

Gonadal Development and Reproductive Cycle of *Heminerita japonica* (Dunker, 1860) from the Coast of Geomundo, Korea

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ABSTRACT

This study aimed to elucidate gonadal development and the reproductive cycle of *Heminerita japonica* inhabiting the intertidal zone of Geomundo, Jeollanam-do, Korea. From April 2013 to March 2014, the condition index (CI), gonadosomatic index (GSI), and gonadal development were examined histologically, and monthly variations in water temperature and salinity were recorded. Water temperature ranged from 10.7 to 24.6 °C, with the highest value in August 2013 and the lowest in March 2014. Salinity ranged from 31.1 to 34.4 psu, with the lowest value in August 2013 and the highest in February 2014. Monthly CI patterns were similar between females and males, peaking in November (female: 43.87 ± 4.07 ; male: 44.49 ± 3.53) and reaching minima in June (female: 23.77 ± 6.07 ; male: 23.18 ± 6.08), indicating regular seasonal periodicity. Based on histological observations, the reproductive cycle was classified into five stages: early development (October-February), late development (November-April), ripe (February-May; females February-May and males March-May), partially spawning (May-July), and degenerative/resting (June-October; females July-October and males June-October). These findings provide baseline information for the conservation and ecological study of *H. japonica*.

Keywords : *Heminerita japonica*; Gonadal development; Reproductive cycle; Condition index

INTRODUCTION

Heminerita japonica is a herbivorous neritid gastropod (Mollusca: Gastropoda: Neritidae) with a shell length of approximately 1 cm, and it is commonly found on bedrock and gravel substrates in the mid- to lower intertidal zones of Korea (Hong *et al.*, 2006). The shell is hemispherical and relatively thick and hard, with four whorls and irregular black-and-white speckling. Because the growth lines are distinct whereas the sutures are obscure, the boundaries between whorls are not clearly

discernible. The body whorl is large and rounded, occupying most of the shell height. The aperture is semicircular; the outer and basal lips are moderately thick; and the columellar lip is wide, straight, and smooth with a glossy surface. The operculum is semicircular and granulated, bearing small projections. Body coloration varies considerably among individuals (Min *et al.*, 2004).

Reproductive biology of gastropods has been extensively investigated in both domestic and international studies (Lee, 1980; Colman *et al.*, 1986; Lasik, 1987; Hahn, 1993; Jeong *et al.*, 1993; Lee, 1998; Na & Lee, 1999; Oh, 2000; Lee, 2002; Song *et al.*, 2002; Kim *et al.*, 2003; Lee, 2004; Kim *et al.*, 2007). Nevertheless, ecological and life-history studies have largely focused on commercially important species, and information remains limited for non-commercial taxa that play key roles in intertidal ecosystems. For *H. japonica*, studies conducted outside Korea have addressed aspects such as taxonomy and

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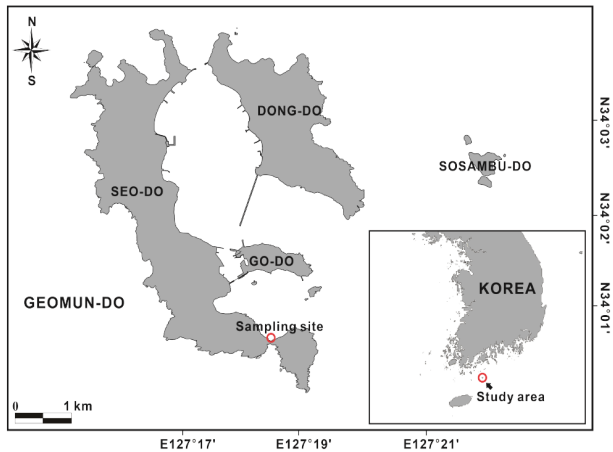


Fig. 1. Map showing the sampling site of *Heminerita japonica* in Geomundo.

community-level characteristics (Nakano & Nagoshi, 1983). However, detailed information on its reproductive biology, including germ-cell development and reproductive cycle, remains insufficient (Lee & Hyun, 2002; Son, 2011). Understanding gametogenesis and reproductive cycles in intertidal gastropods provides fundamental data for interpreting seasonal changes in community structure, biomass, and population dynamics (Kim and Yoo, 2001).

Therefore, the present study aimed to characterize the reproductive cycle of *H. japonica* inhabiting the intertidal zone and to provide baseline information for future ecosystem monitoring. Seasonal variation in environmental factors, including water temperature and salinity, was examined around Geomundo, a representative habitat of *H. japonica*. In addition, temporal changes in the condition index and gonadal development index were analyzed to infer spawning periods, and gonadal development was assessed histologically. Through these approaches, we sought to establish fundamental reproductive biological information for the conservation and ecological study of *H. japonica*.

MATERIALS AND METHODS

1. Experimental animals

H. japonica individuals were collected monthly from intertidal areas of Geomundo, Yeosu,

Jeollanam-do, Korea, for one year from April 2013 to March 2014. Each month, 25 individuals were randomly sampled at the study site (Fig. 1). Collected specimens were transported to the laboratory in insulated containers for subsequent measurements and analyses (Fig. 1).

2. Water temperature and salinity

The water quality in the study area was measured on-site monthly using a digital water temperature meter (YSI-556 MPS; YSI Inc., OH, USA).

3. Condition index

The collected samples were transported to the laboratory, and the shell height, shell length, shell breadth were measured to the nearest 0.01 mm using a Vernier caliper. The total weight was measured to 0.01 g with an electronic scale (PAG2102; OHAUS Inc., NJ, USA). The flesh was separated from the shell by opening the shell, and the flesh weight (FW) and shell weight (SW) were measured to the nearest 0.01 g. Then, the gonads were separated from the fleshy part, and the gonad weight was measured to the nearest 0.01 g. The condition index was obtained using the following equation.

$$\text{Condition index} = \{FW(g) / FW(g) + SW(g)\} \times 100 \quad (\text{Aguirre, 1979})$$

4. Histology

To examine histological changes during gonadal development, dissected gonad tissues were fixed in Bouin's solution for 24 h. The tissues were then dehydrated through a graded ethanol series, cleared, and embedded in paraffin. Serial sections (5 μ m thick) were cut using a microtome, mounted on glass slides, and double-stained with Delafield's hematoxylin and eosin (H&E). The stained sections were examined under a light microscope.

RESULTS

1. Water temperature and salinity

Fig. 2 illustrates the monthly mean water

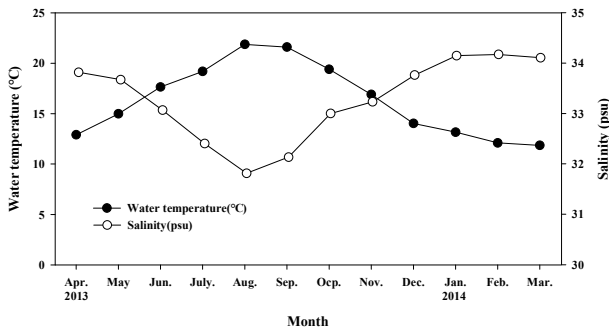


Fig. 2. Monthly variations in water temperature and salinity from April 2013 to March 2014.

temperature and salinity from April 2013 to March 2014. During the study period, water temperature ranged from 10.7 to 24.6°C, peaking at 24.6°C in August 2013 and reaching a minimum of 10.7 °C in March 2014. Monthly mean salinity ranged from 31.1 to 34.4 psu. The lowest salinity (31.1 psu) was observed in August 2013, after which salinity gradually increased, reaching a maximum of 34.4 psu in February 2014.

2. External morphology and gonadal location

The external morphology of *H. japonica* and the location of the gonad are illustrated in Fig. 3. The gonad is located in the posterior region of the spire. As gonadal development progresses, the gonad becomes distinct from the hepatopancreas and is enclosed by a black membrane. Because *H. japonica* exhibits limited external sexual dimorphism, males and females could not be reliably distinguished based on gross observation. However, sex determination was possible through histological examination.

3. Condition index

Monthly variation in the condition index (CI) of *H. japonica* is presented in Fig. 4. The specimens examined in this study ranged from 6.49 to 15.28 mm in shell height and from 0.17 to 1.34 g in total weight. In females, CI was lowest in June (23.77 ± 6.07) and highest in November (43.87 ± 4.07), with an annual mean of 35.31 ± 6.47 . Similarly, male CI was lowest in June (23.18 ± 6.08) and highest in November (44.49 ± 3.53), with an annual mean of

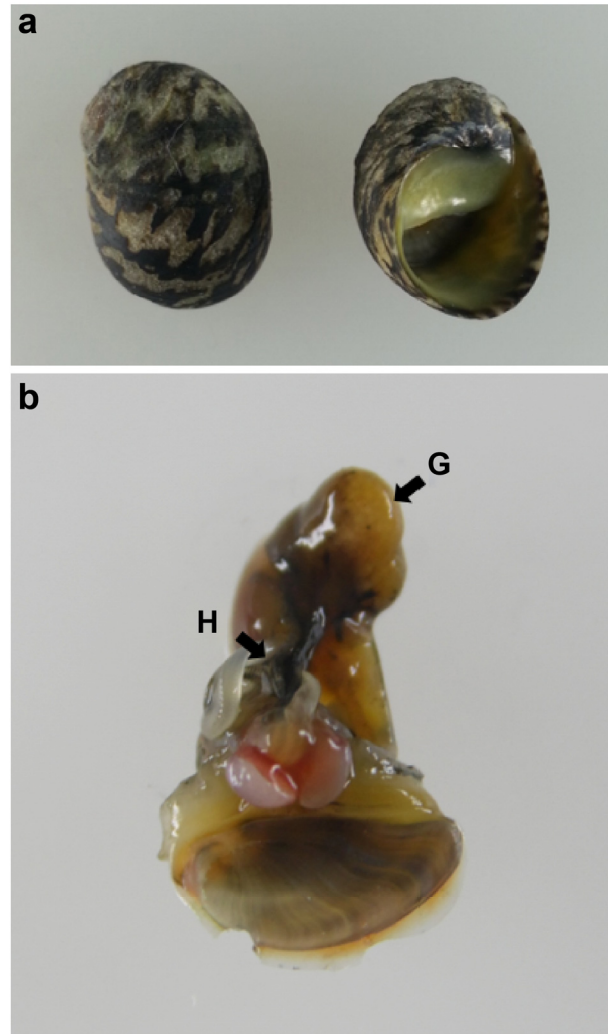


Fig. 3. Structure of a *Heminerita japonica*. (a) Outer morphology. (b) G: Gonad, H: Hepatopancreas.

35.88 ± 6.45 . Overall, both sexes exhibited similar seasonal patterns in CI, indicating consistent seasonal cyclicality.

4. Histological changes in gonads

Based on the histological analysis and the shape and size of germ cells and tissue cells around the germ cells (Redfern, 1974), the developmental process of the gonads was divided into five successive stages for both females and males: early developing, late developing, ripe, partially spawning, and degenerative and resting stages.

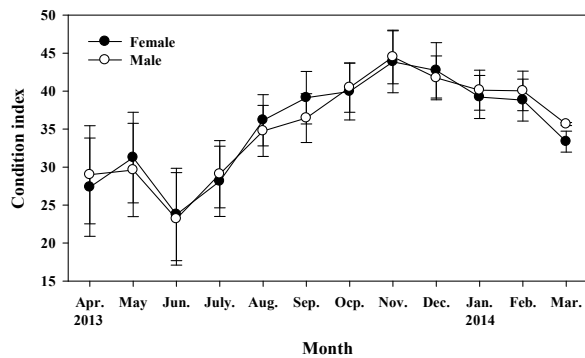


Fig. 4. Monthly condition index of female and male *Heminerita japonica*.

1) Ovary

① Early developing stage

The ovary consisted of numerous oogenic follicles with well-defined boundaries, and oogonia proliferated via mitotic division within the germinal epithelium of the follicles. Oogonia (approximately 5 μm in diameter) and early developing oocytes (10-20 μm) were embedded in the germinal epithelium. Oogonia possessed a distinct, round nucleus and relatively scant cytoplasm. This stage was observed from October to February (Fig. 5A).

② Late developing stage

During this stage, the follicular germinal epithelium became relatively thin, and proliferating oogonia exhibited a gradual increase in cytoplasmic volume, with developing oocytes growing toward the follicular lumen. Initial oocytes measured approximately 25-42 μm. As oocytes reached approximately 50 μm, they became oval to pear-shaped and temporarily formed an egg stalk with a tapered end, extending toward the lumen. Subsequently, the egg stalk disappeared, and oocytes detached from the germinal epithelium, became more spherical, and migrated into the central lumen. This stage occurred from November to April (Fig. 5B).

③ Ripe stage

In the ripe stage, each follicle was densely packed with free mature oocytes, and the ovarian germinal epithelium became markedly thinner. Fully mature

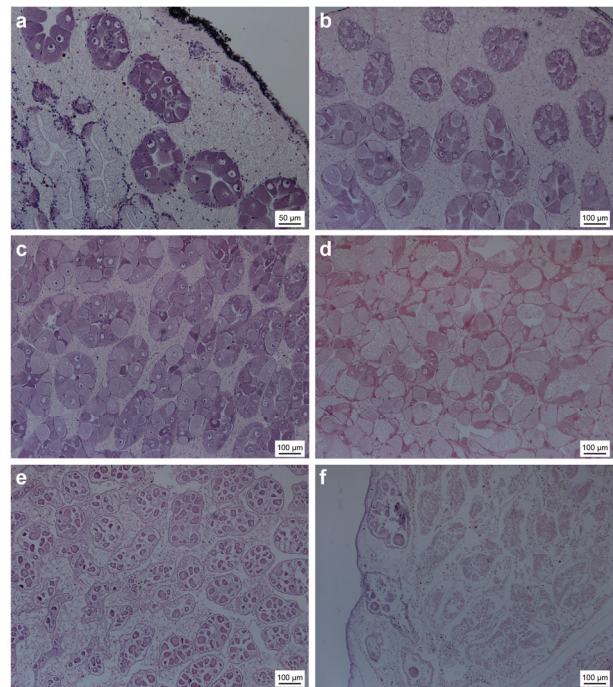


Fig. 5. Histological identification of the ovarian developmental stages in female *Heminerita japonica*. (a) Histological section of the oogenic follicle in the early developing stage. Note oogonia and early developing oocytes attached to follicular walls. (b) Histological section of the oogenic follicle in the late developing stage. Note a number of late developing oocyte in the follicle. (c) Histological section of the follicles in the ripe stage. Note mature and ripe oocytes in the lumen of the follicle. (d) Histological section of the follicles in the partially spawned stage. Note undischarged oocytes in the follicle. (e) Histological section of the follicles in the partially spawned stage. Note undischarged oocytes in the lumen of the follicle after spawning. (f) Histological section of the follicles in the degenerative and resting stage. Note newly formed oogonia on follicular walls and the connective tissues in the follicles after degeneration of the follicles.

oocytes accumulated abundant yolk granules in the cytoplasm and measured approximately 50-55 μm in diameter. Undifferentiated mesenchymal cells and eosinophilic granular cells previously observed around germ cells were no longer apparent. The nucleus was prominent, and granules were concentrated near the nuclear membrane. This stage was observed from February to May (Fig. 5C).

④ Partially spawning stage

Following spawning, the central region of the ovarian follicles became partially empty due to the

release of mature oocytes, while unreleased oocytes remained within the follicles. This stage occurred from May to July (Fig. 5D, E).

⑤ Degenerative and resting stage

After spawning, the remaining immature oocytes in post-spawning follicles underwent degeneration and atrophy. Unreleased oocytes gradually lost stainability, degenerated, and were resorbed. Connective tissue was widely distributed between follicles, and its abundance gradually decreased over time. As degeneration progressed, the follicular germinal epithelium thickened and was reestablished. A small number of oocytes appeared along the germinal epithelium and persisted briefly, representing a short resting period. Subsequently, individuals showing renewed mitotic activity of oogonia in the germinal epithelium were observed. This stage was observed from July to October (Fig. 5F).

2) Testis

The testis consisted of numerous spermatogenic tubules located adjacent to the digestive cecal sac. The spermatogenic follicles were supported by fibrous connective tissue. Based on histological criteria, testicular development was classified into five successive stages, consistent with those defined for ovarian development.

① Early developing stage

Spermatogenic follicles were characterized by a thick germinal epithelial wall. The follicles contained predominantly spermatogonia distributed along the germinal epithelium, together with undifferentiated mesenchymal cells and eosinophilic granular cells. Spermatogonia (approximately 10 μm in diameter) were frequently observed, and spermatocytes (approximately 7-8 μm) were also present. Nuclear structures in early spermatogonia were less conspicuous than those of oocytes; the nuclear reticulum appeared irregular, and chromatin was granular to clumped. This stage was observed from October to February (Fig. 6A).

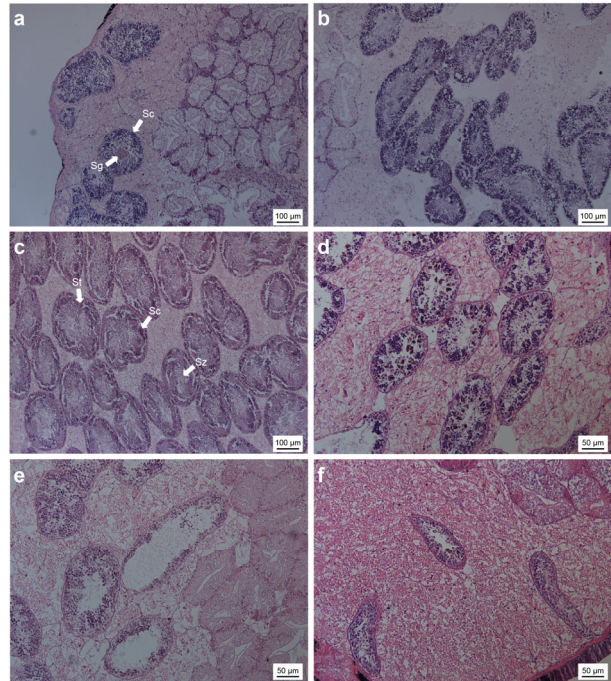


Fig. 6. Histological identification of the testicular developmental stage in male *Heminerita japonica*. (a) Histological section of the spermatogenic follicle in the early developing stage. Note spermatogonia and spermatocytes near the germinal epithelium. (b) Histological section of the follicle in the late developing stage. Note spermatocytes, spermatids and spermatozoa during spermiogenesis. (c) Histological section of the follicles in the ripe stage. Note spermatids and numerous spermatozoa in the lumen of the follicle. (d) Histological section of the follicles in the partially spawned stage. Note undischarged spermatozoa in the lumen. (e) Histological section of the follicles in the degenerating stage. Note degenerating spermatozoa and spermatids in the lumen after release of sperm. (f) Histological section of the follicles in the resting stage. Note newly formed spermatogonia on the germinal epithelium and the connective tissues in the follicle after degeneration of the follicles.

② Late developing stage

The germinal epithelium remained relatively thick. Spermatogonia that had completed proliferation progressed to spermatocytes through the first meiotic division. Within the follicles, the proportion of spermatogonia decreased, whereas spermatocytes and spermatids increased. A limited number of transforming spermatozoa were observed in the follicular lumen. As development progressed, the

spermatogonial layer became reduced and the spermatocyte layer became more prominent. This stage occurred from November to April (Fig. 6B).

③ Ripe stage

Spermatogenic follicles were enlarged and well developed. Spermatocytes and spermatids were mainly distributed along the germinal epithelium, and the follicular lumen was densely filled with mature spermatozoa. Spermatozoa showed a consistent orientation, with heads directed toward the follicular wall and tails toward the lumen. This stage was observed from March to May (Fig. 6C).

④ Partially spawning stage

Following spawning, the density of spermatozoa in the follicular lumen decreased, and some follicles became partially empty. Nevertheless, residual spermatozoa remained within the lumen. Follicles in which spawning had occurred gradually atrophied and exhibited irregular follicular outlines. This stage occurred from May to July (Fig. 6D).

⑤ Degenerative and resting stage

After spawning, spermatogenic follicles became extensively disrupted, and residual spermatozoa degenerated and were resorbed. Connective tissue occupied the spaces left by collapsed follicles. Subsequently, the germinal epithelium was reestablished and thickened, and a small number of spermatogonia reappeared along the germinal epithelium. No pronounced histological changes were observed until new spermatogenic follicles formed. This stage was observed from June to October (Fig. 6E, F).

5. Reproductive cycle

The reproductive cycle of *H. japonica* was assessed histologically based on germ-cell development and was classified into five stages: early developing, late developing, ripe, partially spawning, and degenerative and resting (Figs. 7 and 8).

1) Females

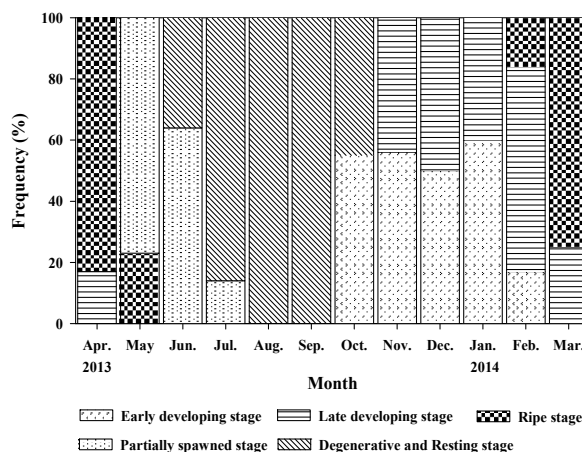


Fig. 7. Frequency of gonadal phases of female *Heminerita japonica*.

In females, the early developing stage occurred from October to February, peaking in January. The late developing stage was observed from November to April, with a peak in February. The early and late developing stages overlapped extensively from November to February. The ripe stage occurred from February to May, peaking in April. The partially spawning stage was observed from May to July, with a peak in May. The degenerative/resting stage occurred from June to October, with the highest frequency in August-September (Fig. 7).

2) Males

Overall, males exhibited seasonal patterns broadly similar to those of females. The early developing stage occurred from October to February, peaking in October. The late developing stage was observed from November to April, with a peak in January, and overlapped with the early developing stage from November to February. The ripe stage occurred from March to May, peaking in April. The partially spawning stage was observed from May to July, with a peak in June. The degenerative and resting stage occurred from June to October, with the highest frequency in August-September (Fig. 8).

Taken together, the reproductive cycle of *H. japonica* in the Geomundo area was characterized by an early developing stage from October to February

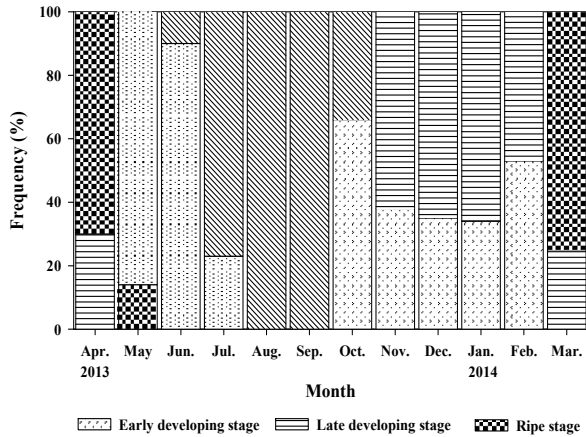


Fig. 8. Frequency of gonadal phases of male *Heminerita japonica*.

and a late developing stage from November to April. The ripe stage occurred from February to May in females and from March to May in males, followed by a partially spawning stage from May to July. The degenerative/resting stage extended from July to October in females and from June to October in males. Both sexes showed largely synchronous maturation; however, females tended to reach maturity slightly earlier than males and entered the partially spawning stage earlier.

DISCUSSION

External factors influencing gonadal development, gametogenesis, maturation, and spawning have been widely documented in marine invertebrates. For example, spawning can be suppressed under conditions of reduced seawater specific gravity (Taki, 1949), and reproductive output is closely linked to food availability for both adults and larvae (Jaramillo and Navarro, 1995). Reproductive patterns also vary geographically; in general, species in high-latitude cold regions often spawn once per year, those in mid-latitude temperate regions may spawn twice per year, and those in low-latitude tropical regions may reproduce over extended periods or year-round (Rand, 1973; Glovani and Diana, 1994).

With respect to spawning seasonality, molluscs have been classified into year-round breeders,

summer breeders (late spring to early fall), and winter breeders (late fall to early spring) (Booolootian *et al.*, 1962). In addition, the number of spawning events differs among species, with reports of annual, biannual, and even triannual spawning cycles (Sarasquete *et al.*, 1990; Brousseau, 1995; Kim *et al.*, 1999; Lee, 1999). In gastropods, gamete development and maturation are generally regulated by multiple environmental and physiological factors, including water temperature, food availability, photoperiod (day length), and endocrine control (Booolootian *et al.*, 1962; Fretter, 1984). In temperate regions, seasonal shifts in water temperature and light conditions are considered major cues initiating gametogenesis and subsequent gonadal maturation (Fretter, 1984).

In the present study, oocytes and spermatogenic cells exhibited rapid growth in March, coinciding with rising water temperature, and spawning activity occurred mainly between May and June when water temperature was approximately 16 °C. These findings suggest that the onset of germ-cell development and spawning in *H. japonica* is strongly associated with seasonal increases in water temperature and changes in light conditions.

Several approaches have been used to estimate bivalve reproductive cycles, including the gonadal index (Yamamoto & Yamakawa, 1985), gonad weight index (Oh *et al.*, 2002), biochemical analyses of gonadal tissues (Strohmeier *et al.*, 2000), histological examination, condition index and flesh-weight ratio, and monitoring of planktonic larval occurrence. In *H. japonica*, monthly CI began to decline from March (female: 33.39 ± 1.38 ; male: 35.66 ± 0.20) as water temperature increased. During the main spawning period, CI decreased further, reaching 31.26 ± 5.97 (female) and 29.62 ± 6.13 (male) in May and the annual minima of 23.77 ± 6.07 (female) and 23.18 ± 6.08 (male) in June. CI subsequently increased during the degenerative/recovery period, indicating a clear seasonal cyclicality. Such post-spawning declines and subsequent recovery in flesh condition have also been reported in several bivalves (e.g., *Tresus keenae*, *Mya arenaria oonogai*, and *Crassostrea gigas*) and gastropods (e.g., *Omphalius rusticus*, *Lunella*

coronata coreensis, and Umboonium thomasi). This pattern likely reflects energetic allocation to rapid germ-cell growth during late developmental stages, followed by depletion of somatic reserves during spawning. The increase in CI during the recovery period may therefore represent replenishment of energy reserves and resorption processes supporting the formation of new germ cells.

After spawning, some bivalves enter a true resting phase, during which residual germ cells in the gonad degenerate and are resorbed (Brousseau, 1995; Chintala & Grassle, 1995), whereas others proceed directly into recovery without an extended resting period. In many gastropods, including abalones (*Haliotis* spp.), *Thais clavigera*, *O. rrusticus*, and *U. thomasi*, gametogenesis resumes soon after spawning, with limited evidence of a prolonged resting phase. In the present study, the reproductive cycle of *H. japonica* was divided into early developing, late developing, ripe, partially spawning, and degenerative and resting stages. Because the gonad entered a resting condition after degeneration while new germ cells were also observed to reappear, gonadal development in *H. japonica* appears to proceed continuously throughout the year, with seasonal modulation in the intensity of gametogenic activity.

ACKNOWLEDGMENTS

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