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Gametogenesis, Mating Behaviour and Spawning of *Octopus ocellatus* (Cephalopoda: Octopodidae) in Western Korea

Pal Won Son[1], Byung-Gyun Kim[2] and Sung Han Kim[3]

[1]*Korea Marine Ecology Institute, Busan 612-020, Korea.*
[2]*Korea Fisheries Resources Agency West Sea Branch, Gunsan 573-030, Korea*
[3]*Faculty of Marine Applied Biosciences, Kunsan National University, Gunsan 573-701, Korea*

ABSTRACT

Gametogenesis, mating behaviour and spawning of *Octopus ocellatus* were investigated by histological study. This species is dioecious, and showed a protandry phenomenon. Ooogenesis (in females) and spermatogenesis (in males) can be classified into 3 stages, respectively. *O. ocellatus* copulates in one of two ways: a male may leap upon a female, mounting her mantle, or a male may sit near the female and extend the hectocotylized third right arm toward her. Spawning occurred between April and June in females, and between March and May in males of *O. ocellatus*. The spawning period was once a year and the peak took place between May and June. A number of flatened follicle cells, which were attached to an oocyte, were involved in vitellogenesis in the cytoplasm of the vitellogenic oocyte (maturing oocyte), and formation of chorion membrane (secondary egg membrane) of the ovarian eggs. Fecundity per female closely related to GSI was 294-660 eggs (average, 429 eggs). The díameters of the ovarían eggs surrounded by chorion membrane were approximately ín the range of 10.10-2.50 mm. Each ovarian egg laid by a female was connected to an egg string. Each egg string was 1-5.5 cm (average 3.6 cm). The total number of eggs laid by a female of this species ranged 218-314, the egg sizes were independent to the size of female adult. this species has a life mode showing some special reproductive characteristics of an annual semelparity as shown in Octopodidae species because we have never seen a female spawning a second time.

Keywords : *Octopus ocellatus*, gametogenesis, mating behaviour, spawning

INTRODUCTION

The octopus, *Octopus ocellatus* (Neocephalopod: Octopodidae), has been found along the coasts of Korea, China, and Japan etc. In Korea, especially, it lives in sandy gravel or silty sand in the subtidal zone on coasts of the southem and western Korea (Lee, 1956; Min *et al.*, 2004), and it is one of the most commercially important edible cephalopods. Intertidal reclamations, reckless overcatching, and water quality degradation might be mainly responsible for the recent rapid reduction of its standing stock. To date, regarding the octopuses, there have been several studies on their taxonomy and ecology (Boyle and Knobloch, 1982; Takashi, 1984 a, b; Mangold, 1990, Aronson, 1991; McQuaid, 1994; Villanueba, 1995; Nixon and Mangold, 1996; Moltschaniwskyj and Doherty, 1995), on the physiology (Taki, 1941; Andrews and Tansey, 1983; Che *et al.*, 1992), reproduction (Smale and Buchan, 1981; Boyle and Knoblock, 1983; Forsythe and Hanlon, 1988; Perez and Haimovici, 1991; Cortez *et al.*, 1995), and morphology (Bairati *et al.*, 1995). Recently, there have been several studies on the development of techniques of the seedling production of the Korean octopuses (Chu and Kim,1990: Kim *et al.*,1997). However, little information is available on oogenesis and spermatogenesis, mating

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Corresponding author : Byung-Gyun Kim
Tel: +82 (63) 440-2660 e-mail: bgkim@fira.or.kr
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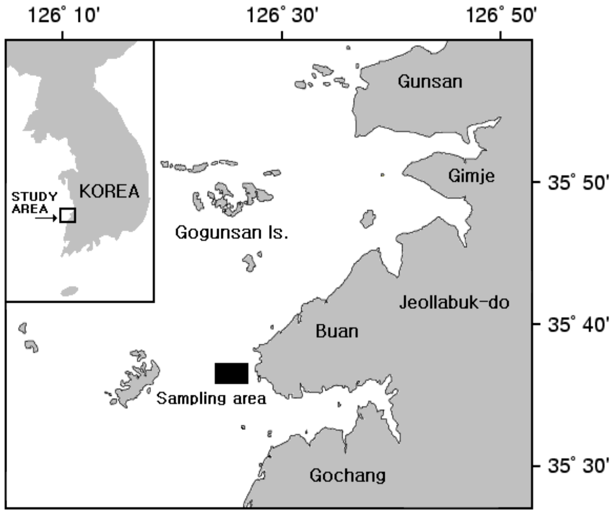

Fig. 1. Map showing the sampling area.

behaviour and spawning behaviour (biochemical synthesis of egg string materials) of *O. ocellatus*. In particular, the processes of mating and spawning behaviours have been investigated in detail using the histological method. Above all, the study of the reproductive behaviour of *O. ocellatus* may be one of the most important tasks in cultural operations for propagation of natural resources. Therefore, the main objectives of the present study are to investigate gametogenesis, mating behaviour, spawning behaviour and fertilization of *O. ocellatus* and to get some information for reproductive and mating behaviours for spawning methods in the indoor rearing tank.

MATERIALS AND METHODS

The specimens of *O. ocellatus* for the histological study were collected monthly by using the octopus pot in the coastal waters off Buan, Korea. from January to December (Fig. 1). After live octopuses were transported to the laboratory, lengths were measured by using a Vernier caliper and total weight was determined using a chemical balance. Seawater temperature was measured at 10:00 A.M. by the Puan hatchery, National Fisheries Research and Development Institute.

For the analysis of the gonadal phases and gametogenesis by light microscopy, histological preparations were made by subjecting the tissues to standard histological procedures and sectioned at 5-7 μm using a rotary microtome. Sections were then mounted on glass slides. stained with either Hansen's hematoxylin-0.5% eosin, Mallory's triple stain or PAS stain, and examined.

Sexually matured ovaries were dissected to investigate fecundity before the spawning period (from February to May).

The natural spawning places and natural laying ovarian eggs in the pot (sea snails shell) at the subtidal zone (about 10-30 m in depth) in the vicinity of the coastal waters of Puan were investigated by a SCUBA diving or trawl nets during the spawning season from April to June when the seawater temperatures increased.

To explore mating and spawning behaviours of the octopus in the indoor rearing tanks, males and females were isolated prior to being paired in tanks. Thereafter, they were paired in the same tank, then their behaviours were investigated by anatomical methods during the copulation and spawning period.

Egg spawnings were observed in the indoor rearing tank at the seawater temperature of 11.0-20.4℃ in the specific gravity ranging from 1.025 to 1.026.

RESULTS

1. Environmental factors of the habitat

Monthly variations in the mean seawater temperature and specific gravity of seawater at the study area were investigated from January to December, 2010 (Fig. 2). The mean sea water temperatures were very low (below 10℃) between December and February, and reached the minimum (5.0℃) in February. And then, the seawater temperatures began to increase from March to July, and reached the maximum (26.8℃) in August. Thereafter `the mean seawater temperatures sharply fell down from September to November.

The mean specific gravity was relatively high from January to April, thereafter, began to decrease rapidly in June when the rainy season began, and reached the minimum (1.021) in August. Then, the mean value

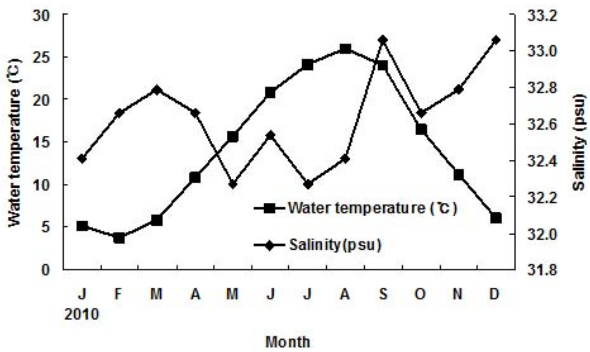

Fig. 2. Monthly changes in the mean seawater temperature and salinity from January to December, 2010.

began to increase from August to December (Fig. 2).

2. Position and morphology of the gonads

O. ocellatus is dioecious organism. The gonads locate medially in posterior region of body and were continuous with pericardíal cavity. The ovary opens into mantle cavity via oviduct(s), oviductal gland and gonopore. the testis opens into mantle cavity via spermduct(s), seminal vesicle. spermatophore producing and storing organs, and gonopore (Fig. 3). Morphologies of female and male gonads showed round in shape in all, the average diameter and extenal colours of ripe female and male gonads were 32 mm (semitransparent light brown in colour) and 17 mm (milky white in colour), respectively. As the gonads were getting mature, transparent elongated eggs covered with chorion were present in the ovarian cavity. At the slight cut by razor blade, the small, rice-like eggs in the oviduct or ovarian cavity of gravid female and milky-white sperms, formed in the spermatophores in the needham's sac in male, could be seen readily. In case of males they have a hectocotylus on the third right arm which is guided to the opening of the oviducts. Therefore, their sexes can be easily distinguishable by external features.

3. Oogenesis and spermatogenesis with germ cell development in gonads

In general, gametogenesis of cephalopods can be classified into oogenesis and spermatogenesis, as shown in other mollusks species. It is the first time

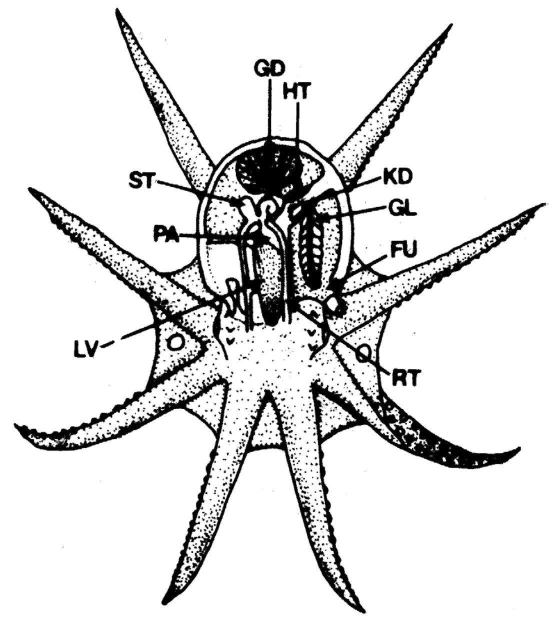

Fig. 3. Anatomy of small octopus, *Octopus ocellatus*. Abbreviations: FU, funnel; GD,gonad; GL, gill; HT, heart; KD, kidney; LV, liver; PA, pancreas; RT, rectum; ST, stomach.

that this studies of oogenesis and spermatogenesis is have not carried out by a histological methology. Based on the morphological features and sizes of germ cell and somatic cells in the ovarian tissues and testicular tissues, oogenesis by the oocyte developmental stage in females can be classified into three successive stages, and also spermatogenesis by the testicular developmental stage in males can be divided into three successive stages. respectively. The criteria used in defining the categories are as follows:

1) Oogenesis by oocyte developmental stage in the ovary

To date, in case of females, oogenesis has been extensively studied by Buckley (1976). According to the method of Buckley (1976), oogenesis of this species can be divided into 3 stages. At Stage I (immature oocyte), the oocytes are not yet surrounded by follicle cells (Fig. 4A). At the beginning of Stage II (maturing oocyte), a maturing oocyte is considered to be a vitellogenic oocyte. in they are surrounded by flattened follicle cells. The cells of the inner layer of

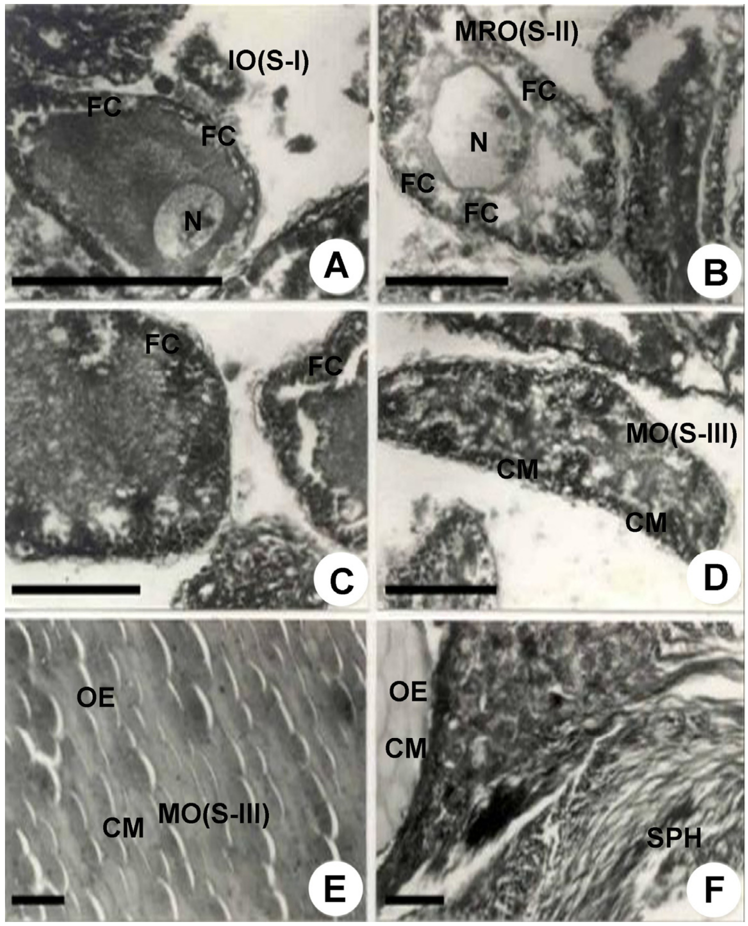

Fig. 4. Photomicrographs showing oogenesis in female *Octopus ocellatus* as seen by light microscopy. **A**, Section of the ovarian lobules in Stage I (immature oocytes). Note oocytes not yet surrounded by follicle cells; **B**, Section of the the ovarian lobules in Stage II (maturing oocytes). Note oocytes surrounded by flattened follicle cells and containig accumulated lipid; **C**, Section of the the ovarian lobules in Stage III (mature oocyte). Note oocytes containing yolk precursors and a number of mature yolk platelets; **D**, Section of the ovarian lobules in the same Stage III (mature oocyte). Note a number of ovarian egg masses covered with the chorion membrane and mixed with numerous spermatozoa in the spermatophores by copulation (hectocotylus) of the males through the opening of the oviducts of the females. Abbreviations: CM, chorion membrane; FC, follicle cell; IO(S-I), Immature oocyte(S-I); MRO(S-II), maturing oocyte(S-II); MO(S-III); N, nucleus; OE, ovarian egg(S-III); SPH, spermatophore. Scale bars indicate 200 μm.

the follicular envelope increase in size as do the oocytes and both accumulate lipids (Figs. 4B, 4C). Stage III (mature oocyte) begins with the formation of yolk platelets and ends with the degeneration of the follicle cells (Figs. 4D, 4E). Particularly, in Stage III, yolk precursors are secreted by the follicle cells and taken up by the oocytes; this stage is known as vitellogenesis. Several ovarian eggs (the oocytes covering with chorion membrane) are shed into the ovarion cavity (Fig. 4F). One may distinguish between immature females, including Stage I and II of Buckley (1976), when the ovary is small and white, maturing females where the ovary increases rapidly in size Stage III of Buckley (1976) and mature females with loose eggs in the ovisac.

2) Spermatogenesis by the teticular developmental stage in the testis

There are a few accounts of *Octopus* spermatogenesis in general and on *O. vulgaris* (Galangau and Tuzet, 1968 a, b). According to the method of classification by Galangau and Tuzet (1968

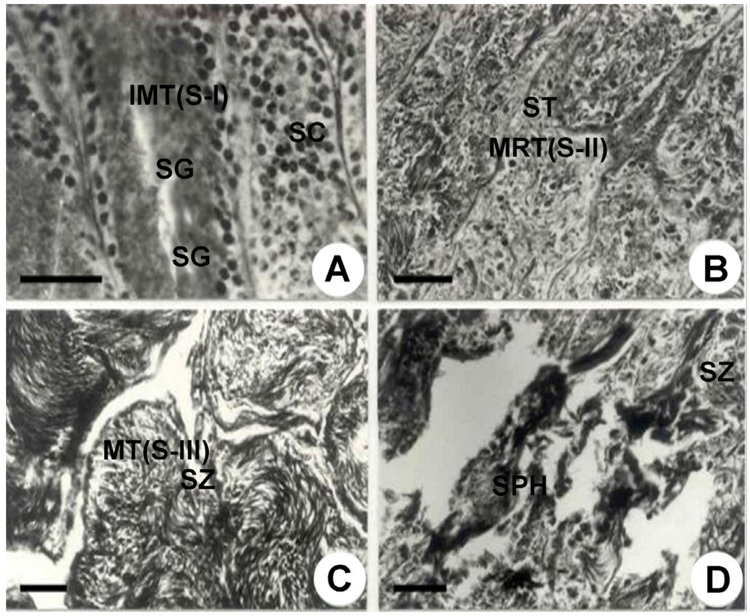

Fig. 5. Photomicrographs showing spermatogenesis in male *Octopus ocellatus* as seen by light microscopy. **A**, Section of the testicular lobules in Stage I (immature testis). Note appearance of spermatogonia, spermatocytes, not yet surrounded with spermatozoa and the whole gonoduct being parent; **B**, Section of the testicular lobules in Stage II (maturing testis). Note spermatocytes, spermatids, a few spermatozoa and containing creamy white vas deferens; **C**, Section of the testicular lobules in Stage III (mature testis). Note a number of spermatozoa in the spermatophores in the Needhams sac. in the testicular lobules **D**, Section of the same Stage III (mature testis in the spermatophores). Note releasing a number of sperm masses in the spermatophores stored in Needhams sac. Abreviations: IMT(S-I) MRT(S-II), maturing testis; MTS-III); SC, spermatocyte; SG, spermatogonia; SPH, speratophore, ST, spermatid; SZ, spermatozoon. Scale bars indicate 50 μm.

a, b), three stages are commonly referred to: Stage I (immature testis): spermatogonia and spermatocytes are present in the testicular lobules (Fig. 5A), whole gonoduct is transparent. In the Stage II (maturing testis), spermatids and a few spermatozoa are found in the testicular lobules (Fig. 5B), the vas deferens is creamy white and thick. In the Stage III (mature testis), spermatids and spermatozoa appear in the testicular lobules (Fig. 5C), and spermatophores are stored in Needhams sac (Fig. 5D). In general, the length of the spermatophores increases with the size of the male. The smallest spermatophores found in *O. ocellatus* in the Buan population had a length of about 10 mm (body weight: 60 g), the largest measured 20 mm (body weight > 65 g).

4. Some characteristics of mating behaviour and fertilization of *O. ocellatus*

Males of this species are distinguished from female externally by the presence of a hectocotylus at an age of 4 or 5 months. According to inspection of the mantle cavity of females, the enlarged gonads appeared from March to May, before approximately one month of spawning. Males and females, which had been isolated prior to being paired in tanks, touched each other's arms briefly with the other’s arms before mating. Hectocotylus on the male’s third right arm entered the mantle cavity of the female. A female usually fends off the male for a while but then submits to the male that will sit next to her or mount her. As shown in Fig. 7, *O. ocellatus* copulates in one of two ways: a male may leap upon a female, mounting her mantle (Fig. 7a), or a male may sit near the female and extend the hectocotylized third right arm toward her (Fig. 7b), there is quick sex recognition, probably by chemotactile cues. and insert the hectocotylus in her mantle cavity to pass the spermatophores. As shown in Fig. 8, a detailed account of the transfer mechanism of the spermatophores is given by Froesch and Marthy (1975). In case of *O. ocellatus*, copulation might

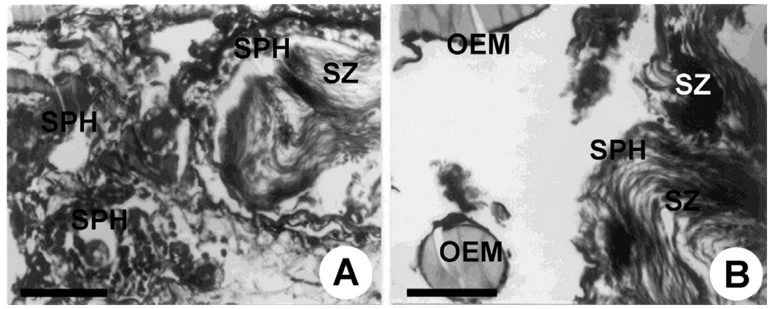

Fig. 6. Photomicrographs showing the spermatophores and several ovarian egg masses, which were inserted into the oviducal cavity of the female from the hectocotylus (the penis) by copulation. **A**, Spermatophores were ejeculated from the hectoctylus (the penis). Note a number of spermatozoa in the spermatophores in the Needam's sac. **B**, occasionally, spermatophores surrounded by the ovarian eggs covered with the chorion membrane, which were observed in the oviducts and ovarian cavity. Abbreviations: OEM, ovarian egg membrane; SPH, spermatophore; SZ, spermatozonn. Scale bars indicate 50 μm.

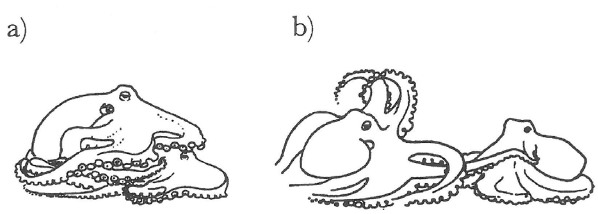

Fig. 7. Mating in *Octopus ocellatus*. (a) Male (top) mounting female. (b) Male (left) at a distance, extending the third right arm, hectocotylus.

continue for two hours or more. As shown in Fig. 8, the hectocotylus is inserted during mating into the distal oviduct, and spermatophores are extruded by the penis from Needham's sac. As reported by a few researchers (Wells and Wells, 1972; Hanlon and Messenger, 1996), a number of spermatozoa released from spermatophores are stored in the oviducal gland (Figs. 6A, 6B; Fig. 8), and the spermatophores are placed in the oviducts. However, empty cases are discarded. The released spermatozoa are stored in the spermathecae of the oviducal glands. The spermtozoids penatrate the wall of the spermathecae and become immobilized. Fertilization takes place in the oviducal glands as the mature egg pass through them on their way out of the oviducts.

Some characteristics of mating behaviours are as follows: the same pair often repeat mating during a week or so. But a male copulates with other females and a female accepts other males. There is no true pair formation. Mating was occassionally observed in the sea, in shallow waters (Woods, 1965). Mating often occurs when the females are immature (Wells and Wells, 1972; Hanlon and Messenger, 1996). Only females ready to lay the eggs consistently fend off the male. They get restless and search for sheltered place where they can lay and brood the eggs without disturbance.

5. Production of egg strings by secretions from the oviducal glands after egg spawning

The outer one of the oviducal gland secrets a mucoprotein at pH 6.6, the central one secretes a mucopolysaccharide at pH. 6.4. While passing through the oviducal glands, the eggs are enveloped by these two secretions. In contract with the seawater (pH 7.8), the secretions combine to gradually from a precipitate, the mucopolysaccharide acting as polymerizer. The mucus of the oviducal glands in mature females at pH 5.2 prevents premature polymerization (Froesch and Marthy, 1975). The two secretions from the oviducal glands, together in strings and attach these to a substrate. The egg strings are glued to theroof of the home. After having cleaned the roof, the female holds on the substrate. The first eggs together with the material from the oviducal glands pass to the small suckers surrounding the mouth. These suckers presumably stick the eggs together by their stalks and attach them to the substrate. Futher eggs are woven into the central stem. Ten to twenty strings may be produced during a night (females rarely spawn during daytime).

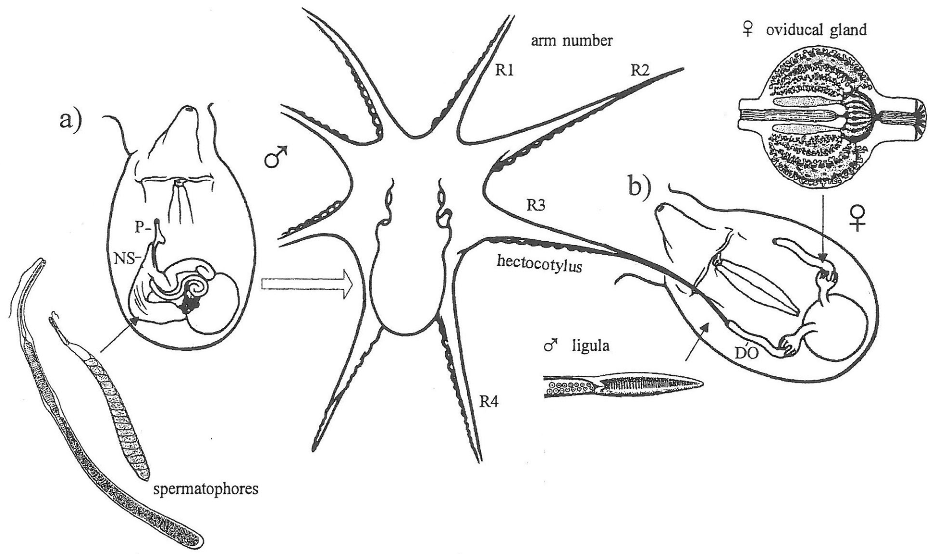

Fig. 8. Octopus reproductive system. (a) Male internal anatomy. Two examples of spermatophores are shown: 8, 15 mm, respectively. Spermatophores are extruded by the penis from Needham's sac (NS) and passed along the hectocotylized third arm during mating. (b) Female internal anatomy. The hectocotylus is presumably inserted during mating intp the distal oviduct (DO) and sperm are stored in the oviduccal gland until eggs are fertilized as they pass from the ovary. An example of the ligula (distal end of the hectocotylus) of Octopus sp. is shown. Digram of the oviducal gland is from Froesch and Marthy (1975).

6. Spawning of ovarian eggs

Most ovarian eggs were laid in shallow water and always attached to substrates. In general, egg masses are found in nature from the sea surface to about 30 m in depth. On rocky shores, females were observed in a hole and sheltered place to lay eggs. However, in case of bottom composing sandy or muddy sediments, they laid their eggs in large moullusc shells or in manmade objects such as bottles, tires, etc. Commony, spawnig of this spescies began to occur approximately 25-30 days after mating behaviour at over 11°C (effective accumlative water temperature of 887°C). Spawning of ovarian eggs occurred once a year during the spawning season, and this species had a characteristics of semelparity like other octopuses. The diameter of small and rice-like elongated eggs, which were laid in empty mollusc shells (*R. venosa*, etc.) in the tank, were approximately 10.10 mm x 2.50 mm. Eggs were surrounded only by the chorion membrane which was formed by the follicular cells of the ovary (Figs. 12A and 12B). An egg With chorion membrane produced an egg stalk, which attached to an egg string. Generally the ends of the strings were attached to the surface of a substrate by means of a secretion so that they hang vertically downwards, but they might sometimes be laid on vertical or near - vertical, surfaces. In this case the egg string formed an overlapping egg-sheet. The number of eggs stalks deposited by a female varis from 218 to 314 (average 262), depending largely on the number of ripe eggs in the ovary (Table 1). Each egg string may be as long as 1-5.5 cm, and the average length of an egg string is approximately 3.6 cm. 10 to 13 eggs per cm of the egg string were connected. The egg size is independent of the female size.

7. Fecundity

To investigate fecundity of sexually matured individuals of this species, number of eggs in the ovary were measured from mature individuals which were

Table 1. Relationship between fecundity and the gonadosomatic index

Date	No.of adults	GSI	No. of egg per ind.	
		Average	Range	Average
March	21	11.6	294-438	345
April	26	18.3	428-660	524
May	28	19.0	336-486	418

regarded as individual having no trace of spawning in the ovary by external features. Fecundity of sexually matured females ranged 294-660 eggs/individual (average, 429 eggs) (Table 1). In this study, fecundity of the individuals having higher GSI was greater than those showing smaller GSI values.

DISCUSSION

The number of follicular ce!ls in cephalopods increase considerably during oocyte development owing to mitotic divisions (Cowden, 1969; Bottke, 1974; Richard, 1970). The number and the arrangement of follicular cells associated with single oocyte differ among molluscs. The developing oocytes become completely surrounded by an increasing number of follicular cells, which often form a syncytium in Octoups vulgaris. According to Huebner *et al.* (1975) and Bast and Telfer (1976), the follicular cells are involved in the synthesis or in the selective transport of particular yolk precursors. On the basis of morphological and histochemical studies, the follicular cells have the following functions: (1) vitellogenesis, (2) the formation of the secondary egg membrane (chorion), (3) the ovulation process, (4) phagocytosis, (5) hormone production, (6) the determination of animal vegetal and bilateral symmetries of the egg, and (7) transportation of the oocyte.

In *O. ocellatus*, morphology of many follicular cells attached to an oocyte during vitellogenesis varied with the gonad developmental stages. As reported in other cephalpods (Bottke, 1974; Selman and Arnold, 1977), the follicular cells of this species also seem to be involved in the synthesis of yolk component, and in the production of substances that form a secondary egg membrane. During the copulation period (from March through May), occasionally, spermatophores, surrounded by the ovarian eggs covered with chorion, were observed in the oviducts and ovarian cavity (Fig. 4F; Figs. 6A and 6B).

In this study, spawnig of *O. ocellatus* began to occur approximately 25-30 days after mating behaviour at over 11°C (effective accumlative water temperature of 887°C). In case of O. dofleini (Gabe, 1975) eggs may be laid approximately 42 days after mating. In general, fecundity of the individuals having higher GSI was greater than those showing smaller GSI values. But regarding to egg sizes, they were not strongly correlated to mother individual sizes. Accordingly, it is assumed that the spawning timing vary with environmental water temperatures (or effective accumulative water temperatures).

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