Thesis for the Degree of Master of Science

Growth and reproduction of the mud shrimp, *Upogebia major* (de Haan, 1841) (Thalassinidea: Upogebiidae) on the intertidal mudflat of the Southern Sea, Korea

by

Kyung Tae Lee

Department of Marine Biology

The Graduate School

Pukyong National University

August 2016

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(남해 갯벌에 서식하는 쏙의 성장과 생식에 관한 연구)

Advisor: Prof. Chul-Woong Oh

by

Kyung Tae Lee

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Kyung Tae Lee

Approved by:

(Chairman) Dr. Hyun-Woo Kim

(Member) Dr. Jong Hun Na

(Member) Dr. Chul-Woong Oh

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CONTENTS

3. Results ………………………………………………………………… 16

LIST OF FIGURES

LIST OF TABLES

Growth and reproduction of the mud shrimp, *Upogebia major* (de Haan, 1841)
(Thalassinidea: Upogebiidae) on intertidal mudflat of the Southern Sea, Korea

Kyung Tae Lee

Department of Marine Biology, The Graduate School,
Pukyong National University

Abstract

Samples of the mud shrimp *Upogebia major* were monthly collected from April 2015 to April 2016 on an intertidal mudflat in Southern Sea of Korea. The sex ratio of the *U. major* significantly equivalent to 1:1 (male = 701, female = 669). The relationship between carapace length (CL) and body weight (BW) was significant (P < 0.001). There was significant difference on the slope of regressions of log CL versus log BW between males and females, indicating sexual dimorphism in growth. The gonadosomatic index (GSI) varied monthly, reaching a maximum in November 2015 and a minimum in February 2016. The highest values of the GSI coincided with the breeding period, and there was a significant difference between the mean GSI of females with non-eyed and those with eyed eggs (P < 0.001), indicating that *Upogebia major* is a consecutive breeder. There was a significant relationship between CL and the number of eggs (EN) in the egg stages ($P < 0.001$), but there was no significant difference in the slope and intercept of the regressions of CL versus EN between females carrying non-eyed and eyed egg stages. Based on the dry weights in the egg stages, reproductive output was determined to be 0.257 ± 0.005. The Von Bertalanffy growth function parameters were $CL_{\infty} = 40.71$ mm, $K = 0.78$ year^{-1}, $C = 0.4$, and $WP = 0.15$ for males, and $CL_{\infty} = 40.48$ mm, $K = 0.62$ year−1, $C = 0.61$, and $WP = 0.95$ for females. The growth performance index (φ′) was higher in males (3.11) than in females (3.01). The dimorphic difference in growth between sexes was discussed in terms of reproductive cycles and moulting.

1. Introduction

Upogebia major (de Haan) is a major species in macrobenthic communities on tidal flats in Southern Sea of Korea. They live in Y-shaped burrows that can extend up to more than 2 meters below the sediment surface (Kinoshita, 2002). Because of the size and abundance of the *U. major* in coastal habitats, their ecological functions and roles have become increasingly important (Kinoshita, 2002; Hong, 2013). Recently, *U. major* has posed a serious threat to the Korean clam industry along the coast of Korea. The extensive burrowing shrimp populations suddenly invaded the tidal flats from 2010 where the clams (*Ruditapes philippinarum*) are raised. As a consequence, clam production has decreased by about 10% over the past three years in some Korean clam beds (Hong, 2013).

Research on the ecology of the *U. major* have focused on burrow structure (Kinoshita, 2002), bio-geochemical processes between the sediment and water (Koike & Mukai, 1983; Kinoshita, 2008), relationship with commensal species (Kato & Itani, 1995; Sato *et al.*, 2001) and life history (Kinoshita *et al*., 2003). These studies suggest that *U. major* influence strongly on benthic metabolism and community structure.

There are some characteristics of reproduction and growth that reported by previous studies in intertidal mudflat of Japan. Breeding season of *U. major* is from November for the previous year to April in Shiranuhi Sea of Japan and from December for the previous year to May in Tokyo Bay of Japan. (Sakamoto *et al*., 1987; Itani, 2001b; Kinoshita *et al*., 2003). An ovigerous female have more than 14,000 eggs in Western Sea of Korea that is double in Tokyo Bay of Japan (Kinoshita *et al*., 2003). Landing female spawn once a season and participates spawning after two and a half years (Kinoshita *et al*., 2003). It seems to have difference of characteristics related different area. Carapace length is approximately 30 mm and mean carapace of ovigerous female is 29.6 mm (Kinoshita *et al*., 2003). New recurits (Landing juveniles) grow rapidly during a year and grow slowly after that period. They start spawning, when carapace length is approximately 2 cm. Estimated lifespan is 4 to 5 years (Kinoshita *et al*., 2003; Kornienko, 2013).

Regarding *U. major*, there is no information on growth and reproductive traits on intertidal mudflat of the Southern Sea, Korea and only one study provides such information in the Western Sea, Korea (Hong, 2013). The aim of this study is to reveal 1) the differences in the size structure of the population, 2) the reproductive aspects and 3) the growth of mud shrimp, *U. major*.

2. Materials and methods

2-1. Field survey

The specimens of *Upogebia major* were monthly sampled in mud flat of Munhang which is located within the Southern Sea of Korea (34.91°N, 127.92°E) (Fig. 1) during April 2015 until April 2016. The specimens were caught with a fishing gear like brush in fishing area and shoveling (0.5 m depths). Shrimps were preserved in 4% neutralized formalin solution. Bottom water temperature (℃) and salinity (ppt) were measured every month in fishing area from Jun 2015 to April 2016. Both parameters were measured from bottom water (0.5 m under the sediment) using a Temperature / salinity meter (30-10 FT, produced by YSI incorporated, Ohio 45387, USA).

2-2. Population structure

Specimens were sexed by inspecting for presence of first pleopods (Kinoshita *et al*., 2003). The sex ratio was based on the proportion of females.

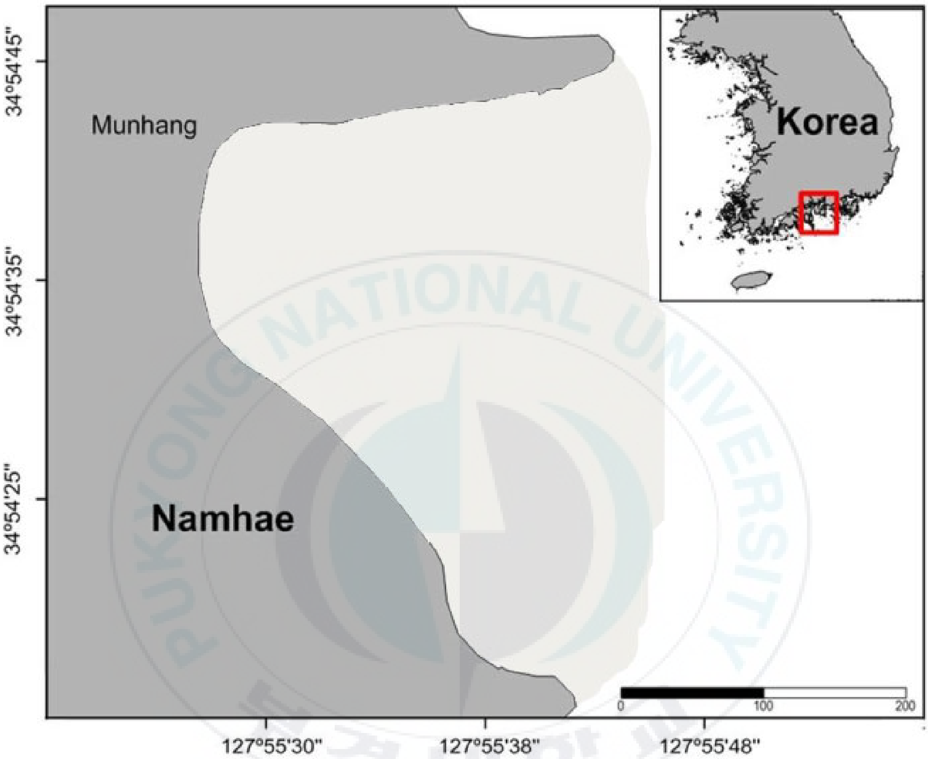


Fig. 1. Map showing sampling stations in the Munhang mudflat of the Southern Sea of Korea.

Population structure was determined based on length-frequency distribution of both sexes. Length-frequency distributions of each sex were constructed using 2 mm length intervals of carapace length, measured from tip of rostrum to edge of the carapace and 2 mm length intervals of abdominal length, measured from edge of carapace to edge of telson.

2-3. Reproductive traits

2-3-1. Ovarian examination

The ovarian stages were determined by size and shape in proportion to the gastric mill, thoracic cavity and abdominal cavity, and external appearance of the ovary (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 weighting to the nearest 0.0001g using an electronic digital balance. GSI was determined by the following formula;

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

Table 1. Ovarian stage of *Upogebia major* in the Southern Sea, Korea (de Haan, 1841).

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 and abdominal cavity	Maturing
Stage 4	Ovary completely filling that space	Ripe
	Similar shape with stage 1 but vestige of breeding	Spent

2-3-2. Egg size

Egg size of ovigerous females was recorded as two stages: (1) non-eyed egg; and (2) eyed egg. 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 (V) 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.

2-3-3. 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 was 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 linear regression in both non-eyed and eyed egg stage were compared to investigate brood mortality.

2-3-4. 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. Relationship between carapace length and fecundity and estimation of reproductive output for all females with spawned eggs were used. Female and egg dry weights were determined by drying at 80℃ for 48 h and weighting to the nearest 0.0001g using an electronic digital balance. Reproductive output (RO) was estimated using dry weight by applying the formula given by Clarke *et al*. (1991):

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

2-3-5. Size at sexual maturity ($\boldsymbol{CL_{50}}$)

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 classes. A logistic curve may be fitted to the proportion of sexually mature females by carapace length. Adapting Campbell (1985) gives:

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

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 constant a and b:

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

2-4. Growth

2-4-1. Relative growth

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 following equation;

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

where a was intercept and b slope. For the relationship carapace length and body weight, the pattern was established by the b-value slope. Pooled regressions are given only when differences between the slopes or intercepts of separate regression were statistically not significant. Intra-specific variation in morphometric relation between sexes was indicated using difference of slope value 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).

2-4-2. Growth parameters

Length-frequency distributions were constructed using 2 mm length intervals of carapace length. Growth was described using the modified Von Bertalanffy growth function (VBGF) (Pauly and Gaschüz, 1979):

$$L_t = L_\infty[1 - e^{[-K(t-t_0)-\frac{CK}{2\pi}sin2\pi(t-t_s)]}]$$

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 the 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 soley 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 1.09 mm (Kinoshita, 1989).

Growth performance of *U. major* 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.

2-5. 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 was differed from the expected 1:1 ratio. Kruskal-Wallis test was used to investigate the monthly mean variation on GSI and the difference in bottom water temperature and salinity between month. 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 males and females and 2) carapace length and the number of eggs of non-eyed and eyed eggs. MINITAB (v. 16), SPSS (v. 12) and R studio (v. 0.99.489) were used for all the statistical analysis and mean value was presented with 95% confidence limit.

3. Results

3-1. Environment factors

In case of environment factors, there was significant difference in bottom water temperature ($H = 40.41$, $df = 10$, $P < 0.001$) and salinity ($H = 27.29$, $df = 10$, $P < 0.01$) between month. Mean bottom water temperature was the highest in August (27.04 ± 0.1℃) and the lowest in February (5.6 ± 0.06℃) (Fig. 2) and salinity was the highest (31.76 ± 0.05‰) in September and the lowest (24.96 ± 3.06‰) in June (Fig. 3).

3-2. Population structure

Of 1,370 specimens (701 males and 669 females), there was no significant difference between percentage of males (51.2%) and of females (48.8%) ($x^2 = 0.7015, v = 1, P > 0.05$) (Fig. 4).

A total 1370 shrimps were collected during sampling between April 2015 and April 2016. There was significant difference in length-frequency distributions of carapace length between males and females respectively (Kolmogorov-Smirnov two-sample test; $Z = 7.5189$, $df = 1368$, $P < 0.001$).

Carapace length (CL) ranged from 16.95 to 38.62 mm for males and 15.84 to 38.91 mm for females, with a mean carapace length of 32.01 ± 0.13 mm for males and 29.98 ± 0.11 mm for females. Males were predominant in larger size classes, whereas females in smaller size (Fig. 5).

There was a significant difference in length-frequency distributions of abdominal length between males and females respectively (Kolmogorov-Smirnov two-sample test; $Z = 4.706$, $df = 1368$, $P < 0.001$). Abdominal length (AL) ranged from 33.16 to 74.4 mm for males and 34.01 to 92.75 mm for females, with a mean abdominal length of 62.18 ± 0.23 mm for males and 65.51 ± 0.27 mm for females. Females were predominant in larger size classes, whereas males were in smaller size (Fig. 6).

3-3. Reproduction

3-3-1. Breeding period

Breeding period was determined by the occurrence of ovigerous female. Ovigerous females of *Upogebia major* were presented in April 2015 and between November 2015 and April 2016 (Fig. 7).

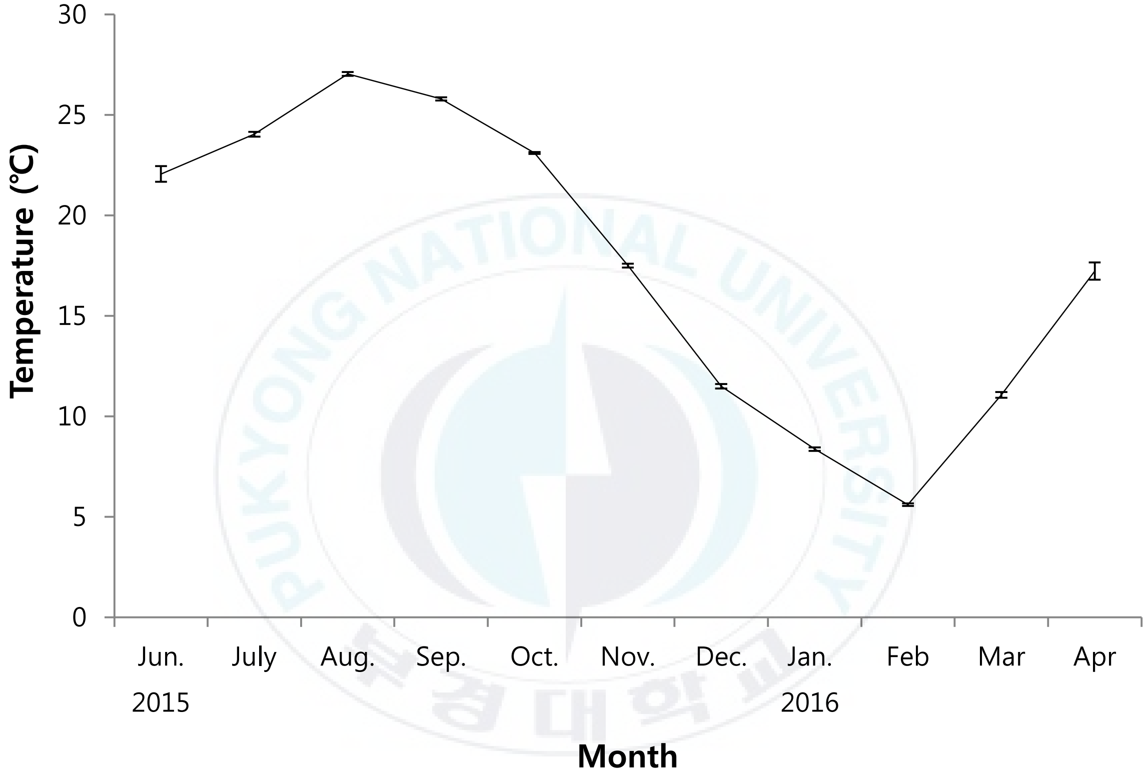


Fig. 2. Seasonal changes of bottom water temperature on mud flat of Munhang in the Southern Sea, Korea.

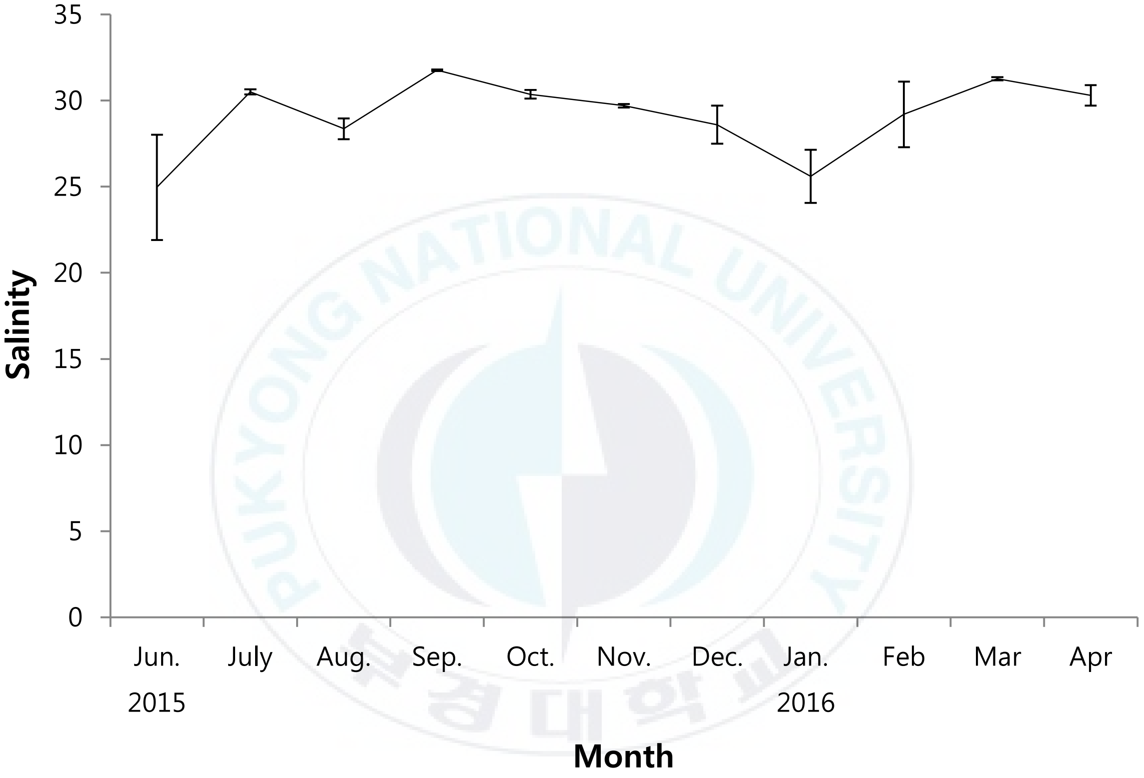


Fig. 3. Seasonal changes of salinity on mud flat of Munhang in the Southern Sea, Korea.

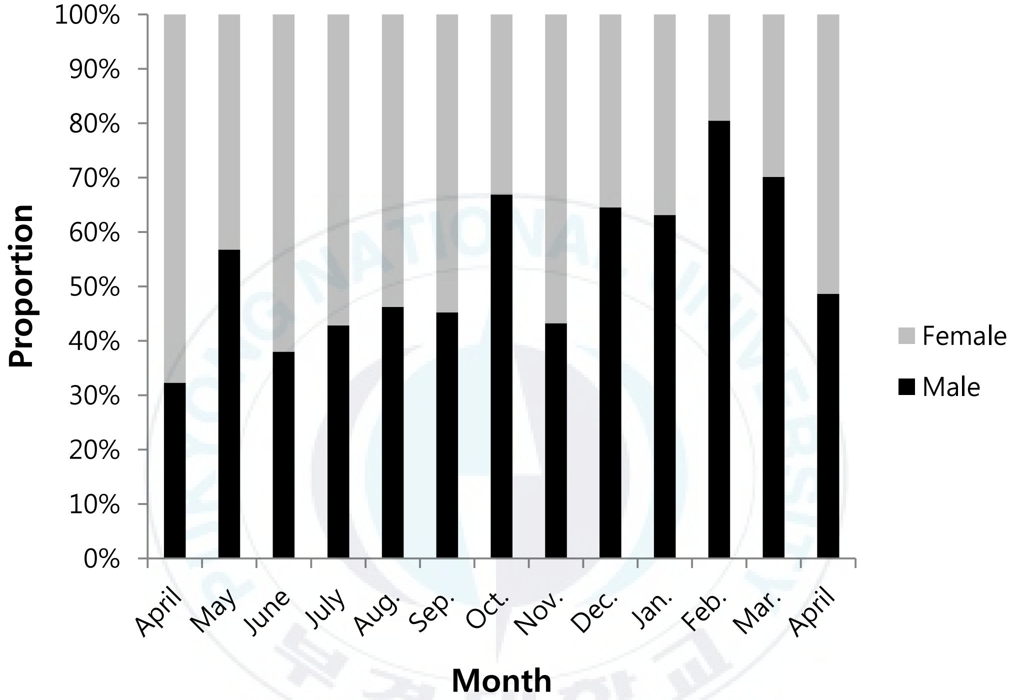


Fig. 4. Sex ratio of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea (X: month, Y: Proportion).

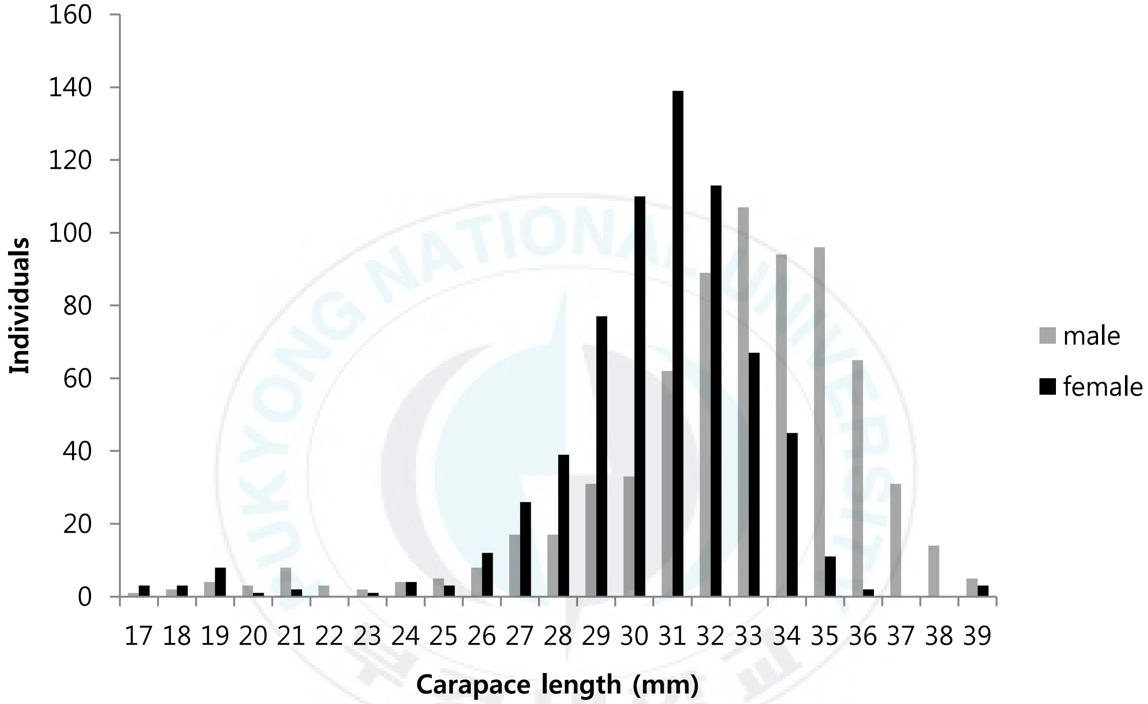


Fig. 5. Carapace length frequency distribution of males and females of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea.

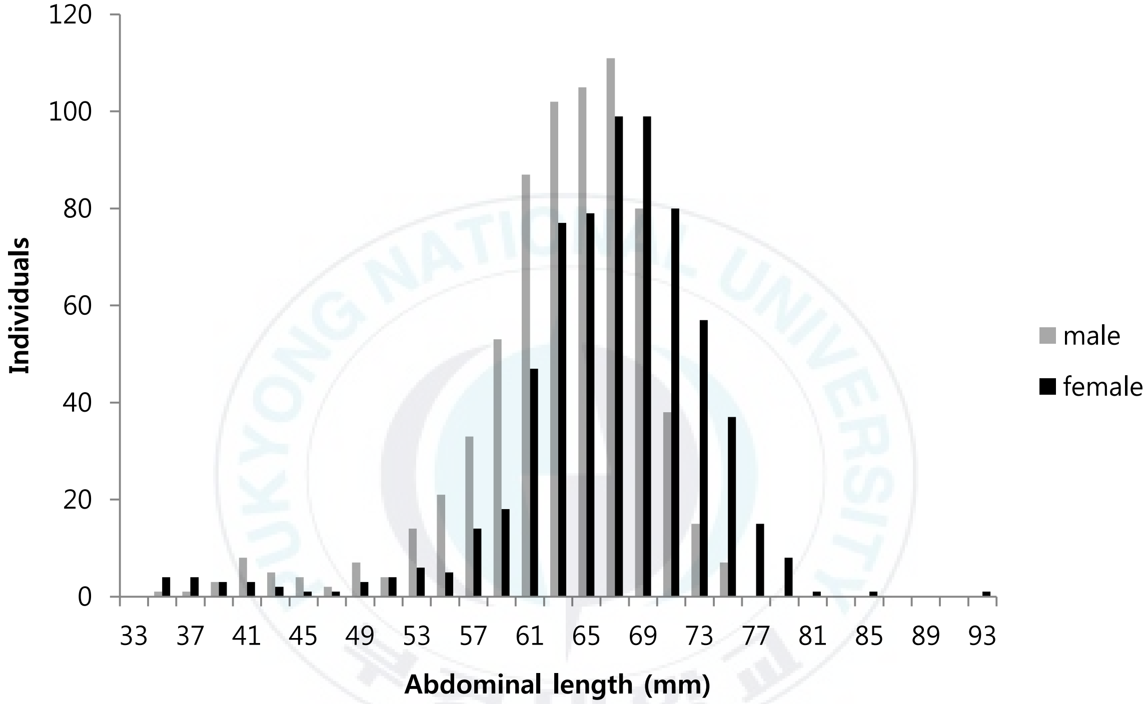


Fig. 6. Abdominal length frequency distribution of males and females of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea.

The mean gonadosomatic index (GSI) started to increase in March, reached a peak in November 2015 (29.29 ± 1.76), and decreased to its lowest value in February 2016 (1.9 ± 0.56) (Fig. 7). GSI values varied significantly each month ($H = 434.16$, $df = 12$, $P < 0.001$).

There was significant difference in mean GSI between of females with non-eyed (mean GSI = 2.64 ± 0.38) and eyed eggs (mean GSI = 7.80 ± 0.45) ($df = 97$, $t = 8.70$, $P < 0.001$), indicating that *Upogebia major* is a consecutive breeder (Fig. 8).

3-3-2. Fecundity and reproductive output

In 163 ovigerous females, 54 females with mean carapace length 30.78 ± 0.41 mm (range, 26.07 to 35.84 mm) were carried 18412.88 ± 960.29 non-eyed eggs (range, 9200 to 31152) and 109 females with mean carapace length 31.01 ± 0.34 mm (range, 25.82 to 38.91 mm) were carried 17368 ± 830.99 eyed eggs (range, 5912 to 38480). Mean egg volume of eyed eggs (0.277 ± 0.002 mm^3, n = 392) was significantly larger than that of non-eyed eggs (0.201 ± 0.001 mm^3, n = 371) ($t = 23.94$, $df = 713$, $P < 0.001$) (Fig. 9).

Log-transformed values of carapace length and number of eggs in females with non-eyed and eyed egg stages both show statistically significant linear relationships (table 2).

In non-eyed stage, the slope of the regressions was approximately 3, which imply that the relationships between the variables were isometry: as female carapace length increases, the number of eggs increases isometrically (Fig. 10). In eyed stage, however, the slope of the regression was less than 3, which imply that the relationships between the variables were negative allometry: as female carapace length increases, the number of eggs increases negative allometrically. There was no significant difference in the slope (ANCOVA: F = 1.83, df = 1, P > 0.05) and intercept (F = 1.53, df = 1, P > 0.05) of regressions of log carapace length versus the number of eggs in the two egg stages (Fig. 11). Reproductive output (± standard deviation) was 0.257 ± 0.005 (n = 163).

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

The 662 of the female *U.major* used in the analysis ranged from 15.84 mm to 38.91 mm. The proportion of mature females by length class

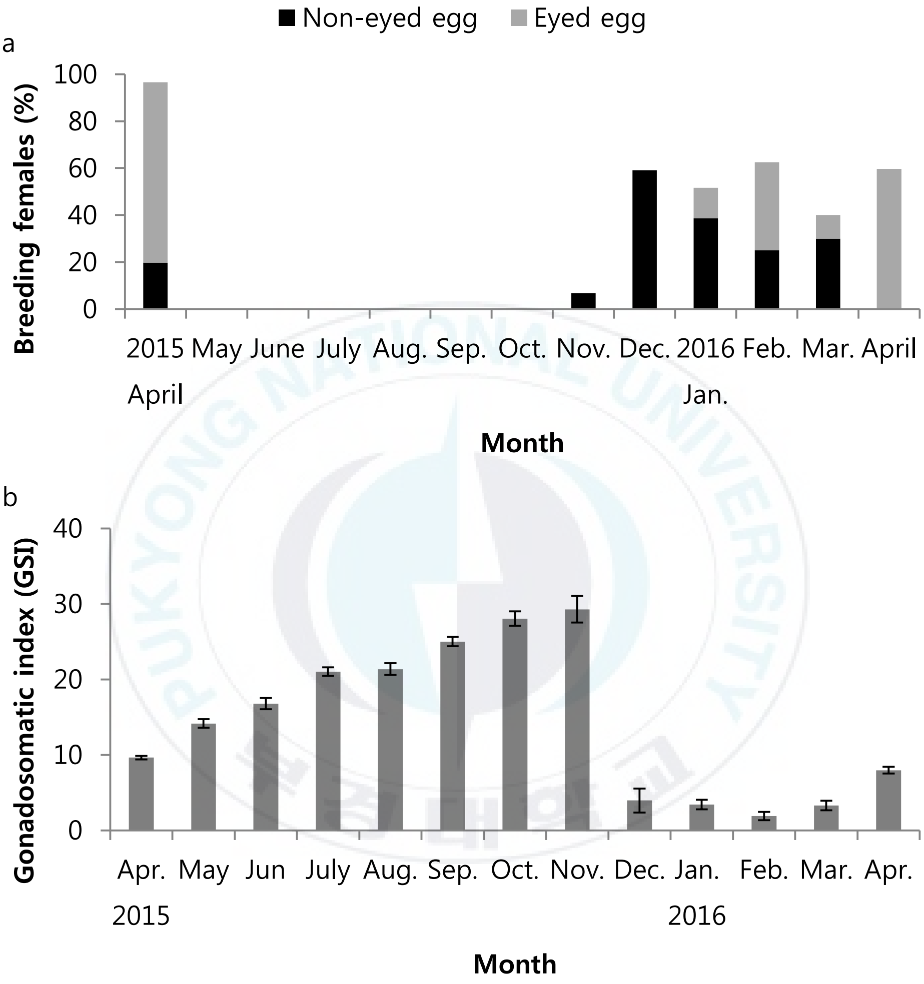


Fig. 7. Monthly changes of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea. a: Proportion of ovigerous females with different egg stages; b: Gonadosomatic index (GSI) of females.

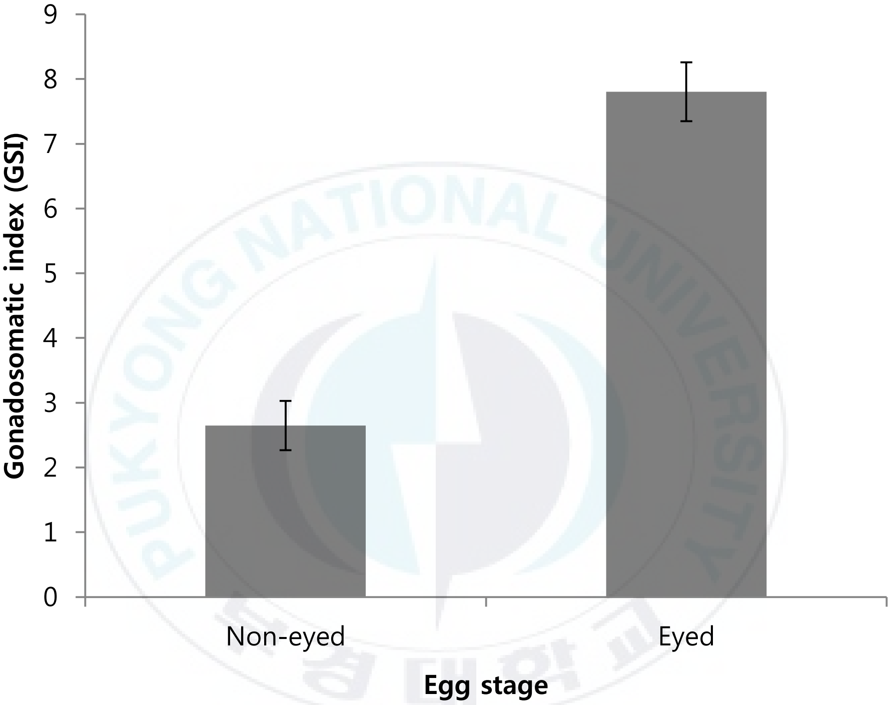


Fig. 8. Gonadosomatic index (GSI) values for each egg stage of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea.

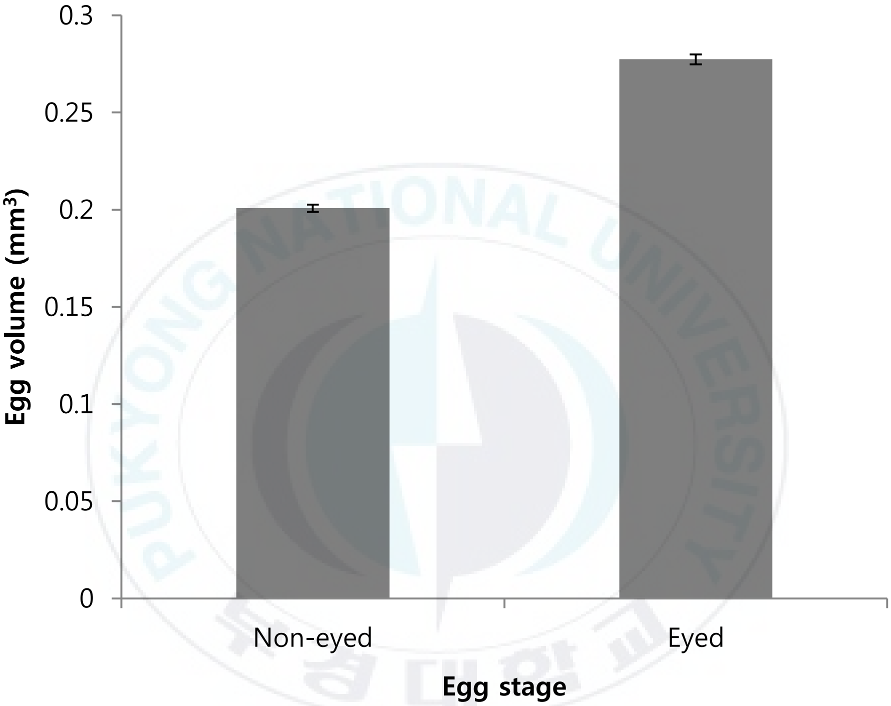


Fig. 9. *Upogebia major* (de Haan, 1841) egg volume for each egg stage.

Table 2. Linear regression of carapace (CL) versus the number of eggs (EN) in non-eyed and eyed egg stages of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea.

Egg stages	Linear regression
Non-eyed	$\ln EN = 2.65(\pm 0.47)\ln CL + 0.69$ $(\mathrm{n} = 41, r^2 = 0.45, P < 0.001)$
Eyed	$\ln EN = 1.62(\pm 0.59)\ln CL + 4.15$ $(\mathrm{n} = 41, r^2 = 0.16, P < 0.05)$

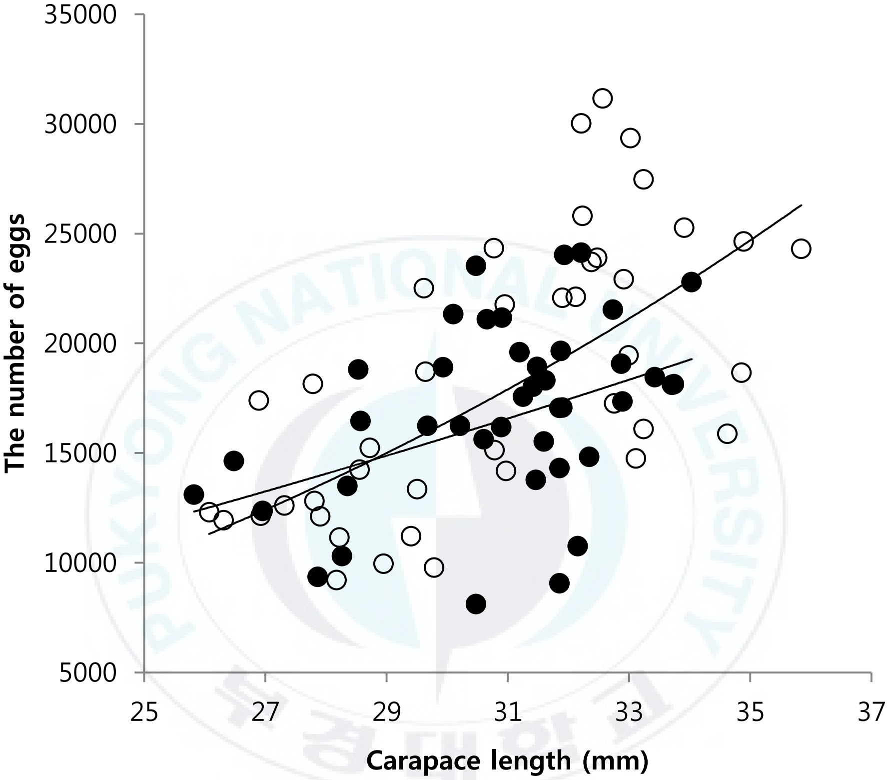


Fig. 10. . Relationship between carapace length and the number of eggs in *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea. solid line: non-eyed egg stage (○); dotted line: eyed egg stage (●).

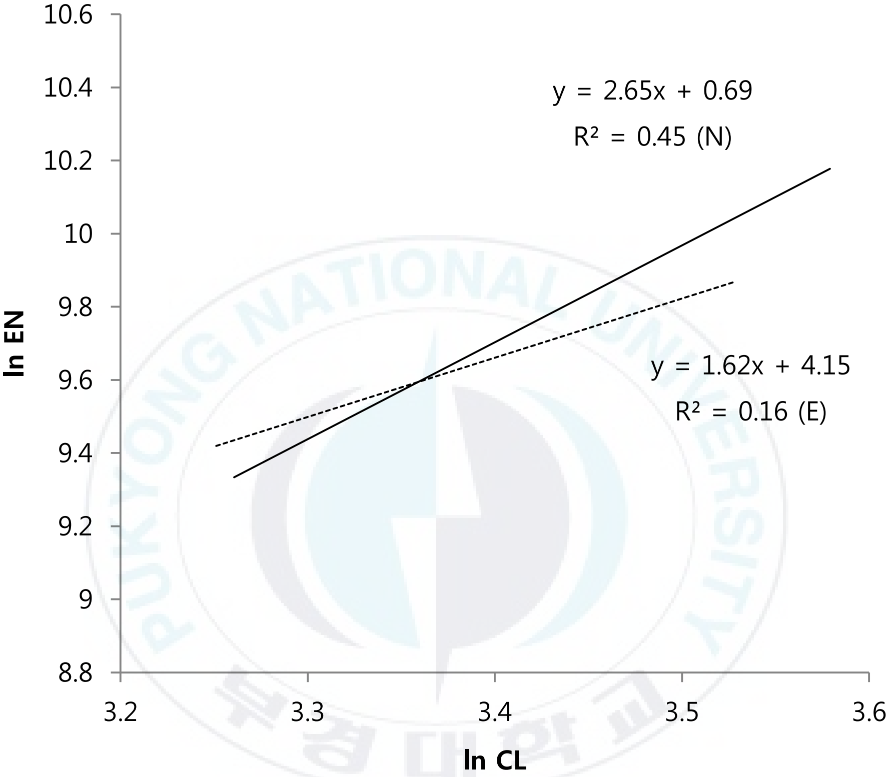


Fig. 11. Linear regression of ln carapace length (CL) and ln number of eggs (EN) on *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea. solid line: non-eyed egg stage; dotted line: eyed egg stage.

increased logistically with length (Fig. 12). The 50% maturity size is 20.28 mm.

$$P = \frac{1}{(1 + e^{(4.63-0.23*CL)})}$$

3-4. Growth

3-4-1. Relative growth

Carapace length (CL) ranged from 16.95 to 38.62 mm for males and 15.84 to 38.91 mm for females.

Body weight (BW) ranged from 3.21 to 79.4 g for males and 1.91 to 43.94 g for females.

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 3).

The relationship between carapace length and body weight was negative allometry for males. In females, however, the relationship between carapace length and body weight was isometry (Fig. 13).

There was a significant difference on slope of regressions of log carapace length versus log body weight between males and females of *U. major* (ANCOVA: $F = 9.39$, $df = 1$, $P < 0.01$) (Fig. 14).

3-4-2. Growth parameters

The Von Bertalanffy growth function parameters estimated by ELEFAN for each sex (Fig. 15) (Table 4). The parameters of asymptotic length (L_∞) and growth coefficient (K) in male is higher than females.

The Von Bertalanffy growth equation is follow (Fig. 16):

$$Male: 40.71\left[1 - e^{[-0.78(t+0.04) - \frac{0.4\times 0.78}{2\pi} sin2\pi(t+0.35)]}\right]$$

$$Female: 40.48\left[1 - e^{[-0.62(t+0.04) - \frac{0.61\times 0.62}{2\pi} sin2\pi(t-0.45)]}\right]$$

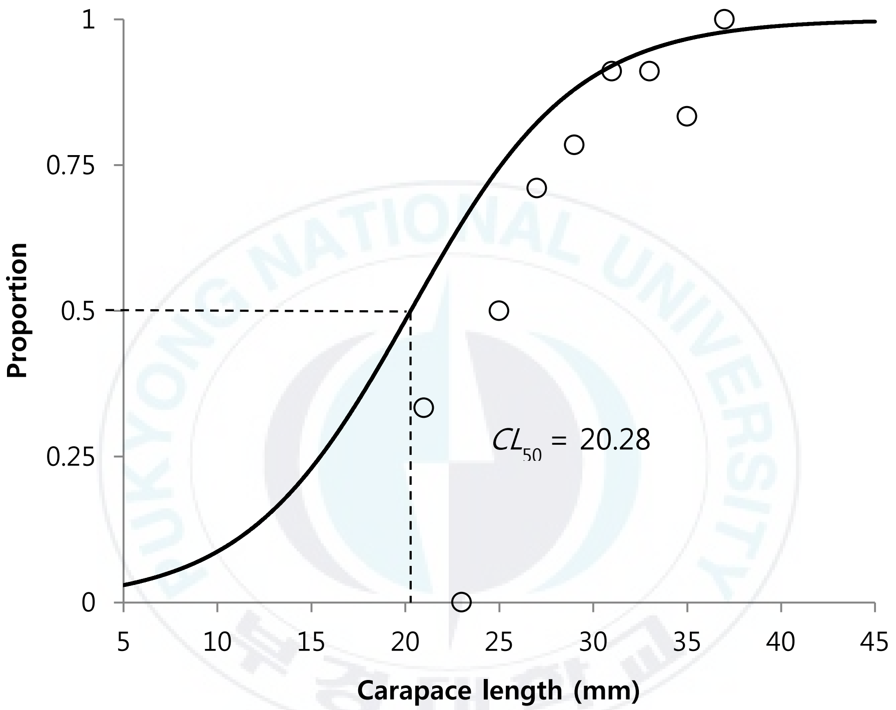
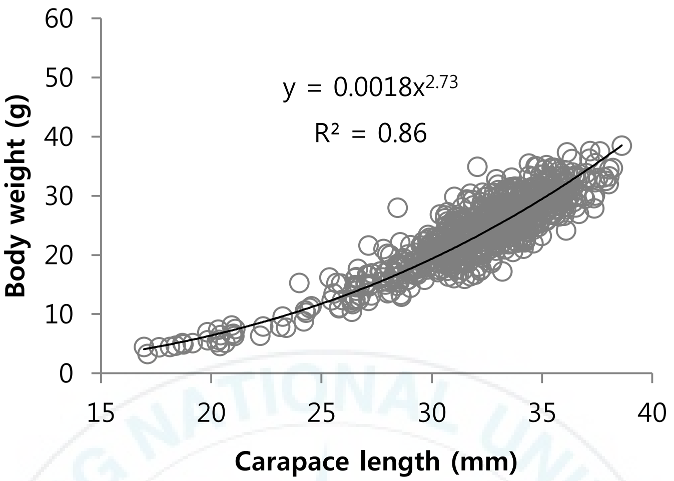


Fig. 12. A logistic function fitting proportion of mature females to carapace length of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea. CL_{50}, which corresponds to a proportion of 0.5, is indicated.

Table 3. Linear regression of carapace length (CL) and body weight (BW) of male and female, mean of carapace length and body weight of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea.

Sex	Linear regression	CL (mm)	BW (g)
Male	$\ln BW = 2.73(\pm 0.04)\ln CL - 6.32$ $(n = 700, r^2 = 0.87, P < 0.001)$	32.01 ± 0.13 mm	23.89 ± 0.25 g
Female	$\ln BW = 2.97(\pm 0.07)\ln CL - 7.01$ $(n = 668, r^2 = 0.72, P < 0.001)$	29.98 ± 0.11 mm	23.18 ± 0.25 g

a



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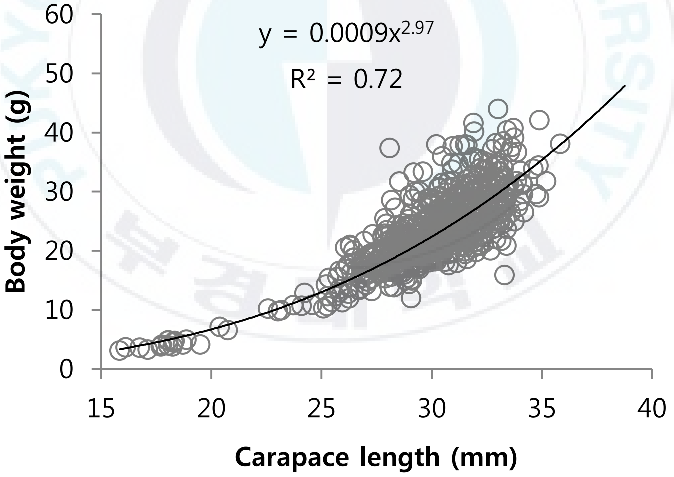

Fig. 13. Relationship between carapace length and body weight of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea. a: males; b: females.

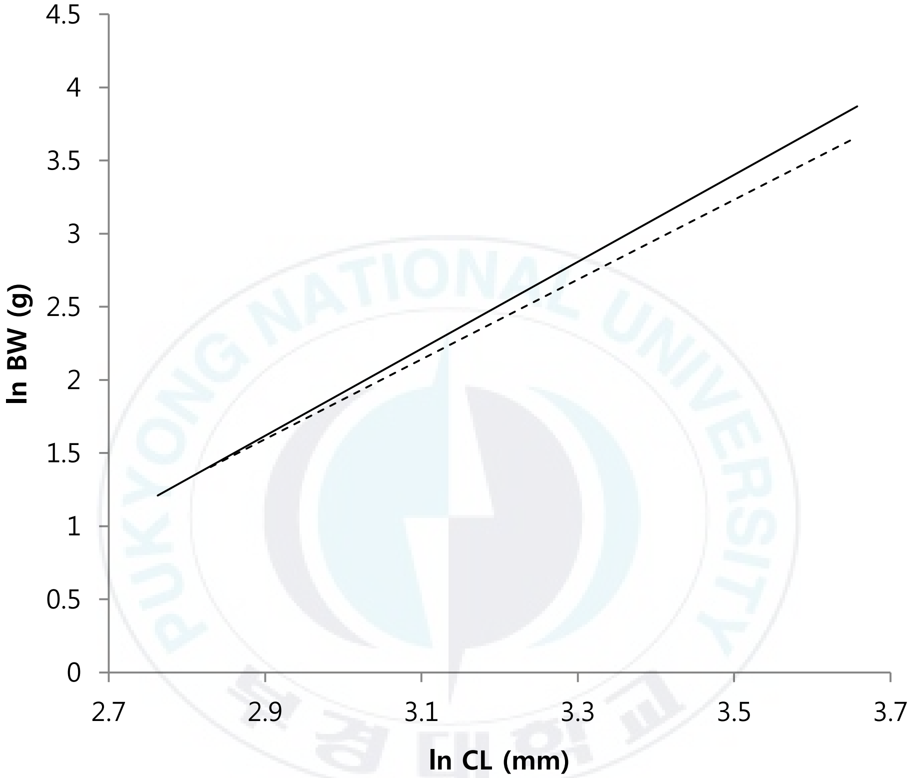

Fig. 14. Relationship between carapace length (CL) and body weight (BW) of *Upogebia major* (de Haan, 1841) in the Southern Sea, Korea. solid line: males; dotted line: females.

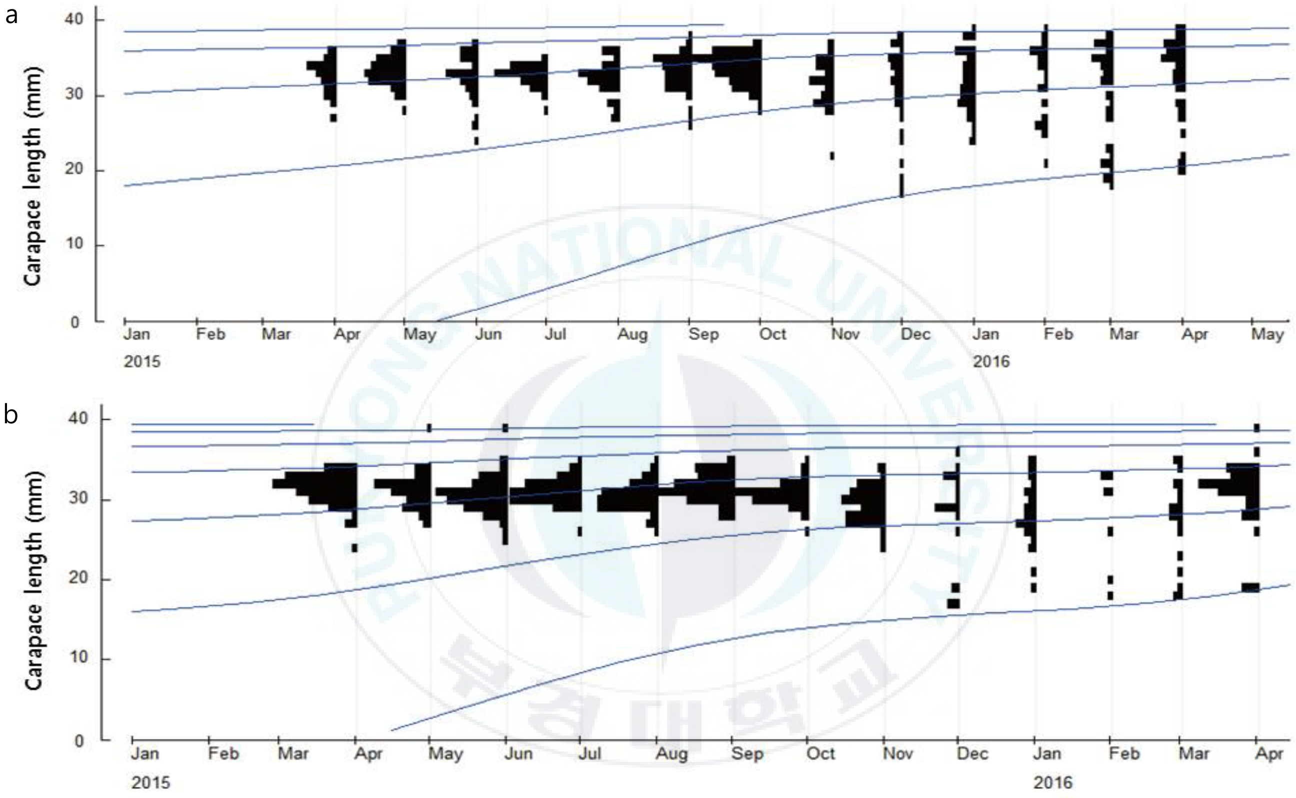

Fig. 15. Length-frequency distribution of males (a) and females (b) of *Upogebia major* (de Haan, 1841) with seasonal von Bertalanffy growth curves superimposed.

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_∞	40.71	40.48
K	0.78	0.62
C	0.4	0.61
WP	0.15	0.95
φ'	3.11	3.01
R_n	0.217	0.219

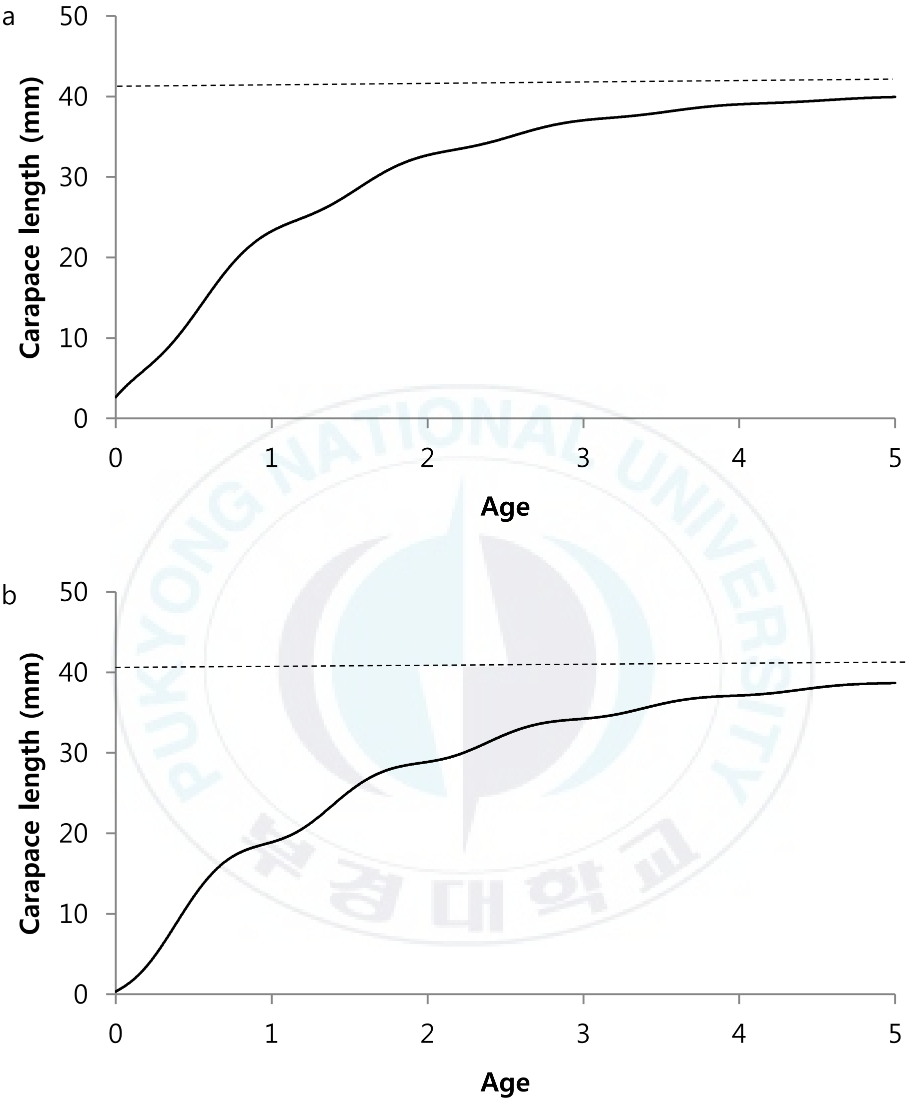

Fig. 16. The von Bertalanffy length-based growth curve. L_∞ is represented by the dashed line. a: male; b: female.

4. Discussion

In present study, the sex ratio of the *U. major* significantly equivalent to 1:1. Many previous studies of *U. major*, higher proportion of males than females has been observed in Western Sea of Korea and Shinhama lagoon of Tokyo Bay (Kinoshita, 2002; Hong, 2013).

In the case of *Upogebia pusilla* (Petagna, 1792), males presented more than females in Northern Aegean sea (T. Kevrekidis *et al*., 1997) but females presented more than males in the Northern Adriatic sea (Dworschak, 1988). Sex ratios throughout the estuary did not deviate significantly from 1:1 in *Upogebia africana* (Ortmann, 1894) (Hodgson *et al*., 2000). Sex ratio of other *Upogebia* species population was high in female (Hill, 1977; Tunberg, 1986; Hanekom & Erasmus, 1989). The reason for these differences are unknown but may in part reflect different sampling protocols (Hodgson *et al*., 2000).

The length-frequency distributions (CL) were significantly different between both sexes, and males were predominant in the larger size classes. In various species of the genus *Upogebia*, maximum carapace length of male was bigger 1-4 mm than that of female (Hill, 1977; Dworschak, 1988; Hanekom & Erasmus, 1989; Hanekom & Baird, 1992; T. Kevrekidis *et al.*, 1997). This showed that adult males of *Upogebia* sp. were generally larger than females (Hanekom & Erasmus, 1989).

Larger size (AL) observed in female indicated a sexual dimorphism as a consequence from reproductive strategy requirement related to parental body size. Growth of abdominal length on female can affect egg production (Felder & Lovett, 1989). This condition appears to reflect a general pattern of development in thalassinids examined to date, and has been concluded in various terms by other investigators (Tucker, 1930; Hailstone & Stephenson, 1961; Dworschak, 1988).

Reproduction is one of the most important life-history features of all organisms (Whertmann *et al*., 2012). The reproduction period of *Upogebia* sp. 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.

Spawning of *U. major* was once a year. It was presented in previous study with *U. major* (Kinoshita *et al*., 2003; Hong, 2013). One spawning period is also characteristic of other *Upogebia* sp., such as *U.* deltaura, *U. pusilla* and *Upogebia pugettensis* (Dana, 1852) (Tunberg, 1986; Dworschak, 1988; Dumbauld *et al*., 1996; Feldman *et al*., 2000) and some populations of *U. africana* have well defined spring and summer breeding cycles, while in other populations, the spring and summer breeding cycles tend to merge, forming a longer breeding season (Hill, 1977; Hanekom & Erasmus, 1989). Therefore, it is characteristic of the reproductive period of *Upogebia* species.

The breeding period of *U. major* started in November and until the end of April (5 months). In previous study, the breeding period of *U. major* was from November to April in Shiranuhi Sea of Japan, December to April in Shinhama lagoon of Tokyo Bay and February to June in the Western Sea of Korea (Kinoshita, 2002; Homg, 2013). It shows difference in beginning of breeding period between the Southern Sea (November 2015) and Western Sea (February 2008) of Korea. Changes in temperature are important in initiating the breeding cycle of *U. africana* (Hamekom & Erasmus, 1989) and beginning of the reproductive period depend mainly on temperature in *U. Pusilla* (T. Kevrekidis *et al*., 1997). It indicates that the breeding period of *Upogebia* sp. depend on temperature, however, there is no information of bottom water temperature in Tae-an at period of the previous study. Therefore, it is difficult to compare between the Western Sea and Southern Sea of Korea with bottom water temperature.

There is oil spill accident as another reason of that difference. In December 2007, there was oil spill accident in Tae-an. After this accident, massive mortality of *U. major* was presented by formation of oil film in sediment (Yu, 2011). Energy of *U. major* is invested for survival rather than gonad development (Kinoshita *et al*., 2003). It seems that difference of breeding period between the Southern Sea and Western Sea of Korea is caused by consumption of energy to increase survival rate during the oil polluted period.

This study revealed no significant difference in slope and intercept in the regression between the number of eggs in two egg stages and carapace length. This indicated that brood loss did not occur.

In present study, egg size of *U. major* showed egg size significantly larger in eyed egg stage than in non-eyed egg stage during development. The increase in egg volume observed similar results for other decapods including thalassinid shrimp in the tidal flat (Table 5). Increase in egg length and volume during incubation is commonly observed in the decapoda (Oh and Hartnoll, 2004). Egg volume increase during embryogenesis was strongly correlated with egg water content increase and suggests egg size increase during development was mainly due to water uptake by the embryo and retention of metabolic water resulting from respiration (Pandian, 1970; Amsler & George, 1984; Petersen & Anger, 1997). The increase in egg volume allows a greater mobility of the embryos and facilitates the release of the larvae (Nazari *et al*., 2000) and generally increases the vulnerability of eggs during incubation (Oh & Hartnoll, 2004). However, the brood loss not occur in present study. Therefore, it seems that brood loss wasn’t influenced by the increase in egg volume.

In present study, RO of *U. major* was 0.257. RO is a life-history trait reflecting the energy inverted in reproduction of decapods (Pianka, 1972). It indicates that females of *U.major* inverted 25.7 % of their body weight into the production of eggs. This value is higher than that of mud shrimps including thalassinid shrimps, such as *Palaemon northropi* (Rankin, 1898), *Betaeus emarginatus* (H. Milne Edwards, 1837), *Alpheus armillatus* (H. Milne Edwards, 1837) and *Calichirus seilacheri* (Harnáez *et al*., 2008) and slightly higher than that of *Calichirus tyrrhena* (Thessalou & Kiortsis, 1997) (Table 6). The results of our study suggest that reproductive investment of *U. major* seem to be relatively higher than that of other shrimps, but there may be different results about reproductive investment per embryo. The number of eggs of *U. major* is more than that of *C. tyrrhena*, but egg volume is lower. It means that reproductive investment per embryo of *U. major* was relatively smaller than that of *C. tyrrhena*, and larger eggs have more yolk (Strathmann and Vedder 1977; Turner and Lawrence 1979; Lawrence et al. 1984; McClintock and Pearse 1986; McEdward 1986). In case of *C. seilacheri*, relatively lower RO come from smaller egg volume, even if this species has egg number, similar to *U. major*.

The slopes of the linear regression between ln CL and ln BW showed significant difference for both sexes, which indicated difference in the relative growth rate. The slope of females was significantly higher than that of males and explained that body weight of females grew faster than males. The faster growth of weight related to carapace length in female of *U. major* may be caused by proportionally greater tissue production in the ovaries compared with that in the testis (Anger and Moreira, 1998) and related to egg production (Felder & Lovett, 1989).

Generally in many crustaceans species, growth of female reduced during breeding period due to the investment of energy in reproductive period such as egg production and care (Hartnoll, 1982), but molting in females *U. africana* and *Upogebia deltaura* (Leach, 1815) occurred approximately one month earlier than in males, suggesting that egg-laying occurs shortly after ecdysis (Hanekom & Baird, 1992). It indicates that body weight of *Upogebia*. sp. may increase rapidly after the ecdysis.

The growth performance indices (φ') were higher in the males than the females. This result indicates that the males grew faster than females, which means that males reached a larger size at the same age than females. There were few studies related growth performance index of the thalassinid shrimps. Similar result is observed in *U. pusilla* but opposite results are observed in *Sergio mirim* (Rodrigues, 1971) and *Callichirus major* (Say, 1818) (Table 7). This does not seem to be the general situation for thalassinid shrimps. The slowest growth season is from January to February for males and November to December for females. The slowest growth period for males is at relatively low water temperature, whereas the period slowest growth for females corresponded to the time when the highest GSI was observed.

The growth rate of female was slower from November to April and faster from May to August. Ovigerous females occurred from November to April. The period of slow growth coincided with breeding season. That reason is due to the long spawning period which extended the intermolt period and therefore caused individuals to grow more slowly. Moulting in female *U. Africana* and *U. deltaura* peaked approximately on month earlier than in males, which suggests that egg laying occurs shortly after ecdysis (Hanekom & Baird, 1992).

Spawning period is approximately from November to April, which was revealed by GSI values and appearance of ovigerous females in reproductive cycle. Females with eyed eggs were occurred from January to April. Evidence for the consecutive breeding of females is significant increase of GSI from non-eyed to eyed egg stages. This indicates that *U. major* can prepare for subsequent breeding events during reproductive period.

Table 5. Comparison of egg volume (mm^3) for a variety of decapods including thalassinid shrimps.

Family	Species	Egg volume		Source
		Non-eyed egg (mm^3)	Eyed egg (mm^3)	
Varunidae	*Helice crassa* (Dana, 1935)	13.37	23.14	Jones & Simons (1983)
	Neohelice granulata (Dana, 1851)	0.013	0.025	Silva *et al*. (2009)
Thalassinidae	*Callichirus seilacheri* (Bott, 1955)	0.227	0.243	Harnáez *et al*. (2008)
	Upogebia major (de Haan, 1841)	0.201	0.277	Present study

Table 6. Comparisons of reproductive output (RO), the number of eggs and egg volume for a variety of mud shrimps.

Family	Species	RO	Egg number	Egg volume (mm^3)	Source
Palaemonidae	*Palaemon northropi* (Rankin, 1898)	0.14	418	0.07	Anger & Moreira (1998)
Alpheidae	*Alpheus armillatus* (H. Milne Edwards, 1837)	0.12	763	0.1	Pavanelli *et al*. (2008)
	Betaeus emarginatus (H. Milne Edwards, 1837)	0.09	285	0.209	Lardies & Wehrtmann (1997)
Thalassinidae	*Callichirus seilacheri* (Bott, 1955)	0.15	17,450	0.243	Harnáez *et al*. (2008)
	Callichirus tyrrhena (Petagna, 1792)	0.20	270	0.86	Thessalou & Kiortsis (1997)
	Upogebia major (de Haan, 1841)	0.257	17,866	0.277	Present study

Table 7. Comparison of growth performance index ($\emptyset'$) for a variety of thalassinid shrimps.

Species	φ'		Source
	Male	Female	
Sergio mirim (Rodrigues, 1971)	2.79	2.84	Pezzuto (1998)
Callichirus major (Say, 1818)	2.24	2.31	Botter-Carvalho *et al*. (2007)
Upogebia pusilla (Petagna, 1792)	2.50	2.34	Dworschak *et al*. (1988)
Upogebia major (de Haan, 1841)	3.11	3.01	Present study

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