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Geschlechtsreifung und Laichreifung bei Teleosteen
--ein Ueberblick¹

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Sexual maturation and spawning maturation in teleostean fishes
--A review¹

by

VOLKER HILGE,

Coastal and Inland Fisheries Institute of the Federal Fisheries
Research Institution, Ahrensburg External Branch ("Institut fuer
Kuesten- und Binnenfischerei der Bundesforschungsanstalt fuer
Fischerei, Aussenstelle Ahrensburg")

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Abstract

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The histological and cytological processes during the maturation of the ovary and oocytes in teleostean fishes are described in order to give a representation of the developmental phases from oogonia to ripe eggs synchronously with the chromosomal activities in the nucleus and the physiological - biochemical changes in the ovary.

¹ The present study is part of a dissertation written at the Kiel External Branch of the Federal Fisheries Research Institution ("Bundesforschungsanstalt fuer Fischerei, Aussenstelle Kiel"), under the direction of Prof. F. THURLOW.

1. Introduction

"Sexual maturation" and "spawning maturation" characterize certain processes of sexual development. The first of these terms refers to the single process of the development of the gonads, from the embryo to the animal capable of reproduction, while the latter comprises the usually cyclical process of the maturation of the genital products.

The development of the ovary and of the oocytes in teleostean fishes also have been the subject of numerous studies. Some of the findings will be presented briefly in the present review. Our purpose is to subdivide the process of ovarian development into natural stages; for only these can serve as the basis 173 for a maturation chart to prevent an inaccurate evaluation of the maturation processes.

In the literature, the terms "oocyte" and "egg" are often used synonymously. I should like to define these two terms in such a way that "oocyte" will refer to the germ cell produced by the oogonial divisions up to the ovulation stage, and "egg" will refer to the cell ready to take up the sperm.

2. Structure and development of ovary and oocytes

In vertebrates, the different organ systems develop at different rates. The gonads do not begin to develop until the coelom is completely formed. Then, the genital primordia unfold their specific growth processes within the coelom.

2.1. The ovary

The ovary is the organ in which the development of the sex cells is completed (WALDEYER 1870). It originates from the mesodermal, dorsal peritoneum, and is suspended dorsally in the body cavity on both sides of the mesentery, attached to the mes-ovaria (HARDER 1964). FRANZ (1910) identified the first primitive germ cells in the mesenteries of the Plaice, and described the germinal epithelium produced by division from these cells. This epithelium is present initially in the form of a ridge, but as it grows, it changes into a fold, densely interspersed with elements of connective tissue. The development of the ovary is completed with the formation of plicate portions of connective tissue towards the inside. It now has a tubular shape.

Histologically, the ovary consists of four different elements: The germinal epithelium arises by continuous division from the primitive germ cells. The stroma and the follicle, which are composed of connective tissue, are surrounded by a pouch of connective tissue. This pouch is traversed by longitudinal, annular, and radial muscles, sometimes stratified concentrically, but sometimes also interwoven (GOETTING 1961). This structure prevents the ovary from rupturing when it expands considerably during the maturation of the eggs. Cranio-caudal contractions of the muscular tube lead to the ejection of the eggs.

2.2. The germ cells

In some species of animals, the two primitive germ cells have been identified at a very early stage. In Ascaris megalocephala, the germ cells appear already after the two-cell stage (KORSCHLDT 1936). In birds and mammals, they can be identified in the primitive streak. Their location implies that they originate from the mesodermal epithelium. Cells which must be designated as primitive germ cells have been identified in the embryos of all classes of vertebrates, from the Cyclostomata to the mammals. They migrate into the gonadal primordia from the intestinal wall (ROMER 1966). It is not yet clear, however, whether they should be considered as the source of all eggs and spermatozoa. Possibly they have only a stimulating function, one of setting the process of gametogenesis in motion. In teleostean fishes, the gametes themselves construct the germinal epithelium.

The oogonia pass through several mitotic divisions, finally reaching the stage of primary oocytes. These may be differentiated from the preceding stage by the presence of nucleoli. The nucleus is relatively large and has darkly staining chromatin. For Platycoecilus, it has been demonstrated that most of the oocytes do not arise from the primordial germ cells, but from the cells of the gonadal epithelium. Also FRANZ (1910) believes that, from the occurrence of only a small number of oogonial mitoses, it may be concluded that many oogonia arise from the medial epithelium, which is initially still inert. The two types--oogonia and primary oocytes--are subsequently visible in microscopic sections of all phases of ovarian development.

2.3. Transitory intersexuality

HARTMANN's (1956) principle of bisexual potency finds confirmation also in the teleostean fishes. This principle states that every germ tract cell has the capacity to develop into sperm or egg. This applies to the developmental period during which the ovary is in the process of formation. Until the transformation of the genital ridge into the genital fold, it is not yet possible to identify the growing organ as an ovary or a testicle. In the Plaice, this can be done only when the incipient formation of the follicle takes place by inward proliferation of connective tissue from the median epithelium. MRSIC (1930) has designated the condition of the preceding phases as transitory intersexuality. In studies concerning the sexual differentiation of juvenile Salmo trutta fario, he proved that in the great majority of these fish, a bisexual gonadal primordium is present. For he found that juvenile animals which, in his opinion, would have developed later as males, first passed through a female phase. Sections through the gonads showed "egg" cells, which underwent involution during the course of further development. Due to a failure to differentiate, animals could even persist in the androgynous state. HÄMPPEL (1948) arrived at the same results in his studies on juvenile Salmo trutta fario and S. trutta lacustris. In both varieties, this author found 54% females, 28% males, and 18% intersexes. With respect to the latter, he assumed that they later develop as males. By administering prolactin,

he was able to change adult fish persisting in the intersex phase into male animals, thus proving that the gonads are governed by the hypophysis. Also other authors have demonstrated the formation of bisexuals and intersexes in various fish species (VAN DEN BROEK 1933). LILLELUND (1961), in his investigations concerning the Smelt, describes this phenomenon in adults as well as in juvenile animals.

2.4. Further development of the oocytes

As already mentioned, the last mitoses of the oogonia give rise to the primary oocytes. These do not undergo any further division until maturation, but they alter their structure by means of various transformations and new formations. These include especially the formation of a follicle. Nucleoli are formed in the nucleus and migrate to the periphery of the nucleus. Simultaneously, the cytoplasmic membrane surrounding the nucleus grows by leaps and bounds, but not very quickly in comparison with the rapid growth of the oocytes which begins later. In his studies on the Plaice, FRANZ (1910) found certain oocyte phases in which development was interrupted by long resting phases.

The primary oocyte membrane is adjoined by a single-layered follicular epithelium. This epithelium exhibits no cell boundaries, but the nuclei are readily visible. During the course of the growth which now begins, a second follicular layer, the theca

folliculi, is added. The nucleoli begin to emerge from the nucleus. The cytoplasm becomes stratified in such a way that the perinuclear zone is followed by a homogenous layer and a colorless layer. In the Gadidae, a layer radially striated in cross section--designated by GOETTING (1961) as the stratum radiatum--appears in the marginal zone. Later, the cortical vacuoles are formed in the marginal zone.

According to FRANZ (1910), the follicle is composed of connective tissue and germinal epithelium. The cells of the inner follicular layer have little chromatin. They become flattened by the pressure of neighboring cells, surround the oocytes, and form the membrana granulosa (BOWERS and HOLLIDAY 1961, POLDER 1961) of the follicle. The outer follicular layer arises by the deposition of connective tissue fibroblasts on the granulosa. The surface of the oocytes adjacent to the follicle cells develops microvilli. At the base of these, a layer designated by FLUEGEL (1967) as the zona radiata externa is deposited. Between this and the oocyte membrane, the zona radiata interna becomes embedded. Its pore canals contain the microvilli as well as processes of the follicle cells. Both are withdrawn at maturity. The microvilli degenerate and the pore canals become closed. This is the process described by FLUEGEL for the formation of the egg membrane in Salvelinus fontinalis, Salmo irideus, Fundulus heteroclitus, Perca fluviatilis and Myoxocephalus scorpius. According to FLUEGEL (1967), the zona radiata ("chorion", corona radiata, cortex radiata,

cortical layer--not to be confused with the stratum radiatum of the Gadidae in an earlier phase of oogenesis) is a formation of the follicle. It is one of the secondary egg membranes. Only the oocyte membrane is primary. Tertiary membranes are formations of the sexual discharge passages (e.g., the gelatinous membrane in Salmo salar).

STERBA (1957) calls attention to special processes of the oocyte membrane which occur in certain fish species. These represent species-specific differentiations serving to attach the membrane to the substrate. They show a great adhesive capacity in water. Their differentiation begins already before the formation of the cortical layers.

According to GOETTING (1961), the first masses of yolk appearing in the Whiting are perinuclear, whereas according to FRANZ (1910), vitellogenesis in the Plaice begins at the periphery. In Carassius auratus, small vacuoles appear at the periphery of the cytoplasm when the oocyte has a diameter of 0.1 to 0.15 mm. Shortly afterwards, vitelline spheres appear between the vacuoles (CHU HUNG WEN and LEE SIN REN 1964). In time, the vacuoles are supplanted and dissolved.

Towards the end of the development of the oocytes, the masses of yolk fuse. The germ cells become transparent and increase their volume considerably by uptake of water. The nucleus migrates from the center to the periphery. The cytoplasm surrounding

the nucleus produces the animal pole, while the portion filled with yolk is called the vegetal pole. This process is known as bipolar differentiation of the cytoplasm. Shortly before the rupture of the follicle, the intercellular spaces between the follicle cells become filled. This is followed by the increase in the volume of the oocyte and ovulation. The egg is released into the lumen of the ovary. A varying number of micropyles may develop on the surface of the egg. The semen reaches the inside of the egg through one of these.

2.4.1. Comprehensive division of stages

SOROKIN (1957), following MEYEN (1939), LAPITSKY (1949) and NAUMOW (1956), divides the phase of rapid growth of the oocytes into four periods:

- (1) Vacuolization of the peripheral zone of the cytoplasm and incipient vitellogenesis,
- (2) the phase of intensive trophoplasmic growth,
- (3) the phase in which the oocyte is filled with yolk, and
- (4) the phase of the transparent oocyte, or the hydration phase. 176

Similarly, GOETTING (1961), following ARNDT (1960b), subdivides the entire development of the oocyte into four phases:

Phase I: Oocyte concentrically structured, the nucleus relatively large and vesicular, its profile circular. Cytoplasm basophilic, as are the one or more nucleoli present. Follicle single-layered.

Phase II: Enlargement of the surface of the nucleus due to undulation. Some nucleoli pass over into the cytoplasm. Stratification of the cytoplasm begins. Somewhat later, cortical vacuoles arise. Formation of the cortical layers begins. Follicle two-layered.

Phase III: Vitellogenesis begins. The cortical vacuoles are supplanted and disappear. Completion of the zona radiata.

Phase IV: The yolk granules fuse. The nucleus departs from the center of the egg. Polar differentiation of the cytoplasm. The oocyte thus loses its concentric structure.

This scheme allegedly applies to marine teleosts as well as freshwater fishes, even though it may be subject to variations within species.

The processes described above do not take place at a uniform speed. Instead, the diameter of the cell increases quite slowly initially during the deposition of the yolk. A rapid enlargement takes place only after the masses of yolk have flowed together, due to the intense swelling connected with the uptake of water. After the egg has been spawned, the perivitelline space develops. This is based on a swelling of the cortical vacuoles along the periphery (ARNDT 1956; DEVILLIERS and THOMOPOULOS 1954). One result of this swelling is the removal of the fertilization membrane.

2.5. Chromosomal processes

During the course of oogenesis, continuous mitoses take place. At the end of this series of divisions, the primary oocyte is present. The next phase is the period of maturation. The preparations for the maturation divisions begin already before the formation of the follicle. FRANZ (1910) reports that in plaice measuring from five to six centimeters in length, this process is already completed before the first winter. The leptotene phase opens the prophase of the maturation divisions, or conjugation. This phase is characterized by the fact that the chromosomes become visible. During the zygotene and pachytene phases, in which the chromosomes are finally close together, there may occur a clumping together of the chromatin due to fixation, the synapsis. The chromosomes do not become visible again until the end of the pachytene. According to STEGNER (1967), the diplotene represents the last substage of the premeiotic prophase before a period in which the chromosomes can no longer be identified. They reappear only shortly before the first maturation division. This leads to the secondary oocyte and the first polar body. Although the cytoplasm is divided unevenly, both cells still harbor the diploid number of chromosomes. Only the second maturation division, which now follows, leads to the mature egg together with its three polar bodies and a haploid number of chromosomes. The polar bodies perish during the course of further development. According to ARNDT (1960a), the first

maturation division in freshwater teleosts takes place already in the ovary shortly before spawning. The second division-- which may be either the division reducing the number of chromosomes or the division reduplicating the chromosomes, since their sequence is not fixed--may be postponed to the time after spawning and penetration by the sperm (HARDER 1964).

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2.6. Chemical changes during the maturation cycle

The processes described above for the growth of the oocyte may be explained by physiological - biochemical processes, through describing the quantitative and qualitative alterations of the material composition of the ovary and oocyte. Thus, NAUMOW (1956) pointed out that in the Murmansk Herring, which spawns in the late spring, a special composition of the blood corresponds to certain maturation stages. He related this to the hemoglobin content of the blood, which reaches its maximum values at the time of a maximum fat content and an optimal condition of the fish, viz., during the phase of the slow growth of the egg, at the beginning of yolk deposition (Table 1).

These values decrease at spawning maturity, reaching their lowest point in the spent fish. They do not rise again until the beginning of a new maturation period.

However, the periodical variations of the hemoglobin content during maturation are not the only chemical changes which have been studied. WENGI (1963) traced the cyclical

Datum ¹	Hämoglobingehalt ² (mg %)
Oktober ³ 1938	64,0-64,1
November 1938	64,5-65,5
Mai/Juni-1939	53,4-53,6
Juni/Juli ⁴ 1939	55,1-57,5

Table 1. Variation of the hemoglobin content of the blood in the Murmansk Herring (After NAUMOW 1956)

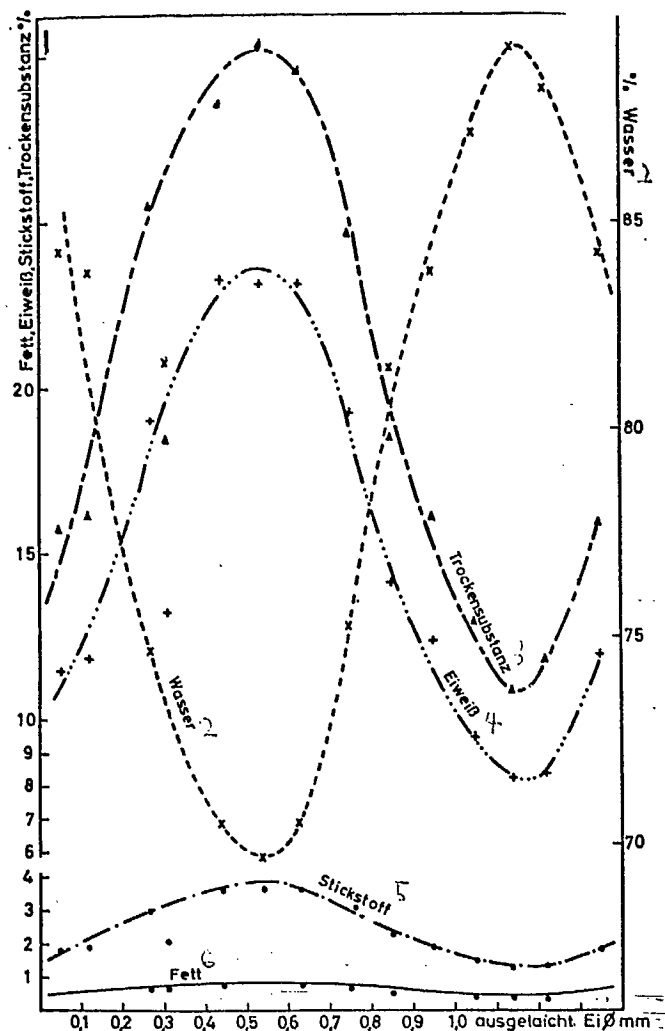
Key: 1- date 2- hemoglobin content 3- October 4- May-June 5- June-July (Read commas as decimal points.)

Monat ¹	Körperfettgehalt ² (%)
Juli/August ³	17
Oktober ⁴	12
Dezember ⁵	6-11
Januar ⁶	5-10
April	2- 3
Juni ⁷	13

Table 2. Variations of the content of body fat in the spring herring of the western Baltic Sea during the annual maturation cycle (After LUEHMANN 1952)

Key: 1- month 2- body fat content 3- July-August 4- October 5- December 6- January 7- June

variations in the material composition of the ovary in Baltic Sea codfish on the basis of, e.g., water content, content of dry matter, and protein content. Thus, he demonstrated that the water content decreased constantly during vitellogenesis down to 63%, with a sudden rise only at the time of swelling, to reach a maximum value of 88% in the flowing ovary, corresponding approximately to the value during the initial phases of ovarial maturation. The curve plotted for contents of dry matter and protein followed a course exactly the opposite to that of the water percentage. It increased steadily with the increasing average diameter of the egg during yolk deposition, up to 30% dry matter, falling to 12% in the flowing ovary. According to MENGI's data, spent ovaries, and also immature ovaries, contain about 16% dry matter (See graph).



Chemical changes in the ovary of codfish in the western Baltic Sea during the maturation cycle (From MENGI 1963)

Key: 1- Fat, protein, nitrogen, and dry matter 2- water
 3- dry matter 4- protein 5- nitrogen 6- fat 7- spent egg
 (Read commas as decimal points.)

The curve plotted for the water content of the cod ovary has been confirmed by H.M. HOFMANN (1971). She studied also Plaice and flounder from the western Baltic, and found a curve resembling that of the Cod for both species. Also EHLEBRACHT (1971),

who studied the conditions of Baltic herring spawning in spring and those spawning in autumn, arrived at essentially the same findings. In both races, the spent ovary has a high water content, but this decreases steadily during the maturation of the egg until the time of the intraovarial uptake of water, then rises rapidly. Once again, the curves found for contents of dry matter, protein, and fat showed the opposite pattern.

The maturation process is related also to the content of body fat in the fish. LUEHMANN (1952) showed that in herring of the western Baltic spawning in the spring, there is a relation between the body-fat content and the condition of the gonads. 178 Especially prominent phases were the beginning of a new maturation period, with a body-fat content up to a maximum of 17%, and the end of the spawning process, with the lowest fat reserves, at 2-3%. During the maturation of the gonads between these two phases, the fat content decreased continuously. However, the degradation of the fat reserves is not determined exclusively by the maturation cycle. In herring spawning in autumn, the minimum content did not coincide with the phase of the spent ovary; instead, it was distinctly higher than in the spring spawners, at 6-8%, and fell to 4% only in late winter. Hence, a certain amount of fat was still required in order to cover the energy requirements during the winter (Table 2).

Table 3 shows the extent to which especially the water content characterizes the changes in the cod ovary during the

Reifegrad n. MAIER	Gonadengew. in % vom Körpergew. 2 (%)	Gonaden- gewicht 3 (g)	Wassermenge 4 im Ovar		Gewicht d. 5 Trockensubst. im Ovar	
			(%)	(g)	(%)	(g)
II	0,9	9	84	7,6	16	1,4
III	2,9	29	72	20,9	28	8,1
IV	7,2	72	70	50,4	30	21,6
V	12,3	123	82	100,2	18	22,8
VI	19,8	198	88	174,2	12	23,8
VII	9,1	91	84	76,4	16	14,6

Table 3. Changes in the weight of water and dry matter, respectively, in the ovary of a female codfish (1000 grams fresh weight) during the course of the maturation cycle (calculated according to values reported by BERNER 1960 and MENGI 1963)

Key: 1- maturation stage (according to MAIER) 2- weight of the gonads in percent of the body weight 3- weight of the gonads 4- amount of water in the ovary 5- weight of dry matter in the ovary (Read commas as decimal points.)

course of the maturation process. BERNER (1960) has calculated the average percentage of the weight of the gonads in relation to the body weight for cod in the central region of the Baltic. Using the values reported by MENGI (1963) for the changes in the material components of the cod ovary during the course of the maturation period, we can now trace the changes in the absolute weight of water and dry matter, respectively, in relation to a codfish weighing 1000 grams.

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Table 3 shows distinctly that with the dry matter remaining about constant, only water is responsible for the sharp rise in the weight of the gonads during maturation phases IV to VI. The water content increases about seven times during yolk deposition, but the content of dry matter increases about 15 times. During the regeneration of the ovary, the content of dry matter must decrease again to one-tenth of its value in the spent ovary.

The process of the construction of the next generation of oocytes already takes place along with the processes of degradation, viz., the resorption of the follicle and unspawned eggs. The high water content of the spent ovary indicates a considerable amount of intraovarial fluid.

Beginning with phase IV, hardly any further transport of material into the ovary takes place. The slight increase may perhaps be explained by the fact that it is already to the benefit of the next generation of oocytes. But this would imply that the development of the oocytes from the reserves to the mature egg ready for spawning requires longer than a year.

2.7. The duration of the maturation of the gonads

The developmental period leading to the mature spawn may vary in duration. The time of the first spawning maturity is known for most fish species. In sturgeon (Acipenser sturio and A. huso), eels, or Hemichromis bimaculatus, it occurs after a number of years; in smelts, anchovies, Gobius or Taurulus, it is already reached at the end of the first year of life. Geographical aspects play an important role within a species. Thus, the Atlantic Codfish is sexually mature after five to eight years, while the Baltic Cod matures already after two or three years. The tropical Cyprinodontidae are only a few weeks or months old when they spawn for the first time. These fishes reach spawning maturity several times each year.

In spite of all these differences in time, it must be assumed that the process of the maturation of the oocytes is similar in all species, and this with respect to sexual maturation as well as the periodically recurrent spawning maturity. The latter cycle--which frequently lasts one year--applies to arctic - boreal and boreal species, not to the Cyprinodontidae mentioned above. PETERS (1957) demonstrated with Hemichromis bimaculatus that a new spawn matured within 6 to 22 days if the previous spawn had been lost due to non-fertilization of the eggs or if an ovary had been removed operatively prior to spawning maturity.

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2.8. Spawning types

Different types of spawners--viz., one-time spawners and intermittent spawners--are differentiated. Whereas fishes of the former type deposit their mature eggs in a single act of spawning, sometimes within a few hours, those belonging to the latter type require a longer period of time for oviposition: for, their oocytes do not all mature at the same time; instead, they reach full maturity in batches. KAZANSKY (1949) considers the reason for partial spawning to be the uneven course of vitellogenesis in the oocytes. In his opinion, there are two reasons for this:

(1) A difference in the rate at which the yolk is laid down in the cytoplasm, with the consequent formation of two or three more or less clearly differentiated groups of oocytes to be spawned in the same season; and

(2) A lack of uniformity in the growth of the oocytes, not only during vitellogenesis, but also during vacuolization. This leads to the formation of many groups of oocytes which may be spawned.

Perhaps intermittent spawning represents an adaptation to the large number of eggs. Fishes with heavy losses of eggs and larvae produce large numbers of eggs. But these can not all mature simultaneously, due to a lack of space (NIKOLSKY 1963). Finally, KAZANSKY (1949) classifies the fishes according to their manner of spawning.--In classifying according to spawning types, we must note whether the spawning period of the individual or that of a whole stock is intended.

(1) Fishes with a short spawning period; and

(2) fishes with a long spawning period.

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The second group is subdivided as follows:

(a) Those spawning several times without a sharp differentiation between oocytes and mature eggs;

(b) those spawning several times with a distinct differentiation between these groups; and

(c) fishes spawning once with a long spawning period.

QUASIM (1956) subdivided fishes into two groups, viz., those with a long spawning period in a southern range of distribution from the Mediterranean to the North Sea, and those with a short spawning period and northern distribution from the Channel to the Arctic. The former deposit their eggs over a period of five or six months in spring and summer, the latter within three or four months in winter and at the beginning of spring.

Table 4. Classification of the maturation processes in teleostean oocytes

<u>Germ cell phase</u> (according to ARNDT and GOETTING)	<u>Chromosomal activity</u>	<u>Physiological-biochemical processes</u>	
		body-fat con- tent of spring herring (accord- ing to LUEHMANN)	water con- tent of the ovary in Baltic Cod (according to MENGI)
I. Oogonia; primary oocytes; one or more nucleoli; single-layered follicle	mitotic divisions; conjugation of chromosomes		
II. Undulation of nuclear membrane; nucleoli pass into the cytoplasm; development of cortical vacuoles; beginning of the formation of the zona radiata; follicle two-layered	loosening of the chromosomes; DNA not detectable	maximum fat content (17%)	high water content (84%)
III. Vitellogenesis; cortical vacuoles become supplanted; zona radiata complete; intensive growth of oocytes		fat content decreases steadily	lowest water content (70%)
IV. Vitelline spheres fuse; nucleus departs from the center; bipolar differentiation of the cytoplasm; hydration; secondary oocyte, mature egg	DNA again visible; meiotic divisions; haploid chromosome number	lowest fat content (2-3%)	maximum water content (88%)

Using the anchovy Engraulis ancrasicholus as an example, GOETTING (1961) has pointed out that external factors influence the spawning period. For, this species spawns from April to September in the Mediterranean and in the Atlantic, but in June and July in the North Sea. GOETTING concludes that different populations in different major geographical areas of distribution show a different spawning behavior. From this, he concludes that the maturation type is not fixed genetically, but determined by metabolic physiology.

HICKLING and RUTENBERG (1936) compared the maturation types of pike and sardines with those of herring and haddock. They concluded from the distribution of the groups of oocytes that the shorter and more exact the spawning period was, the more distinctly the maturing germ cells were separated from the spawning reserves. GOETTING (1961) called this type the discontinuity type with northern distribution, as opposed to the continuity type for fishes with southern distribution. In the latter, the generations of eggs can not be clearly differentiated with respect to size. The fishes of these two types differ in the histological pattern of their ovaries. In the second type, continuous gradations between the different oocyte phases may be observed. This is not the case in the discontinuity type, which shows clearly separated groups of oocytes.

Summary

The processes of the maturation of the oocytes, described above, are listed in Table 4, which describes the developmental phases from the oogonium to the ripe egg synchronously with the chromosomal activities taking place in the nucleus and the physiological - biochemical processes in the ovary.

The first germ-cell stage comprises the development from the oogonium to the primary oocyte with a single-layered follicle. This phase is characterized by slow growth of the cytoplasmic membrane surrounding the nucleus and by the appearance of nucleoli. The most important changes in this phase occur in the nucleus. The oogonial mitoses are followed by the commencement of the first maturation division in the young oocyte, with the chromosomes heaped close together.

In the second stage, the chromosomes loosen again. At this point, the processes of division are interrupted, and the DNA is no longer visible. Hence, the changes which now take place in the structure of the oocyte are all the more important. The nuclear membrane undulates and the nucleoli gradually pass into the cytoplasm. Cortical vacuoles appear at the periphery of the cell. The formation of the zona radiata externa begins and the follicle becomes double-layered. The third stage, which now follows, is characterized by the enlargement of the oocyte associated with vitellogenesis. The cortical vacuoles are supplanted.

The formation of the zona radiata interna marks the completion of the cortical layer. In the fourth stage, important changes take place in the nucleus and in the cytoplasm. The DNA reappears. The meiotic divisions continue, terminating in the ripe egg, which is characterized by a haploid number of chromosomes. The vitelline spheres fuse and the nucleus departs from the center of the oocyte. Polar differentiation of the cytoplasm forms an animal portion and a vegetal portion. The oocyte enlarges considerably in a short period of time by uptake of water. This marks the end of the process of the maturation of the oocyte in the ovary.

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Author's address

Dr. VOLKER HILGE, Bundesforschungsanstalt für Fischerei, Institut für Küsten- und Binnenfischerei, Außenstelle Ahrensburg, D-207 Ahrensburg, Wulfsdorfer Weg

(Federal Fisheries Research Institution, Coastal and Inland Fisheries Institute, Ahrensburg External Branch ... W. Germany)