CANADIAN TRANSLATION OF FISHERIES AND AQUATIC SCIENCES

No. 4873

Oogenesis and a maturity scale for the ovaries of the Sevan trout, Salmo ischchan (Kessler).

by

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Original Title: Ovogenez i shkala zrelosti yaichnikov sevanskoi foreli Salmo ischchan (Kessler).

From: Biol. Zh. Arm. 19: 58-71, 1966.

Translated by the Translation Bureau (JN)
Multilingual Services Division
Department of the Secretary of State of Canada

Department of Fisheries and Oceans
Pacific Biological Station
Nanaimo, BC

1982

24 **pages typescript**

CTFAS 4873

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU

MULTILINGUAL SERVICES DIVISION

CANADA

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS

DIVISION DES SERVICES MULTILINGUES

TRANSLATED FROM – TRADUCTION DE	INTO – EN
Russian	English

AUTHOR – AUTEUR

I. T. Negonovskaya

TITLE IN ENGLISH – TITRE ANGLAIS

Cogenesis and a maturity scale for the ovaries of the Sevan trout, Salmo ischchan (Kessler).

TITLE IN FOREIGN LANGUAGE (TRANSLITERATE FOREIGN CHARACTERS)
TITRE EN LANGUE ÉTRANGÈRE (TRANSCRIRE EN CARACTÈRES ROMAINS)

Cvogenez i shkala zrelosti yaichnikov sevanskoi foreli Salmo ischchan (Kessler).

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET, TRANSCRIRE EN CARACTÈRES ROMAINS.

Biologicheskii zhurnal Armenii

REFERENCE IN ENGLISH – RÉFÉRENCE EN ANGLAIS

Biological Journal of Armenia

PUBLISHER – ÉDITEUR	DATE OF PUBLICATION / DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL / NUMÉROS DES PAGES DANS L'ORIGINAL
Academy of Sciences of the Armenian SSR [USSR]	YEAR / ANNÉE	VOLUME	ISSUE NO. / NUMÉRO	58 - 71
PLACE OF PUBLICATION / LIEU DE PUBLICATION				NUMBER OF TYPED PAGES / NOMBRE DE PAGES DACTYLOGRAPHIÉES
Erevan, Armenian SSR	1966	19	4	24

REQUESTING DEPARTMENT / MINISTÈRE-CLIENT: Fisheries and Oceans

TRANSLATION BUREAU NO. / NOTRE DOSSIER N°: 1035813

BRANCH OR DIVISION / DIRECTION OU DIVISION: S.I.P.E.

TRANSLATOR (INITIALS) / TRADUCTEUR (INITIALES): J. N.

PERSON REQUESTING / DEMANDÉ PAR: F.P.J. Velsen

YOUR NUMBER / VOTRE DOSSIER N°: ----------

DATE OF REQUEST / DATE DE LA DEMANDE: 15 June 1982

UNEDITED TRANSLATION
For information only
TRADUCTION NON REVISEE
Information seulement

AUG AOUT 10 1982

SOS-200-10-6 (REV. 2/68)
7530-21-029-5333

Biologicheskii zhurnal Armenii (Biological Journal of Armenia), Vol. 19, No. 4, pp. 58 - 71. 1966.

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Oogenesis and a maturity scale for the ovaries of the Sevan trout, Salmo ischchan (Kessler)

I. T. Negonovskaya

The investigation of oogenesis and the compilation of a maturity scale for the ovaries is the first necessary stage in the study of the sexual cycles of fishes. For some representatives of the families Cyprinidae, Percidae, Salmonidae and Acipenseridae fairly detailed information is available on these questions, though with respect to many species of fishes this information is still very scanty. In particular this concerns species of the genus Salmo. Here one may speak only of some individual data belonging to various (mainly the last) stages of oogenesis of some of the representatives of this genus - the Atlantic salmon, Salmo salar (8, 16), and the Sevan trout, Salmo

* The numbers in the right-hand margin indicate the corresponding pages in the original text. (Tr.).

ischchan (13, 14). A maturity scale for the ovaries of the Atlantic salmon is present in the study of L. S. Berg (2), though this was not compiled on the basis of a study of the oogenesis of the subject under consideration, but was taken only as an example from the study of K. A. Kiselevich (7), who proposed a five-step scale for determining the degree of maturity of the gonads of the Caspian shad.

On the basis of the literature data concerning oogenesis in salmonids (1, 5, 6, 9, 10, 15, 24, 29) some idea may be obtained about some of the features of this process, that are characteristic of this family as a whole. Thus, in the egg cells of the studied species of fishes (whitefish, Caspian inconnu, Atlantic salmon, some Far-Eastern salmons) there is noted the formation of similar inclusions: vacuoles appearing in the peripheral layers of the cytoplasm in the early stages of oogenesis, fatty inclusions and yolk. However the sequence of the appearance of these is different in different species of fishes. In the egg cells of the Ludoga whitefish, Coregonus lavaretus ludoga, there initially appear the first droplets of oil and then the vacuolization of the cytoplasm commences (10). In the chum, Oncorhynchus keta, and the sockeye, Oncorhynchus nerka, in contrast, initially there occurs a partial vacuolization of the cytoplasm and then the oil and yolk become formed (24). As to the vacuolar inclusions in the oocytes of salmonids, these are apparently identical to those vacuoles, containing a mucopolysaccharide substance, which are characteristic in general of the egg cells of bony fishes and which are in essence cortical alveoli (18, 27, 28). A phenomenon that is inherent to the oogenesis of salmonids, possessing large eggs, may be considered to be

the displacement of the nucleus towards the animal pole, which occurs during the process of trophoplasmatic growth of the egg cells long before they complete their growth (19, 24, 29). Finally, a characteristic feature of all of the salmonids is the process of the coalescence of the lump-like yolk into a compact homogeneous mass during the period of the preparation of the oocytes prior to ovulation.

Possessing several features that are common to all, the process of oogenesis in each of the above-mentioned species undoubtedly has its own characteristic features both with respect to the morphology as well as in the duration of the individual stages. This, in particular, gives rise to the necessity for carrying out special studies of the development of the egg cells in each new species. 59

Serving as material for the present study were the ovaries of various races of the Sevan trout. It should be noted, however, that from the morphological aspect no fundamental differences were found in the oogenesis of the different races, and therefore below a single description will be given of this process for the Sevan trout in general.

The material, collected over a four-year period (1958-1961), embraces almost all of the seasons of the year and various stages of the life cycle of the trout: the growth period, the period when the trout prepare for spawning and acquire the breeding coloration, and the spawning period. In total, about 1300 ovaries of the Sevan trout were examined in histological preparations. The material was fixed with Bouin's fixative and was embedded in paraffin in the usual way. 5 to 7 μ thick sections were stained with Heidenhain's haematoxylin, and also with Heidenhain's Azan stain.

The data obtained showed that the egg cells of the trout pass through several developmental phases, each of which is characterized by a particular, qualitatively distinct process.

The study was commenced from the moment when the egg cells enter into the period of protoplasmic growth. The preceding period of oogonial division, and also of the nuclear transformations of the oocytes, was not considered by us. Within the period of the protoplasmic growth many authors (11, 12) distinguish two phases of development of the oocytes: the phase of the juvenile oocyte and the phase of the oocyte with a one-layered follicle. The differences in the structure of the egg cells at these two stages of development, in so far as may be judged by the available data, mainly concern their volumes and the structure of their envelope: the younger oocytes possess only an ectoplasmic membrane, while subsequently around them there is formed an envelope of follicular epithelium. In the Sevan trout, as shown by the data obtained, it was not possible to draw a distinct boundary between these two phases. Nevertheless, during the process of protoplasmic growth its egg cells not only increase in volume but also change their structure in a particular fashion, which is manifested even in one and the same preparation of an ovary, since the trout is characterized by having a marked asynchrony in the development of the oocytes (especially in the early stages of maturity of the ovaries). Refraining from distinguishing any particular phases, we will only describe those forms of egg cells of the period of protoplasmic growth, which we were able to observe.

A most striking feature is that in the comparatively smallest oocytes (diameter 50 - 100 μ) the plasma is most intensively stained and most frequently appears homogeneous (Figure 1a). The nucleus in such darkly stained egg cells is displaced right up against the boundary of the cell, and the cells themselves may take on various irregular forms under the pressure of the surrounding oocytes. In larger oocytes, which, as previously, still have an excentrically situated nucleus, within the plasma two sections with a differing density of coloration become more and more differentiated (Figure 1 b, v): against the overall more lightly coloured background of the cytoplasm there becomes differentiated a darkly coloured section, adjacent to the nucleus and having a very variable form. As the egg cell grows one may see how the nucleus gradually moves into the center, while the darkly coloured portion of plasma, earlier represented by a compact area, stretches out, breaks up into separate fragments and becomes arranged around the nucleus in the form of a ring (Figure 1 g, d, e, zh). During the process of the subsequent growth of the oocyte the fragments of this ring become smaller and smaller and more and more lightly coloured, they move away towards the periphery, take on the form of weakly coloured flocculi and, finally, disappear completely (Figure 1 z, i, k, l). The oocyte of the Sevan trout, having attained the completion of protoplasmic growth (diameter 400 - 500 μ), has a centrally situated nucleus and a homogeneous lightly coloured plasma (Figures 1 l, 2).

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The trophoplasmatic growth of the oocytes of the Sevan trout, as in other salmonids, is accomplished by means of three kinds of inclusions: cortical vacuoles, oil droplets and yolk.

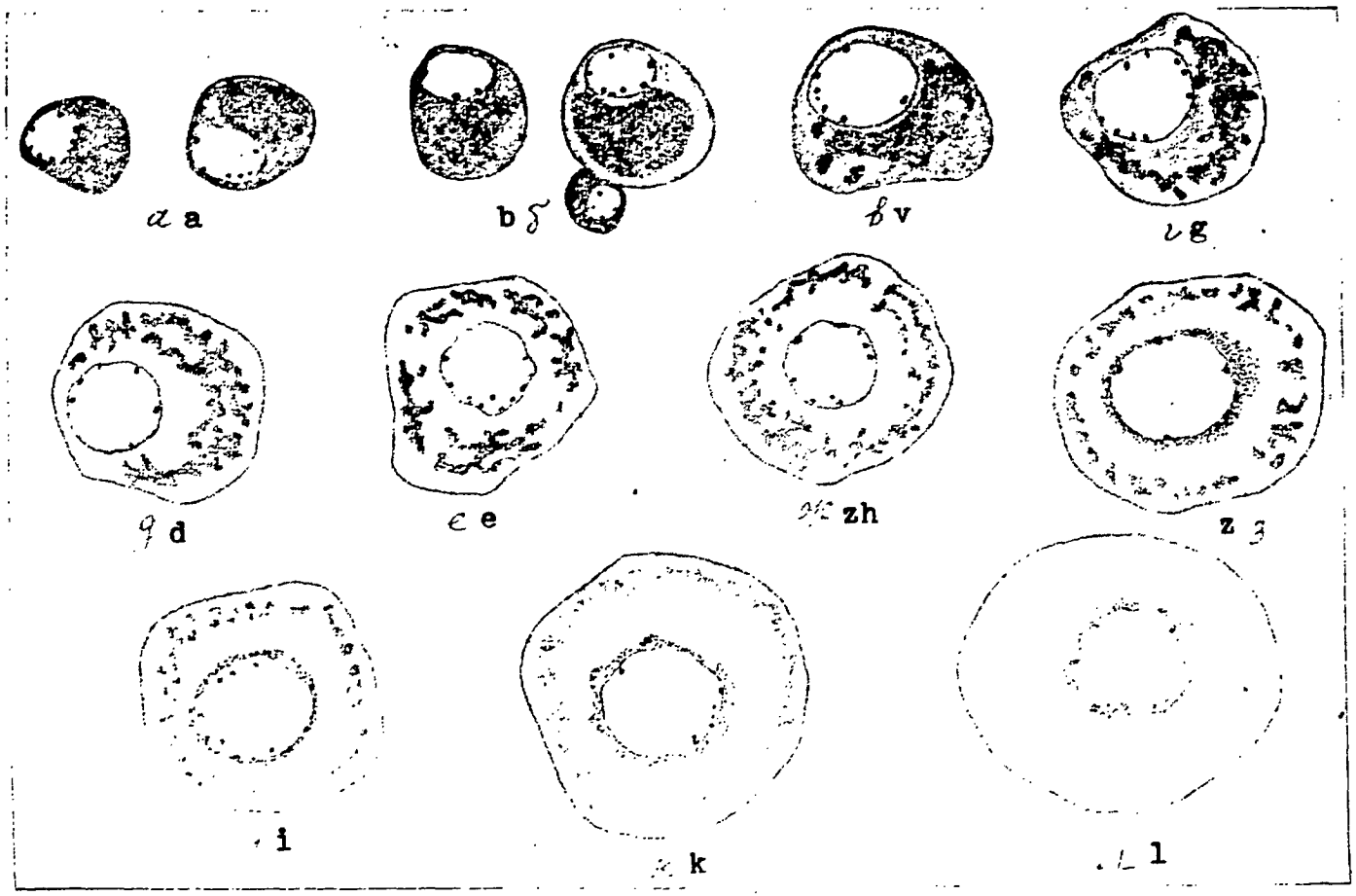

Рис. 1. Овоциты форели в период протоплазматического роста. ок. 7, об. 20, рисовальный аппарат РА-4, рисунки выполнены на уровне предметного столика микроскопа с одного препарата яичника.

Figure 1. Trout oocytes during the period of protoplasmic growth. Ocular X7, objective X20, drawn with an RA-4 apparatus: drawings made at the level of the microscope stage from one ovary preparation.

The accumulation of these by the oocytes occurs in a definite sequence, in accordance with which during the period of the trophoplasmatic growth we may differentiate several phases. These may be arbitrarily designated as the phase of vacuolization, the phase of oil formation and the phase of yolk formation.

The phase of vacuolization commences with the appearance of small droplets of a substance which is stained a light-bluish colour with aniline blue, in the peripheral layers of the plasma of the oocyte (Figure 3). As they grow they are transformed into round vacuoles, the number and dimensions of which gradually increase. On account of the accumulation of only this type of inclusions the oocyte of the Sevan trout increases in size, on average, to 900 μ in diameter, while the zone of vacuolization within the oocyte extends from the periphery towards the center to approximately 2/5 of its radius (Figure 4).

The subsequent growth of the oocyte now proceeds by means of two kinds of inclusions: the cortical vacuoles and the oil droplets; and the oocyte enters into the phase of oil formation. In the preparations the sites of deposition of the oil are detected by the cavities which arise as a result of the dissolution of the oil during fixation and the subsequent treatment with alcohols. The first small droplets of oil appear in the plasma zone around the nucleus, which is free of the vacuolar inclusions, and they form a ring around the nucleus (Figure 5). This ring gradually becomes wider due to an increase in the number and an enlargement of the oil droplets and, finally, it connects up with the zone of cortical vacuoles, which is growing in from the periphery (Figure 6). The diameter of the oocyte at this time attains a size of 1200 - 1400 μ.

Рис. 2. Овоциты форели на последних ступенях периода протоплазматического роста. Микрофотография, ок. 7, об. 20.

Рис. 3. Фаза вакуолизации цитоплазмы. Микрофотография, ок. 7, об. 20.

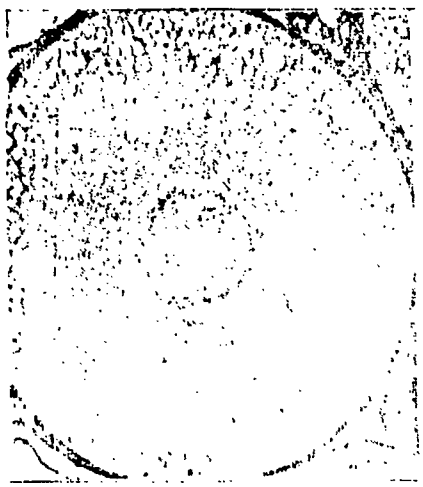

Рис. 4. Фаза вакуолизации цитоплазмы. Микрофотография, ок. 7, об. 20.

Рис. 5. Фаза жиробразования в овоцитах форели. Микрофотография, ок. 7, об. 20.

Figure 2. Trout oocytes in the last stages of the period of protoplasmic growth. Photomicrograph, oc. X7, ob. X20.

Figure 3. Phase of vacuolization of cytoplasm. Photomicrograph, oc. X7, ob. X20.

Figure 4. Phase of vacuolization of cytoplasm. Photomicrograph, oc. X7, ob. X20.

Figure 5. Phase of oil formation in trout oocytes. Photomicrograph, oc. X7, ob. X20.

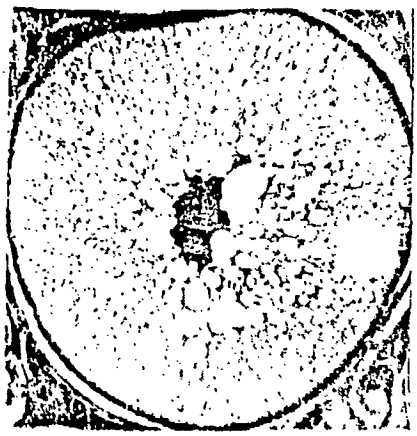

Рис. 6. Фаза жирообразования в ооцитах форели. Микрофотография, ок. 7, об. 8.

Рис. 7. Фаза желткообразования при центральном положении ядра. Микрофотография, ок. 7. об. 8.

Рис. 8. Фаза желткообразования при центральном положении ядра. Микрофотография, ок. 7, об. 3.

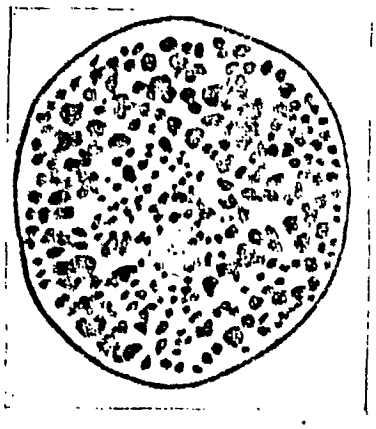

Рис. 9. Фаза миграции ядра к анимальному полюсу. Микрофотография, ок. 7, об. 3.

Figure 6. Phase of oil formation in trout oocytes. Photomicrograph, oc. X7, ob. X8.

Figure 7. Phase of yolk formation with a central position of the nucleus. Photomicrograph, oc. X7, ob. X8.

Figure 8. Phase of yolk formation with a central position of the nucleus. Photomicrograph, oc. X7, ob. X3.

Figure 9. Phase of migration of the nucleus towards the animal pole. Photomicrograph, oc. X7, ob. X3.

The following phase of development of the egg cells of the Sevan trout is characterized by the appearance of yolk within the cells, on account of the accumulation of which there occurs an extremely intensive growth of these egg cells, and in the end result this yolk makes up the bulk of the contents of the mature egg. Initially the process of yolk formation is accompanied by a no less intensive accumulation of oil, but subsequently it becomes predominant. The first yolk inclusions in the form of small granules, as well as of larger yolk spherules, which stain to a light blue colour with the Azan method, appear either in the portions of the cytoplasm around the nucleus amidst the oil droplets or they form a peripheral annular zone, or else they appear simultaneously in both of these places (Figure 7). Subsequently the process of yolk formation proceeds most intensively in the central region of the oocyte, where the mass of yolk globules, staining to a red colour (with azocarmine according to Heidenhain's method) as it becomes denser, proliferates and pushes out towards the periphery the zone of cortical vacuoles; this latter zone becomes more and more narrow (Figure 8). This stage of development of the trout egg cells, as previously, is characterized by a central positioning of the nucleus. The diameter of the largest egg cells that retain this structural plan is 2000 - 2500 μ. After this one may observe how the nucleus migrates from the center towards the animal pole (Figure 9) and, as the oocyte grows, it approaches nearer and nearer to this point (Figure 10). The polar differentiation of the oocyte is intensified during the course of its development not only due to the migration of the nucleus but also in connection with the

characteristic distribution within it of the different fractions of the yolk. Fine-grained yolk accumulates in the animal region, while coarsely floccular yolk occupies the vegetal region. The displacement of the nucleus towards the animal pole, occurring during the process of the growth of the oocyte, seems to us to be a qualitatively new phenomenon in comparison with those which we observed up to this time. In addition, during this period a considerable acceleration in the growth of the oocyte may be noted. All of this taken together leads us to think that it would be desirable to differentiate this stage of the development of the oocyte as an independent phase, which we have arbitrarily designated as the phase of the migration of the nucleus towards the animal pole. Then the preceding stage may be called the phase of yolk formation with a central position of the nucleus. At the end of the phase of migration of the nucleus the egg cells attain their definitive size (diameter 4500 - 5000 μ), while the nucleus approaches almost right up against the membrane of the oocyte (Figure 11). In the fixed ovum it may be seen through the membrane in the form of a white spot.

The trout egg cells, having completed their growth, still continue to remain for a long time within the tissue of the ovary. During this period no new formation of substances now occurs within them, but there may be observed a fundamental reorganization of their internal structure, due to which they acquire the structure of mature eggs and prepare themselves for ovulation. Since a description of these processes has already been presented by us (13), we will speak very briefly about them here.

As in the other salmonids, in the egg cells of the Sevan trout during the period of maturation there occurs a coalescence of the floccular yolk into a compact spherical mass, while the cytoplasm, separating away from the yolk and oil, becomes concentrated close to the animal pole. In the trout the process of the coalescence of the yolk commences in the center of the oocyte and gradually embraces the whole of its vegetal region. The loose floccular yolk is preserved for the longest time in the animal region (Figure 12). In the composition of the nucleus there occur significant changes, associated with meiosis: the nuclear membrane breaks down and the karyoplasm flows out into the cytoplasm; the nucleoli, which undergo several complex morphological transformations, disappear. During this period the various patterns of the first maturation division have been observed and described, right up to the formation of the metaphase spindle of the first maturation division.

The whole complex of processes, associated with the preparation for ovulation of the oocytes, terminating the trophoplasmatic growth, is considered by us as a new phase of the development of the oocytes, which we arbitrarily call the phase of the pre-ovulation structural transformations of the oocyte, which has attained its definitive size. Then the following and last stage of oogenesis will be the phase of the mature ovulated egg. This last, as was already mentioned above, is characterized by the complete coalescence of the yolk and by the presence of the plasmatic disc on that part of the surface of the spherical yolk mass, which is facing the animal pole (Figure 13). The oil droplets are situated in the boundary zone between the yolk and

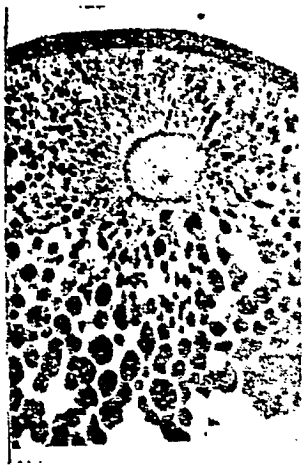

Рис. 10. Фаза миграции ядра к анимальному полюсу. Микрофотография, ок. 7, об. 3.

Рис. 11. Овоцит форели, закончивший трофоплазматический рост. Микрофотография, ок. 7, об. 3.

Рис. 12. Фаза предовуляционных преобразований структуры овоцита, закончившего рост — частичное слияние желтка, переход ядра в мейотическое состояние. Я — ядро. Микрофотография, ок. 7, об. 3.

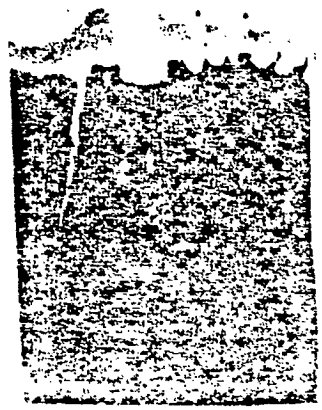

Рис. 13. Фаза зрелого яйца форели. Микрофотография, ок. 7, об. 3.

Figure 10. Phase of the migration of the nucleus to the animal pole. Photomicrograph, oc. X7, ob. X3.

Figure 11. Trout oocyte, having completed trophoplasmatic growth. Photomicrograph, oc. X7, ob. X3.

Figure 12. Phase of pre-ovulation structural transformations of the oocyte, having completed growth - partial coalescence of the yolk, transition of nucleus into meiotic state. n - nucleus. Photomicrograph, oc. X7, ob. X3.

Figure 13. Phase of mature trout egg. Photomicrograph, oc. X7, ob. X3.

the cytoplasm. In the cortical layer of the plasmatic disc close to the micropyle there is found the metaphase spindle of the second maturation division, lying perpendicularly to the surface of the egg. 66

It should be noted that the question, as to in which phase of meiosis ovulation occurs in the trout, remained unclear for some time. On the one hand, it was stated in several studies that in the mature eggs of the brook trout the metaphase spindle of the first maturation division is present (21, 22, 23). The same conclusion, which was subsequently found to be erroneous, was also made by the present author in a study of the maturation processes of the eggs of the "gegarkuni"* Sevan trout (13). In all of these cases the circumstance which led the investigators into error was that these authors were unable to find close to the metaphase spindle, present in the mature unfertilized trout egg, any traces of a previous first maturation division, such as a reduction body** or a reduction slit. On the other hand, data from studies devoted to the investigation of meiosis and fertilization in representatives of Far-Eastern salmonids (17, 25) indicate that in these, as in most other fishes, ovulation occurs at the metaphase of the second maturation division. It was natural to assume that in the case of the trout an error was made and to attempt to obtain evidence for this. Such evidence, though indirect, is provided by the data on the processes of fertilization in the "gegarkuni" Sevan trout. Examining the egg cells of this trout at various time intervals after their insemination, we found in them the extrusion of only one, i.e. the

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* "gegarkuni" - a fast growing form of the Sevan trout. (Tr.).

** A literal translation of the Russian "redukrtsionnoe telo". This is the polar body, which latter term is hereinafter used in this translation. (Tr.).

the second polar body, after which there occurred the fertilization proper, the fusion of the pronuclei, and the cleavage divisions commenced. Serving as the basis for these conclusions were the following data: 20 minutes after insemination (incubation at a temperature of 6-8°C) an early anaphase configuration was found in the trout egg (Figure 14a), and after 1 hour this was already a late anaphase (Figure 14b). Then the beginning of the formation of the polar body was observed. The meiotic configuration becomes elongated and its apical end, together with the surrounding plasma, protrudes above the surface of the plasmatic disc (Figure 14v - 1 hour and 20 minutes after insemination). After 1 hour and 45 minutes the unthreading of the polar body occurs (Figure 14g), after which commences the formation of the female pronucleus. We can see the stages of this process in Figure 14d (2 hours and 30 minutes after insemination) and Figure 14 e (3 hours and 30 minutes after insemination). 5 hours after insemination the female and male pronuclei are found deep inside the embryonic disc, touching one another (Figure 14zh), and 1 hour later they are already in the process of fusing (Figure 14z). 7 hours after insemination one can see one of the initial stages of the formation of the metaphase spindle of the first cleavage division (Figure 14i), and after 1 more hour the spindle configuration is already formed to a considerable degree (Figure 14k). 10 hours after insemination the embryonic disc of the trout egg is found to be divided into two blastomeres.

The data presented provide evidence that in the fertilized trout egg there is completed the second maturation division and that, therefore, the ovulation in the trout is carried out

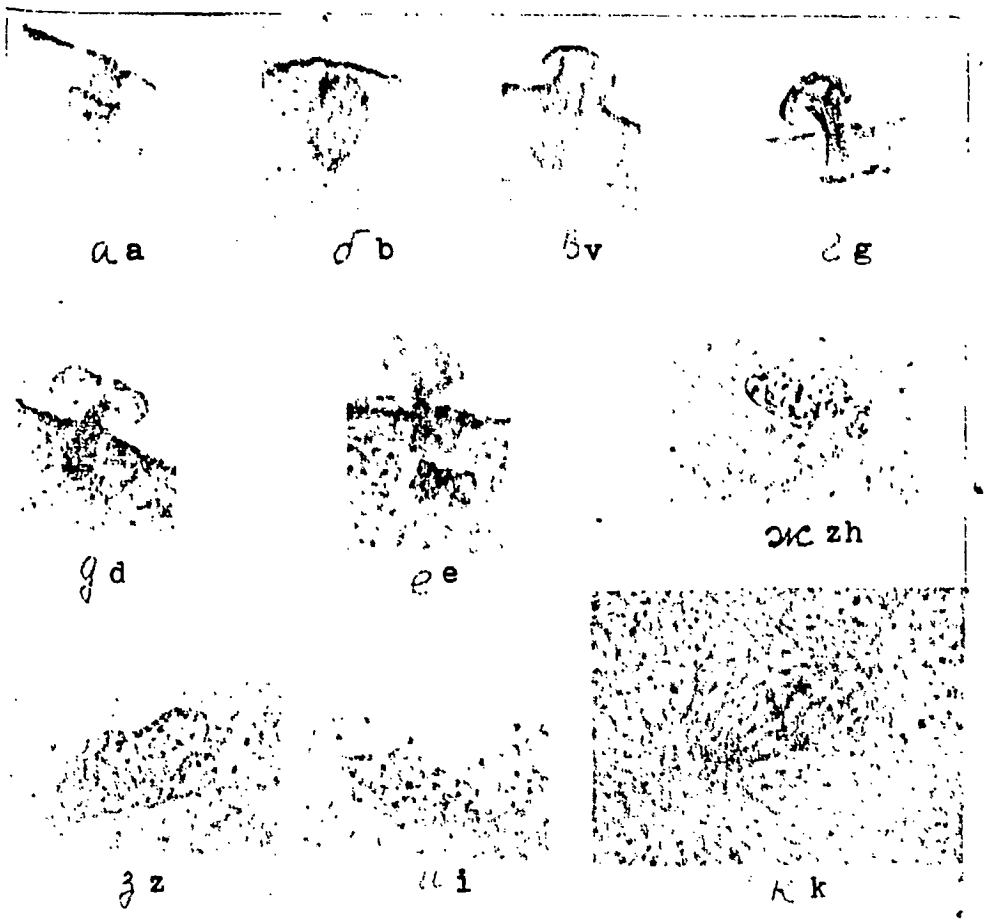

Рис. 14. Завершение II деления созревания, оплодотворение и начало I деления дробления в осемененных яйцах севанской форели гегаркуни. Микрофотографии. ок. 7, об. 90.

Figure 14. Completion of the second maturation division, fertilization and commencement of the first cleavage division in inseminated eggs of the "gegarkuni" Sevan trout. Photomicrographs, oc. X7, ob. X90.

during the metaphase period of the second maturation division. From this it may be concluded that the spindle figure which we find in the oocyte of the Sevan trout, still enclosed in the tissue of the ovary but already containing the fully coalesced yolk, also pertains to the second maturation division. In its location and size this spindle does not differ from that which

is found in the ovulating egg. Previously we also assigned this meiotic figure erroneously to the first maturation division (13).

Concerning the overall division of oogenesis in the Sevan trout into phases, it should be noted here that we selected as indicators of the initiation of a new phase the beginning of some or other qualitatively new process that was occurring within the egg cell: the synthesis of a new substance, the beginning of the bipolar differentiation of the oocyte etc. Over the course of each of the described phases of development there naturally occur certain changes in the structure of the egg cell, 68
but these changes are basically of a quantitative character: there is an increase in the mass of substances synthesized by the cell, the nucleus comes to lie comparatively closer to the animal pole etc. As will be shown later, the rate of growth of the trout oocyte increases as it enters into each new phase of development.

It should be noted that in the process of trophoplasmatic growth of the egg cells in the masu (Oncorhynchus masu) (29), as well as the chum (Oncorhynchus keta) and sockeye (Oncorhynchus nerka) (24), stages have been distinguished which are in principle similar to those in the Sevan trout. The authors distinguish the following stages in the development of the egg cells: stage of vitelline vesicles (cortical vacuoles), stage of oil droplets, primary, secondary and tertiary yolk stages - based on the degree of filling of the oocyte with yolk (in the Sevan trout all of these are united in the phase of yolk formation with a central position of the nucleus), the stage of migration of the nucleus, the pre-maturation stage (in the trout this

corresponds to the phase of the pre-ovulation structural transformations of the oocyte that has completed its growth) and the definitive maturation stage (in the trout - the phase of the mature egg).

Over the course of the period of protoplasmic growth the structure of the egg cells of the Sevan trout changed in a particular manner, as has been shown above. These changes mainly concerned the location of the nucleus and the state of the cytoplasm. A ring of darkly coloured cytoplasmic fragments around the nucleus, superficially similar to that which is present in the oocytes of the Sevan trout at certain stages of its development, has been described by several authors in the oocytes of certain other species of fishes under the name of a circumnuclear ring. According to the data of N. L. Gerbil'skii (3, 4) in the mirror carp this structure represents a fatty-lipoid substance and has a seasonal character. It is present in the oocytes during the winter and spring, but disappears in the summer. It is not possible to say anything about the nature and significance of the similar formation in the egg cells of the trout or to make any analogies between this and the circumnuclear ring in the oocytes of other fishes on the basis of the available data. We are justified only in noting that in the Sevan trout this structure appears, becomes modified and disappears in connection with the growth and development of the egg cell and in no way has a seasonal character, as in the carp, since it is found in the oocytes during the period of protoplasmic growth irrespective of the season of the year.

In the maturity scale for the ovaries of fishes, which has been accepted at the present time by ichthyologists and fish culturists (11, 12, 20 et al.), the various stages of maturity of the ovaries are characterized in the following manner: first - in the ovary there are present oogonia, oocytes in the period of the synaptic pathway and oocytes entering into the period of protoplasmic growth. Second - an older generation of oocytes is in various stages of protoplasmic growth. Over the course of the third stage there proceeds the trophoplasmatic growth of an older generation of oocytes. Finally, the fourth stage of maturity of the ovaries is characterized ~~is characterized~~ by the presence in them of oocytes that have attained their definitive size, while the fifth stage is characterized by the presence of mature ovulated eggs. In the Sevan trout, as has 69
been shown above, the period of the trophoplasmatic growth of the egg cells is divided into four phases, in accordance with which within the third stage of maturity of the ovaries we may distinguish four substages.

Taking into consideration all that has been presented above, one may represent the maturity scale for the ovaries of the Sevan trout in the following manner:

Stage I - ovaries in the form of short, flat, pale-pink strands; the oviferous lamellae are not visible with the naked eye, they can be distinguished only under a magnifying glass. The ovaries contain oocytes in the period of the synaptic pathway and at the very beginning of the period of protoplasmic growth.

Stage II - ovaries in the form of wider pink small ribbons. The oviferous lamellae are clearly distinguishable

with the naked eye, though the egg cells are poorly visible. The latter are passing through the period of protoplasmic growth.

Stage III: III-A - ovaries of a greyish-pink colour, egg cells of older generation distinguished by the naked eye in the form of small light-coloured dots. They are in the phase of vacuolization of the cytoplasm; III-B - ovaries light-grey or whitish-grey, oocytes 1 - 1.5 mm in diameter and they are in the phase of oil formation; III-V - ovaries of a light-yellow or yellow colour, the egg cells with a diameter of 1.5 - 2.5 mm are in the phase of yolk formation with a central position of the nucleus; III-G - ovaries large, of an orange colour, egg cells large but they have not yet attained their definitive size, 2.5 - 4 mm in diameter, they are in the phase of the migration of the nucleus towards the animal pole.

Stage IV - ovaries bright-orange, they occupy a large part of the body cavity of the fish, the egg cells of the older generation have attained the definitive dimensions, 4.5 - 5 mm in diameter (phase of pre-ovulation structural transformations of the occyte that has completed growth).

Stage V - the mature eggs have passed out of the ovaries into the body cavity of the fish, the eggs pass out of the genital opening when the abdomen of the fish is pressed or when the body of the fish is bent.

The females of the Sevan trout possessing gonads in maturity stages II, III-A, III-B, III-V and in the beginning of III-G have the characteristic appearance of the feeding (non-spawning) trout - a light colour of the integument, a silvery lustre of the scales, and a flexible and well-fattened body.

During the period when the ovaries of the trout approach the end of substage III-G there appear in the trout the first features of the breeding coloration: scales that were more difficult to scrape off than in the non-spawning fish, the genital papilla enlarges, mucus appears on the surface of the body. When the ovaries pass into stage IV of maturity the spawning coloration is already clearly expressed in the females: the characteristic dark-olive colour of the body, the change in form of the head etc.

It should be noted that the term "yalovaya" trout,* accepted both in the scientific literature on the fishes of Lake Sevan as well as by workers in the fishery, does not refer to any sterility of the fish but only to an immature state of its genital products and the corresponding physiological state of its organism. 70

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* The Russian word "yalovaya", translated above by "non-spawning", literally means "barren". (Tr.).

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