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Gametogenesis and Reproductive Cycle of the Cockle, *Fulvia mutica* (Reeve)*

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새조개, *Fulvia mutica* (Reeve)의 生殖細胞形成過程 및 生殖週期*

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雌雄同體型 二枚貝인 새조개, *Fulvia mutica*, 의 資源管理 및 養殖을 爲한 基礎生物學的 硏究로서, 1980年 10月부터 1981年 9月까지 月別로 採集한 麗水近海産 材料를 對象으로 生殖細胞形成過程 및 生殖週期를 組織學的 方法에 依해 調査하였다.

生殖巢는 複雜한 管狀構造를 가진 많은 卵巢小囊과 精巢小囊들이 서로 混在된 雌雄同體型을 나타내고 있다. 發達初期의 生殖巢에서 成長中인 生殖細胞와 함께 好酸性 顆粒細胞와 不分化間充組織들이 豊富하게 나타나고 있으며, 生殖巢가 成熟함에 따라 漸次 消失되어 간다.

完熟卵의 크기는 57~67 μm으로 젤라틴狀의 皮膜에 둘러싸여 있고, 變態를 마친 完熟精子는 精巢小囊의 內腔中央에 波狀의 精子束을 形成한다.

새조개의 生殖週期는 分裂增殖期, 成長期, 成熟期, 放出期, 退化期 및 回復期의 連續的인 6段階로 나눌 수 있었으며, 産卵期는 水溫 20°C 內外의 5~10月로써, 그 盛期는 6~7月과 9月인 것으로 나타났다.

特히, 5月의 早期産卵個體들은 生殖巢를 곧 回復發達시켜 9, 10月 放卵群에 다시 參與하는 것으로 推定되었다.

Introduction

The cockle, *Fulvia mutica* (Reeve), is one of the important commercial bivalves in the western Pacific coast. According to the Yearbook of Fisheries Statistics by Office of Fisheries, the Republic of Korea, total landing of this species in Korean waters was 13,195 metric tons from 1974 to 1980. With increasing demand of this clam, this clam draws a particular attention of the mariculturists. However the basic biological studies on this species are not much available.

A work on the spawning season in ecological aspect (Inoue, 1955) and a few other works which also partly dealt with the spawning season of *F. mutica* (Yoshida, 1953 ; Nishihiro, 1980 ; etc.) have been reported. Especially, the gonad of *F. mutica* is known hermaphroditic (Inoue, 1955 ; Matsuoka *et al.*, 1968 ; Tanaka, 1969). Up to now, the writers could not find out any histological study on the gametogenesis and the reproductive cycle about the monoecious species of bivalves, while the reproductive cycle and

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the gametogenesis have been reported on the various dioecious species of bivalves. i.e., *Venus mercenaria* (Loosanoff, 1937 b), *Pinctada martensii* (Tateishi and Adachi, 1957 ; Uemoto, 1958 ; Lee, 1972), *Chlamys farreri* (Kanno and Tanita, 1961), *Patinopecten yessoensis* (Wakui and Obara, 1967 ; Maru, 1976 ; Mori *et al.*, 1977), *Spisula solidissima* (Ropes, 1968), *S. sachalinensis* (Takahashi and Takano, 1970), *Corbicula fluminea* (Lee and Chung, 1980), etc.

This paper deals with gametogenesis, spawning season, reproductive cycle of *Fulvia mutica* by histological methods.

Materials and methods

From October 1980 to September 1981, 30 to 45 individuals of *F. mutica* were collected monthly by commercial dredge in Gamak Bay, the southern area of Yeosu (Fig. 1).

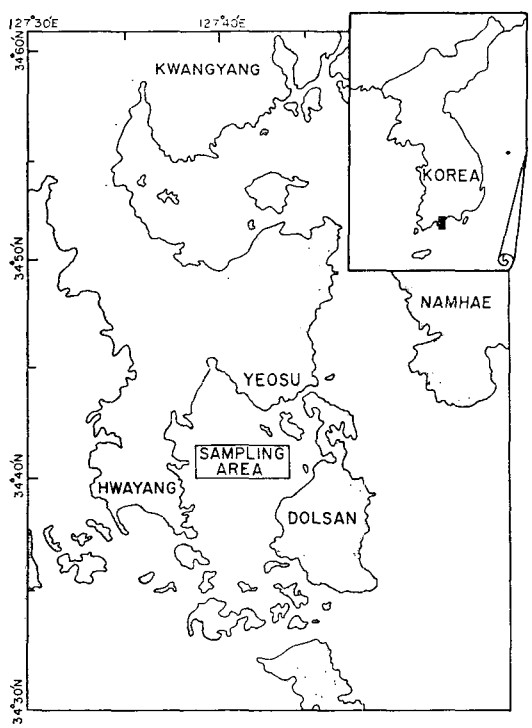


Fig. 1. Map showing the area where the specimens for the study were collected.

First, shell length, shell height, shell breadth, total weight, meat weight and shell weight of all the specimens were measured, and then fatness, [Meat weight/(Meat weight + Shell weight) × 100], was computed by the method of Momoyama and Iwamoto (1979). The gonadal portion located at the beginning of the foot was cut into 5 to 7 *mm* in thickness (Fig. 2) for fixation in Bouin's solution. The fixed specimens were sectioned into 5 to 6 *μm* in thickness by the paraffine method and stained with Hansen's haematoxilin-eosin and Mallory's triple stain.

The sea-water temperatures in the adjacent area of Yeosu where the specimens for the study were collected from October 1980 to September 1981 were quoted from unpublished records of National Fisheries Research and Development Agency, Korea.

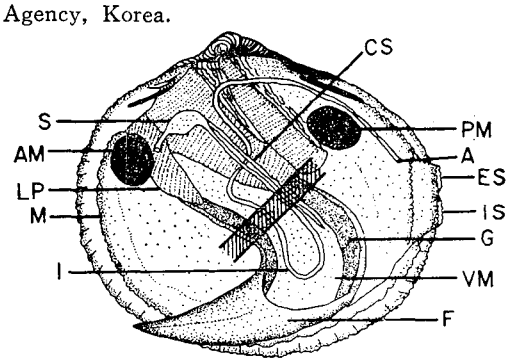


Fig. 2. Anatomy of *Fulvia mutica*.
A: Anus, AM: Anterior adductor muscle, CS: Crystalline style sac, ES: Exhalant siphon, F: Foot, G: Gonad, I: Intestine, IS: Inhalant siphon, LP: Labial palp, M: Mantle, PM: Posterior adductor muscle, S: Stomach, VM: Visceral mass.
▨: Position of the histological specimen cut.

Results

1. Position and structure of gonads

Gonads are located between the beginning of the gill and the bended part of the foot (Fig. 2). By the histological examination, the gonads showed to be hermaphroditic and lay between

tne liver and the outer fibromuscular layers compacted by connective tissue fibers and muscle fibers. The simple cuboidal epithelium was situated on these muscular layers. Gonad tubules attached to the connective tissue fibers of the lowest part of the muscular layers and then formed the ovarian sacs and the testicular tubules (Pl. I—Fig. 1). The gonads contained a number of ovarian sacs and testicular tubules which showed complicated tubular structure.

The basement membrane of the ovarian sac and testicular tubule contained many gonial cells along its wall in the early stage of gonadal development. It consisted of duplicate membranes made of connective tissue which showed blue colour in Mallory's triple stain and inner one of these membranes had the function as the germinal epithelium.

As the development proceeded, the gonads extended their volume toward the ventral direction of the animal and showed milky white in colour. Especially, from this time gonads developed well around the crystalline style sac.

The distended gonads before the spawning extended ventrally, occupying the space between the muscular layers and the visceral mass. At this time, if they are slightly scratched by any means, ripe eggs and sperms readily flow out.

It happened to be observed that the testicular tubules in mature stage contained one or two, sometimes three mature oocytes in their lumens, but in general, female germ cells were in the ovarian sac and male germ cells in the testicular tubule (Pl. I—Fig. 2).

2. Gametogenesis

1) Oogenesis

Ovarian sacs of early development stage were gradually increased in number, showing the complicated tubular structure ramified. In the beginning of this stage, most of the germinal epithelia were in contact with each other. Oogenesis occurred in the germinal epithelium and a large number of oogonia and small oocytes appeared along the germinal epithelium of the ovarian sac. Every oogonium measuring about 10 μm in diameter had a round nucleus containing a nucleolus in its center. Nucleus and nucleolus, at that time, were distinct in appearance, while the cytoplasm of oogonium was very poor (Pl. I—Fig. 3).

A great deal of both eosinophilic cells and undifferentiated mesenchymal tissues were also seen along the germinal epithelium in this time (Pl. I—Fig. 4).

As the growth of ovarian sacs advanced, rapid proliferation of oogonia progressed in a parallel manner, while oogonia which were produced earlier suspended the mitosis and began to grow in their volume toward the center of the lumen (Pl. I—Fig. 5). The early growing oocyte also had a round nucleus containing a basophilic nucleolus and its cytoplasm began to grow in volume. As a rule, the nucleus in the early growing oocyte was situated near the germinal epithelium. However, when the oocytes grew 16—24×23—37 μm, each of them made a egg-stalk connected to the germinal epithelium and each nucleus moved to the distal part of the oocyte. From this time, the oocyte increased its cytoplasm more than that of early stage and its nucleus enlarged to be a germinal vesicle having a relatively small nucleolus (Pl. I—Fig. 6).

When the oocytes grew 27—34×50—58 μm in their size, most of them were attached to the germinal epithelium of the ovarian sac by the egg-stalk but some of them were free in the lumen and gradually became round or oval. On the other hand, eosinophilic cells and mesenchymal tissues seen in the early development stage were markedly decreased (Pl. I—Fig. 7).

When the oocytes grew 28—36×56—65 μm in size, the ovarian sacs crowded with each other and were filled with the mature oocytes in their lumens. The mesenchymal tissues, however, were very few and the germinal epithelium

became very thin. Even this time, it was observed that there were still a few growing oocytes of the early development stage on the thin epithelium (Pl. I—Fig. 8).

In mature stage, ripe oocyte measuring about 60 μm in diameter was surrounded by gelatinous membrane and its cytoplasm contained a large number of yolk granules and a little lipid granules. It had a enlarged germinal vesicle measuring 31 to 39 μm in diameter and a basophilic clear nucleolus (Pl. I—Fig. 9).

When spawning occurred, ripe oocytes in the ovarian sac were released in the surrounding environment. At this time, there were a few ripe oocytes undischarged as well as young oocytes (Pl. II—Fig. 10). Almost immediately after the spawning, the undischarged oocytes in the lumen were undergoing the cytolysis and then each ovarian sac was contracted.

Sooner or later, the rearrangement of the newly formed ovarian sacs, and the appearance of the new eosinophilic cells and mesenchymal tissues followed. Then ovarian sac had a new function and began to form oogonia on the germinal epithelium (Pl. II—Fig. 11).

On the other hand, according to the writers' close observation the ovarian sacs in the gonad which spawned in May were characterized in July and August by the presence of a few unspawned oocytes and degenerating oocytes in their lumen, and by early growing oocytes and oogonia on the germinal epithelium (Pl. II—Fig. 12).

2) Spermatogenesis

Testicular tubules, as already shown in the ovarian sacs, also formed a complicated tubular structure. In the early development stage, the spermatogonia were actively proliferating among the eosinophilic cells and the mesenchymal tissues which were abundunt on the germinal epithelia of the testicular tubules (Pl. II—Fig. 13).

As the growth of the testicular tubules advanced, rapid proliferation of the spermatogonia progressed in a parallel manner. However, the spermatogonia which were formed earlier gradually increased in size, and their nuclei changed markedly. This growth caused a shift of the cells, that is, spermatocytes moved toward the lumen of the tubule. These spermatocytes showed a flowing structure toward the center of the lumen (Pl. II—Fig. 14).

Through the further development of gonad, each of the testicular tubules increased its volume and formed stratified layers composed of spermatogonia, spermatocytes, spermatids and spermatozoa in groups on the germinal epithelium (Pl. II—Fig. 15).

Most of the spermatids formed by meiosis in the mature stage underwent transformation into highly differentiated spermatozoa except for spermatocytes and spermatids in small numbers near the germinal epithelium. Then in each testicular tubules, bundles waving slightly spirally were formed by spermatozoa of which heads oriented to the basement membrane and tails to the center of the lumen (Pl. II—Fig. 16).

Toward the beginning of spawning, the testicular tubule lost the bundle structure formed by countless spermatozoa in its lumen and discharged the spermatozoa to the surrounding environment through the sperm duct with the simple cialiated columnar epithelium (Pl. II—Fig. 17).

After the spawning, a few of remaining spermatozoa were scattered in their shrunken lumen but they began to degenerate. By the time of spawning completion, contracting of the testicular tubules occurred and finally only the trace of them remained there. Even at this time, it was possible to find out a few residual spermatozoa in the lumen (Pl. II—Fig. 18).

Thereafter the basement membrane became thick again and began to produce new spermatogonia on it. At this time, as has been mentioned in the oogenesis, new eosinophilic cells and mesenchymal tissues appeared a great deal on the germinal epithelium.

3. Fatness and environmental water temperature

Monthly changes of the fatness are shown in Fig. 3. In October when the water temperature was falling, the fatness was 50.9, the lowest of all over the period of the experiment, but thereafter it was highly increased during the winter season and by January it reached 61.9. Fatness, however, remained fairly constant, the ranged 59.7—62.6 during the spring season from February to May. In June the fatness was 62.9, the highest value during the period of the experiment. But in July and in September the fatness dropped abruptly. It was, however, noticeable that the fatness in August was similar to that of July without a big difference between the two.

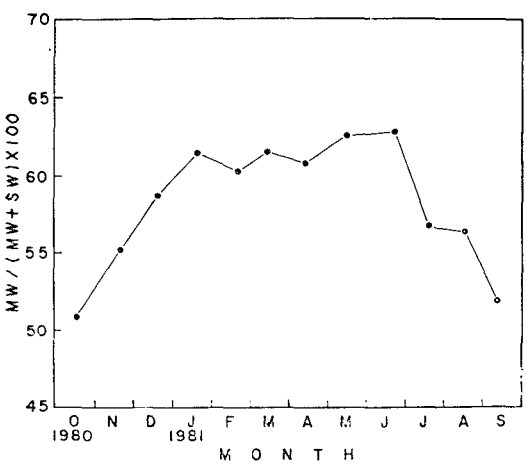


Fig. 3. Monthly changes of fatness.
MW:Meat weight, SW:Shell weight.

Fig. 4 shows the monthly mean water temperatures around the area where the specimens for the study were collected. The water temperature decreased to the lowest of 4.1℃ in January and thereafter it rose gradually up to 23.9℃ in August, and it again began to decrease slowly from September.

4. Reproductive cycle

In this study the reproductive cycle which was more or less continuous could be classified into six stages : multiplicative, growing, mature, spent, degenerative and recovery stage as shown in Fig.4.

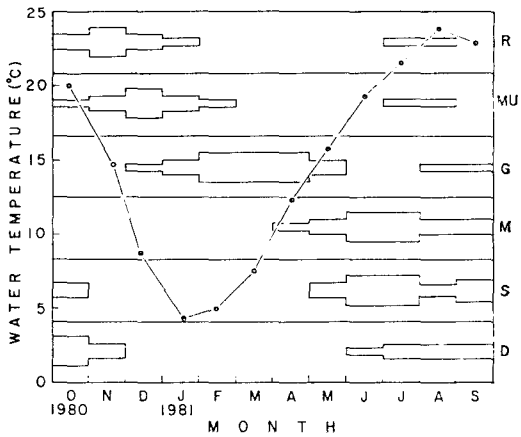


Fig. 4. Gonadal phases of *Fulvia mutica* and changes of mean water temperature from October 1980 to September 1981.
R: Recovery stage, MU: Multiplicative stage, G: Growing stage, M: Mature stage, S: Spent stage, D: Degenerative stage.

1) Multiplicative stage

The gonad tubules located near the outer muscular layer began to develop toward the visceral mass and to extend their lumens. In this stage, each germinal epithelium propagated oogonia and spermatogonia and the ovarian sac was distinguished from the testicular tubule. Individuals of the multiplicative stage appeared from October to February and the main season was December to January. The proliferation of the primary germ cells was also shown in the gonads of some specimens in July and August.

2) Growing stage

In this stage, the primary germ cells suspended the mitosis and then grew into the oocytes and the spermatocytes. The gonad tubules of this stage gradually increased in their volume and reached the largest volume in April. With the growth of the gonad, the oocytes lost their

egg-stalks and were freed in the lumen. In the late period of this stage, the spermatozoa appeared in the lumen of the testicular tubules. The individuals of growing stage appeared from December to May, the main growing season being from February to April. Some of the specimens in August and September also had the growing gonads.

3) Mature stage

After having been freed in the ovarian sac, the oocytes became round in shape and were filled up in the lumen. The spermatozoa became arranged in bundles waving slightly spirally towards the center of the lumen. In this stage, because the gonads were full grown with distended gonadal mass, the visceral mass became much depressed. Mature gonads were found from April to September, peak period being June and July.

4) Spent stage

After the ripe eggs and the sperms were spawned, the lumen became emptied but some ripe germ cells remained undischarged in the contracting lumen. The spawning began in May and lasted till October. Two peak spawnings occurred, one in June and July, and the other in September.

5) Degenerative stage

After having discharged the eggs and sperms, the gonadal mass decreased and the undischarged germ cells were degenerated in the contracted lumen. This stage began in June and continued till November The main degeneration occurred in October.

6) Recovery stage

This stage is the period when the germinal epithelium of the newly formed gonad tubule is activated again. The individuals of this stage were mainly found from October to January. Some individuals in July and August also had the gonad in the recovery stage.

Discussion

Fulvia mutica has been reported to be monoecious by Iroue (1955) and Tanaka (1969), etc., although most marine bivalves belong to the dioecious.

Reddiah (1962) reported that three categories of sexuality might be distingished among the pectinids in Manx waters as below,

1. Species which are hermaphroditic throughout their life-time without sex reversal.
2. Species with seperate male and female phases which undergo sex reversal and with hermaphrodites for a short time.
3. Species which are dioecious.

By the result of present histological observation, it is found that *Fulvia mutica* belongs to type 1 such as *Pecten maximus*, *P. opercularis* (Dakin, 1909), *P. irradians* (Gutsell, 1930) and *P. albicans* (Tanaka, 1971).

It happened to be observed that the testicular tubules in mature stage contained one or two, sometimes three mature oocytes in their lumen. This phenomenon has also been reported on *Pinctada martensii* (Tateishi and Adachi, 1957; Uemoto, 1958), *Venerupis japonica* (Nishikawa *et al.*, 1968), *Patinopecten yessoensis* (Maru, 1976, 1978), ect. Each observers termed such oocyte "testis-ovum". Tateishi and Adachi (1957) reported that if oogonia had appeared on the basement membrane of the testicular tubule having testis-ovum, sex reversal of *Pinctada martensii* might have occurred, while Uemoto (1958) reported that testis-ovum was originated by the development of oocyte which was formed accidently in male gonad, because he could not find oogonia present in the testicular tubules. *P. martensii* has been virtually known as dioecious species by Lee (1972), etc. If the evidence that *P. martensii* shows a sex reversal in some stage of life is true, it should belong to type 2 by

Reddiah (1962). According to the detailed observation in this study, because the writers could not find the appearance of oogonia on the basement membrane of the testicular tubules having testis-ovum, it is not sufficient to confirm that sex reversal occurs in *Fulvia mutica*. Moreover, since *F. mutica* is monoecious, such an assumption is not acceptable. It is, however, uncertain what this testis-ovum is derived from. Further study on the origin of the testis-ovum is demanded to clarify this problem.

The nutritive materials concerning with gonadal development have been reported in several papers. i.e., phagocytic-nutritive cell in *Venus mercenaria* by Loosanoff (1937 a), somatic cell in *Spisula sachalinensis* by Takahashi and Takano (1970), undifferentiated mesenchymal tissue and eosinophilic cell in *Pinctada martensii* by Lee (1972) and in *Corbicula fluminea* by Lee and Chung (1980). Lee and Chung (1980) stated, because the undifferentiated mesenchymal tissue and eosinophilic cells which were aburdunt around the basement membrane in multiplicative stage were gradually disappeared with the growing of gonad tubules, that they could be considered as a kind of nutritive materials. The observations in the present study showed the same results as Lee and Chung's.

Inoue (1955) reported that the fatness of *Fulvia mutica* was low during the main spawning season. Matsuoka *et al.* (1968) discussed that low fatness in the months which gonads of *F. mutica* were not found was to be related with the spawning. As shown in Figs. 3 and 4, the fatness of each individual collected for this study was lowest in October when spawning was completed. Thereafter it rapidly increased till January and reached the highest value in June. These trends indicate that the meat portion increases proportionally to the growth and maturity of the gonad. On the contrary, the fatness rapidly fell down in July and September. In August, it is, however, about the same with that of July. These trends indicate that the peak spawning occurs twice a year between June and July, and in September. This well agrees with the reproductive cycle by the histological observation of gonad.

Especially, the fact that fatness in August did not fall as deep as in July and September indicates the possibility of the secondary spawning in September by the individuals once spawned in May. This is well supported by the results of histological observations that some individuals of July and August showed the gonadal phase of the growing stage.

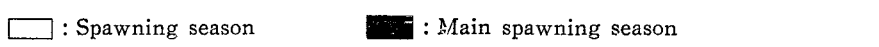
In the relations between the environmental water temperature and the gonad development, the water temperature rises in the main growing season from February to April and shows around 20℃ during the spent stage. This water temperature in the spent stage closely agrees with that in the induced spawning (20℃) by Hotta (1977) and that in the development (18 to 20℃) by Matsuoka *et al.* (1968).

Osanai *et al.* (1980) stated the gonadal maturation of *Patinopecten yessoensis* could be stimulated either by rising or decreasing temperature. Sastry (1963) mentioned that matured scallops in the laboratory spawned in response to elevated temperature. Kikuchi and Uki (1974) summarized that the adult abalones which were kept under controlled condition and after obtaining 1500° in, so called, integral water temperature, could respond to artificial stimuli to induce spawning. In this study, it seems that sexual maturity and spawning of *Fulvia mutica* under the natural condition are also closely related to the water temperature as implied by the authors, mentioned above.

Spawning seasons of *F. mutica* reported by several authors are summarized in Table 1. Some variations of the spawning seasons among the various localities seem to be mainly due to the differences of the water temperature fluctuations during a year in given localities. This is well supported by the fact that the spawning season under present study in adjacent area of Yeosu agrees with that of Yoshida (1953) in Chinhae Bay in Korea.

Table 1. Comparison of the spawning seasons of *Fulvia mutica* (Reeve) in various localities

Author	Locality	Month (J F M A M J J A S O N D)
Yoshida (1953)	Chinhae, Korea	
Inoue (1955)	Yamaguchi, Japan	
Matsuoka *et al.* (1968)	Kyoto, Japan	
Tanaka (1969)	Yokohama, Japan	
Ogushi *et al.* (1971)	Yamaguchi, Japan	
Ogushi *et al.* (1973)	Yamaguchi, Japan	
Nishihiro (1980)	Kyoto, Japan	
Present authors (1982)	Yeosu, Korea	



Summary

The structure of gonads, gametogenesis and reproductive cycle of the cockle, *Fulvia mutica*, were studied mainly by histological observation.

The materials were monthly sampled in the southern area of Yeosu from October 1980 to September 1981.

F. mutica was monoecious. The gonads were situated between the liver tissues and the outer fibromuscular layers compacted by the connective tissue fibers and muscle fibers beneath the outermost layer of simple cuboidal epithelium. The gonad was composed of a number of the ovarian sacs and the testicular tubules which form the tubular structure. Testicular tubules in the mature stage sometimes contained "testis-ova".

The undifferentiated mesenchymal tissues and the eosinophilic cells were abundantly distributed on the germinal epithelium in the early development stage. With the further development of the ovary and testis, these tissues and cells gradually disappeared. The undifferentiated mesenchymal tissues and the eosinophilic cells are related to the growing of the oocytes and spermatocytes.

Early multiplicating oogonium was about 10 μm in diameter. As the oocytes grow to 27—34×50—58 μm by increasing cytoplasm, the oocytes connected to the basement membrane by their egg-stalks. The ripe eggs were about 60 μm in diameter and they were surrounded by gelatinous membrane. Most male germ cells in mature stage were transformed into the spermatozoa and they formed the sperm bundles.

After spawning, undischarged ripe eggs and spermatozoa remained in the ovarian sac and the testicular tubule respectively for some time, then they finally degenerated. Especially the early spent ovarian sacs in May did not contract significantly and then they took part in the secondary maturation within two or three months during the summer season.

The monthly changes of the fatness well agreed with the reproductive cycle.

The reproductive cycle of *F. mutica* could be classified into six successive stages : multiplicative, growing, mature, spent, degenerative and recovery stage.

It seems that the spawning season is closely related to the water temperature, and the spawning occurs from May to October at about 20°C in water temperature. The peak spawning seasons appeared twice a year between June and July and in September.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. The gonads are located between the liver and the outer fibromuscular layers compacted by connective tissue fibers and muscle fibers beneath the epithelial layer.

Fig. 2. The testicular tubules containing testis-ova in their lumen in mature stage.

Fig. 3. The transverse section of an ovarian sac showing the oogonia and the early growing oocytes along the germinal epithelium.

Fig. 4. A great deal of the undifferentiated mesenchymal tissues and the eosinophilic cells on the basement membrane of the early growing stage.

Fig. 5. The growing oocytes in the ovarian sac. The oocytes are growing into the lumen.

Fig. 6. An oocyte connected by the egg-stalk to the germinal epithelium.

Fig. 7. Section of the late growing ovary. There are little mesenchymal tissues and few eosinophilic cells.

Fig. 8. The ovarian sacs of mature stage. The mature oocytes fill up the lumen.

Fig. 9. The transverse section of the ripe oocytes. A large number of yolk granules are found in the cytoplasm and the nucleolus in the large germinal vesicle.

PLATE II

Fig. 10. The spent ovary. Note a few undischarged oocytes which are in the ovarian sacs after spawning.

Fig. 11. A shrunken ovarian sac of recovery stage. The basement membrane is activating and the oogonia begin to appear on the germinal epithelium.

Fig. 12. The ovarian sacs of the gonad in the specimens collected in July. The oogonia, growing oocytes, undischarged oocytes and degenerating eggs coexist in the same ovarian sac.

Fig. 13. Section of a testicular tubule of multiplicative stage. Numerous spermatogonia proliferate on the germinal epithelium.

Fig. 14. Section of a testicular tubule of growing stage. Numerous spermatogonia and spermatocytes appear along the germinal epithelium.

Fig. 15. A part of transverse section of a late growing testicular tubule with the spermatogenetic cells in various stages of development.

Fig. 16. Section of a testicular tubule of mature stage. Countless spermatozoa with the tails oriented toward the center of the testicular tubule, are forming the bundles waving slightly spirally.

Fig. 17. The mass of the spermatozoa is exiting through the sperm-duct.

Fig. 18. Section of a degenerating testicular tubule with shrunken appearance.

PLATE I

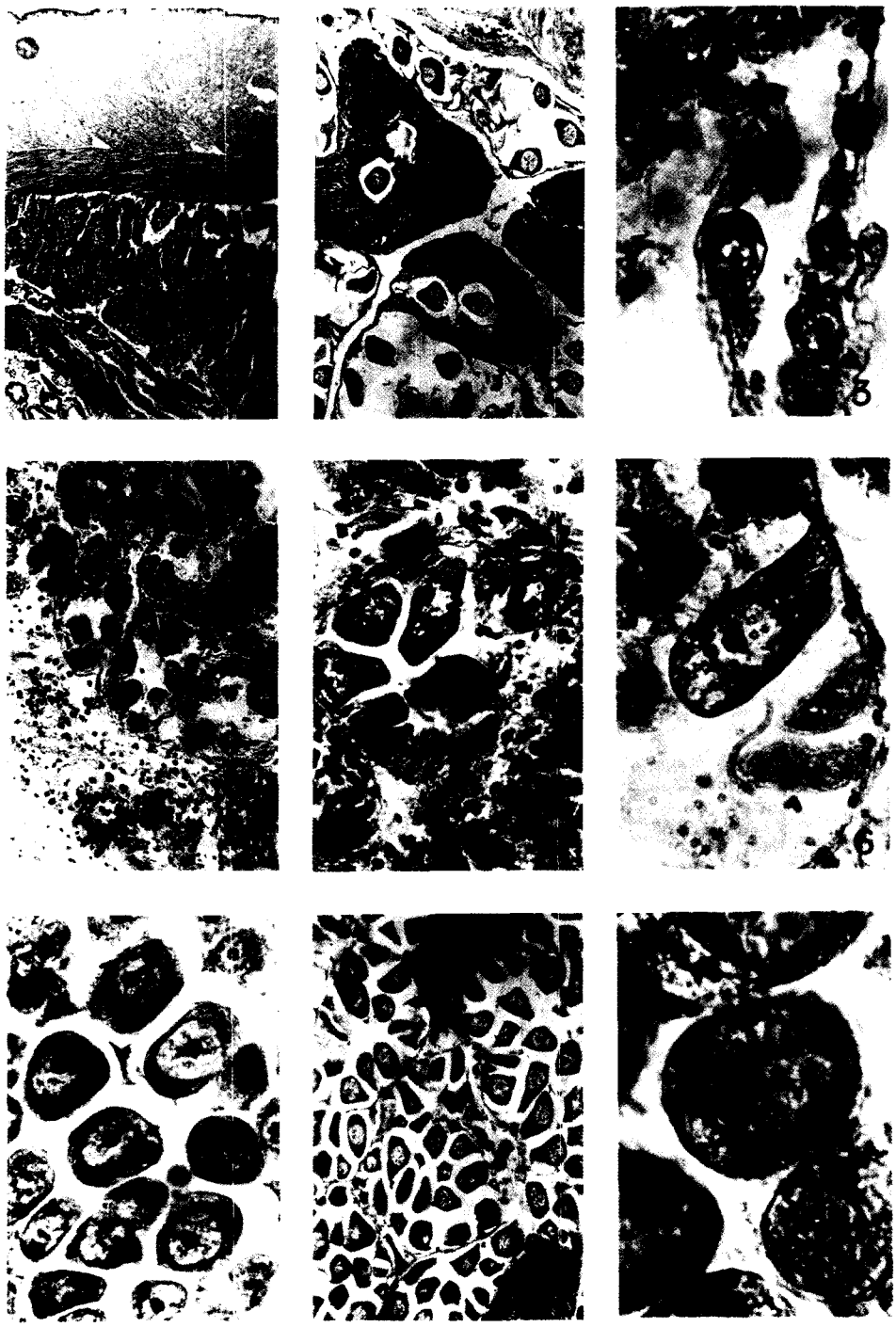

PLATE II