Zoological Studies **58:** 29 (2019)
doi:10.6620/ZS.2019.58-29

Zoological Studies

Open Access

Early Larval Development and Annual Gametogenesis of the Brooding Oyster *Ostrea circumpicta* (Pilsbry, 1904) in the Shallow Subtidal Benthic Ecosystem in Jeju Island, Off the South Coast of Korea

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Received 23 March 2019 / Accepted 29 June 2019 / Published 19 September 2019
Communicated by Benny K.K. Chan

The subtropical brooding oyster *Ostrea* (= *Striostrea*) *circumpicta* (Pilsbry, 1904) occurs at high density in the shallow, subtidal, rocky bottom in Jeju Island, off the south coast of Korea, where the sea surface temperature and salinity varies annually from 13 to 25°C and 30 to 33 ppt, respectively. In this study, the annual gametogenesis and early larval development of *O. circumpicta* was examined, using histology and scanning electron microscopy (SEM). Histology indicated that the females and males initiated gonial mitosis in September, shortly after sexual resting in August. In December, ripe eggs first appeared in the follicles, and most of the females exhibited fully mature oocytes in May, as the water temperature reached 17 to 18°C. Spawning females were dominant in June and July, when the trochophore and strait-hinged veliger larvae were also identified in the branchial chambers, their size ranging from 111 to 130 μm and 135–205 μm in diameter, respectively. The veliger larvae in the brooding chamber exhibited a well-developed velum and digestive tract, suggesting that the larvae are engaged in feeding in the branchial chamber. Unlike other marine bivalves in temperate coastal ecosystems, *O. circumpicta* has a long period of gonad maturation and a short resting phase. It has been believed that such a long period of reproductive maturation is associated with a low level of food in the environment and the comparatively large size of the oocytes, which may require a relatively longer time to accumulate necessary nutrients to produce large eggs in a food-poor environment.

Key words: *Ostrea circumpicta*, Larval development, Gametogenesis, Microscopy, Jeju Island Korea.

BACKGROUND

The subtropical larviparous oyster *Ostrea* (= *Striostrea*) *circumpicta* (Pilsbry, 1904) is widely distributed in the tropical to subtropical northwest Pacific Ocean, from Jeju Island to Taiwan, Hong Kong, southern Japan, and southern China (Hirase 1930; Bernard et al. 1993; Kwon et al. 1993; Okutani

Citation: Lim NL, Lee HM, Jeung HD, Noseworthy RG, Jung S, Choi KS. 2019. Early larval development and annual gametogenesis of the brooding oyster *Ostrea circumpicta* (Pilsbry, 1904) in the shallow subtidal benthic ecosystem in Jeju Island, off the south coast of Korea. Zool Stud **58:**29. doi:10.6620/ZS.2019.58-29.

2000; Min et al. 2004). In the shallow, subtidal, rocky substrate in Jeju Island, *O. circumpicta* occurs at a high density, and is often encrusted with various sessile flora and fauna including soft corals, sponges, and small algae, which play a crucial role in the ecosystem by providing substrata for other benthic organisms (Je et al. 2002; Kang et al. 2004a). Despite its abundance and ecological importance, few studies have been carried out on the life history of this larviparous oyster. Kang et al. (2004a) observed, for the first time, microscopic features of the larvae and gonads of *O. circumpicta* collected from Munseom Island, off the south coast of Jeju Island. They reported that females collected in early summer brood the early veliger larvae (115–135 µm) in their infra-branchial chamber. Although they reported the spawning and appearance of larvae, complete annual gametogenesis of *O. circumpicta* has yet to be investigated.

Located off the south coast of Korea, Jeju Island (33.10° to 33.50°N, 126.10° to 127.0°E) is a typical volcanic island with a well-developed rocky shoreline. Coastal Jeju Island is a complex region, where three major water masses from the north and northwest are mixed. The warm Tsushima Current branches from the northeastward flowing Kuroshio Current and travels through the southern coastal area of the island, giving this area somewhat warmer water temperatures. The prevailing winds from the Pacific Ocean are southeasterly in summer, and also help to raise the water temperature. Due to the blending of warm and cool currents around the island, Jeju has a high diversity of marine flora and fauna (Oh et al. 1994; Lee 1999; Kang et al. 2005; Lee et al. 2019). Munseom Island, an uninhabited island located off the southern coast of Jeju (33°13'25"N, 126°33'58"E), is well known for its high species diversity and richness of marine flora and fauna (Je et al. 2002, Fig. 1). Munseom is characterized by rocky, volcanic intertidal and subtidal zones that are subjected to strong wave action. The rocky substrata are covered with a rich assortment of sessile fauna such as oysters, barnacles, and numerous species of hydrozoans. Surface water temperature and salinity in this area vary annually from 14 to 22°C and from 32.2–34.4 psu, respectively (Choa and Lee 2000; Lee et al. 2000). In the shallow subtidal of southern Jeju Island, numerous species of mollusks have been identified; some species occur only in Jeju Island (Je et al. 2002; Noseworthy et al. 2007 2016; Limpanont et al. 2010). According to Min et al. (2004), there are 17 oyster species in Korean waters; *O circumpicta* occurs only in Jeju Island, mainly on the south coast.

The present study investigated seasonal changes

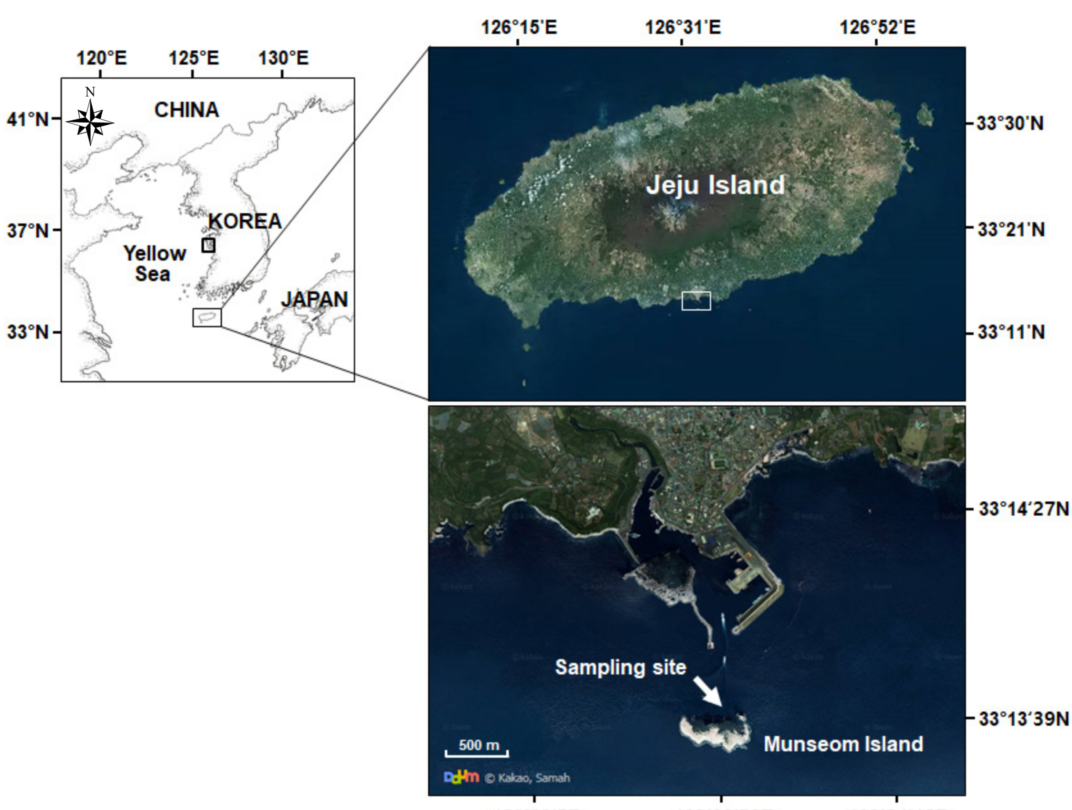

Fig. 1. Map showing the sampling location, Munseom Island, off the south coast of Jeju Island.

in the gonad and early larval development of *O. circumpicta* from the southern coast of Jeju Island using histology and scanning electron microscopy (SEM). This is the first study to report on the annual reproductive cycle and larval development of this brooding oyster.

MATERIALS AND METHODS

From September, 2003 to September, 2004, adult oysters with shell lengths ranging from 50–80 mm were collected monthly using SCUBA, from Munseom Island at depths of 5–7 m (Fig. 2). Seasonal changes in the surface seawater temperature and salinity of the sampling site during sampling were obtained from the National Oceanographic Research Institute of Korea (NORI). The monthly mean chlorophyll *a* level in each sampling period was collected from the NASA EARTHDATA database (https://earthdata.nasa.gov/, USA). The chlorophyll *a* varied from 0.3 (July 2004) to 1.7 μg/L (October 2003), while the surface seawater temperature varied from 14 to 25°C, and salinity ranged from 24.2 to 32.1 psu during the sampling period (Fig. 3).

To examine gonad development, a longitudinal section was cut from the middle of the body, including the gills and gonad. The tissue sections were fixed in Davidson's fixative for 48 hrs and dehydrated in ethanol. The dehydrated tissues were embedded in paraffin, sectioned at 6 μm, stained with Harris' hematoxylin, and counter stained with eosin Y. The histological preparations were examined under a light compound microscope to evaluate the gonad maturation level. Based on the microscopic appearance of the gonad, the reproductive stages of each specimen were assigned to one of six categories according to Siddiqui and Ahmed (2002): 1) resting, 2) early developing, 3) late developing, 4) ripe, 5) partially spawned, and 6) spent. Egg diameter in randomly-selected microscopic fields was also measured from the histological preparation, using image analyzing software.

During May and August, the presence of larvae in the branchial chamber was examined directly under a dissecting light microscope. As the shells were opened, the gills which may contain the larvae were gently washed using filtered seawater; the filtrates were harvested and examined under a microscope, and the size, *i.e.*, distance of the longest axis, was measured using image analyzing software. For SEM observation, the larvae collected from the infra-branchial chamber were fixed in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.3 at 4°C), then washed for 30 mins in the same buffer. The fixed specimens were finally dehydrated in an ethanol series, freeze-dried, and coated with platinum. The platinum-coated larvae were examined under a JEM 1200EX-II SEM (JEOL, Japan). Shell development during the larval period was categorized according to the criteria described by Marin and Luquet (2004).

RESULTS

Microscopic features of the gonad and annual gametogenesis

Histology revealed that 40% of the female oysters collected in September, 2003 were in the late developing stage. During early and late developing stages, oogonia and oocytes propagated along the germinal epithelia (Fig. 4a, b). Female oysters in the late developing stage

Fig. 2. Animal and shell of *O. circumpicta*. ▲, Gonad, ➤, Gills.

were characterized by greatly expanded and coalesced follicles, and the cytoplasm became less basophilic than in the early developing stage (Fig. 4b). Spermatogonia and spermatocytes appeared in the follicles during the late developing stage (Fig. 5a), in December. During the late developing phase, the spermatocytes developed into spermatids, and several groups of spermatids were distributed in the center of the follicle; groups of spermatocytes were arranged along the spermatogenic follicles (Fig. 5b).

In February, as the surface seawater temperature increased from 14 to 17°C; the females became sexually mature, exhibiting fully mature oocytes containing large nuclei with nucleoli; and the follicles were greatly expanded (Fig. 4c). During this month, the ripe males also appeared, demonstrating expanded follicles containing a large number of concentrated spermatids and spermatozoa (Fig. 5c). In May, most males were actively engaged in spawning, exhibiting scattered masses of spermatozoa and vacated testis (Fig. 5d). Spawning males were observed until July; spent testis was recognized from some individuals (Fig. 5e).

Spawning females first appeared in May, exhibiting free mature oocytes in the lumen of the follicles, while the follicles became partially empty (Fig. 4d). The spawning females could be observed until July, as the SST increased from 17°C to 20°C. In July and August, most oysters were in the spent stage exhibiting a few relict oocytes in the follicles (Fig. 4e). During this stage, the follicles were mostly vacated, and the follicle area become reduced to a great extent. In males, most follicles appeared empty, while some residual spermatozoa and spermatids become degenerated (Fig. 5e). Sexually undifferentiated oysters appeared in August and September, and no gametogenic cells could be identified from the thin follicle wall (Figs. 4f, 5f).

Seasonal changes in frequency distribution in the different reproductive stages are plotted in figure 6. In females, ripe oysters could be seen from December to July, while spawning females could be seen during June and July. The high percentage of spawning/spent oysters in June and July indicated that *O. circumpicta* spawned during this period. Contrary to the females, spawning males were first observed in May, and spawning in males continued until July, suggesting that the major spawning period of this species in Jeju Island is June and July.

Figure 7 plots monthly variation in the oocyte size. In the early developing stage, young oocytes (60 μm in diameter) were dominant during September and October. Fully mature eggs began to appear in March, and were dominant in May, measuring 104 μm in diameter. The proportion of mature eggs decreased in June, possibly due to infernal fertilization. Histology revealed that *O. circumpicta* in Jeju Island carries the oocytes in the gonad all year round, representing a characteristic of tropical/subtropical oysters.

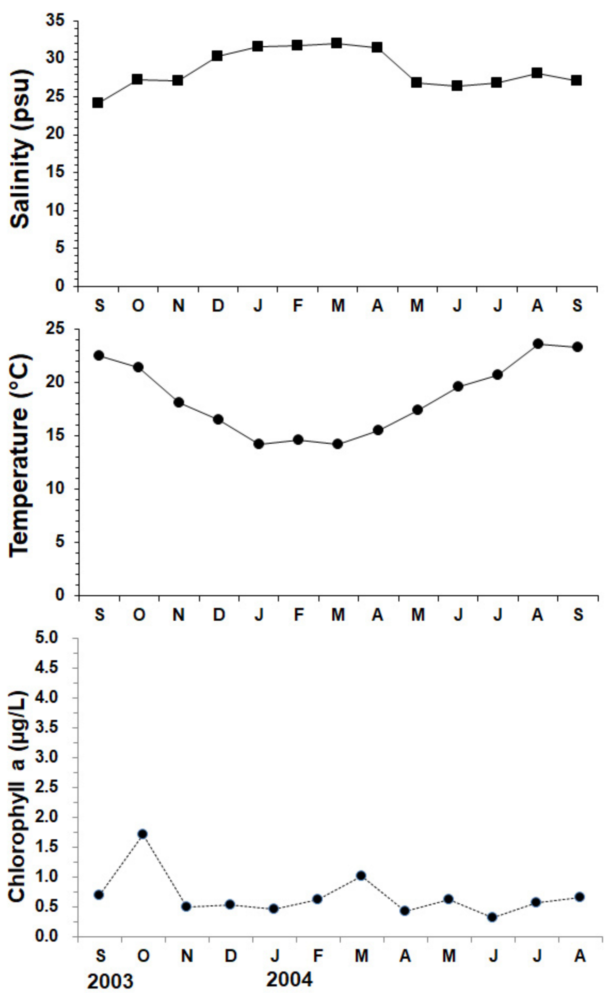

Fig. 3. Monthly variations in the surface water temperature, salinity and chlorophyll *a* at the sampling location from September 2003 to September 2004. The sea surface temperature and salinity data were obtained from Korea Hydrographic and Oceanographic Agency, and the chlorophyll *a* were referred from NASA EARTHDATA (https://earthdata.nasa.gov/, USA)

Larval development

Trochophore and veliger larvae first appeared as early as May. In June, 50% of the females reared the larvae in their gill chambers. The proportion of the females exhibiting D-shaped veliger and/or trochophore larvae declined in July to 29%, and none of the females examined in August exhibited the larvae in the gill chambers (Table 1). The data suggest that spawning and subsequent larval rearing in *O. circumpicta* was finished by July in southern Jeju Island.

Histology also confirmed the presence of the trochophore and veliger larvae in the infra-branchial chamber in the mantle cavity in June and July (Fig. 8a, b); the former consisted of a rudimentary shell and foregut (Fig. 8c), and the latter showed well-developed organs including locomotory cilia, digestive gland, esophagus, rudimentary gill, intestine, mantle, retractor muscle, rudimentary shell, stomach, velum, and visceral cavity (Fig. 8d). Under SEM observation, sizes of the trochophores ranged from 111 μm to 130 μm (Fig. 9a), and the veligers ranged from 135 μm to 205 μm in shell length (Fig. 9b, 9c). Characteristics of the veliger larvae observed from SEM included relatively small size, straight hinge, and absence of the rim of prodissoconch II; it was concluded that the shell stage of the veliger larvae observed in the present study belonged to prodissoconch I (Fig. 9d).

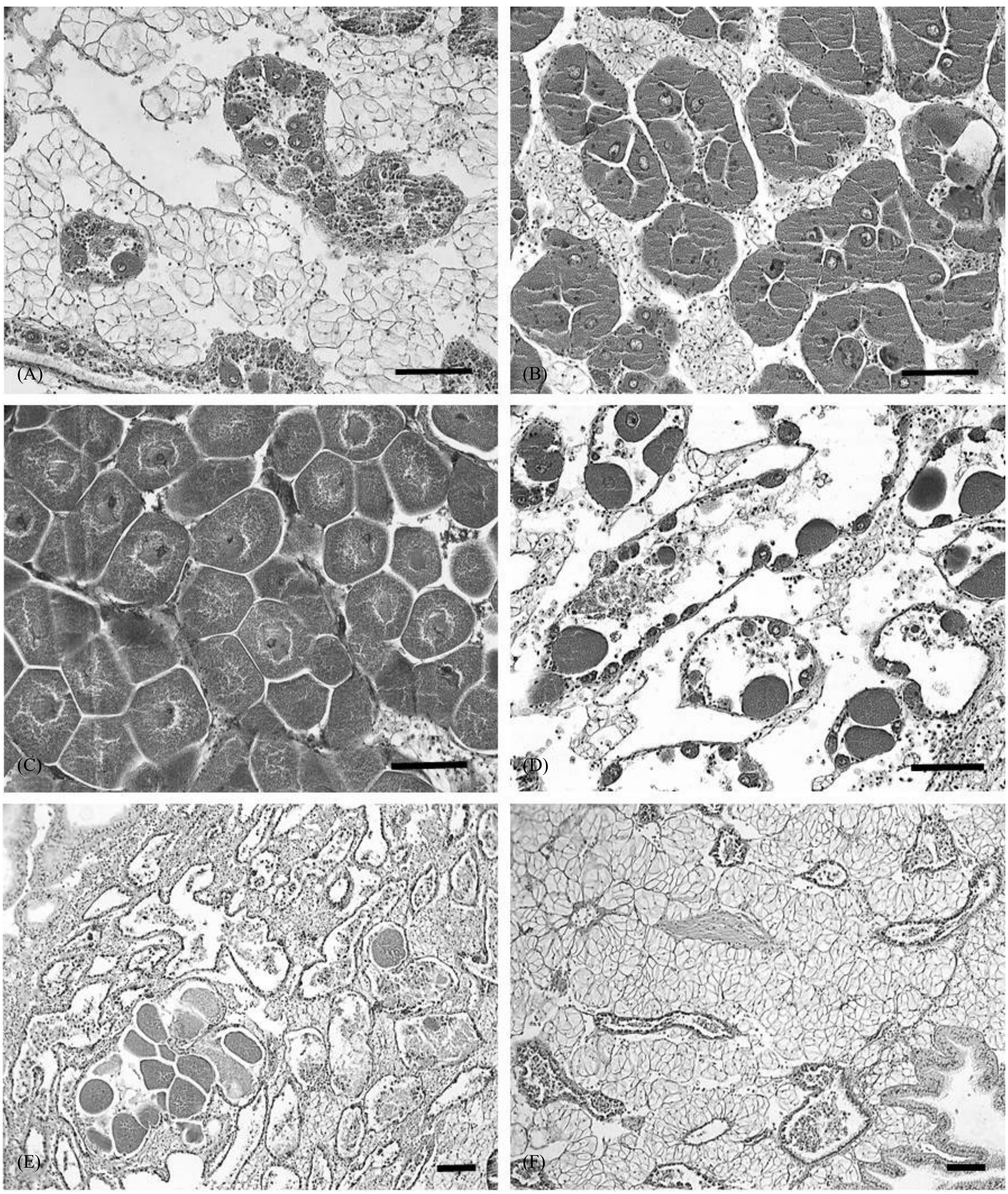

Fig. 4. Photomicrographs of reproductive stages of female *O. circumpicta*. (A) early developing, (B) late developing, (C) ripe, (D) partially spawned, (E) spent/absorbing, (F) resting.

DISCUSSION

According to the World Register of Marine Species (WoRMS 2019), the genus *Ostrea* (Linnaeus, 1758) includes 17 accepted living species, while approximately 400 synonymized and unaccepted species names have been assigned to the genus worldwide. In the north-west Pacific region, currently four species of brooding oysters have been identified, including *O. circumpicta*, *O. denselamellosa*, *O. stentina*, and *O. futamiensis* (Bernard et al. 1993; Kwon et al. 1993; Okutani 2000; Min et al. 2004; Hamaguchi et al. 2017). In Korean waters, where 17 living oyster species have been recognized, *O. circumpicta* is limited in distribution to Jeju Island, where the sea surface water temperature ranges from 13 to 26°C annually (Min et al. 2004; Kang et al. 2004b; Hong et al. 2013). Recently, Song et al. (2017) reported the presence of

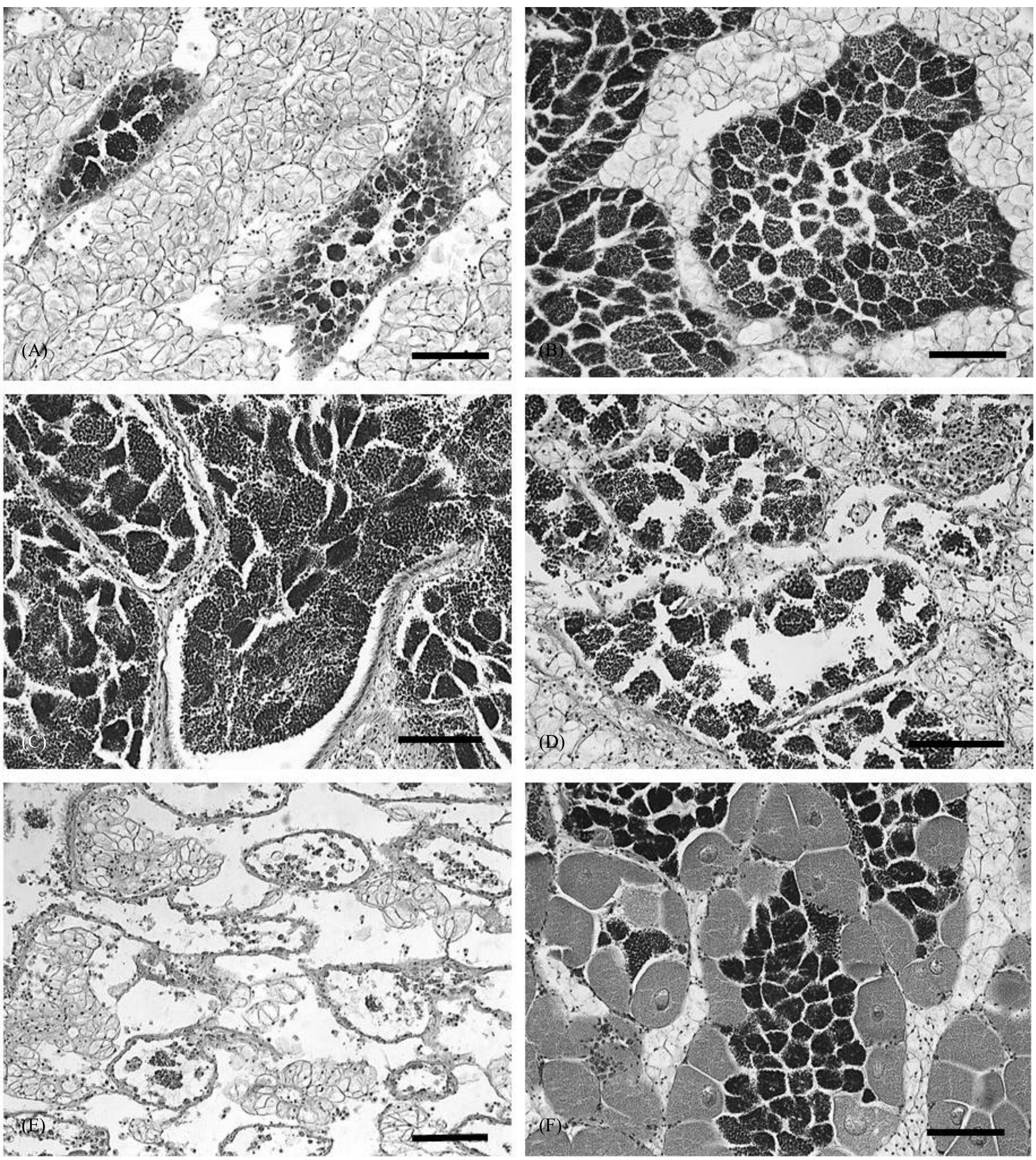

Fig. 5. Photomicrographs of reproductive stages of male *O. circumpicta*. (A) early developing, (B) late developing, (C) ripe, (D) partially spawned, (E) spent/absorbing, (F) resting.

O. circumpicta subtidally in Dokdo Island in the East/Japan Sea (37°14'26.8"N, 13151'54.6"E), a typical offshore island where the Tsushima current supplies warmer water from the south. In the northwest Pacific region, *O. circumpicta* has also been reported from the sub-tropical East China Sea, at Kyushu and the Seto Inland Sea in Japan (Hirase 1930; Bernard et al. 1993; Okutani 2000). Like other species in the genus *Ostrea*, *O. circumpicta* harbors its larvae in the branchial chamber; however, studies on its annual reproductive cycle are limited (Kang et al. 2004a).

This study is the first to examine the annual reproductive cycle of an *O. circumpicta* population on the shallow, subtidal, rocky substrate in Jeju Island. It is noticeable that *O. circumpicta* exhibits a short period of reproductively resting stage in August and a relatively longer period of gonad maturation. Shortly after resting in summer, the oysters initiated gonial mitosis in September and they first spawned in May, indicating that gonad growth takes approximately 8 months. It is also noticeable that the spawning activity of the females is limited to a short period, from late May to July. During this period, the females also exhibited early developing larvae such as trochophores and veligers in the mantle cavity. Histology also indicated that *O. circumpicta* carries the early developing larvae during June and July, suggesting that the spawning period coincides with the early larval brooding period. Accordingly, the annual gametogenesis of *O. circumpicta* can be summarized as a short period of resting and early developing, *i.e.*, gonial mitosis, in summer to early fall, maturing of the gametes in late fall to late spring, and spawning with the larvae developed and released in summer (Fig. 10).

Several studies have reported that bivalves distributed in warmer water have a short period of resting or no inactive/resting phase, due to the warmer water temperature which enables the oyster to actively remain in gametogenesis. In the tropical lagoons in French Polynesia, black-lip pearl oysters do not have a resting stage during their annual reproductive cycle, where the SST ranges 22–29°C annually (Pouvreau et al. 2000; Le Moullac et al. 2012). No sexual rest was also reported from the southern Gulf of Hammamet on the eastern coast of Tunisia, as the dwarf oyster

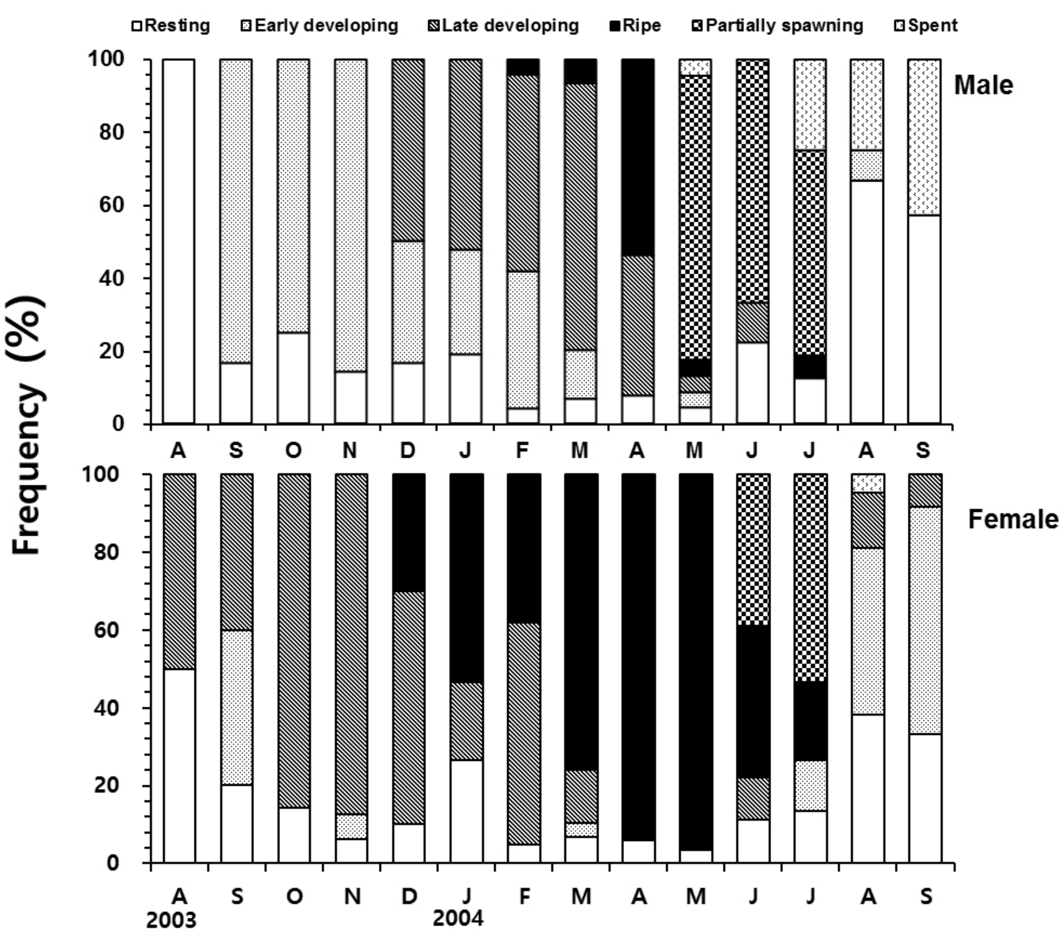

Fig. 6. Frequency distribution of gametogenic stages of *O. circumpicta*.

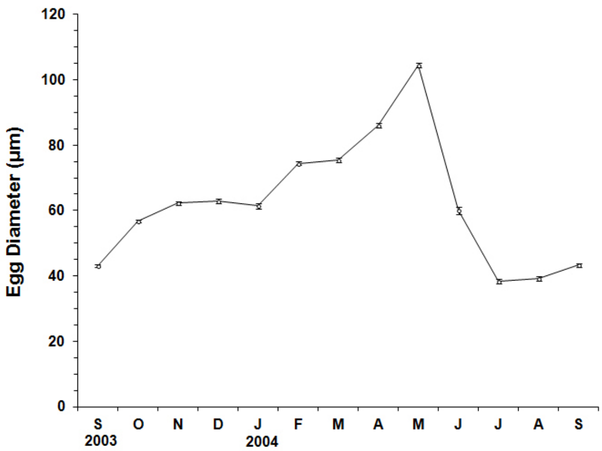

Fig. 7. Monthly mean changes in egg size of *O. circumpicta*.

Ostreola (= *Ostrea*) *stentina* exhibited gametes all year round (Salah et al. 2012). In a lagoon in the southern Gulf of California where the SST varies from 19–31°C seasonally, *Crassostrea corteziensis* rested for a month during its annual reproductive cycle (RodrÍguez-Jaramillo et al. 2008). Unlike other tropical and/or subtropical oysters, the tropical rock oyster *Striostrea prismatica*, on the southern coast of Ecuador, has a distinct sexual resting period from June to August (Loor and Sonnenholzner 2016).

Temperature is one of the key environmental factors that govern the annual gametogenesis of marine bivalves, especially in temperate waters, where the SST fluctuates seasonally with a wide range. On the south coast of Korea, where the SST ranges 9 to 26°C annually, the Pacific oyster, *Crassostrea gigas*, exhibits

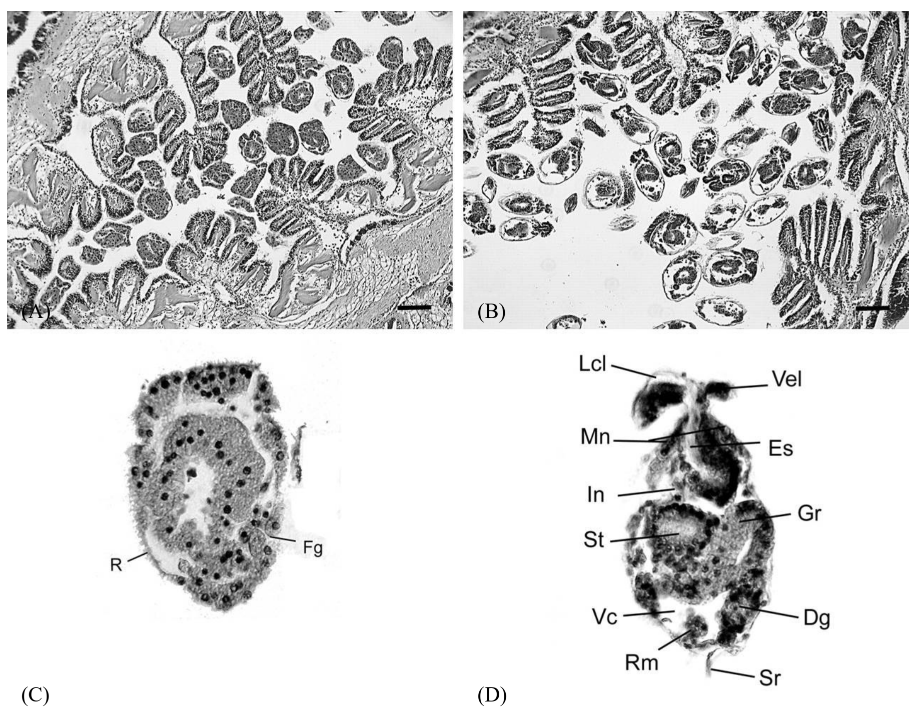

Fig. 8. Light microscopic images of *O. circumpicta* larvae in infrabranchial chamber. (A) trochophores; (B) veligers; (C) single trochophore (R, rudimentary shell; Fg, foregut); (D) Frontal section of larval of *S. circumpicta* stained with Hemotoxylin and Eosin. (Lcl, locomotory cilia; Dg, digestive gland; Es, esophagus; Gr, rudimentary gill; In, intestine; Mn, Mantle; Rm, retractor muscle; Sr, rudimentary shell; St, stomach; Vel, velum; Vc, visceral cavity)

Table 1. Percentage of the female oysters brooding the trochophore and/or veliger larvae in the infra-branchial chamber

Period		Percentage
	May	0
2004	June	50
	July	29
	August	0

a series of discrete gonad development phases in an annual reproductive cycle, which are closely linked to changes in water temperature (Kang et al. 2000; Ngo et al. 2002 2006; Mondol et al. 2016). In Gamakman Bay, on the south coast, *C. gigas* attached to subtidal long-lines spawned in June and July, when the SST ranged from 22–25°C. After spawning is completed, this species has a 4 months of resting stage, from

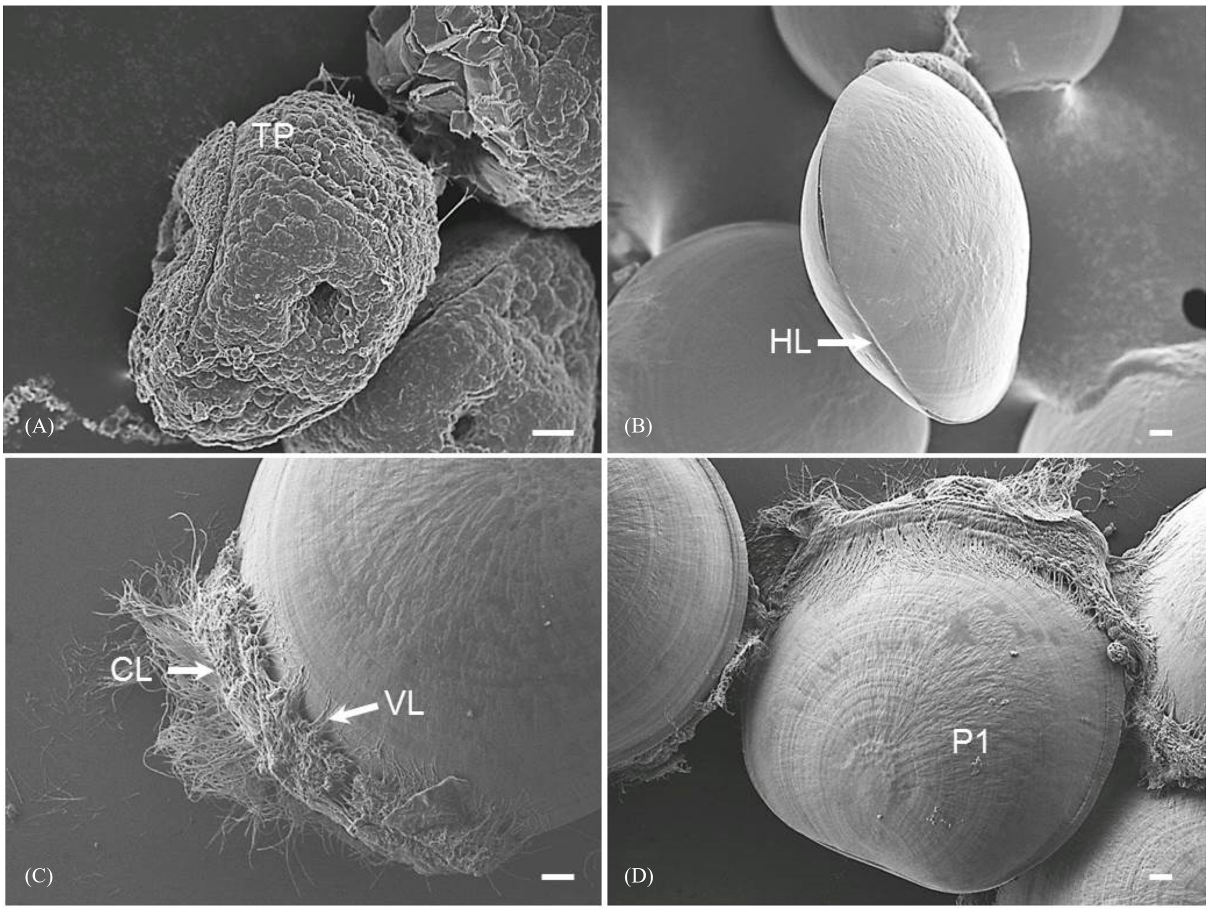

Fig. 9. Scanning electron microscopic images of *O. circumpicta* larvae. (A) trochophore, (B) hinge; (C) velum; (D) veliger, lateral view. TP: trochophore, IC: infrabranchial chamber, HL: straight hinge line; CL, cilium; VL, velum; P1, prodissoconch I.

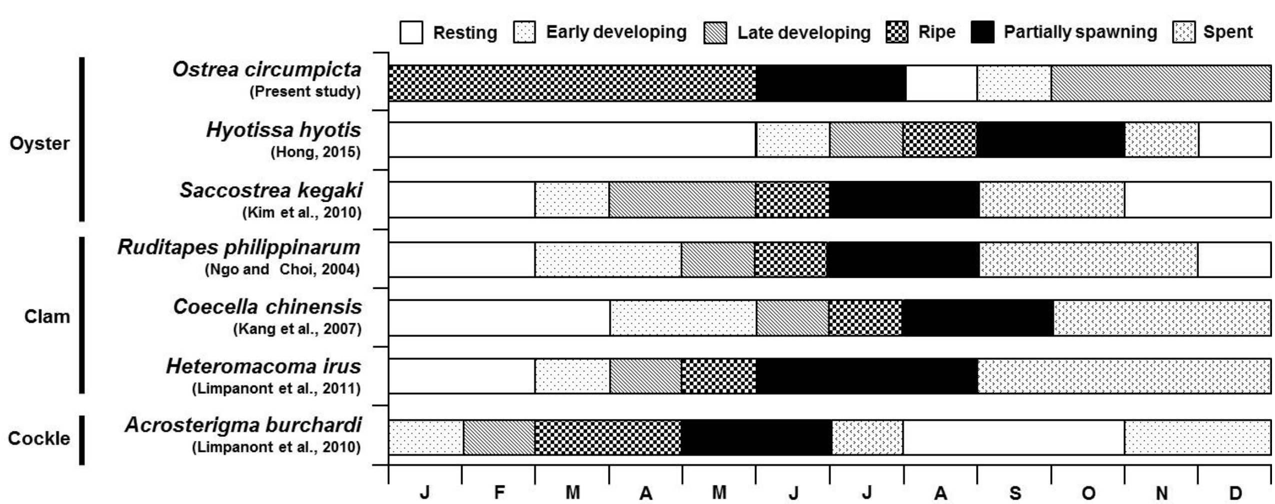

Fig. 10. Comparison of gametogenic stages of seven bivalve species from Jeju Island.

October to January, then resumes gametogenesis the following spring (Mondol et al. 2016). Similarly, the Pacific oysters in Gosung Bay, also on the south coast, showed 3 months of a reproductively inactive phase, *i.e.*, resting, from December to March, although the oysters in Gosung Bay had a longer period of spawning from June to September (Ngo et al. 2002). In Incheon Bay on the west coast, where the SST is comparatively cooler in winter and spring, *C. gigas* on a tidal flat exhibited 6 months of resting period, from August to February, and a short period of spawning during July and early August (Lee 2010). According to da Silva et al. (2009), the flat oyster, *O. edulis*, in Galicia, Spain takes several months of resting after a short period of spawning in summer.

In figure 10, we summarize the annual reproductive cycle of marine bivalves reported from the intertidal to shallow subtidal in Jeju Island. Among the seven species of oysters occurring in Jeju Island, *O. circumpicta* shows the longest period of gonad maturation, from October (late developing) to May (ripe), while other oysters, such as *Hyotissa hyotis* and *Saccostrea kegaki*, have 2–3 months of maturation in spring and early summer (Kim et al. 2010; Hong 2015). Such a short period of gonad maturation observed from those two tropical/subtropical oysters is also evident in other marine bivalves in Jeju Island; intertidal clams *Ruditapes philippinarum*, *Coecella chinensis*, and *Heteromacoma irus* take 2 to 3 months of gonad maturation in spring, then spawn in summer (Ngo and Choi 2004; Kang et al. 2007; Limpanont et al. 2010 2011).

The relatively longer phase of gonad maturation observed in *O. circumpicta* could be, in part, linked to the size of the mature eggs and food availability in the environment. Like other oysters, *O. circumpicta* is a suspension feeder, acquiring its food from the water column by filtering water. In Jeju Island, the chlorophyll *a* concentration in coastal areas, a proxy of the amount of food available for filter feeders, is relatively lower than the levels reported from other studies carried out in Korean waters (Fig. 3). Affan (2006) reported chlorophyll *a* content in the surface waters at the sampling site of this study, the southern coast of Jeju Island, ranging from 0.1, February, to 1.9 µg/L, April. Uddin et al. (2012) also reported a chlorophyll *a* concentration in a lagoon on the east coast of Jeju Island where the level varied from 0.5 to 2.6 µg/L annually. Compared to the chlorophyll *a* levels reported from the south and west mainland coasts, ranging 0.5–10.0 µg/L, (Kang et al. 2000; Uddin et al. 2012; Mondol et al. 2015), the levels reported from Jeju Island are somewhat lower. Thus, it is believed that suspension feeders in coastal Jeju Island may filter a relatively smaller amount of food, which may affect growth and sexual maturation, resulting in slow gonad maturation, although additional studies should be carried out to test this hypothesis. In this study, the maximum size of the oocytes was recorded as 170 µm in May, which is 2 to 3 times larger than the oocytes of clams and cockles in Jeju Island (Ngo and Choi 2004; Kang et al. 2007; Limpanont et al. 2010 2011). The large size of oocytes is a characteristic of brooding oysters. As summarized by Castaños et al. (2005), the mean diameter of the oocytes of *O. edulis* in England is reported to be 150 µm, and the oocyte size of *O. chilensis* in Chile ranged from 220–323 µm in diameter. It is believed that *O. circumpicta* eggs are lecithotrophic, like other eggs of brooding oysters, containing comparatively higher nutritional reserves to be used by the early developing larvae in the mantle cavity (Waller 1981; Foighil and Taylor 2000; Castaños et al. 2005).

Based on histology and light microscopy of *O. circumpicta* collected from the shallow subtidal on the south coast of Korea in June 2002, Kang et al. (2004a) first reported the presence of the trochophore and veliger larvae in its branchial chamber, confirming that *O. circumpicta* is a brooding oyster. The veliger larvae were characterized by well-developed cilia and incompletely-developed adductor muscles, as they ranged from 115-135 µm in diameter. According to Castaños et al. (2005), brooding oysters brood the veliger in the mantle cavity, *i.e.*, infra-brachial chamber, for a few days to a month, depending upon the species and water temperature. They also summarized the size of veliger larvae released from different species of brooding oysters; the size varied from 110 µm (*O. puelchana*, San Matias Gulf, Argentina) to 541 µm (*O. chilensis*, Chile).

In this study, the trochophores and the veligers were also observed in summer, mostly in June. From SEM images of the early developing larvae collected from the mother oysters in June, 2004, the size of the veligers was estimated, ranging from 135 µm to 205 µm in shell length. Compared to the size reported by Kang et al. (2004a), the veliger larvae observed in this study were somewhat larger, although the two studies used different methods to measure the size. It is probable that some veliger larvae that were analyzed in this study are fully grown and ready to be released, since they are approximately twice as large as the fully mature eggs. In histology, the veliger larvae also exhibited well-developed organs including locomotory cilia and digestive glands, suggesting that they are about to be released and start feeding on food particles in the water column; however, the incubation period in the branchial chamber was not determined in this study.

CONCLUSIONS

The annual reproductive cycle and larval brooding of *Ostrea circumpicta* in subtidal Jeju Island was investigated, using histology and SEM. The annual reproductive cycle of this brooding oyster was characterized by a short period of resting after completing spawning and larval rearing, and a long period of gonad development for several months. The brooding of trochophore and veliger larvae in the infra-branchial chamber was observed in a limited manner from May to July. The relatively long period of oocyte maturation observed in *O. circumpicta* was believed to be linked to the relatively larger size of the oocytes and the low level of available food in the water column in southern Jeju Island.

Acknowledgment: This study was supported in part by a project, "Marine ecosystem-based analysis and decision-making support system development for marine spatial planning "20170325", from the Ministry of Oceans and Fisheries of Korea. This research was also supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (2019R1A6A1A03033553).

Authors' contribution: N-L Lim analyzed all the datasets, including oyster histology and SEM, and wrote the manuscript. H-M Lee reviewed annual gametogenic patterns of marine bivalves on Jeju Island and prepared figure 10. H-D Jeung examined larval development images in SEM, and collected the environmental data. R.G. Noseworthy reviewed and polished the English in this study. S. Jung reviewed the manuscript and added statements in the discussion. K-S Choi engaged in the sampling, data analysis, preparing the manuscript and corresponding with the journal.

Competing interests: All authors declared that they have no competing interests.

Availability of data and materials: The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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