Korean J Biol Sci 3: 375-383, 1999

Gametogenesis and Reproductive Cycle of the Rock Shell, *Reishia (Thais) clavigera* (Neogastropoda: Muricidae), on the West Coast of Korea

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Key Words:
Reishia clavigera
Gonadal development
Gametogenesis
Reproductive cycle
First sexual maturity

Gonadal development, gametogenesis, reproductive cycle, and first sexual maturity of *Reishia clavigera* were investigated monthly from July 1998 to June 1999 through cytological and histological observations. *R. clavigera* had separate sexes, and was an internal fertilizer. The male penis was located near the two tentacles. The ovary and testis were composed of a great number of oogenic lobules and spermatogenic tubules, respectively. The size of ripe oocyte ranged from 130 to 140 μm in diameter. The peripheral cytoplasm of the germinal vesicle of the ripe oocyte in many cases were surrounded by smaller yolk granules, while the eccentric cytoplasm was occupied with larger ones. The reproductive cycle of *R. clavigera* could be classified into five successive stages: early active, late active, ripe, spawning, and recovery. Spawning of females occurred from early July to August when the seawater reached above 24.8℃. Spawning of males occurred from early June to August in the water above 22.8℃. Minimum size for sexual maturity of both sexes was above 10.0 mm in shell height. Each egg capsule was a cylinder or spindle in shape, 4-6 mm in length and 1-2 mm in width. Colors of newly spawned egg capsules showed yellowish white or pale yellow, while those with veliger larvae showed pale black, and released larvae or dead egg capsules showed black violet. The fecundity in an egg capsule ranged from 70 to 91 eggs (mean=80.28 eggs).

The rock shell, *Reishia (Thais) clavigera* (Neogastropoda: Muricidae), is found on a rock in the intertidal zone of the coasts of Korea and south of Hokkaido Island, Japan. It is one of the edible gastropods, but excessive eating causes stomachaches (Yoo, 1976; Kown et al., 1993).

Owing to an imposexual phenomenon caused by TBT (tributyltin), a kind of endocrine disruptor compound, this species is known as an indicator species of marine pollutions. The hypobranchial gland of *R. clavigera* and *R. bronni* which belong to the family Muricidae gives off a fetid odor, namely, methyl mercaptan and dimethyl disulfide (Shiomi et al., 1982). Tanaka (1949) and Kon et al. (1966) reported that *R. clavigera* and *Neverita didyma* kill young oysters and other bivalves by boring the shells.

Past studies of the Muricidae include aspects of classification (Yoo, 1976; Kwon et al., 1993), injuring mechanisms (Tanaka, 1949), seasonal changes of the gonads (Kon et al., 1966), volatile sulfur compounds (Shiomi et al., 1982), reproductive ecology (Chung et al., 1993), and cytological studies on testicular maturation (Chung and Kim, 1997). To date, histological study on the reproductive biology of *R. clavigera* is not known. In this study, the gonadal development, gametogenesis, reproductive cycle, and first sexual maturity of this species were defined through histological observations.

Materials and Methods

The materials used were collected monthly from the rocky intertidal zone of Taehang, Puan-gun, Chollabuk-do, on the west coast of Korea, from July 1998 to June 1999 (Fig. 1). The total number of 475 individuals, ranging from 3.6 mm to 38.5 mm in shell height, was collected. After the specimens were transported alive to the laboratory, the height and width of the shells were measured to the nearest 0.1 mm by a vernier caliper, and the total weight, flesh weight, and shell weight were weighed to the nearest 0.01 g by an electronic balance. The sex of matured clams was determined by the presence of the penis.

To observe histological changes involved in gonadal development, the gonad containing a part of the visceral masses was removed and fixed in Bouin's

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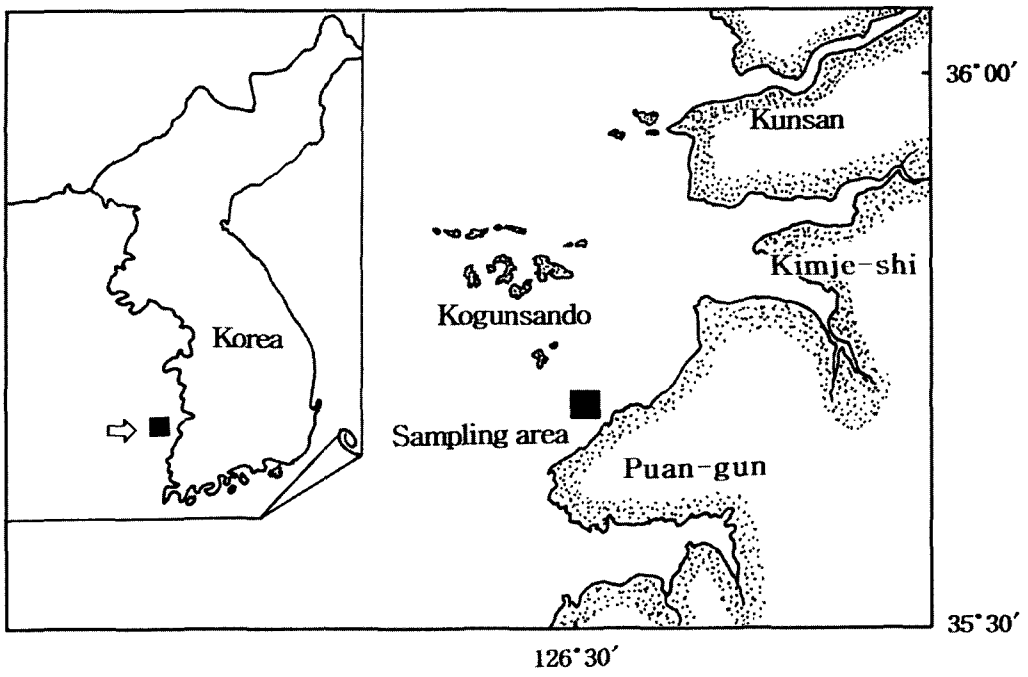

Fig. 1. A map showing the sampling area.

solution (a mixture of saturated picric acid, formalin, and glacial acetic acid with the proportions of 75, 25, and 5) for 24 h. The fixed specimens were processed according to standard techniques (dehydrated in ethyl alcohol and embedded in paraffin). The embedded tissues were serially sectioned at 4-5 μm by a rotary microtome. The sections were attached on glass slides, stained with Bohmer's hematoxylin-1% alcoholic eosin, mounted in Canada balsam, and examined under a light microscope. To investigate the fecundity in egg capsules, a total of 318 egg capsules were collected at the sampling area from July to August 1998.

The percentages of the first sexual maturity were histologically investigated to confirm the shell heights of the specimens involved in reproduction before and after the breeding seasons.

Unpublished data of water temperatures, measured at 10:00 a.m. by the Kunsan branch, Seohae Fisheries Institute, National Fisheries Research and Development Institute, were used for this study.

Results

Position and structure of the gonad

Reishia clavigera had distinct sexes, and was an internal fertilizer. The gonad was widely located on the surface of the liver which was located in the posterior spiral part in the shell (Fig. 2). The immature gonad was thinly distributed on the liver. With the progress of maturation, the external colors of the ovary and testis appeared to be light yellow and yellowish brown, respectively. At this time, if the gonads are slightly scratched by any means, ripe eggs and spermatozoa easily flow out. The male could readily be discriminated by the presence of the penis.

Ovarian development and oogenesis

The ovary, composed of a number of oogenic lobules, was placed between the liver and the outer layers composed of the simple columnar epithelial cells and connective fibromuscular tissues.

From September to the following June, the oogonia were actively propagated on the wall of the oogenic lobule. Each oogonium was round or oval in shape, 8-9 μm in diameter, and had a round nucleus containing a conspicuous basophilic nucleolus in its center. However, the cytoplasm of oogonium was very poor. A number of mesenchymal tissues and eosinophilic granular cells were also seen near the lobular wall at that time. A few early growing oocytes (20-30 μm in diameter) were attached to the lobular wall by an egg-stalk, but they did not have yolk granules yet in their cytoplasm (Fig. 3A).

As the growth of the ovary proceeded, the oogenic lobules gradually increased in volume and size. From October to the following July, most of the oocytes grew to 60-70 μm in diameter, each oocyte had an egg-stalk connected to the lobular wall, and the nucleus in the oocyte, that is, germinal vesicle with a distinct nucleolus, moved to the distal part of the oocyte. At this time, with the initiation of yolk formation, the cytoplasm of the oocyte was filled with various yolk granules in size and volume (Fig. 3B).

From February to September, most of the oocytes

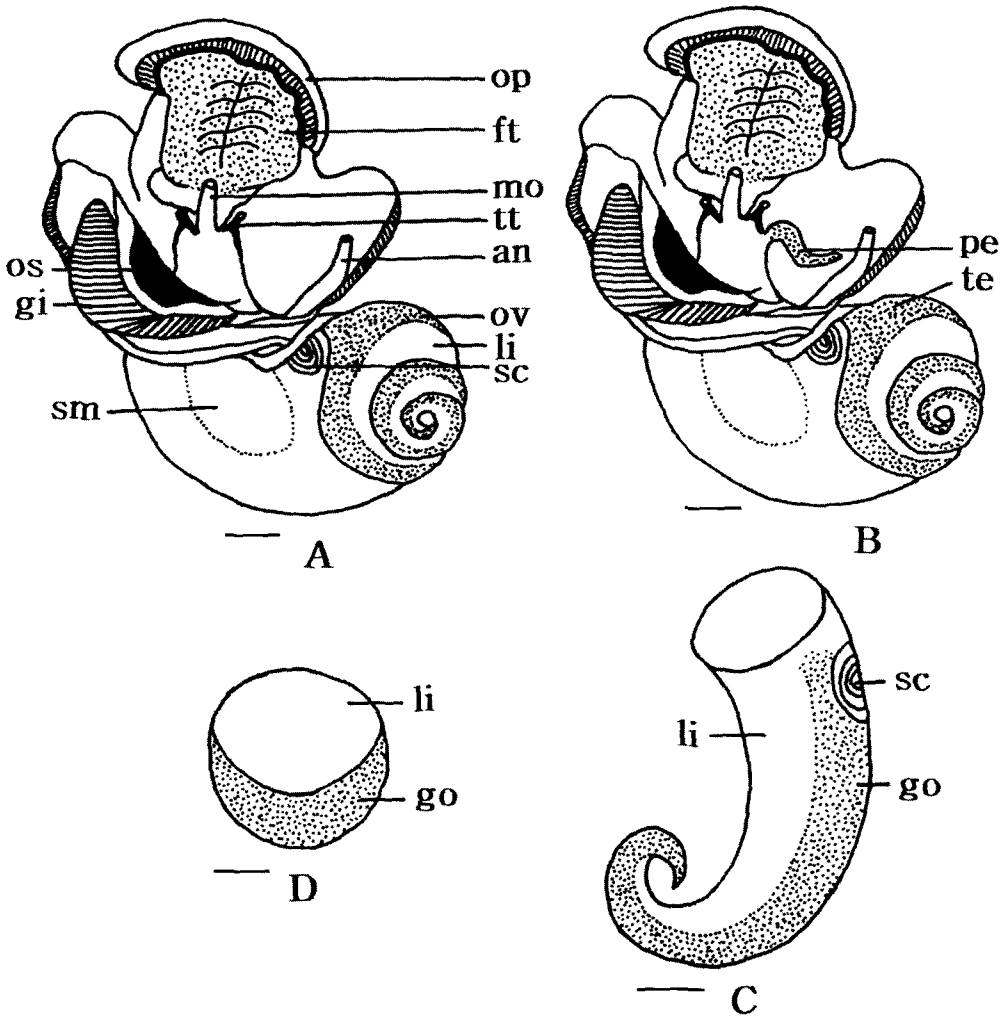

Fig. 2. Anatomy of *Reishia clavigera*. A, Organs of a female. B, Organs of a male. C, Posterior appendage showing gonad and liver. D, Cross section of posterior appendage showing gonad and liver. an, anus; ft, foot; gi, gill; go, gonad; li, liver; mo, mouth; op, operculum; os, osphradium; ov, ovary; pe, penis; sc, stomachal cecum; sm, stomach; te, testis; tt, tentacle. Scale bars=1 mm (D), 3 mm (C), and 4 mm (A, B).

which had grown up to 110-120 μm in diameter became polygon in shape, and each oogenic lobule was filled with mature oocytes. However, the oocytes forming yolk granules and a few early growing oocytes were still found on the lobular wall. The eosinophilic granular cells and mesenchymal tissues existed in very few numbers and the lobular wall became very thin (Fig. 3C). The ripe oocyte (130-140 μm in diameter) contained a great number of yolk granules in its cytoplasm. As ovarian maturation progressed, the peripheral cytoplasm of the germinal vesicle of oocyte tended to surround smaller yolk granules, while the eccentric cytoplasm was occupied with larger ones. At this time, as the oocytes closely came in contact with one another by very thin egg membranes, it became difficult to distinguish the borders (Fig. 3D).

From July to August, the ripe oocytes in the oogenic lobules were discharged in the surrounding environment. At this time, a number of yolk granules, which were caused by the rupture of the undischarged ripe oocytes as well as growing oocytes, still remained in the lumen of the lobule (Fig. 3E).

After spawning, the undischarged oocytes in the lumen of the lobule underwent cytolysis, and then each oogenic lobule was contracted. The outer layers of the ovary composed of the simple columnar epithelial cells and connective fibromuscular tissues tended to thicken again. New oogonia, eosinophilic granular cells, and mesenchymal tissues appeared in newly formed oogenic lobules (Fig. 3F).

Testicular development and spermatogenesis

The testis, as already shown in the ovary, was also placed between the liver and the outer epithelial layers and composed of numerous spermatogenic tubules.

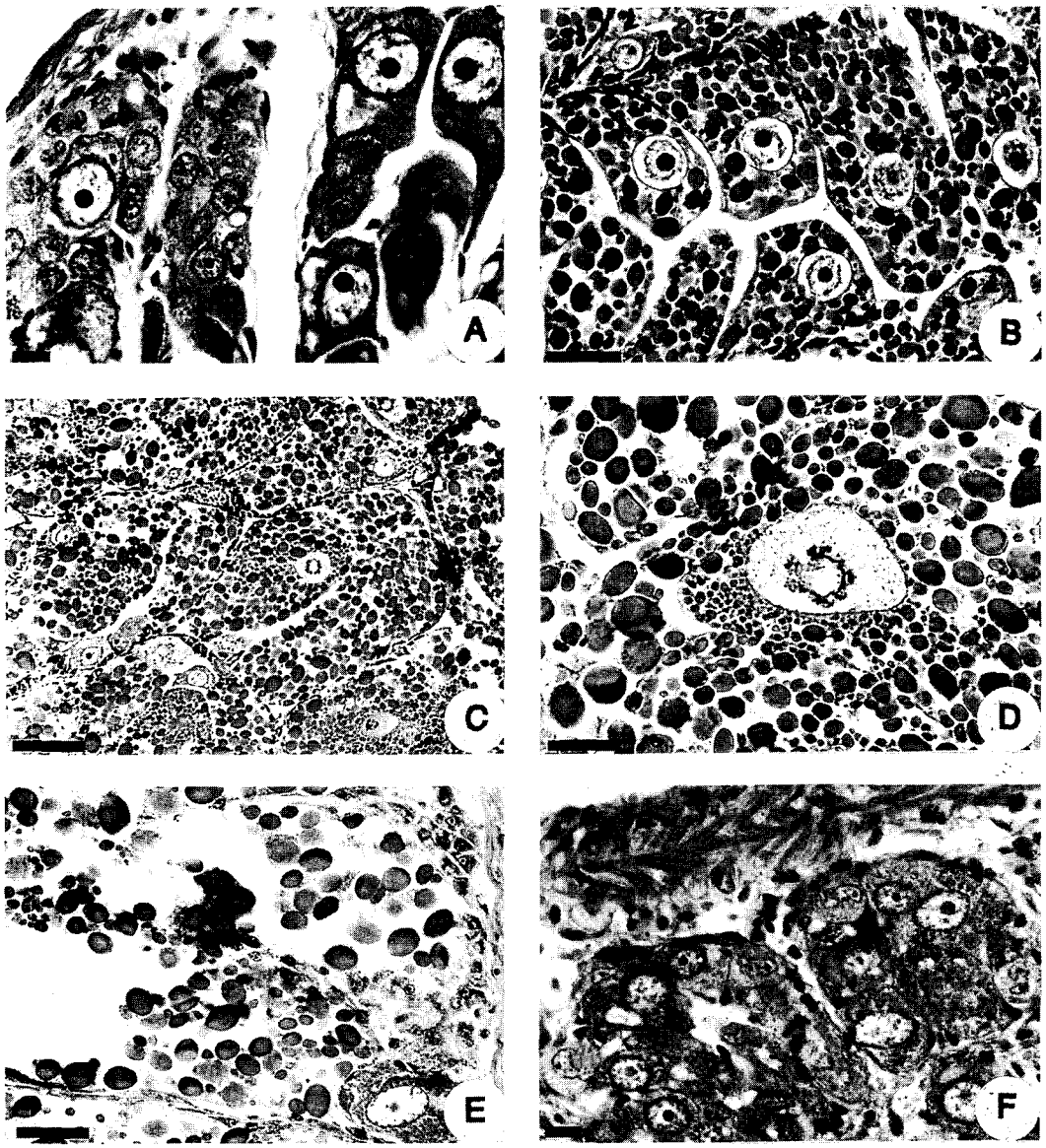

Fig. 3. Photomicrographs of gonadal phases of female *Reishia clavigera*. A, Section of the oogenic lobule in the early active stage in November. Note a number of oogonia and eosinophilic granular cells in the lobule. A few early growing oocytes are attached to the lobular wall by an egg-stalk, but they do not have yolk granules in their cytoplasm yet. B, Section of the lobule in the late active stage in March. Cytoplasm of the oocyte is filled with various yolk granules in size and volume. C, Section of the lobule in the ripe stage in June. Each oogenic lobule is filled with the mature oocytes. There are still a few early growing oocytes in the lobule. D, Section of the lobule in the same stage as above in July. Note a distinct germinal vesicle in the center of the picture which is surrounded with smaller yolk granules. E, Section of the lobule in the spawning stage in August. Note a number of yolk granules which were caused by the ruptures of the undischarged ripe oocytes as well as a growing oocyte are still in the lumen of the lobule. F, Section of the lobule in the recovery stage in September. The outer layer of the ovary thickens again. New oogonia as well as eosinophilic granular cells appear in newly formed oogenic lobule. Scale bars=10 μm (A, F), 30 μm (D), 40 μm (B, E), and 80 μm (C).

The spermatogenic tubules perpendicularly projected inwards from the outer testicular wall. From August to the following April, the spermatogonia were round in shape, 7-8 μm in diameter, and actively proliferated alone or in small groups on the wall of the spermatogenic tubule. The nucleus of spermatogonium was 5-6 μm in diameter, and the basophilic nucleolus was seen in the center of the nucleus. A few spermatocytes appeared in the lumina of spermatogenic tubules (Fig. 4A).

From September to the following July, as the growth of testis advanced, the spermatogonia grew to the primary and secondary spermatocytes, and then these spermatocytes developed into spermatids. The diameters of spermatocytes and spermatids were 4-5 μm and 2-3 μm, respectively. At this time, the spermatogenic tubule formed multiple layers composed of spermatogonia, primary and secondary spermatocytes, and spermatids (Fig. 4B).

From December to the following September, number

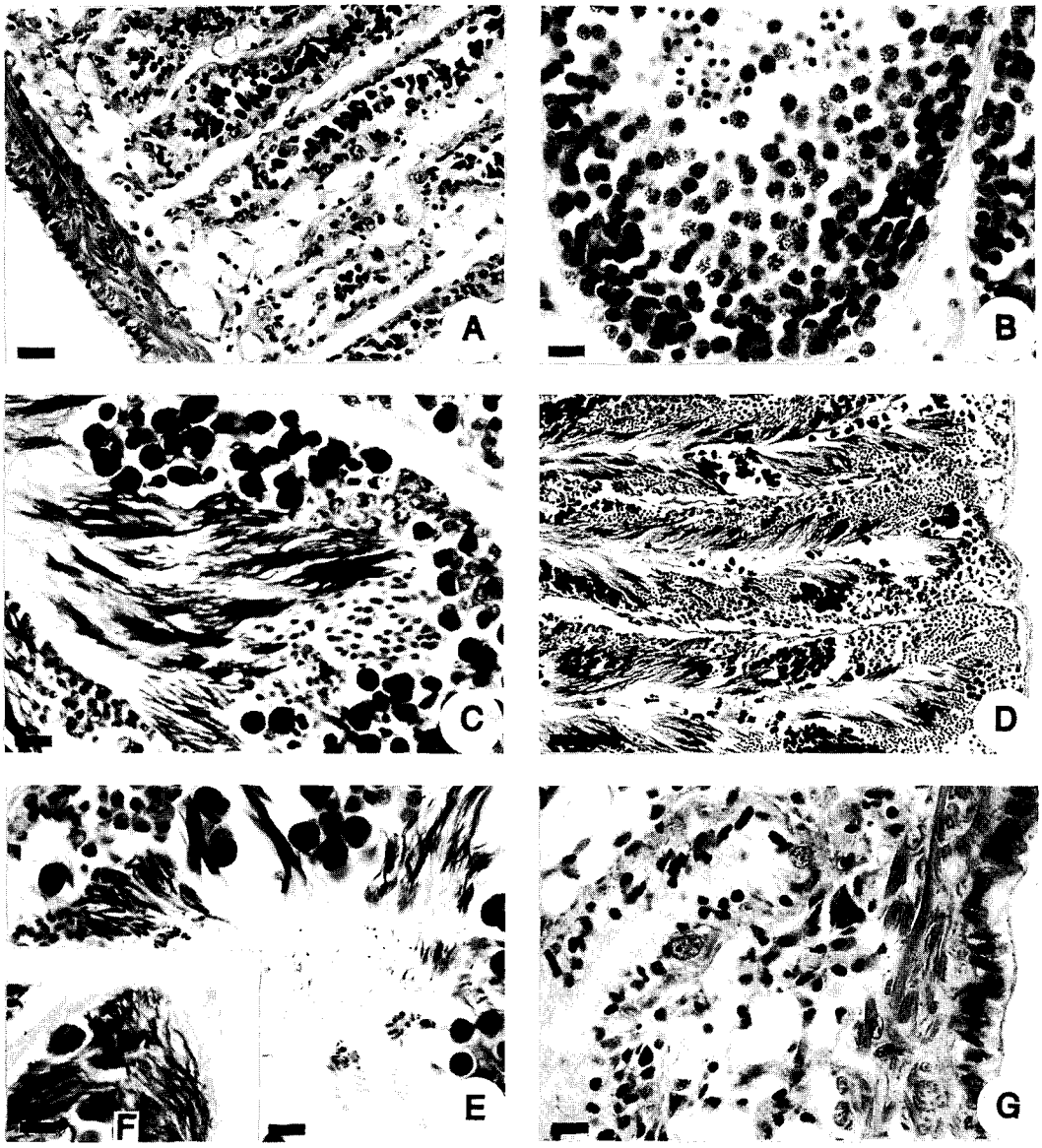

Fig. 4. Photomicrographs of gonadal phases of male *Reishia clavigera*. A, Section of the spermatogenic tubule in the early active stage in November. The tubules perpendicularly project inward from the outer testicular wall. Note the spermatogonia and spermatocytes in the tubule. B, Section of the tubule in the late active stage in February. Note numerous spermatogonia, spermatocytes, and spermatids in the lumen. C, Section of the tubule in the ripe stage in June. A great number of spermatozoa which completed spermiogenesis filled up the lumen of the tubule. Their heads orient to the tubular wall, and tails to the center of the lumen. Note the various stages of the cells under spermatogenesis. D, Section of the tubule in the same stage as above in July. E, Section of the tubule in the spawning stage in August. Note a number of undischarged spermatozoa and residual substances in the lumen of the tubule. F, Cross section of the vas deferens which is occupied with the mass of the spermatozoa in August. G, Section of the tubule in the recovery stage in September. The outer layer of the testis thickened again. New spermatogonia as well as eosinophilic granular cells and mesenchymal tissues appear in newly formed spermatogenic tubule. Scale bars=10 μm (B, C, E, F, G), 20 μm (A), and 80 μm (D).

of spermatogonia, spermatocytes, and spermatids in the mature spermatogenic tubule gradually decreased, while the spermatozoa which completed the process of spermiogenesis filled up the lumen of the tubule. Heads of spermatozoa oriented toward the tubular wall and tails toward the center of the lumen. In some areas the ripe spermatozoa formed homogeneous masses, while others swirled toward the center of the tubule. At this time, the outer layer of the testis and the tubular wall became very thin, but the volume of the testis became large (Figs. 4C and D).

In early June, countless spermatozoa in the tubule were transported to the vas deferens which were convoluted between the testis and liver before initiating copulation. At this time, the lumen of the tubule became considerably empty. However, a number of various spermatogenic cells were still remaining in the lumen (Figs. 4E and F).

A few remaining spermatogenic cells were degenerated in the lumen of the tubule. As mentioned in the

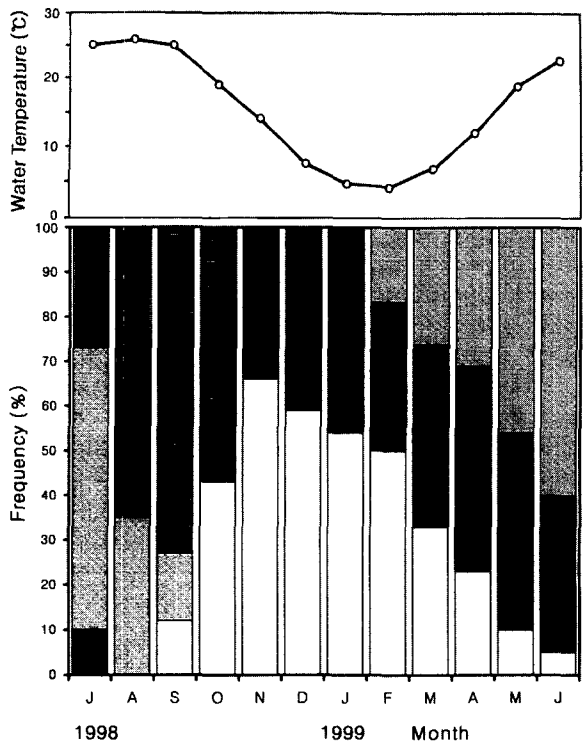

Fig. 5. Frequency of female *Reishia clavigera* with gonads in each developmental phase and monthly changes of the mean water temperature from July 1998 to June 1999. □, early active phase; ■, late active phase; ⊡, ripe phase; ▥, spawning phase; ▤, receovery phase.

process of oogenesis, the outer layers of the testis thickened again, new spermatogonia, eosinophilic granular cells, and mesenchymal tissues appeared in newly formed spermatogenic tubules (Fig. 4G).

Reproductive cycle

By studying the monthly changes of the morphological features and sizes of germ cells during gametogenesis in the gonad, the reproductive cycle of *R. clavigera* could be classified into five successive stages: early active, late active, ripe, spawning, and recovery stage as shown in Figs. 5 and 6.

Early active stage: The oogenic lobules and spermatogenic tubules located near the outer epithelial layers began to develop toward the livers. In this stage, the oogonia and spermatogonia propagate on the lobular and tubular walls, respectively. Therefore, the ovary and testis could be easily distinguished by a histological method. Females and males in the early active stage were found from September to the following June and August to the following April, respectively. The main season occurred in November in both sexes.

Late active stage: In this stage, the oocytes began yolk formation in their cytoplasms, and most oocytes were attached to the lobular wall by an egg-stalk. The

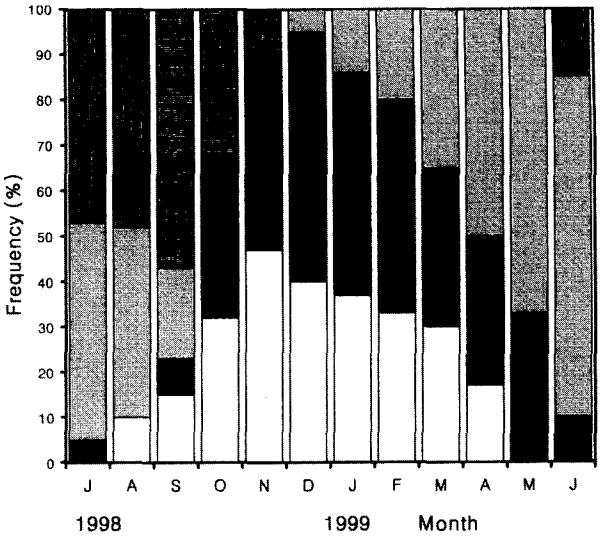

Fig. 6. Frequency of male *Reishia clavigera* with gonads in each developmental phase from July 1998 to June 1999. □, early active phase; ■, late active phase; ⊡, ripe phase; ▥, spawning phase; ▤, receovery phase.

spermatogonia developed into the spermatocytes and spermatids, therefore each spermatogenic tubule formed stratified layers composed of various spermatogenic cells. Females and males in the late active stage were found from October to the following July and September to the following July, respectively.

Ripe stage: In this stage, the gonad became the thickest of all stages, while the outer layers, the lobular and tubular walls became the thinnest. The lumina of lobules were filled with ripe oocytes and the cytoplasm of each oocyte contained a large number of yolk granules. The mature spermatozoa filled up the lumen of the spermatogenic tubule, but a few of spermatogonia, spermatocytes, and spermatids were still in the tubule. Females and males in the ripe stage were found from February to September and December to the following September respectively. The main season in females and males was July and June, respectively.

Spawning stage: In this stage, the lumen of oogenic lobule gradually became empty, but a great number of undischarged yolk granules and a few growing oocytes were also found in the lumen. The lumen of the spermatogenic tubule gradually became empty, but undischarged spermatozoa, spermatocytes, and spermatids were also found in the lumen. Spawning of females occurred from early July to August when the water temperature reached above 24.8℃. However, spawning of males occurred from early June to August in seawater above 22.8℃. The main spawning in females and males occurred in August and July, respectively.

Recovery stage: In this stage, the outer epithelial layers of the gonad thickened again. New oogonia and

Fig. 7. External features of egg capsules of *Reishia clavigera*. Scale bar=1 cm.

spermatogonia appeared in the newly formed oogenic lobular and spermatogenic tubular wall. Females and males in the recovery stage were found from August to December and July to November, respectively.

Observation of the egg capsules

A great number of egg capsules were attached in a group on the solid substrata (especially rock). Morphology of each capsule was cylindrical or spindly shaped, 4-6 mm in length, and 1-2 mm in width (Figs. 7 and 8). Newly spawned egg capsules seem yellowish white or pale yellow, while those with veliger larvae colored pale black, and released larvae or dead egg capsules black Violet. The fecundity, namely, number of eggs in an egg capsule ranged from 70 to 91 eggs (mean=80.28 eggs) (Fig. 8 and Table 1). The egg capsules appeared from early July to mid-August.

First sexual maturity

The first sexual maturity of a total 260 specimens (131 females and 129 males) of *R. clavigera* ranging from 4.0 to 21.9 mm in shell height was histologically investigated in order to determine the heights of the shell taking part in reproduction from May to October.

As shown in Table 2, individuals of 7.9 mm and less in shell height could not take part in reproduction in both sexes. Females and males ranging from 8.0 to 9.9 mm in shell heights participated in reproduction at a rate of 33.3% and 31.3%, respectively. Percentages of the first sexual maturity of female and male specimens ranging from 10.0 to 11.9 mm in shell heights

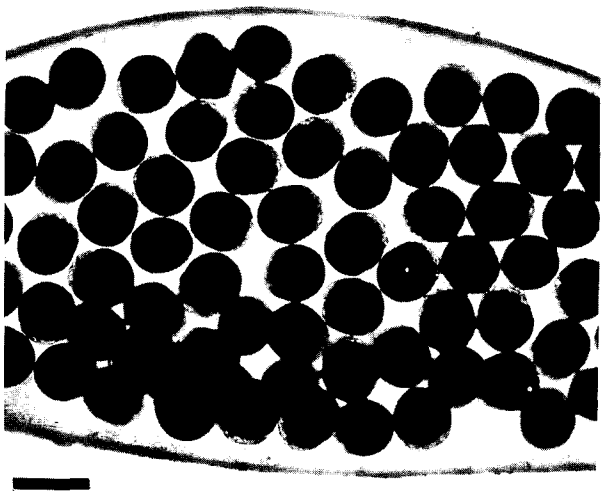

Fig. 8. Photomicrograp of eggs in an egg capsule of *Reishia clavigera*. Scale bar=0.2 mm.

were 53.3% and 56.3%, respectively, and 100% of those over 16.0 mm in shell height in both sexes took part in the reproduction.

Discussion

Many authors reported that gonadal development and maturation, gametogenesis, and reproductive cycle of most marine mollusks were related to exogenous factors. For example, Taki (1949) described that the low specific gravity of seawater suppressed the spawning of *Meretrix lusoria*. Giese (1959), Griffiths (1977), and Jara-millo and Navarro (1995) reported that the breeding seasons of marine bivalves were closely related to the abundance of food for adults and their planktotrophic larvae. Kennedy and Krantz (1982) and Glovani and Diana (1994) described that the duration of spawning varied geographically, that is, long duration of spawning were shown at lower latitude localities and short duration of spawning at higher latitude localities. Webber and Giese (1969) and Brousseau (1995) reported that the role of water temperature in triggering release of gametes and gonadal developments was not clear. While several authors (Chang and Lee, 1982; Chung et al., 1993; Lee et al., 1999) reported that in the relation between the environmental water temperature of the habitat and gonadal development, gonadal development was closely related to the increase in water temperature.

Table 1. Fecundity in an egg capsule of *Reishia clavigera*

Date	No. of examined egg capsules	Fecundity in an egg capsule	No. of total eggs	Mean fecundity per egg capsule
Jul. 5, 1998	81	75~88	6,517	80.46
Jul. 15, 1998	80	71~90	6,335	79.19
Aug. 1, 1998	75	70~91	6,247	83.29
Aug. 15, 1998	82	72~89	6,429	78.40
Total	318		25,528	80.28

Table 2. Shell height of *Reishia clavigera* at first sexual maturity

Shell height (mm)	Female			Male		
	No. of individuals examined	No. of matured individuals	Maturity (%)	No. of individuals examined	No. of matured individuals	Maturity (%)
4.0~ 5.9	15	0	0	15	0	0
6.0~ 7.9	14	0	0	13	0	0
8.0~ 9.9	15	5	33.3	16	5	31.3
10.0~11.9	15	8	53.3	16	9	56.3
12.0~13.9	15	9	60.0	15	10	66.7
14.0~15.9	16	15	93.8	14	13	92.9
16.0~17.9	14	14	100	15	15	100
18.0~19.9	13	13	100	12	12	100
20.0~21.9	14	14	100	13	13	100
Total	131	78		129	77	

In this study, spawning of most females occurred from early July to August when the water temperature was above 24.8℃, however, spawning of a few females commenced in late June. Spawning of males occurred from early June to August when the water temperature was above 22.8℃. Therefore, it is assumed that gonadal development, sexual maturation, and spawning of *R. clavigera* are closely related to the water temperatures.

In some marine mollusks, gonad passes into the resting or inactive stage after spawning, and then the germ cells are no longer found in the gonad (Lee et al., 1997, 1999; Lee, 1998). In this study, the reproductive cycle of *R. clavigera* was divided into 5 stages, namely, early active, late active, ripe, spawning, and recovery stage through histological observations. After spawning, the gonad of this species immediately passed into the recovery stage without resting or inactive stage. Accordingly, it is supposed that gonadal development and gametogenesis of this species continuously occur throughout the year.

Boolootian et al. (1962) stated that most marine mollusks have their own unique breeding patterns. And Boolootian et al. (1962) divided breeding patterns of the mollusks into three categories, namely, (1) year-round breeders which spawn throughout all seasons, (2) winter breeders which spawn from late fall to early spring of the following year, and (3) summer breeders which spawn from late spring to early fall. Number of annual spawning seasons of mollusks showed various patterns: once a year in *Turbo cornutus* (Lee, 1980), *Rapana venosa* (Chung and Kim, 1997), and *Scapharca subcrenata* (Lee, 1998); twice a year in *Tapes japonica* (Ko, 1957) and *Fulvia mutica* (Chang and Lee, 1982); and three times a year in *Ruditapes philippinarum* (Sarasquete et al., 1990). In this study, spawning of *R. clavigera* occurred from early July to August. Consequently, it is assumed that *R. clavigera* belongs to the summer breeders, and the spawning of this species occurs once a year.

Amio (1963) reported that the eggs of marine herbivorous gastropods showed various colors such as orange, yellowish red, or deep green, while the eggs of carnivorous ones showed pale yellow or white. Chung et al. (1993) stated that the eggs of *Rapana venosa* were well protected in egg capsules (yellowish white in color) and were pale yellow. In this study, *R. clavigera* belonged to the marine Neogastropoda and the carnivore, their yellowish eggs existed in the egg capsules, and newly spawned egg capsules showed yellowish white or pale yellow in color. These observations corresponded with the above-mentioned reports.

Fujinaga (1985) reported that *Neptunea arthritica* (Neogastropoda) produced 20-80 egg capsules per individual. And Chung et al. (1993) reported that *Rapana venosa* (Neogastropoda) produced 296-409 egg capsules per individual, and the fecundity in an egg capsule is 984-1,241 eggs. In *R. clavigera*, the number of egg capsules, which was produced from an individual, could not be investigated at the sampling area. However, the fecundity in an egg capsule was 70-91 eggs (mean=80.28 eggs). Therefore, it is assumed that the fecundity in an egg capsule varies with genera, species, habitats, and other environmental factors in neogastropods.

Acknowledgements

I am grateful to Prof. Pyung-Rim Chung at Inha University College of Medicine, for his valuable comments. This work was supported by the research fund from Jeonju University (1999).

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[Received September 13, 1999; accepted October 10, 1999]