introduced fish. Under the present-day conditions, it becomes necessary to depend on culture procedures. Attempts at introduction of the autumn 292
chum and pink were carried out in the Samur farm of the Dagestan ASSR and the Kizanskii fish farm on the Volga (Tamarin, 1965, 1972; Magomedov, 1970, 1972). Eggs were transported from Sakhalin from 1963 to 1967. The

first return of sexually mature individuals was observed in 1964, and was most abundant in 1966. The chum entered the Terek, Sulak and many small rivulets, as well as into the Volga. It was taken off the shores of Iran. Some individuals matures at the age of two years, most at three. Such rapid maturation can be explained by the southern position of the feeding area and by the abundance of food. We also consider as a hopeful sign the capture in the Caspian Sea of an adult specimen of the pink. The Caspian Sea is rich in food invertebrates and small fish, whereas there are only a few predatory fish left. The abundance of the local salmon has dropped sharply and its mass culture is difficult. All this offers good chances for culturing Pacific salmon in the Caspian. Following the establishment of specialized fish culture bases, the Caspian can be converted into an excellent salmon reservoir. Of course, this calls not simply for any salmon, but for certain intraspecific groups. For culturing in the Caspian one can reccommend the autumn chum from the Sakhalin, the autumn-spawning chinook, coho and masou of Primor'e. One can also hope for success in culturing autumn-spawning pink. Recommendations on selection of salmon for introduction in other European seas, lakes and (hydroelectric) reservoirs are contained in previous publications (Smirnov, 1962a, 1971, 1972a).

Experiments have confirmed the possibility of rearing of Pacific salmon in the lower reaches of the Caspian rivers. Since fish culture operations with this salmon involve a period from the autumn until the sptring, the fish culture bases prepared for them can be used for rearing of acipenserids or other valuable fish which spawn in the spring and summer. Construction of comprehensive fish culture enterprises, functioning round the year is also more interesting from the economic point of view.

Possible Future Directions of Improvements in Environment. Under the conditions of poor runs of spawners (natural improvers of spawning grounds) and increasing influence of anthropogenic factors on nature the problem of preservation of spawning resources becomes more acute. At the same time, the technical complexity of carrying out the routine improvement of many thousands of spawning habitats, scattered over huge territories is quite obvious (Cherfas, 1956). There are no grounds for expecting the availability of a great deal of manpower and techinical assistance. Means at our disposal must be expended very carefully. The solution to this problem is kept in mind, particularly in the rationalized program for the work of fisheries environmental improvement stations (Nikol'skii, 1956).

The fatal influence of disturbance of the water supply regime and of freezing on eggs and larvae is well known. As one of the measures al- 293
lowing optimisation of the conditions on spawning grounds is construction of small barriers (dams) (Wickett, 1952, 1958; Krogius and Krokhin, 1954;Nikol'skii. 1956; Vasil'ev, 1959b). It must be noted, however, that scientists differ in opinion as to the role of these barriers and the best way to build them. Having reviewed literature data on this topic and also those of his own experiments, Levanidov (1969) arrived at the conclusion that construction of barriers is justified in those places where reproduction of salmon is under the control of man. In his view, during severe winters, barriers in spawning grounds which are mainly supplied by subsoil stream, do not prevent freezing and death of eggs.

As the technical possibilities of our national economy improve, the possibility of hydrotechnical improvement of the basic type becomes wider. To such measures belongs, for example, construction of artificial spawning grounds and incubation channels. Work is being conducted on the improvement of their design and methods of exploitation. Artificial spawning grounds produce much higher numbers of young than the natural ones (MacKinnon, 1963; Strekalova, 1965; 1968; Dill, 1967; McDonald, 1969).

The improved supply of food to the young is of great importance to the enhancement of salmon stocks. In his monograph, Levanidov (1969) takes note of the greater productivity of limnocrenes in comparison with side channels and the more rapid growth in them of the juvenile autumn chum. By erecting barriers across streams and their side channels, they can be made similar to limnocrenes. In this way, writes Levanidov, salmon hatcheries can be built on the base of natural spawning grounds. It is also known that as the result of the destruction of carcasses the habitat becomes richer in biogenic substances and its feeding capacity is enhanced (Krokhin, 1959, etc.). When the spawning grounds are not filled sufficiently with spawners, the necessity arises of introduction of fertilizers into spawning and rearing waters. The rapid pace of development of the chemical industry allows us to suppose that practical application of this measure will become possible.

A drop in abundance of salmon can cause changes in the biocoenotic relationships in the rearing habitats which would favour predators and trophic competitors of young salmon (Krogius and Krokhin, 1954). In such instances the necessity arises for biological inprovement of waters, organisation of predator control and control of the food competitors of young salmon. It must be stressed that the determination of the specifies composition of predators and competitors, of harm they cause, as well as the development of methods for regulation of their numbers call for special research. Among effective measures of biological improvement is the acclimation work discussed above, which allows acceleration of the recovery of impoverished stocks, improvement of their composition and creation of new stocks of valuable forms of salmon.

On Development and Improvement of Salmoniculture. In recent decades in the Far East, old fish farms were reconstructed and new ones built; 294
their productivity has improved and the scale of salmoniculture has become significantly greater. Fish culture plays an increasingly important role in the productivity of the commercial stocks and its shortcomings can now be reflected in the economy of the fishing industry. In consequence, greater demands are placed on the level of the biological techniques used and on the establishment of biological quality control in fish culture enterprises.

At the base of the successful conduct of any fisheries operations and establishment of biological control lies correct understanding of the biology of the cultured species during different stages of their ontogeny. The increase in the volume of information on biology of salmon, special features of ecology of intraspecific groups and characteristics of development, creates the basis for improved biological techniques and increased productivity of salmoniculture. It must be noted, however, that reports on the characteristics of the individual populations of Pacific salmon are still very fragmentary.

The increased role of farm fish culture in the salmon husbandry and its change from an auxiliary means to that producing commercial stocks, sharpens attention to many problems. One of them is the selection of the species for culture and the evaluation of the characteristic features of its biology. The selection is made more difficult by the significant differences between intraspecific forms, the ecology of which is not yet fully studied. And yet, from the relationship between the ecology of the selected forms and the concrete conditions of their culture depends to a large extent the success of fish culture undertakings. As has been said above, the representatives of the genus Oncorhynchus differ from the Atlantic salmon in the short phase of their freshwater life, which makes their culture simpler. However, this characteristic differs in individual species and intraspecific forms. Juveniles of the pink live in the rivers for a fairly short period of time, the chum which reproduce in small rivers--slightly longer; the life cycles of the autumn-spawning chinook are not very prolonged in freshwater, etc. These fishes are more simple and cheaper to culture; they should be preferred also in the organisation of salmon husbandry in the lower reaches of regulated rivers. Moreover, it is in the interest of development of the salmon industry that the list of the cultured species be extended. We consider as an inescapable task for the immediate years organisation of mass rearing of such valuable species as chinook and coho. We must undertake rearing of the masou of Primor'e, which in its quality much exceeds the Sakhalin masou. Biological techniques of rearing of sockeye deserve serious attention. Specialists of various countries attempted development of artificial production of migrating sockeye. The lack of sufficient success, in our opinion, is due to the concentration of attention on the generative-limnophilic form, the young of which live particularly long in fresh water and feed on plankton. In our view, the generative-rheophilic form is much more suitable for artificial reproduction.

The broad ecological and morpho-biological variability characteristic of the Pacific salmon indicates their plasticity. This characteristic promotes selection, allows us to modify salmon in the desired direction and to enhance their commercial value (Donaldson, 1970; Donaldson et al., 1973). The possibility seems very promising of bringing together by means of hybridization and selection of qualities which are valuable from the point of view of industry and which are "scattered" among various intraspecific forms. Interspecific hybrids of the first generation among which are forms distinguished by accelerated development, high rate of growth and rapid maturation could be widely used for commercial production (Smirnov, 1969). 295

Reports on the biology of salmon and experience in production make it clear that an important ecological prerequisite for successful culture of these fish is the harmony between the quality of water, its thermal and hydrochemical regime and the requirements of the cultured species. It is necessary, therefore, that the specialization of the fish farms (or their individual parts) be related to the character of the water sources. In farms supplied with river water it would be incorrect to rear salmon adapted to development in ground water. The importance of water quality to successful fertilization, incubation of eggs and rearing of larvae is a sufficiently well known fact. We would like to stress the importance of water quality for acceleration of maturation of spawners, as well as for development in the young fish a "sense of native river", with which we directly link the return of the spawners to the places of the release of the young.

Fish culture practice shows the economic advantage of increasing the capacity of the fish culture establishments, which, however, is often limited by the low availability of spring water sources during the winter. One of the ways to solve this problem might be introduction into the salmoniculture of the Far East of equipment which is more economical in water use.

In fish hatcheries, salmon embryos hatched from eggs are kept in apparatus and rearing impoundments with different substrate. Having studied the development of the chum, Disler (1951) noted that the rearing ponds with smooth sandy bottoms do not meet the requirements of the free embryos (pre-larvae). Working in Adotymovskii farm, with a similar rearing pond, we arrived at a similar conclusion. It has been demonstrated experimentally that the young salmon reared in gravel is more resistant to temperature differences, to strong current and is less susceptible to destruction by predators than those that are reared in the apparatus with a smooth bottom (Vibert, 1953b). The character of natural environment, structure, behaviour of salmon before emergence from their redds, as well as experimental data show that rearing ponds with clean gravel bottoms, well washed by water, are much more suitable for the requirements of free salmon embryos (Disler, 1954, 1957; Smirnov, 1954a, 1963b, Cherfas, 1956). This must be taken into account, when further improvements are planned for 296
salmon in rearing ponds.

In the salmoniculture of the Far East the young of the pink and chum have not been fed in the farm, because it has been observed that these species migrate into the sea early. Currently, the fact that they should be fed has received wide acceptance from fish culturists and those interested in acclimation. Beside the morph-functional data, which show the necessity of timely food supply to larvae, the usefulness of rearing was indicated by the relationship noted by various authors, between size and the survival rate of the young salmon (Krogius and Krokhin, 1948; Foerster, 1954; Levanidov, 1964a; Kanid'ev, 1966; Kanid'ev and Levanidov, 1968). The organisation of feeding of the juveniles allows us also to attempt regulation of the catadromous migration. The relationship between the success of salmoniculture and the provision of the young with biologically fully adequate food is well known. It must be stressed that the creation of an appropriate food base to a large extent determines the possibilities of commercial production of salmon living in the rivers for prolonged periods.

In view of the fact that in the rearing ponds the conditions in some aspect or another differ from the natural environment, the cultured fish develops reactions not typical to the species and the formation of natural conditioned reflexes is more difficult, which causes higher mortality among the young fish after their release into natural waters (Cherfas, 1956; Isaev et al., 1965). It becomes necessary to weaken the effects of domestication and to develop in the cultured fish before its release into the natural habitat natural reactions to different natural stimuli (Manteifel', 1970). The most important task is to develop hunting and defensive reflexes, although this does not exhaust the problem.

Essentially accomplished in various ways. Satisfactory results are achieved by keeping the young fish before release in specially prepared sections of the natural habitat, rich in food, or in the ponds (Vasil'ev, 1954; Levanidov, 1954a, 1969; Smirnov, 1963b). In the Sakhalin farms a method

has been evolved of rearing hatchery fish in fenced off parts of rivers and ponds with the use of artificial and natural food (Kanid'ev, 1966; Kanid'ev and Levanidov, 1968; Kanid'ev et al., 1970). The use of artificial food allows a sharp increase in planting density, which is very important in large-scale salmon culture, and the presence of natural food improves the value of the diet. By using it, the young fish develops hunting reflexes typical for the species. Introduction into such habitats of a small number of predators promotes the development of defensive reflexes. In experiments with various fishes the possibility of development of defensive reactions without direct contact with predators has been demonstrated (Popov, 1953; Gerasimov, 1971; etc.). In the juvenile chum, sockeye and
trout, conditioned defensive reflexes were developed both in the presence 297
of short-duration contact with predators and by the use of their models and electric current as unconditioned stimulus (Tarrant, 1964; Kanid'ev, 1966; Kanayama and Tuge, 1968).

In addition to rearing young fish to a certain age and the developing in it of natural reflexes, the effectiveness of salmoniculture is determined by correct selection of time and ecological conditions favourable for release of the young into natural habitats. In this case also, one must carefully take into account characteristic features of the species and populations dealt with, as well as specific characters of the water, their fauna, composition of predators, time and place of their concentrations and, finally, duration of development in the river and near its mouth of abundant food organisms.

Until recently, the possibility of significant influence of fish culture on the commercial stocks of abundant species of Pacific salmon was assessed very cautiously. The development of commercial fish culture brings sizeable corrections to this assessment. Interesting in this respect is the example of the Sakhalin district. Up to 20% of the stocks of pinks and up to 85% of those of the autumn chum began to be produced there in fish culture establishments. In the south-west of the island the culture-production has replaced natural reproduction of the autumn chum and the fish culturists are supporting its abundance at the level much higher than before. This success allows us to evaluate optimistically the future of the far-eastern salmon industry, if salmoniculture in various regions will be undertaken at the right time and on a solid scale and if the improvement in biological techniques will continue.

Naturally, the development of salmoniculture calls for considerable capital investment. It must be remembered, however, that such investment pays for itself rapidly. When placed on a right footing, the profitability of the salmon farms is similar to that of the best fish farms. For example, in 1964--1968 the annual return of chum into Kalinin fish farm was about 5 thousand centners (500 metric tons, translator's note) and the processing of one centners of salmon caught cost the farm about 8 rubles; later, annual return of production of this farm increased to 8 thousand centners (Kanid'ev, Krykhtin and Lagunov, 1969; Kanid'ev, Kostyunin and Salmin, 1970; "Izvestiya", 4th of January 1973, No.4).

Farm production of Pacific salmon is the most effective method of enhancement of its stocks. Through the development of the commercial salmoniculture we can arrive at planned productivity of commercial stocks, stabilisation and an increase in catches of valuable salmonid fishes. Large-scale farm production of Pacific salmon is undoubtedly profitable and

is a very convenient way of utilisation of food resources of the seas and the ocean. Feeding migrations of salmon extend thousands of miles. While on the move, these voracious fish feed on most diverse organisms, grow very rapidly and at the end of their lives return for reproduction 298
to the places where the young were released. Having covered the Far East with a network of well equipped fish culture establishments and releasing into the sea large numbers of the young of various species and intra-specific forms, man with the aid of these inveterate "travellers" can utilise food resources of huge marine and oceanic aquatories without the use of an expensive fleet.

CONCLUSION 299

A comparative morpho-ecological study of the development of Pacific salmon revealed principal features of their ontogeny, a system of morpho-functional and behavioural adaptations typical to the group, as well as the special features of individual species and intraspecies forms.

For the success of oviposition and creation for the offspring of favourable conditions of existence, the nuptial changes of the spawners, their characteristic behaviour and the building of spawning redds are of great importance. The ability of the offspring to develop in the ground brought about of a complicated set of morphological, physiological, bio-chemical and behavioural characters of the embryos and larvae. Due to the high strength of the membranes and the turgor, the eggs of salmon can withstand high pressure. The embryos are supplied with large stores of nutrient substances and develop for a long time at the expense of endogenous feeding. Because of the low oxygen content in water washing the nests, and because of the large size of the eggs, salmon possesses adaptations facilitating respiration: their eggs are rich in carotenoids, the embryos develop early strong embryonic organs of respiration, protoplasmic and special neuro-muscular movements are observed. While inside the membrane, the embryos accumulate products of nitrogen metabolism, thus preventing pollution of the nest environment. After hatching, embryos develop positive tactile reaction, photophobia and positive reaction to water currents. Abundant discharge of mucus protects their gills and body surface from silting, and rythmic movements of pectoral fins ensure constant change of water at respiratory surfaces. These fish attain large size in their redds, high level of differentiation and mobility, and become able to ingest fairly large objects. The emergence from the nests is preceded by the loss by larvae of photophobia and positive tactile reaction. The larval period of development is abbreviated; it includes one stage of mixed feeding. The juvenile period consists of several stages. Facts available confirm the view that in the process of historical establishment of the group of fish dealt with here changes involved not individual features, properties or sections of life cycle but the entire organism during different times of existence. A special type of ontogeny was formed, specific links developed with the abiotic and biotic conditions, as well as species and population structure.

The example of the Pacific salmon shows that the method of reproduction and development, characteristic of the lithophilic fish which
bury their eggs, allowed them to occupy an extremely large range, in some 300
species extending from subtropical to Arctic regions, to reproduce in waters of various types and during different seasons, to feed in fresh waters and the seas and to produce abundant stocks.

In the course of its life, salmon repeatedly changes its environment. From time to time, while passing from one stage to the next, the entire organism undergoes qualitative change and so do its interrelationships with the environment. Ontogenetic changes correspond with the change in the temperature, gaseous, salinity and illumination regimes, with the change of locality and character of biotic links. Investigations have shown basic similarity between the means of reproduction and development and the system of adaptations of all representatives of this group. At the same time, various species and intraspecific groups possess specific morphofunctional features, which are manifest at all periods and stages and at different times during the development, and are related to the characteristic features of the environment and its changes. This morphobiological variability shows broad parallelism, which can be explained by the common type of ontogeny.

The study of our own and literature data has convinced us also that species and ecologically distinct intraspecific groups occupy for reproduction waters and spawning grounds of a definite type. The places of spawning differ in geomorphological, hydrological and hydrochemical characteristics, in quality of ground, abundance of food, its composition, etc. The special character of the conditions of development and reproduction is manifest also in the size of the spawning areas and concentration of spawners on them. Moreover, the dynamic properties of the salmon differ, its fecundity and the type of oviposition, intensity with which the fish acts on the spawning substrate (effect of natural ground improvement), density of filling of the ground with eggs and the depth at which they are laid, as well as the quantity of carcass material, reflected in the quantity of food in the water. Therefore, not only the fish themselves select the place for reproduction, but they change it, imparting to the environment of their offspring specific character.

Since salmon develop for a long time in their redds, many characteristics of the species and intraspecific forms are related to the regime of their water supply and the quality of the water. Sockeye and coho reproduce in places of emergence of ground water, the thermal, gaseous regimes and salinity composition of which differ significantly from the mainstream water and the subsoil streams. Characteristics to these waters is especially low oxygen content and high saturation with carbonic acid. As the result of the characteristics of their environment, the eggs of these species are smaller than those of others, their membranes are thinner and the eggs are distinguished by high carotenoid content; the embryonic organs of respiration develop in these species more strongly and earlier. The most extensive differences occur in intraspecific forms using habitats of a different kind. A good example of such divergence are the hereditary-rheophilic and generative-limnophilic forms of sockeye. Significant are the differences between migratory and landlocked forms. The differences in the thermal regime of ground waters washing the spawning grounds promotes 301
isolation (development) of groups with different spawning seasons. The stability of the places of emergence of ground waters, their often narrow localization and different properties are well known. With these characteristics of spawning grounds is to some extent connected the accuracy of the return of spawning fish to the places of their birth, leading in turn to the reproductive and genetic isolation of small groups and complication in the structure of the species. The sockeye is characterized by a particularly complex specific and population structure.

In the remaining species of Pacific salmon there is more or less definitive divergence in colonisation of spawning grounds, supplied with waters of different origin. The pink typically uses river spawning grounds, supplied with subsoil water and extending over vast large areas. Since the subsoil streams are derived from the mainstream water, the regime of such spawning grounds is less stable and depends on the climatic character of the region, seasonal, daily and periodical changes in the quality of the mainstream water. Temperature favourable for reproduction exists in them in the summer, which promoted the formation of summer-spawning races. During severe winters extreme conditions often occur in these spawning grounds. The salt content, thermal and gaseous regime of the subsoid water, just like those of the mainstream water, are uniform along sections of the rivers of considerable length and sometimes in the neighbouring tributaries and rivers. This promotes reproduction of populations uniform from the morpho-biological point of view and of considerable abundance. The hydrological regime of mountain rivers is unstable, their bed changing systematically during floods; also changing is the position of the localities suitable for reproduction of salmon. In such situations there was no chance of fixing strict relationships with any particular parts of rivers. Consequently, in species like pink homing is less definitely expressed. In sections with steep slopes and clean stone and sand beds the subsoil streams are well aerated and the pink developes in sufficiently high oxygen content. This is reflected in the quality of the eggs, development of embryonic respiration organs and other characters. Fauna of such localities is poor. Their food potential is even more diminished due to cleaning of the ground during the spawning. Feeding of large numbers of juveniles becomes impossible under such conditions, and the pink descends to the estuarine areas rich in food particularly early.

The summer-spawning masou, chum and chinook occupy different habitats on river spawning grounds. Masou moves for reproduction into the upper reaches of the rivers and into small tributaries, where the spawning areas are limited and its nests are scattered widely; this to a large extent determines low abundance of masou populations. The Kamchatkan chinook spawns, as a rule, in the sectors with rapid current and solid, large-stone ground, where smaller salmon cannot reproduce.

Displacement of spawning for autumn in the pink and masou is observed 302
where warmer water is mixed with subsoil streams, as well as in the regions with mild climate. Autumn- and winter-spawning chinook and chum of the Paleoamur region reproduce in places which are washed with ground water, that retain for a long time spawning temperatures; a similar picture is observed in the places of reproduction of coho and generative-rheophilic sockeye. The regime of these spawning grounds is more stable and this is reflected in the dynamics of the population abundance. Similar localities are found both in large and small rivers, in upper and lower courses, all of which is reflected in the characteristics of the spawners and the biology of the juveniles. It is the colonisation of this type of spawning grounds to which the origin and existence of autumn- and winter-spawning races of the chum and chinook, and other ecologically analogous species are linked.

This work has shown significant differences of the ecology of the summer- and autumn-spawning chum of the Paleoamur region and of the seasonal races of chum in the rivers of Kamchatka, determined by the differences in the geological past and hydrological regime of the corresponding basins. Evidence is quoted of the many sided nature of morpho-biological differences and stability of the racial characters. It is stressed that due to the intraspecific ecological variability not only the seasons of reproduction of salmon are extended, but also the ranges, utilized spawning surfaces and food resource, thereby ensuring high abundance of species. This has been convincingly corroborated by the examples of intraspecific differentiation and high abundance of the chum in the western part of its range and those of the chinook in the eastern part; low abundance of chinook in the western part of its range is due to the ecological uniformity of its populations.

By morpho-biological characteristics of juveniles there can be distinguished two groups of species: larvae after emergence from the ground and juveniles of chum, pink, and sockeye lead a gregarious life, while juveniles of coho, chinook and masou disperse throughout the habitat, for some time occupy individual territories and aggressively defend them. The young of the former group have streamlined (high, thin) bodies, low unpaired fins and short paired ones and dark spots on the sides of the body are poorly marked or absent. The feeding of numerous gregarious juveniles requires an abundant and constantly available food base. For this reason the pink and chum migrate early into the estuarine areas of the rivers, rich in food, and the young of the sockeye move into the pelagic zone of lakes where they feed on plankton (from stream spawning grounds not linked with lakes or large limnocrenes sockeye migrates into the seas earlier). The young of chinook, coho and masou have high bodies and long paired and high unpaired fins with elongated anterior branching rays. Their larvae develope long and broad preanal folds, which are retained for a long time. Such shape of body and fins allows the juveniles to perform vigorous jumps upwards, catch food objects swimming by and rapidly return to the original place.

Characteristic of these species is early intense pigmentation and well expressed spotty colouration of the body, due to which the young are not easily visible against the background of the stoney bottom. The characteristic mode of hunting extends very widely the range of the food. The diet of the juveniles, particularly of coho and masou, in large proportions consists of aerial and terrestrial insects. Dispersal throughout the habitat allows them more fully to utilise food resources. All this favours extension of the freshwater period of life; in these species exist dwarf males as well as landlocked forms. 303

The study of ecology of reproduction and morpho-biological characteristics of the species and intraspecific forms allowed elucidation of some principles of distribution of salmon in individual regions and basins. Reports of this type were used in preparation of recommendations on transplantation and acclimation of the most valuable forms. The timeliness of these measures is increased under the conditions of intensive marine fishery and commercial utilisation of the river valleys and hydro-electric constructions, which radically change spawning grounds and make salmon production more difficult. Under these conditions close attention should be given to the species and intraspecific forms which are able to develop in low oxygen content and which live in fresh water relatively briefly.

The structure of the species and populations, ecology of reproduction and special features of development of various intraspecific forms should be carefully taken into account when the rules are being made for fisheries, habitat improvement and, of course, for salmoniculture. Morpho-biological variety of the Pacific salmon offers rich possibilities for selection and hybridization.

High nutritional quality, rapid maturity and growth, euryphagia, short freshwater life cycle, ability to produce populations of high abundance and other qualities make the Pacific salmon extremely interesting as the object of large-scale artificial production. Commercial production of these fish is a rational and economically convenient way of intensive utilization of food resources of the inland waters, but particularly of those of the open spaces of the seas and the ocean.

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BIOLOGY, REPRODUCTION AND DEVELOPMENT OF PACIFIC SALMONS

The monography represents a generalization of the original ecologo-morphological investigations of Pacific salmons (*Oncorhynchus*, *Salmonidae*) performed by the author for many years. A brief historical outline of Far East salmon investigations is given and data about times of spawning, spawning grounds, conditions of development in nature and in hatcheries are compiled. Special attention is paid to description of the stepwise development of *Oncorhynchus keta, O nerka* (anadromous and residual forms), *O. gorbuscha, O. tschawytscha, O. kisutch* and *O. masu*. The material is illustrated by photographs and numerous accurate drawings of the living specimens made by the author. The data on egg and sperm qualities of different species are listed. Detailed morphological and behavioral characteristics of embryos, larvae, young and adult fish of species mentioned presented, the lithophilous egg-burying group of fish being examined as a whole. Peculiarities of population structure, directions and factors of intraspecific differentiations and geographical distribution of representatives of the genus *Oncorhynchus* are discussed. In conclusion the questions concerning the introduction, intensification of natural reproduction and technological improvment of Pacific salmons hatcheries are considered.

The book may be of interest for ichthyologists, embryologists, pisciculturists as well as teachers, students and postgraduates of biological and piscicultural colleges.

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