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Histological Studies on the Reproductive Cycle and First Sexual Maturity of the Pomfret, *Pampus echinogaster* (Perciformes: Stromateidae) on the West Coast of Korea

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서해산 덕대의 생식주기와 군성숙도에 관한 조직학적 연구

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Abstract

The reproductive cycle, egg diameter compositions, spawning season and first sexual maturity of the pomfret, *Pampus echinogaster*, were investigated by histological analyses and morphometric data. The reproductive cycle of this species can be divided into six successive stages in females: early developing stage (February to March), late developing stage (March to April), mature stage (April to June), ripe and spawning stage (June to early August), recovery and resting stage (August to October), and immature stage (October to February). Males can be divided into five successive stages: developing stage (February to April), mature stage (March to June), ripe and spent stage (June to August), recovery and resting stage (August to October), and immature stage (October to February). According to the frequency distributions of egg diameters in a spawning season, *P. echinogaster* is a polycyclic species that spawns two times or more during the spawning period. The percentages of *P. echinogaster* that had reached first sexual maturity over 50% in males from 12.1 to 15.0 cm in body lengths, while in females, those from 15.1 to 18.0 cm in body lengths reached over 50%. And both sexes were 100% for fishes over 21.1 cm in body length.

Key words : *Pampus echinogaster*, Reproductive cycle, Spawning season, Spawning frequency, First sexual maturity

Ⅰ. Introduction

The pomfret, *Pampus echinogaster* (Vasilewsky), is distributed along the coasts of Korea, the East China Sea, and Japan. On the west coast of Korea, this fish is mainly found in the East China Sea and coastal waters around Jaun-Do, Muan-gun, and Jollanam-do, Korea. This species is a commercially important edible fish (Kim et al., 2005). However, overfishing has led to the need for a more sustainable fishing regimen. For the propagation and resource management of *P. echinogaster*, it is important that its reproductive ecology be fully understood. It is especially, important to study the reproductive cycle, spawning season, spawning frequency and first sexual maturity of this species

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by histological analyses and morphometric data.

To date, several aspects of the reproductive ecology of *P. echinogaster* have been studied, including gonadal maturation (Jin, 1989), growth and reproduction (Lee, 1989), deformities (Higashikawa et al., 1984), population biology (Oh et al., 2009) studies have been conducted.

Although there have been several studies of reproduction conducted, there are still gaps in our knowledge of the reproductive ecology of *P. echinogaster,* and information useful to management and aquaculture production of this organism is lacking. Accordingly, studies of the reproductive cycle associated with gonadal development and spawning season of this species are required to understand the unique characteristics of its reproductive life cycle. In particular, understanding the reproductive cycle and the spawning period will provide necessary information for determination of the age and recruitment period (Kim and Lee, 1984; Jun, 2003; Lee et al., 2003; Kang et al., 2004, 2015; Lim et al., 2012). Moreover, information regarding the potential annual capacity of reproduction and monthly relative frequencies of egg diameter compositions during the spawning period are required to estimate the spawning frequency (Jun, 2003; Lee et al., 2003; Kang et al., 2004).

To date, because biological terms for each article has not been well established, various biological terms, that were associated with fish reproductive biology, have created confusion in the terminology used. However, recently, a book published ("Reproductive biology and Phylogeny of fishes (Agnathans and bony fishes), many researches in the field of reproductive biology were made up of more than 60 years. The book, pointing out that a large number of reproductive biological terms should be revised.

In particular, so far been logged in error "zona radiata" should be corrected to the "zona pellucida". And also, various error recorded terminololgies associated with oocyte developmental stages and the reproductive cycle should be revised in this paper. Therefore, in order to check these biological terms, it is very important to confirm and use this book for biological terms for (Jamieson, 2009).

Therefore, the purpose of the present study is to describe the reproductive cycle, spawning season and first sexual maturity of *P. echinogaster* to enable adequate management of this natural resource.

Ⅱ. Materials and methods

Sampling methodology: Specimens of the Korean pomfret, *Pampus echinogaster*, were collected monthly by the stow net in the neighboring waters of Jaun-Do, Muan-gun, Jollanam-Do, Korea, from January to December, 2006. A total of 595 fish ranging from 6.3 to 32.5 cm in body length were collected during the study period. Fish were transported alive to the laboratory and body length, gonad weight and total meat weight were measured. Unpublished data of seawater temperatures measured daily at 10:00 a.m. at the Mokpo Regional Maritime Affairs and Fisheries Office were used for this study.

Histologic analysis: For light microscopic examination of histologic preparations, female ovarian tissues were removed from shells and preserved in Bouin fixative for 24 h and then washed with running tap water for 24 h. Tissue were then dehydrated in alcohol and embedded in paraffin molds. Embedded tissues were sectioned at 5–7 μm thickness using a rotary microtome. Sections were mounted on glass slides, stained with Hansen hematoxylin–0.5% Eosin and PAS stain, and examined using a light microscope. After histologic preparations produced by histolocal methods mentioned earlier, (1) the ovarian cycle; and (2) the size at first sexual maturity were analyzed by histologic preparations.

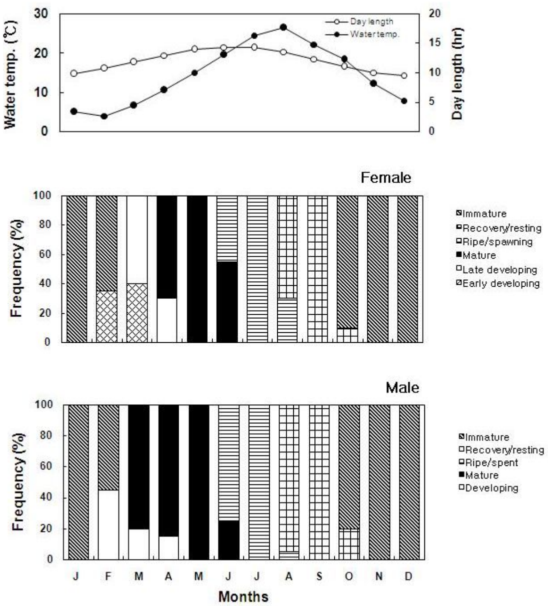
Monthly changes in oocyte size-frequency distributions: Monthly changes in oocyte size-frequency distributions were investigated to estimate the number of spawnings by observation of histological tissue sections from April to August. To investigate monthly oocyte size-frequency distributions, in each month about one thousand eggs that were cut centrally in the histological sections were measured, and then plotted and graphed using the frequency curve method of Pearse (Pierce, 1966).

Size at first sexual maturity: For the study of the size at first sexual maturity, a total of 496 gonadal preparations (6.3-32.5 cm in body length) were histologically examined for evidence of maturation and spawning from April to August, 2006. The size equivalent to 50% of size at sexual maturity was estimated to be the biological minimum size for natural resource management.

Ⅲ. Results and discussions

External morphology of the gonads: The body of the Korean pomfret is in the compressiform, unlike common ovary, one ovary is curved to right and left hands caudally, the ovary on the right and left hands, which is a asymmetric and relatively large size, suspended dorsally within the coelom by the mesovarium. The ovary of this species is a saccular structure (cystovarian condition) which contains a lumen or ovocoel. The developmental morphology of this saccular ovary of this species is unique among vertebrates. The female gonad is located at a part of the intestine along the vertebra on the dorsal posterior part symmetrical.

In general, the ovaries of teleost fish can be classified into two basic conditions based on the anatomical deposition of the germinal tissue: 1) the gymnovarian condition and 2) the crystovarian condition (Hoar, 1957). The ovarian structure of *P. echinogaster* belongs to the crystovarian condition, as reported in *K. bicoloratus* (Jun, 2003), *Coilia nasus* (Lee et al., 2003) and *H. otakii* (Kang, 2002; Kang et al., 2004). The ovary of *P. echinogaster* is separated into right and left lobes that are asymmetric in shape. Unlike in general the testis, one testis is curved to right and left hands caudally, which is an asymmetric and the lobule type, attached to the dorsal wall of the body by a mesorchium. And it is converged in a central efferent duct system, which is open to the exterior through the urogenital pore. The male gonad is located at a part of the intestine along the vertebra on the dorsal posterior part symmetrical. Testicular morphology can generally be classified into two types: 1) tubule type and 2) lobule type (Nagahama, 1983). According to the results of histological observations, *P. echinogaster* has lobule type testes, as reported in *K. bicoloratus* (Jun, 2003), *Coilia nasus* (Lee et al., 2003), *H. otakii* (Kang, 2002; Kang et al., 2004) and *P. argenteus* (Chung et al., 2008). The testes of *P. echinogaster* are separated into right and left lobes, which are asymmetric in shape, and united in the posterior seminal vesicle.



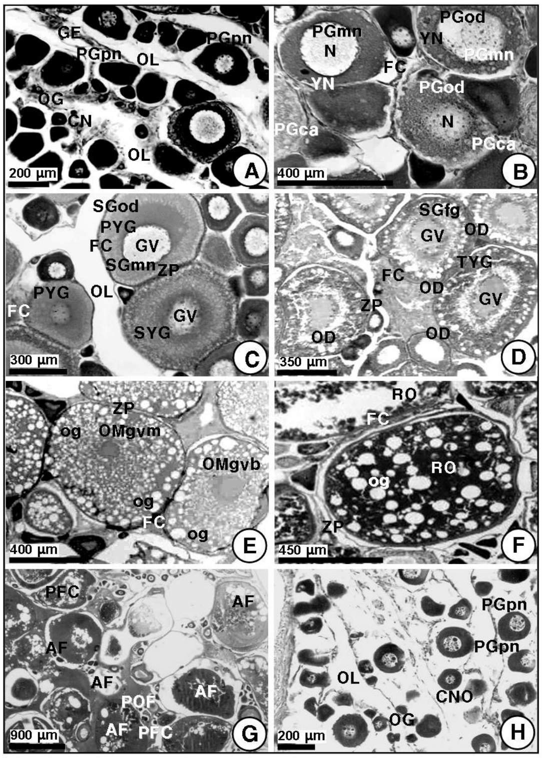
[Fig. 1] Water temperature, day length and frequency of gonadal phases female and male *Pampus echinogaster* from January to December, 2006.

Reproductive cycle: Based on morphological characteristics, sizes and growth characteristics of germ cells determined by histological observations, the reproductive cycle according to gonad developmental stages of this species can be classified into six successive stages in females and five successive stages males: in females, the early developing stage, late developing stage, mature stage, ripe and spawning stage, recovery and resting stage and immature stage; while in males, the developing stage, mature stage, ripe and spent stage, recovery and resting stage, immature stage ([Fig. 1]). In this study, we used various technical terms reported by Jamieson (2009).

Ovary

Early developing stage: The ovary of this species is composed of a number of ovarian lobules. In the ovarian lobules oogonia and early developing oocytes in the germinal epithelium are seen bordered by the ovarian lumen. In this stage, oogonia (approximately 15 μm in diameter) in the oogonia proliferate stage, oocytes in the chromatin nucleolus stage (25-35 μm in diameter) and perinucleolar oocytes (about 100-250 μm in diameter) or the primary growth oocytes were found in the ovarian lobules of the ovary. Especially, in the primary growth oocytes, three or several nucleoli appeared around the inner membrane of the nucleus, and a yolk nucleus was found in the cytoplasm of the oocyte in this stage, the ooplasm of the oocytes in the chromatin nucleolus stage and perinucleolor oocytes showed the haematoxylin-basophilic cytoplasms showing dark blue in color, as reported in other teleosts (Jun, 2003; Kang et al., 2008; Chung et al., 2008). In particular, in the primary growth oocytes (approximately 350-450 μm in diameter) contained a developing zona pellucida on the vitelline envelope ([Fig. 2 A]).

In this stage, a number of cortical alveoli were found in the cytoplasm of the perinucleolar oocyte in the primary growth stage. At this time, the zona pellucida on the vitelline envelope of perinucleolar oocyte continued to develop during the primary growth stage. In particular, in the primary growth oocyte, cortical alveoli and oil droplets were the main inclusion that appeared in the ooplasm in the primary growth oocyte ([Fig. 2 B]). Female individuals in the early developing stage were found between February and March when seawater temperatures were relatively low and day lengths showed short photoperiod ([Fig. 1]).



[Fig. 2] Photomicrographs of the gonadal phases showing ovarian development in female pomfret (A-H). A. Transverse section of the ovarian lobules in the early developing stage. Note oogonia (OG) on germinal epithelium (GE) in the ovarian lumen (OL), the oocytes in the chromatin nucleolus stage (CN), perinucleolar oocytes in the primary growth stage (PGpn). B. Section of the ovarian lobules in the same stage. Note multiple nucleoli (PGmn) appeared around the inner membrane of the nucleus and yolk nucleus (YN), oil droplets (PGod) and cortical alveolar (PGca) in the cytoplasm of the oocytes in the primary growth stage. C. Section of the ovarian lobules in the late developing stage. Note multiple nucleoli (SGmn) in the germinal vesicle (GV), oil droplets (SGod) primary yolk globules (PYG), secondary yolk globules (SYG), and follicle cells (FC) on the zona pellucida (ZP) in the secondary growth stage in the ovarian lumen (OL). D. Section of the ovarian lobules in the mature stage. Note a number of oil droplets (OD) in the cytoplasm, and follicle cells (FC) on the zona pellucida (ZP) of the full-grown oocytes (SGfg). E. Section of the ovarian lobules in the same stage. Note a germinal vesicle migration (OMgvm) to the animal pole and germinal vesicle breakdown oocyte hydration (OMgvb), and follicle cells (FC) on the zona pellucida (ZP) during the period of oocyte maturation containing oil globules (og) in the cytoplasm. F. Section of the ovarian lobules in the ripe and spawning stage. Note undischarged ripe ova (RO) containing a number of oil globules (og) in the cytoplasm, and a number of follicle cells (FC) on the zona pellucida (ZP). G. Section of the ovarian lobules in the recovery and resting stage. Note residual postovulatory follicles (POF) or postovulatory follicle complexes (PFC), and a number of atretic follicles (AF) in the degenerated oocytes. H. Section of the ovarian lobules in the immature stage. Note residual oogonia (OG), oocytes in the chromatin nucleolus (CNO), and perinucleolar oocytes in the primary growth stage (PGpn) appeared in the ovarian lumen (OL) of the ovarian lobules.

Late developing stage: In particular, the secondary growth oocytes, which have appeared in this stage, can be divided into two oocytes according to morphological characteristics: the early and late secondary growth oocytes. Early secondary growth oocytes (approximately 500-600 μm in diameter) were found in the ovarian lumens of the ovarian lobules from March, In particular, multiple nucleoli, seven or more, irregularly situated within the germinal vesicle, as reported in other teleosts (Lee et al., 2003; Jun, 2003; Chung et al., 2008;

Kang et al., 2008). And the late secondary growth oocytes (about 620-700 μm in diameter) were filled with a number of primary and secondary yolk globules containing the eosinophilic cytoplasm ([Fig. 2 C]). Female individuals in the late developing stage were found between March and April when seawater temperatures were increased and day lengths begin to increase (Fig. 1).

Mature stage: Full-grown oocytes were filled with a number of tertiary yolk globules. At this time, a well-developed zona pellucida appeared on the vitelline envelope of the full-grown oocyte, and a number of oil droplets encircled the germinal vesicle, peripheral to which were yolk globules. At this time, follicle cells encircled the yolked oocytes in the secondary growth stage containing primary and secondary yolk globules ([Fig. 2 D]). During the period from April to June, oocytes in the germinal vesicle migratory stage and full-grown oocytes (approximately 750-800 μm in diameter) in the oocyte maturation stage were found. At this stage, most oocytes contained numerous mature yolk globules and a number of oil globules in the cytoplasm, and a well-developed zona pellucida appeared on the vitelline envelope. At this stage, oil droplets were fused to become oil globules. Oil globules and yolk globules surrounded the germinal vesicle and were mixed with yolk globules, consequently, they became homogeneous yolk globules in the eosinophilic cytoplasm, and a well-developed zona pellucida appeared on the vitelline envelope, as have seen in other teleosts (Lee et al., 2003; Jun, 2003; Chung et al., 2008; Kang et al., 2008). During this stage from April to June, eccentric germinal vesicle appeared, oil droplets coalesced, germinal vesicle migrated to the animal pole, oocyte hydrated, and germinal vesicle breakdown occurred ([Fig. 2 E]). Female individuals in the mature stage appeared from April to June when seawater temperatures are gradually increased, and day lengths showed a long photoperiod ([Fig. 1]).

Ripe and spawning stage: The ovarian follicles in the ovaries were filled with a number of ripe ova containing a number of oil globules. In this study, the ovarian lobules were ovulated, and fully ripe ova (approximately 800-900 μm in diameter) were ovulated, as reported with other teleosts (Lee et al., 2003; Chung et al., 2008). At this time, the ovulatory follicle layers were detached from the zona pellucida of ripe ova, and residual traces of several ovulated oocytes appeared near the undischarged oocytes in the ovarian lobules of the ovary ([Fig. 2 F]). Female individuals in the ripe and spawning stage appeared from June to early August when seawater temperatures are increased and day lengths showed a long photoperiod ([Fig. 1]).

Recovery and resting stage: During the recovery stage, the residual follicle cells and overlying germinal epithelium were broken. After ovulation, remaining undischarged oocytes degenerated and gamete atresia is resorbed, and the postovulatory follicle complex and residual trace of ovulatory follicle appeared near the degenerated oocytes. Most eosinophilic secondary growth oocytes with the follicle layers in the ovarian lobules were degenerated and contracted. Thereafter, the connective tissue occurred in the lobules and also rearrangement of several newly formed oogonia were rearranged along the lobular walls of the lobules. And also undischarged oocyte in the chromatin nucleolus stage without follicle layers and the primary growth oocyte (or perinucleolar oocyte) in the ovarian lobules were existed continually without degeneration or contraction as reported in other teleosts (Lee et al., 2003; Chung et al., 2008). Most ovarian lobules were rearranged and recovered gradually in the spent stage ([Fig. 2 G]). Female individuals in the recovery and resting stage were found from August to October when seawater temperatures were gradually decreased and the day lengths showed a short photoperiod over a long period of time ([Fig. 1]).

Immature stage: In this stage, oogonia in the oogonial proliferating stage, oocytes in the chromatin nucleolus stage and perinucleolar oocyte in the primary growth oocytes appeared in the ovarian lobules over a long period time. At this time, the cytoplasms of oogonia, oocytes in the chromatin nucleolus stage and perinucleolar oocytes (or the primary growth oocytes) in the ovarian lumen of the ovarian lobules showed basophilic stainability ([Fig. 2 H]). After degeneration of residual oocytes and follicle layers, newly formed oogonia and oocytes in chromatin nucleolus stage or perinuclear stage were rearranged near the connective tissues in the ovarian lobule in the immature stage over a long period of time (Lee et al., 2003; Chung et al., 2008). Female individuals in the immature stage were found from October to February when seawater temperatures were gradually decreased and day lengths showed a short photoperiod over a long period of time ([Fig. 1]).

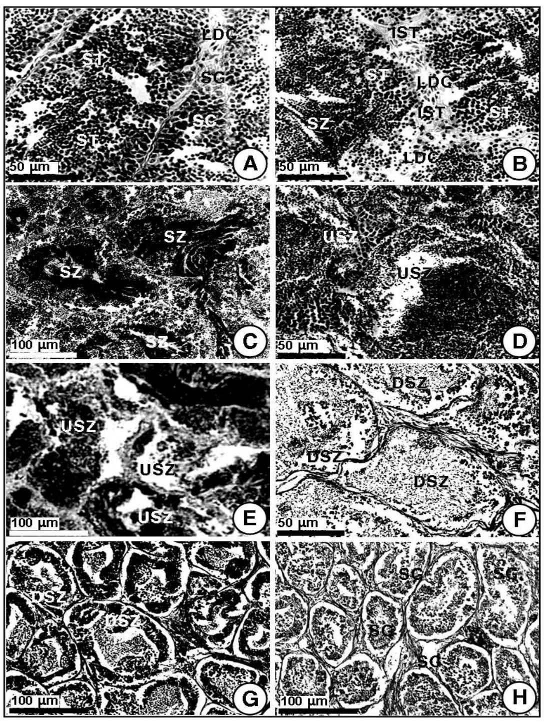
Testis

Developing stage: Testicular development and spermatogenesis occurred in the seminiferous lobules of the testis. During spermatogenesis, a few spermatogonia and a number of spermatocytes and spermatids appeared in the lobules, and a small number of spermatozoa during spermiogenesis were found in the cysts of the lobules near the Leydig cells in the interstitium as reported in other teleosts (Chung et al., 2010). At this stage, particularly, a number of well-developed Leydig cells containing eosinophilic cytoplasm (red in color) appeared in the interstium between lobules during the maturation division for spermatogenesis ([Fig. 3 A]). Male individuals in the developing stage were found from February to April, when seawater temperatures were relatively low and day lengths were short ([Fig. 1]).

Mature stage: In the mature stage, the lobules in the testes were filled with a small number of spermatocytes, spermatids and spermatozoa that had completed spermatogenesis. At this stage, a number of well-developed Leydig cells containing the eosinophilic cytoplasm appeared in the interstium between seminiferous lobules during spermatogenesis ([Fig. 3 B, C]). Male individuals in the mature stage appeared from March to June, when seawater temperatures were increased and day lengths were the longest ([Fig. 1]).

Ripe and spent stage: In this stage, male individuals containing sexually ripe testis began to appear ([Fig. 3 D]), a large number of spermatozoa were actively discharged during the period of June and July, and a number of undischarged residual spermatozoa appeared in the seminiferous lobules. In particular, at this stage, several well-developed Leydig cells were present in the interstium between seminiferous lobules ([Fig. 3 E]). Thus, some similar phenomena appeared in the Leydig cells in this species were observed in other teleosts (Chung et al., 2010). Male individuals in the ripe and spent stage appeared from June to August, when seawater temperatures are gradually increasing and day length is gradually becoming longer ([Fig. 1]).

Recovery and resting stage: After spermiation, remaining spermatozoa and spermatids degenerated and gamete atresia in the recovery stage were resorbed from August ([Fig. 3 F]), after which connective tissue develops in the lobules and rearrangement of several newly formed spermatogonia in the lobules occurs in the resting stage ([Fig. 3 G]). Male individuals in the recovery and resting stage appeared over a long period of time from August to October, when seawater temperatures were gradually decreased and day lengths were gradually becoming short photoperiod ([Fig. 1]).

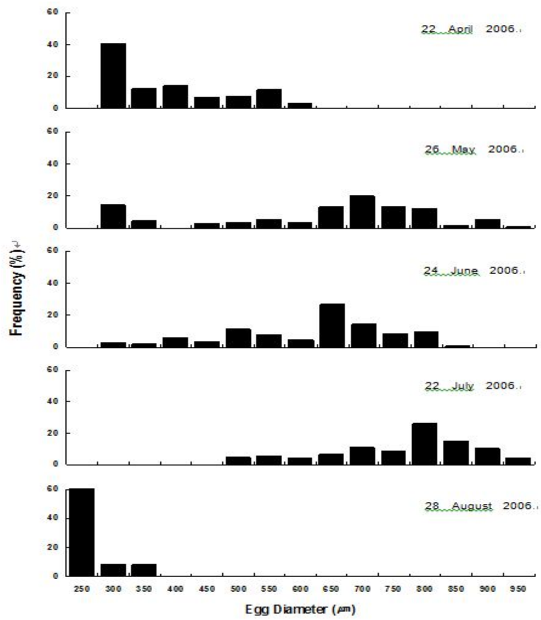


[Fig. 3] Photomicrographs of the gonadal phases showing testicular development in male pomfret (A-H). A. Transverse sections of the testicular lobules in the developing stage. Note The cysts in the lobules of the testis (including spermatogonia (SG), spermatocytes (SC) and spermatids (ST), and several Leydig cells (LDC) in the interstitium (IST) between the lobules during the period of active maturation division); B, C. Sections of the lobules in the mature stage. Note numerous spermatozoa (SZ), a large number of spermatids (ST) and a number of spermatocytes (SC), at this stage, a number of Leydig cells (LDC) in the interstitium (IST) between lobules; D, E. Sections of the lobules in the ripe and spent stages. Note undischarged spermatozoa (USZ) in vacant parts of the lobules because of releasing of spermatozoa; F, G. Sections of the lobules in the recovery and resting stage. Note residual degenerating spermatozoa (DSZ) in the lobules and degenerated spermatozoa (DSZ) in the gradually contracted seminiferous lobules; H. Section of the lobules in the immature stage. Note the rearrangement of newly formed a few spermatogonia (SG) on the germinal epithelium near the connective tissues after degeneration of the seminiferous lobules.

Immature stage: A number of spermatogonia and spermatocytes were found in the lobules of the testis ([Fig. 3 H]). The individuals in the immature stage were found from October to February when seawater temperatures were gradually decreased and day lengths showed a short photoperiod over a long period of time ([Fig. 1]).

Relative frequency of ovarian egg diameter composition during the spawning season: To estimate the number of spawn frequency during the spawning season, monthly changes in relative frequency distributions of the egg diameters from the beginning of ovarian maturation in April to the end of spawning in August 2006 were measured ([Fig. 4]). In April 2006, the relative frequency of the egg diameter mode of 300-600 μm (medium size group) consisted of the main mode, and in May, the egg diameter modes were divided into a median sized group of approximately 450 μm and a large sized group of approximately 850 μm. In June, the large sized group disappeared due to spawning; however, an egg diameter mode of about 650 μm gradually formed. In July, the egg diameter modes of 800-900 μm (large size group) comprised the main oocyte group, while in August this group disappeared because of spawning, and undischarged oocytes and eggs with a diameter of below 300 μm (small size group) comprised the main egg diameter modes. Based on the results of monthly changes in the egg diameter modes, spawning in *P. echinogaster* occurred from May to July, and it is assumed that this species is a polycyclic species that spawns two or more times during one spawning season.

First sexual maturity: As shown in <Table 1>, a total of 496 (260 females and 236 males) individuals of *P. echinogaster* were investigated histologically to determine the body lengths of fish that reach maturation and participate in reproduction from April (before spawning) to late August (after spawning). The percentages of sexually mature female and male individuals ranging from 6.3 to 9.0 cm in body length were 0%, while 23.1% and 27.3% of female and male individuals, respectively, ranging from 9.1-12.0 cm in body length were sexually mature. Additionally, 44.4% and 53.3% of female and male individuals, respectively, ranging from 12.1-15.0 cm in body length were sexually mature, while 59.4% and 78.3% of female and male individuals ranging from 15.1-18.0 cm in body length were sexually mature.



[Fig. 4] Monthly changes in relative frequency distribution of the ovarian egg diameter in female *Pampus echinogaster*.

<Table 1> Body length of first sexual maturity of *Pampus echinogaster* from April (before spawning) to late August (after spawning)

Body length (cm)	Female		Male	
	Number	Maturity (%)	Number	Maturity (%)
6.3-9.0	21	0	23	0
9.1-12.0	26	23.1	22	27.3
12.1-15.0	36	44.4	30	53.3
15.1-18.0	32	59.4	23	78.3
18.1-21.0	26	88.5	34	94.1
21.1-24.0	35	100.0	38	100.0
24.1-27.0	32	100.0	31	100.0
27.1-30.0	28	100.0	25	100.0
30.1-32.5	24	100.0	10	100.0
Total	260		236	

However, all female and male individuals of body lengths greater than 21.1 cm were sexually mature. Based on the percentages of sexually mature younger female and male individuals ranging from 12.1-15.0 cm in length, sexual maturation and the beginning of participation in reproduction occurred somewhat faster among male individuals than females (<Table 1>).

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