Thesis for the Degree of Master of Science

Growth and reproduction of the Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan 1844) in the coastal area of Tongyeong, Korea

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Advisor: Prof. Chul-Woong Oh

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Abstract

Growth and reproduction of the Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan 1844), were investigated based on samples from July 2014 to August 2015 in the Tongyeong, Korea. A total of 2,621 samples was collected (1,380 females and 1,241 males) during the study period. The number of female was observed more frequently than that of male ($P < 0.001$). The mean body length (BL) was 128.54 ± 0.38 mm in females and 126.87 ± 0.42 mm in males, respectively. The mean body weight (BW) was 31.23 ± 0.28 g in females and 31.06 ± 0.32 g in males, respectively. The females were larger than males in BL ($P < 0.01$). There was a significant difference in the length-frequency distributions between females and males ($P < 0.05$). A linear regression analysis using natural log transformed data of females was $\ln BW = 2.8498(\pm 0.0235)\ln BL - 10.4339$ and $\ln BW = 2.8727(\pm 0.0272)\ln BL - 10.5153$ of males, respectively. We found no significant difference in the slopes of the regression between ln BL and ln BW for the both sexes ($P > 0.05$), but a significant difference in the intercepts of the regression for the both sexes ($P < 0.01$). The Von Bertalanffy growth function parameters were BL_∞ = 184.5 mm, K = 0.72 year^{-1}, C = 0.36, and WP = 0.45 for females and BL_∞ = 183.75 mm, K = 0.82 year^{-1}, C = 0.38, and WP = 0.22 for males. The growth performance indices (φ') were 4.39 for females and 4.44 for males. The gonadosomatic index (GSI) varied monthly. GSI reached a maximum in May and a minimum in November. The highest values of the GSI coincided with the spawning period of *O. oratoria*. Larger individuals of *O. oratoria* have earlier spawning season than smaller ones. The size at sexual maturity (BL_{50}) of females was estimated as 96.5 mm.

1. Introduction

Oratosquilla oratoria (De Haan 1844) (Crustacea: Stomatopoda) is known as Japanese mantis shrimp. They have distributed North-western Pacific (e.g. Korea, Japan, Taiwan, China and Vietnam) and are found from 10-20 m depth with muddy or sandy-mud substrates (Ahyong 2012). In East Asia, a number of *O. oratoria* are commercially exploited (Hamano et al. 1987; Ahyong 2012; Schram et al. 2013).

Generally, the mantis shrimp have important roles as the predator (crustacea, fish, mollusca and annelida) and the prey (fish and seabirds) in marine ecosystem (Kubo et al. 1959; Griffiths and Blaine 1988; Ahyong, 2012; Schram et al. 2013). They live in burrow at day-time and are active during night-time (Caldwell 1991). The brooding females are tolerated in their burrow during incubation season (Hamano and Matsuura 1984; Caldwell 1991; Wortham-Neal 2002). Some study reported that burrowing behavior affects seasonal variations in sex ratio (Griffiths and Blaine, 1988; Haddy et al. 2007; Mili et al. 2011).

There were some previous studies on growth and reproduction in the coastal area of Japan. The growth of *O. oratoria* had been mainly studied from monthly size frequency distribution because crustaceans have no hard parts as age markers (Hamano and Morrissy 1992; Chang et al. 2012). The longevity of *O. oratoria* was estimated at 2-4 years (Hamano et al. 1987; Nakata 1987; Ohtomi and Shimizu 1988; Hamano and Morrissy 1992). The spawning period of *O. oratoria* fell approximately into summer (Kubo et al. 1959; Yamazaki and Fuzi 1980; Hamano et al. 1987; Ohotomi et al. 1988; Torisawa et al. 1998; Kodama et al. 2004; Kodama et al. 2006; Nakajima et al. 2010). Recently, Kodama et al. (2004) found that spawning period of *O. oratoria* were bimodal pattern according to individual size of females.

Since life-history characteristics differed greatly among localities, the study of growth and reproduction is important to understanding its population dynamics. In Korea, there has been only one study on the seasonal pattern of larval occurrence of *O. oratoria* (Yeon and Park 2011). The present study is to describe some traits of growth and reproductive biology of *O. oratoria* such as sex ratio, growth pattern and spawning periods in Korea.

2. Materials and methods

Oratosquilla oratoria were sampled monthly from July 2014 to August 2015 except February 2015 in Tongyeong, Korea. Samples were collected using gill net during the night-time. They were placed in the cool box with ice to preserve the freshness for laboratory analysis. In the laboratory, the samples were determined the sex. Body length (BL) and body weight (BW) of each individual were measured.

2-1. Sex ratio

Sex was determined by the presence or absence of paired penes. The penes were found on the inner base of a pair of pereopods on the eighth thoracic segment (Kubo et al. 1959; Wortham-Neal 2002). Overall and seasonal variation of monthly sex ratio were expressed as the proportion of females.

2-2. Length-frequency distribution

The length-frequency distributions were constructed to reveal the population structure of all individuals using 5 mm length intervals of the body length. The body length (Kubo-BL; BL) was measured by Kubo's method (Kubo et al. 1959) which measured from base of the rostrum to anterior edge of the median notch of the telson to the nearest 0.01 mm with Vernier calipers.

2-3. Morphometric relationship

The BL was measured with the same method as mentioned earlier, and body weight (BW) was measured to the nearest 0.01 g using a digital balance. A linear regression analysis using log-transformed data was conducted to determine the relationship between BL and BW by the following equation:

$$\ln \mathrm{BW} = a + b \times (\ln \mathrm{BL})$$

where a is the intercept and b is the slope.

2-4. Growth

The length-frequency distributions were constructed using 1-cm length intervals of Kubo-body length (BL). Growth was described using a modified Von Bertalanffy growth function (VBGF) (Pauly and Gaschüz 1979):

$$BL_t = BL_\infty[1 - e^{[-K(t-t_0)-\left(\frac{CK}{2\pi}\right)sin2\pi(t-t_s)]}]$$

where BL_t is the asymptotic body length, K the intrinsic growth rate, t_0 the age at which the length of mantis shrimp is 0, C the amplitude of seasonal growth oscillation, t_s the age at the beginning of growth oscillation, and $WP = t_s + 0.5$ the time of year when growth is slowest.

Growth curves were estimated from the length-frequency distributions using the ELEFAN program in FiSAT II (Gayanilo et al. 2005), which is a non-parametric method to fit the modified VBGF through modes. The R_n value gives an estimator of the goodness of fit. ELEFAN estimates the growth parameter (BL_∞, K, C and WP) without standard errors. According to Pauly (1987), t_0 estimates cannot be obtained solely from the length-frequency data so only ELEFAN routines allow for their calculation. Thus, t_0 was estimated using the relationship described by Lopes Veiga (1979).

$$t_0 = \frac{1}{K}(ln\frac{BL_\infty - BL_h}{BL_\infty})$$

where BL_h is the body length at hatching. In this paper, the value used for L_h was 1.86 mm BL (values converted from size at 1st zoeal stage described by Hamano and Matsuura 1987).

Growth performance of *O. oratoria* was determined a growth performance index (φ') (Pauly and Munro 1984):

$$\varphi' = 2\log_{10} BL_\infty + \log_{10} K$$

The growth performance index is preferred for growth comparison rather than comparison of BL_∞ and K individually, because these two parameters are correlated. The growth performance index is more robust than either BL_∞ or K individually as it takes into account the negative correlation between the two parameters, and fulfills the requirement for a simple single parameter for comparison of growth.

2-5. Ovarian examination

Ovarian observation was conducted to investigate the maturity of females. The maturity of females was based on their external appearance of the ovary and the degree of development of the sexual cement glands. Females have paired ovaries that lie along the length of the thorax, abdomen and telson. The cement gland can be observed through thoracic sternite. The ovarian and cement gland stages were determined according to Deecaraman and Subramoniam (1983b) and Wortham-Neal (2002) illustrations of their shape and color, respectively. In present study, the ovarian stages were determined by 5 stages: immature, developing, maturing, ripe and spent (Table 1). The body and ovarian dry weights were determined by drying at 80℃ for 48 h and weighing them to the nearest 0.1 mg using an electronic digital balance. The gonadosomatic index (GSI) was determined with the expression:

$$\text{GSI} = (\text{ovarian dry weight}/\text{body dry weight}) \times 100$$

Table 1. Ovarian and cement gonad stage modified from Deecaraman and Subramoniam (1983b) and Wortham-Neal (2002)

Stages	Descriptions	Present study
Stage 1	The ovaries are tubular, fine fragile and translucent with black pigments over its outer membrane. The cement glands represent no development in the ventral thoracic region.	Immature
Stage 2	The ovaries are faint yellow. The cement glands begin to develop medially	Developing
Stage 3	The ovaries are yellow with granular aspect and large extends. The cement glands form three white parallel stripes.	Maturing
Stage 4	The ovaries are bright golden with fuse ovaries. The cement gland are fully developed and form 3 dense white bends, connected medially.	Ripe
Stage 5	The ovaries become cloudy or dirty yellow in color. The cement glands are similar with stage 1 or stage 2	Spent

2-6. Size at sexual maturity (BL_{50})

The proportion of sexually mature females except stage 1 and 2 in ovarian development was obtained for each size class. The proportion of mature females by size was fitted to the logistic equation:

$$P = 1/(1 + e^{-(a+b\mathrm{BL})})$$

where a and b are parameters. The parameter estimates for this equation were made with a correlation analysis between P and BL after linearization. Size at sexual maturity (BL_{50}), which is defined as the BL of 50% of shrimps in the reproductive state, was calculated from the ratio between the constants a and b:

$$BL_{50} = -(a/b)$$

2-7. Statistical analysis

A χ^2 test was used to determine whether the observed overall and monthly sex ratio of both sexes differed from the expected 1 : 1 ratio, respectively. The difference between the length-frequency distributions of the two sexes was determined by the Kolmogorov-Smirnov two-sample test. The difference in BL between sexes was tested by one-way analysis of variance (ANOVA). An analysis of covariance (ANCOVA) was used to compare the differences in the slopes and intercepts of the regressions between the BL and BW values of the males and females. The Kruskal-Wallis test was used to investigate the monthly mean variation in the GSI. MINITAB (v.16) and SPSS (v.12) were used for all statistical analyses.

3. Results

A total of 2,621 specimens (1,380 females and 1,241 males) of *O. oratoria* was captured during the sampling period. Many individuals with attached barnacles were observed in September 2014. Soft-shelled individuals were also observed in October and November 2014.

3-1. Sex ratio

The overall sex ratio of females and males was 1.1:1. Thus, the percentage of females (52.4%) was significantly greater than that of males (47.6%) ($\chi^2 = 7.27, df = 1, P < 0.01$; Fig. 1). The sex ratio of both sexes were monthly varied.

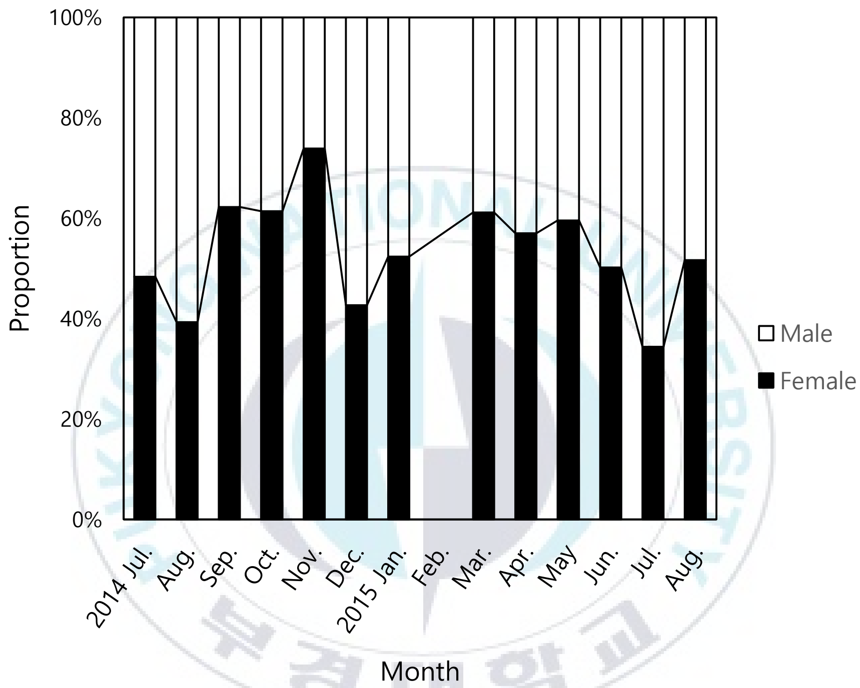

Fig. 1. Sex ratio of *Oratosqulla oratoria* (De Haan 1844) in Tongyeong, Korea.

3-2. Length-frequency distribution

The mean BL was 128.54 ± 0.38 mm (range $86.76 - 171$ mm) in females and 126.87 ± 0.42 mm (range $91.05 - 172$ mm) in males, respectively. Mean BL of females was significantly larger than that of male ($F = 8.08, df = 1, P < 0.01$). There was a significant difference in the length-frequency distributions between females and males (Kolmogorov-Smirnov two-sample: $P < 0.05$; Fig. 2).

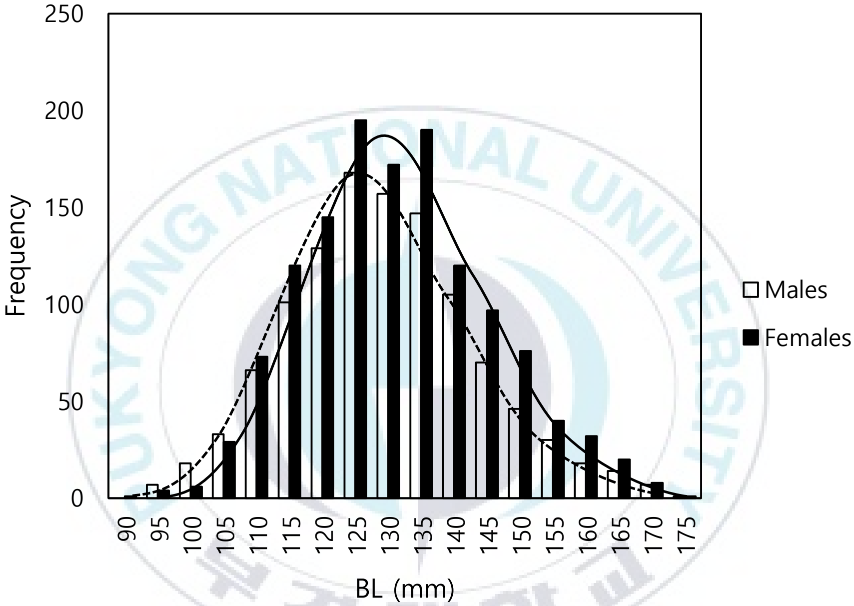

Fig. 2. Length-frequency distribution of males and females of *Oratosqilla oratoria* (De Haan 1844) during study period in Tongyeong, Korea (solid line: female; dotted line: male).

3-3. Morphometric relationship

The relationship between BL and BW of both sexes was determined by linear regression using natural log transformed data (Table 2; Fig. 3). The mean BW was 31.23 ± 0.28 g (range $10.39 - 70.91$ g) in females and 31.06 ± 0.32 g (range $11.86 - 75.22$ mm) in males, respectively.

We found no significant difference in the slopes of the linear regression between ln BL and ln BW for the both sexes (ANCOVA: $F = 0.455, df = 1, P > 0.05$), but a significant difference for the intercepts of the linear regression for the both sexes (ANCOVA: $F = 55.039, df = 1, P < 0.001$; Fig. 4).

Table 2. Linear regression of body length (BL) and body weight (BW) of males and females, mean ± standard error of BL and BW of *Oratosquilla oratoria* (De Haan 1844) in Tongyeong, Korea

Sex	Linear regression	BL (mm)	BW (g)
Female	$\ln BW = 2.8498(\pm 0.0235)\ln BL - 10.4339$ ($n = 1{,}328, r^2 = 0.9170, P < 0.001$)	128.54 ± 0.38	31.23 ± 0.28
Male	$\ln BW = 2.8727(\pm 0.0272)\ln BL - 10.5153$ ($n = 1{,}116, r^2 = 0.9092, P < 0.001$)	126.87 ± 0.42	31.06 ± 0.32

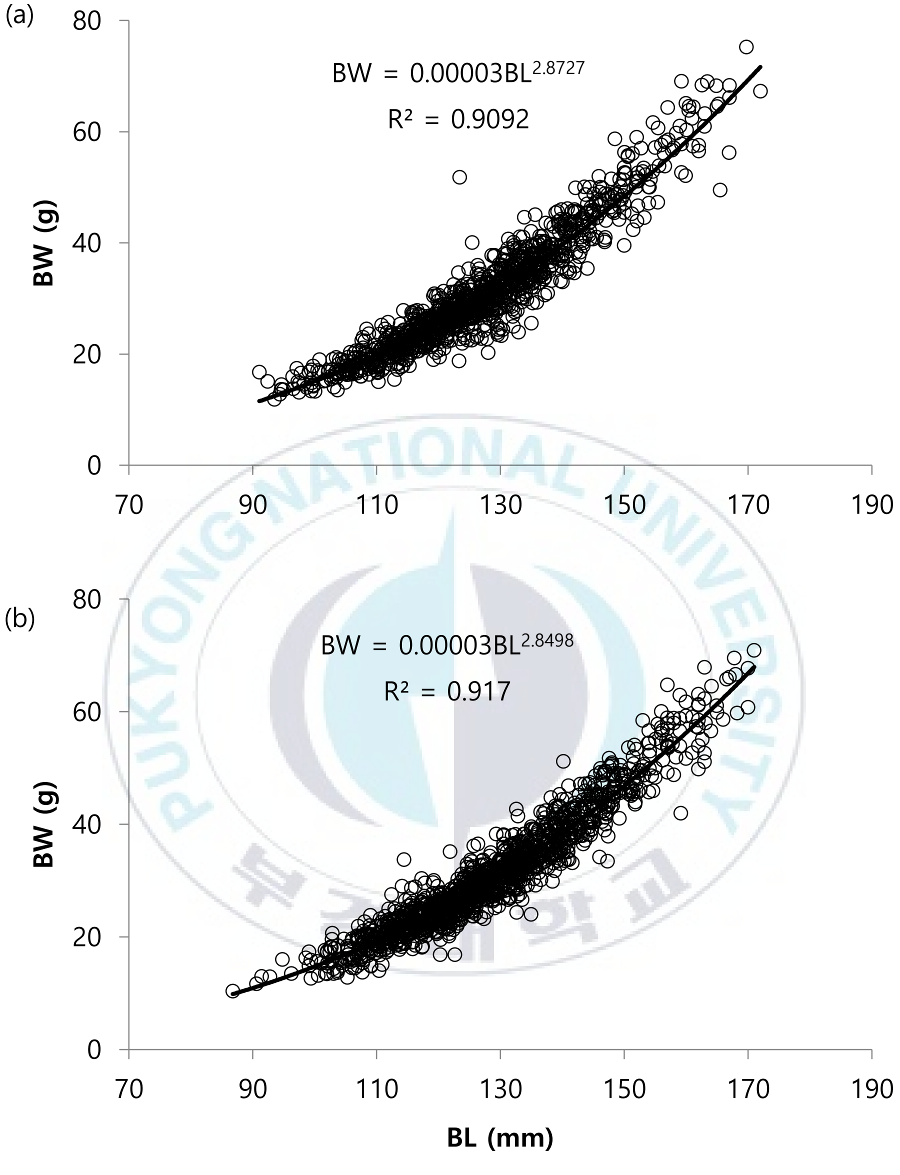

Fig. 3. Relationship between body length (BL) and body weight (BW) of *Oratosquilla oratoria* (De Haan 1844) in Tongyeong, Korea (a: female; b: male).

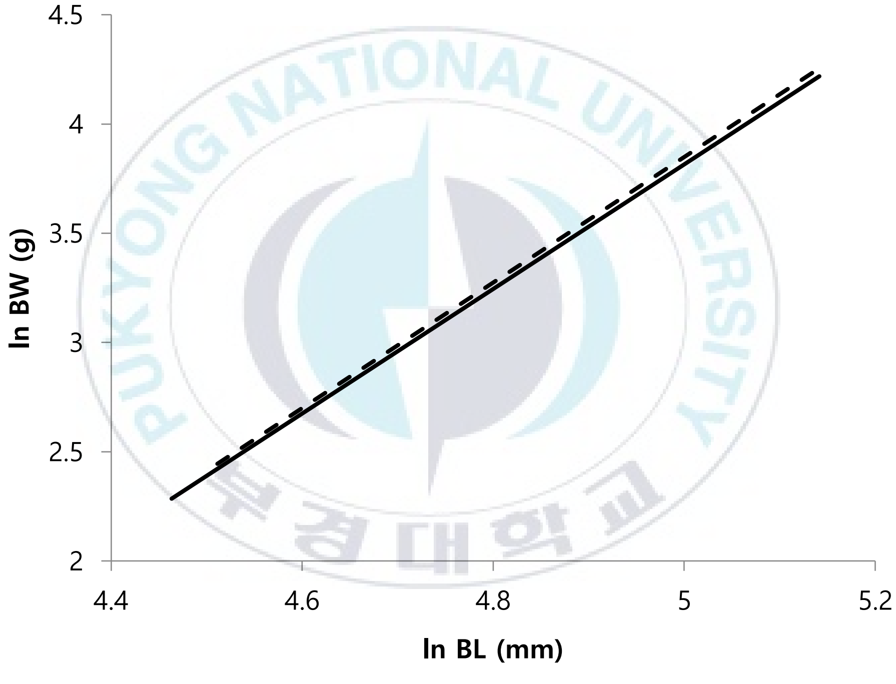

Fig. 4. Relationship between body length (BL) and body weight (BW) of *Oroatosquilla oratoria* (De Haan 1844) in Tongyeong, Korea (solid line: female, dotted line: male).

3-4. Growth

The Von Bertalanffy growth parameter was estimated to investigate the seasonal growth traits for each sex (Fig. 5).

Asymptotic length (BL_{∞}) was higher in females (184.8 mm BL) than males (183.75 mm BL). Growth coefficient (K) was lower in females $(0.72\,yr^{-1})$ than males $(0.82\,yr^{-1})$ (Table 3). The growth curve showed a seasonality growth rate (*C*) of 36% for females, 38% for males. The slowest growth season (*WP*) is May in females and February in males.

The Von Bertalanffy growth equations for the each sex were (Fig. 6):

$$\text{Female: } 184.8[1 - e^{[-0.72(t+0.01)-\left(\frac{0.36\times0.72}{2\pi}\right)sin2\pi(t+0.05)]}]$$

$$\text{Male: } 183.75[1 - e^{[-0.82(t+0.01)-\left(\frac{0.38\times0.82}{2\pi}\right)sin2\pi(t+0.28)]}]$$

The growth performance indices (φ') were 4.39 in females and 4.44 in males.

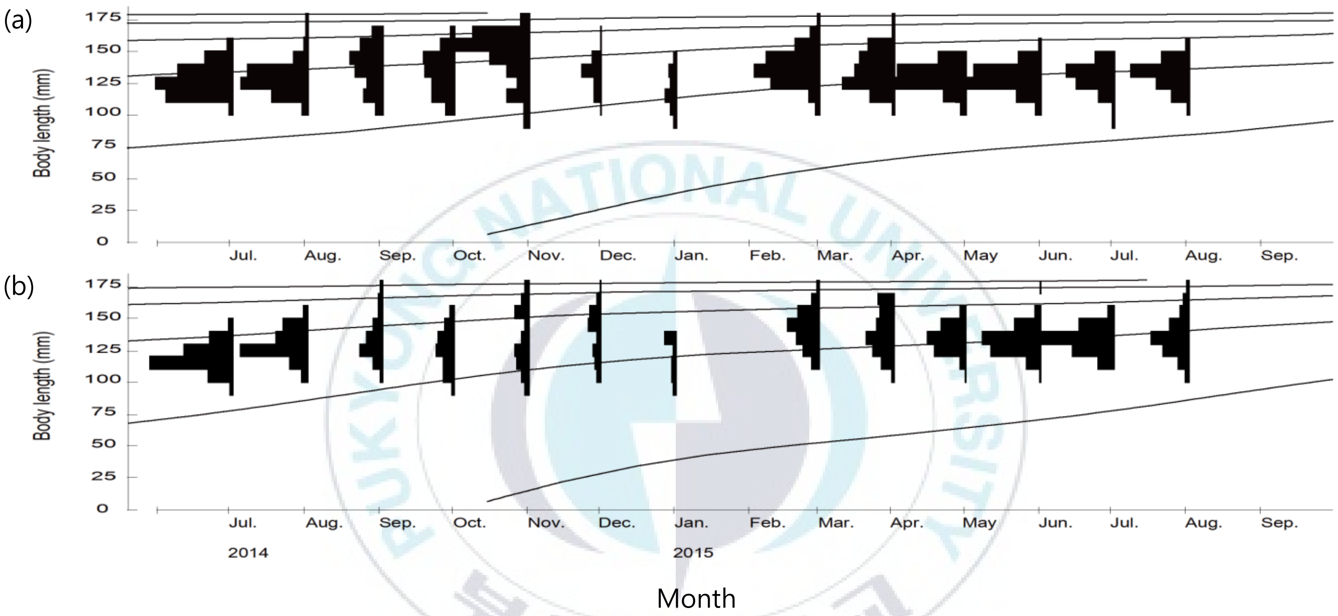

Fig. 5. Length-frequency distribution of *Oratosquilla oratoria* (De Haan 1844) with seasonal Von Bertanlanffy growth curves ((a) female; (b) male).

Table 3. Estimated parameters of the ELEFAN analysis for females and males of *Oratosquilla oratoria* (De Haan 1844) in Tongyeong, Korea (BL_∞: asymptotic length (mm); *K*: growth coefficient (yr^{-1}); *C*: amplitude of growth oscillation; *WP*: winter point; R_n: score function)

Growth parameter	Female	Male
BL_∞	184.8	183.75
K	0.72	0.82
C	0.36	0.38
WP	0.45	0.22
R_n	0.332	0.272

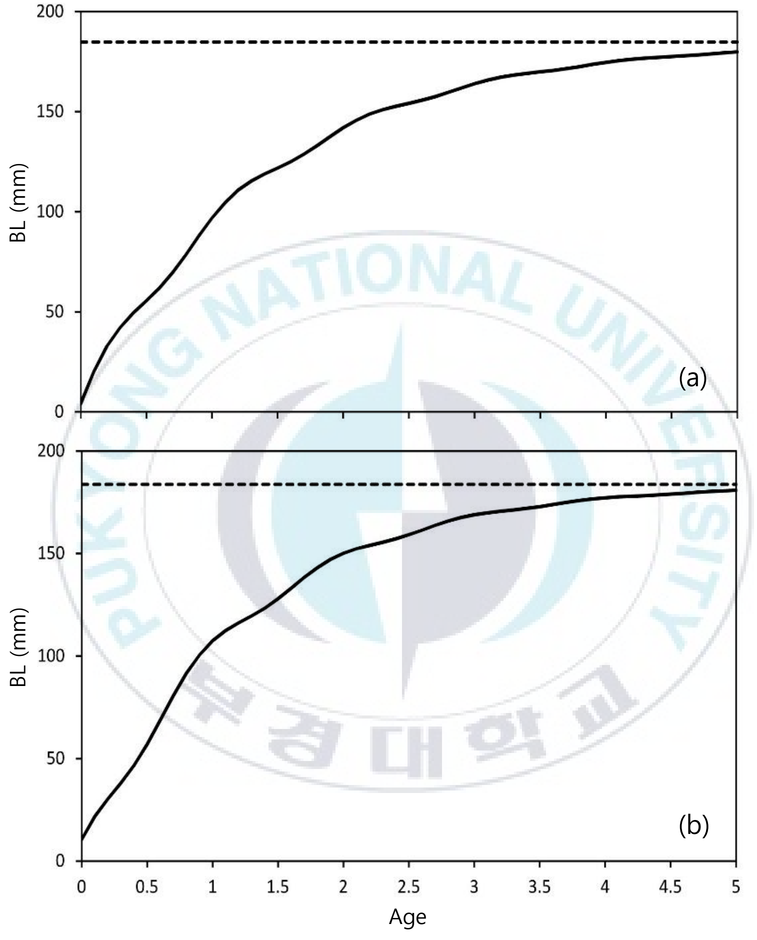

Fig. 6. The Von Bertalanffy growth curve of *Oroatosquilla oratoria* (De Haan 1844) in Tongyeong, Korea. L_{∞} is represented by the dashed line (a: female; b: male).

3-5. Spawning period

The spawning period was determined by the gonadosomatic index (GSI) and the ovarian stages of females. The GSI values differed significantly from one month to the next ($H = 612.285, df = 12, P < 0.001$).The monthly GSI were mainly peaked in May 2015 (15.92) and sub-peak in winter (December 2014) (Fig. 7).

To observe the GSI variation at each size class, the monthly variation of GSI were performed at size class of 10 mm BL interval (Fig. 8). Under 110 mm BL classes, a particular GSI peak was not found. In 110-120 mm BL classes, a main peak of GSI was found in July. In 120-130 mm BL classes, the GSI values occurred in bimodal peaks in May and July. In 130-150 mm BL classes, a main peak of GSI was found in May. In the more than 150 mm BL classes, unusually high levels of GSI was observed in August 2014.

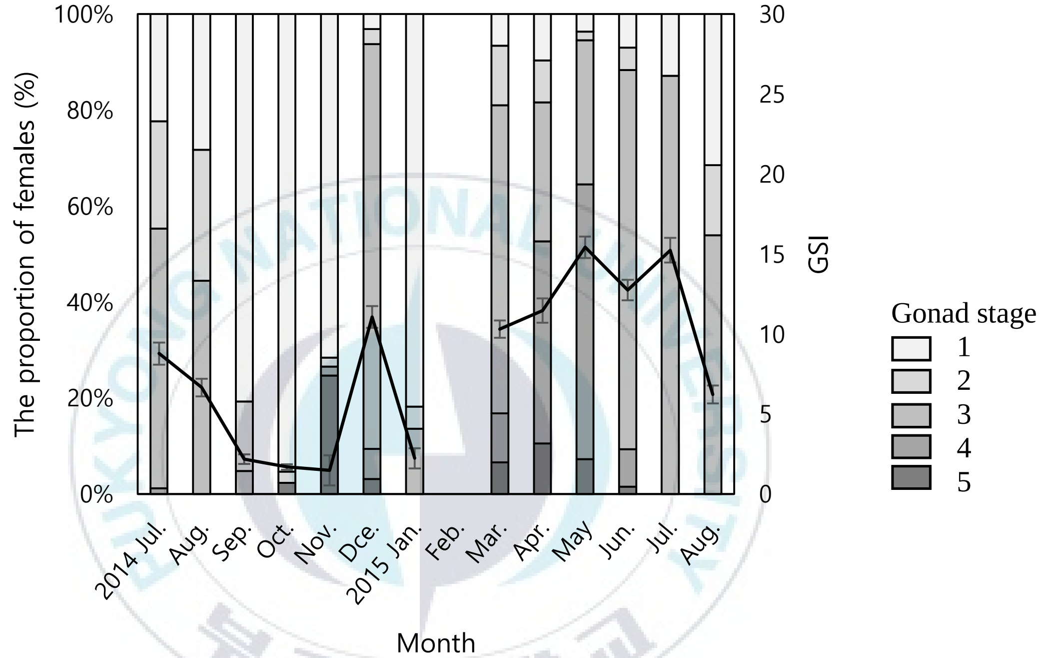

Fig. 7. The proportion of females with different gonad stages and gonadosomatic index (GSI) of *Oratosquilla oratoria* (De Haan 1844) in Tongyeong, Korea.

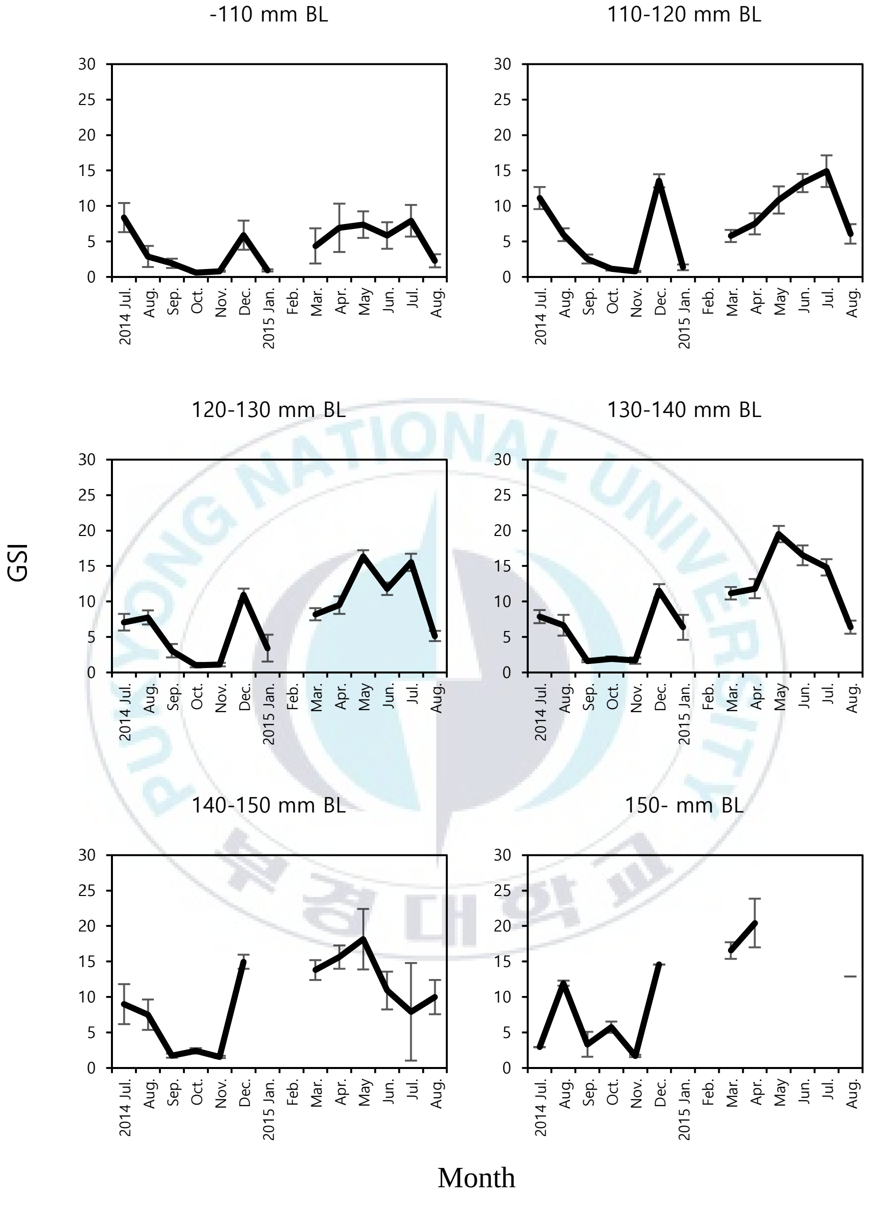

Fig. 8. The proportion of females with different gonad stages and gonadosomatic index (GSI) by size classes of *Oratosquilla oratoria* (De Haan 1844) in Tongyeong, Korea.

3-6. Size at sexual maturity (*BL_{50}*)

The size at sexual maturity (BL_{50}) of females was estimated as 96.5 mm (Fig. 9). The observed smallest mature size was 94.78 mm in this study. The proportion of mature females by size was fitted to the logistic equation with length as followed:

$$P = \frac{1}{1 + e^{-0.11(\mathrm{BL}-102.24)}}$$

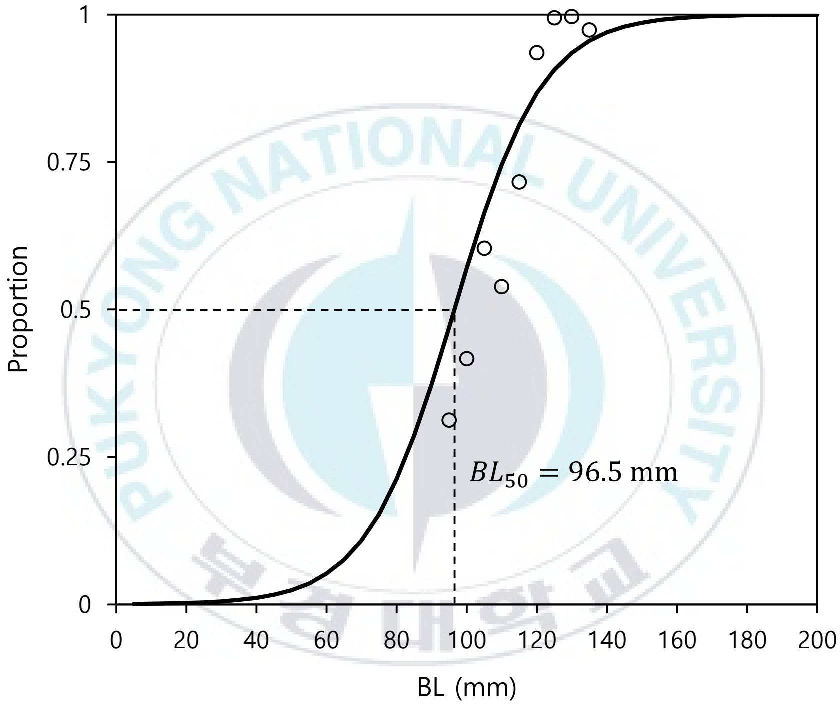

Fig. 9. A logistic function fitting proportion of mature females to body length (BL) of *Oratosquilla oratoria* (De Haan 1844) in Tongyeong, Korea. BL_{50}, which corresponds to a proportion of 0.5, is indicated.

4. Discussion

The overall sex ratio of females was higher than that of males. Although the number of females occupied larger proportion than that of males during observed period, the sex ratio varied seasonally. The sex ratio of males was significantly higher in summer than other seasons. Females of *O. oratoria* were underrepresented in the catch during spawning season (Torisawa et al. 1998). Generally females of stomatopod shirmps brood their eggs in their maxillipeds in the burrow to avoid danger such as injured and killed by predator (Hamano and Matsuura 1984). They provide with care to clean eggs and to circulate water using the maxillipeds in the burrow (Caldwell 1991). In previous studies, burrowing behavior during spawning season decreases catchability of females and affects seasonal change in sex ratio (Griffiths and Blaine 1988, Maynou et al. 2004, Haddy et al. 2007).

The length-frequency distributions were significantly different between both sexes, and females were predominance in the larger size classes compared to males. The predominance of females in larger size might be related to the agonistic behavior of males. As males have to fight with competitor for mating partners, the mortality of males gradually increase in larger size (Wardiatno and Mashar 2010).

The slopes of the linear regression between ln BL and ln BW showed no significant difference for both sexes, which indicated no difference in the relative growth. However, the intercepts of the linear regression for the both sexes were significantly different, which suggest that BW of males were larger than that of females in given BL. This result indicated that initial growth might be different in both sexes.

Seasonal Von Bertalanffy growth parameters of females of *O. oratoria* were estimated higher L_∞ value and lower K value than those of males. The growth parameters in *O. oratoria* were different between both sexes. The growth performance indices were higher in the males than in the females. This result suggests that male grew slightly faster than females. Therefore, males reached a larger size at the same age than females. Similar results were observed in the previous studies of *O. oratoria* (Ohtomi and Shimizu 1988; Hamano and Morrissy 1992; Ohtomi and Shimizu 1994; Table 4).

The growth rate of *O. oratoria* in both sexes have been influenced by seasonality. The phase of slowest growth for females coincided with the time of spawning periods and increasing GSI values whereas the slowest growth period for males appears at the time of low water temperature.

Hartnoll (1985) reported that growth and reproduction are antagonistic in terms of energy cost in crustaceans. Reproduction of females must always restrict their growth because the energy cost is required for ovary maturation. Therefore, a possible explanation for the sexual dimorphism of growth is that the energy which is cost to attain sexual maturity in males is less than that in females (Kodama et al. 2009).

Table 4. Comparison of growth performance indeices (φ') for *Oratosquilla oratoria*

Population	φ'		Author(s)
	Female	Male	
Tokyo Bay	4.01	4.09	Ohtomi and Shimizu (1988)
Seto Inland Sea	4.01	4.04	Hamano and Morrissy (1992)
Tokyo Bay	4.33	4.34	Ohtomi and Shimizu (1994)
Tongyeong	4.39	4.44	Present study

In this study, the maturity of females was determined to both their external appearance of the ovary and the degree of development of the cement glands. The cement glands secretes a sticky substance composed of mucoid sulphated acidmucopolysaccharide substance. Reproductive mature females developed cement glands form three white parallel stripes under the sixth, seventh and eighth thoracic sternites (Wortham-Neal 2002). Wortham-Neal (2002) has proposed two functions of cement material in mantis shrimp; 1) help the embryos form a mass and 2) aid the females in attaching the eggs in her maxillipeds. Moreover, the activities of these glands are controlled by same reproductive hormones regulating the ovarian development (Deecaraman and Subramoniam 1983a). Vila et al. (2013) also described synchrony in development of the ovary and cement glands.

The main spawning period of *O. oratoria* was approximately in summer (Kubo et al. 1959; Yamazaki and Fuzi 1980; Hamano et al. 1987; Ohtomi et al. 1988; Torisawa et al. 1998; Kodama et al. 2004; Kodama et al. 2006; Nakajima et al. 2010). Larger individuals of *O. oratoria* have earlier spawning season than smaller ones. Monthly changes in the GSI values of *O. oratoria* were also reported from previous studies (Ohtomi et al., 1988, Kodama et al. 2004; Kodama et al. 2006). Kodama et al. (2004) reported that the GSI values of large females (≥ 10 cm) peaked around May whereas the small (< 10 cm) were around August in Japan.

The difference of spawning season by size was considered as size related maturation (Kodama et al. 2004; Kodama et al. 2006). Ohtomi and Shimizu (1996) reported that females of *O. oratoria* could spawn eggs after one year from hatching. In this study, some of *O. oratoria* of 2 years old or 1 year old with fast-growing had earlier spawning season. Others which were 1 year old with slow-growing had later spawning season.

Some large females (>150 mm BL) had still mature ovaries during the late spawning season. Kodama et al. (2004) reported several possible explanations for this result. One is that spawning failure occurred in early spawning seasons because females did not reach the minimum size at maturity. However, proposed size (≥ 10 cm) was not applied in this study. Another possible explanation is multiple spawning. In some cases, multiple spawning of more than two times has been reported under rearing condition (Kodama et al. 2003). Females who lost the egg mass were again developed and the second egg is 40 days after the first spawning (Hamano and Matsuura 1984).

The GSI values were dramatically high in December and drop in January. Since there was very low catch during winter season from December to February, the GSI vales were over or under estimate compared with other season. El-sherif et al. (2012) reported that some mature ovaries persisted in the ovary and ovarian regeneration occurred in spent phase. In Japan, GSI of *O. oratoria* again begin to increase in the winter season (Yamajaki and Fuzi 1980; Torisawa et al. 1998). Although the number of individuals in the winter season was low compared with other season, GSI values tended to increase from winter in this study.

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