Thesis for the Degree of Master of Engineering

Population dynamics of the Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan, 1844) in the coastal area of Goheung, Korea

by

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Population dynamics of the Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan, 1844) in the coastal area of Goheung, Korea

(한국 고흥 연안에 서식하는 갯가재의 개체군 동태)

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by
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최 하 경

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요 약

본 연구는 남해 고흥 연안에 서식하는 갯가재 (*Oratosquilla oratoria* (De Haan, 1844))의 개체군 동태를 조사하기 위해, 2020년 2월부터 2021년 6월까지 매월 표본을 채집하여 성장, 생식, 사망률, 생식 산출력 등 생식생물학적 특성을 연구하였다.

연구 기간 동안 표본은 3,197마리 (수컷 1,521마리, 암컷 1,676마리)가 채집되었으며, 암컷의 비율이 높게 관찰되었다(수컷: 암컷 비율, 1: 1.1). 암수의 체장빈도분포에는 유의한 차이가 있었으며, 갑각장 (CL)과 체중 (BW)의 회귀직선의 기울기에 있어서 암수의 상대성장에서 유의한 차이를 보였다 (ANCOVA; $F=53.27$, $P<0.001$). 계절적 Von Bertalanffy 성장식의 매개변수는 이론적 최대갑장 (CL_∞), 성장계수 (K), 계절적 성장 변동계수 (C)를 나타내며, 수컷은 $CL_\infty=41.52$ mm, $K=0.67$ yr^{-1}, $C=0.41$이며, 암컷은 $CL_\infty=35.1$ mm, $K=0.82$ yr^{-1}, $C=0.38$로 추정되었다. 성장비교지수 (φ')는 수컷과 암컷 각각 3.06, 3.00으로 추정되었다. 총 사망률 (Z)은 어획물 곡선법에 의해 3.25 yr^{-1}, 어획 사망률 (F)은 2.28 yr^{-1}, 자연 사망률 (M)은 0.97 yr^{-1}로 추정되었다. 가입 패턴은 연간 두 번의 최대가입률을 보였다. 생식도 숙도 지수(Gonadosomatic index: GSI)는 4-6월에 최대값을, 2월에 최소값을 보였다. 군성숙체장(CL_{50})은 24.43 mm로 계산되었다. 포란수와 갑각장의 관계식은, $F=3.1773CL^{3.0087}$ ($n=50$, $r^2=0.90$, $P<0.001$)이다.

Population dynamics of the Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan, 1844) in the coastal area of Goheung, Korea

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Abstract

Population dynamics of the Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan, 1844), were investigated from February 2020 to June 2021 in Goheung, Korea. A total of 3,197 samples (1,521 males and 1,676 females) were collected during the period. The number of females was observed frequently than males (male : female ratio, 1 : 1.1). There was a significant difference in the length-frequency distribution between both sexes. The slopes of the linear regression of carapace length (CL) and body weight (BW) between males and females showed significant difference in allometric growth. The parameters of Von Bertalanffy growth function were CL_{∞}=41.52 mm, K=0.67 yr^{-1}, C=0.41, and WP=0.23 for males, and CL_{∞}=35.1 mm, K=0.82 yr^{-1}, C=0.38 and WP=0.12 for females. The growth performance index (φ') was 3.06 in males and 3.00 in females. Total mortality (Z) was estimated at 3.25 yr^{-1} by length-converted catch curve, fishing mortality (F) at 2.28 yr^{-1}, and natural mortality (M) at 0.97 yr^{-1}. The recruitment pattern showed two peaks of recruitment per year. The GSI values was monthly varied, and reached highest in April to June, and lowest in February. The size at sexual maturity (CL_{50}) was calculated as 24.43 mm. Fecundity was expressed as a function of CL, resulting an equation of $\mathrm{Fecundity} = 3.1773CL^{3.0087}$.

1. Introduction

The Japanese mantis shrimp, *Oratosquilla oratoria* (De Haan, 1844) (Crustacea: Stomatopoda), is distributed in the north-western Pacific, such as Korea, Japan, Taiwan, China and Vietnam (Ahyong, 2012). It can be found on all coasts in Korea. *O. oratoria* inhabits in muddy or sandy-mud substrates around under 10-20 m and usually grows up to 130-155 mm in total length (Ahyong, 2012). The main spawning season of mantis shrimp is summer, and the peak month is June (Hamano *et al.*, 1987).

The basic morphological characteristics of the mantis shrimp are as follows. Total length is about 140 mm long and body color is light brown with four red lines on its back. There are two antennae and five pairs of thoracic legs, and the first antenna is divided into three parts. Among the five pairs of thoracic legs, the second leg is called the raptorial claw.

The mantis shrimps are actively captured in many countries including Korea. In Japan, although mantis shrimp accounts for more than 40 % of the catch, the resource level is rapidly deteriorating, maintaining a catch of 1,080 tons in 1989 and dropping to 57 tons in 2005.

In addition, *O. oratoria* has an important ecological niche. The role of mantis shrimp is mainly as predator, preying on small crustaceans, polychaeta and small fish, and as prey for benthic fish (Hamano and Matsuura, 1986). Comparing the population of the species currently being collected in this area, it is expected that other species would change depending on the mantis shrimp that prey on small crustaceans. Also, it can be confirmed that mantis shrimp show overall top dominance in Goheung, Korea (Table 1).

Research on mantis shrimp has being studied abroad in several countries. In Japan, there is a previous study on the population dynamics of *Oratosquilla oratoria* (Narita *et al.*, 2007). In Korea, large numbers of mantis shrimp are caught all over the country. However, although it has been proven to be ecologically useful, population dynamics has not been investigated. Only two studies have been conducted in Korea; the development and distribution of mantis shrimp larvae (Yeon and Park, 2011) and the growth and reproduction of mantis shrimp in Tongyeong (Kim *et al.*, 2017).

The purpose of this study is to investigate 1) reproduction, and 2) population dynamics of the mantis shrimp.

Table 1. Total number of crustaceans collected in Goheung during the study period

	2020-Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	2021-Jan	Feb	Mar	Apr	May	Jun	Total
Alpheus japonicus	480	86	77	216	4	10	9	44	123	405	241	340	24	269	294	185	10	2817
Alpheus rapax	66	12	36	100	11	5	3	18	6	29	5	8		10	11	7	1	328
Arcania undecimspinosa			2	2	2		1	1	16	94		15		14	5	29		181
Batepenaeopsis tenella	880	422	12	26	3	4	763	1953	24	3130	3753	1157	292	75	124	111	31	12760
Charybdis bimaculata	1826	867	276	1400	585	660	64	41	55	714	153	34	252	13	1683	2173	563	11359
Charybdis japonica			1		7	11	33		6	8	1			7	1	1		76
Crangon hakodatei	619	4044	322	2264			3	5	418	2096	8685	1818	1028	1398	1089	206	1	23996
Diogenes edwardsii			8		3	27	13	13	6	1	1	2			7	7		88
Entricoplax vestita			4			2		1	2	3	2	1			2	4		21
Eriocheir sinensis												2						2
Eucrate crenata				2		2		2	8	16	3	34		1	4	45		117
Heikeopsis japonica			3	4	34	56	7	2	7	25	1	19		6	71	81		316
Heptacarpus futilirostris													1		9	14		24
Latreutes planirostris	9	54	11	26		30	1		3	15	137	412	80	38	40	16		872
Leptochela gracilis	2	95		10				1			105	327	3		6	3		552
Lysmata vittata	1		18	3					2	1	43	52	1		12	20		153
Metapenaeus joyneri	437		3	2				12	51	55	681			49	32			1322
Oratosquilla oratoria	**70**	**419**	**680**	**349**	**103**	**46**	**31**	**162**	**481**	**435**	**106**	**11**	**9**	**91**	**149**	**53**	**47**	**3242**
Palaemon carinicauda	1	7					4			7		183		21	4			227
Palaemon modestus	1		15		1		3	1				127	40		1	2		191

Continued)

Parthenope validus						2												2
Pinnaxodes major			1						1			5		2	1			10
Portunus trituberculatus						7	4	27	12	1	28	1		1				81
Trachysalambria curvirostris	182	497	41	415	543	115	43	436	2334	27	356	12		9	24	216	22	5272
Tritodynamia rathbuni			1	1					1		5	19		2		9		38
Total	4574	6503	1511	4820	1296	977	982	2719	3556	7062	14306	4579	1730	2006	3569	3182	675	64047

2. Materials and Methods

2-1) Sample collection

Samples of the mantis shrimp, *Oratosquilla oratoria*, were collected monthly from February 2020 to June 2021 in Goheung, Korea. Samples were collected by using 8 m beam trawl with 18 mm size mesh (trawl length: 22 m) during day-time. Water temperature and salinity were measured monthly by YSI for marine environmental factors. Collected samples were preserved in 10 % neutralized formaldehyde.

2-2) Sex ratio

Sex was determined by the presence of paired penes. The penes were located on the base of a last pair of pereopods on the eighth thoracic segment (Wortham-Neal, 2002). Sex ratio was presented as the proportion of females.

2-3) Sample analysis

The carapace length (CL), from the base of the rostrum plate to the posterior edge of the carapace, was measured up to the nearest 0.01 mm using Vernier calipers. Body wet weight (BW) was determined to the nearest 0.01 g using an electronic balance. Population size (P) was calculated by the equation

$$P = C/A$$

where C is a catch number, and A is a swept area.

2-3.1) Length-frequency distribution

Length-frequency distribution (LFD) was constructed to indicate population structure between sexes using 5-mm intervals of CL.

2-3.2) Morphometric relationship

A linear regression between CL and BW was conducted by using log-transformed data. The equation is

$$ln\,BW = a + b \times ln\,CL$$

where, a is an intercept and b is a slope.

The relationship between CL and body length (BL) was determined respectively by the equation

$$BL = a + b \times CL$$

where a and b are parameter of intercept and slope, respectively.

2-4) Growth

Growth was described using the modified Von Bertalanffy Growth Function (VBGF) (Pauly and Gaschütz, 1979):

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

where CL_∞ is the asymptotic carapace length, K is the intrinsic growth rate, t_0 is the age at which the length of mantis shrimp is 0, C is the amplitude of seasonal growth oscillation, t_s is the age at the beginning of growth oscillation, and WP (t_s+0.5) is the time of year when growth is slowest.

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

$$t_0 = \frac{1}{K}\left(\ln \frac{CL_\infty - CL_h}{CL_\infty}\right)$$

where CL_h is the carapace length at hatching.

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

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

The growth performance index is preferred for growth comparison rather than comparison of CL_{∞} and K individually, since two parameters are correlated.

2-5) Mortality

Total mortality was estimated in ELEFAN using two methods: a linearized, length-converted catch curve (Pauly, 1984) and a Jones and van Zalinge (1981) plot. Z can be estimated by using the estimated K from the VBGF because the output is Z/K. Fishing mortality (F) and natural mortality (M = Z - F) can also be estimated by ELEFAN. Recruitment pattern was also studied.

2-6) Ovarian examination

Ovarian observation was conducted to investigate the maturity of females. Ovaries are located overall parts of thorax, abdomen and telson. Ovarian stages were expressed in 5 stages according to Deecaraman and Subramoniam (1983) and Worthan-Neal (2002); (□) Immature, ( ) Developing, ( ) Maturity, ( ) Ripe, and ( ) Spent. The body and gonad of each were dried at 60 for 72 h in order to measure the body and gonad dry weight. Dry weight was measured to the nearest 0.001 g using an electronic digital balance. The gonadosomatic index (GSI) was determined by the equation:

$$\mathrm{GSI} = \frac{Dry\ \ ovarian\ \ weight}{Dry\ \ body\ \ weight} \times 100$$

2-7) Size at sexual maturity (CL_{50})

The proportion of sexually mature female was indicated with gonad development stage 3 or higher. The proportion of mature females by size (P) was fitted to the logistic equation:

$$P = 1/(1 + e^{-(a+bCL)})$$

where *a* and *b* are parameters.

Size at sexual maturity (CL_{50}), which was defined as the CL of 50 % of mantis shrimps in the reproductive state, was calculated by the ratio of the parameters *a* and *b*:

$$CL_{50} = -(\frac{a}{b})$$

2-8) Fecundity

Fecundity was estimated by using mature female shrimps with gonad stage and . Parts of ovarian were dissected for each mature individual. Each of the samples was dried and weighted to the nearest 0.001 g. Before drying, gonad particles were counted under a microscope (Zeiss Stemi SV-6) by using dissecting needles and forceps. Total fecundity (F) was determined through the equation (Kodama et al., 2004):

$$\mathrm{F} = F_s \times \frac{GW_t}{GW_s}$$

where F_s is the number of particles in a sample, GW_t is the total weight of the gonad, and GW_s is the weight of the dissected gonad.

Relationship between fecundity and CL was determined by linear regression analysis:

$$\mathrm{F} = aCL^b$$

where *a* and *b* are parameters.

2-9) Statistical analysis

A x^2 test was used to determine whether the observed overall sex ratio of both sexes differed from the expected 1:1 ratio. Correlation analysis was performed to indicate the relationship between temperature and population size. The difference between length-frequency distribution of the both sexes were determined by the Kolmogorov-Smirnov two sample test. Linear regression analysis with natural log transformed data was used to indicate the relationship between; carapace length and body weight for both sexes, and carapace length and fecundity. An analysis of covariance (ANCOVA) was used to compare the differences in slopes and intercepts of the regression between body weight and both sexes. Monthly mean values of GSI were tested by Kruskal-Wallis test. MINITAB (v. 16) and SPSS (v. 27) were used for all statistical analysis.

3. Results

3-1) Population structure

A total of 3,197 specimens (1,521 males and 1,676 females) were sampled during the period. The ratio between male and female was 1:1.1. The proportion of females (52.4 %) was significantly greater than males (47.6 %) ($x^2 = 62.08, df = 16, P < 0.001$; Fig. 1).

The estimated population size was higher in summer to fall and lower in winter. Population size (P) ranged from 0.22 (2021 Jan.) to 5.35 (2020 Jun.). A correlation analysis showed a significant correlation between population size and seawater temperature ($r = 0.605$, $P < 0.05$; Fig. 2a). However, there was no significant correlation between population size and salinity ($r = -0.082, P > 0.05$; Fig. 2b)

3-2) Length-frequency distribution

The mean CL was 18.44 ± 6.82 mm (range 6.59 – 40.15 mm) in males and 16.41 ± 6.57 mm (range 4.91 – 34.57 mm) in females. There was a significant difference in the length-frequency distribution between males and females (Kolmogorov-smirnov two-samples test, $Z = 3.908, P < 0.001$; Fig. 3). Mean CL of males was significantly larger than that of females.

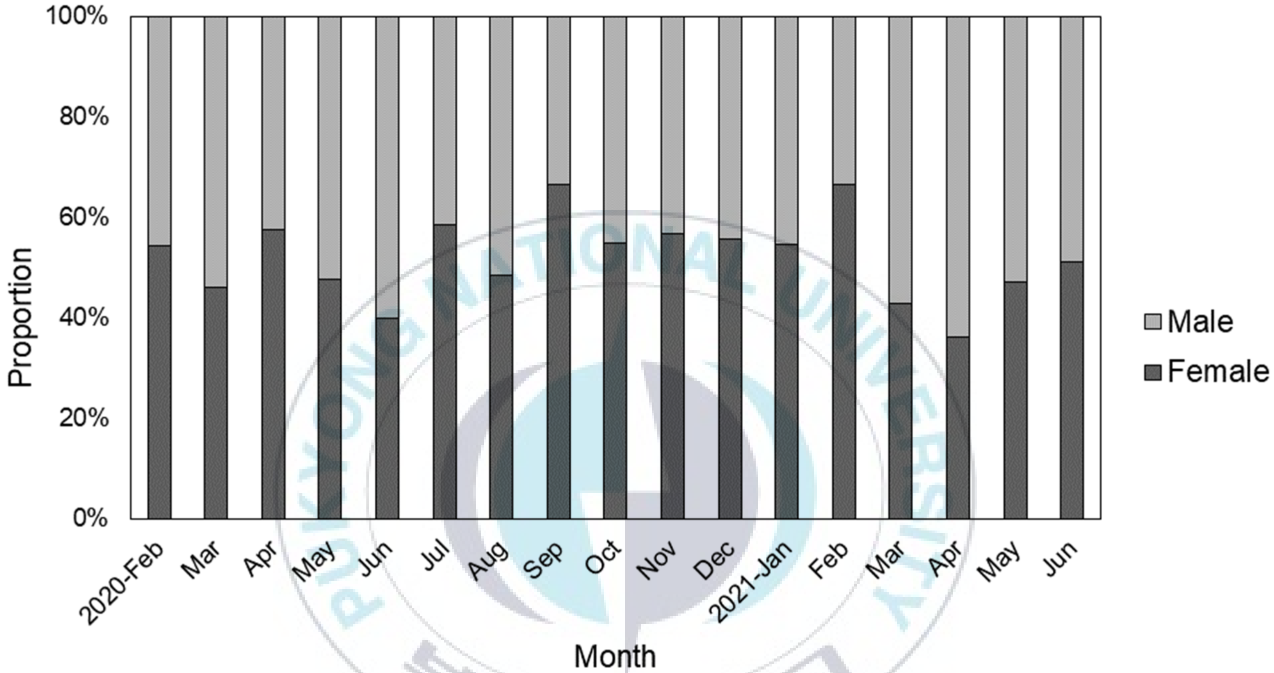
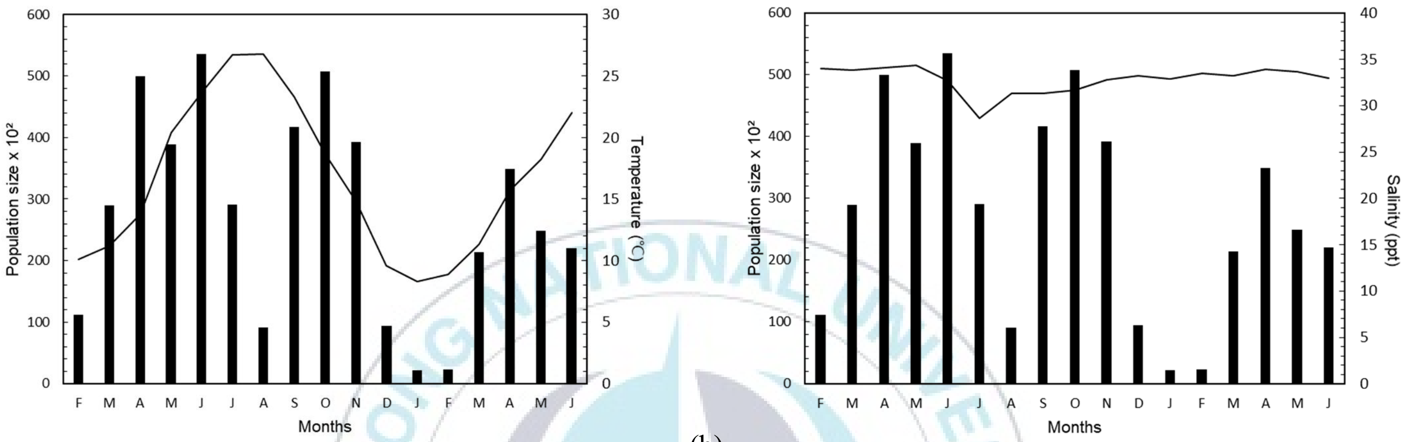


Figure 1. Monthly proportions of males and females of *Oratosquilla oratoria* (De Haan, 1844)



(a) (b)

Figure 2. Population size of *Oratosquilla oratoria* (De Haan, 1844) with seawater temperature (a), and salinity (b) during sampling period in Goheung

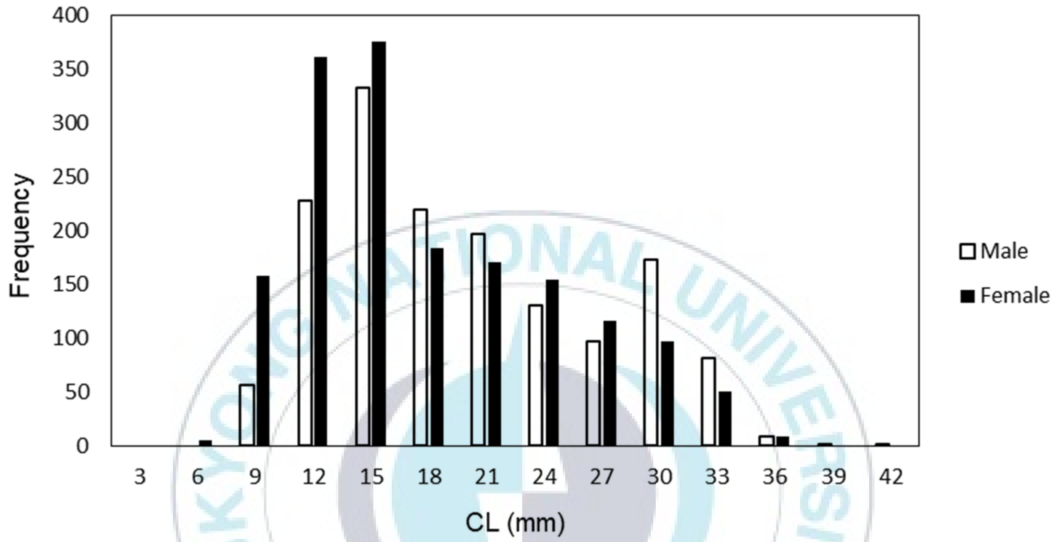


Figure 3. Length-frequency distribution of males and females of *Oratosquilla oratoria* (De Haan, 1844)

3-3) Morphometric relationship

The relationship between CL and body length (BL) was determined by linear regression. The equation was:

$$\mathrm{BL} = 2.6134 + 4.2494\mathrm{CL} \quad (r^2 = 0.9842, n = 3197, P < 0.001)$$

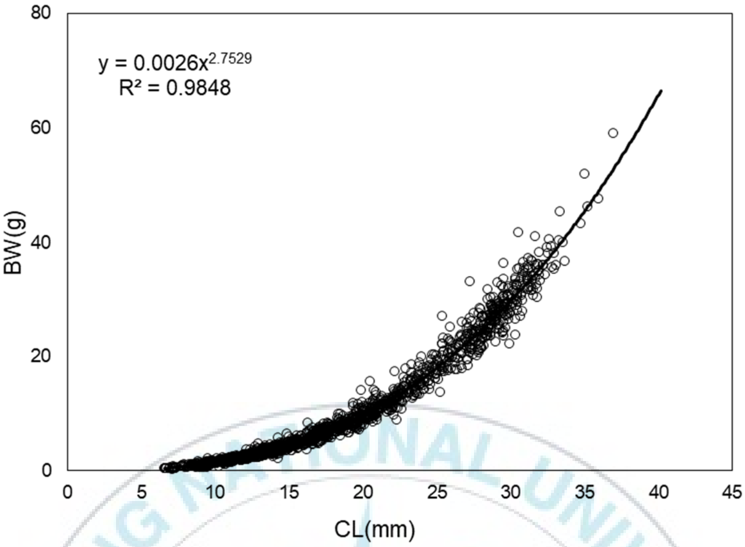
The relationship between CL and BW of each sexes was determined by linear regression using natural log transformed data (Table 2; Fig. 4)

There was a significant difference in the slopes of the linear regressions of ln CL and ln BW for both sexes (ANCOVA; $F = 53.27,\ P < 0.001$; Fig. 5).

Table 2. Linear regression of carapace length (CL) and body weight (BW) of male and female, mean ± standard error of carapace length, body weight of *Oratosquilla oratoria* (De Haan, 1844)

Sex	Linear regression	CL (mm)	BW (g)
Male	$\ln BW = 2.7529\ (\pm 0.0088) \ln CL - 5.9690$ $(\mathrm{n} = 1521, r^2 = 0.9848, P < 0.001)$	18.44 ± 0.17	10.52 ± 0.26
Female	$\ln BW = 3.0464\ (\pm 0.0089) \ln CL - 6.8831$ $(\mathrm{n} = 1676, r^2 = 0.9858, P < 0.001)$	16.41 ± 0.16	7.89 ± 0.22

(a)



(b)

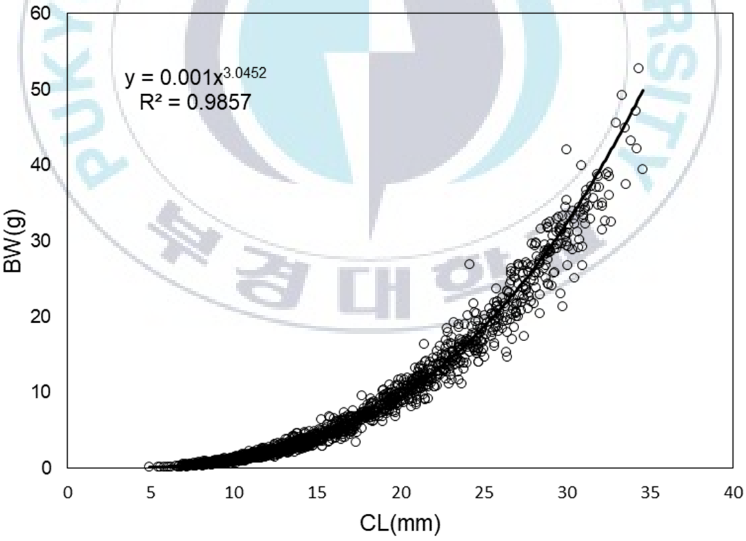


Figure 4. Relationship between carapace length (CL) and body weight (BW) of *Oratosquilla oratoria* (De Haan, 1844) in Goheung, Korea; (a): Males, and (b): Females

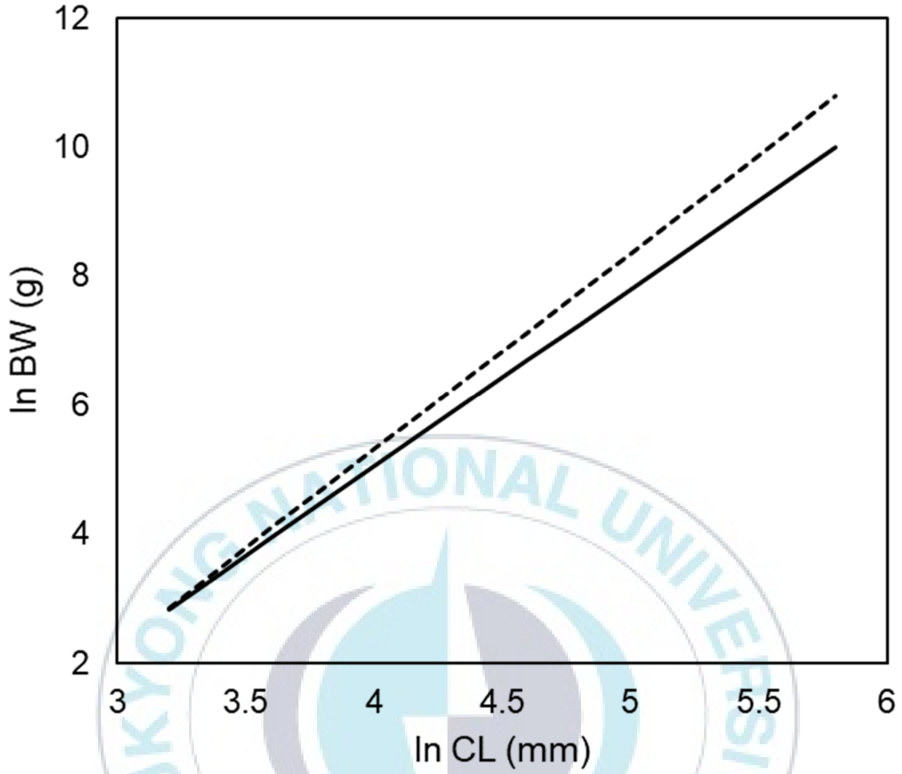


Figure 5. Linear regression of ln carapace length and ln body length of *Oratosquilla oratoria* (De Haan, 1984) (Solid line: Males; Dotted line: Females)

3-4) Growth

The Von Bertalanffy growth parameter for both sexes was determined by ELEFAN to investigate the growth of species (Fig. 6).

Asymptotic length (CL_∞) was slightly higher in males (41.52 mm) than females (35.1 mm). Growth coefficient (K) was higher in females (0.82 yr^{-1}) than males (0.67 yr^{-1}). The growth curve showed a seasonality growth rate (C) of 41 % for males, and 38 % of females. The slowest growth season (WP) was February in males and January in females (Table 3).

The Von Bertalanffy growth equations for both sexes were determined as (Fig. 7):

$$CL_t = 41.52\left[1 - e^{\left[-0.67(t+0.02)-\left(\frac{0.41\times0.67}{2\pi}\right)\sin 2\pi(t+0.27)\right]}\right] \text{ for males,}$$

$$CL_t = 35.1\left[1 - e^{\left[-0.82(t+0.02)-\left(\frac{0.38\times0.82}{2\pi}\right)\sin 2\pi(t+0.38)\right]}\right] \text{ for females.}$$

The growth performance index (φ') was 3.06 for males and 3.00 for females.

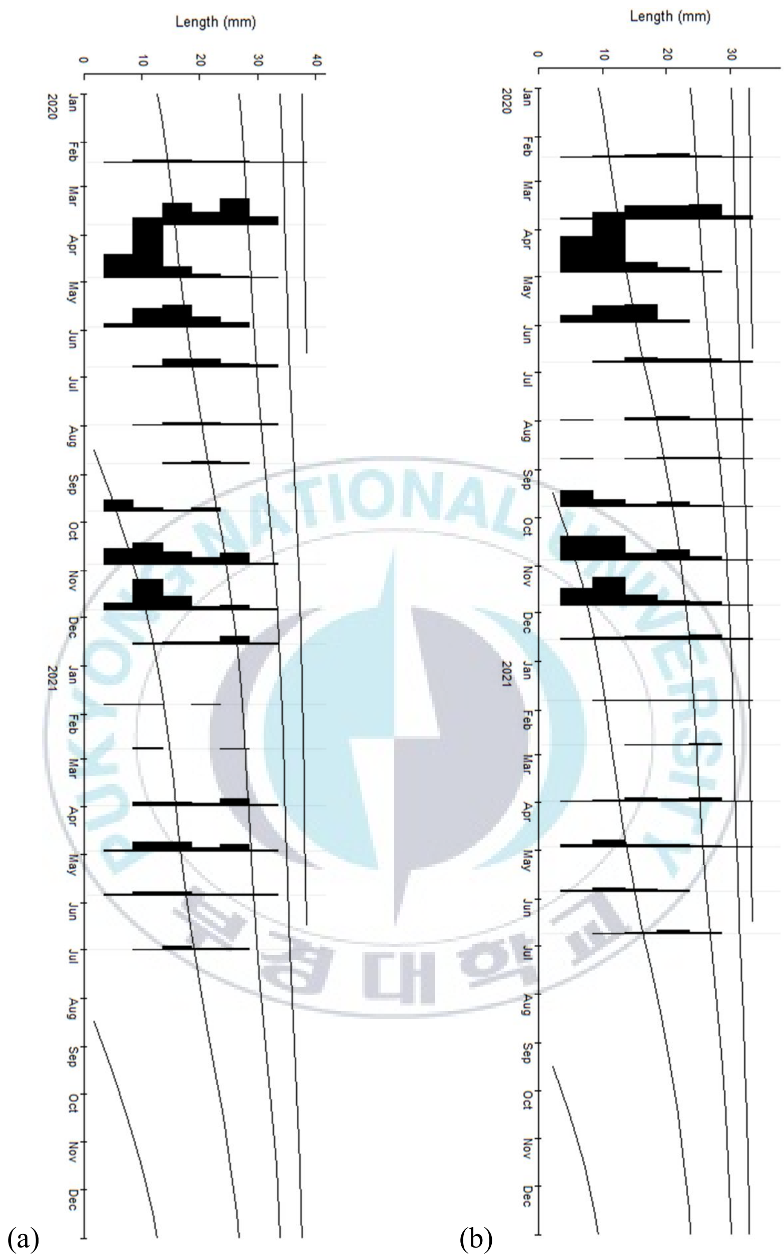
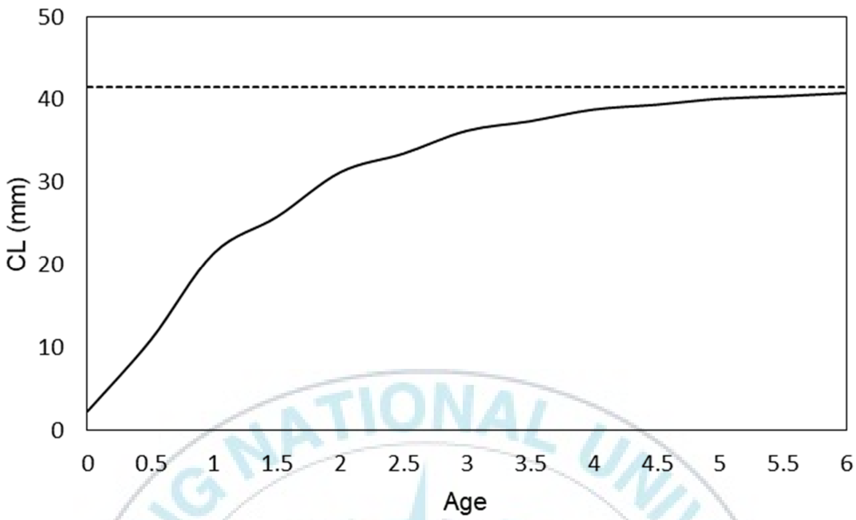


Figure 6. Length-frequency distribution of *Oratosquilla oratoria* (De Haan, 1844) with seasonal Von Bertalanffy growth curves; (a) Males, and (b) Females

Table 3. Estimated parameters of the ELEFAN analysis of length-frequency distribution for males and females of *Oratosquilla oratoria* (De Haan, 1844). (CL_{∞}: Asymptotic length (mm); K: Growth coefficient (yr^{-1}); C: Amplitude of growth oscillation; WP: winter point; R_n: Score function)

Parameters	Males	Females
CL_{∞}	41.52	35.1
K	0.67	0.82
C	0.41	0.38
WP	0.23	0.12
R_n	0.482	0.389

(a)



(b)

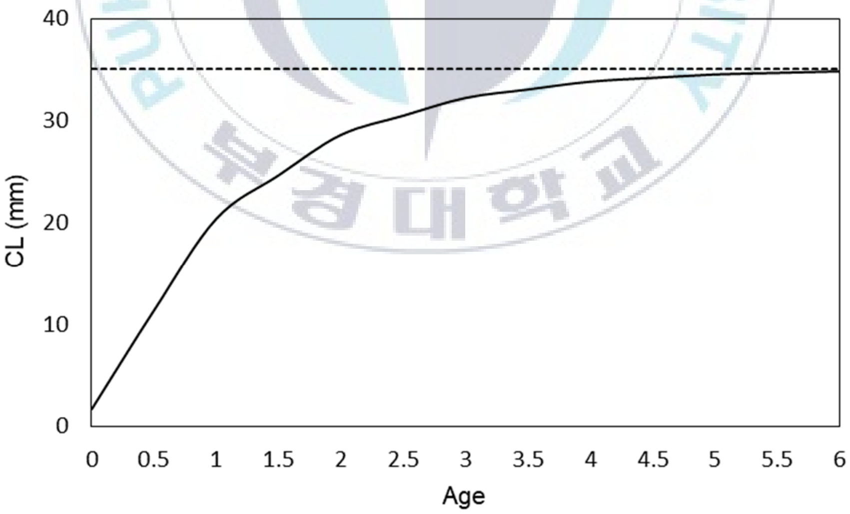
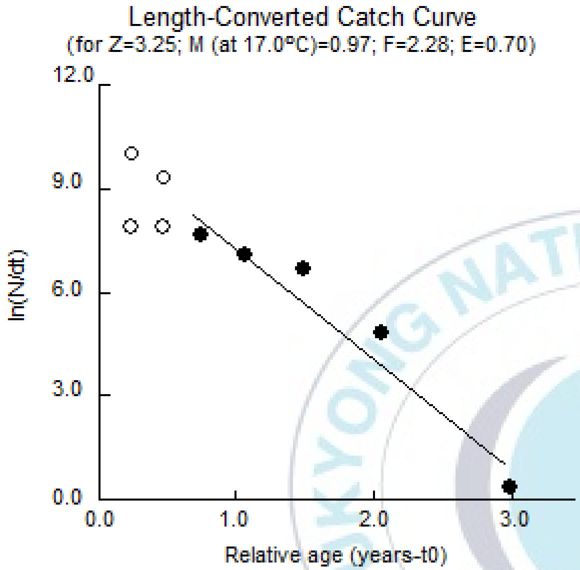


Figure 7. The Von Bertalanffy growth curve of *Oratosquilla oratoria* (De Haan, 1844); (a) Males, and (b) Females; (Dotted line: CL_{∞})

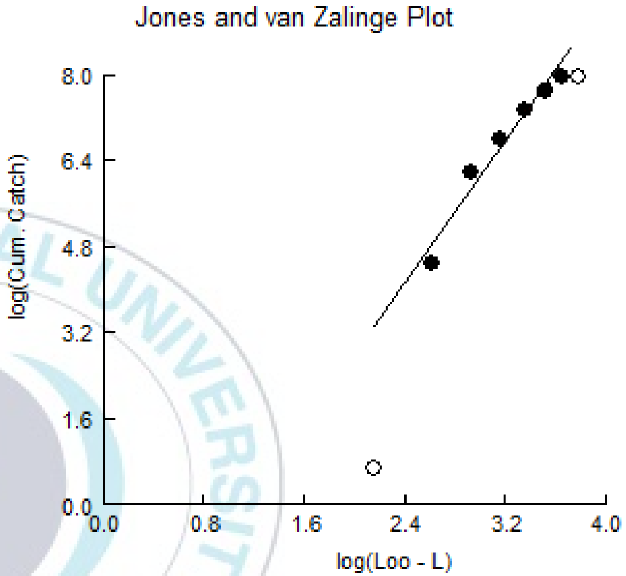
3-5) Mortality & Recruitment pattern

Total mortality (Z) was 3.25 yr^{-1} (Fig. 8a) when calculated from the length-converted catch curves, and 3.21 yr^{-1} (Fig. 8b) from Jones & van Zalinge's plot. Fishing mortality (F) and natural mortality (M) from the length-converted catch curves were 2.28 yr^{-1} and 0.97 yr^{-1}, respectively. The exploitation ratio (E=F/Z) was 0.70.

Recruitment pattern, obtained from FiSAT , determined that recruitment peak appear two times in one year (Fig. 9).



(a)



(b)

Figure 8. Length-converted catch curve (a) and Jones and van Zalinge plot (b) for *Oratosquilla oratoria* (De Haan, 1844)

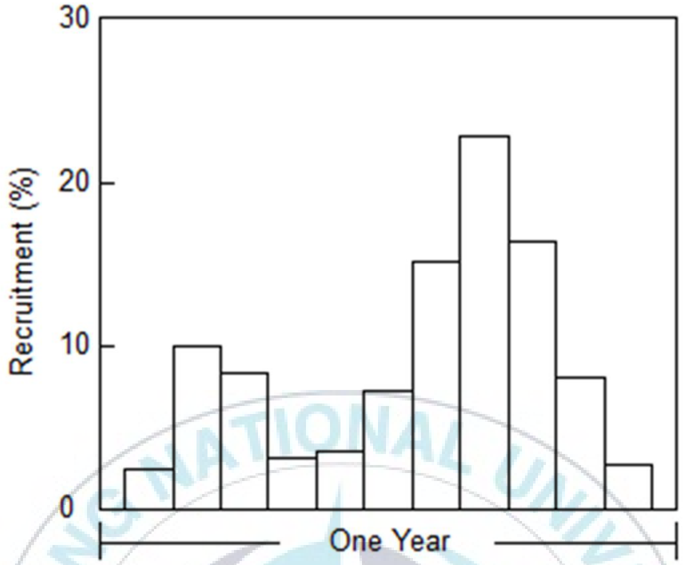


Figure 9. Recruitment pattern of *Oratosquilla oratoria* (Da Haan, 1844)

3-6) Spawning period

The spawning period was determined by the proportion of female gonad stages and the gonadosomatic index (GSI). The GSI mainly peaked in the period from April to June (late-spring to summer) and sub-peaked in January (winter) (Fig. 10). The GSI values were significantly different between months ($H = 191.43,\ df = 16,\ P < 0.001$).

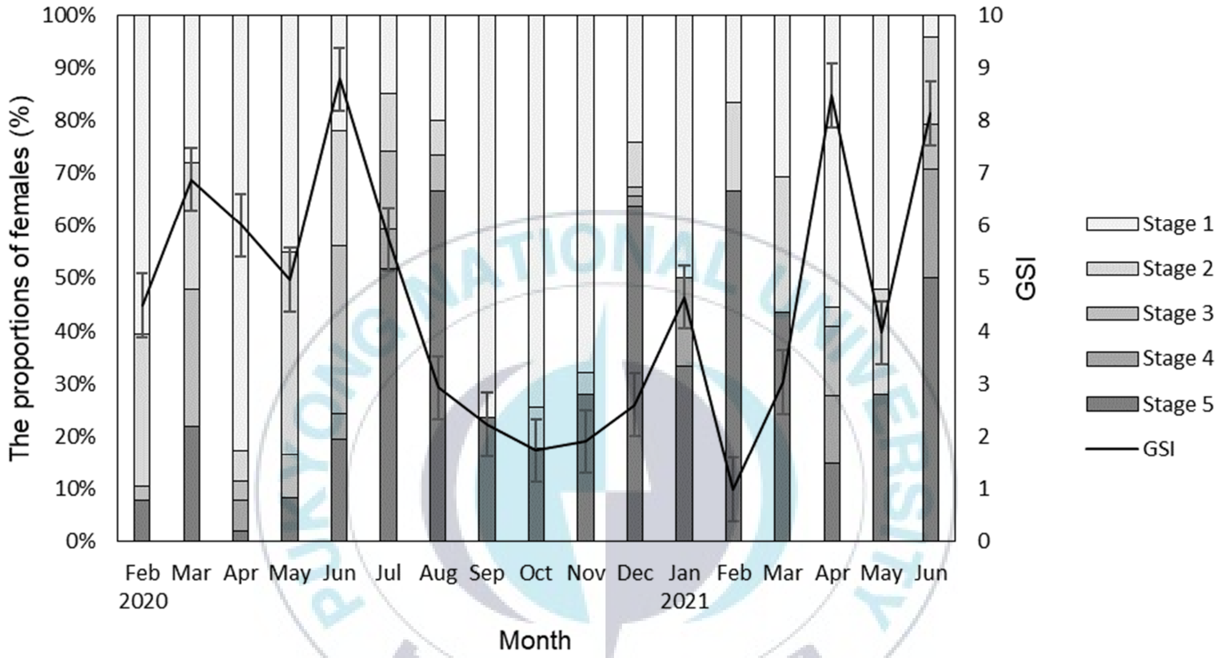


Figure 10. Monthly values of GSI and the proportions of female gonad stage of *Oratosquilla oratoria* (De Haan, 1844)

3-7) Size at sexual maturity (CL_{50})

The observed size of mature females ranged from 12.19 – 34.57 mm in this study. The size at sexual maturity (CL_{50}) of females was estimated as 24.43 mm. The proportion of sexually matured females by size (P) was determined by fitting a logistic equation with length as followed (Fig. 11):

$$\mathrm{P} = 1/(1 + e^{-(5.1203 - 0.2096CL)})$$

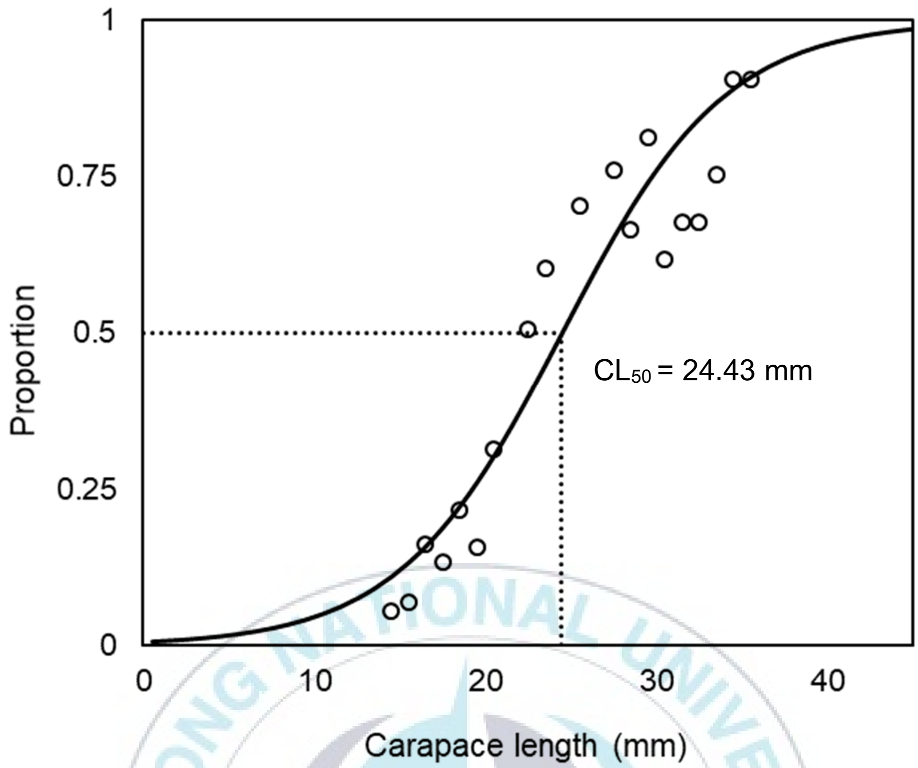


Figure 11. A logistic function determining the proportion of sexually matured females to carapace length (CL) of *Oratosquilla oratoria* (De Haan, 1844) in Goheung. The dotted line corresponds to a proportion of 0.5

3-8) Fecundity

A total of 50 individuals with gonad stage at 3 and 4 were investigated for the determination of fecundity. The relationship between carapace length (CL) and fecundity (F) is calculated by the equation (Fig. 12):

$$\mathrm{F} = 3.1773CL^{3.0087} \quad (n = 50, r^2 = 0.90, P < 0.001)$$

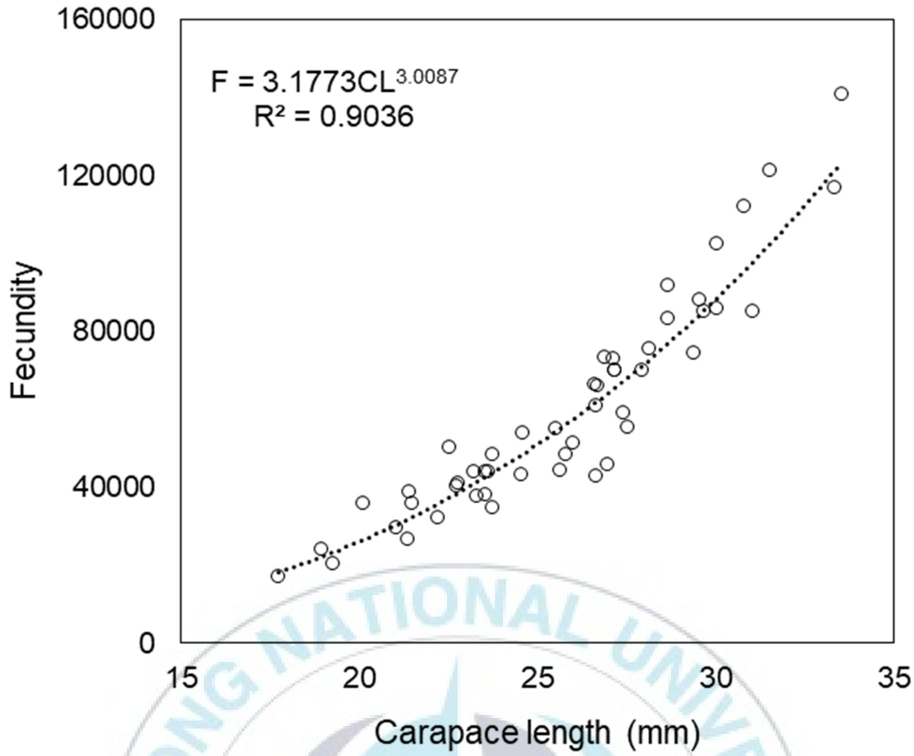


Figure 12. Relationship between fecundity (F) and carapace length (CL) of *Oratosquilla oratoria* (De Haan, 1844) in Goheung, Korea

4. Discussion

Population size increases when the temperature rises. This suggested that there is a correlation between the temperature and the number of individuals. However, exceptionally, the population was very small in July and August despite the warm temperatures. This could be explained by increased jellyfish population size which is co-occurred under warm temperature regime (Purcell, 2005). Large jellyfish bloom affects fishery catch such as shrimp and crabs (Jiang *et al.*, 2008). Due to this influence, it could be disturbed by jellyfish population when the beam trawl was pulled up, thus affecting the composition and total amount of fisheries. It means a decline of crustacean population due to a surge in jellyfish in summer, resulting in sharp decrease in catch of mantis shrimp in this study.

The sex ratio of *Oratosquilla oratoria* was significantly greater in females than males. Similar result can be found in *Harpiosquilla raphidea* (Wardiatno and Mashar, 2010), *Xiphopenaeus kroyeri* (Grabowski *et al.*, 2014), and *Metapenaeus affinis* (Gerami *et al.*, 2013). Female-biased sex ratio arise for several reasons. Sex reversal in penaeid shrimps and growth difference between sexes in decapod crabs lead to changes in sex ratio (Wenner, 1972). However, approximately from March to May in both 2020 and 2021, the proportions of males were higher than females compared to other seasons. Higher male proportions can be explained by natural habits of female around spawning period. Female mantis shrimps are adopted to a burrowing life while reproduction occurs (Hamano and Matsuura, 1984). In this reason, catch of females can decrease at the period of spawning season.

There was a significant difference in LFD between both sexes. Generally, frequency of females was larger, but it can be seen that as the length of carapace increases, the frequency of males increases. Two evidence can be presented. Due to the nature of spawning, females need to allocate energy to reproduction (Roa and Ernst, 1996), whereas males can allocate more energy to growth. Therefore, females are expected to be smaller in size than males. For other reason, in this case, it could be a problem with the sample itself. For most crustaceans, females are significantly larger than males in length-frequency distribution (Segura and Delgado, 2012; Papaconstantinou and Kapiris, 2003; Kalogirou *et al.*, 2017) Since the mesh size of net is small in this study, small individuals may have been caught much more than large individuals. In addition, some months have few samples to be collected under unfavorable weather condition. Therefore, subsequent experiments will be made for larger individuals.

Slopes of linear regression between carapace length and body weight showed significant difference for males and females, which results that the relative growth between both sexes are different. Slope was smaller than 3 in males, but larger than 3 in females. Allometric growth in carapace length and body weight was indicated (Hartnoll, 1982) as negative allometric growth in males and positive allometric growth in females. In previous study (Kim *et al.*, 2017), there was no significant difference between slopes. The differences between the two studies come from variation in size of individual for the relationship. Previous study employed commercial size or larger size, and this study smaller size than that. Different results may have been derived depending on the size of the population.

Parameters in seasonal Von Bertalanffy growth function showed different factors between males and females. Females had lower CL_∞ value and higher K value than males. C and WP values were higher in male. Growth performance index (φ') was higher in males than females, suggesting that male grew faster than females. Other previous studies of *O. oratoria* presented similar results (Ohtomi and Shimizu, 1988; Hamano, 1990; Kim *et al.*, 2017; Table 4). Differences in growth parameters arise from the differences in the main purpose of energy use between males and females. Males grow larger to make courtship and copulation more efficiently (Hartnoll, 1985).

Table 4. Comparison of growth performance index (φ′) for *Oratosquilla oratoria* (De Haan, 1844) in various areas.

Area	φ'		Authors
	Male	Female	
Tokyo Bay	4.09	4.01	Ohtomi and Shimizu, 1988
Hakata Bay	1.79	1.77	Hamano, 1990
Tongyeong	4.44	4.39	Kim *et al.*, 2017
Goheung	3.06	3.00	This study

The GSI values of *O. oratoria* are generally known to increase in summer and decrease at winter (Torisawa et al., 1998). In Torisawa et al. 1998, the GSI gradually increased from April to June, decreased in July, and began to increase again after October until November. The female GSI values in this study have been determined to peak at June in 2020 and from April to June in 2021. Sub-peak was calculated in 2021 January. The main spawning period of *O. oratoria* was summer. In this study, however, multiple spawning could be suggested from recruitment pattern. Two GSI peaks were found in a year. In several cases, mantis shrimp have two spawning period. Previous study showed that the first spawning season took place in May to June for more than 1-year-old individuals, and the second in July to September for 0-1-year-old individuals (Kodama et al., 2006). CL_{50} was calculated as 24.43 mm and with the Von Bertalanffy growth equation, the age at CL_{50} corresponded to approximately 1.5-year-old. It can be seen that they mature from 1-year-old, and from this, main spawning occurring mainly at 1.5 years old can be supported.

Recruitment pattern presents that percentage of recruitment peaks twice in one year. This result is consistent with that of GSI monthly changes. The age of first juvenile stage of *O. oratoria* is 36-59 days (2-3 months) (Hamano and Matsuura, 1987), implying that it takes 2-3 months until recruitment. From this, it can be confirmed that the recruitment rate increases according to the spawning period.

The total mortality (Z) of *O. oratoria* was 3.25 and 3.21, estimating similar results for both methods. The mortality rates are different among mantis shrimps (Table 5) (Wardiatno and Mashar, 2012; Arshad *et al.*, 2015; Warahma *et al.*, 2021). Natural mortality (M) was similar to other species, but fishing mortality (F) was dramatically higher than others, resulting in higher total mortality (Z). In this study, exploitation ratio (E) value was 0.70 which is higher than optimal value (=0.5). This means that fishing mortality is the major cause of mortality of *O. oratoria* and control of fishing mortality is needed to sustain the species.

Table 5. Comparison of mortality (M, F, Z) for a variety of Stomatopoda species (Value of Males (Females), where two values are shown).

Species	M (yr^{-1})	F (yr^{-1})	Z (yr^{-1})	E	Authors
Oratosquilla oratoria	0.97	2.28	3.21	0.70	This study
Harpiosquilla raphidea	0.473	0.347	0.820	0.42	Wardiatno and Mashar, 2012
Harpiosquilla harpax	2.247 (1.674)	1.837 (1.585)	4.084 (3.259)	0.449 (0.486)	Arshad *et al.*, 2015
Gonodactylus chiragra	0.76 (0.80)	0.52 (0.75)	1.28 (1.55)	0.41 (0.48)	Warahma *et al.*, 2021

The development stages of gonad were isochronic among different parts of the ovary (Kodama *et al.*, 2004), which indicates that whole gonad develop simultaneously. In previous study, the relationship of fecundity was calculated with body length (Kodama *et al.*, 2004). As a result of converting the relationship between carapace length and fecundity through the relation between carapace length and body length, the equation with an exponent of 2.81 is derived, which indicates negative allometric growth. However, the slope of regression equation between fecundity and carapace length in this study fell into 3 in 95 % confident interval, suggesting isometric growth.

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