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ARTICLE

The Annual Gametogenesis of the Mussel, *Mytilus unguiculatus* (*coruscus*) (Valenciennes, 1858), Occurring in the Shallow Subtidal of Ulleungdo Island in Korea

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Abstract

The mussel *Mytilus unguiculatus* (*coruscus*) (Valenciennes, 1858) occurs at high density on the shallow subtidal hard bottom of Ulleungdo Island off the east coast of Korea, where it plays a crucial role as a primary consumer in the shallow, coastal, benthic ecosystem. In this study, we monitored seasonal variation in the condition index, gonad growth, and subsequent spawning of this species at Ulleungdo to obtain substantial information on its reproductive traits. From May to July 2013, the condition index (CI) dropped dramatically, indicating that *M. unguiculatus* (*coruscus*) spawned during this period. The CI also dropped from March to April in 2014 and then increased in May. Histology revealed that the onset of gonial mitosis in males and females occurred in September and October, and individuals in the spawning stage were observed in April 2014 and May 2013, when the surface seawater temperature (SST) ranged from 14 to 15 °C. The monthly mean oocyte diameter measured from the digitized images of the gonad also indicated that most females spawned completely in July. In summary, the annual reproductive cycle of *M. unguiculatus* (*coruscus*) at Ulleungdo could be categorized into (1) onset of gonial mitosis in late summer to early fall, (2) active growth of gonad cells ready for spawning during winter and spring, and (3) spawning and reabsorption of the residual gametes during late spring and summer. Seasonal changes in the gonads are closely linked to temporal changes in the SST.

Keywords *Mytilus unguiculatus* (*coruscus*) · Mussel · Gametogenesis · Ulleungdo Island · East · Japan Sea

1 Introduction

Sessile marine bivalves, such as mussels and oysters, often dominate the shallow subtidal hard bottom in coastal marine environments, where they play a crucial role as primary consumers, filtering small phytoplankton and bacteria (Lassen et al. 2006; Kecinski et al. 2018). Mussels and oysters often form beds or reefs in shallow temperate regions and are traditionally exploited as shellfish resources (Haupt et al. 2010; McLeod et al. 2014; Herbert et al. 2016; Andriana et al. 2020). *Mytilus unguiculatus* (*coruscus*) (Valenciennes, 1858) is widely distributed in the upper sublittoral rocky bottom in the East/Japan Sea, along the south and west coasts of Korea (Je et al. 1990; Okutani 2000; Kulikova et al. 2011; An and Lee 2012; Yang et al. 2015; Lutaenko and Noseworthy 2012, 2019). According to Vekhova (2013), *M. unguiculatus* (*coruscus*) is a slow-growing species. The age of individuals with a shell length of 80–90 mm, collected from Vostok Bay (i.e., Peter the Great Bay) in the East/Japan Sea, was estimated at 9–11 years old. This species also commonly occurs in the upper subtidal rocky bottom at Ullengdo, in the East/Japan Sea, where its density has declined, possibly due to overfishing and lack of proper management (Ulleung-Gun 2014).

Located 120 km off the east coast of Korea, Ulleungdo is characterized by a relatively warm surface water temperature during the winter due to the East Korean Warm Current (EKWC; Lee et al. 2016; Baek and Kim 2018). The rocky littoral and shallow sublittoral zones at Ulleungdo are enriched with macro-benthic flora and fauna, especially including several species of mussels (Je et al.

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1990; Cha and Kim 2013; Kang et al. 2013). Such high species diversity of macro-benthic organisms, with a high density in the shallow subtidal at Ulleungdo, can be, in part, explained by high primary production in the environment due to coastal upwelling that supplies nutrients to the primary producers in the shallow coastal ecosystem (Shin et al. 2018; Lee et al. 2020).

M. unguiculatus (*coruscus*) is one of the common benthic animals at depths of 0–5 m in the shallow rocky subtidal area in Ulleungdo. Despite this abundance, limited studies have been carried out on the reproductive ecology of this mussel in Ulleungdo (KIOST 2019). In this study, using histology, we first surveyed the annual gametogenesis of *M. unguiculatus* (*coruscus*) occurring in the shallow subtidal rocky bottom at Ulleungdo.

2 Materials and Methods

2.1 Sampling Effort

Specimens (107.7–121.0 mm in shell length, SL) used in this study were collected monthly (20–30) from May 2013 to May 2014 using SCUBA at Jukdo located on the east coast of Ulleungdo Island (Fig. 1). The specimens were transferred immediately to the laboratory, where the shell length (SL, mm) of each individual was measured (Fig. 2). The tissue-wet weight (TWWT, g) was measured using an electronic balance. The sex of each individual could be identified by the color of the mantle—where the gonad is located; the females are orange in color, while the males are creamy-white (Fig. 2).

The surface seawater temperature (SST) and salinity variation in the sampling area were referenced from Yang

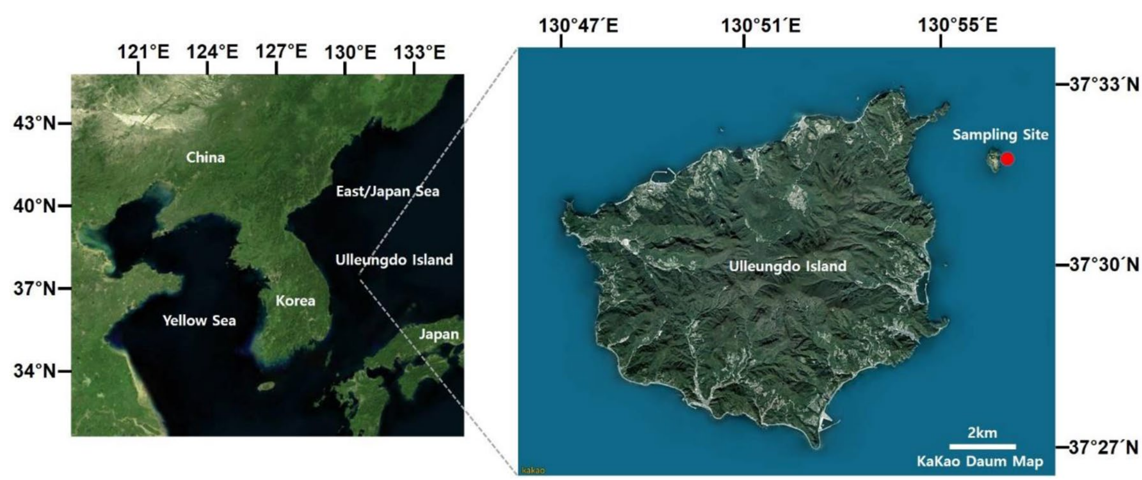

Fig. 1 Location of study area. The red dot indicates the sampling site off the east coast of Ulleungdo Island, Republic of Korea

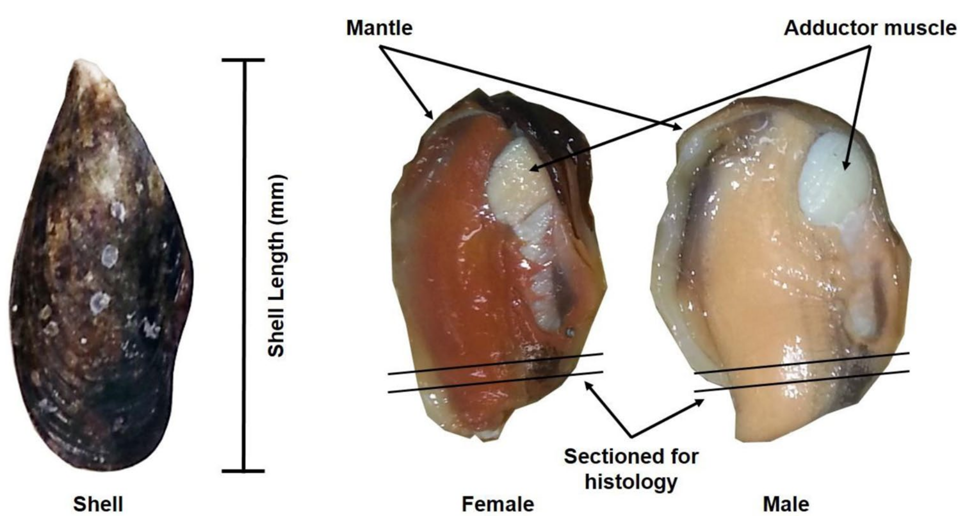

Fig. 2 Method of shell length measurement (left), and morphological features of female and male of *Mytilus unguiculatus* (*coruscus*) (right)

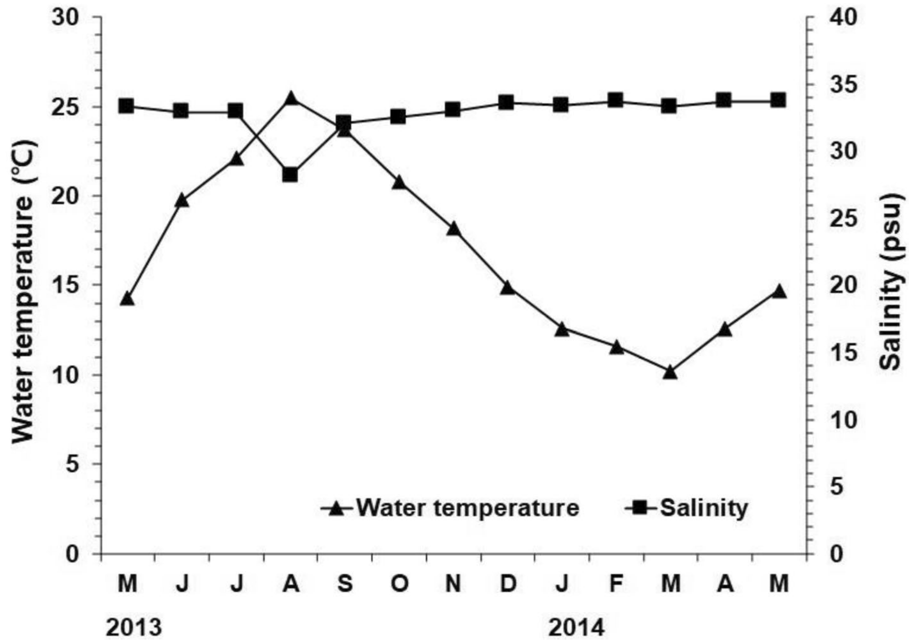

Fig. 3 Seasonal variation in surface seawater temperature and salinity at Ulleungdo Island, Korea from May 2013 to May 2014

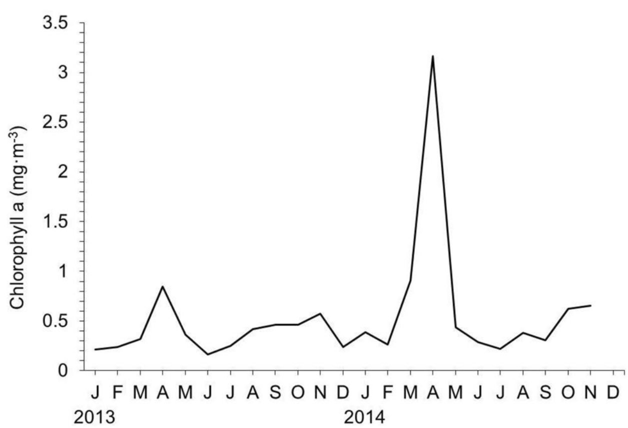

Fig. 4 Time series, area-averaged chlorophyll concentration based on Giovanni data from NOAA (http://giovanni.gsfc.nasa.gov/giovanni)

Table 1 Biometric data of shell length (SL, mm), shell height (SH, mm), shell width (SW, mm), and tissue wet weight (TWWT, g) of *Mytilus unguiculatus* (*coruscus*) collected from May 2013 to May 2014 at Ulleungdo Island, Korea

Period	*N*	SL	SH	SW	TWWT
May 2013	30	119.2 ± 2.9	58.5 ± 1.4	42.2 ± 1.2	34.02 ± 2.5
Jun	30	110.9 ± 1.4	54.8 ± 1.0	39.8 ± 0.6	25.37 ± 0.8
Jul	30	113.7 ± 1.0	56.1 ± 0.5	40.4 ± 0.5	21.79 ± 0.5
Aug	20	116.3 ± 1.3	56.9 ± 0.6	44.4 ± 0.5	26.46 ± 0.8
Sep	30	114.2 ± 1.2	56.0 ± 0.7	42.0 ± 0.5	27.16 ± 0.6
Oct	25	121.0 ± 1.2	60.0 ± 0.8	43.4 ± 0.5	31.08 ± 1.0
Nov	30	116.9 ± 1.1	56.7 ± 0.6	41.8 ± 0.6	25.90 ± 0.7
Dec	30	109.5 ± 1.0	54.6 ± 0.6	38.8 ± 0.5	26.38 ± 1.0
Jan 2014	N.D				
Feb	30	111.2 ± 1.7	52.0 ± 0.7	43.0 ± 0.5	22.64 ± 1.0
Mar	30	112.2 ± 1.5	53.0 ± 0.8	42.3 ± 0.7	26.49 ± 0.9
Apr	30	107.7 ± 1.7	53.9 ± 1.2	41.2 ± 0.7	23.42 ± 1.1
May	30	117.5 ± 1.5	57.2 ± 0.7	42.7 ± 0.6	34.76 ± 1.0

Each value represent mean ± standard error (SE). *N.D* no data

et al. (2017), who reported the monthly mean of the SST and salinity at Ulleungdo from May 2013 to May 2014. Yang et al. (2017) obtained the mean SST and salinity of the study site from the Korea Hydrographic and Oceanographic Administration (Ulleungdo Island Observatory, 130° 54′ 49″ E, 37° 29′ 29″ N). During the study, the SST and salinity varied annually from 10.2 to 25.5 °C and 28.2 to 33.7 psu, respectively (Fig. 3). The monthly mean chlorophyll-a concentration in the study site was referred from the GIOVANNI database (http://giovanni.gsfc.nasa.gov/giovanni), and monthly mean chlorophyll-a concentration ranged from 0.16 to 3.16 mg·m^{-3} (Fig. 4).

2.2 Annual Gametogenesis

A 2-mm-thick piece of tissue containing the gonad was excised and the wet weight of the section measured, then fixed in Davidson's fixative for 48 h (Fig. 2). The remaining body tissue was freeze-dried and weighed using an electronic balance. The condition index (CI) of individuals was determined as the ratio of the dry tissue weight to the dry shell weight (Table 1).

The fixed tissues went through the standard histological procedure including dehydration in a series of elevated concentrations of ethanol and subsequent embedding in paraffin. The paraffin block was sliced to 6 μm using a microtome (Leica, Germany), and then stained with Harris' hematoxylin and eosin Y. The degree of gonad development was categorized into six stages as (1) early developing, (2) late-developing, (3) ripe, (4) partial spawning, (5) spent, and (6) resting stages according to Lee et al. (2007). To trace the annual gametogenesis, we also measured the oocyte diameter (OD) from the digitized microscopic images of the gonad using Image Pro-Plus (Media Cybernetics, USA).

3 Results

3.1 Microscopic Features of Testis and Ovary

Figures 5 and 6 demonstrate the microscopic features of the male and female gonads. During the resting stage, no gametogenic cells are observed in the follicles and the sex cannot be distinguished (Figs. 5a, 6a).

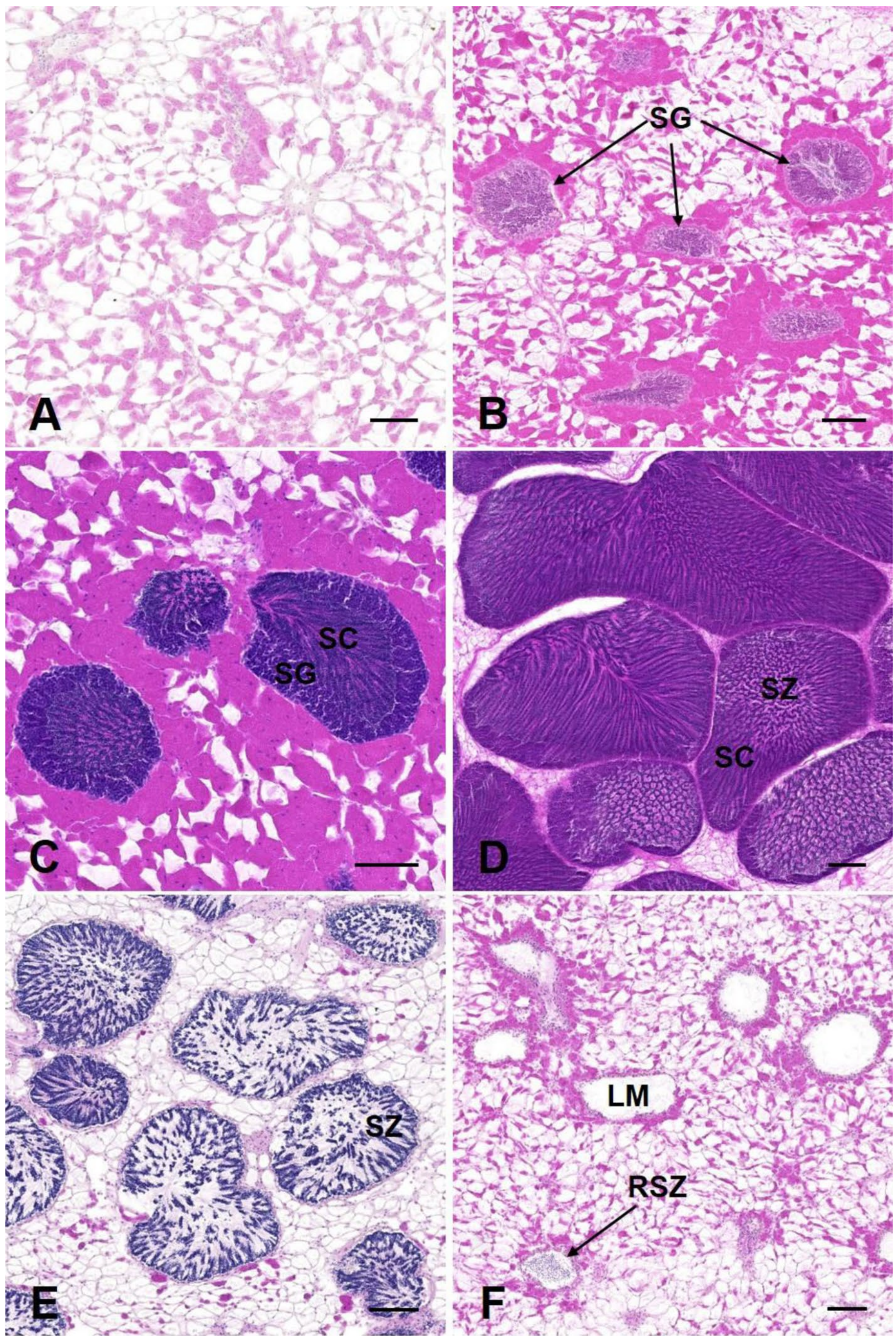

Fig. 5 Photomicrographs of different gonad development stages of male mussel. **a** Resting stage, **b** early developing stage, **c** late-developing stage, **d** ripe stage, **e** partially spawning stage, and **f** spent stage. *SG* spermatogonia, *SC* spermatocytes, *SZ* spermatozoa, *RSZ* relict spermatozoa, *LM* lumen. Scale bar: 100 μm

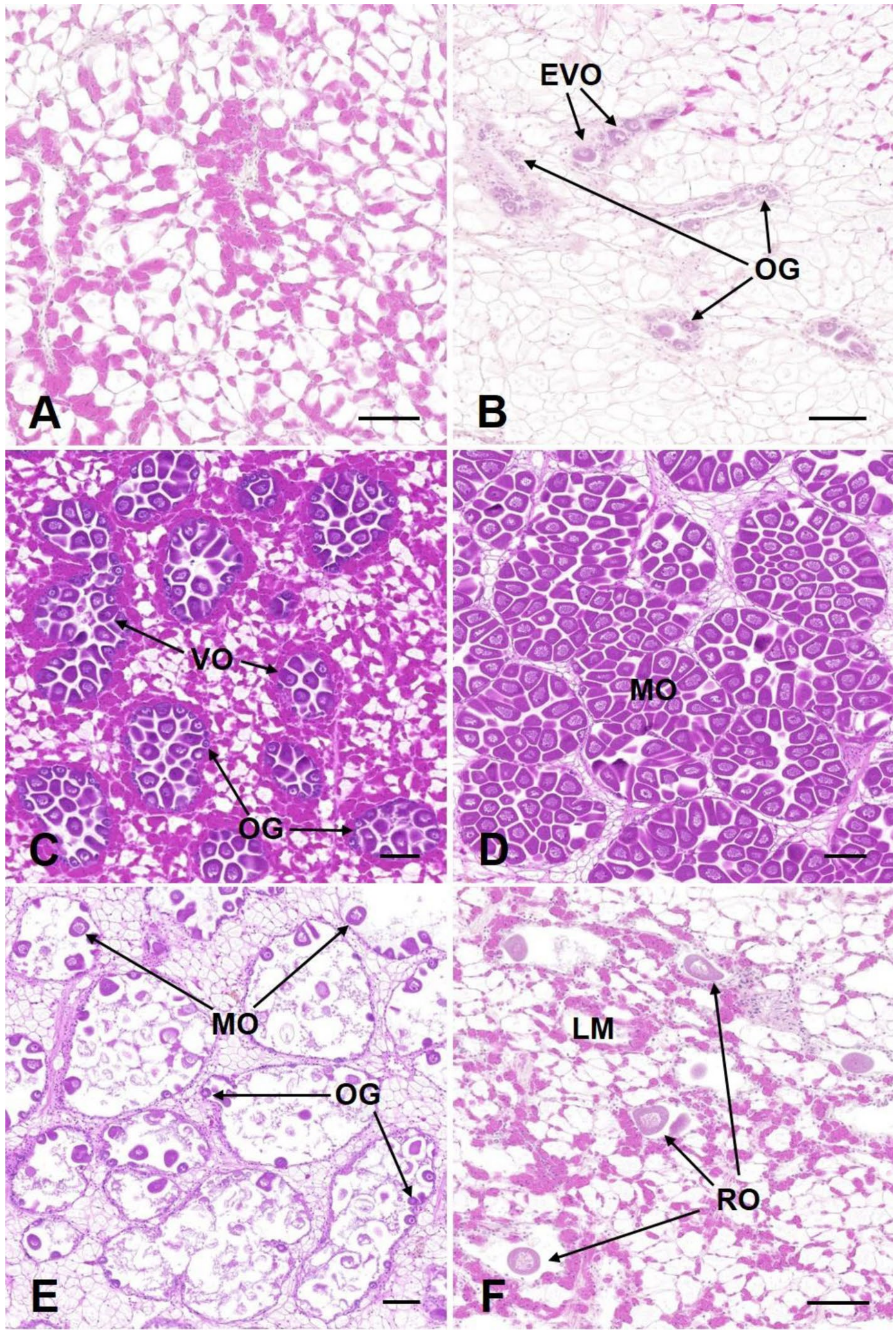

Fig. 6 Photomicrographs of different gonad development stages of female mussel. **a** Resting stage, **b** early developing stage, **c** late-developing stage, **d** ripe stage, **e** partially spawning stage, and **f** spent stage. *OG* oogonia, *EVO* early vitellogenic oocytes, *VO* vitellogenic oocytes, *MO* mature oocyte, *RO* relict oocyte, *LM* lumen. Scale bar: 100 μm

Individuals in the early developing stage (i.e., gonial mitosis) exhibit small spermatogonia (Fig. 5b) and oogonia (Fig. 6b) on the follicle walls. The size of the oogonia, measured from the digitized microscopic images, ranges from 20 to 50 μm.

During the late developing stage, the spermatogonia are spread around the extended inner follicle wall, and spermatocytes are concentrated in the center of the testis (Fig. 5c). In the ovaries, a few individual oogonia are found along the follicle wall, whereas more mature and larger vitellogenic oocytes are observed in the center of the ovaries. In this stage, several vitellogenic oocytes can be observed in the follicle wall (Fig. 6c).

In the ripe stage, the mature spermatozoa occur at high density in the testis, and the spermatocytes surround the spermatozoa at the edge of the follicles (Fig. 5d). In this stage, the ovaries are densely packed with the size of the mature oocytes being over 50 μm in diameter (Fig. 6d).

As spawning commenced, the sizes of the testes and ovaries become reduced due to the release of spermatozoa and oocytes (Figs. 5e, 6e). In the ovaries, the residual mature oocytes can be seen in the follicles with numerous oogonia attached to the follicle wall (Fig. 6e).

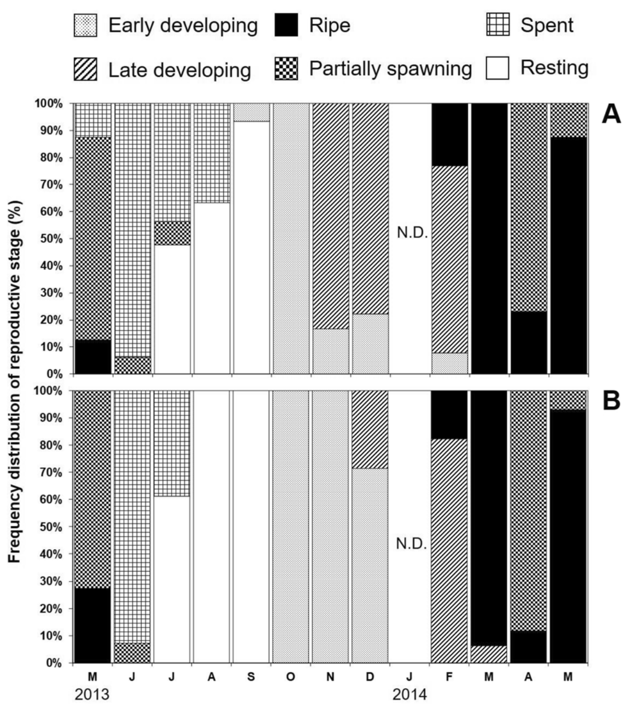

Fig. 7 Frequency distribution of different reproductive stages of *Mytilus unguiculatus* (*coruscus*) gonads observed monthly during the study period. **a** Male mussel and **b** female mussel. *N.D.* no data

During the spent stage, the size of the testis and ovary are greatly reduced and characterized by empty lumen. In the ovaries, a small number of residual eggs can be identified in the reduced follicles (Figs. 5f, 6f).

3.2 Annual Reproductive Cycle

Figure 7 plots the frequency distribution of the different reproductive stages of *M. unguiculatus* (*coruscus*) analyzed in this study. Individuals in the early developing stage were observed as early as September (6.7%), while all those collected in October (100%) were in this stage. In November when the SST was recorded as 18.5 °C, the species was in the late-developing stage (83.3%) and the proportion of individuals in this stage was reduced in December (28.6%). In February, the males (23.1%) and females (17.6%) exhibited mature gametes in the follicles, and the proportion increased in March. The histology suggested that both males and females spawned in April and May when the SST ranged from 14 to 15 °C. Histology also indicated that this species has a reproductively resting period from July to September, when the SST ranged from 22 to 24 °C.

3.3 Oocyte Growth

The OD ranged from 5.7 to 100 μm annually, and the monthly mean OD varied from 17.5 (October) to 55.5 μm (March, Fig. 8). During October and November, when most of the females were in the early developing stage, the mean OD increased from 17.5 to 21.4 μm. In February, as a certain

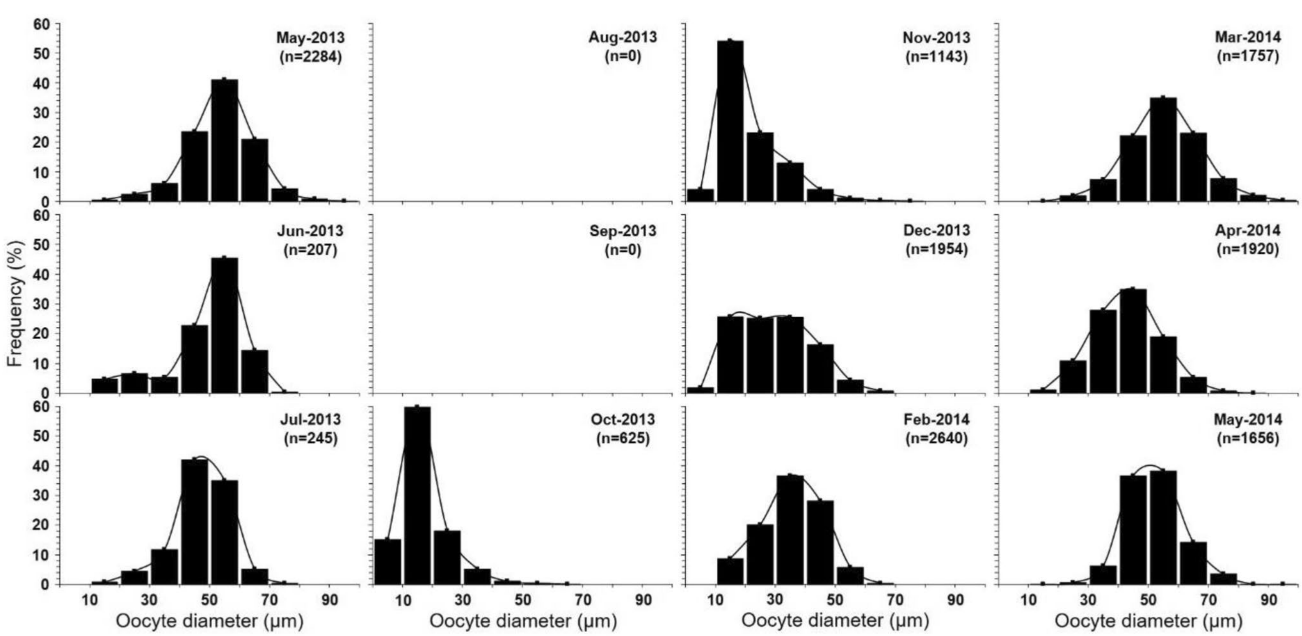

Fig. 8 Frequency distribution of annual oocyte diameter of female *Mytilus unguiculatus* (*coruscus*)

portion of females exhibited mature eggs in the follicles, the mean OD reached 35.6 µm. During the ripe stage observed from March to May, the monthly mean OD remained stable, showing a range from 52.0 (May) to 55.5 (March).

3.4 Condition Index

The monthly mean CI of *M. unguiculatus* (*coruscus*) at Ulleungdo ranged from 0.065 to 0.106 (Fig. 9). In May 2013, the CI was 0.087 and thereafter began to decline, reaching the lowest level of 0.065 in July. The CI levels increased gradually from July 2013 to March 2014 (0.084), then decreased before demonstrating a significant decrease in April (0.065), and thereafter eventually increased to the highest recorded value in May (0.106). This variation in the CI was closely related to changes in gonadal development and spawning patterns described below.

4 Discussion

The CI is a useful index to monitor the annual gametogenesis of marine bivalves since a substantial number of gametes are released during spawning. Several studies have reported that the CI of marine bivalves reaches its annual highest when they are ripe and ready to spawn, whereas the lowest can be found during post-spawning period (i.e., spent or resting stage, Kim et al. 2005; Moura et al. 2008; Yang et al. 2016). According to Seed and Suchanek (1992), the blue mussel *M. edulis* also exhibits a noticeable decline in CI during spawning. According to Lee et al. (2007), CI of *M. unguiculatus* (*coruscus*) occurring on the west coast of Korea ranged from 0.12 and 0.37 annually, and the CI showed its annual highest prior to spawning in February. Similarly, Wi et al. (2003) reported that, on the south coast of Korea, the CI of *M. unguiculatus* (*coruscus*) exhibited its annual peak in January when the mussels were ripe and ready to spawn. According to Mladineo et al. (2007), seasonal variation in the CI of the horse-bearded mussel *Modiolus barbatus,* in Mali Ston Bay in Croatia, is closely linked to the annual reproductive cycle, as an increase in CI coincided with the gonad development in spring. In this study, *M. unguiculatus* (*coruscus*) at Ulleungdo exhibited a strong temporal variation in CI. Histology indicated that *M. unguiculatus* (*coruscus*) at the study site completed spawning in June and most of the mussels were in the resting phase during July and August. Like other marine bivalves, *M. unguiculatus* (*coruscus*) might discharge a substantial amount of the gametes during spawning, and the low CI recorded during post-spawning period is possibly due to the weight loss before and after the spawning.

Seasonal variation in environmental factors such as water temperature, salinity, and food availability are known to affect the growth, gametogenesis, and biochemical composition of marine bivalves (Giese 1959; Okumus and Stirling 1998; Saxby 2002). In particular, SST is one of the most crucial factors that govern an annual gametogenesis of marine bivalves (Mann 1979a, b; Dohmen 1985). According to Seed and Suchanek (1992), the onset and duration of reproductive cycles in *Mytilus* spp. vary latitudinally, and mussels in the warmer waters of the Northern Hemisphere reproduce earlier than those in the north. In this study, histology indicated that *M. unguiculatus* (*coruscus*) at Ullengdo

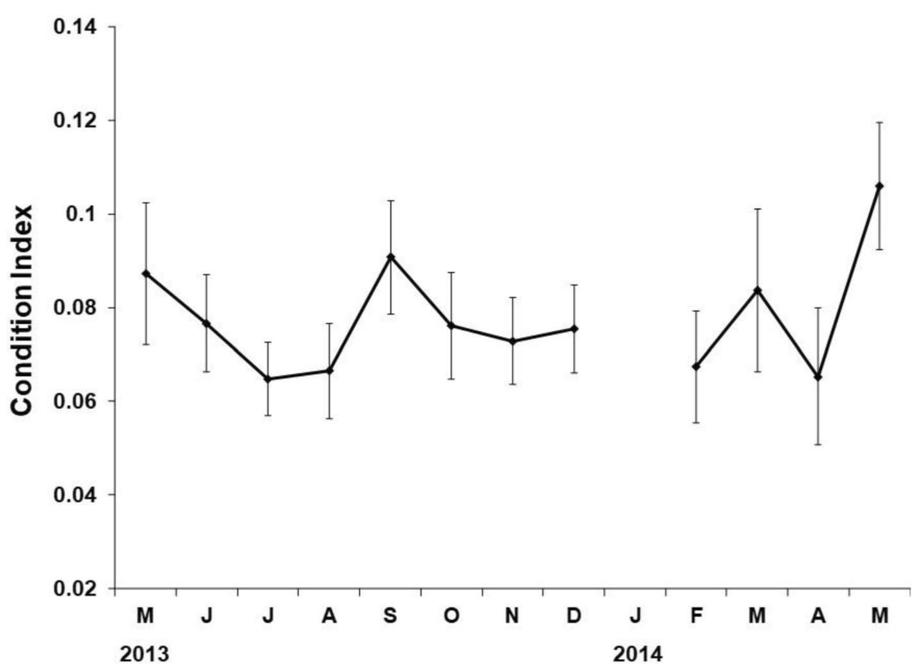

Fig. 9 Monthly mean value on condition index of *Mytilus unguiculatus* (*coruscus*) calculated from May 2013 to May 2014

(37° 32′ N) spawns during April and July with a peak in April or May, when the SST ranges from 13 to 22 °C. Lee et al. (2007) also examined the annual reproductive cycle of *M. unguiculatus* (*coruscus*) occurring on the west coast (35° 37′ N) using histology, where the SST varied from 4 to 28 °C seasonally. According to Lee et al. (2007), this species on the west coast spawns during February and April, when the SST ranges from 4 to 12 °C, which is somewhat earlier than the spawning period of *M. unguiculatus* (*coruscus*) in Ulleungdo Island. Wi et al. (2003) also investigated the annual reproductive cycle of *M. unguiculatus* (*coruscus*) inhabiting a subtidal rocky bottom on the south coast of Korea (34° 38′ N), where the SST ranged annually from 7 (January) to 25 °C (August). Wi et al. (2003) reported that *M. unguiculatus* (*coruscus*) at an offshore island spawns during February and April, and they initiate gonial mitosis in November and December. According to Wi et al. (2003), *M. unguiculatus* (*coruscus*) is considered a winter spawner as its spawning mostly occurs when the SST remains comparatively low.

The spawning period of *M. unguiculatus* (*coruscus*) Ulleungdo, as revealed in this study, lies between April and May, when the SST ranged approximately from 13 to 15 °C. Compared to the period reported from the west and the south coasts, the spawning period of *M. unguiculatus* (*coruscus*) at Ulleungdo is somewhat later, or the Ulleungdo population spawns during the warmer water period. Such a spatial variation in an annual mussel reproductive cycle was reported for the blue mussel, *M. edulis,* in England, as the population on the west coast spawns earlier than the east coast (Seed 1975). The blue mussels in Fairfield (41° 08′ N, Brousseau 1983) also spawn approximately a month earlier than the population in the northern Magdalen Island (47° 34′ N, Myrand et al. 2000). Along with the SST, marine pollution often influences maturation and subsequent spawning of marine mussels. Rouabhi et al. (2019) investigated the annual reproductive cycle of *M. galloprovincialis* in Algeria (35° 42′ N). In the port of Oran, Algeria, *M. galloprovincialis* showed two distinct spawning peaks, in November and February, and another one in March and June. In their study, the mussels showed a certain level of gonad degradation and atresia in the follicles. Such abnormal gonad development was believed to be associated with the coastal pollution in the port.

In 2014, *M. unguiculatus* (*coruscus*) Ulleungdo spawned over two months in April and May, which is believed to be linked to sufficient food supply in the water column. According to Seed and Suchanek (1992), a prolonged period of spawning in marine bivalves is often associated with favorable food conditions in the environment. In this study, we estimated the monthly chlorophyll a level in the study area using the GIOVANNI database, which ranged from 0.16 to 3.16 mg/m^3. According to the database, the chlorophyll a level in the study site in April 2014 was approximately three times higher than the level in April 2013, suggesting that the food availability for *M. unguiculatus* (*coruscus*) was much more favorable in April 2014. Several studies have reported that the phytoplankton biomass of Ulleungdo is high in the spring. Lee et al. (2020) measured the primary production in the water column around Ulleungdo in the spring. They reported that the phytoplankton abundance at coastal Ulleungdo is significantly higher than offshore, possibly due to coastal upwelling in the spring (Hyun et al. 2009; Yoo and Park 2009). Shin et al. (2018) investigated the coastal upwelling and the net primary production (NPP) at Ulleungdo from 2002 to 2012 and reported that the NPP shows its annual peak in April. Accordingly, we believe that the late spring phytoplankton bloom in the study area strongly supports mussel gonad maturation and subsequent spawning at coastal Ulleungdo.

In summary, we first investigated the annual reproductive cycle of the mussel, *M. unguiculatus* (*coruscus*), occurring on a shallow rocky bottom at Ulleungdo, off the east coast of Korea. Histology indicated that this species at Ulleungdo spawned in April and May when the SST varies from 13 to 15 °C. Compared to the spawning period reported from the south and west coast of Korea, the spawning period of *M. unguiculatus* (*coruscus*) at Ulleungdo is 2–3 months later. Such spatial differences in spawning patterns are believed to be attributable to differences in environmental factors, such as water temperature and available food. We also believe that the findings of the present study will contribute toward ensuring the successful recruitment of *M. unguiculatus* (*coruscus*) and thereby promote a subsequent increase in the wild mussel population at Ulleungdo.

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