



Report on the Annual Gametogenesis and Tissue Biochemical Composition in the Gray mussel, *Crenomytilus grayanus* (Dunker 1853) in the Subtidal Rocky Bottom on the East Coast of Korea

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Abstract

The Gray mussel *Crenomytilus grayanus* occurs in high density in the shallow rocky subtidal zone on the east coast of Korea, where the mussel dominates the shallow subtidal benthic community. In this study, we first examined the annual gametogenesis and temporal changes in the tissue composition, which provides crucial information to the management of the mussel on the east coast. Based on histological analysis, oogenesis and spermatogenesis commenced in September, as the small oogonia ($16.67 \pm 4.87 \mu\text{m}$ in diameter) and spermatogonia developed on the follicle walls, respectively. In March, the mature oocytes ($46.55 \pm 9.91 \mu\text{m}$ in diameter) and spermatozoa dominated the follicle. During May and June, most of the males and females spawned when the surface seawater temperature (SST) increased from 15.5 to 22.3 °C. The total carbohydrate level in the tissue increased dramatically from April to May, which coincided with the chlorophyll-*a* maximum occurring in April. Condition index, a ratio of tissue weight to shell weight, also increased from February to May and then declined in June, suggesting that most mussels released the gametes through spawning during these months. Our data suggest that *C. grayanus* is a spring spawner, and the onset of gametogenesis and subsequent spawning is closely linked to the seasonal changes in the water temperature and food availability in the water column.

Keywords *Crenomytilus grayanus* · East Coast of Korea · Gametogenesis · Gray mussel · Spring spawner · Total Carbohydrate

1 Introduction

An annual reproductive cycle of marine bivalves in the temperate ecosystems includes a series of gametogenesis which is often categorized into several distinguished reproductive phases, including resting, the onset of the gonial mitosis, maturation of the oocytes and spermatocytes, and release of the gametes from spawning males and females (Lowe et al. 1982; Thompson et al. 1996; Racotta et al. 2003; Drummond et al. 2006). Such gonadal changes are regulated by biotic and abiotic parameters, including photoperiod, available food in the water column, water temperature, and salinity (Bayne 1976; Hofmann et al. 1992; Urrutia et al. 1999; Kang et al. 2009). In a temperate coastal environment, algal blooms in spring or fall supply a substantial quantity of foods to the suspension-feeding bivalves, and the assimilated foods are stored and mobilized during the gametogenesis (Bayne 1976; Beninger and Lucas 1984; Gabbott and Peek

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1991; Thorarinsdottir and Gunnarsson 2003). The energy required for gametogenesis and subsequent spawning is supplied from the somatic tissues such as a mantle, adductor muscles, and siphons, which are stored previously or directly from recently absorbed and assimilated food (Gabbott 1983; Ahn et al. 2003; Uddin et al. 2007; Lee et al. 2015; Hong et al. 2020). Understanding the reproductive cycle of marine mussels is crucial since it is one of the key species in a shallow subtidal benthic ecosystem.

Similar to oysters, mussels are vital shellfish resources in many countries, as mussels are captured or cultured at an industrial scale (Gosling 2003). The global mussel production has increased gradually over the past decade, from 1.77 million metric tons (MT) in 2006 to 68.21 million MT in 2016 (FAO 2016). In Korean waters, the introduced Mediterranean mussel *Mytilus galloprovincialis* is farmed exclusively in small bays on the south coast using suspended long-lines. In marine bivalve aquaculture, the planktonic larvae in the water are often induced to settle on artificial substrata, and the settled larvae are served as the seeds. Accordingly, understanding the annual gametogenesis is crucial to forecast the spawning period and subsequent spat harvest from the environment (Ventilla 1984; Arakawa 1990; Ngo et al. 2006; Uddin et al. 2007, 2012; Mondol et al. 2016). Unlike the south coast, the rocky shallow east coast of Korea is dominated by the Gray mussel *Crenomytilus grayanus*, which occurs at a high density on a shallow subtidal rocky substrate (Galysheva 2008; Lutaenko and Noseworthy 2019; Selin and Dulenina 2012). The Gray mussel has a high potential as an aquaculture species on the east coast due to

the larger size and high nutritional values. Studies on the reproduction of the Gray mussel are yet to be available on the east coast, while it is crucial for successful aquaculture development.

Endemic to the east coast of Korea, *Crenomytilus grayanus* is one of the key species in the shallow subtidal hard bottom of the benthic ecosystem in terms of biomass and abundance. Currently, crucial information about the growth rate and the annual reproductive cycle of the Gray mussel is yet to be available. In this study, we first report seasonal changes in the tissue biochemical composition and the annual reproductive cycle of the Gray mussel occurring on the east coast of Korea.

2 Materials and Methods

2.1 Sampling Effort

Using SCUBA, we collected the Gray mussels monthly from a depth of 2–3 m rocky bottom on the east coast of Korea (37° 45' N, 128° 59' E) from September 2012 to August 2013 (Fig. 1). Thirty adult mussels with shell length (SL) ranging from 88 to 107 mm were collected monthly (Table 1). The sea surface temperature (SST), chlorophyll-a, and salinity data were referenced from the Giovanni online data system (NASA GES DISC <https://giovanni.gsfc.nasa.gov/giovanni>). Salinity in the study area ranged from 32.3 to 33.7 g/L annually. The SST in the study area ranged annually from 9.5 in

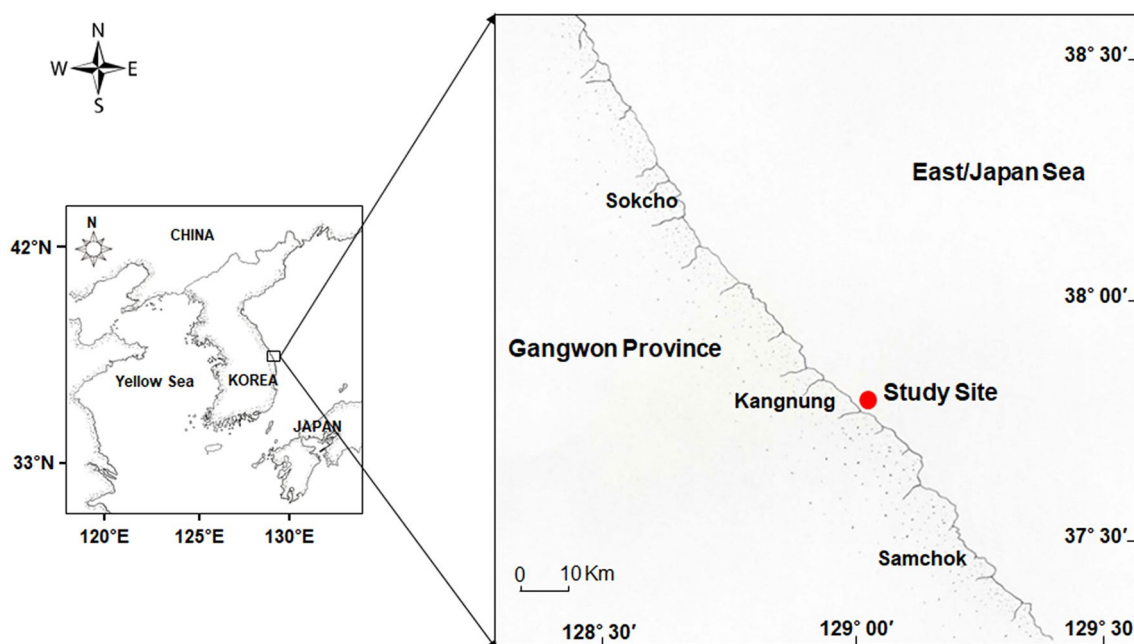


Fig. 1 Location of study area on the east coast of Korea

Table 1 Summary of the sampling effort

Month	<i>N</i>	SL (mm)	Sex ratio
		Mean \pm SD	F: M: I
2012			
S	30	107.0 \pm 8.5	1.3: 1: 2.7
O	30	99.2 \pm 7.9	10: 19: 1
N	30	99.8 \pm 8.1	1.5: 2.5: 1
D	30	91.3 \pm 5.2	1: 1.1: 0
2013			
J	30	100.1 \pm 5.7	1.1: 1: 0
F	30	95.6 \pm 8.6	1: 1: 0
M	30	96.2 \pm 7.2	1: 1.7: 0
A	30	88.3 \pm 6.2	1: 1.3: 0
M	30	95.9 \pm 9.1	1: 2: 0
J	30	100.8 \pm 4.6	1: 1.7: 0
J	30	93.7 \pm 6.2	1: 0.9: 1.1
A	30	89.4 \pm 10.9	1: 1.5: 12.5

The values represent the monthly mean and standard deviation

N numbers of mussels used in analysis, *SL* standard length in mm, *M* male mussel, *F* female mussel, *I* indifferent mussel

January to 29.5 °C in August, while the chlorophyll-*a* level varied from 0.35 μ g/l in June to 1.8 μ g/l in April (Fig. 2).

2.2 Biometry and Histology

After recording the SL, the soft tissue was removed from the shell and weighed by mg using an electronic balance. For histology, a 2–3 mm thick section was removed dorso-ventrally from the middle of the body which contained mantle tissue, gonad, gill, and digestive track then fixed in Davidson's fixative. The tissue sections were dehydrated using an ascending series of alcohol and embedded in paraffin. The paraffin blocks were sliced to a thickness of 6 μ m, stained with Harris's hematoxylin, and counterstained with eosin Y. Microscopic images of the gonad in different reproductive stages were digitized using a digital camera connected to a microscope. The maturity of the gonads was grouped into six stages according to Drumond et al. (2006) and Mondol et al. (2016), (1) resting, (2) early developing, (3) late-developing, (4) ripe, (5) partially spawning, and (6) spent. The oocyte size (i.e., the diameter) was measured from the digitized microscopic images of the gonads using ImageJ software (National Institute of Health, USA). The remaining tissues were freeze-dried and weighed by mg using an electronic balance. Condition index (CI) was determined as a ratio of the dry tissue weight to the dry shell weight.

$$CI = (\text{dry tissue weight}/\text{shell dry weight}) \times 100.$$

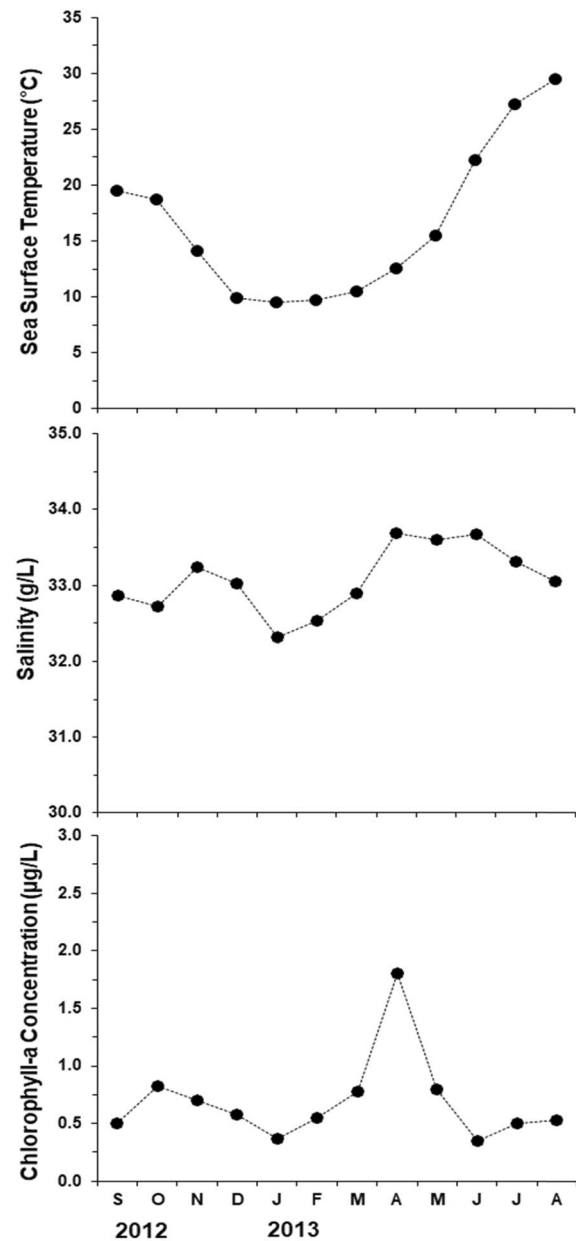


Fig. 2 Seasonal variation in seawater temperature, salinity and chlorophyll-*a* concentration in the study site

2.3 Total Carbohydrate and Total Protein Analysis of Tissue

The freeze-dried Gray mussel tissue stored at -70 °C was homogenized to determine the total carbohydrate and total protein levels. The total protein content in the tissue was estimated spectrometrically according to Lowry et al. (1951) using bovine serum albumin as a standard. Total carbohydrate in the tissue was assessed using the phenol-sulfuric method (Dubois et al. 1956), with dextrose anhydrous as the standard material.

3 Results and Discussions

3.1 Annual Gametogenic Cycle

Figure 3 shows the monthly changes in the gametogenesis observed in the female and male Gray mussels. When the SST reached its annual highest during August and September, the Gray mussels were in the reproductively resting stage, exhibiting no gametes in the mantle. Based on the histological analysis, the oogenesis and spermatogenesis commenced in September as the SST was 19.5 °C; 34.8% and 28.6% of the females and the males were engaged in the stages. The proportion of females and males in the late-developing stage increased steadily from October to February, from 9.1 to 100% and 45–85.7%, respectively. In histology, mature oocytes could be observed in the follicles in March and April (63.6%), whereas mature spermatozoa were observed a month earlier in February. In May, 41.2% of the males and 54.5% of the females were spawning as the SST elevated to 15.5 °C. In June, the proportion of the Gray mussels in spawning reduced to 9.1% and 10.5% in females and males, respectively, suggesting that most of the Gray mussels spawned in May. In June, most of the mussels were in the spent stage, with the females at 90.9% and the males at 89.5%.

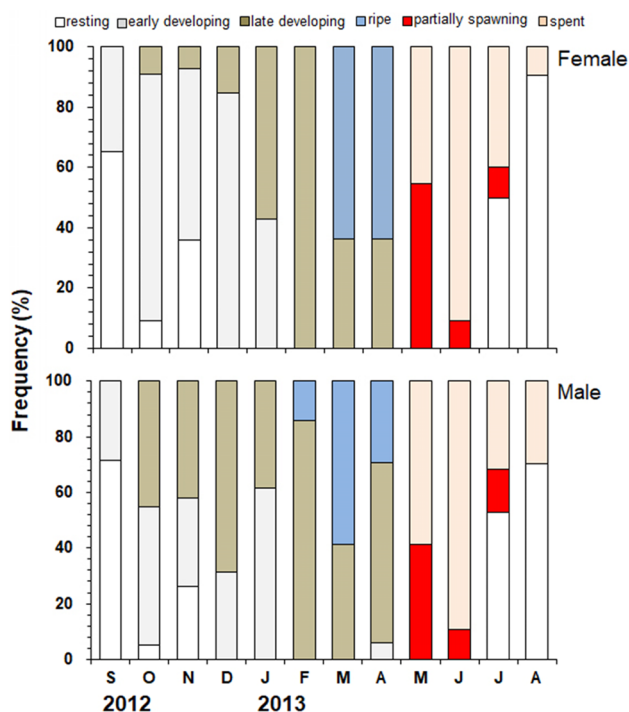


Fig. 3 Frequency distributions of the reproductive stages of the female and male mussels

From the digitized gonad microscopic images, the oocyte sizes were assessed monthly (Fig. 4). Oocyte diameter ranged from 10.50 to 68.84 μm, with the monthly mean size ranging from 16.67 ± 4.87 μm in September to 50.39 ± 8.82 μm in July. Small oocytes size ranging, 10–30 μm in diameter were dominant in the early developing stage from September to October. As the gametogenesis progressed, the oocyte sizes increased to 25–45 μm in diameter. When the Gray mussels are mature and ready to spawn during March and April, the oocyte diameter reached 50–55 μm.

Endemic to the coastal East/Japan Sea, *C. grayanus* has a wide distribution from the Sea of Okhotsk, Kurils, the Peter the Great Bay, and the coastal East/Japan Sea (Min et al. 2004; Galysheva 2008; Belcheva et al. 2011; Selin and Dulenina 2012; Lutaenko and Noseworthy 2019). Despite their popularity, no studies have investigated the annual gametogenesis of *C. grayanus* in the endemic area. Accordingly, this study first reports on the annual reproductive cycle. Histology applied in this study first revealed the annual gametogenesis of the Gray mussel occurring on the shallow subtidal rocky bottom on the east coast. The Gray mussels have an extended period of gonial mitosis (i.e., early developing) from September (19.5 °C) to January (9.5 °C) with a comparatively short period of spawning in May and June when the SST elevated from 15.5 to 22.3 °C. The reproductive pattern of *C. grayanus* obtained in this study can provide crucial information about the appropriate time for natural spat collection during the post-spawning period and the sustainable fishery of the mussels in the study area. A limited number of studies have reported the annual gametogenesis of the mussels occurring on the coastal rocky intertidal and subtidal of the east coast of Korea, where several mussels species, including *C. grayanus*, *M. galloprovincialis*, *M. trossulus*, and *M. coruscus* have been reported (Min et al. 2004; Lutaenko and Noseworthy 2019). Yang et al. (2021) first reported the annual gametogenesis of the mussel *M. coruscus* occurring in the shallow subtidal in Ulleungdo Island off the east coast, which is somewhat comparable to the annual reproductive cycle of *C. grayanus*. According to Yang et al. (2021), *M. coruscus* occurring on a shallow subtidal zone of Ulleungdo Island off the east coast commence their gametogenesis in September when the SST 24 °C and both the male and female spawn in April and May.

Table 2 summarizes the annual gametogenesis pattern of different species of mussels reported from the temperate region, including the Gray mussel investigated in the present study. It is noticeable that *M. coruscus* distributes on the south and east coast of Korea, as well as in the coastal East China Sea commence the oogenesis in late summer to fall and spawn and they spawn in spring as the SST ranges 10–13 °C (Wi et al. 2003; Lee et al. 2007; Zhu et al. 2018; Yang et al. 2021). Sprung (1983) also reported spawning of the blue mussel *M. edulis* in the North Sea in April and

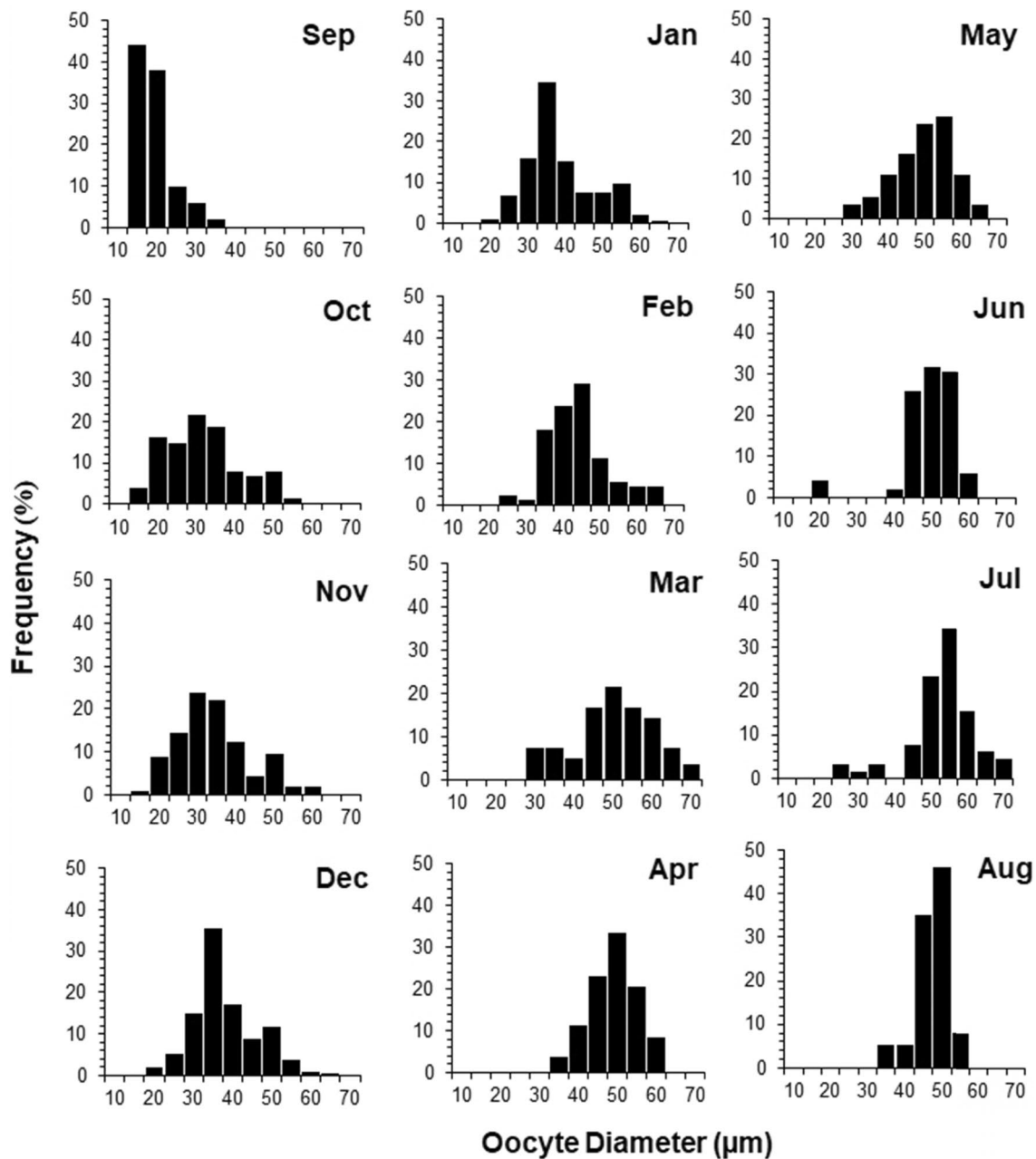


Fig. 4 Frequency distribution of oocyte diameter size classes determined monthly

June when the SST ranged from 6 to 14 °C. Accordingly, the annual gametogenic pattern of *C. grayanus* occurring on the east coast of Korea is comparable to *M. coruscus* and *M. edulis* occurring in the North Sea, and they are considered as spring spawners. Contrary to the blue mussel, the Mediterranean mussel *M. galloprovincialis* in the Bay of Biscay Spain commenced the oogenesis in April, and they spawned in October as the SST reached 18 °C. Similarly, as an invasive species in the Tokyo Bay, the Mediterranean mussels spawn in October, and the mussels continued their spawning until March (Okaniwa et al. 2010).

Marine bivalve aquaculture utilizes wild spats harvested during post-spawning as the seeds in many cases (Arakawa 1990; Semenikhina et al. 2008). Our study indicated that most of the Gray mussels release their eggs and sperms into the water column during May and June, while the larval period and subsequent settling time remain unknown in this study. Yaroslavtseva and Sergeeva (2009) investigated the larval period of the Gray mussel at a laboratory condition and reported that the larvae spend approximately four to five weeks in planktonic stages as the temperature remains 22 °C. Accordingly, we believe that *C. grayanus* larvae in

Table 2 Summary of annual reproductive cycle of different species of the mussel reported from temperate region

Species	Oogenesis		Spawning		Oocyte size	Location	References
	Month	SST (°C)	Month	SST (°C)			
<i>M. coruscus</i>	Nov	~ 17	Feb–Apr	< 10	60–80	Gyeokpo, Korea (35° 37' N, 126° 27' E)	Lee et al. (2007)
<i>M. coruscus</i>	Nov	~ 14	Feb–Mar	~ 11–12	60–80	Hansan Bay, Korea (34° 38' N, 128° 33' E)	Wi et al. (2003)
<i>M. coruscus</i>	Sep	29.1	Mar	12	67	Nanji Island, China (27° 27' N, 121° 05' E)	Zhu et al. (2018)
<i>M. coruscus</i>	Sep	24	Apr–May	14–15	NA	Ulleung Island, Korea (37° 29' N, 130° 48' E)	Yang et al. (2021)
<i>M. edulis</i>	Nov	~ 9	Apr–Jun	6–14	78	Helgoland, Germany (54° 10' N, 7° 53' E)	Sprung (1983)
<i>M. galloprovincialis</i>	Nov	21	Oct–Mar	17–19	NA	Tokyo Bay, Japan (35° 19' N, 139° 37' W)	Okaniwa et al. (2010)
<i>M. galloprovincialis</i>	Apr	~ 16	Oct	~ 18	NA	Bay of Biscay, Spain (43° 28' N, 3° 45' W)	Azpeitia et al. (2017)
<i>C. grayanus</i>	Sep	19.5	May–Jul	15.5	47	Gangneung, Korea (37° 45' N, 128° 59' E)	Present study

the coastal East/Japan Sea may settle mostly in late July and early August, although the settling time may vary year to year variation in the water temperature and food availability.

3.2 Total Carbohydrate and Total Protein

The total carbohydrate content in the Gray mussel ranged annually from 86 (January) to 392 mg/g (July) (Fig. 5). A noticeable decline in the total carbohydrates was observed from November (276 mg/g) to January (86 mg/g), coinciding with a low level of chlorophyll-*a* during fall and early spring in the water column. The carbohydrate level increased considerably from April (74 mg/g) to May (202 mg/g), coinciding with the dramatic incline of chlorophyll-*a* during this period. The total carbohydrate level in the tissue remained higher in summer from June (169 mg/g) to August

(173 mg/g), although the Gray mussels were in the post-spawning phase.

Contrary to the total carbohydrate, the total protein level in the dry tissue varied within a small range. The monthly mean total protein was highest in September (290 mg/g), while it was lowest in April (124 mg/g) (Fig. 6).

Marine bivalves store carbohydrates in their tissues, and the stored energy is used in growth, gametogenesis, and metabolic maintenance (Beninger and Lucas 1984). The monthly mean carbohydrate levels in the Gray mussel ranged from 86 (January) to 392 mg/g dry tissue in July, and a dramatic increase in the total carbohydrate was observed from April (114) to May (322 mg/g dry tissue). Such a dramatic increase in the total carbohydrate can be explained, at least in part, by the high level of food availability in the water column in April; the chlorophyll-*a* level showed its annual maximum this month, possibly due to a local phytoplankton

Fig. 5 Seasonal changes in the total carbohydrate (mg/g dry tissue) in *Crenomytilus grayanus* over the study period. The values represent mean ± standard error (SE), and the vertical bar in each value represents the standard error

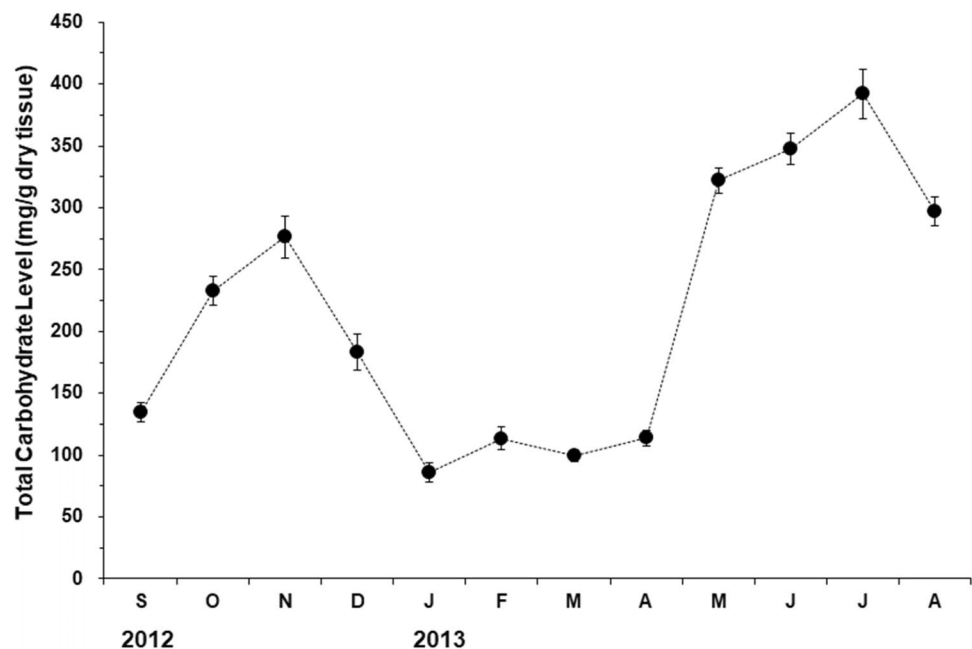


Fig. 6 Monthly mean total protein level (mg/g dry tissue) in *Crenomytilus grayanus* over the study period. The values represent mean \pm standard error (SE), and the vertical bar in each value represents the standard error

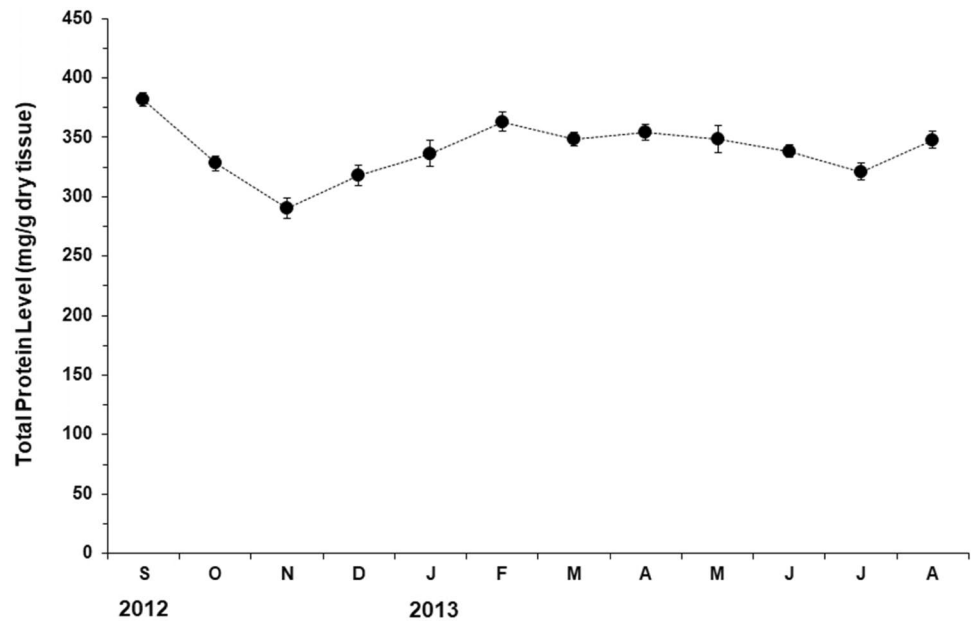


Table 3 Comparison of the average total carbohydrate of different *Mytilus* with *C. grayanus*

Species	Total carbohydrate (mg/g DW)	References
<i>M. galloprovincialis</i>	115	Leontowicz et al. (2008)
<i>M. galloprovincialis</i>	178	Kopp et al. (2005)
<i>M. edulis</i>	298	Kopp et al. (2005)
<i>M. edulis</i>	131	Chi et al. (2012)
<i>C. grayanus</i>	217	Present study

TCH total carbohydrate content

bloom during this period. Gabbott and Whittle (1986) also reported a rapid increase in glycogen content in *M. edulis* in Wales, U.K., which coincided with the increased food level in the environment in summer. We list the average carbohydrate content of different mussel species with *C. grayanus* in Table 3. As the table indicates, the Gray mussel contains a comparatively higher amount of carbohydrates, suggesting that these mussels have high marketability and can be a potential aquaculture species.

The total carbohydrate content of the Gray mussel declined dramatically from November to January, which coincided with the active growth of the oocytes and spermatocytes, as the histology revealed. During this period, the oocyte size also increased, as well as the reproductive stage becomes progressed from early developing to late-developing. Contrary to the total carbohydrate content, the CI remained slightly varied while the total protein level increased during this period. Accordingly, we believe that the Gray mussel mobilized the stored carbohydrate and

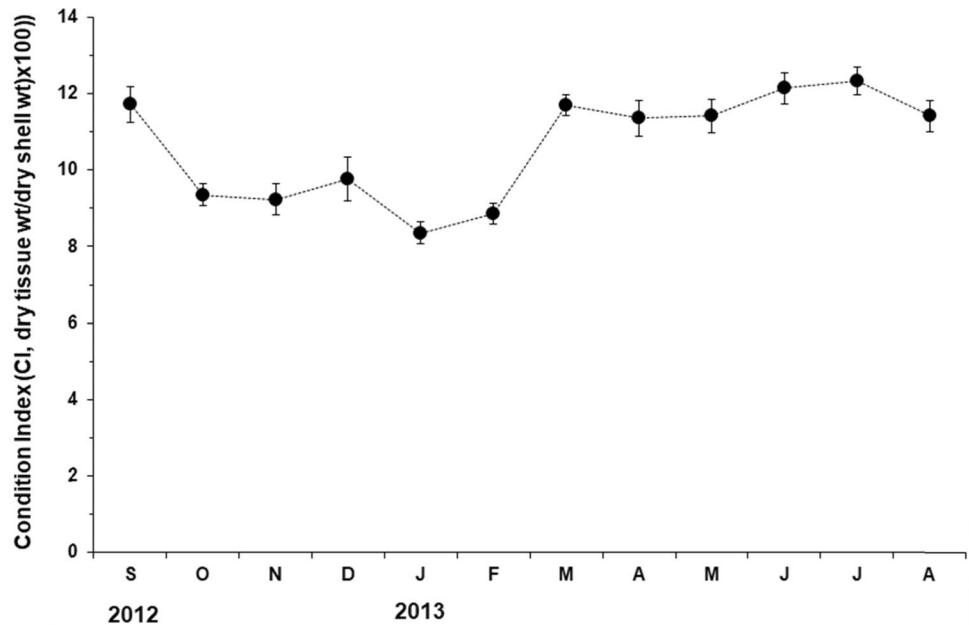
converted it into the yolk protein in the case of females. The total carbohydrate level increased dramatically from April to July, despite spawning in May and June. The Gray mussels seem to spend not much energy on the spawning activities, and they store the assimilated energy during the spring phytoplankton bloom as carbohydrates.

Figure 7 shows the monthly variation in CI of the mussels, ranging from 8.4 (January) to 12.3 (July) during the study. CI declined from 11.7 (September) to 9.4 (October) during late fall, and CI remained low during the winter. It was noticeable that CI increased markedly from February (8.4) to March (11.7), then the monthly mean CI remained stable until August (9.4).

CI is used widely in monitoring physiological and nutritional conditions of marine bivalves, and most of the studies define CI as a ratio of dry or wet tissue weight to the shell weight (Lucas and Beninger 1985; Davenport and Chen 1987; Orban et al. 2002; Kim et al. 2017; Lee et al. 2020). In the present study, we defined the CI of the Gray mussel as a ratio of the dry tissue to the shell weight, which showed a small range of variation (8.4–12.3) in an annual reproductive cycle. The lowest CI observed in January coincided with the annual minima of the chlorophyll-*a*, suggesting that the mussels in the study site were in poor nutritional condition due to low food availability in the environment. CI increased markedly from February to March and April, which coincided with the rapid increase in chlorophyll-*a* concentration in the water column. Accordingly, it is believed that the spring phytoplankton bloom plays a crucial role in the fattening of the mussel on the east coast of Korea.

CI of mussels often declines significantly after spawning due to the release of the gametes. Mladineo et al. (2007)

Fig. 7 Monthly mean condition index [(dry tissue wt/dry shell wt) × 100] in *Crenomytilus grayanus* over the study period. The values represent mean ± standard error (SE), and the vertical bar in each value represents the standard error



examined monthly variation in the CI of the horse-beared mussel *Modiolus barbatus* in the Adriatic Sea, observed a subsequent decline in CI during the post-spawning period in late summer. Similarly, *M. galloprovincialis* in the Black Sea demonstrated an evident seasonal decline in CI after spawning due to the release of gamete during the spawning (Celik et al. 2012). In this study, the CI of the Gray mussel did not change much after spawning in June and July compared to April when the mussels were ready to spawn. As a result, we postulate that the Gray mussels on the east coast of Korea produce a comparatively small quantity of gamete in an annual reproductively cycle, resulting in a slight variation in CI before and after the spawning.

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