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Thesis for the Degree of Master of Science

Reproductive traits of two crangonid shrimps, *Crangon hakodatei* and *Metacrangon sinensis* (Crustacea, Decapoda) in the Geoje Island, South Korea

by

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Department of Marine Biology

The Graduate School

Pukyong National University

February 2019

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(거제도에 서식하는 자주새우류의 생식특성 연구)

PUKYONG NATIONAL UNIVERSITY
부경대학교

Advisor: Prof. Chul-Woong Oh

by
Pil Gyu Jung

A thesis submitted in partial fulfillment of the requirements
for the degree of

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

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CONTENTS

PUKYONG NATIONAL UNIVERSITY 부경대학교

LIST OF FIGURES

PUKYONG NATIONAL UNIVERSITY 부경대학교

LIST OF TABLES

PUKYONG NATIONAL UNIVERSITY 부경대학교

Reproductive traits of two crangonid shrimps, *Crangon hakodatei* and *Metacrangon sinensis*
(Crustacea, Decapoda) in the Geoje Island, South Korea

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Abstract

Fecundity of two crangonid shrimps, *Crangon hakodatei* and *Metacrangon sinensis*, were examined. Despite their essential ecological role, two crangonid shrimps' fecundity is barely known. Various parameters were used to define fecundity; number of eggs, reproductive output, egg dry weight and egg size. As fecundity is considered as one of the fundamental elements to understand species reproductive strategies, comparisons were made afterwards. Ovigerous females of *Crangon hakodatei* (7.15-17.84 mm CL) carried 738 to 10,238 eggs per brood, whereas *Metacrangon sinensis* females (3.69-7.45 mm CL) carried 8 to 38 eggs per brood. The number of eggs varied according to the body size in both early and late stages of egg development. The reproductive output (RO) of *C. hakodatei* was 0.16 in average, based on dry weights in early eggs, whereas *M. sinensis* had average value of 0.14. Brood mortality, which is a common phenomenon in crustaceans, was independent of female size and estimated to be a 38.43%. However, it was observed that brood loss did not occur during the incubation period in *M. sinensis;* perhaps due to small sample size. Mean egg volume and length significantly increased from non-eyed to eyed egg stages in both species. On the other hand, mean dry weight of eggs decreased as it alters from non-eyed to eyed stage. As reflected by the different egg numbers and size, their reproductive strategies are obviously opposed. Examining these two shrimps' fecundity would ultimately expand our understandings of the diversity of reproductive strategies found in the family Crangonidae.

1. Introduction

The crangonid shrimps inhabit in the littoral and the sublittoral areas of the Northern Hemisphere (Campos *et al*., 2012), especially in the cold and temperate waters of Northern Atlantic and Pacific oceans. In present, there are 219 species in 23 genres within the Crangonidae family worldwide (Holthuis, 1993; De Grave and Fransen, 2011), while 18 species of family Crangonidae are known to be inhabiting in Korean waters (Holthuis, 1980; Hayashi and Kim, 1999; Kim, 2015). Among these, two species of crangonid shrimps, *Crangon hakodatei* Rathbun, 1902 and *Metacrangon sinensis* Fujino and Miyake, 1970 are commonly found nearby the Geoje Island, Southern coast of Korea (Cho *et al*., 2013).

Crangonid shrimps provide essential functionality to the benthic communities in sustaining ecological balance by acting as vital food supply and also as predator to small organisms (Seikai *et al*., 1993; Mori, 1998). Despite their ecological significance, only few crangonid shrimps in Korean Waters have attracted much attention; previous researches were mainly focused on targeted species. *C. hakodatei* was included in the targeted species, where its larval development, feeding ecology, and the population dynamics were investigated (Choi *et al*., 2002; Li and Hong, 2003; Maher *et al*., 2013). On the other hand, *M.*

sinensis has only been studied with the aim to reveal the morphological or taxonomical features (Kim, 2005; Komai, 2011). These two crangonid shrimps' fecundity, reproductive output, and brood loss are rarely known.

Fecundity is considered one of the most fundamental elements to understand species' life history and reproductive patterns, and even their reproductive strategies (Bauer, 1986; Clarke, 1979, 1987; Ito, 1978; Pereira *et al.*, 2017). As with other caridean shrimps, crangonid shrimps are external brooders which enables to estimate fecundity more efficiently. Due to its significance and convenience, numerous researches have been conducted for crangonid shrimps on aspects of fecundity (Haefner, 1972; Natsukari and Iwasaki, 1987; Jay, 1989; Oh and Hartnoll, 1999; Bilgin and Samsun, 2006; Li *et al.*, 2011). The most widely known parameters proposed to define fecundity in crustaceans are reproductive output, egg dry weight and egg size. Brood loss must be also considered when estimating reproductive output for better accuracy. This loss indicates reduction of reproductive output during their incubation period and consequently affect reproductive potential of species. To estimate brood loss, comparisons of fecundity between the early and late stages of egg development is generally applied (Perkins, 1971; Oh and Hartnoll, 2004). In addition to this, estimating fecundity could be indices for intra- and interspecific comparisons of reproductive traits. Intraspecific variations of the reproductive output have been used in defining population characteristics (Hines, 1982; Torres *et al*., 2007), while interspecific comparisons have provided foundations for theoretical consideration of life history strategies (Torres *et al*., 2007).

This paper is intended to evaluate and compare the reproductive traits of two crangonid shrimps (*C. hakodatei* and *M. sinensis*) populating in the Geoje Island, Korea. To proceed, three major approaches were implemented for each species then compared; (1) fecundity, reproductive output and brood mortality, (2) the differences in egg properties according to embryonic development and (3) the relationship between the ovary and female weights depending on embryonic stages. Ultimately, these data would broaden our understandings of the diversity of reproductive strategies found in the crangonid shrimps and stimulate further research on crangonid shrimps inhabiting in Korea.

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2. Materials and Methods

2-1. Sample collection

The ovigerous females of *C. hakodatei* and *M. sinensis* were collected on bottom substrates with shrimp beam trawls (40 – 60m depth) in the Geoje Island, Southern coast of Korea (34°42'N, 128°42'E) (Fig. 1). Sampling was conducted from October 2017 to April 2018. Seven months is not sufficient enough to define species, since summer broods were excluded; Usage of shrimp beam trawl was prohibited from May to mid-October in this region for recovery of shrimp stocks. However, this study intends to be a preliminary work to provide guideline information since researches regarding *C. hakodatei* and *M. sinensis* are limited.

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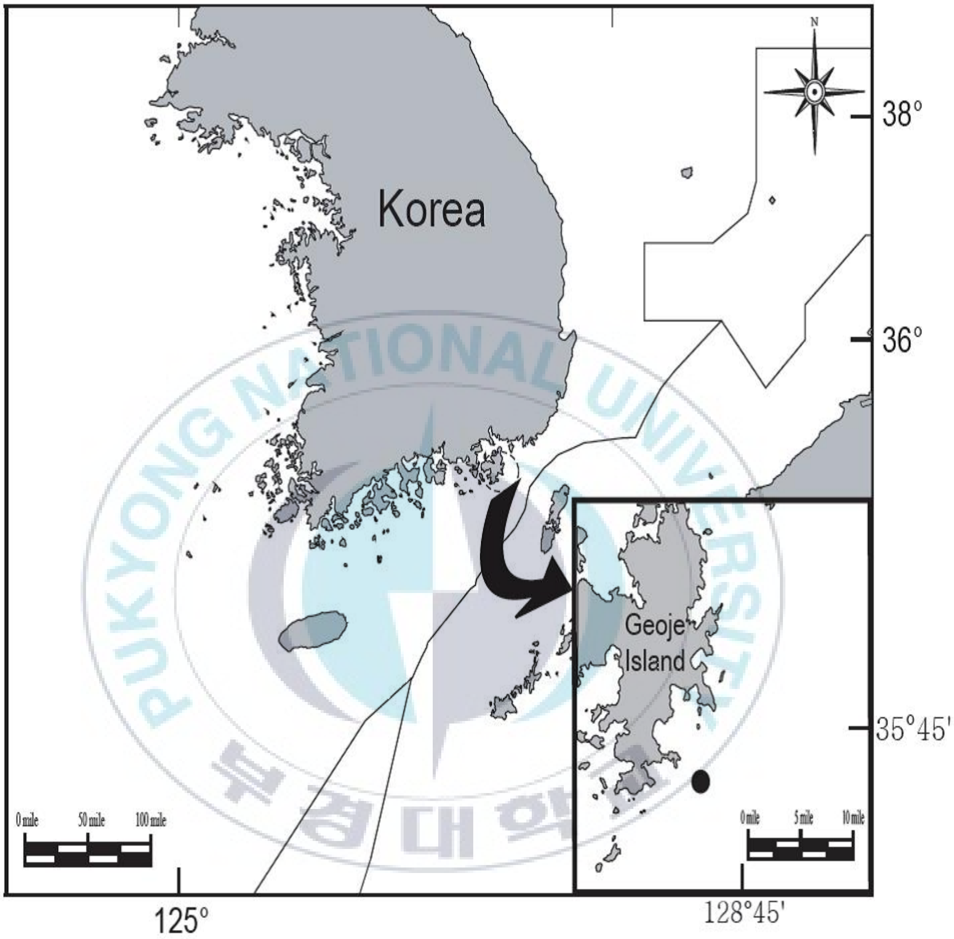

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Figure 1. Sampling area of *Crangon hakodatei* and *Metacrangon sinensis* in the Geoje Island, Southern coast of Korea.

2-2. Preservation and measurement

Samples were fixed in 10% neutralized formalin for a day, then transferred in 70% ethanol for preservation. Among samples, only ovigerous females in good conditions (i.e., no damage and egg mass undisturbed) were selected. Obtaining a wide-range of carapace length, and similar numbers of early and late stage eggs were the top priority. In total, approximately 192 ovigerous *C. hakodatei* and 57 of *M. sinensis* were analyzed. The morphometric measurements of samples were obtained such as carapace length (CL, distance between the anterior tip of rostrum and the posterior-median carapace margin) and total length (TL, distance between from the anterior tip of rostrum to the posterior end of telson) were measured to the nearest 0.01 mm using Vernier calipers.

2-3. Fecundity and Reproductive output (RO)

Egg stages of ovigerous females were categorized into two stages: (1) non-eyed (early) and (2) eyed-eggs (late), based on the absence or presence of eye pigments. Under ambiguity due to its small size, microscope was used to determine its stage. The embryo mass was carefully stripped from the pleopods using fine forceps and placed on a Petrie dish. Any setal or extraneous matters around the eggs were detached for better vision and count. Eggs were directly counted to minimize any bias which might arise from the indirect methods. To estimate reproductive

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output (RO) and evaluate carapace length-fecundity relationship, only data from females with non-eyed eggs were used to avoid potential error caused by brood loss. On the other hand, data from females with eyed eggs were used to estimate brood loss during incubation. After the process of egg-extrusion, ovaries according to the stages were dissected. Along with the female's body, eggs and ovaries were oven dried at 60℃ for 48 h for dehydrations and weighed to the nearest 0.0001g using an electronic digital balance. The reproductive output (RO) was determined using dry weights by applying the formula introduced by Clarke *et al.*, (1991):

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

2-4. Egg properties

Before the drying procedure, a subsample of approximately 10 eggs were selected for the measurements. The major and the minor axes of eggs, which includes the chorionic membrane tightly adhered to the egg surface, were measured using a binocular microscope. Eggs were treated as ellipsoid form and egg volume (EV) was calculated by the following formula:

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

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

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2-5. Statistical analysis

Linear regression analysis was performed to examine the relationship between carapace length (CL) and egg number (EN). To assure the homogeneity of variances and distribution of residuals, all data were log transformed before the analysis. An analysis of covariance (ANCOVA) was used to compare the slope and intercept between the two embryonic stages. If the slopes were not significantly different, common slope was determined and the elevations were tested. If the elevations were significantly different between the embryonic stages, brood loss was quantified by the following formula;

$$100\ [1\text{-}\exp\ (a_l\text{-}a_e)]$$

Where a_l is the intercept for the late egg stages, while a_e is the intercept for the early egg stages. The mean differences in egg volume, length and dry weights of egg and ovary between the stages were tested with student *t*-test.

All statistical analyses were conducted with MINITAB (version 18.0) and differences were considered significant at the 95% confidence level ($P < 0.05$) in all comparisons.

3. Results

3-1. Fecundity and Reproductive output (RO)

The 74 females of *C. hakodatei* with non-eyed eggs were analyzed. The carapace length ranged from 7.15 – 17.84 mm and fecundity ranged from 738 to 10,238 eggs. The regressions between carapace length (CL) and egg number (EN) in the females with non-eyed and eyed eggs revealed statistically significant linear relationships. The slope of the regression in non-eyed stage was less than 3, which indicates that the relationship between the variables are negative allometry. In contrast, the slope was close to 3, indicating that an isometric relationship was observed in eyed egg stage (Fig. 2).

Non-eyed egg: $ln\ \mathrm{EN} = 2.588\ (\pm\ 0.34)\ ln\ \mathrm{CL} + 1.577\ (n = 74,\ r^2 = 0.84,\ P < 0.001)$,

Eyed egg**:** $ln\ \mathrm{EN} = 2.813\ (\pm\ 0.28)\ ln\ \mathrm{CL} + 0.494\ (n = 51,\ r^2 = 0.84,\ P < 0.001)$.

During the early stage, the significant positive regressions between *ln* egg dry weight (Edwt) and *ln* female dry weight (Fdwt) were found (Fig. 3).

$ln\ \mathrm{Edwt} = 1.337\ (\pm\ 0.23)\ ln\ \mathrm{Fdwt} - 3.744\ (n = 74,\ r^2 = 0.88,\ P < 0.001)$. Reproductive output (RO) (± SD), determined from the data was 0.16 (± 0.04) (n = 74).

In *M. sinensis*, 51 females with non-eyed eggs were examined. The carapace length ranged from 3.69 – 7.45 mm and the number of eggs per brood ranged from 8 to 33. The relationships between the CL and the EN per brood revealed statistically significant linear relationship. The slopes for both stages were less than 3, which represents the negative allometric relationships (Fig. 4).

Non-eyed egg: ln EN= 1.74 (± 0.1511) ln CL – 0.171 ($n = 51$, $r^2 = 0.83$, $P < 0.001$),

Eyed-egg: ln EN= 1.67 (± 0.0263) ln CL – 0.164 ($n = 6$, $r^2 = 0.99$, $P < 0.001$).

The relationship between ln Edwt and ln Fdwt were significantly positive (Fig. 5).

ln Edwt = 1.128 (± 0.20) ln Fdwt – 2.506 ($n = 51$, $r^2 = 0.75$, $P < 0.001$). When quantified by the formula, reproductive output (RO) (± SD) for this specie was 0.14 (± 0.03) ($n = 51$).

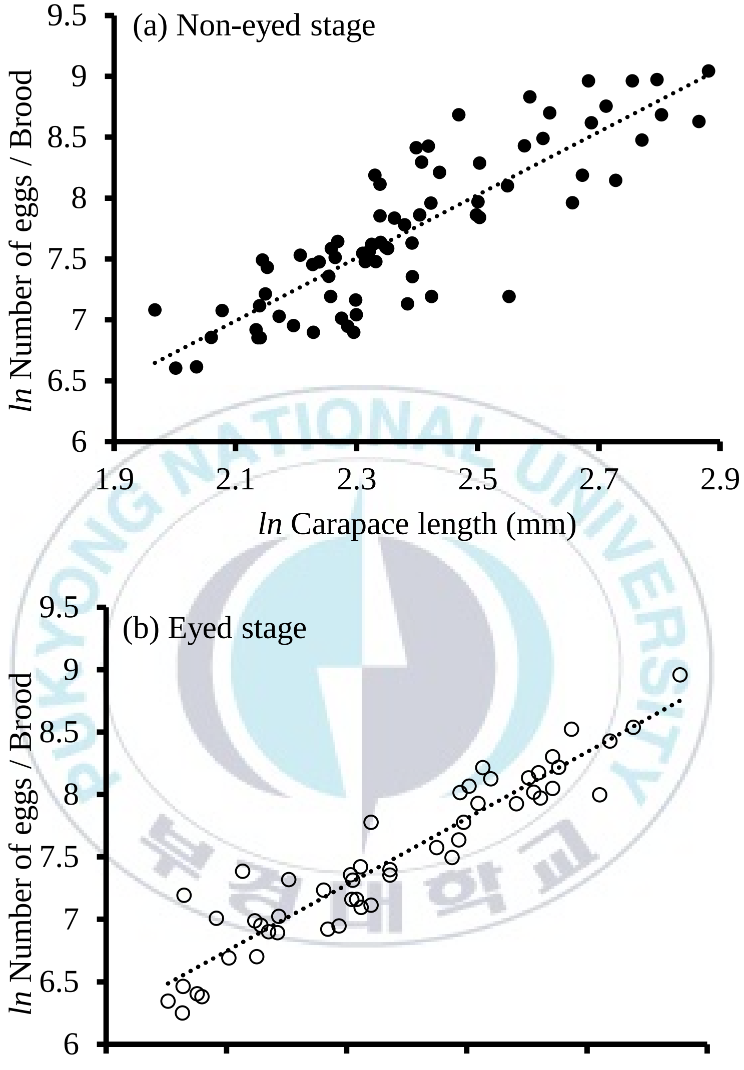

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Figure 2. Relationship between *ln* carapace length (CL) and *ln* number of eggs per brood (EN) in *Crangon hakodatei*. (a) Black circle indicates the non-eyed stage and (b) open circle indicates the eyed stage.

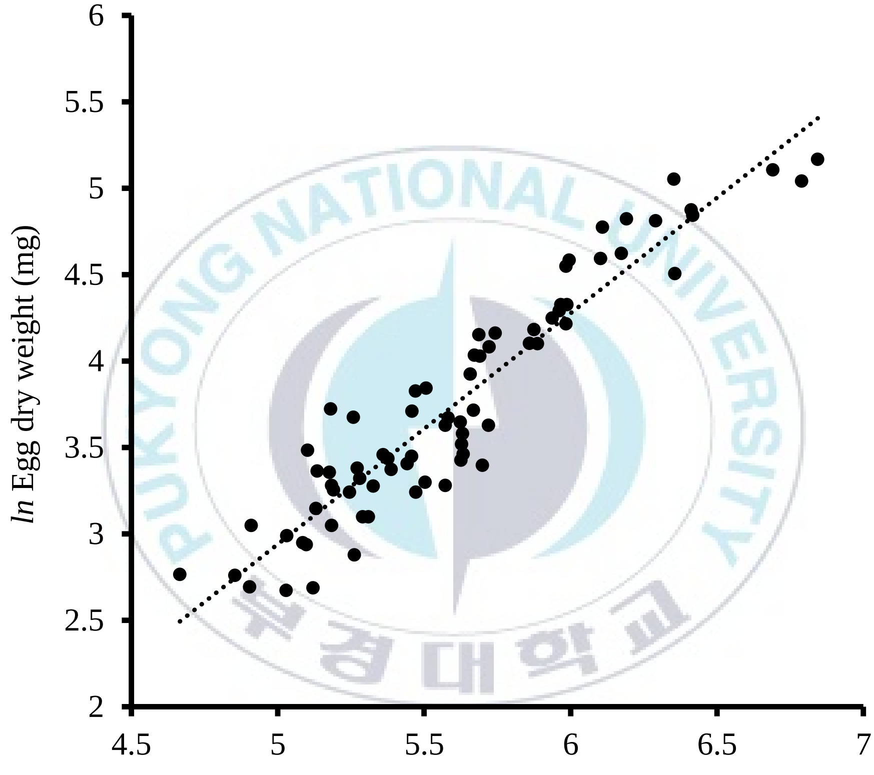

Figure 3. Relationship between *ln* female dry weight (Fdwt) and *ln* egg dry weight (Edwt) in *Crangon hakodatei*.

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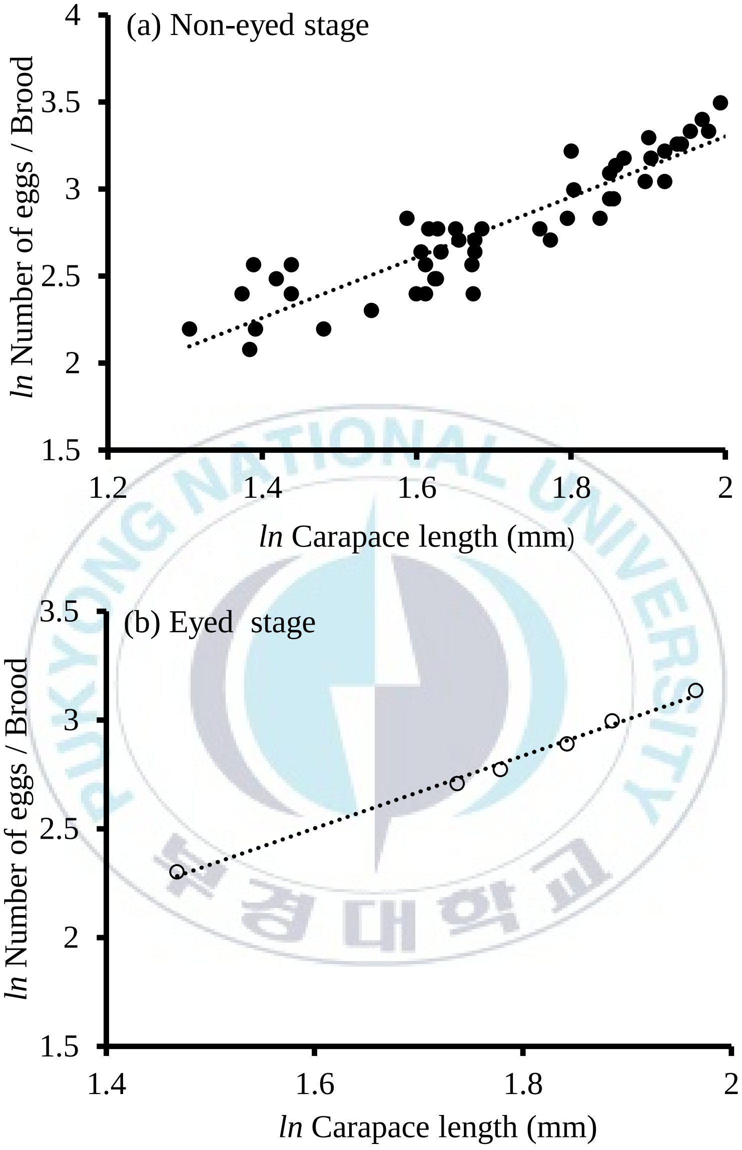

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Figure 4. Relationship between *ln* carapace length (CL) and *ln* number of eggs per brood (EN) in *Metacrangon sinensis*. (a) Black circle indicates the non-eyed stage and (b) open circle indicates the eyed stage.

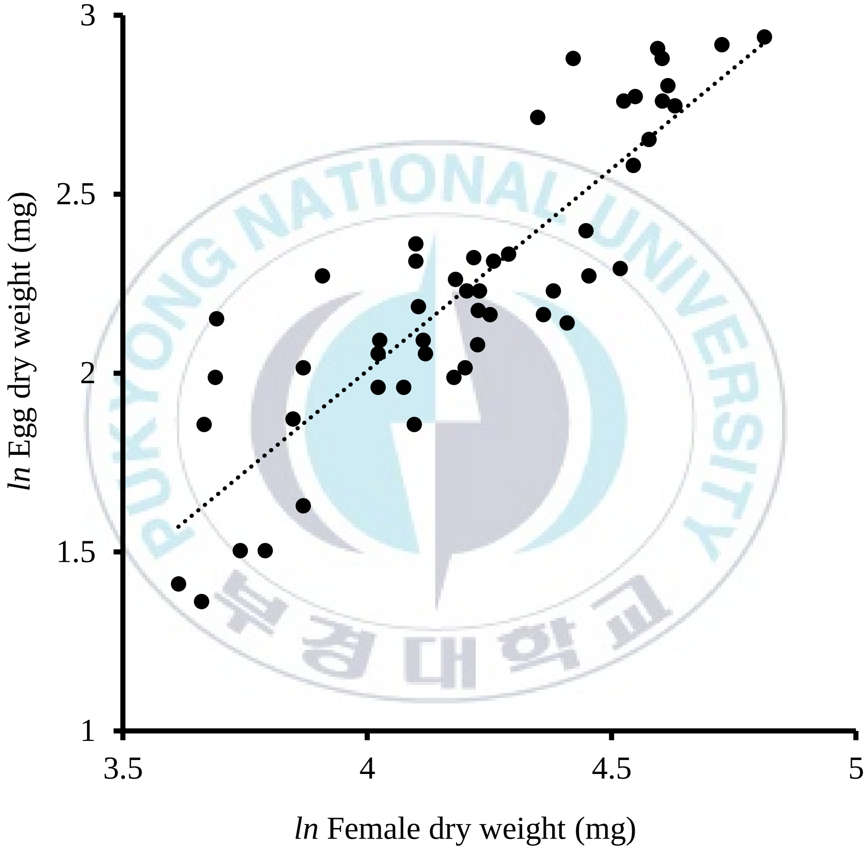

Figure 5. Relationship between *ln* female dry weight (Fdwt) and *ln* egg dry weight (Edwt) in *Metacrangon sinensis*.

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3-2. Brood mortality

The regressions between carapace length and egg number of *C. hakodatei* were compared for both stages to examine brood loss. ANCOVA indicated that the slopes of the regression were not significantly different ($F = 1.28$, $df = 1, 121$, $P > 0.25$). However, elevations were significantly different after the recalculation of a common slope ($F = 67.68$, $df = 1, 120$, $P < 0.001$) (Fig. 6). Results support that there was a significant brood loss occur during their incubation period. Based on the common slope regression, brood mortality between the two stages was 38.43%.

Same approach was taken to measure the brood loss in *M. sinensis*. ANCOVA results demonstrated that the slopes of the regression were not significantly different between two stages ($F = 0.03$, $df = 1, 53$, $P > 0.8$). When common slope was applied, the intercepts were not significantly different ($F = 3.60$, $df = 1, 52$, $P > 0.05$) (Fig. 7). This statistical analysis indicates that brood loss did not occur during the incubation period.

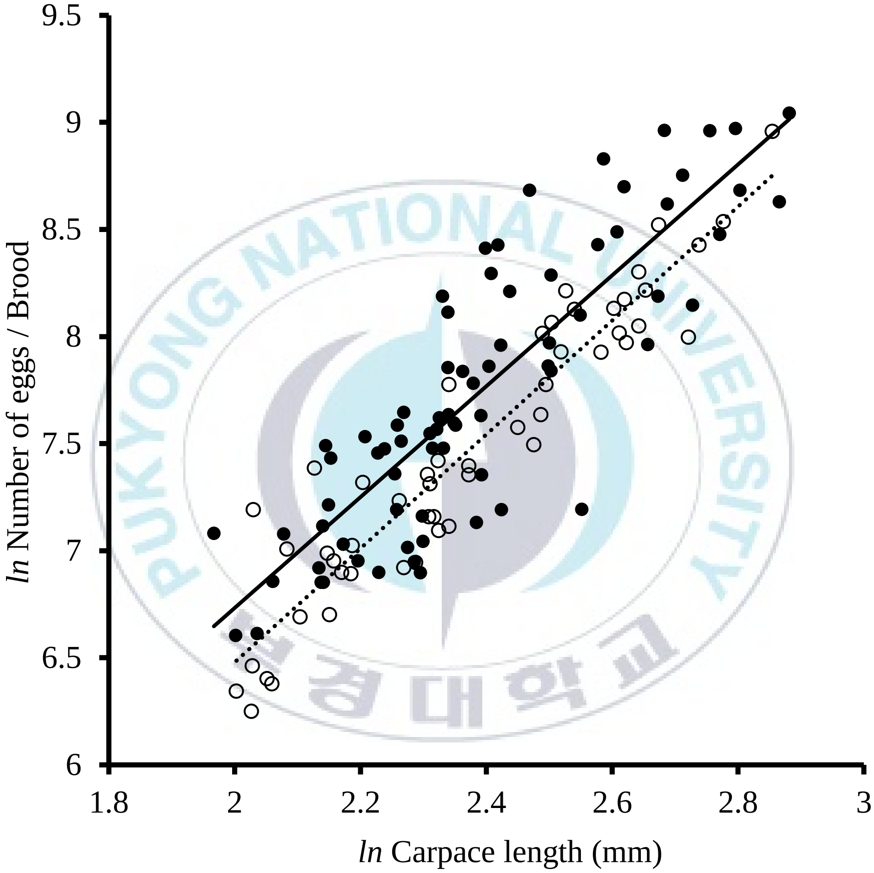

Figure 6. Regression of *ln* egg number (EN) on *ln* carapace length (CL) of ovigerous female *Crangon hakodatei* with non-eyed (black-circle) and eyed eggs (open-circle).

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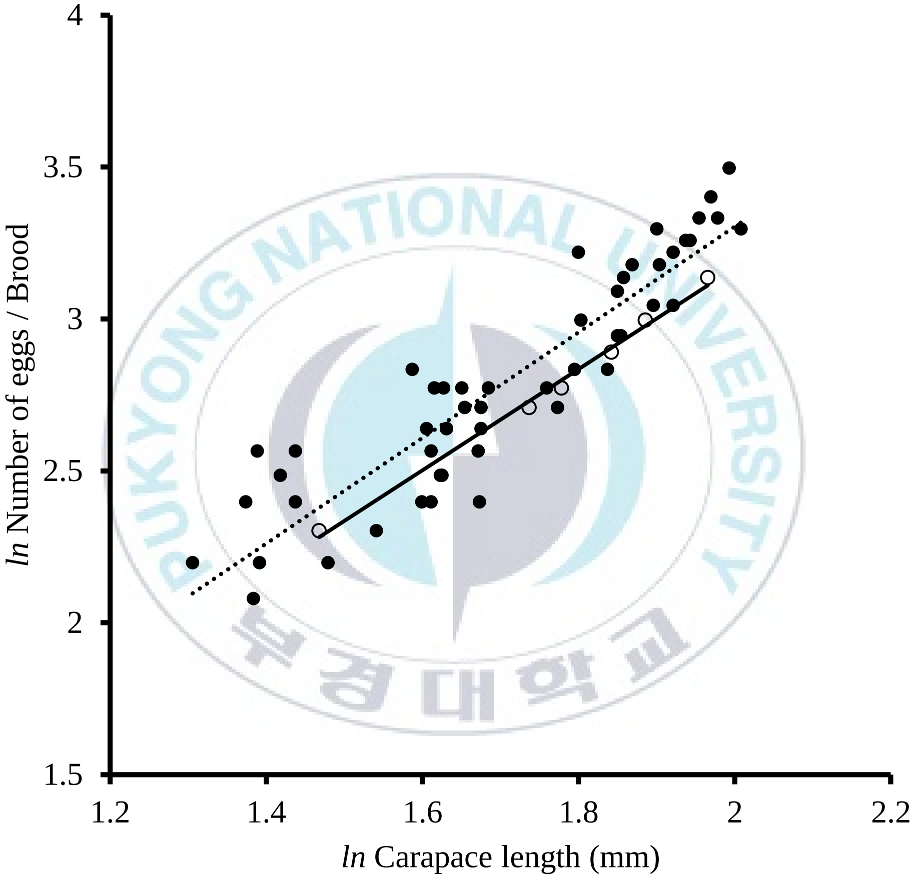

Figure 7. Regression of *ln* egg number (EN) on *ln* carapace length (CL) of ovigerous female *Metacrangon sinensis* with non-eyed (black-circle) and eyed eggs (open-circle).

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3-3. Egg properties (volume, length and dry weight)

Mean egg volume of *C. hakodatei* between two embryonic stages were significantly different indicating that eyed egg stage was larger than non-eyed egg stage (Student t-test, $P < 0.001$). Mean egg volume (± SE) increased about 103.85% from non-eyed stage (0.052 ± 0.003 mm^3, $n = 74$) to eyed stage (0.106 ± 0.003 mm^3, $n = 51$). Mean egg length (± SE) significantly increased by 34.62% from (0.52 ± 0.009 mm) in non-eyed stage to (0.70 ± 0.010 mm) in eyed stage ($P < 0.001$). In contrast, mean dry weight of eggs (± SE) decreased 88% from non-eyed (0.049 ± 0.004 g) to eyed stages (0.025 ± 0.003 g) ($P < 0.001$) (Fig. 8).

In *M. sinensis*, the mean egg volume of eyed eggs (1.78 ± 0.042 mm^3, $n = 6$) was significantly larger than that of the non-eyed eggs (1.09 ± 0.140 mm^3, $n = 48$) (Student t-test, $P < 0.05$). Mean egg volume increased about 63.30% from non-eyed to eyed egg stage. Mean egg length also significantly increased by 17.01 % from non-eyed stage (1.47 ± 0.016 mm) to eyed stage (1.72 ± 0.045 mm) ($P < 0.05$). On the other hand, mean dry weight of eggs decreased by 52.24%, from (0.0102 ± 0.0005 g) in non-eyed eggs to (0.0067 ± 0.0013 g) in eyed-egg stages ($P < 0.05$) (Fig. 9).

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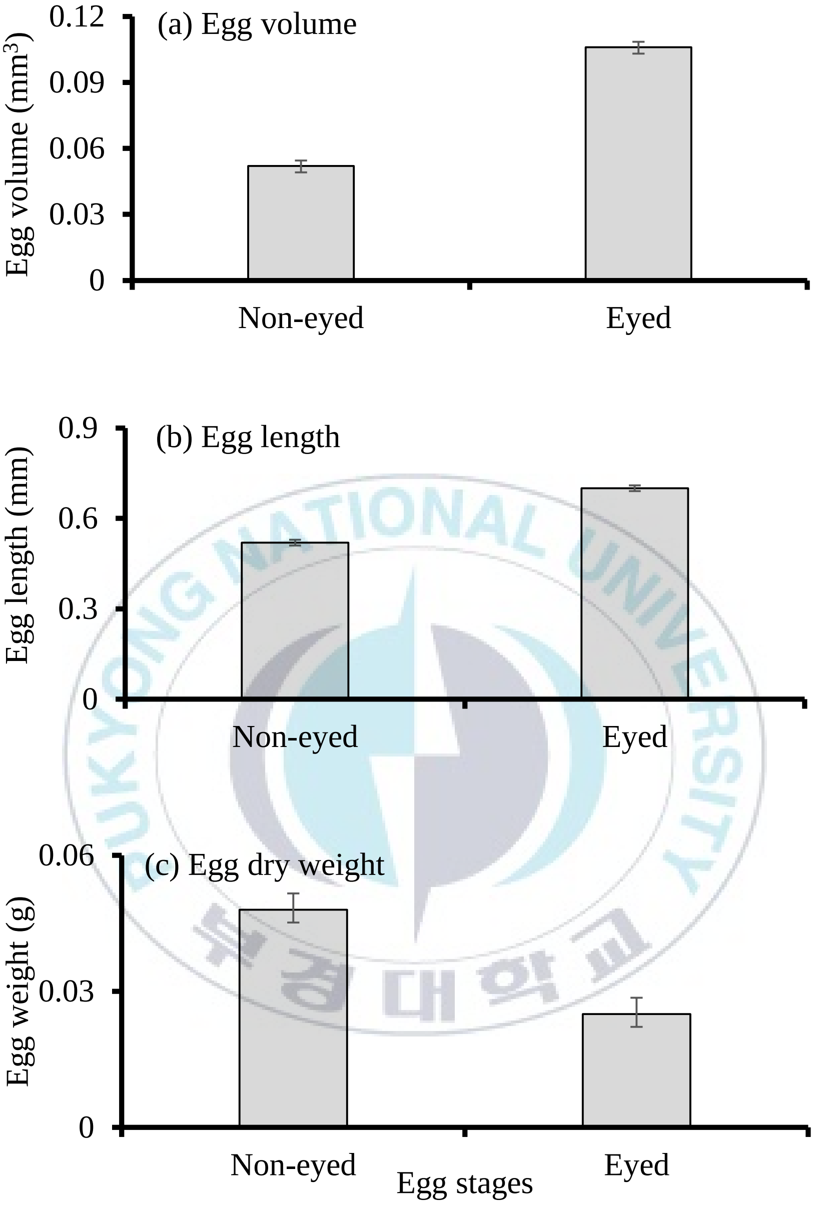

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Figure 8. Changes in (a) mean egg volume, (b) length and (c) dry weight of eggs with ± standard error, during embryonic development in *Crangon hakodatei*.

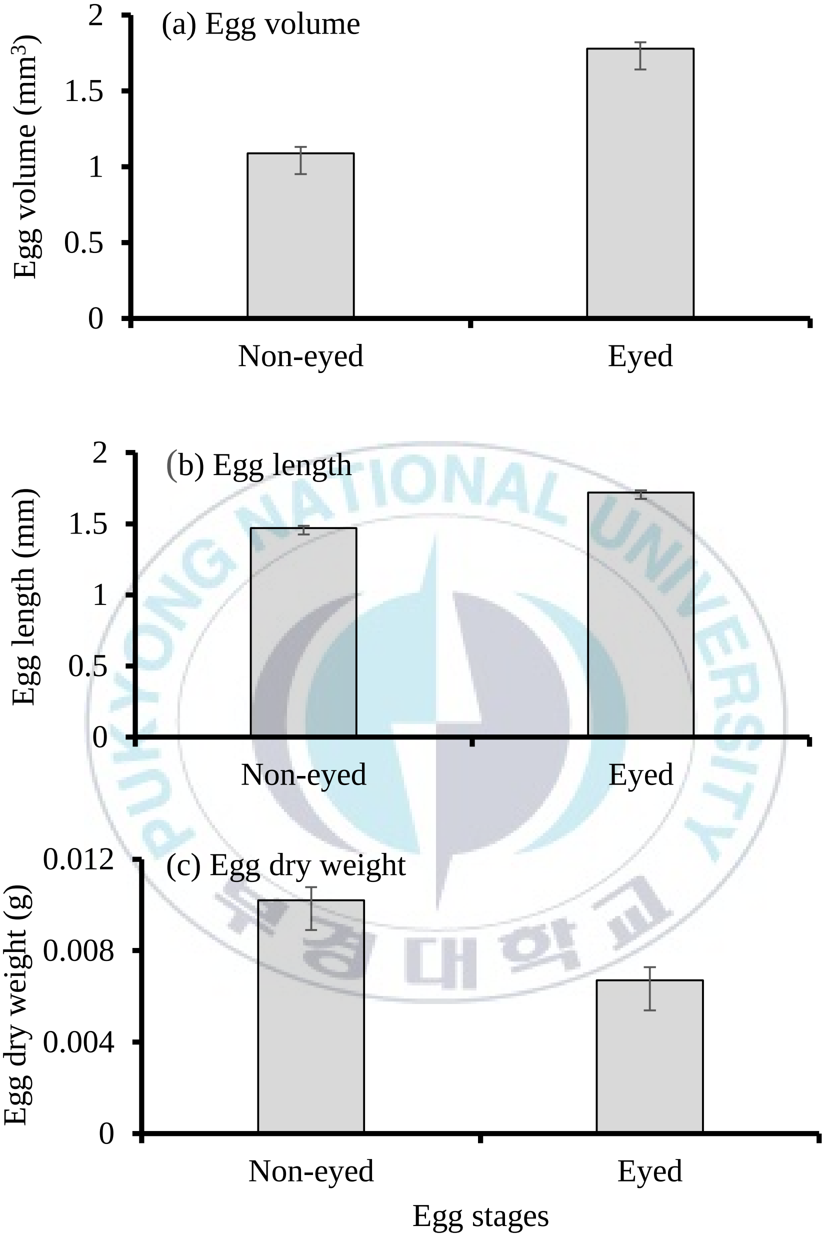

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Figure 9. Changes in (a) mean egg volume, (b) length and (c) dry weight of eggs with ± standard error, during embryonic development in *Metacrangon sinensis.*

3-4. Ovarian dry weight

The carapace length (CL) and ovarian dry weight (Odwt) of *C. hakodatei*, were significantly correlated in both females with non-eyed and eyed eggs (Fig. 10).

Non-eyed egg: ln Odwt = 3.151 (± 0.33) ln CL - 12.34 ($n = 37$, $r^2 = 0.52$, $P < 0.001$)

Eyed egg: ln Odwt = 2.908 (± 0.22) ln CL – 11.070 ($n = 56$, $r^2 = 0.68$, $P < 0.001$)

To investigate whether the regression between Odwt and CL differed between two stages, the differences in slope and elevation of the two regressions were tested. ANCOVA revealed that slopes did not significantly differ between the two stages ($F = 0.21$, $df = 1, 89$, $P > 0.6$). However, when common slope was applied, the intercepts differed significantly ($F = 154.47$, $df = 1, 88$, $P < 0.001$). This indicates that there was a significant increase in mean Odwt from non-eyed to eyed stage.

The relationship between CL and Odwt were also significantly correlated in both stages of *M. sinensis* (Fig. 11).

Non-eyed egg: ln Odwt = 3.122 (± 0.18) ln CL – 12.006 ($n = 27$, $r^2 = 0.70$, $P < 0.001$)

Eyed egg: ln Odwt= 2.460 (± 0.06) ln CL- 10.310 ($n = 6$, $r^2 = 0.98$, $P < 0.001$)

Same method was applied as above. ANCOVA revealed that the slopes did not significantly differ between the stages. ($F = 1.33$, $df = 1, 31$ $P > 0.2$). When common slope was introduced, the intercepts were significantly different (*F* = 44.63, *df* = 1, 30, $P < 0.001$). There was a significant increase in mean Odwt from non-eyed to eyed egg stage.

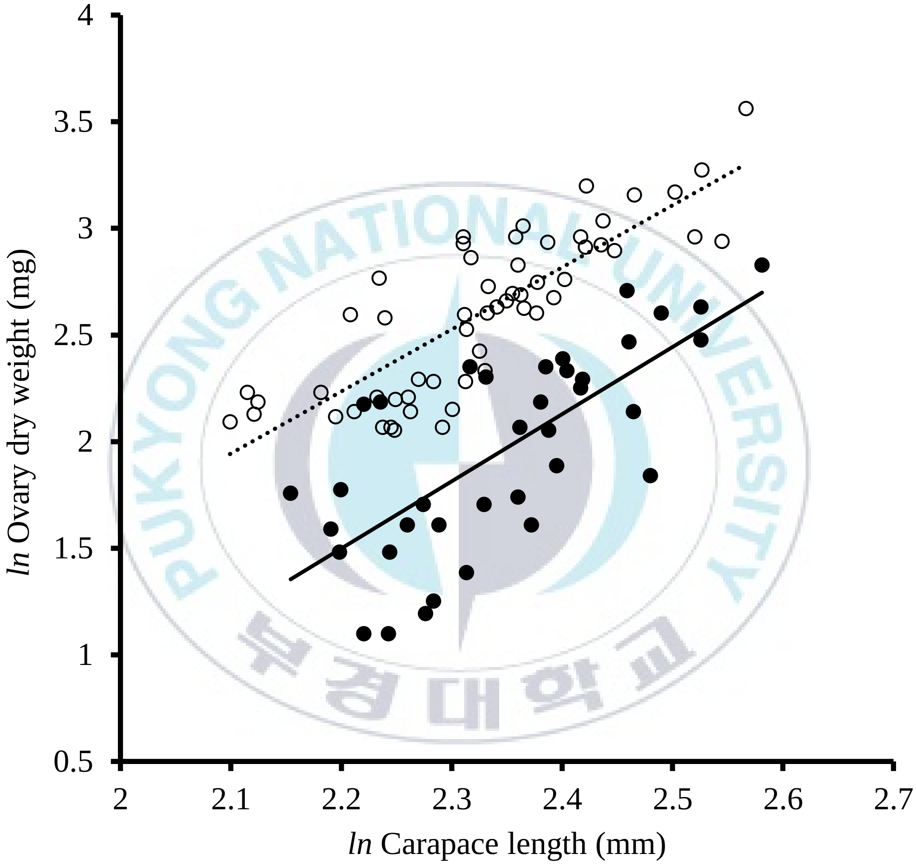

Figure 10. Regression of *ln* ovarian dry weight (Odwt) of *ln* carapace length (CL) of ovigerous female *Crangon hakodatei* with non-eyed (black-circle) and eyed (open-circle).

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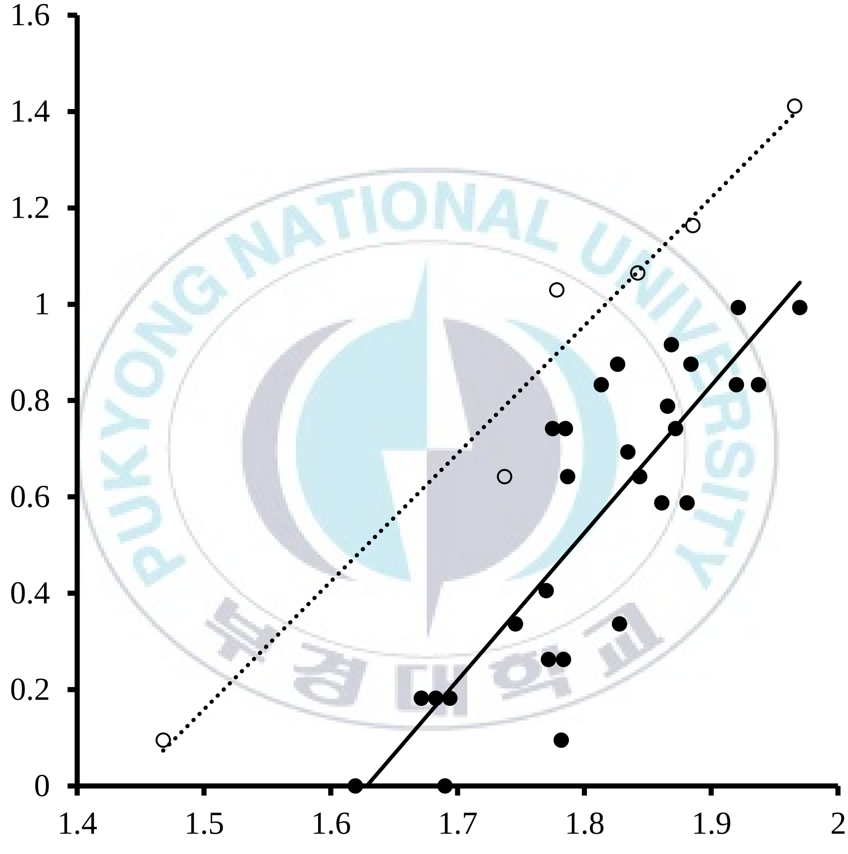

Figure 11. Regression of *ln* ovarian dry weight (Odwt) on *ln* carapace length (CL) of ovigerous female *Metacrangon sinensis* with non-eyed (black-circle) and eyed (open-circle).

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4. Discussions

4-1. Fecundity and Reproductive Output (RO)

In this study, it was amply demonstrated that brood size and female body size are positively correlated for both species. This relationship was consistent with previous studies of caridean shrimps (Clarke *et al*., 1991; Corey and Reid, 1991; Kim and Hong, 2004) and crangonid shrimps in the narrower sense of taxonomy (Boddeke, 1982; Hong and Oh, 1989; Oh and Hartnoll, 1999[b]; Li *et al*., 2011; Viegas *et al*., 2012). This correlated relationship certainly induces that size plays a critical role in egg production. Space in the abdomen, where they accommodate embryos, would expand correspondingly to the females' size (Clarke, 1993). Moreover, depending on the decapod species, there is a trade-off between growth and reproduction in terms of energy investigation. Larger specimens would have more energy resources to utilize, allowing them to allocate more energy toward gonad maturation (Baeza, 2006). In contrast, small specimens tend to investigate more energy in growth (Calado and Dinis, 2007).

As Table 1 presents, the maximum fecundity of crangonid shrimps differ tremendously. *Crangon* species generally produce over thousands of embryos, whereas comparatively low fecundities have been documented in other genera. This wide disparity between the species or even genera is most likely due to the different female body size. However, other biological factors must be considered to elucidate this interspecific variations. First, habitat characteristics; Sub-polar and bathyal species are known to be having larger but fewer eggs than those living in temperate area (Lacoursière-Roussel and Sainte-carie, 2009). Second, habitat adaptation associated with different reproductive strategies; In general, the egg size tends to be larger but fewer in number with increasing depth and also require longer periods of larval development as an adaption to endure the food-scarcity condition in deeper water (King and Butler, 1985). The differences in maximum fecundity between two studied shrimps fits into this category. The *Metacrangon* species usually populate in deeper environments than are *Crangon* species (Table 2). Furthermore, the fecundities also could vary intra-specifically (by region) as indicated by different numbers observed in *C. crangon* (3,630 and 8,708) (Table 1). It has been reported that the size of embryo increases simultaneously with the latitude but, inversely related with embryo number (Echeverría-Sáenz and Nelson, 2011). Therefore, latitudinal or seasonal aspects also deserve considerations.

When reproductive output (RO) was quantified, brood weight averaged 16% of female body weights in *C. hakodatei* and 14% in *M. sinensis* respectively. Among various caridean shrimps, the average RO value varies from 10% to 44% (Clarke *et*

PUKYONG NATIONAL UNIVERSITY

al., 1991) and from 12 to 24% in crangonid shrimps (Clarke, 1987) (Table 3). Both of our results fell within the range RO value of crangonid shrimps. In comparison, the average RO value of other crustaceans such as deep-sea crabs is limited to be less than 10% (Hines, 1988). Hence, the observed value and other data support that this average RO value is a general range of crangonid shrimp.

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Table 1. Maximum fecundity of crangonid shrimps.

Genus	Species	Maximum Fecundity	Reference
Crangon	*C. affinis*	4,088	Hong and Oh (1989)
	C. allmani	7,000	Allen (1960)
	C. crangon	3,630	Bilgin and Samsun (2006)
		8,708	Tiews (1970)
	C. uritai	13,824	Li *et al.* (2011)
	C. hakodatei	10,238	Present study
Metacrangon	*M. sinensis*	33	Present study
	M. jacqueti	288	Wenner (1978)
Notocrangon	*N. antarcticus*	348	Bluhm and Brey (2001)
Sclerocrangon	*S. boreas*	184	Ingram (1979)

PUKYONG NATIONAL UNIVERSITY
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Table 2. Maximum depth reported in crangonid shrimps.

Genus	Species	Maximum depth (m)	Reference
Crangon	*C. affinis*	< 200	Hayashi and Kim (1999)
	C. crangon	< 50	Gibson *et al*. (2008)
	C. hakodatei	< 70	Choi *et al*. (2002)
		< 250	Hayashi and Kim (1999)
	C. propinquus	< 40	
	C. uritai	< 40	Li and Hong (2011)
Metacrangon	*M. hanoa*	< 353	Komai and Ahyong (2010)
	M. hikurangi	< 1171	
	M. proxima	< 280	Komai (2011)
	M. similis	< 412	
	M. sinensis	< 150	Fujino and Miyake (1970)
	M. teina	< 636	Komai and Ahyong (2010)

PUKYONG NATIONAL UNIVERSITY 부경대학교

Table 3. Reproductive output of caridean shrimps

Family	Species	Reproductive Output	Reference
Crangonidae	*Argis lar*	0.12	Seo *et al.*(2014)
	Crangon crangon	0.17	Clarke (1987)
	Crangon uritai	0.23	Li *et al.* (2011)
	Notocrangon antarcticus	0.12	Clarke (1987)
	Philocheraus trispinosus	0.14	Oh and Hartnoll (1999)
	Sabina sepetemcarinata	0.14	Clarke (1987)
Hippolytidae	*Lebbeus groenlandicus*	0.18	Bae (2014)
Pandalidae	*Pandalus gracilis*	0.34	Oh *et al.* (2008)

4-2. Brood mortality

In both species, the slopes of the regression between brood and female size according to embryonic stages were not significantly different. Based on the differences observed in intercepts, brood loss in *C. hakodatei* was 38.43%. It has been reported that, percentage of brood loss varies from 12% to 74% in caridean shrimps (Oh and Hartnoll, 1999), whereas 17% to 33% in crangonid shrimps (Hong and Oh, 1989). Brood loss of *C. hakodatei* was relatively higher compare to the average loss of other crangonid shrimps', but was still within the range of caridean shrimps. However, brood loss did not occur in *M. sinensis*. This unusual result was perhaps associated with their reproductive strategy, but most likely due to insufficient sample size used in this study (*n* = 6).

The numerous causative factors of brood loss have been suggested such as maternal cannibalism, parasite issue, mechanical loss and even the sampling method (Penha-Lopes *et al*., 2007). Nemertean parasites and *Argeia pugettensis* are the ideal parasite examples that affect brood loss in crustaceans (Kuris and Wickham, 1987; Seo *et al*., 2014). The presence of nemertean parasites were barely reported in crangonid shrimps nor caridean shrimps. Having characteristics such as frequent ecdysis or specialized appendages for grooming, would reduce the probability of parasite attachments (Kuris and Wickham, 1987). On the other hand, *A. pugettensis* was observed in crangonid shrimps inhabiting in Korea (Seo *et al*., 2014). However, there was no sign of any parasite in this study, thus parasitism was discarded from the reason of brood loss. The one of the major factors that yield brood loss in crangonid shrimps is perhaps their burrowing behavior. As they burrow, exposed eggs on their abdomen would collide with substrates, which makes it vulnerable to egg loss. Moreover, the embryo requires more oxygen as they enter later stage due to the process of cell differentiation (Dick *et al.,* 1998). This demand of more oxygen would make females to exhibit pleopods beating more frequently, resulting more brood loss.

4-3. Egg properties

The tendency of increment in egg volume and length but reduction in weight during embryonic developments are generally observed in the decapod shrimps (Wear, 1974; Boddeke, 1982; Oh and Hartnoll, 2004; Bilgin and Samsun, 2006). The volume increment of *C. hakodatei* (103.85%) and *M. sinensis* (63.30%) in this study were within the range described (50% to 175%) in decapods (Wear, 1974). The volume increment percentage tends to vary from species to species. In *C. crangon*, egg volume increased approximately 135% (Oh and Hartnoll, 2004) 69.03% in *C. uritai* (Li *et al*., 2011) and 17% in *A. lar* (Seo *et al*., 2014). Equivalent to the egg volume, egg length also increased as they enter later stage. The egg length increment of *C. hakodatei* (34.62%) was larger than *M. sinensis* (17.01%), but less than that of *C. crangon* (48%) and *P. trispinosus* (41%) (Oh and Hartnoll, 1994; 2004). This variations in either egg volume or length among species might be related to their different water depth preferences. Shrimps in deeper water generally have slower rates of egg growth during development than those inhabiting in coaster waters (King and Butler, 1985). Unlike the egg volume and length, dry weights of embryo decreased in both species by 88% in *C. hakodatei* and 52.24% in *M. sinensis* respectively during their embryogenesis. This reduction in egg dry weights is associated with increased water contents for cellular mobility and changes in biochemical compositions of crangonid shrimps during embryogenesis (Green, 1965).

4-4 Breeding characteristics

The ovigerous females of *C. hakodatei* and *M. sinensis* were constantly present throughout the 7 months of sampling. This observation indicates that two studied shrimps are possibly consecutive breeders. Another evidence to support this assumption is the significant increments in ovarian weight from the non-eyed stage to eyed-stage, which were observed in both species. This increment indicates that they are developing ovaries concurrently with their active reproductive cycle, so that they can prepare for the following breeding events. Also, most species of crangonid shrimps are known to exhibit consecutive breeding as documented in numerous previous researches (Allen, 1960; Modlin, 1980; Corey, 1987; Hong and Oh, 1989).

The most precise way to determine breeding seasons of caridean shrimps is finding the peaks of reproductive activity, which is reflected by the gonadosomatic index (GSI). According to Han and Li (2015), two discrete spawning peaks of *C. hakodatei* living in the Yellow Sea, China were March to April and August to September. At the same location, *M. sinensis* were present throughout the year but breeding peaks are unrevealed (Fujino and Miyake, 1970). In the present study, sampling period was relatively too short to access the GSI value as they usually require at least 1-year of sampling. Therefore, defining breeding seasons of these two shrimps were difficult. Understanding breeding season of species are crucial to manage these resources more efficiently. Further research is inevitable in this perspective.

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