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Reproductive Biology and Scale of Maturity Stage of Reproductive System  
of Female Squid (*Illex illecebrosus*)

by

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Abstract

Oogenesis and the development of the reproductive organs in *Illex illecebrosus* females was studied. The sample analyses were obtained from the area between Cape Hatteras and the Grand Bank in 1966-1983. To investigate the oogenesis, 10 gonads were taken from the females with the mantle length of 15-30 cm at all maturity stages (except spawning). Approximately 2,000 specimens were studied to obtain knowledge of the development of the reproductive system organs during the ontogenesis. More than 50,000 females were sampled to analyse the maturation dynamics and the distribution during their life cycle. Data on the spawning and spent females were obtained for *Illex argentinus*.

The term "development phase" is used to indicate some particular qualitative state of an oocyte constituting a part of a more general stage in its development which is termed "period". Each period consists of several development phases. "Development stage" is a set of features determining the gonad state. "Maturity stage" is a state of the reproductive system as a whole (gonad, oviducts, nidamental and oviductal glands).

No oogonies or premeiotic oocytes were observed on the histological gonad sections from the analyzed females. The youngest generation was represented by the oocytes of the protoplasmic growth period. This period includes the first, second and the third phases of the previtellogenesis, when a simple follicle is formed and the diameter of the oocytes increases from 15 to 217  $\mu$ m around the long axis. The oocytes at their third phase of the previtellogenesis are of a specific goblet form. A staining by "Sudan" at the protoplasmic growth period does not reveal any fat traces in the oocytes.

The protoplasmic development period is followed by an intercalary one consisting of two phases: "complex follicle" and "hydrotation". At these phases, the follicle cells penetrate into the oocyte surface in the capillaries passage place forming the meridional folds. Then the cytoplasm "sinks" separating from the cell capsule which allows to presume a quick oocyte hydrotation.

During the intercalary period when viewing the gonad under the microscope even at low magnification the oocytes with a reticular pattern are clearly visible. The oocyte staining by "Sudan" during the intercalary growth period does not show any fat tissues as well.

The following period - trophoplasmic growth (vitellogenesis) is subdivided into three phases ("vacuolization", "yolk accumulation" and "expulsion of a follicle"). Central part of a protoplasm is slowly filled with yolk. The reticular pattern first disappears from the side surfaces of the oocyte and then from its vegetative pole. The "expulsion of a follicle" phase is characterized by a specific phenomenon when the "expulsed" follicle folds form regular scallop on the section edge which is similar to the "maturing stage" described by N. Jakahosi, T. Yahata (1973) for *Jodarodes pacificus*. In the largest and most developed oocytes a clear non-structural band-future chozion - is defined between the very thin layer of a cytoplasm and the

follicle epithelium. The oocyte diameter during this period increases from 210-315  $\mu$  at the "vacuolization" phase up to 400-600  $\mu$  at the "expulsion of a follicle" phase.

In the gonads where we find the oocytes at the "expulsion of a follicle" phase, there are always oocytes at almost all the earlier phases of the development: a continuous asynchrononous development of the oocytes is characteristic of *I. illecebrosus* as well as of *Loligo pealei* (Burukovsky and Vovk, 1974) and *Sthenoteuthis pteropus* (Burukovsky *et al.*, 1977). This phenomenon makes it difficult to discriminate between the gonad development stages and thus, a method is advised based on the phases and periods of the more developed oocytes.

Seven development (d.s.) stages are suggested to discriminate in *I. illecebrosus* gonad:

I d.s. Formation of the oocytes. A period of development from the oogonia to the first previtellogenesis phase.

II d.s. Increase of a number of the oocytes in the ovary; the most developed oocytes are at the second previtellogenesis phase.

III d.s. The oocytes tend to develop autonomically; more developed oocytes are at the third previtellogenesis phase ("simple follicle").

IV d.s. Preparatory. Most developed oocytes are at the "expulsion of a follicle" phase.

V d.s. Maturing gonad. Most developed oocytes are at the ripe egg phase.

VI d.s. Mature gonad. The empty-spaced follicles can be found in the ovary which serves as evidence of "sinking" of the ripe eggs into the oviduct.

VII d.s. Spent. The gonad stops functioning.

The comparison between the gonad development stages and the development of the accessory organs (oviducts and nidamental glands) in connection with the conception of breaking the contradiction between a tendency to produce a maximum number of eggs and the necessity to spawn them during a very short period of time which is characteristic of a nektonic monocyclic predator (Burukovsky *et al.*, 1977) allowed us to suggest a scale of the maturity stages of a reproductive system in short-finned squid (Table 1).

In the process of a female ooteneses which main function is a reproduction, five major reproductive ecological stages are distinguished:

1. The formation of a reproductive system and the intensive somatic growth during the feeding period. Two substages may be identified: (a) pelagic, plankton-nektonic (maturity stage I; ML 1.2-200 mm, mainly up to 140 mm; duration of 3-5 months; pelagic layers in the open sea and slope waters, and (b) near-bottom, nektonic (maturity stage II, ML 100-280 mm; duration of 3-6 months; shelf and slope waters). The duration of the whole stage is 8-9 months.
2. Maturation (increase of a composite of the generative growth). It starts at maturity stage III when the females stop their feeding and begin the spawning migration (ML 170-300 mm; duration of 1-2 months; shelf-slope waters) and proceeds during the spawning migration (maturity stages III-IV; ML 190-310 mm; duration of 1-2 months). At the end of this stage the females migrate into the pelagic layers of the continental slope area. The duration of this stage is 2-3 months.
3. Accumulation of ripe eggs in the oviducts (constant spawning into oviducts). The generative growth dominates. The females are at maturity stages V<sub>1</sub>-V<sub>3</sub>; ML is 190-310 mm; duration of 0.3-0.7 month. Mainly in the spawning areas, in the pelagic layers of the slope region.
4. Spawning (true spawning). The females are at maturity stage VI. Several egg masses are spawned at some intervals during which new ripe eggs though less intensively but still are formed and the females couple with the males for a few times. The animals at this stage are found in the pelagic waters above the continental slope during the period of 0.1-0.5 month.

5. Spent. The extremely exhausted females at maturity stage VII; soon they are in the pelagic slope waters.

The differences in the feeding conditions within the species range determine the differences in the spawning female lengths as well as the duration and orientation of the spawning intensity in time (Lange, 1981; Froerman and Dubinina, 1984; Froerman, 1984).

In the process of the species range formation, the shifting of its reproductive and feeding parts in the northeastern direction into the areas of the increased water mass dynamics and the non-balanced production cycle which is characteristic of the boreal zone, is the reason for a protraction of the spawning seasons which peaks predetermine the feeding season of the young squid to coincide with the maximum values of the zooplankton biomass. Hence, possible evolution of *Illex illecebrosus* can be likened to that of *Illex argentinus* and *Todarodes pacificus*.

(FULL TEXT OF THIS PAPER WILL BE AVAILABLE IN ABOUT 2 MONTHS)

(see over for Table 1)

Table 1. Scale of maturity stages of female *Illex illecebrosus*.

Maturity stage	Stage of Ovary development (d.s.): dia. of developing oocytes (D), coefficient of ovary development (OW/BW, %)	State of ovary (O), oviduct (OV) and oviductal gland (OVG)	State and length of nidamental gland NDL/ML (%)	Coefficient of maturity RSW/BW (%)
I	I.d.s.; D < 0.05 mm; OW/BW < 0.03-0.12 ( $\bar{x}$ = 0.05)	O and OV are transparent and threadlike.	Threadlike, transparent, poorly visible; 0.03-11.3 ( $\bar{x}$ = 5.8)	0.045-0.15 ( $\bar{x}$ = 0.1)
II	II.d.s.; D < 0.1 mm OW/BW = 0.06-0.4	O is grey semitransparent; in early part of stage, ovary is scepter-shaped and conic at the end. OV is flat and transparent. OVG are semitransparent.	Band-shaped, semitransparent, well visible; 0.6-16.4 ( $\bar{x}$ = 10.7)	0.08-0.45 ( $\bar{x}$ = 0.35)
III	III.d.s.; More advanced oocytes are generally goblet-shaped. D < 0.3 mm (0.1-0.25 mm) OW/BW = 0.18-1.67 ( $\bar{x}$ = 0.3)	O is white-grey, with slightly noticeable grain structure on the periphery. OV are well detectable with slight indication of their spiral structure. OVG are dense, grey-white.	Lance-shaped, grey; they increase somewhat in volume; 1.2-23.4 ( $\bar{x}$ = 16.1)	0.2-2.2 ( $\bar{x}$ = 1.0)
IV	IV and V.d.s.; D = 0.3-1.0. The more advanced oocytes have reticular pattern. OW/BW = 0.32-7.2 ( $\bar{x}$ = 1.4)	O expands greatly; its grains are well pronounced. Spiral structure of OV is very evident. OVG are white and tough.	Ellipse-shaped, grey-white; large expansion later in stage; 18.8-32.7 ( $\bar{x}$ = 22.9)	0.7-11.6 ( $\bar{x}$ = 3.0)
V <sub>1</sub>	VI.d.s.; D = 0.9-1.0 mm OW/BW = 3.0-10.0*	Mature oocytes appear in OV; less than 10% of all oocytes in O and OV.	Ellipse-shaped, white; 27.0-42.0 ( $\bar{x}$ = 38.0)	6.4-12.7*
V <sub>2</sub>	VI.d.s.; D as at stage V <sub>1</sub> . OW/BW = 5.0-8.0*	Accumulation of mature eggs continues in OV, 10-60% of the total volume of oocytes.	Generally same as V <sub>1</sub> but more expanded; 40.0-50.0 ( $\bar{x}$ = 43.0)	11.6-27.7*
V <sub>3</sub>	VI.d.s.; D as at stages V <sub>1</sub> and V <sub>2</sub> ; OW/BW = 3.5-7.2*	OV filled with mature eggs, 60-90% of total volume of oocytes. Ovary size is as at maturity stage III-IV. Usually 1-4 clusters of unused spermatophores on gills or near them.	Same as V <sub>2</sub> but more expanded; tough; 42.0-52.0 ( $\bar{x}$ = 46.0)	22.0-28.7*
VI**	VI.d.s.; D as at stages V <sub>1</sub> , V <sub>2</sub> and V <sub>3</sub> ; OW/BW = 3.0-6.4*	Mature eggs are few in OV as at V <sub>1</sub> and early V <sub>2</sub> . O is small as at III. There are usually 1-3 used and 1-2 new clusters of spermatophores near gills.	Grey-white, slightly fallen, shrunk; 36.0-48.2 ( $\bar{x}$ = 46.0)	9.0-18.0*
VII**	VII.d.s.; spent ovary OW/BW = 0.3-1.0*	Residual oocytes in OV, but ovary is destroyed. Liver is small and loose. Mantle is thin and very shrunk.	Grey, fallen, flat. 35.0-42.0 ( $\bar{x}$ = 39.0)	0.8-2.0*

\* Mean values were not determined (number of specimens <10-15).

\*\* Stages by data for *Illex argentinus*.