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Gonadal Development and Reproductive Cycle of the Top Shell, *Omphalius rusticus* (Gastropoda: Trochidae)

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Key Words:
Gastropoda
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Gonadal development
Reproductive cycle
Gonad index
First sexual maturity

Gonadal development, reproductive cycle, gonad index, meat weight rate, and first sexual maturity of the top shell, *Omphalius rusticus* were investigated monthly by histological observations. Specimens were collected from the west coast of Korea during the period from January to December in 1999. *O. rusticus* is dioecious and oviparous. The gonad is widely situated on the surface of the digestive gland located in the posterior spiral meat part in the shell. The ovary and the testis were composed of a number of oogenic follicles and several spermatogenic follicles, respectively. Ripe oocytes were approximately 120-130 μm in diameter. The meat weight rate peaked in June (27.7%), and then rapidly decreased in September (19.5%). Monthly changes in the gonad index in both sexes reached the maximum in June, and then sharply decreased in September. Percentages of first sexual maturity of female and male snails ranging from 9.0 to 9.9 mm in shell heights were 58.3% and 54.5%, respectively, and 100% in those over 11.0 mm in both sexes participated in reproduction. Reproductive cycle of this species can be categorized into five successive stages: in females, early active (October to April), late active (December to June), ripe (April to September), spawning (July to September) and recovery (September to January); in males, early active (November to March), late active (December to June), ripe (April to September), spawning (July to September) and recovery (September to December). Gonadal development, gametogenesis, reproductive cycle, and spawning were closely related to the seawater temperature.

The top shell, *Omphalius rusticus* (Gastropoda: Trochidae) is a marine mollusc inhabiting underneath rocks in the intertidal zone of the coasts of Korea and Japan. It is one of the edible gastropods and is herbivorous (Kwon et al., 1993).

So far, there have been some reports on *Omphalius* spp: aspects of classification (Choe and Yoon, 1990; Kwon et al., 1993), Korean and local names (Lee and Baek, 1982; Je, 1989), a feeding stimulant assay (Sakata et al., 1988), ecological studies (Lee and Jwa, 1988; Lee et al., 1995), and the distribution and community structure (Lee, 1991; Lee and Hyun, 1991). To date, however, no histological study on the reproductive biology of *O. resticus* has been reported.

Due to marine pollution, changes in marine environments (marine reclamation and exploitation of the tidal flats), and reckless fishing, yields and habitats of this species have gradually decreased. To study reproductive biology of this species for maintenance of natural resources, its reproductive cycle, gonad index, meat weight rate, and first sexual maturity were investigated by histological observations. Therefore, studies on gametogenesis, reproductive cycle, and spawning season of *O. rusticus* will be provided as basic information for propagation and culture of natural resources.

Materials and Methods

Specimens of the top shell, *O. rusticus* were collected monthly by hand from the rocky intertidal zone of Daehang-ri, Buan-gun, Jeollabuk-do, on the west coast of Korea, from January to December, 1999 (Fig. 1).

A total of 275 snails (4.0-24.2 mm in shell height) used for histological observations. The specimens were kept alive during transportation to the laboratory, and their shell heights and widths were measured to the accuracy of 0.1 mm by a vernier caliper, and the total weight, meat weight (MW) and shell weight (SW) were measured to the accuracy of 0.01 g with an electronic balance. To investigate correlations between gonadal phases and changes in body weight, the meat weight rate (MWR) was calculated by the following formula (Momoyama and Iwamoto, 1979):

$$MWR(\%) = \frac{MW(g)}{MW(g) + SW(g)} \times 100$$

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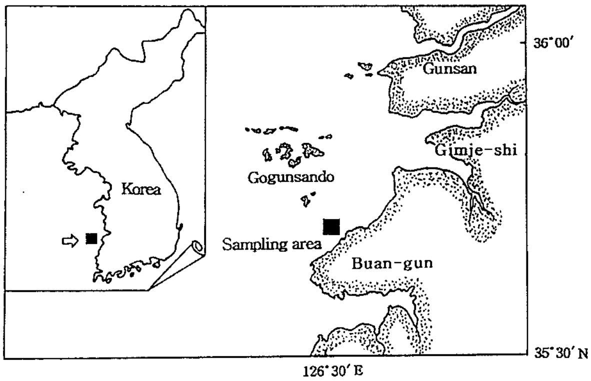

Fig. 1. Map showing the sampling area.

To estimate gonadal development, reproductive cycle, and spawning period, the mean gonad index (GI) was calculated for each sample (Yamamoto and Yamakawa, 1985; Shibata, 1993) as follows:

$$GI = \frac{\text{Diameter of gonad } (D')}{\text{Total diameter of cross section } (D)} \times 100 \quad \text{(Fig. 2)}$$

To examine gonadal phases, the soft body of the snail was exposed by breaking the shell with a hammer. The posterior appendage including the gonad and digestive gland was then dissected by surgical instruments, and fixed in Bouin's solution for 24 h. The fixed specimens were subjected to standard histological specimen preparation procedures (dehydrated in ethanol and embedded in paraffin). Serial sections were made (4 μm to 5 μm). Sections were mounted on glass slides, stained with Bohmer's haematoxylin-1% alcoholic eosin, mounted in balsam, and examined under a light microscope.

Percentages of first sexual maturity were investigated histologically to confirm shell heights of the specimens undergoing reproduction during breeding seasons.

Results

Position and the external features of the gonad

Sex of *Omphalius rusticus* is separate. The gonad was widely situated on the surface of the digestive gland

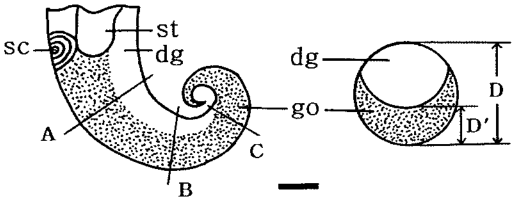

Fig. 2. Schematic illustrations of the gonad and adjacent regions of *Omphalius rusticus* and cross section of B region. A, B, and C indicate the sections for measurements of the gonad index. These three sections were equally spaced. dg, digestive gland; go, gonad; sc, stomachal caecum; st, stomach. Scale bar=2.5 mm.

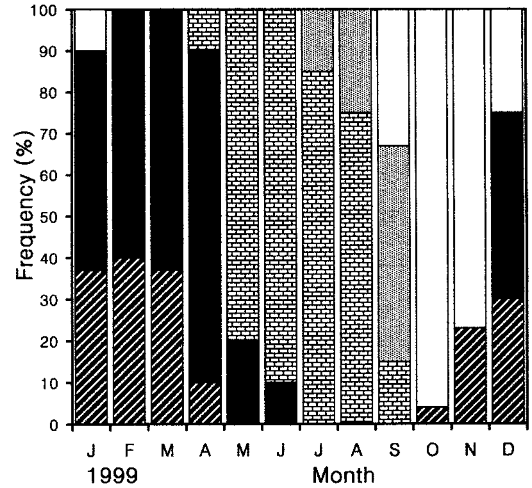

Fig. 3. Frequency distribution of gonadal phases of the female top shell, *Omphalius rusticus* from January to December, 1999. early active phase (▨), late active phase (■), ripe phase (▤), spawing phase (▒), and recovery phase (□).

located in the rear of the spiral meat part of the shell (Fig. 2). The immature gonad was thinly distributed on the surface of the digestive gland. As the gonadal maturation proceeded, the gonad was thickly distributed on the digestive gland. The external color of the mature ovary was green, and that of the mature testis milky yellow. Therefore, both sexes could be readily distinguished by their external colors. When mature gonads were gently scratched, ripe eggs and sperms readily flowed out. However, after spawning, the gonad became dark brown or dark blue. At this time, the sex of the snails could not be readily distinguished by color.

Gonadal phase and reproductive cycle by histological observation

Based on monthly changes of the morphological fea-

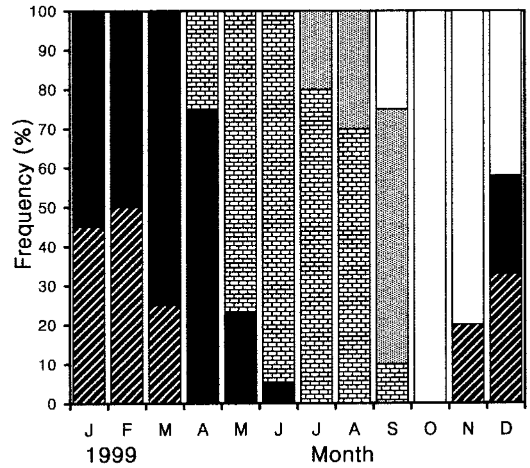

Fig. 4. Frequency distribution of gonadal phases of the male top shell, *Omphalius rusticus* from January to December, 1999. early active phase (▨), late active phase (■), ripe phase (▤), spawing phase (▒), and recovery phase (□).

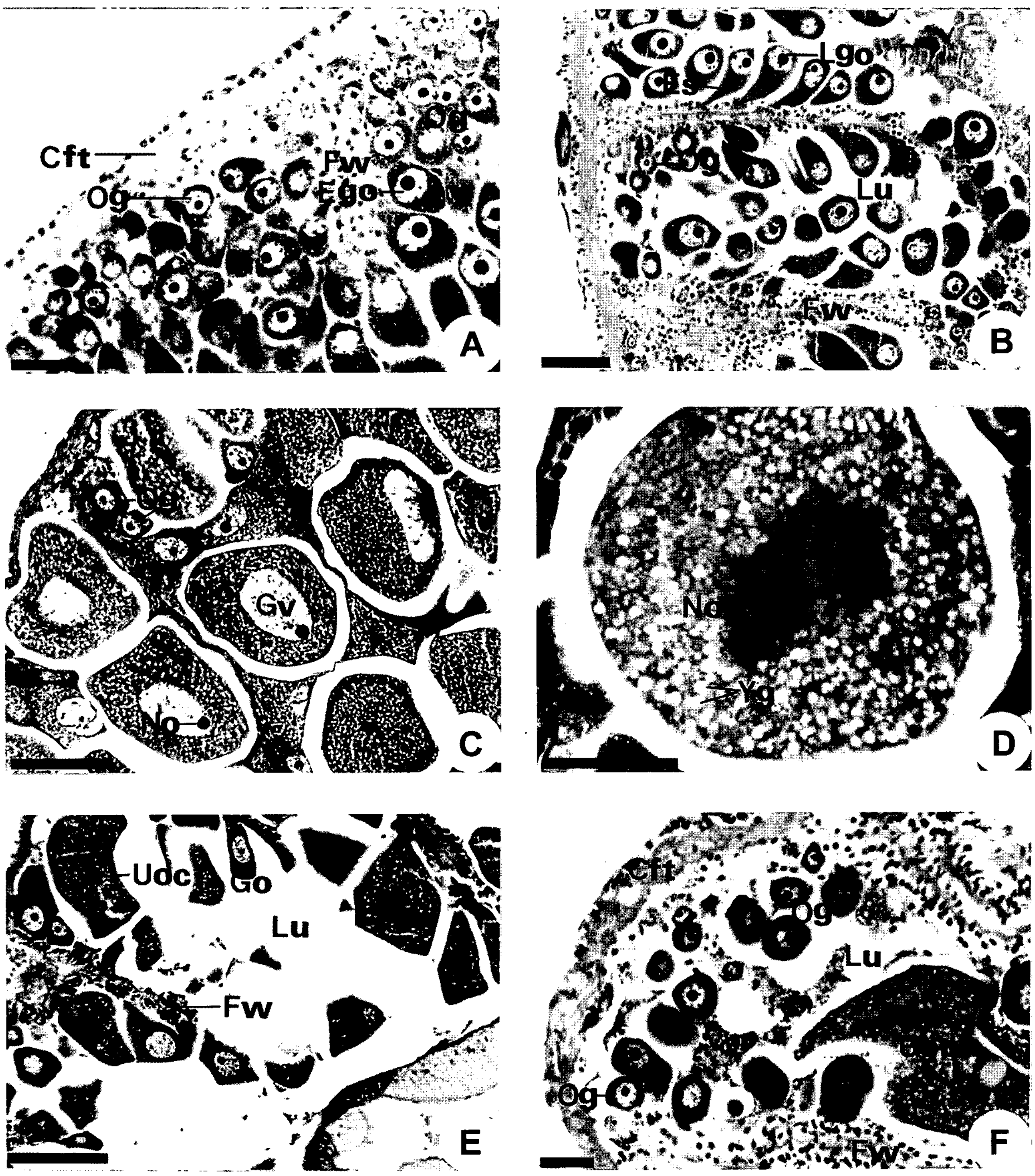

Fig. 5. Photomicrographs of gonadal phases of the female top shell, *Omphalius rusticus*. A, Transverse section of the oogenic follicles in the early active stage collected in January. B, Section of the follicles in the late active stage collected in March. C, Section of the ripe oocytes in the ripe stage collected in June. D, Section of the fully ripe oocyte in the ripe stage collected in July. E, Section of the follicles in the spawning stage collected in September. F, Section of the follicles in the recovery stage collected in November. Cft, connective fibromuscular tissue; Ego, early growing oocyte; Es, egg stalk; Fw, follicular wall; Go, growing oocyte; Gv, germinal vesicle; Lgo, late growing oocyte; Lu, lumen; Mo, mature oocyte; No, nucleolus; Og, oogonia; Uoc, undischarged oocyte; Yg, yalk granule. Scale bars=25 µm(A, F), 40 µm(D), 80 µm(C, E), and 100 µm(B).

tures and the sizes of the germ cells during gamtogenesis in the gonad, the reproductive cycle of *O. rusitcus* can be divided into five successive stages: early active, late active, ripe, spawning, and recovery as shown in Figs. 3 and 4.

Early active stage

In females, a great number of oogonia and a few early growing oocytes were present on the wall of the oogenic follicles. The oogonia and the early growing oocytes were about 10 µm and 25-30 µm in diameter,

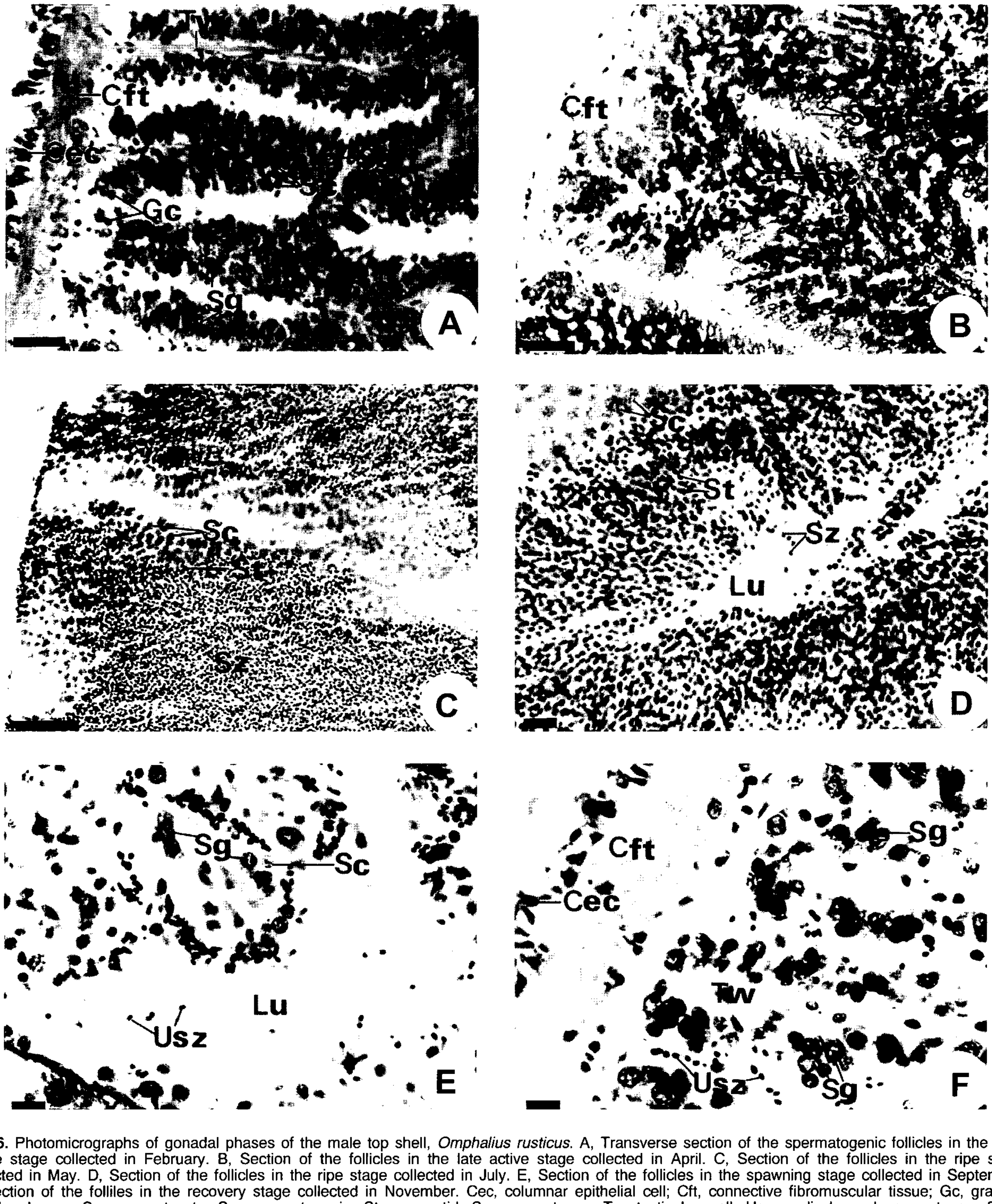

Fig. 6. Photomicrographs of gonadal phases of the male top shell, *Omphalius rusticus*. A, Transverse section of the spermatogenic follicles in the early active stage collected in February. B, Section of the follicles in the late active stage collected in April. C, Section of the follicles in the ripe stage collected in May. D, Section of the follicles in the ripe stage collected in July. E, Section of the follicles in the spawning stage collected in September. F, Section of the folliles in the recovery stage collected in November. Cec, columnar epithelial cell; Cft, connective fibromuscular tissue; Gc, granular cell; Lu, lumen; Sc, spermatocyte; Sg, spermatogonia; St, spermatid; Sz, spermatozoa; Tw, testicular wall; Usz, undischarged spermatozoa. Scale bars=10 μm(D, E, F), 25 μm(A, B), and 30 μm(C).

respectively. Every oogonium was round or oval in shape, and had a round nucleus including a conspicuous nucleolus in the center. At this time, its cytoplasm was very poor. Only a few early growing oocytes were attached to the follicular wall by egg stalks (Fig. 5A). The females in early active stage was found from October (4%) to April (10%), with maximum frequency in February (40%).

In males, the spermatogenic follicles projected inward perpendicularly from the outer testicular wall that is composed of simple columnar epithelial cells and connective fibromuscular tissues. A number of the spermatogonia, spermatocytes, mesenchymal tissues, and eosinophilic granular cells appeared in the follicles. The diameters of spermatogonia and spermatocytes were 8-9 µm and 5-6 µm, respectively. Each spermatogonium had a conspicuous nucleus (6-7 µm in diameter), and the basophilic nucleolus was observed in the center of the nucleus (Fig. 6A). The males in early active stage was found from November (20%) to March (25%), with maximum frequency in February (50%).

Late active stage

In females, a number of late growing oocytes ranging from 45 µm to 55 µm appeared in the oogenic follicles. Most of the oocytes had egg stalks attached to the oogenic follicles. At this time, the nucleus in oocyte, i.e., the germinal vesicle, moved to the distal part of the oocyte (Fig. 5B). The females in late active stage occurred from December (45%) to June (10%), with maximum frequency in April (80%).

In males, spermatogonia and spermatocytes in the spermatogenic follicle grew to spermatocytes and spermatids (3-4 µm in diameter), respectively. At this time, various germ cells including spermatogonia, spermatocytes, and spermatids were observed in the follicles (Fig. 6B). The males in late active stage occurred from December (25%) to June (5%), with maximum frequency in March (75%) and April (75%).

Ripe stage

In females, each oogenic follicle was filled with mature oocyte with its diameter about 100-110 µm. However, a few early growing oocytes were found on the wall of the oogenic follicle. At this time, the outer layers were composed of simple columnar epithelial cells and connective fibromuscular tissues, and the follicular walls became very thin (Fig. 5C). The ripe oocyte which had grown up to 120-130 µm in diameter became round or oval in shape. A large number of yolk granules were evenly distributed in the cytoplasm of the ripe oocyte (Fig. 5D). The females in ripe stage appeared from April (10%) to September (15%), with maximum frequency in June (90%).

In males, except a few spermatogonia, spermatocytes and spermatids on the follicular wall, most of the spermatogenic cells began to undergo transformation into spermatozoa. Countless spermatozoa occupied the majority of the lumen. As already shown in the ovarian development, the outer layers and follicular walls of the testis became very thin. At this time, mesenchymal tissues and eosinophilic granular cells existed in very few numbers (Figs. 6C and D). The males in ripe stage appeared from April (25%) to September (10%), with maximum frequency in june (95%).

Spawning stage

In females, the ripe oocytes in the oogenic follicles were discharged into the surrounding environment and a few of ripe undischarged oocytes as well as growing oocytes remained in the follicles. At this time, the lumen of the follicle became considerably empty (Fig. 5E). The spawning stage took place from July (15%) to September (52%).

In males, a great number of ripe spermatogonia in the lumen of the follicle were discharged into the surrounding water. Thereafter, the lumen became considerably empty. However, a few undischarged spermatozoa and spermatogenic cells in various developmental stages were still visible in the follicle (Fig. 6E). The spawning stage took place from July (20%) to September (65%).

Recovery stage

In females, after spawning, the undischarged eggs in the lumen of the follicle underwent cytolysis, and each follicle was contracted and degenerated. Thereafter, the outer layers of the ovary were composed of connective fibromuscular tissues, and the walls of the follicles tended to thicken again. Newly formed oogonia appeared in the follicle (Fig. 5F). The recovery stage occurred from September (33%) to January (10%), and the maximum frequency of this stage appeared in October (96%).

In males, after spawning, the undischarged spermatids and spermatozoa in the lumen of the follicle were subjected to cytolysis, and each follicle was contracted and degenerated. And then, newly formed spermatogonia, mesenchymal tissues, and eosinophilic granular cells appeared along the follicular wall (Fig. 6F). The recovery stage occurred from September (25%) to December (42%), and the maximum frequency appeared in October (100%).

Monthly changes in the meat weight rate and water temperature

Monthly changes in the meat weight rate (MWR) and water temperature are shown in Fig. 7. From February to April, when the mean water temperature gradually increased, the MWR values also gradually increased and reached the maximum (27.7%) in June. Then, the values rapidly decreased from July to September when the mean water temperature reached above 24.2℃. Thereafter, the values gradually increased from September to the following February, and the temperature gradually decreased during this period.

Monthly changes in gonad index

Monthly changes in gonad index (GI) values are shown in Fig. 8. The GI values in the female gradually began to increase from January to April and reached maximum (49.7) in June. Then, the GI vales sharply

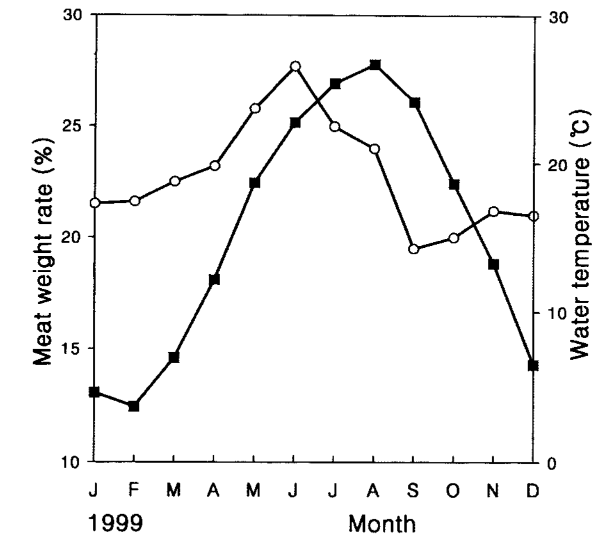

Fig. 7. Monthly changes in the mean meat weight rates (○) of the top shell, *Omphalius rusticus* in relation to water temperature (■) from January to December, 1999.

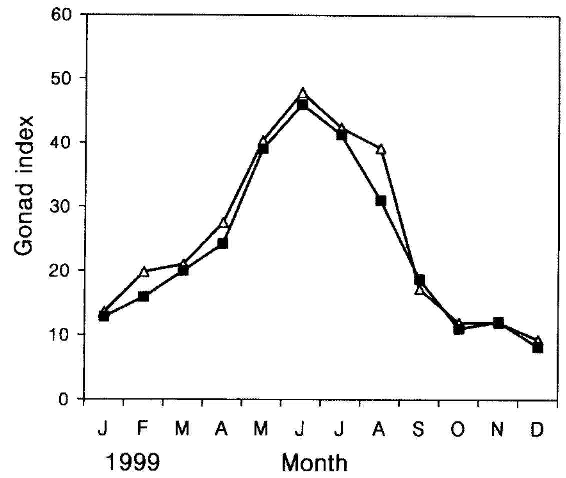

Fig. 8. Monthly changes in the mean gonad indices of male (■) and female (△) the top shell, *Omphalius rusticus.*

decreased from July to September, and gradually decreased from September to December. The monthly changes of the GI values in the male were similar to those in the female.

First sexual maturity

First sexual maturity of 183 *O. rusticus* (94 females and 89 males) ranging from 5.0 to 13.9 mm in shell height was investigated histologically to determine the heights of the shell taking part in reproduction from June to October, 1999.

As shown in Table 1, individuals of 7.9 mm and less in shell height could not participate in reproduction in both sexes. Females and males ranging from 8.0 to 8.9 mm in shell heights took part in reproduction at a rates of 38.5% and 37.5%, respectively. Percentages of first sexual maturity of female and male specimens ranging from 9.0 to 9.9 mm were 58.3% and 54.5%, respectively, and 100% in those over 11.0 mm in both sexes. To conserve natural resources of this species, therefore, individuals of 0.9 mm and less in shell height must not become a prize to a reckless captor.

Discussion

With regard to nutritive materials for gonadal development and gametogenesis in aquatic invertebrates, there have been several reports: sperm-morula in *Mya arenaria* by Coe and Turner (1938), K cells in the purple snail *Purpura clavigera* by Kon et al. (1966), somatic cells in the surf clam, *Spisula sachalinesis* by Takahashi and Takano (1970), and yellowish granules in the marsh clam *Lamproula gottschei* by Lee (1997).

Chung et al. (1998) and Lee (1999b) reported that the mesenchymal tissues and eosinophilic cells were abundant in the oogenic and spermtogenic follicles of the early gametogenic stage. These tissues and cells then gradually disappeared with gonadal development. Therefore, they could be considered as nutritive materials. In the present study, the results were similar to those of others' reports mentioned above.

Several authors described that gonadal development, gametogenesis, reproductive cycle, and spawning in molluscs were correlated with exogenous environmental factors such as specific gravity of seawater (Taki, 1949), photoperiodism (Simpson, 1982), abundance of food for adults and their planktotrophic larvae (Jara-millo and Navarro, 1995), water temperature (Kim et al., 1999; Lee, 1999a), an endogenous factor, that

Table 1. Shell height of first sexual maturity of the top shell, *Omphalius rusticus*

Shell height (mm)	Female			Male		
	No. of individuals examined	No. of matured individuals	Maturity (%)	No. of individuals examined	No. of matured individuals	Maturity (%)
5.0~ 5.9	10	0	0	12	0	0
6.0~ 6.9	9	0	0	11	0	0
7.0~ 7.9	11	0	0	9	0	0
8.0~ 8.9	13	5	38.5	8	3	37.5
9.0~ 9.9	12	7	58.3	11	6	54.5
10.0~10.9	10	8	80.0	12	10	83.3
11.0~11.9	10	10	100	7	7	100
12.0~12.9	11	11	100	9	9	100
13.0~13.9	8	8	100	10	10	100
Total	94	49		89	45	

is, the endocrine system (Euler and Heller, 1963). The water temperature has been the subject of much discussion. Yamamoto and Yamakawa (1985) and Brousseau (1995) stated that the role of water temperature in triggering release of eggs and spermatozoa was not clear. However, in the present study, the gonadal development and gametogenesis in *Omphalius rusticus* almost coincided with the rising seawater temperature, and the spawning periods in both sexes occurred from July to September when the temperature was 25.4-24.2℃. Therefore, it is supposed that gonadal development, gametogenesis, maturation, and spawning of this species are closely correlated with the water temperature.

Yamamoto and Yamakawa (1985) reported that the gonad index value in *Turbo cornutus* kept low during the early active stage. The value gradually increased during the late active stage, and then reached the maximum during the ripe stage. The gonad index value in *Crassostrea virginca* peaked during its ripe stage and dropped rapidly during the spawning stage (Brousseau, 1995). Sasaki (1987) stated that the reproductive cycle of *S. sachalinensis* based on changes in the gonad index comprised of four phases: rapid gonad-growth (growing phase), prior to spawning following maturation (maturing phase), releasing (spawning phase), and low in reproductive activity (resting phase). In the present study, the gonad index values in both sexes gradually increased from January and peaked (47.9 in female and 46.0 in male) in June. Thereafter, the values rapidly decreased from July (40.1 in female and 41.3 in male) to September (17.2 in female and 18.7 in male) when the seawater temperature was relatively high (above 24.2℃). Therefore, it is supposed that the spawning in both sexes occurs from July to September, and the monthly changes in the gonad index nearly coincide with the gonadal development and reproductive cycle.

Lee et al. (1999) and Lee (1999b) reported that the meat weight rate and condition factor increased with the growth and maturity of the gonad and decreased with the spawning. In this study, the meat weight rate of *O. rusticus* gradually increased from February to April and peaked in June. Then the values abruptly decreased from July to September when spawning occurred. Therefore, it is assumed that monthly changes in the meat weight rate of this species coincide well with the reproductive cycles based on the histological observations of the gonad.

Most marine invertebrates have their own unique breeding patterns. Boolootian et al. (1962) stated that their breeding habits can be divided into three types: year-round breeders, summer breeders, and winter breeders. A number of annual spawning periods of molluscs showed various types: once (Breusseau, 1995; Lee, 1999a), twice (Shibata, 1993; Kim et al. 1999; Lee, 1999b), and three times (Sarasquete et al., 1990) per year. In the present study, this species spawned between July and September, when the seawater temperature ranged 24.2-25.4℃. Therefore, it is suggested that this species is a type of summer breeders, and the spawning period of *O. rusticus* is once a year.

Chung (1997) and Chung et al. (1998) reported that after spawning, reabsorption of the undischarged or hopeless germ cells is found in the oogenic and spermatogenic follicles of many bivalves. Dorange and Le Pennec (1989) and Xie and Burnell (1994) stated that the atresia of the undischarged gametes in the follicles takes place to reallocate the reproductive energies and other metabolic activities among developing gametes. In the present study, after spawning, the undischarged germ cells in the gonads of *O. rusticus* gradually degenerated and were reabsorbed. Therefore, it is supposed that this species may have a mechanism to reabsorb the undischarged germ cells in order to provide the reproductive energy for the developing gametes.

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