Thesis for the Degree of Master of Science

Reproduction and growth of the spiny lebbeid shrimp, *Lebbeus groenlandicus* (Fabricius, 1775) (Caridea, Hippolytidae) in the deep-water of the East Sea, Korea

by

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Reproduction and growth of the spiny lebbeid shrimp, *Lebbeus groenlandicus* (Fabricius, 1775) (Caridea, Hippolytidae) in the deep-water of the East Sea, Korea (동해 심해에 서식하는 가시배새우의 생식과 성장)

Advisor: Prof. Chul-Woong Oh

by

Ho Jin Bae

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Abstract

Reproduction and growth of the spiny lebbeid shrimp, *Lebbeus groenlandicus* (Fabricius, 1775) are investigated in the East Sea of Korea from January 2012 to April 2013. An understanding of the reproductive strategies of a species is critical for understanding its population dynamics and biogeographic patterns (Ramírez-Llodra, 2002). Deep sea species would not undergo the seasonal periodicities in breeding shown by their relatives in shallower water subject to annual change in water temperature, but, instead, breeding would take place year-round (Orton, 1920). Population parameters are necessary in order to understand the health of any fishery to determine appropriate management measures (Nwosu, 2008). The proportion of females was significantly greater than that of males (male:female ratio, 4.6:5.4). Females were predominant on larger class size than males.

Significant differences on slopes of carapace length versus body weight linear regression between sexes indicate sex-specific differences in allometric growth. The gonadosomatic index (GSI) varied monthly, reaching a maximum in November 2012 (10.28) and a minimum in March 2013 (2.15). Monthly variations in the proportions of ovigerous females showed all months. The highest values of the GSI coincided with the breeding period of *L. groenlandicus*. There was significant difference between the mean GSI of females with non-eyed and eyed eggs, indicating that *L. groenlandicus* is a consecutive breeder. There was a significant correlation between carapace length and the number of eggs at early egg stages. There was significant difference in the slope of the regressions of carapace length versus the number of eggs between females carrying non-eyed and eyed egg stages, indicating that there was brood loss during the incubation period. Based on dry weights in early egg stages, reproductive output was determined 0.18 ± 0.006. The von Bertalanffy growth function parameters were $CL_\infty = 38.80\,mm, K = 0.48\,yr^{-1}, C = 0.5, WP = 0.4$ for males and $CL_\infty = 43.64\,mm, K = 0.41\,yr^{-1}, C = 0.6, WP = 0.6$ for females. The growth performance index (φ') is 2.86 for males and 2.89 for females. This study verified the biological characteristics of *L. groenlandicus* inhabiting the deep sea in the East Sea of Korea. The present study will help manage fisheries resources based on ecological parameters, which was provided from the study.

1. Introduction

Most shrimp species are found in tropical and subtropical regions, with a marked decrease in number towards temperate and cold regions (Castilho *et al.*, 2008). Hippolytid shrimps are distributed in neritic, from the littoral zone through shelf depths, with few deep-sea species (Bauer, 2004). Shrimps of the genus *Lebbeus* inhabit cool temperate to arctic waters in the northern Pacific Ocean (Wicksten, 1982). The spiny lebbeid shrimp, *Lebbeus groenlandicus* (Fabricius, 1775) is broadly distributed in the northern Pacific Ocean, from the Bering Sea and Puget sound to East Sea and northern Japan, at depth ranging from 200 m to 400 m on the continental slope and ocean floor (Kim and Choi, 2006).

An understanding of the reproductive strategies of a species is critical for understanding its population dynamics and biogeographic patterns (Ramírez-Llodra, 2002). Deep sea species would not undergo the seasonal periodicities in breeding shown by their relatives in shallower water subject to annual changes in water temperature, but, instead, breeding would take place year-round (Orton, 1920). These traits are very different in various habitat and species.

Growth is as important as reproduction. Fecundity determines population size. If they are hatched and grew, population size is able to grow. Early stage individual grows faster than adult. Fast growth of early stage individual is able to decrease the threat from predators, get swimming ability and develop reproductive ability.

The study of *L. groenlandicus* is the only one which described larval stage in Alaska (Haynes, 1977). Despite importance of reproduction and growth, studies of the ecology and reproductive characteristic of *L. groenlandicus* are little.

The aim of this study is to reveal 1) the differences in the size structure of the population, 2) the reproductive traits and 3) the von Bertalanffy growth equation of deep water shrimp, *L. groenlandicus*.

The hypotheses are no significant difference 1) of sex ratio and length-frequency distribution between sexes, 2) in the reproductive traits (relationship between non-eyed and eyed eggs, reproductive output) between non-eyed and eyed eggs, 3) of the slope and the intercept of the linear regression and 4) in growth between sexes.

2. Materials and methods

2-1. Sample collection

Lebbeus groenlandicus specimens were monthly sampled in the East Sea of Korea during January 2012 until April 2013. Samples were collected in the depth range of 200 – 400 m, using otter trawl. Shrimps were preserved in 10% neutralized formalin solution.

2-2. Sex ratio

Samples were identified by Kim (1977) separated according to sex and measured. Sex was determined to the naked eye based on the presence or absence of the appendix masculina on the endopodite of the second pleopod (Bauer, 2004) (Fig. 1). The sex ratio was based on the proportion of females.

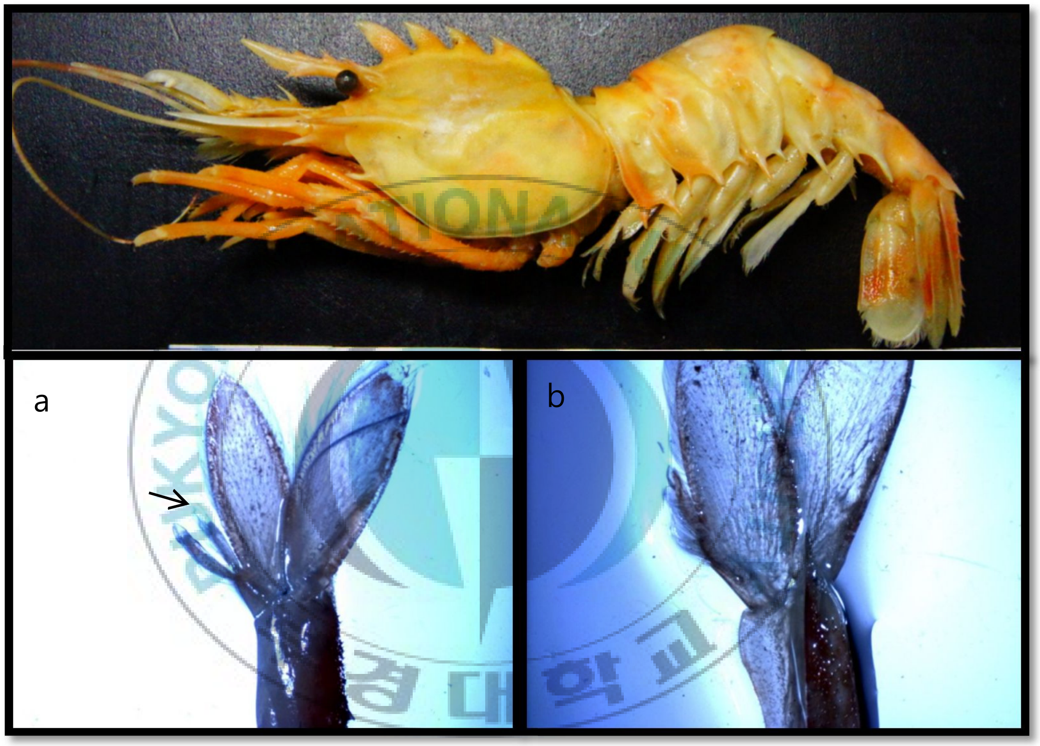

Fig. 1. Morphology of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. Top is the entire body and bottom is the second pleopod. a: male; b: female; arrow: appendix masculina.

2-3. Length-frequency distribution

Population structure was determined based on length-frequency distribution of both sexes. Length-frequency distributions of each sex were constructed using 1 mm length intervals of carapace length, measured from the base of the eyestalk to posterior edge of the carapace.

2-4. Morphometric relationship

Morphometric relationship was investigated between carapace length and body weight. Carapace length was measured with the same method as used on length-frequency distribution measurement, while body weight was measured using digital balance to the nearest 0.01 g after all remain water was removed from shrimp body. The relationship between carapace length (CL) and body weight (BW) were analyzed linear regression using natural log transformed data and calculated separately for males and females, presented by allometric graph on both sex separately. Linear regression test used this following equation;

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

where, a was intercept and b was slope. For the relationship carapace length and body weight, the pattern was established by the b-value slope ($b = 3$, isometry; $b < 3$, negative allometry and $b > 3$, positive allometry). Pooled regressions are given only when differences between the slopes or intercepts of separate regressions were statistically not significant.

Intra-specific variation in morphometric relation between different sexes was indicated using slopes value differences between regressions of two sexes. According to Anger and Moreira (1998), different intercepts are difficult to interpret, because this parameter may represent an extrapolation below the range measured, and its comparison may have little biological meaning. By contrast, the slope should be a more useful growth parameter, indicating a different degree of dependence among size dimensions (Anger and Moreira, 1998).

2-5. Ovarian examination

The ovarian stages were determined according to Bauer's (1986) illustrations of size and shape in proportion to the gastric mill and thoracic cavity, and external appearance of the ovary. In present study, the ovarian stages were determined by modified Bauer's illustrations (Table 1). Four main stages of development were established: immature (stage 1, 2); maturing (stage 3); ripe (stage 4); spent. Body and ovarian dry weight were determined by drying at 80℃ for 48 h and weighing to the nearest 0.0001 g using an electronic digital balance. GSI was determined by the following formula;

$$\text{GSI} = \frac{Ovarian\ dry\ weight}{Body\ dry\ weight} \times 100$$

Table 1. Ovary stage modified from Bauer (1986)

Stages	Descriptions according to Bauer (1986)	Present study
Stage 1	No noticeable development	Immature
Stage 2	Vitellogenic oocytes distinct but ovary small	
Stage 3	Ovary filling at least half the space above the cardiac stomach	Maturing
Stage 4	Ovary completely filling that space	Ripe
	Similar shape with stage 1 but vestige of breeding	Spent

2-6. Egg size

Egg size of ovigerous females was recorded as two stages: (1) non-eyed egg; and (2) eyed egg (Fig. 2). Eggs were carefully stripped from pleopods using fine forceps. For egg volume calculation, 10 eggs were selected before drying. These were measured along the major and minor axes (including the chorionic membrane tightly adhering to the egg surface), using a binocular microscope with a calibrated eyepiece. Eggs were treated as ellipsoids and volume quantified by the formula:

$$V = \frac{4}{3}\pi r_1 {r_2}^2$$

where r_1 is half the major axis and r_2 is half the minor axis.

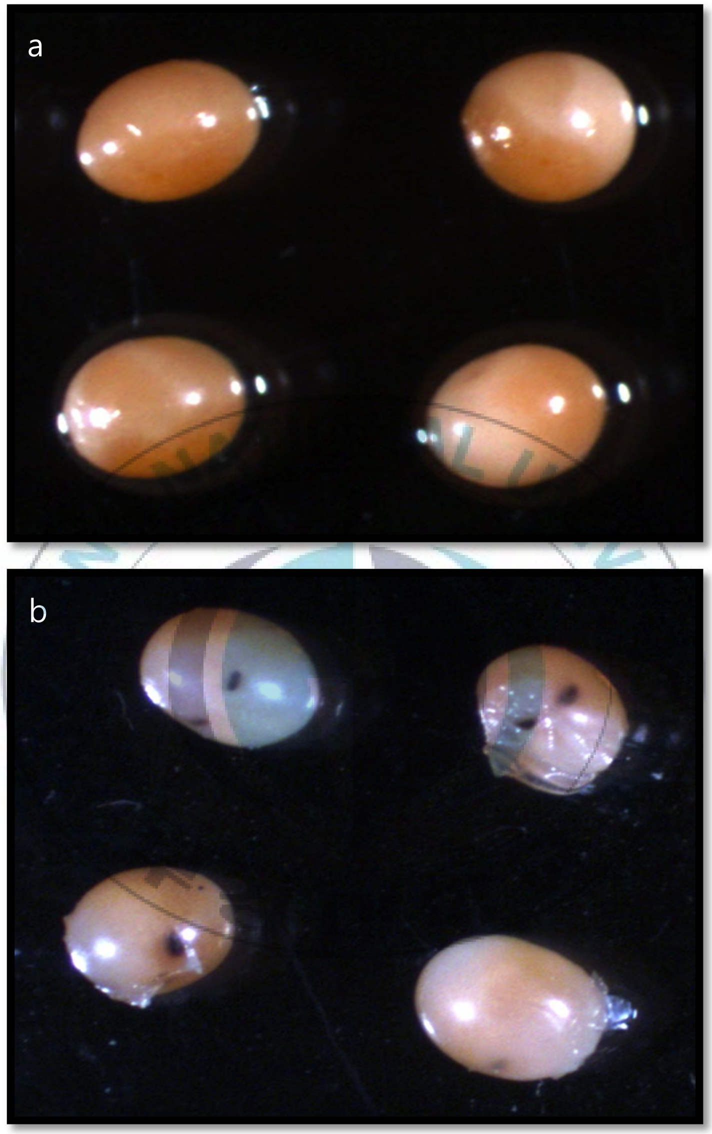

Fig. 2. Egg stage of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. a: Non-eyed stage eggs; b: Eyed stage eggs.

2-7. Relationship between body size and the number of eggs

The relationship between carapace length and the number of eggs was estimated using data of ovigerous females with non-eyed and eyed eggs. The size and fecundity data were natural log transformed so that the data conform more closely to the assumptions of linear regression analysis regarding homogeneity of error variance over the range equation. Linear regression test on natural log transformed data of carapace length (CL) and the number of eggs (EN) was used to find the relation between body size and the number of eggs, with following equation:

$$\ln EN = a + b \ln CL$$

where, a was intercept and b was slope, consider a constant rate of increase. For the relationship carapace length and the number of eggs, the pattern of allometry was established with the same method on carapace length - body weight relationship. Slope and intercept of both non-eyed and eyed egg stage linear regression were compared to investigate brood mortality.

2-8. Fecundity and reproductive output (RO)

Eggs were carefully stripped from pleopods using fine forceps and any setal material or extraneous matter was removed. All of the eggs were counted directly to eliminate error which might be caused by indirect methods. For carapace length - fecundity relationship and reproductive output estimation all females with spawned eggs were used. Female and egg dry weights were determined by drying at 80℃ for 48 h and weighing to nearest 0.0001 g using an electronic digital balance. Reproductive output (RO) was estimated using dry weight by applying the formula given by Clarke *et al.* (1991):

$$RO = \frac{total\ mass\ of\ egg\ batch}{mass\ of\ female}$$

2-9. Size at sexual maturity (CL_{50})

The proportion of sexually mature females, based on the number of non-ovigerous and ovigerous females exceeding stage 2 in ovary development was obtained for each size class. A logistic curve may be fitted to the proportion of sexually mature females by carapace length. Adapting Campbell (1985) gives:

$$P = \frac{1}{(1 + e^{-(a+b\cdot CL)})}$$

where a and b are parameters. The parameter estimation of this equation was made by correlation analysis of variable P and CL after linearization. Size at sexual maturity (CL_{50}) is the carapace length which corresponds to a proportion of 0.5 in reproductive condition. It was calculated from the ration between the constants a and b:

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

2-10. Growth

Length-frequency distributions were constructed using 1 mm length intervals of carapace length. Growth was described using the modified von Bertalanffy growth function (VBGF) (Pauly and Gaschüz, 1979):

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

where L_∞ is the asymptotic length, K is the intrinsic growth rate, t_0 is the age at which the length of shrimps 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 length-frequency distributions using the ELEFAN program in FiSAT II 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 estimates the growth parameters(L_∞, K, C and WP) without standard errors. According to Pauly (1987), t_0 estimates cannot be obtained solely from the length-frequency data, so ELEFAN routines alone allow their calculation. Thus t_0 was estimated using the relation described by Lopes Veiga (1979).

$$t_0 = \frac{1}{K}(\ln\frac{L_\infty - L_h}{L_\infty})$$

where L_h is the carapace length at hatching. In this paper, the value used for L_h was 1.4 mm CL [values converted from 6.9 mm TL in 1st zoeal stage described by Haynes (1977)].

Growth performance of *L. groenlandicus* was using a growth performance index (φ′) (Pauly and Munro, 1984):

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

The growth performance index is preferred for growth comparison rather than comparison of L_∞ and K individually, because these two parameters are correlated. The growth performance index is more robust than either L_∞ 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.

2-11. Statistical analysis

The differences in the length-frequency distribution between the two sexes were determined with the Kolmogorov-Smirnov two-sample test. Chi-squared test was used to determine if the observed ratio of male to female sex ratio was differed from the expected 1:1 ratio. Kruskal-Wallis test was used to investigate the monthly mean variation on GSI. Student *t*-test was used to investigate the difference in egg volume and the difference of GSI values between non-eyed egg and eyed egg stages. Linear regression analysis with using natural log transformed data was used for investigate the relationship between carapace length - body weight on each sex and carapace length - fecundity on both egg stages. Analysis of covariance (ANCOVA) was used to compare the difference in slope and intercept of regressions on relation between; 1) carapace length and body weight of male and female and 2) carapace length and the number of eggs of non-eyed and eyed eggs. MINITAB (v.16) and SYSTAT (v.13) were used for all the statistical analysis and mean value was presented with 95% confidence limit.

3. Result

3-1. Sex ratio

Of 2,964 specimens (1,365 males and 1,599 females), percentage of females (53.9%) was significantly greater than that of males (46.1%) $(x^2 = 9.25, df = 1, P < 0.01)$ (Fig. 3).

3-2. Length-frequency distribution (LFD)

A total 2,964 shrimps were collected during sampling between January 2012 and April 2013. Kolmogorov–Smirnov two-sample test revealed a significant difference in the length-frequency distributions of the males and females $(P < 0.001)$. Females were predominant in larger size classes, whereas males were in smaller size (fig. 4).

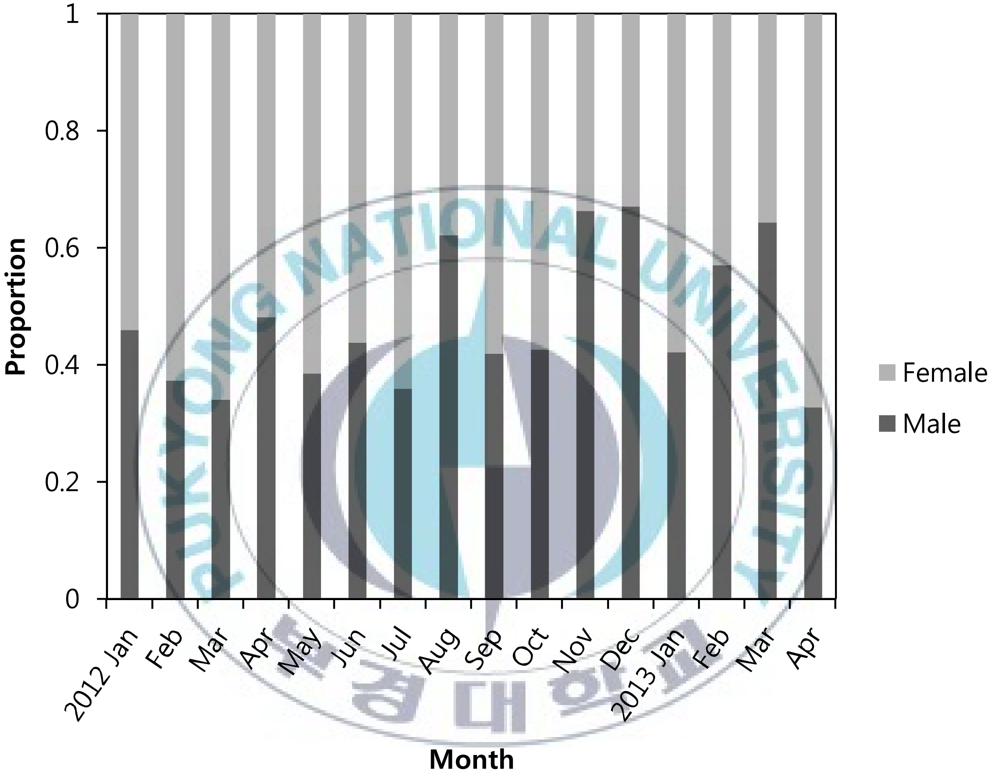

Fig. 3. Sex ratio of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea.

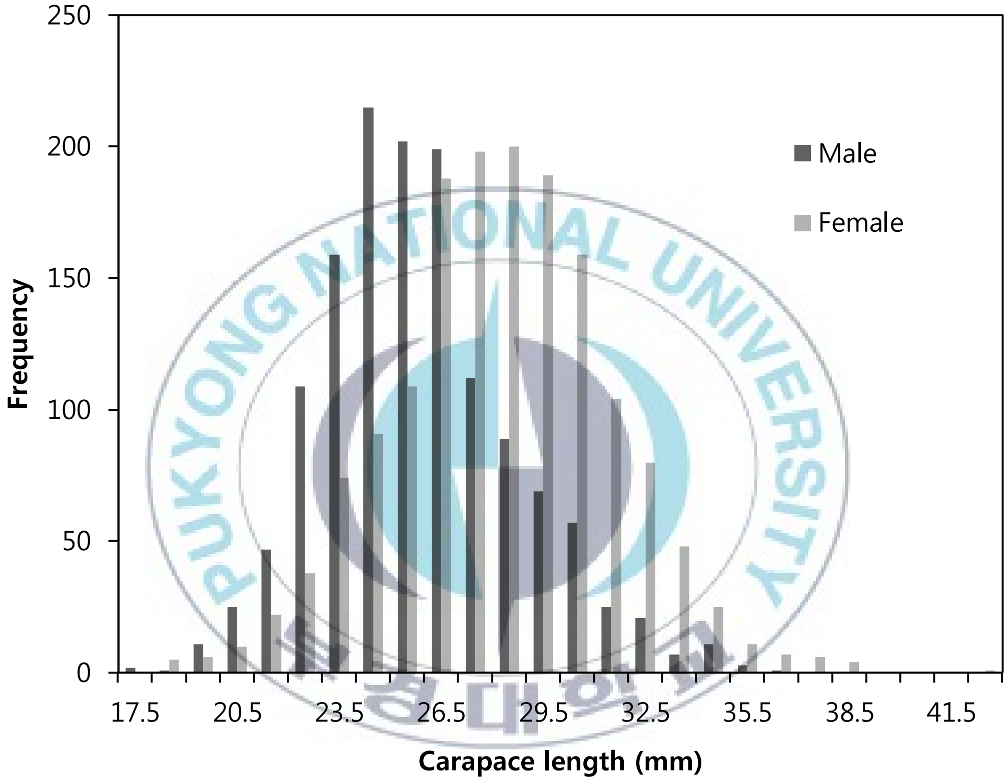

Fig. 4. Length-frequency distribution of males and females of *Lebbeus groenlandicus* (Fabricius, 1775) during study period in the East Sea, Korea.

3-3. Morphometric relationship

The body size of males was smaller than females. Mean carapace length of males was 25.84 ± 0.08 mm (range, 17.03 – 36.72 mm), while that of females was 28.23 ± 0.08 mm (range, 18.48 – 42.4 mm). Mean body weight of males was 19.51 ± 0.18 g varied from 5.83 – 54.71 g and females 27.21 ± 0.25 g varied from 6.09 – 67.45 g.

The relationship between carapace length and body weight was analyzed by linear regression using natural log transformed data of both variables on each sex (table 2).

Table 2. Linear regression of carapace length (CL) and body weight (BW) of male and female, mean ± standard error of carapace length and body weight of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea.

Sex	Linear regression	CL (mm)	BW (g)
Male	$\ln BW = 2.6808\ (\pm 0.0613) \ln CL - 5.7822$ $(n = 1365, r^2 = 0.8439, P < 0.001)$	25.84 ± 0.08	19.51 ± 0.18
Female	$\ln BW = 2.9453\ (\pm 0.0657) \ln CL - 6.5831$ $(n = 1575, r^2 = 0.8291, P < 0.001)$	28.23 ± 0.08	27.21 ± 0.25

The relationship between carapace length and body weight was negative allometry for male *L. groenlandicus* expressed by the slope on linear regression of male, which is smaller than 3. In female, however, the relationship between carapace length and body weight was isometry expressed by the slope on linear regression of female, which is approximately 3 (Fig. 5).

A significant difference on slope of regressions of log carapace length versus log body weight between male and female, was found indicating a sex-specific difference in the morphometric relationship among carapace length and body weight of between male and female of *L. groenlandicus* (ANCOVA: $F = 142.70, df = 1, P < 0.001$) (Fig. 6).

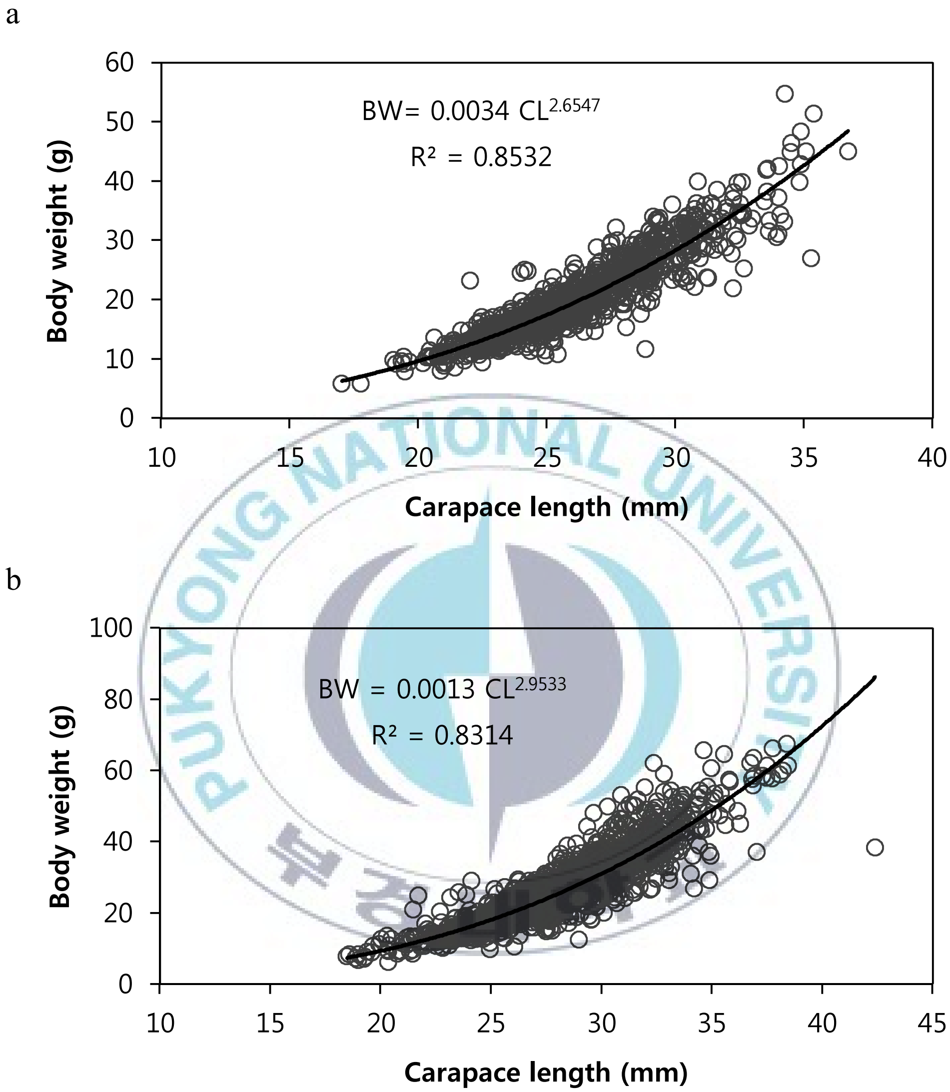

Fig. 5. Relationship between carapace length and body weight of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. a: males; b: females.

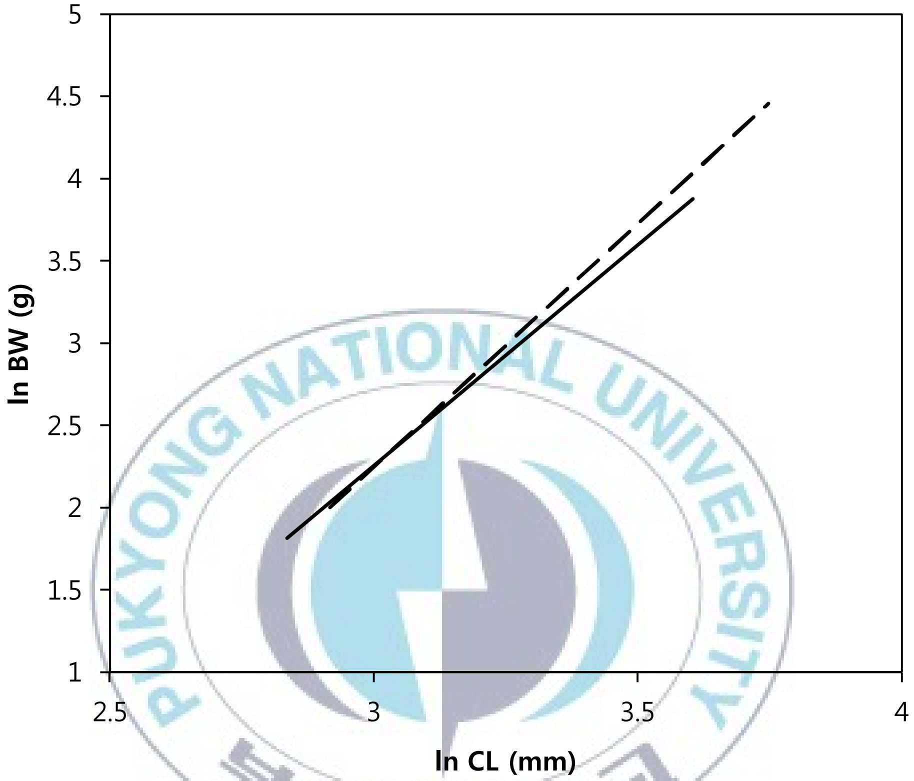

Fig. 6. Relationship between carapace length (CL) and body weight (BW) with natural log transformation of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. solid line: males; dotted line: females.

3.4 Breeding period

Breeding period was determined by the occurrence of ovigerous female. Ovigerous females of *L. groenlandicus* were present all months (fig. 7a).

The GSI started to increase in April, reached a peak in November 2012 (10.28), and decreased to its lowest value in March 2013 (2.15) (Fig. 7b). GSI values varied significantly each month ($H = 139.07, df = 15, P < 0.001$).

GSI values of females with non-eyed and eyed egg stages were significantly different (Student *t*-test, $P < 0.05$) (Fig. 8).

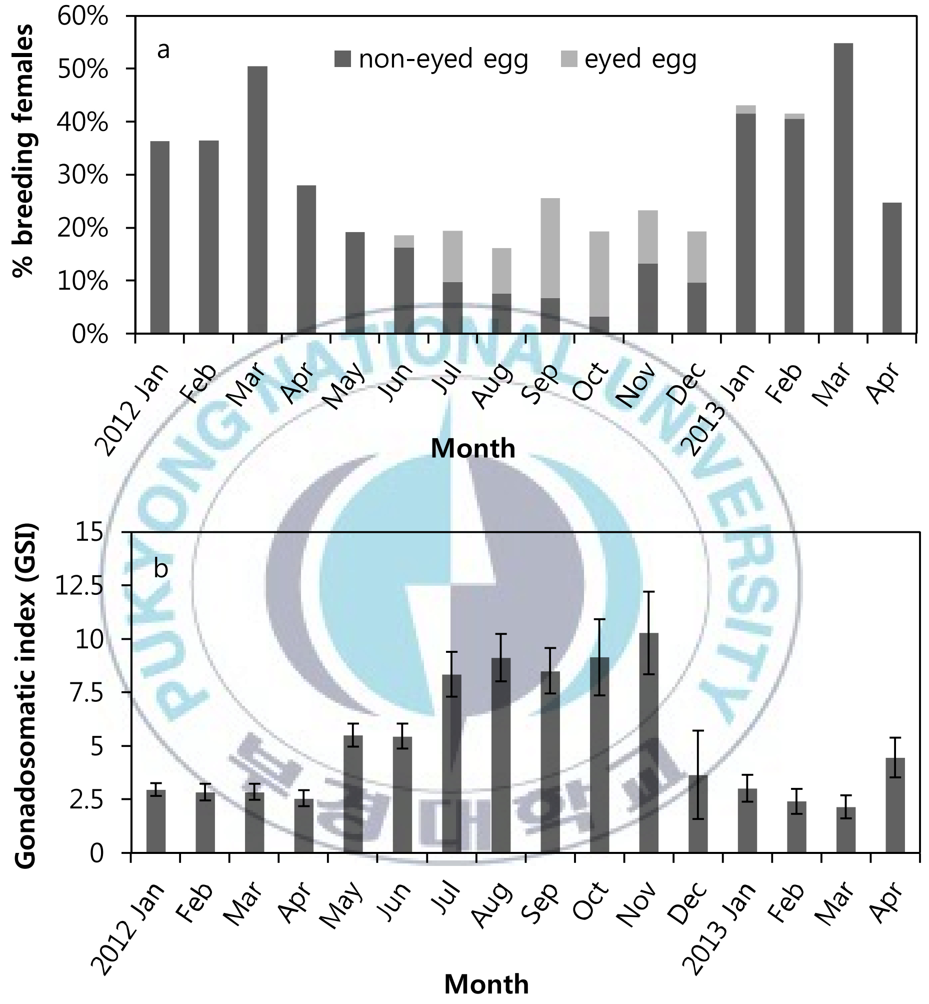

Fig. 7. Monthly variation of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. a: in the proportion of ovigerous females with different egg stages; b: in gonadosomatic index (GSI).

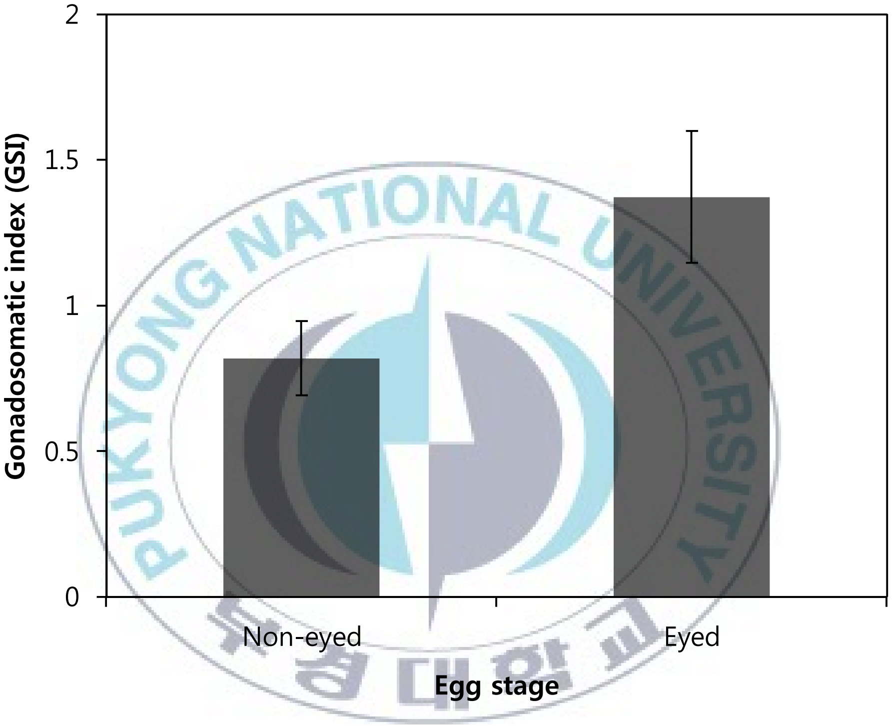

Fig. 8. Mean ± standard error of goandosomatic index (GSI) values for each egg stage of *Lebbeus groenlandicus* (Fabricius, 1775).

3-5. Fecundity and reproductive output

In 182 ovigerous females, 155 females with mean carapace length 28.90 ± 0.17 mm (range, $24.12 - 35.55$ mm) were carried $1{,}089.59 \pm 32.16$ non-eyed eggs (range, $463 - 2{,}600$) and 27 females with mean carapace length 32.10 ± 0.41 mm (range, $28.46 - 36.93$ mm) were carried $1{,}668.26 \pm 74.87$ eyed eggs (range, $923 - 2{,}726$). Mean egg volume of eyed eggs ($3.51 \pm 0.13\ mm^3, n = 51$) was significantly larger than that of non-eyed eggs ($2.91 \pm 0.06\ mm^3, n = 123$) (Student *t*-test, $P < 0.001$) (Fig. 9).

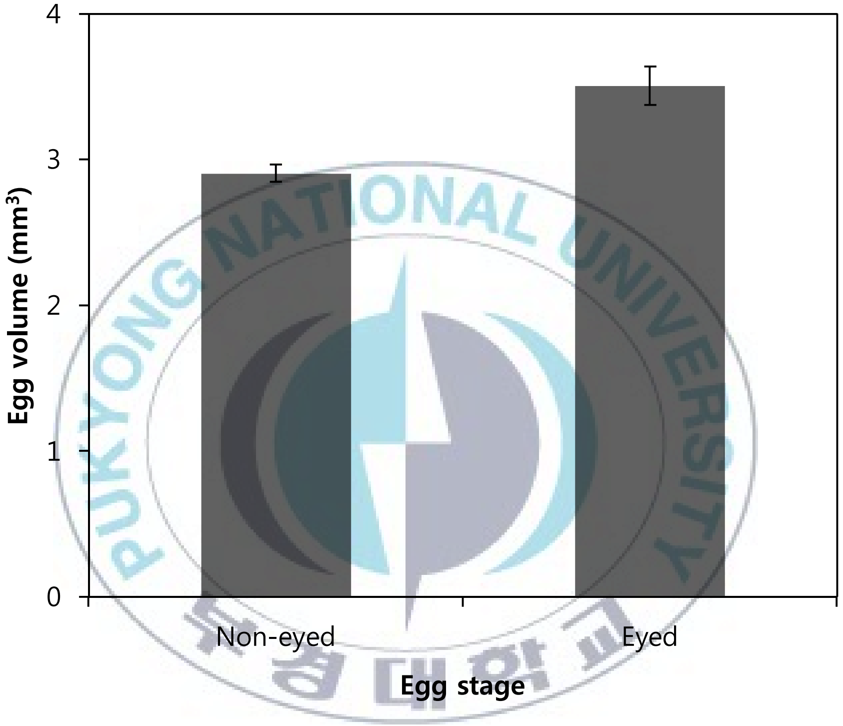

Fig. 9. Mean ± standard error of egg volume of *Lebbeus groenlandicus* (Fabricius, 1775) for each egg stage.

Loge-transformed values of carapace length and the number of eggs in females with non-eyed and eyed egg stages both show statistically significant linear relationships (table 3).

In non-eyed stage, the slopes of the regressions are approximately 3, which imply that the relationships between the variables are isometry: as female carapace length increases, the number of eggs increases isometrically (fig. 10). In eyed stage, however, the slopes of the regressions are less than 3, which imply that the relationships between the variables are negative allometry: as female carapace length increases, the number of eggs increases negative allomerically.

ANCOVA revealed significant difference the number of eggs in the two egg stages as functions of carapace length, indicating brood loss during incubation $(F = 6.40, df = 1, P < 0.05)$ (Fig. 11).

Reproductive output (± standard deviation) was 0.18 ± 0.006 $(n = 352)$.

Table 3. In non-eyed and eyed egg stages, linear regression of carapace length (CL) versus the number of eggs (EN) of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea.

Egg stages	Linear regression
Non-eyed	$ln\,EN = 3.1743\ (\pm 0.5687)\ ln\,CL - 3.7360$ $(n = 154, r^2 = 0.4429, P < 0.001)$
Eyed	$ln\,EN = 1.3857\ (\pm 1.3093)\ ln\,CL + 2.5906$ $(n = 27, r^2 = 0.1597, P < 0.05)$

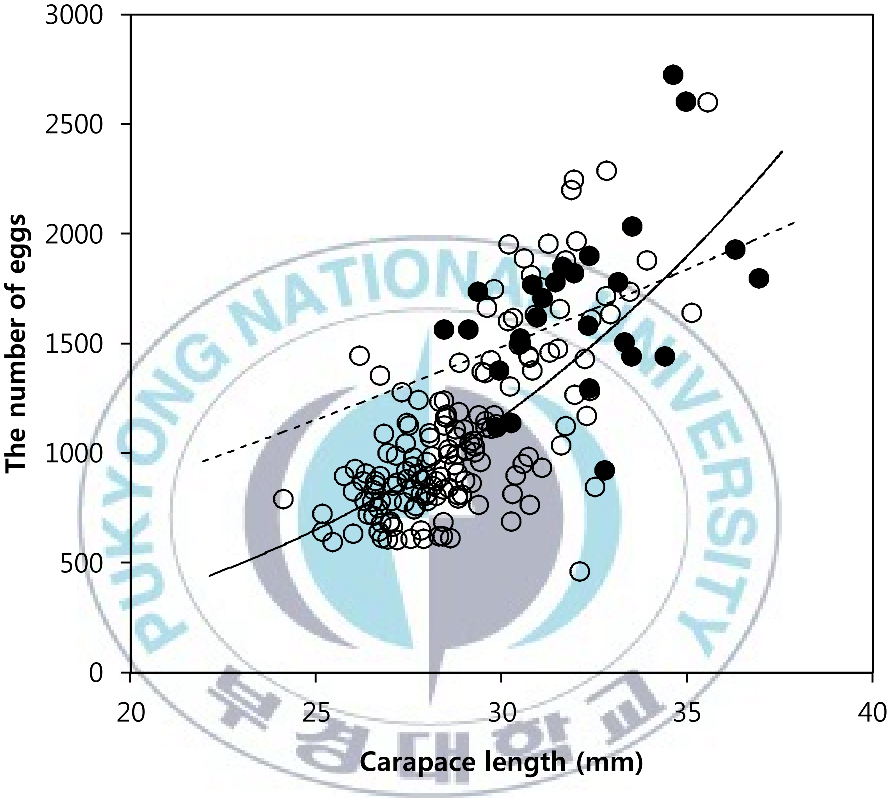

Fig. 10. Relationship between carapace length and the number of eggs on *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. solid line: the non-eyed egg stage (○); dotted line: the eyed egg stage (●).

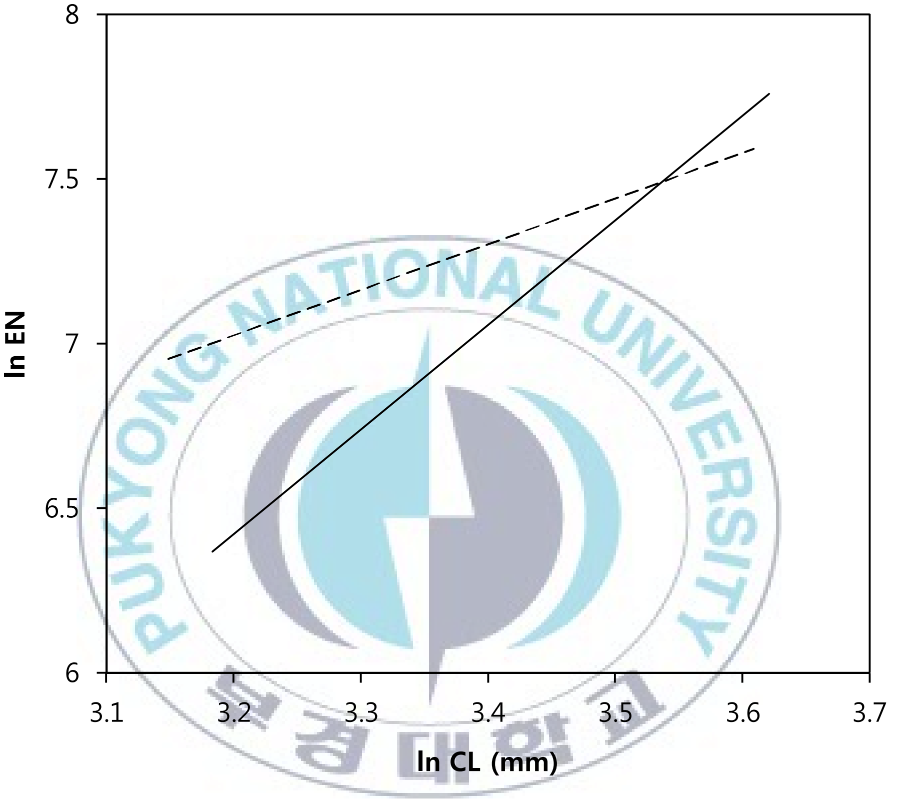

Fig. 11. Linear regression of ln carapace length (CL) and ln number of eggs (EN) on *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. solid line: non-eyed egg stage; dotted line: eyed egg stage.

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

During study period, the 861 of the female *L. groenlandicus* used in the analysis ranged from 10.5 mm to 42.5 mm. The proportion of mature females by length class increased logistically with length (Fig. 12). The 50% maturity size is 22.80 mm.

$$P = \frac{1}{1 + e^{(10.03 - 0.44\,CL)}}$$

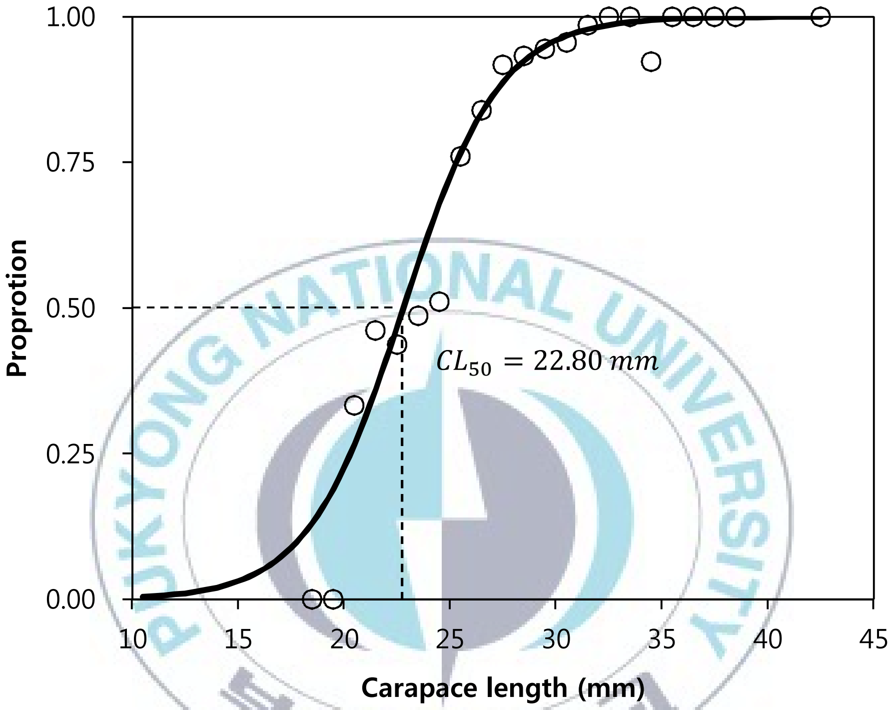

Fig. 12. A logistic function fitting proportion of mature females to carapace length of *Lebbeus groenlandicus* (Fabricius, 1775) in the East Sea, Korea. CL_{50}, which corresponds to a proportion of 0.5, is indicated.

3-7. Growth

The von Bertalanffy growth function parameters estimated by ELEFAN for each sex (Fig. 13) (Table 4). The parameter of asymptotic length (L_∞) in females (43.64 mm CL) is higher than males (38.80 mm CL). However, the parameter of growth coefficient (K) in females ($0.41yr^{-1}$) is lower than males ($0.48yr^{-1}$).

The von Bertalnffy growth equation is follow (Fig. 14):

$$\text{Male}: 38.80[1-\exp\left[-0.48(t+0.1)-\frac{0.5\times 0.48}{2\pi}\sin 2\pi\,(t+0.08)\right]]$$

$$\text{Female}: 43.64[1-\exp\left[-0.41(t-0.1)-\frac{0.6\times 0.41}{2\pi}\sin 2\pi\,(t+0.08)\right]]$$

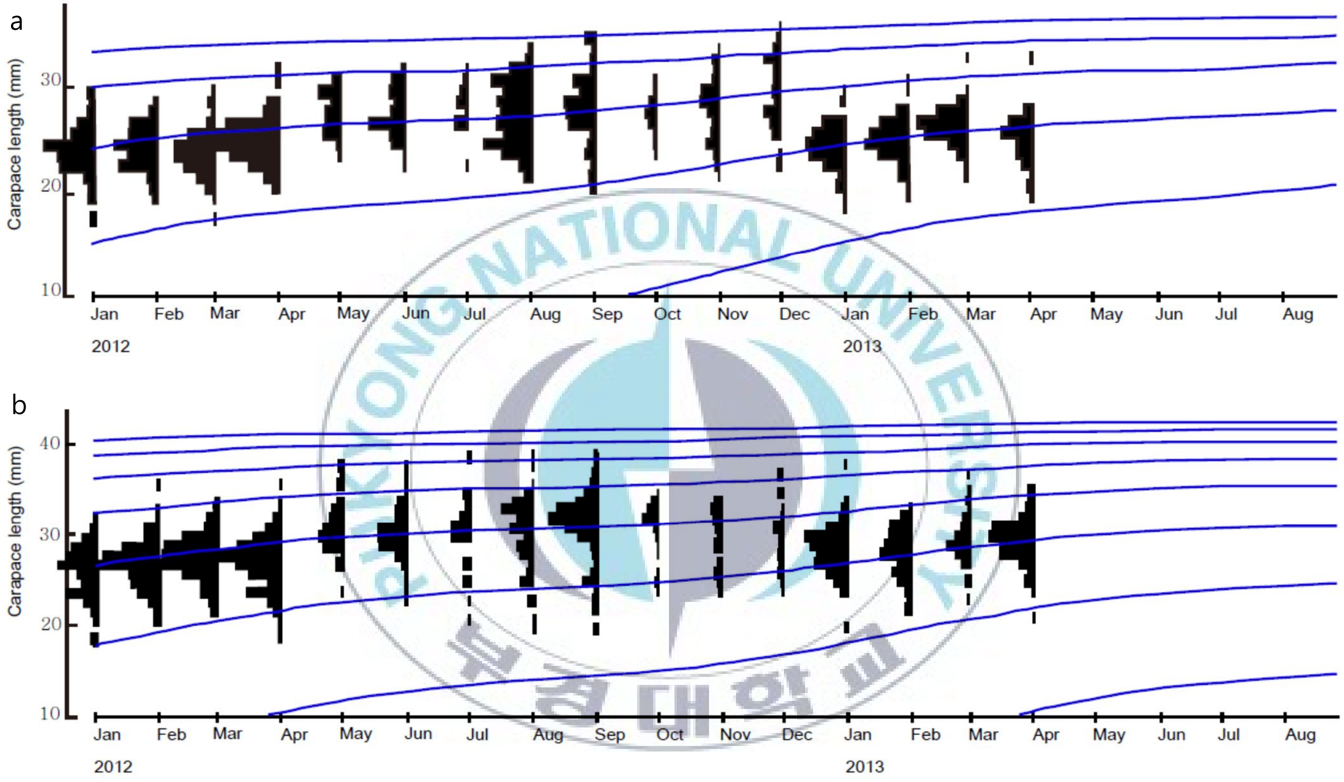

Fig. 13. Length–frequency distribution of males (a) and females (b) of *Lebbeus groenlandicus* with seasonal von Bertalanffy growth curves superimposed.

Table 4. Parameter estimation of the ELEFAN analysis of length-frequency distribution for males and females: L_∞: asymptotic length (mm); K: growth coefficient (yr^{-1}); C: amplitude of growth oscillation; WP: winter point; φ': growth performance index; R_n: score function.

	Males	Females
L_∞	38.80	43.64
K	0.48	0.41
C	0.5	0.6
WP	0.4	0.6
φ'	2.86	2.89
R_n	0.312	0.230

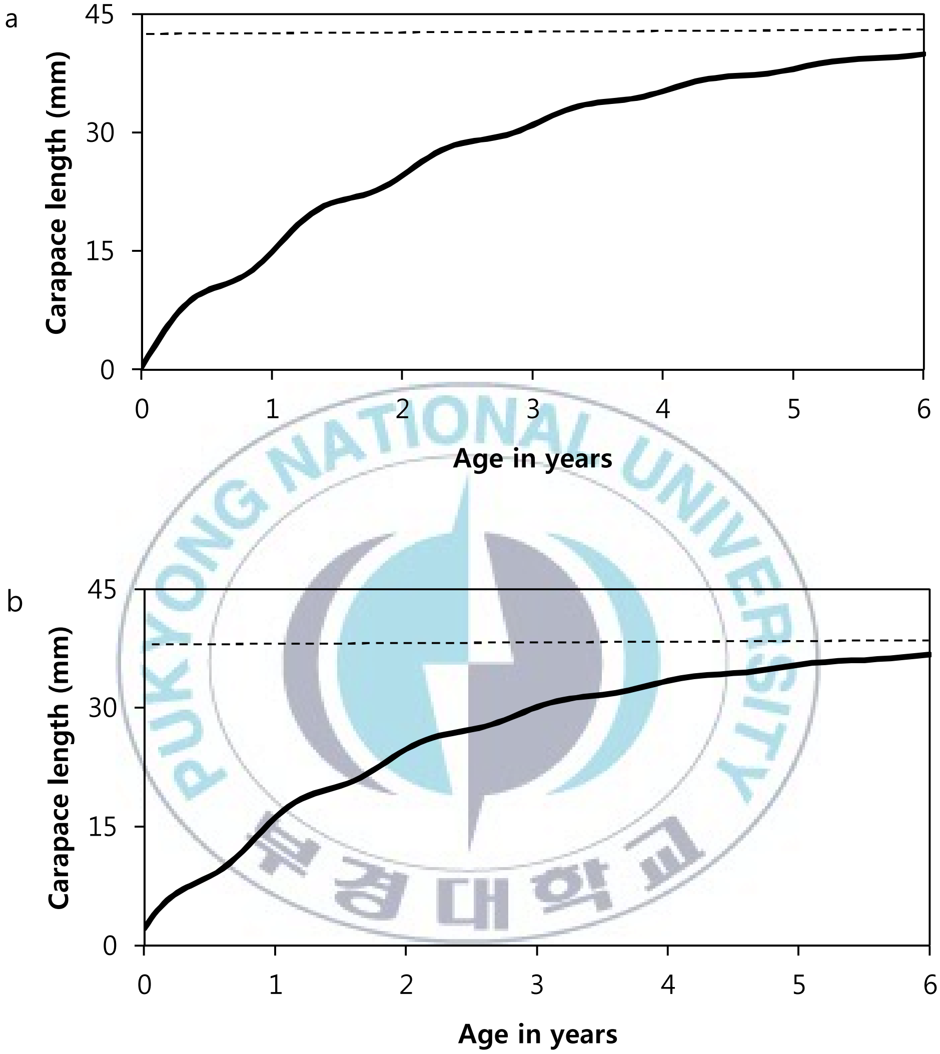

Fig. 14. The von Bertalanffy length-based growth curve. L_∞ is represented by the dashed line. a: male; b: female.

4. Discussion

4-1. Sex ratio

The sex ratio of the *Lebbeus groenlandicus* population in the East Sea is high in female. Unequal sex ratio, which is common in crustacean populations (Lizárraga-Cubedo *et al.*, 2008), can be explained by variation between sexes in; mortality and migration patterns (Kim *et al.*, 2008); net dodging ability due to difference in swimming ability between sexes (Yamane *et al.*, 2003).

Higher proportion of females than males has been observed in hippolytid shrimps, such as *Tozeuma carolinense*, *Heptacarpus futilirostris*, *Hippolyte inermis* and *H. obliquimanus* (Ewald, 1969; Oya, 1987; Cobos *et al.*, 2005; Terossi and Mantelatto, 2010). All of these showed sexual ratios in favor of females.

This indicated that sexual ratio in favor of females is the characteristic of hippolytid shrimps.

4-2. Length-frequency distribution (LFD)

Large size on females indicated a sexual dimorphism as a consequence from reproductive strategy requirement related to parental body size and mating system. This condition holds for the many hippolytid species in which adult females are lager, on average, than males (Bauer, 2004). Large size on females in the population has been recorded in other deep-water shrimps such as; *Argis lar*, *Plesionika martia* and *Heterocarpus ensifer* (Lozano-Álvarez *et al.*, 2007; Kocak *et al.*, 2012; Seo *et al.*, 2012).

Small size on males is beneficial in escaping the notice of predators, reducing the risk of predation and getting female because of the higher agility (Berglund, 1981; Correa, 2003; Bauer, 2004). Furthermore, energy needs and habitat requirements may be lower (Bauer, 2004). Contrastively, large size on females can produce the number of eggs directly proportional to her body size (Bauer, 2004) and increase the mean survival to maturity of offspring produced (Hartnoll, 1985).

It was indicated and more explained in the morphometric relationship between males and females observed in this study.

4-3. Morphometric relationship

Slope values on linear regression were significant difference between sexes, which indicated the morphometric relationships among carapace length versus body weight of *L. groenlandicus*. Female slope value was significantly higher than male and interpreted as a faster body weight increase in females than in males. Sexual dimorphism also is reported in deep sea shrimp, such as *Pandalus borealis*, *Argis dentata, A. toyamaensis* and *A. lar* (Anderson, 1991; Komai, 1997; Park, 2010; Seo *et al.*, 2012).

The faster weight gain in relation to carapace length in female *L. groenlandicus* on this study may be caused by proportionally greater tissue production in the ovaries compared with that in the testis (Anger and Moreira, 1998). Although, generally in many crustaceans species, female growth reduced during breeding period due to the investment energy more in reproductive period such as egg production and care (Hartnoll, 1982) inhibits growth by reducing molt increment and extending the intermolt period (Hartnoll, 1985).

4-4. Breeding period

Reproduction is one of the most important life-history features of all organisms (Whertmann *et al.*, 2012). The reproduction period of caridean shrimps is characterized by the presence of ovigerous females, the frequency of which may vary during different seasons, indicating peaks of reproductive activity for each population.

In *L. groenlandicus* spawning was a once during the year. One spawning period is also characteristic of other hippolytid shrimps, such as in *Hippolytie obliquimanus*, *Heptacarpus pictus* (Bauer, 1976; Terossi and Mantelatto, 2010). Therefore, it is characteristic of the reproductive period of hippolytid shrimps.

Pinheiro & Fransozo (2002) proposed two categories of continuous reproduction: (1) continuous reproduction, when the monthly percentages of ovigerous females are similar; (2) seasonal-continuous reproduction, when ovigerous females occur in all months, but in different percentages, and it is possible to recognize some peaks in some seasons.

The population of *L. groenlandicus* showed seasonal-continuous reproduction, characterized by the presence of ovigerous females in almost all months, with a peak in March.

4-5. Fecundity

Fecundity is the number of eggs offspring produced by an organism in a given time (Daintith and Martin, 2010). It is important components of fitness, which is dependent on lifetime reproductive performance (Sastry, 1983).

A significant positive allometric relationship was observed between carapace length and the number of eggs in non-eyed eggs, which indicates that the number of eggs is relatively greater at larger body sizes. However, a significant negative allometric relationship was observed between carapace length and the number of eggs in eyed eggs, which indicates that relative the number of eggs is smaller at larger body sizes.

ANCOVA revealed significant difference the number of eggs in the two egg stages as functions of carapace length. This is indicated that brood loss occurred. This loss of eggs can occur due to a diversity of factors, such as egg volume increase, parasites, mechanical stress, shrimp behavior as related to egg carrying position, predator dodging movement, failure of eggs to attach to pleopodal setae and egg predation (Kuris, 1991; Oh and Hartnoll, 1999; Oh *et al.*, 2002; Puspitasari, 2012).

Egg size (length or volume) is easily measured and is one of the most widely reported parameters in studies of marine invertebrate reproductive biology (Clarke, 1993). Increase in egg length and volume during incubation is commonly observed in the decapoda (Oh and Hartnoll, 2004). The large eggs slow development but also allow the larva to proceed to a more advanced stage before hatching, in some cases to a miniature adult (Clarke, 1992). The increase in egg volume allows a greater mobility of the embryos and facilitates the release of the larvae (Nazari *et al.*, 2000).

In the present study, *L. groenlandicus* showed an approximately 21% larger egg size in eyed egg stage than in non-eyed egg stage during development. In general, shrimps distributed in coastal waters show more rapid rates of egg growth during development than shrimps distributed in deep-water (Seo *et al.*, 2012) (Table 5). In the case of *L. groenlandicus*, the increase in egg volume observed corroborates similar results for other decapods, including hippolytid shrimps in the deep water.

Table 5. Comparison of egg volume for a variety of caridean shrimps.

Family	Species	Egg volume Non-eyed egg (mm^3)	 Eyed egg (mm^3)	Increasing proportion (%)	Source
Pandalidae	*Pandalus eous* Makarov, 1935	0.83	0.93	12	Park (2010)
Crangonidae	*Argis toyamaensis* (Yokoya, 1933)	8.10	8.96	11	Park (2010)
	Argis lar (Owen, 1839)	1.52	1.78	17	Seo *et al.*(2012)
Hippolytidae	*Eualus biunguis* (Rathbun, 1902)	0.71	0.89	25	Chun *et al.*(2011)
	Lebbeus groenlandicus (Fabricius, 1775)	2.91	3.51	21	present study

4-6. Reproductive output

Reproductive output is a life-history trait reflecting varying numbers and sizes of larvae (Hartnoll, 1985). Reproductive output expressed as the biomass of the reproductive products per unit biomass of the female (Pianka, 1972; Thessalou-Legaki and Kiortsis, 1977).

This study suggested that different reproductive output among the deep water shrimps is a reproductive strategy influenced by different family (Table 6). Reproductive output of *L. groenlandicus* is higher than *A. lar* and smaller than *P. borealis*. These showed an interspecific comparison of reproductive output in deep-water shrimp, which reflects from difference in the reproductive strategies of shrimps.

Table 6. Comparison of reproductive output for a variety of deep-water caridean shrimps.

Family	Species	Reproductive output (mean)	Source
Pandalidae	*Pandalus borealis* Krøyer, 1838	0.25	Clarke *et al.* (1991)
Crangonidae	*Argis lar* (Owen, 1839)	0.12	Seo *et al.* (2012)
Hippolytidae	*Lebbeus groenlandicus* (Fabricius, 1775)	0.18	present study

4-7. Size at sexual maturity

Size at sexual maturity is a crucial indicator of the reproductive capacity of populations, and may distinct considerably even in closely related species (Robertson & Butler, 2003). The results of present study suggested that 50% of the females of *L. groenlandicus* are mature at 22.80 mm CL.

Robertson & Butler (2003) suggested that the size at sexual maturity may be influenced by, among other factors, the high rates of predation that juvenile organisms are subjected to, which in turn favor the occurrence of an early reproduction in species.

4-8. Growth

Seasonal von Bertalanffy growth analyses showed that L_∞ was higher and K was lower in the female *L. groenlandicus*. This resulted in similar growth performance indices between sexes, despite the differences in von Bertalanffy growth parameters between males and females.

The growth performance index (φ') can be used for averaging growth parameters obtained from the von Bertalanffy growth function of a particular species (Sparre and Venema, 1992) and is a useful tools for comparing growth under a variety of environmental conditions (Pauly, 1991).

The growth performance index (φ') is different among the deep-water shrimps (Table 7). The growth performance index (φ') of *A. foliacea*, *S. melantho* and *L. groenlandicus* is higher in female than male. This indicates that female is faster in growth than male. On the other hands, the growth performance index (φ') of *P. martia* is lower in female than male. This result confirmed a slightly higher growth rate in male than in female.

The growth performance index (φ') of *L. groenlandicus* is lower than other shrimps except *P. martia*. This reason might be the asymptotic length (L_∞) and habitat. The asymptotic length of *A. foliacea* (male, 47.2 mm; female, 64.09 mm) and *A. antennatus* (69.1 mm) is significantly higher than *L. groenlandicus* (male, 38.8 mm; female, 43.64 mm). In habitat depth, *S. melantho* (187 – 242 m) is distributed shallower water than *L. groenlandicus* (200 – 400 m).

The growth performance index (φ') of *P. martia* is lower than *L. groenlandicus*. In habitat depth, *P. martia* (165 – 550 m) is distributed similar but asymptotic length (L_∞) (23.63 mm) is lower than *L. groenlandicus*.

The growth season of *L. groenlandicus* is fall and winter season. WP of male is 0.4, which from April to May are slowest growth season. WP of female is 0.6, which from July to August are slowest growth season. The slowest growth period for males is relatively low water temperature. The period slowest growth for females corresponded to the time when the highest GSI was observed.

Table 7. Comparison of growth performance index (φ′) for a variety of deep-water shrimps.

Species	φ′		Source
	Male	Female	
Aristeus antennatus (Risso, 1816)	3.41		Ragonese and Bianchini (1996)
Solenocera melantho De Man, 1907	2.97	3.21	Ohtomi and Irieda (1997)
Aristaeomorpha foliacea (Risso, 1827)	3.10	3.28	Papaconstantinou and Kapiris (2003)
Plesionika martia (A. Milne-Edwards, 1883)	2.44	2.42	Kocak *et al.* (2012)
Lebbeus groenlandicus (Fabricius, 1775)	2.86	2.89	present study

Overall observations of growth, GSI, ovigerous female rate and female with eyed egg stage rate were shown in fig. 16. The growth rate of female was slower from June to October and faster from January and April. However, GSI was higher from July to November and lower December to April. The growth rate and GSI were totally contrary. That reason is due to the long spawning period which extended the intermolt period and therefore caused individuals to grow more slowly.

We found that the spawning period is approximately from January to March. GSI values, on the other hand, were higher in November. We found that females begin to developing their ovaries during December and mostly spawn until March. In addition, females with eyed eggs were occurred from June to January. This suggests that females spawning in March possibly spawned again the next year. Evidence for the consecutive breeding of females is significant increase of GSI from non-eyed to eyed egg stage; this indicates that *L. groenlandicus* can prepare for subsequent breeding events during an active reproductive cycle. Multiple spawning may be an alternative to a single spawn that produces larger eggs or an annual migration of females into shallow water to spawn because increase food availability (Seo *et al.*, 2012).

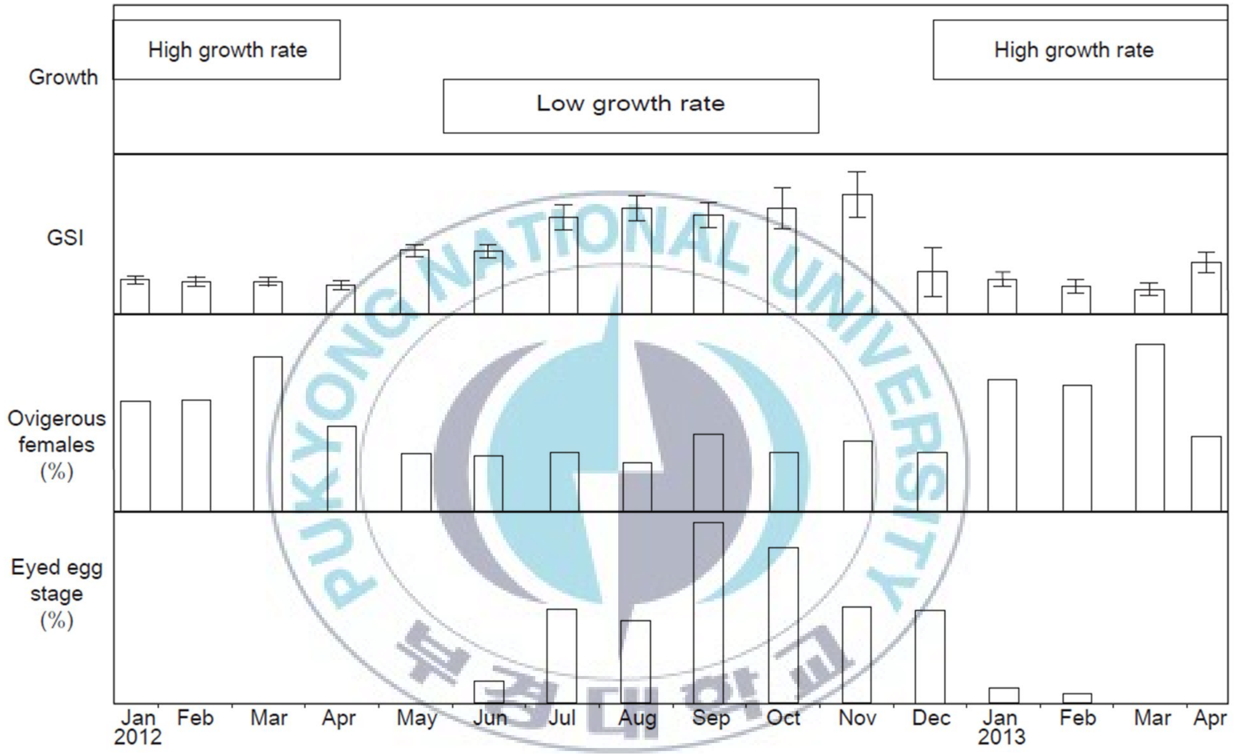

Fig. 15. Life history traits based on growth, GSI, ovigerous female rate (%) and females with eyed egg stage (%) of *Lebbeus groenlandicus* in the East Sea, Korea.

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