Thesis for the Degree of Master of Engineering

Growth and reproduction of the red-banded lobster *Metanephrops thomsoni* (Bate, 1888) around Jeju Island, Korea

by

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Growth and reproduction of the red-banded lobster *Metanephrops thomsoni* (Bate, 1888) around Jeju Island, Korea (제주 연안역에서 가시발새우의 성장과 생식)

Advisor: Prof. Chul-Woong Oh

by
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Growth and reproduction of the red-banded lobster *Metanephrops thomsoni* (Bate, 1888) around Jeju Island, Korea

한 동 주

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요약

가시발새우 (*Metanephrops thomsoni*)의 성장과 생식에 대한 연구는 제주 인근 해역에서 2021 년 3 월부터 2022 년 3 월까지 이루어졌다. 총 5,430 마리의 표본이 채집되었다. 월별로 체장빈도 분포는 암, 수 간에 차이가 있었다. 수컷의 평균 두흉갑장 (CL)은 26.25 ± 4.77 mm 였고 전중 (BW)은 16 ± 9.3 g 이었다. 암컷의 평균 CL 은 25.43 ± 3.93 이고 BW 는 14.35 ± 6.70 g 으로 수컷이 유의하게 더 컸다. CL 과 BW 의 관계는 수컷 $y = 0.0005CL^{3.1701}$ 암컷 $y = 0.0005CL^{3.1606}$ 으로 나타났다. 생식도 지수 (GSI)는 6 월과 9 월에 2 번의 정점이 나타났다. 포란 암컷은 연구기간 중 5 월을 제외한 모든 달에서 관찰되었다. 6 월에서 12 월까지 포란 암컷의 평균 CL 이 감소하는 추세를 보였다. 가시발새우의 포란수 (EN)는 미발안난의 경우 평균 406.99 ± 90.46, 발안난의 경우 평균 233.21 ± 86.85 로 나타났다. 미 발안난과 발안난의 부피평균에서는 유의한 차이가 있었으며, 난 단계별 CL 에 따른 EN 과의 관계식은 미발안난 $\ln EN = 18.716\ (\pm\ 3.00) \ln CL - 175.31$ 발안난 $\ln EN = 12.147\ (\pm\ 3.66) \ln CL - 135.14$ 으로 나타났다. 두 난 단계의 회귀직선의 기울기는 유의한 차이가 없었지만 (ANCOVA, $F = 0.39$, $df = 113, 1$, $P > 0.05$) 절편에서는 유의한 차이를 보였으며 (ANCOVA, $F = 148.89$, $df = 114, 1$, $P < 0.001$) 이를 통해 나타낸 난 손실률은 42.3% 였다. 군성숙체장 (CL_{50})은 23.21 mm 였으며, 생식 산출력 (RO)은 0.066 ± 0.026 이였다. Von Bertalanffy 성장 매개변수와 성장비교지수 (φ)는 암, 수 각각 다음과 같았다. 수컷: $CL_\infty = 44$ mm, $K = 0.69$, $C = 0.10$, $WP = 0.50$, $\varphi' = 3.13$; 암컷: $CL_\infty = 42.3$ mm, $K = 0.55$, $C = 0.09$, $WP = 0.58$, $\varphi' = 2.99$. 암, 수 간 성장 매개변수 차이는 CL_∞와 K에서 나타났다.

1. Introduction

Metanephrops thomsoni, the red-banded lobster, are found mainly in the sandy mud bottom at about 200 m. They are mainly distributed in parts of the South Sea of and distributed in the East China Sea, Japan, Taiwan, the South China Sea, the Philippines, and Australia.

Previous studies on red-banded lobster are conducted on embryogenesis (Hamasaki & Matsuura, 1987) and egg loss (Matsuura & Hamasaki, 1987) in Japan. Hamasaki & Matsuura (1987) mentioned that embryonic development period is the fastest. Hamasaki & Matsuura (1987) and Choi et al. (2008) observed egg loss of *M. thomsoni*. Population biology and mitochondrial genome were studied in Korea (Choi et al., 2008; Ahn et al., 2016).

M. thomsoni has been utilized as fisheries resource in Korea, and many trawler ships have flowed into the *M. thomsoni* fishery since 2016. As a result, the catch of *M. thomsoni* increased from 62,116 tons in 2016 to 206,142 tons in 2018. *Nephrops norvegicus* biomass caught by the seabed by trawler fishing may represent a large proportion of the benthic biomass and production in the areas (Johnson et al., 2013). *M. thomsoni* and *N. norvegicus* have similar life histories, as slow-moving benthic ecosystem predators, and burrowing habitants (Johnson et al., 2013; Choi et al., 2008). Johnson et al. (2013) and Choi et al. (2008) suggested that fishing effort in *M. thomsoni* may have critical roles in the flows of carbon and nutrients through marine communities. In addition to trophic interactions, *M. thomsoni* may interact with benthic species and sediment-water column fluxes through activities that shape the habitat: the construction of burrows and sediment resuspension.

Most of commercial crustaceans have been studied on minimum catchable size regulations, age and growth, reproduction, and ecology for fisheries management. However, there is no research on size at sexual maturity as a reference point for minimum catchable size and reproductive aspects to determine the closed season of *M. thomsoni*. Therefore, this study is to investigate growth, and reproduction for fishery management of *M. thomsoni*.

2. Materials and Methods

2-1. Sample collection

M. thomsoni specimens were monthly sampled in the coastal area of Jeju Island, Korea from March 2021 to March 2022 (Fig. 1). Samples were collected in the depth range of 80–110 m, using bottom seine trawl and mesh size was 60 mm. Collected samples are preserved in 10% neutralized formalin solution.

2-2. Sex ratio

Sex was determined by the shape of the first swimmeret. Males have boney swimmerets, and females have feathery swimmerets (Fig. 2). The sex ratio of the sample was expressed as the proportion of females. The carapace length (CL) was measured to the nearest 0.01 mm with vernier calipers, as the distance from the base of the eyestalk to the posterior edge of the carapace.

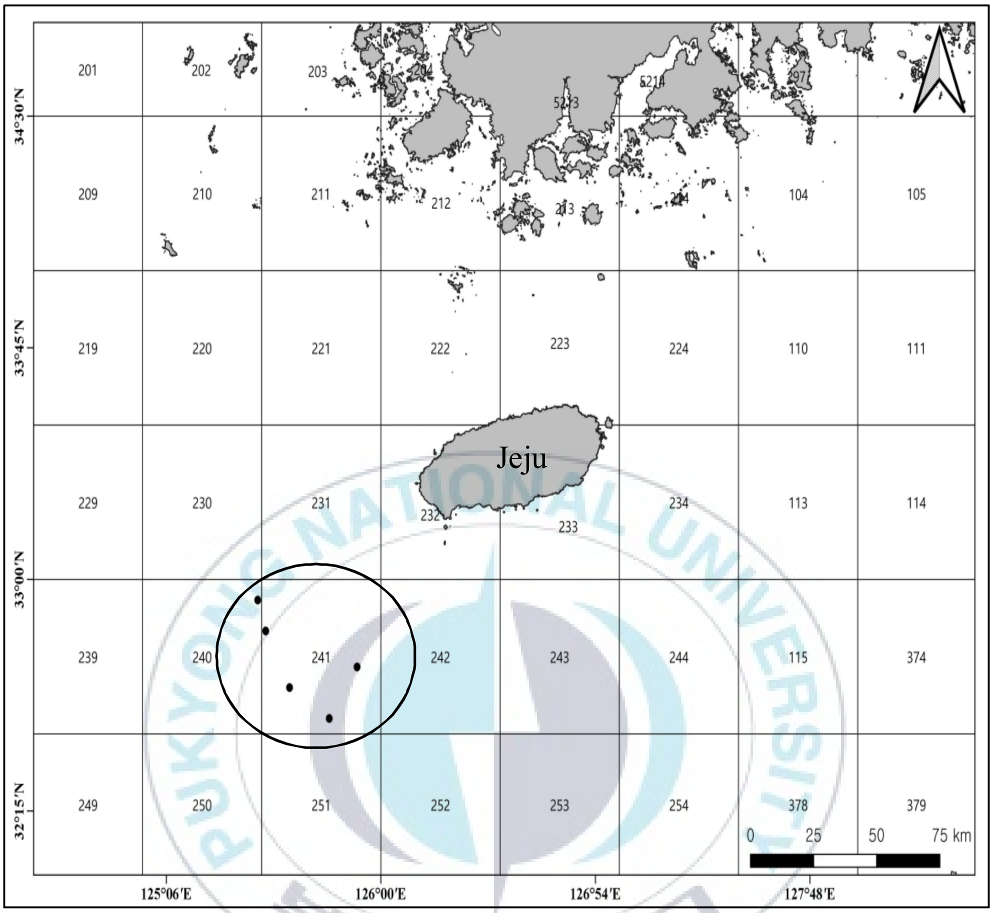


Fig. 1. Map showing sampling area of *Metanephrops thomsoni* (Bate, 1888) around Jeju Island, Korea.

Fig. 2. Swimmeret morphology of *Metanephrops thomsoni* (Bate, 1888) around Jeju Island, Korea. a: male; b: female

2-3. Length-frequency distribution

Population structure was revealed through length-frequency distribution of both sexes. Length-frequency distribution of each sex was constructed using 1 mm length intervals of carapace length.

2-4. Morphometric relationship

Morphometric relationship between carapace length (CL) and body weight (BW) was analyzed. CL was measured as mentioned in the sex ratio part, and BW was measured using a digital balance to the nearest 0.01 g after all remain water was removed from lobster body. Linear regression was analyzed to reveal the relationship between CL and BW with using natural log-transformed data. The equation is:

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

where *a* and *b* were intercept and slope, respectively.

2-5. Ovarian examination

An ovarian observation was conducted to investigate the female reproductive cycle. The maturity of ovary was expressed in five stages according to Becker et al. (2018): (1) immature; (2) development; (3) maturity; (4) spent; (5) recovering (Table 1). In order to measure the dry weight of body and ovary, each individual was dried for 48 h at 60 and measured to the nearest 0.0001 g using digital electronic balance. The gonadosomatic index (GSI) was determined by the following equation:

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

Table 1. Ovarian stage modified from Becker et al. (2018).

Stage	Descriptions according to Becker (2018)	Present study
0	Threadlike translucent immature ovary of a juvenile female.	Immature
2	Progressing stages of ovary: restricted to the thorax	Developing
3	Progressing stages of ovary: extend into the pleon	Maturity
4	Progressing stages of ovary: extend into the second pleomer and can be very swollen	
B	Egg	Spent
1a	Recovering (earliest) ovary stage	Recovering
5a	Ovary is spent and therefore collapsed	
5b	Ovary occurs in females which have not spawned and fully resorb the ovary instead	
1b	Full resorption of the ovary is completed	

2-6. Mean CL of ovigerous females

Monthly CL average of ovigerous females was investigated. From March 2021 to February 2022, the ratio of ovigerous females in the monthly CL class interval was calculated. The monthly CL class interval was divided into 5 mm.

The monthly ovigerous females CL average was determined by the following equation:

$$\text{Mean CL of ovigerous females} = \frac{\sum a_i b_i}{\sum b_i}$$

where *a* was monthly ovigerous females class interval average and *b* was monthly ovigerous females (n) / monthly total females (n)

2-7. Egg volume

Egg size of ovigerous females was recorded as two stages: (1) non-eyed egg and (2) eyed egg. In order to measure egg volume, the eggs in the pleopods are carefully separated using fin 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 (ZEISS SteREO Discovery. V8) 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

2-8. Relationship between the number of eggs (EN) and carapace length (CL)

The relationship between the number of eggs (EN) and carapace length (CL) was estimated for ovigerous females carrying non-eyed and eye eggs. Linear regression analysis using natural log transformed data of EN and CL was used to determine the relationship between body size and the number of eggs, with following equation:

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

where a is intercept and b is slope. Slope and intercept of both non-eyed and eyed egg stage in the regressions were compared to investigate egg loss. The percentage of egg loss was estimated from the intercepts by following equation:

$$\text{Egg loss } \% = 100(1 - \exp(\mathrm{a}' - \mathrm{a}))$$

where a' and a are intercepts of two equations (a' < a).

2-9. Fecundity and reproductive output (RO)

Eggs were carefully stripped from pleopods using fine forceps, and any setal material or extraneous matter was removed. All eggs were counted directly because indirect methods can cause errors. 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 60 for 48 h and weighing to the nearest 0.0001 g using an electronic digital balance. Reproductive output (RO) was estimated using dry weight by the following equation:

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

2-10. Size at sexual maturity (CL_{50})

The proportions of sexually mature females were measured based on individuals with ovarian stage of 3 or higher. The proportion of mature females according to the carapace length was fitted to the logistic equation:

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

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}) correspond to the proportion of 50% of the sexually mature females. It was calculated from ratio between the constants *a* and *b*:

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

2-11. Growth

The 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 & Gaschüz, 1979):

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

where L_∞ is the asymptotic carapace length, K is the intrinsic growth rate, t_0 is the age at which the length of lobster 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 & Sparre, 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 estimated the growth parameters (L_∞, K, C and WP) without standard errors. t_0 estimates cannot be obtained solely from the length-frequency data (Pauly, 1987), so ELEFAN routines alone allow their calculation. Thus t_0 was estimated using the relation (Lopes Veiga, 1979).

$$t_o = \ t + \frac{1}{K}\left(ln\frac{L_\infty - L_h}{L_\infty}\right)$$

where L_h is the carapace length at hatching.

Growth performance of *M. thomsoni* was using a growth performance index (φ') (Pauly and Munro, 1984):

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

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.

2-12. Statistical analysis

Chi-square test was performed to determine whether the observed ratio of both sexes differed from the expected 1:1 ratio. Differences in length-frequency distributions between the two sexes, whether the two sexes came from the same distribution, were determined by the Kolmogorov-Smirnov two-sample test. Student *t*-test was used to investigate the difference in CL between sexes, egg volume, and GSI values between non-eyed egg and eyed egg stages. The monthly mean difference in the GSI was tested by one-way analysis of variance (ANOVA). The Tukey HSD test was performed to compare changes in monthly mean CL of ovigerous females. Analysis of covariance (ANCOVA) was used to determine the difference in intercept and slope of regressions on relation between; 1) carapace length and body weight of both sexes and 2) carapace length and the number of eggs for eyed and non-eyed eggs. 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. Likelihood ratio test (Kimura, 1980) was used to test the differences between the estimated parameters of both sexes in von Bertalanffy length-based growth curve. MINITAB (v. 18), SPSS (v. 26), R, and automatic differentiation model builder (ADMB) were used for all statistical analysis, and mean value was presented with a 95% confidence limit.

3. Results

3-1. Sex ratio

A total of 5,430 specimens (2,672 males and 2,758 females) of *M. thomsoni* was collected during the sampling period. There was no significant difference in sex ratio between male and female ($x^2 = 22$, $df = 20$, $P > 0.05$) (Fig. 3).

3-2. Length-frequency distribution

A total 5,430 lobsters were collected during sampling from March 2021 to next February 2022 (Fig. 4). The mean CL was 26.25 ± 4.77 mm (range 14.41-43.15 mm) in males and 25.43 ± 3.93 mm (range 11.52-43.15 mm) in females. There was a significant difference in mean CL between males and females (Student *t*-test, $t = 6.962$, $df = 5{,}428$, $P < 0.001$). A statistical analysis showed a significant difference in the length-frequency distribution of the both sexes (Kolmogorov-Smirnov two sample test, $P < 0.001$).

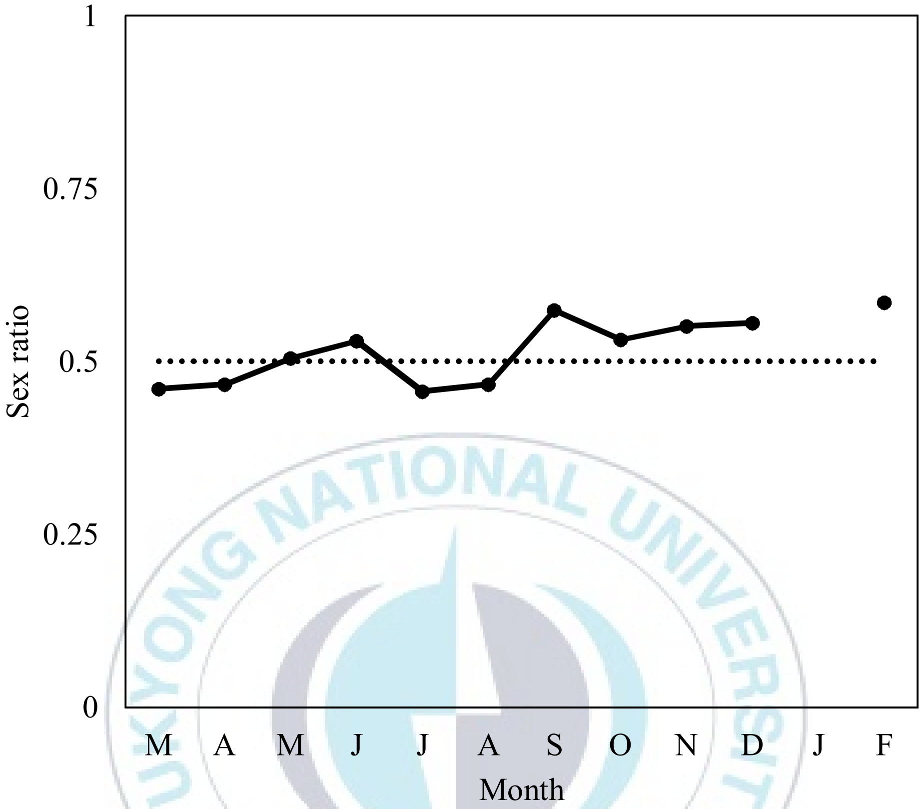


Fig. 3. Variations in the sex ratio of *Metanephrops thomsoni* (Bate, 1888).

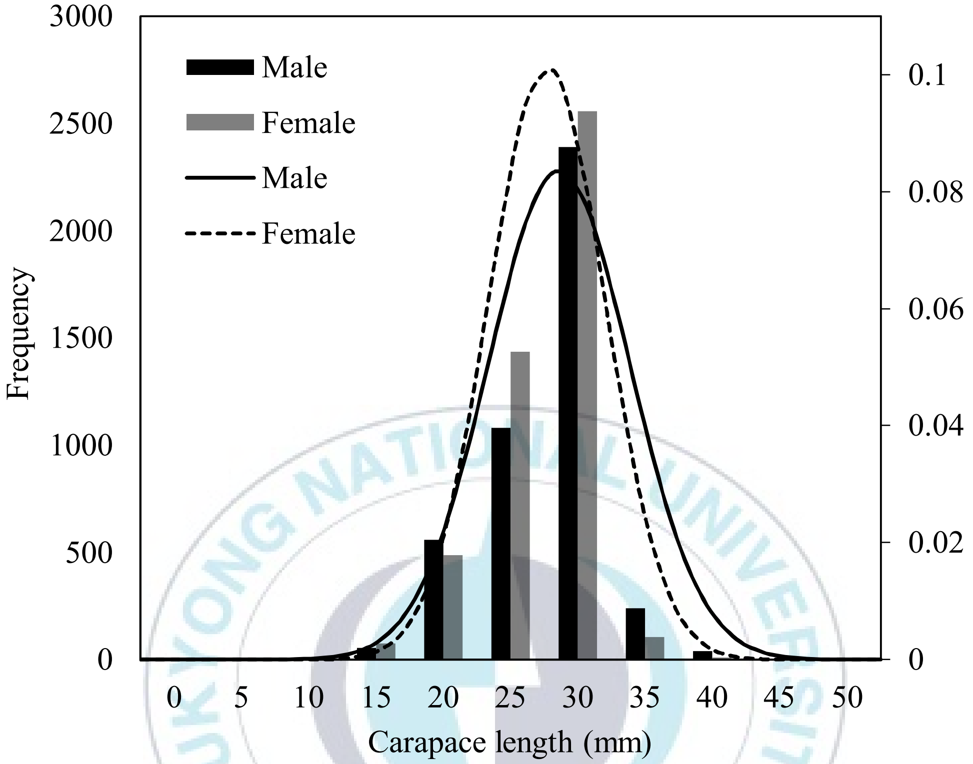


Fig. 4. Length-frequency distribution of males and females of *Metanephrops thomsoni* (Bate, 1888) during study period.

3-3. Morphometric relationship

The body size of females was smaller than that of males. Mean body weight (BW) was 16 ± 9.3 g (range 1.59-65.37 g) in males and 14.35 ± 6.70 g (range 1.06-49.58 g) in females.

The relationships between carapace length (CL) and body weight (BW) of males and females were analyzed by linear regression using natural log transformed data (Table 2).

In both sexes, the relationship between CL and BW was positive allometric (Fig. 5). There was no significant difference in slope of regression of log carapace length versus log body weight between male and female (ANCOVA, $F = 0.525$, $df = 1, 5412$, $P > 0.05$) (Fig. 6).

Table 2. Regression analysis between carapace length (CL) and body weight (BW) of male and female of *Metanephrops thomsoni* (Bate, 1888).

Sex	Linear regression (Slope ± 95% ln *CL*)	CL (mm) (Mean ± SD)	BW (g) (Mean ± SD)
Male	$\ln BW = 3.1719\ (\pm\ 0.012) \ln CL - 7.6966$ $(\mathrm{n} = 2669, r^2 = 0.9721, P < 0.001)$	26.66 ± 4.99	17.01 ± 9.83
Female	$\ln BW = 3.1624\ (\pm\ 0.01) \ln CL - 7.6476$ $(\mathrm{n} = 2747, r^2 = 0.9790, P < 0.001)$	25.54 ± 4.26	14.74 ± 7.35

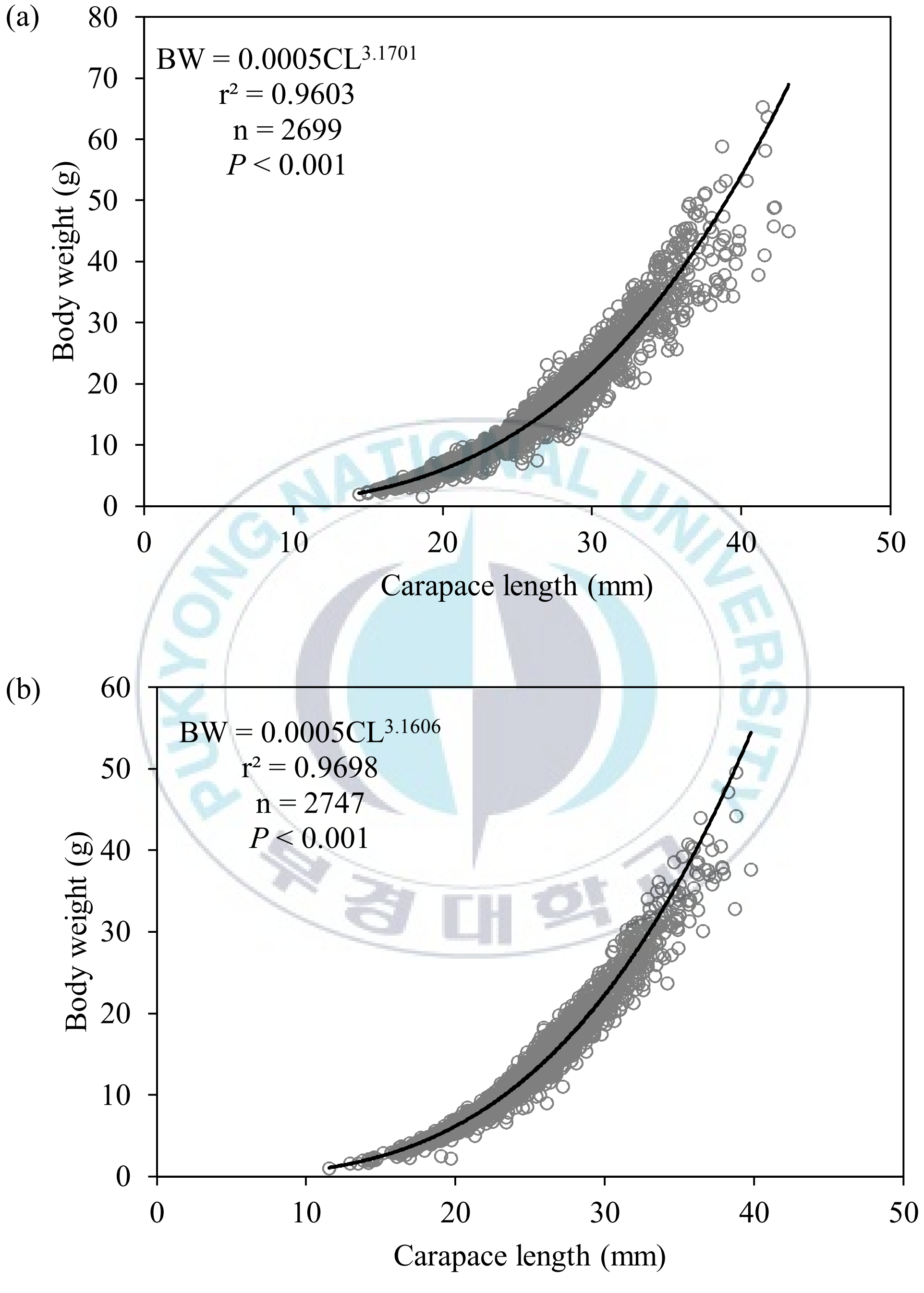


Fig. 5. Relationship between carapace length (CL) and body weight (BW) of *Metanephrops thomsoni* (Bate, 1888). a: males; b: females.

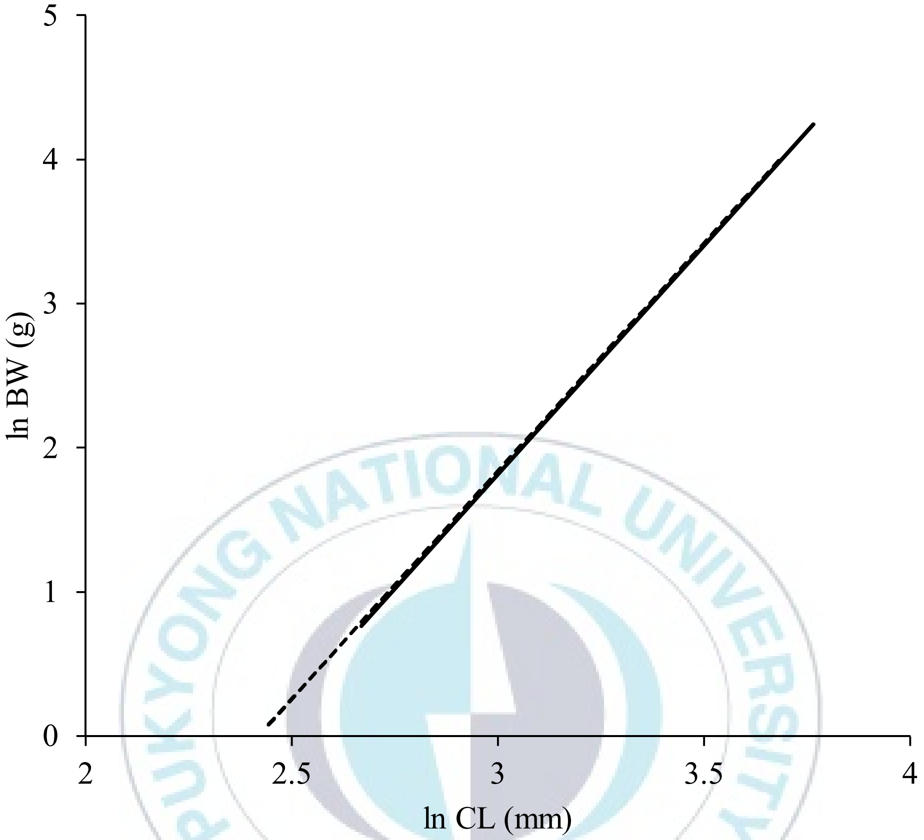


Fig. 6. Relationship between carapace length (CL) and body weight (BW) of *Metanephrops thomsoni* (Bate, 1888), assuming a common slope. Solid line: males; dotted line: females.

3-4. Breeding period

The breeding period was determined by both the ovarian stages of females and the gonadosomatic index (GSI). Ovigerous females was observed in all month except May 2021 (Fig. 7).

The GSI started to increase in April, reached a peak in June (8.64), and decreased to its lowest value in December (5.98). There was a significant difference in the monthly GSI (ANOVA, $F = 7.82$, $df = 10$, $P < 0.001$) (Fig. 8). Mean CL of ovigerous females tend to decrease from June to December (Tukey HSD, $P < 0.001$) (Fig. 9).

There was a significant difference in the GSI value with non-eyed and eyed egg stages showing higher GSI in eyed stage (Student *t*-test, $t = 6.17$, $df = 302$, $P < 0.05$) (Fig. 10). This result indicates that females of *M. thomsoni* are consecutive breeders.

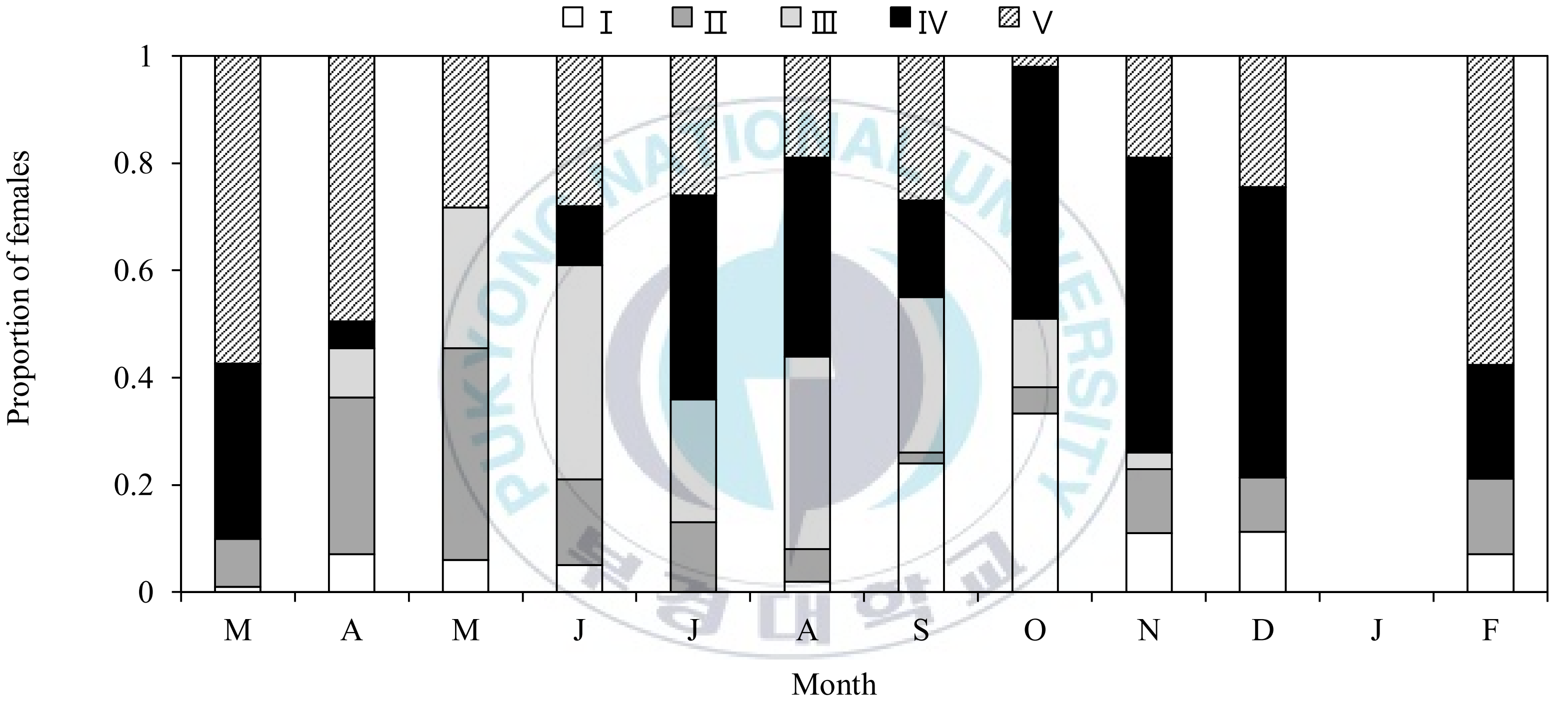


Fig. 7. Variations in proportion of female *Metanephrops thomsoni* (Bate, 1888), according to the five ovarian stages.

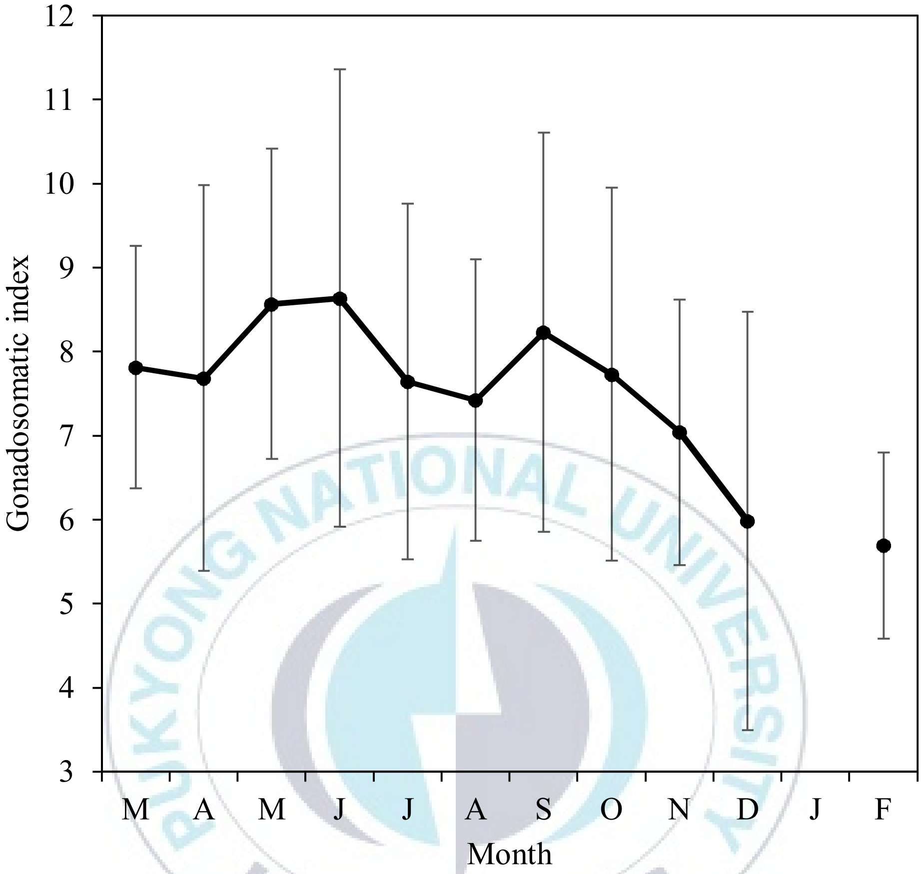


Fig. 8. Change in monthly gonadosomatic index of *Metanephrops thomsoni* (Bate, 1888) during the sampling period.

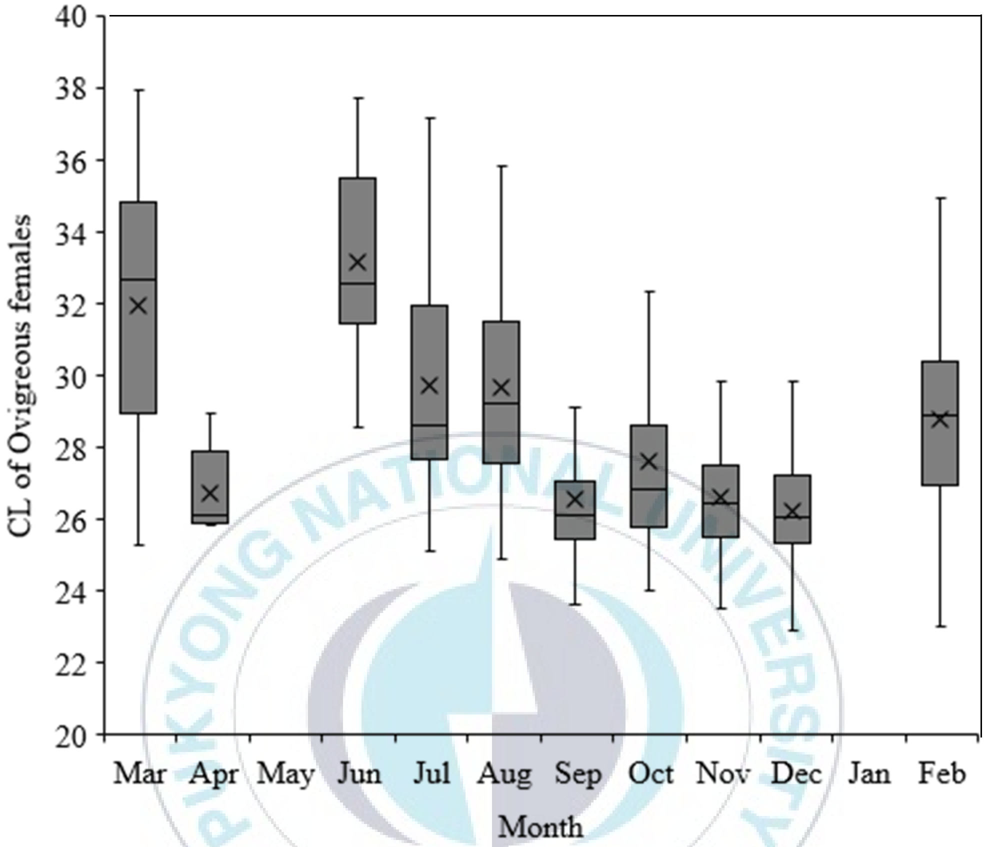


Fig. 9. Change in monthly mean CL of ovigerous females of *Metanephrops thomsoni* (Bate, 1888) during the study period.

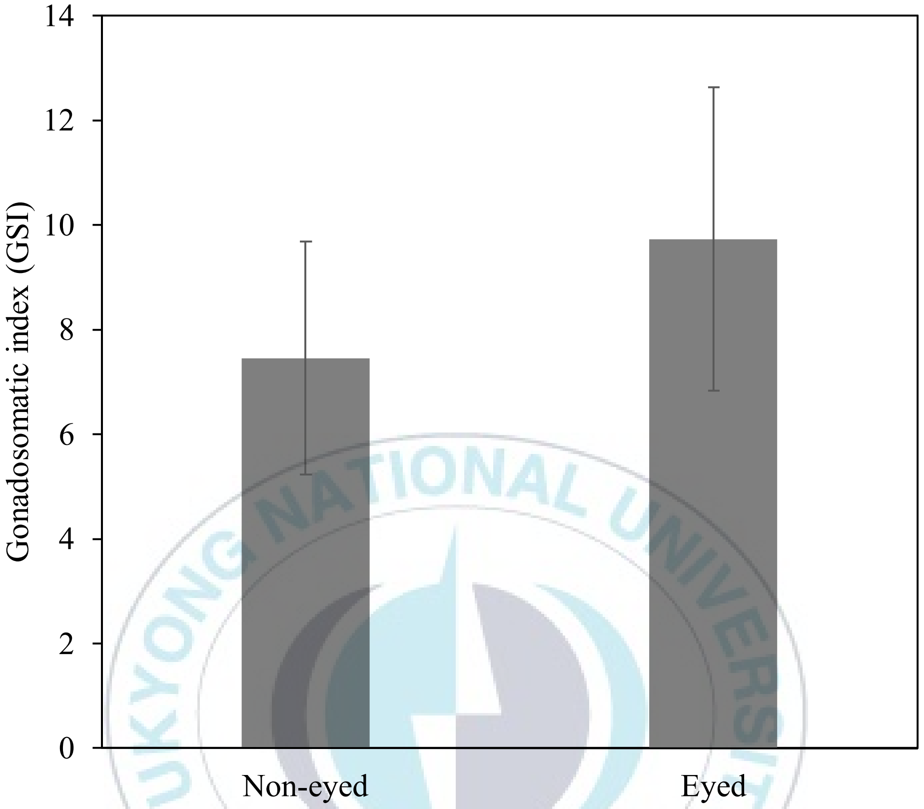


Fig. 10. Mean gonadosomatic index, with standard deviation of the two egg stages of *Metanephrops thomsoni* (Bate, 1888)

3-5. Fecundity and reproductive output

Total 117 ovigerous females, 75 females with mean carapace length 30.32 ± 3.33 mm (range 26.08–37.79 mm) were carried 406.99 ± 90.46 non-eyed eggs (range 24–609), and 42 females with mean carapace length 30.32 ± 3.26 mm (range 25.51–37.94 mm) were carried 233.21 ± 86.85 eyed eggs (range 543–609).

Mean egg volume of eyed eggs (2.28 ± 0.46 mm^3, n = 100) was significantly larger than non-eyed eggs (1.53 ± 0.22 mm^3, n = 100) (Student *t*-test, t = 19.463, df = 198, $P < 0.001$) (Fig. 11).

The relationships between carapace length (CL) and the number of eggs (EN) for females with non-eyed and eyed egg stages were analyzed, as shown in Table 3.

There was no significant difference in the slopes of the linear regression between ln CL and ln EN for the two egg stages (ANCOVA, F = 0.39, df = 1, 113, $P > 0.05$), but a significant difference in the intercept of the linear regression for the two egg stages (ANCOVA, F = 148.89, df = 1, 114, $P < 0.001$) (Fig. 12). Therefore, a common slope was recalculated from the data. In this study obtained the new regression equations having a common slope and passing through the mean values of both the carapace length and the number of eggs in two phases (Fig. 13). Decrease in values of the intercept with progress of embryonic development indicates that egg loss occurred during incubation. The percentage of egg loss between two egg stages was estimated as 42.3%.

Reproductive output (RO) was 0.066 ± 0.026 (n = 160).

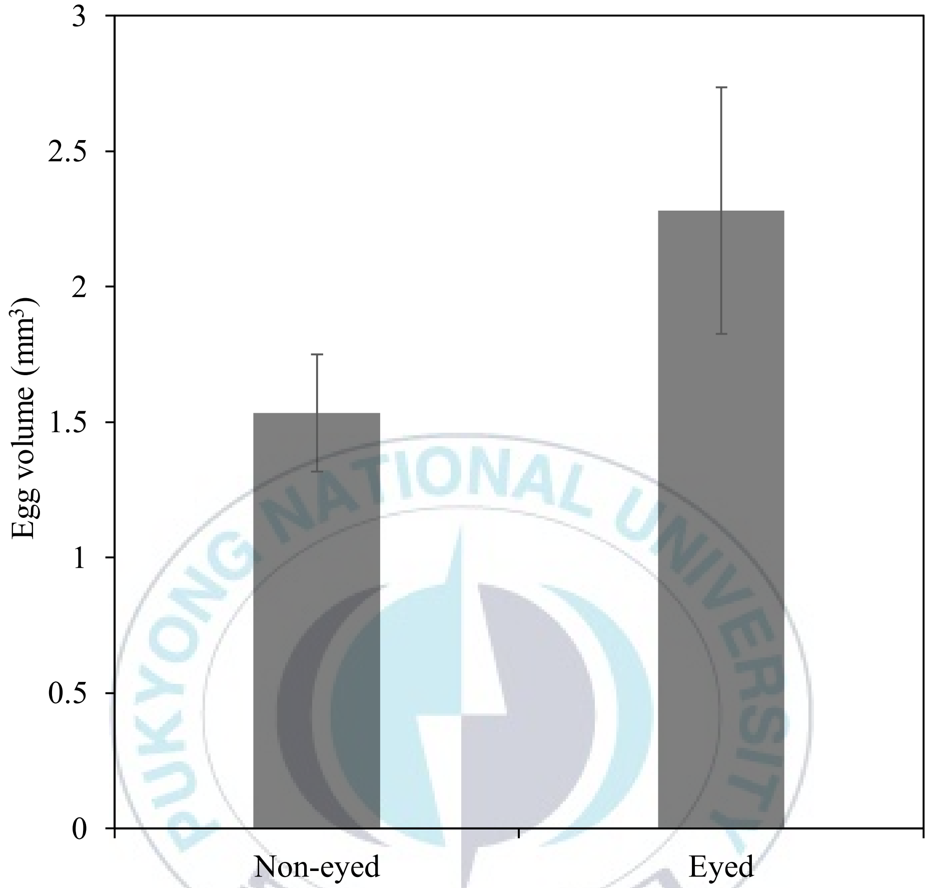


Fig. 11. Mean egg volume, with standard deviation of *Metaneprhops thomsoni* (Bate, 1888) for the two egg stages.

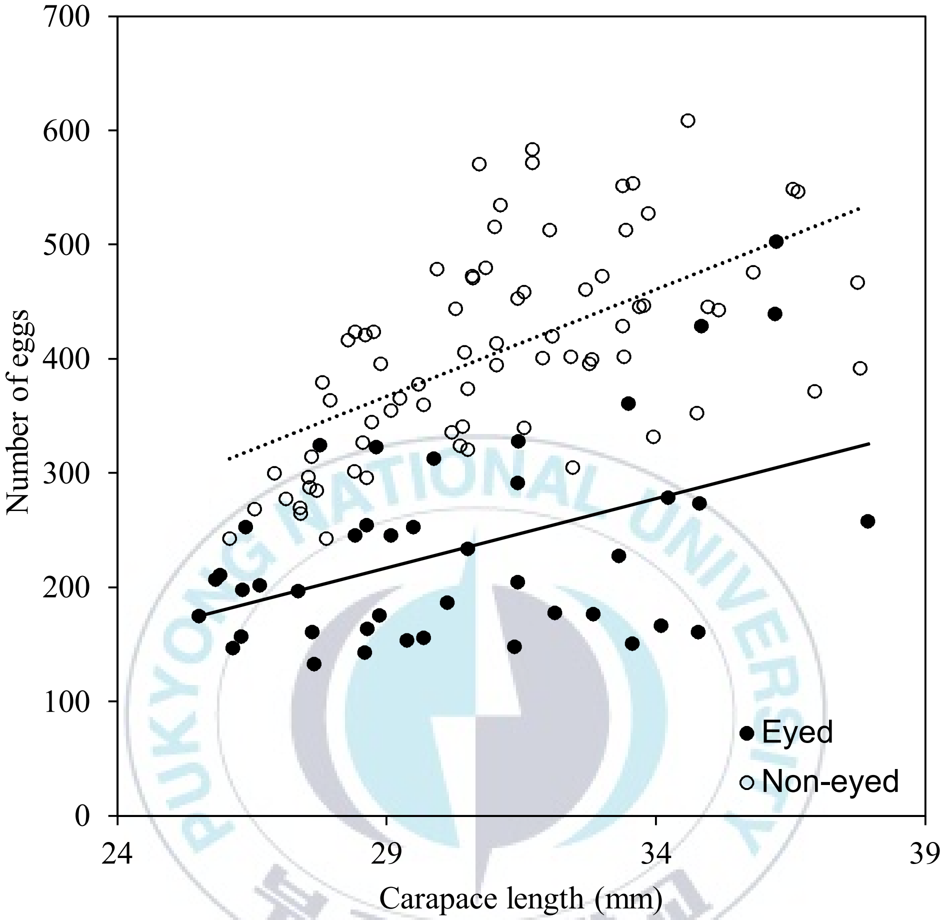


Fig. 12. Linear regression of number of eggs (EN) and ln carapace length (CL) of females of *Metaneprhops thomsoni* (Bate, 1888) with non-eyed (○) and eyed (●) eggs.

Table 3. Relationships between ln the number of egg (EN) and ln carapace length (CL) of *Metanephrops thomsoni* (Bate, 1888).

Egg stages	Relationship	Linear regression (± 95% ln *CL*)
Non-eyed	EN versus CL	$\ln EN = 18.716\ (\pm\ 3.00) \ln CL - 175.31$ $(\mathrm{n} = 75, r^2 = 0.3471, P < 0.001)$
Eyed	EN versus CL	$\ln EN = 12.147\ (\pm\ 3.66) \ln CL - 135.14$ $(\mathrm{n} = 42, r^2 = 0.2164, P < 0.01)$

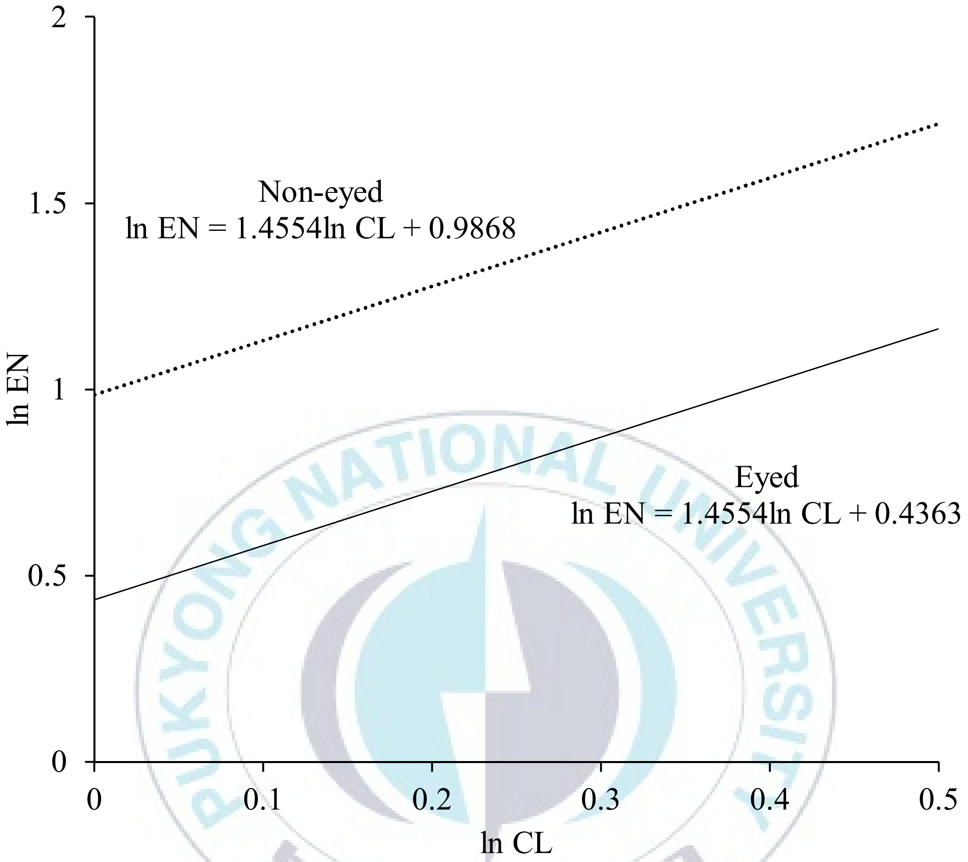


Fig. 13. Recalculated equations showing the relationship between the carapace length (X) and number of eggs (Y) of *Matanephrops thomsoni* (Bate, 1888) assuming a common slope. Solid line: eyed; dotted line: non-eyed.

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

Total 851 of the females *of M. thomsoni* used in the analysis ranged from 11.5 mm to 42.5 mm. The proportion of sexually mature females by length class was calculated by fitting a logistic equation (Fig. 14). The size at sexual maturity ($\boldsymbol{CL_{50}}$) of females was estimated as 23.21 mm.

$$P = \frac{1}{1 + e^{(54.93 - 2.36CL)}}$$

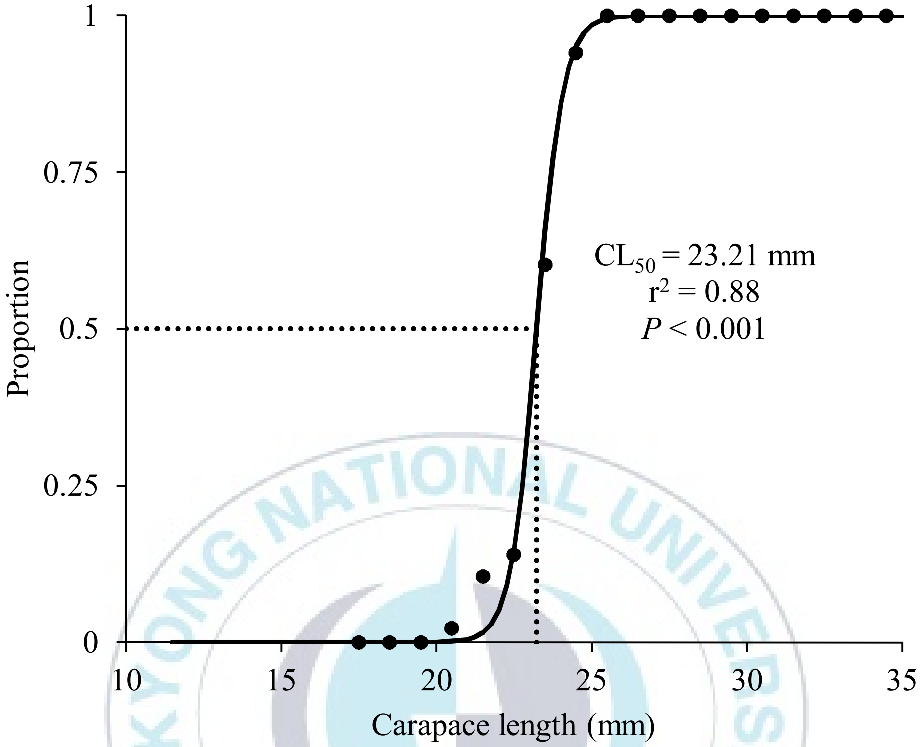


Fig. 14. A logistic function fitting proportion of mature females to carapace length of *Metanephrops thomsoni* (Bate, 1888). CL_{50}, which corresponds to the proportion of 50% of mature females, was 23.21 mm.

3-7. Growth

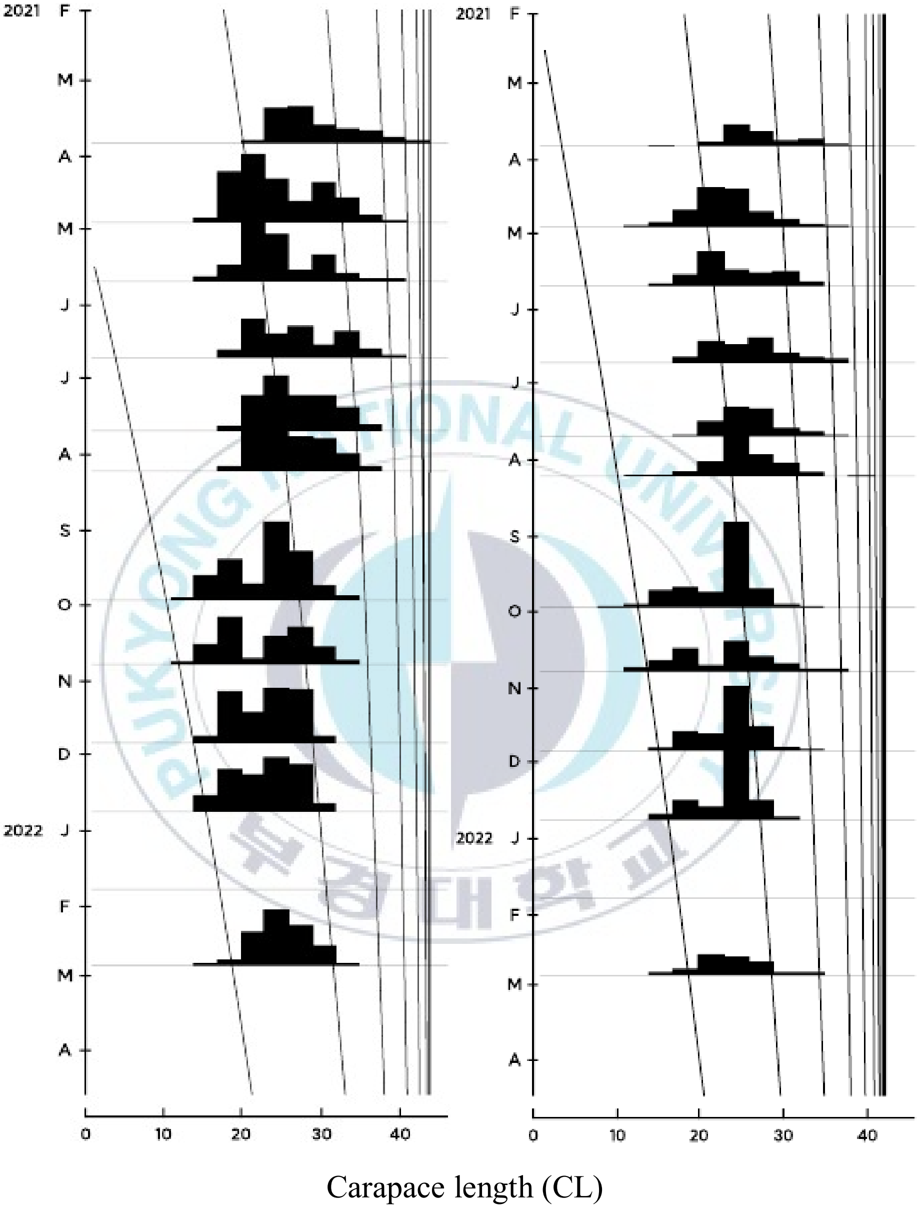
The von Bertalanffy growth parameter was estimated by ELEFAN for both sexes. Asymptotic length ($\boldsymbol{CL_\infty}$) was higher in males (44 mm) than females (42.3 mm). Growth coefficient (*K*) also was higher in males (0.69 $\boldsymbol{yr^{-1}}$) than females (0.55 $\boldsymbol{yr^{-1}}$). Seasonality growth rate (*C*) was 10% for males, 9% for females. The slowest growth season (WP) is June in males and July in females. The growth performance index ($\boldsymbol{\varphi'}$) were 3.13 in males and 2.99 in females (Table 4). The length-frequency distribution showed that there was an appreciable modal shift in the length of the cohorts with time (Fig. 15).

The von Bertalanffy growth function is follow (Fig. 16):

$$\textbf{Male}:\ \boldsymbol{44[1-e^{[1-e^{[-0.69(t+0)-(\frac{0.1\times0.69}{2\pi})sin2\pi(t+0)]}}]}$$

$$\textbf{Female}:\ \mathbf{42.3[1-e^{[1-e^{[-0.55(t+0)-(\frac{0.09\times0.55}{2\pi})sin2\pi(t+0.08)]}}]}$$

The differences in length-based growth curves between both sexes were compared by the method of Kimura’s likelihood ratio test (Kimura, 1980). This method allows the testing of several hypotheses to compare the two curves by analyzing one or more growth parameters simultaneously (Table 5).


(a) Male

(b) Female

Fig. 15. Length-frequency distribution of males (a) and females (b) of *Metanephrops thomsoni* (Bate, 1888) with seasonal von Bertalanffy growth curves superimposed.

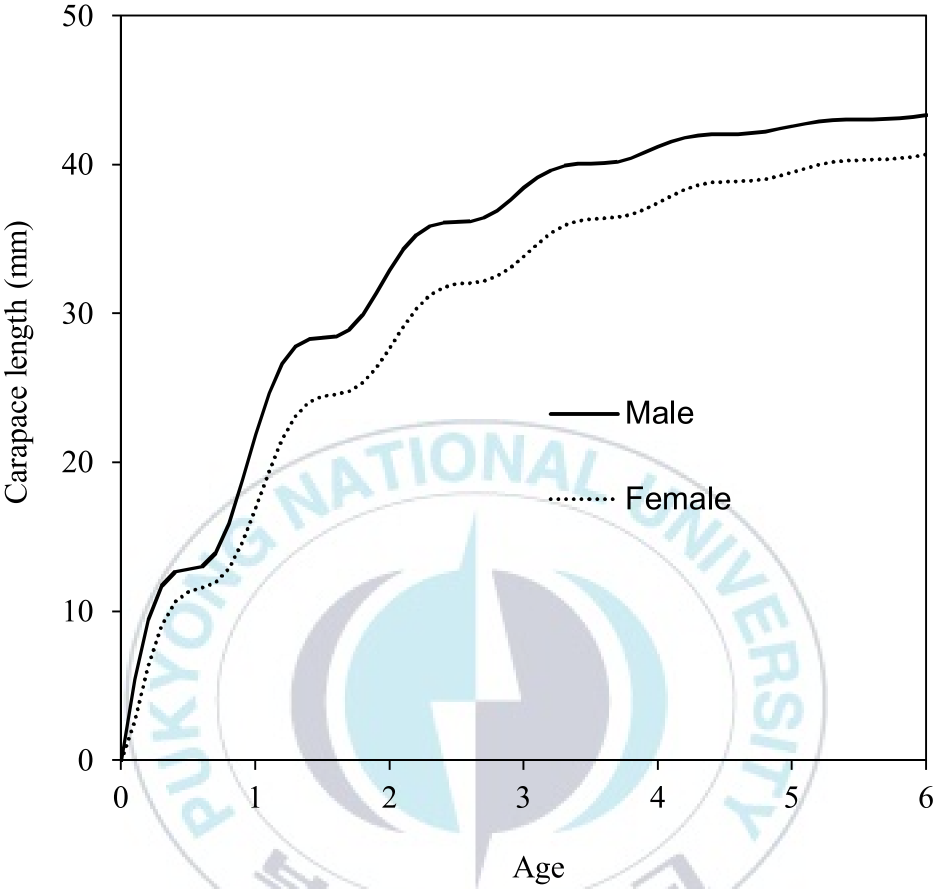


Fig. 16. Average growth curves for males and females of *Metanephrops thomsoni* (Bate, 1888) based on von Bertalanffy growth curve. Solid line: males; dotted line: females.

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

Parameter	Males	Females
CL_∞	44	42.3
K	0.69	0.55
C	0.10	0.09
WP	0.50	0.58
φ'	3.13	2.99
R_n	0.26	0.20

Table 5. Von Bertalanffy parameters between both sexes, compared using the Kimura method's likelihood ratio test (Kimura, 1980). 1: females and 2: males, RSS: residual sum of squares.

Hypothesis	Linear constraints	$L_{\infty 1}$	$L_{\infty 2}$	K_1	K_2	t_{01}	t_{02}	C_1	C_2	t_{s1}	t_{s2}	RSS	x^2	P
H_0	CL_∞	42.91	42.91	0.50	0.82	0.00	0.05	0.09	0.11	0.00	0.05	7.93	4.44	< 0.05
H_1	K	40.14	45.47	0.64	0.64	0.02	0.00	0.10	0.09	0.04	0.00	10.69	7.73	< 0.05
H_2	t_0	41.65	44.30	0.54	0.71	0.00	0.00	0.09	0.11	0.00	0.00	5.30	0.00	> 0.05
H_3	C	41.65	44.30	0.54	0.71	0.00	0.00	0.09	0.09	0.00	0.00	5.30	0.00	> 0.05
H_4	t_s	41.65	44.30	0.54	0.71	0.00	0.00	0.09	0.11	0.00	0.00	5.30	0.00	> 0.05

4. Discussion

4-1. Sex ratio

In this study, there was no significant difference in sex ratio. *Metanephrops mozambicus*, there was also no significant difference in sex ratio (Berry, 1969; Robey, 2013). However, in *N. norvegicus*, males outnumberd females (Barnes & Bagenal, 1951).

This difference could be caused by oxygenate activities and burrows. *M. mozambicus* females would have to spend more time outside their burrows to oxygenate eggs (Berry, 1969). In *N. norvegicus*, burrows have two entrances which facilitate water flow over the eggs of sheltered females (Rice & Chapman, 1971). This is another means of oxygenating eggs for females, so the ratio of males was more dominant than females in *N. norvegicus* (Barnes & Bagenal, 1951; Thomas, 1964; De Figueiredo & Thomas, 1967). This study had observed oxygenation activity to *M. mozambicus*, leading to no significant difference in sex ratio.

4-2. Growth

There was a significant difference in length-frequency distribution of both sexes, and males were predominant in the bigger size classes. These results are identical to study of; *Metanephrops rubellus* and *Metanephrops binghami* (Cusba et al., 2017; Severino-Rodrigues et al., 2018).

Size difference between sexes are caused by competition related to reproduction. If breeding burrows are scarce, males should compete more intensely to monopolize them. Mating success of males depend on both competitions for burrows and their ability to attract females. Males are bigger than females, as males compete to defend breeding burrows from which they attract potential mates (Forsgren et al., 1996; Kvarnemo & Ahnesjö, 1996).

There was no significant difference between males and females in the slope of the relationship between carapace length and body weight. Juveniles of *palinurus elephas* migrate rapidly from shallow settlements to deeper habitats in winter or spring (Goñi et al., 2001). Similar ontogenetic migrations have been described in other Palinurid lobsters (Herrnkind, 1980; Morgan, 1982; Lyons, 1986). The smallest juveniles of *M. thomsoni* could be excluded from the sampling, so the growth rates of both sexes in the relationship are not different. Therefore, further studies will be focused on bias, which could be occurred at sampling.

In this study suggested that 50% of the females of *M. thomsoni* are mature at

23.21mm CL. This result was smaller than *M. binghami* (30.55 mm) and *M. chllengeri* (30.1 mm) (Paramo & Saint-Paul, 2012; McCarthy et al., 2018). CL_{50} is used as a parameter to establish the minimum catchable size. The CL_{50} for *N. norvegicus* studied on the Portuguese coast were 21-32 mm, 37.5 mm, and 47-51 mm (ICES, 2006; Ayza et al., 2011). Ayza et al. (2011) suggested that CL_{50} can be influenced by several factors, such as behavior and fishing pressures during the breeding cycle. Therefore, in order to obtain the CL_{50}, which determines minimum catchable size of *M. thomsoni*, biological research is required to know the reproductive cycle and the factors that affect the success of spawning, which are necessary for the management of fisheries (Cusba et al., 2017).

Seasonal von Bertalanffy growth parameters showed that L_∞ (males: 44 mm, females: 42.3 mm) and *K* (males: 0.69, females: 0.55) were higher in the male *M. thomsoni*. Difference in growth performance index (φ') between both sexes could be attributed to difference in reproductive pattern an energy investment. The growth performance index (φ') can be used for averaging growth parameters obtained from the von Bertalanffy growth function of a particular species (Sparre, 1998) and is a useful tool for comparing growth under a variety of environmental conditions (Pauly, 1991).

The growth performance index (φ') is different among the *Metanephrops* genus lobsters (Table 6). *N. norvegicus*, showed that the parameters for calculating growth performance index (φ') L_∞ and K are different depending on the location and method (Haynes et al., 2016) (Table 7). Numerical methods have also been developed to the convert length-frequency data used in this study into age composition, but such approaches are only reliable when direct age readings are available to confirm the age composition of length cohorts. Thus, further studies using the recently developed direct age determination methods, such as gastric ossicle analysis or lipofuscin analysis, are needed (Kilada & Driscoll, 2017).

Table 6. Comparison of the growth performance index (φ') in genus *Metanephrops* lobster.

Genus	Species	φ'		Reference
		Male	Female	
Metanephrops	*M. thomsoni*	3.13	2.99	Present study
	M. mozambicus	3.42		Robey (2013)
	M. australiensis	3.14	3.19	Wallner & Phillips (1995)
	M. velurinus	3.22	3.16	Wallner & Phillips (1995)
	M. sibogae	3.1	3.16	Wallner & Phillips (1995)

Table 7. Comparison of the growth parameters for *Nephrops norvegicus* across Atlantic areas.

Location	Male		Female		Method	Reference
	K	L_∞	K	L_∞		
Skagerrak	0.138	72.9	0.056	64.9	Tag & recapture	Ulmestrand & Eggert (2001)
Scottish West	0.166	57	0.228	46.6	Tag & recapture	Bailey & Chapman (1983)
Irish Sea (east coast)	0.16	60	0.1	56	Unknown	ICES (2000)
Irish west coast	0.161	70.8	0.077	55.2	Tag & recapture	Haynes et al. (2016)
Portugal (northern)	0.38	88.3	0.38	64.5	ELEPHAN	Ayza et al. (2011)
Portugal (south)	0.14	78.9	0.12	71.3	FISHPARM	Mytilineou et al. (1998)
Spain (Atlantic)	0.13	83.4	0.12	70.7	Length-cohort analysis	Sardà et al. (1998)

4-3. Reproduction

In this study, ovigerous females appeared from June to next April. Yamada et al. (1986) reported that ovigerous females of *M. thomsoni* appeared from September to next April in the East China Sea. The appearance period of ovigerous females was earlier in this study than that of Yamada's study. *N. norvegicus* females incubation period varies from 6 to 10 months depending on latitude (Powell & Eriksson, 2013). Difference in incubation period of *M. thomsoni* between these two studies could be explained by differential environment factors.

This study showed that mean CL of ovigerous females tend to decrease from June to December. In *M. thomsoni*, the bigger ovigerous females appeared first in June-August, and smaller females close to sexual maturity appeared after September. Choi et al. (2008) suggested that *M. thomsoni* females have several spawning times during the breeding season from September to next April, which is a characteristic of multiple breeding. In this study, large ovigerous females appeared first, and small ovigerous females appeared later, suggesting that *M. thomsoni* had a longer incubation period. Therefore, *M. thomsoni* is not a multiple breeding, but a consecutive breeding, and this reproductive pattern can be also found in *N. norvegicus* (Powell & Eriksson, 2013).

Fecundity is a vital parameter that permits the estimation of the reproductive potential and future stock size of a given species or population (Hattori &

Pinheiro, 2001). Furthermore, it is a crucial component of fitness, dependent on lifetime reproductive performance (Sastry, 1983). Therefore, when studying the fecundity of crustaceans, it is essential to note differences in egg size or any change in egg numbers during development.

In this study, egg volume (EV) of the eyed egg stage was significantly bigger than eyed egg and non-eyed egg stages. Egg size, fecundity, and egg loss for the genus *Metanephrops* is shown in Table 8. The size of the eggs has been found to increase with the duration and extent of egg development (Mori et al., 1998). Generally, bigger eggs are also associated with smaller broods, better egg or larval survival, and abbreviated free-living larval periods (Pollock, 1997). The incubation period of *M. thomsoni* was 11 months, which is longer than that of *N. norvegicus* (6-10 months; Farmer, 1975).

There was no significant difference in the slope of the relationship between EN and CL but a significant difference in the intercept for eyed egg and non-eyed egg stages. The egg loss estimated form the intercept difference was 42.3%.

The egg losses are typically attributed to reasons such as incomplete formation of egg envelope during oocyte maturation (Talbot & Harper, 1984), disease, cannibalism, predation, habitat abrasion, water temperature, failure to adhere to pleopods during extrusion (Wear, 1976; Estrella & Cadrin, 1995; Goñi et al., 2003), natural egg loss (Campbell & Brattey, 1986; Matsuura & Hamasaki, 1987) and poor attachment and interference or disturbance during egg laying

(Talbot et al., 1984). In crustacean stock assessment, egg loss can be affecting on recruitment process of fisheries resources and thus should be incorporating into spawning stock-recruitment model.

Table 8. Egg size (mm), fecundity and egg loss (%) of *Metanephrops* species and *Nephrops norvegicus* previously studied.

Species	Egg size (mm)	Carried eggs	Egg loss (%)	Reference
M. thomsoni	1.67-2.67	133-609	42.30	Present study
	1.78-2.66	210-880	20-40	Choi et al. (2008), Matsuura & Hamasaki (1987)
M. challengeri	2.08-3.15	800 (Max)	44	Fenaughty (1989), Balss (1914)
M. mozambicus	1.95-2.83		10	Berry (1969), Robey & Groeneveld (2014)
M. australiensis	2.8 (Max)			Bruce (1966)
M. boschmai	1.9 (Max)			Holthuis (1964)
M. japonicus	2.1-4.0			Okamoto (2005)
M. binghami		102-781		Paramo & Saint-Paul (2012)
N. norvegicus	1.2-1.56	600-4500	30-75	Smith (1987), Bell et al. (2013)

Our study showed that the value of RO was 0.066 ± 0.026 (n = 160). The RO of *Pleuroncodes monodon* and *Panulirus argus* was 0.03 and 0.49 (Guzmán et al., 2016; Baeza et al., 2016). The RO of *M. thomsoni* was similar to that of deep-sea lobster *P. monodon*, but smaller than *P. argus*. The main influencing factor of RO is temperature, which affects the abundance of food for larvae (Goodbody, 1965; Lancaster, 1990) and the maintenance of gametogenesis and ovarian development, which define the species' reproductive period (Bauer, 1992). The differences in RO between the other species, give rise to varied brood sizes, and subsequently lead to changes in annual egg production. The RO can also vary with age and nutrient levels in the diet and between broods for a species with multiple breeding patterns within a single productive period, or as a function of the primiparous or multiparous female condition (Oh, 2011).

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6. Reference

Ahn, D. H., Min, G. S., Park, J. K., & Kim, S. (2016). The complete mitochondrial genome of the red-banded lobster *Metanephrops thomsoni* (Crustacea, Astacidea, Nephropidae): a novel gene order. *Mitochondrial DNA Part A*, *27*(4), 2663-2664.

Ayza, O., Tuset, V. M., & González, J. A. (2011). Estimation of size at onset of sexual maturity and growth parameters in Norway lobster (*Nephrops norvegicus*) off the Portuguese coast. *Fisheries Research*, *108*(1), 205-208.

Baeza, J. A., Simpson, L., Ambrosio, L. J., Mora, N., Guéron, R., & Childress, M. J. (2016). Active parental care, reproductive performance, and a novel egg predator affecting reproductive investment in the Caribbean spiny lobster Panulirus argus. *BMC Zoology*, *1*(1), 1-15.

Bailey, N., & Chapman, C. J. (1983). A comparison of density, length composition and growth of two *Nephrops* populations off the west coast of Scotland. *ICES CM*, 1-10.

Balss, H. (1914). Ostasiatische Decapoden II. Die Natantia und Reptantia. *Abhandlungen der Bayerischen Akademie der Wissenschaften, 2*(10), l-101.

Barnes, H., & Bagenal, T. B. (1951). Observations on *Nephrops norvegicus* (L.) and on an epizoic population of *Balanus crenatus* Brug. *Journal of the Marine Biological Association of the United Kingdom*, *30*(2), 369-380.

Batoy, C. B., Sarmago, J. F., & Pilapil, B. C. (1987). Breeding season, sexual maturity and fecundity of the blue crab, *Portunus pelagicus* (L.) in selected coastal waters in Leyte and vicinity, Philippines. *Annals of Tropical Research*, *9*(3), 157-177.

Bauer, R. T. (1992). Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. *Invertebrate Reproduction & Development*, *22*(1-3), 193-202.

Becker, C., Cunningham, E. M., Dick, J. T., Eagling, L. E., & Sigwart, J. D. (2018). A unified scale for female reproductive stages in the Norway lobster (*Nephrops norvegicus*): evidence from macroscopic and microscopic characterization. *Journal of Morphology*, *279*(12), 1700-1715.

Bell, M., Tuck, I., & Dobby, H. (2013). *Lobsters: biology, Management, Aquaculture and Fisheries*, 2nd ed. Oxford: John Wiley & Sons.

Berry, P. F. (1969). The biology of *Nephrops andamanicus* Wood-Mason (Decapoda, Reptantia). *Investigational report of the Oceanographic Research Institute of South Africa 22*, 1-55

Bruce, A. J. (1966). *Nephrops australiensis* sp. nov, a new species of lobster from northern Australia (Decapoda Reptantia). *Crustaceana*, *10*(3) 245-258.

Campbell, A., & Brattey, J. (1986). Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(4), 772-780.

Choi J. H., Kim J. N., Kim M. H., Chang D. S., Yoo J. T., & Kim J. K. (2008). Population biology and feeding habits of the nephroid lobster *Metanephrops thomsoni* (Bate, 1888) in the East China Sea. *Journal of Environmental Biology*, *29*(4), 453-456.

Cusba, J., Paramo, J., & Salcedo-Reyes, J. C. (2017). Morphometric relationships and size at sexual maturity of the deep-sea Caribbean lobster *Metanephrops binghami* (Decapoda: Nephropidae) in the Colombian Caribbean. *Universitas Scientiarum*, *22*(2), 145-160.

De Figueiredo, M. J., & Thomas, H. J. (1967). On the biology of the Norway lobster, *Nephrops norvegicus* (L.). *ICES Journal of Marine Science*, *31*(1), 89-101.

Estrella, B. T., & Cadrin, S. X. (1995). Fecundity of the American lobster (*Homarus americanus*) in Massachusetts coastal waters. *ICES Marine Science Symposia, 199*, 61-72.

Farmer, A. S. D. (1975). Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). *FAO Fisheries Synopses (FAO). no. 112*.

Fenaughty, C. (1989). Reproduction in *Metanephrops challengeri*, *Unpublished report MAF Fisheries, Wellington,* 1-46.

Forsgren, E., Kvarnemo, C., & Lindström, K. (1996). Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution*, *50*(2), 646-654.

Gayanilo, F. C., & Sparre, P. (2005). FAO-ICLARM stock assessment tools II: FiSAT II: user's guide (No. 8). Rome: Food and Agriculture Organization of the United Nations.

Goñi, R., Quetglas, A., & Renones, O. (2003). Size at maturity, fecundity and reproductive potential of a protected population of the spiny lobster *Palinurus elephas* (Fabricius, 1787) from the western Mediterranean. *Marine Biology*, *143*(3), 583-592.

Goñi, R., Reñones, O., & Quetglas, A. (2001). Dynamics of a protected Western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap surveys. *Marine and Freshwater Research*, *52*(8), 1577-1587.

Goodbody, I. (1965). Continuous breeding in populations of two tropical crustaceans, *Mysidium columbiae* (Zimmer) and *Emerita portoricensis* Schmidt. *Ecology*, *46*(1-2), 195-197.

Guzmán, F., Olavarría, L., & Urzúa, Á. (2016). Seasonal variation in reproductive parameters of the squat lobster Pleuroncodes monodon from a South Pacific population. *Invertebrate Reproduction & Development*, *60*(2), 137-144.

Hamasaki, K., & Matsuura, S. (1987). Embryonic development of *Metanephrops thomsoni* (Bate, 1888) (Crustacea, Decapoda, Nephropidae). *Journal of the Faculty of Agriculture Kyushu University*, *31*(4), 391-403.

Hattori, G. Y., & Pinheiro, M. A. A. (2001). Fecundity and embryology of *Pachycheles monilifer* (Dana, 1852) (Anomura, Porcellanidae) at Praia Grande, Ubatuba, SP, Brazil. *Nauplius*, *9*(2), 97-109.

Haynes, P. S., Browne, P., Fullbrook, L., Graham, C. T., Hancox, L., Johnson, M. P., Lauria, V., & Power, A. M. (2016). Growth in *Nephrops norvegicus* from a tag-recapture experiment. *Scientific Reports*, *6*(1), 1-11.

Herrnkind, W. F. (1980). *Spiny lobsters: patterns of movement. Biology and management of lobsters: Physiology and Behavior.* New York: Academic Press.

Holthuis, L. B. (1964). On some species of the genus *Nephrops* (Crustacea Decapoda). *Zoologische Mededelingen*, *39*(10), 71-78.

ICES. (2000). Report of the Study Group on Life History of *Nephrops*. ICES Document CM. 2000/G: 06.

ICES. (2006). Report of the Workshop on *Nephrops* Stocks. ICES Document CM. 2006/ACFM: 12.

Johnson, M. P., Lordan, C., & Power, A. M. (2013). Habitat and ecology of *Nephrops norvegicus*. *Advances in Marine Biology*, *64*, 27-63.

Kilada, R., & Driscoll, J. G. (2017). Age determination in crustaceans: a review. *Hydrobiologia*, *799*(1), 21-36.

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, *77*(4), 765-776.

Kvarnemo, C., & Ahnesjo, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution*, *11*(10), 404-408.

Lancaster, I. (1990). Reproduction and life history strategy of the hermit crab *Pagurus bernhardus*. *Journal of the Marine Biological Association of the United Kingdom*, *70*(1), 129-142.

Little, G. (1968). Induced winter breeding and larval development in the shrimp, *Palaemonetes pugio* Holthuis (Caridea, Palaemonidae). *Crustaceana. Supplement*, 19-26.

Lopes Veiga, E. C. (1979). Fitting von Bertalanffy growth curves in short-lived fish species. A new approach. *Investigación Pesquera*, *43*(1), 179-181.

Lyons, W. G. (1986). Problems and perspectives regarding recruitment of spiny lobsters, *Panulirus argus*, to the south Florida fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(11), 2099-2106.

Matsuura, S., & Hamasaki, K. (1987). Loss of Eggs Attached to the Pleopods in *Metanephrops thomsoni* (Bate,1888). *Journal of the Faculty of Agriculture Kyushu University*, *31*(4), 405-410.

McCarthy, A., Tuck, I., & Jeffs, A. (2018). Estimates for the size at onset of maturity for New Zealand scampi (*Metanephrops challengeri*). *Bulletin of Marine Science*, *94*(3), 699-718.

Morgan, G. R. (1982). Rock (spiny) lobster of western Australia. *Fishery Bulletin*, *80*(3-4), 475-486.

Mori, M., Biagi, F., & De Ranieri, S. (1998). Fecundity and egg loss during incubation in Norway lobster (*Nephrops norvegicus*) in the North Tyrrhenian Sea. *Journal of Natural History*, *32*(10-11), 1641-1650.

Mytilineou, C., Castro, M., Gancho, P., & Fourtouni, A. (1998). Growth studies on Norway lobster, *Nephrops norvegicus* (L.), in different areas of the Mediterranean Sea and the adjacent Atlantic. *Scientia Marina*, *62*, 43-60.

Oh, C. W., (2011). Population biology of the swimming crab *Portunus Trituberculatus* (Miers, 1876) (Decapoda, Brachyura) on the Western Coast of Korea, Yellow Sea. *Crustaceana, 84*(10), 1251-1267.

Okamoto, K. (2005). Survival, egg loss, hatching larvae and molting of ovigerous Japanese lobster, *Metanephrops japonicus* in captivity. *Bulletin of Shizuoka Prefectural Fisheries Experiment Station (Japan), 40,* 35-40

Paramo, J., & Saint-Paul, U. (2012). Spatial structure of the Caribbean lobster (*Metanephrops binghami*) in the Colombian Caribbean Sea. *Helgoland Marine Research*, *66*(1), 25-31.

Paramo, J., & Saint-Paul, U. (2012). Spatial structure of the Caribbean lobster (*Metanephrops binghami*) in the Colombian Caribbean Sea. *Helgoland Marine Research*, 66(1), 25-31.

Pauly, D. (1987). *A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. Length-based Methods in Fisheries Research*. Kuwait: International Center for Living Aquatic Resources Management.

Pauly, D. (1991). Growth performance in fishes: rigorous description of patterns as a basis for understanding causal mechanisms. *Aquabyte, 4*(3), 3-5

Pauly, D., & Gaschutz, G. (1979). A simple method for fitting oscillating length growth data, with a program for pocket calculators. ICES Document CM 1979/G: 24.

Pauly, D., & Munro, J. L. (1984). Once more on the comparison of growth in fish and invertebrates. *Fishbyte*, *2*(1), 1-21.

Pollock, D. E. (1997). Egg production and life-history strategies in some clawed and spiny lobster populations. *Bulletin of Marine Science*, *61*(1), 97-109.

Powell, A., & Eriksson, S. P. (2013). Reproduction: life cycle, larvae and larviculture. *Advances in Marine Biology*, *64*, 201-245.

Rice, A. L., & Chapman, C. J. (1971). Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and *Goneplax rhomboides*. *Marine Biology*, *10*(4), 330-342.

Robey, J. (2013). An assessment of abundance trends and biology of langoustines (*Metanephrops mozambicus*) and pink prawns (*Haliporoides triarthrus*) from the deep-water trawl fishery off eastern South Africa (Doctoral dissertation. Unpublished Doctoral Dissertation. University of KwaZulu-Natal, Westville.

Robey, J., & Groeneveld, J. C. (2014). Fecundity of the langoustine *Metanephrops mozambicus* Macpherson, 1990 (Decapoda, Nephropidae) in eastern south africa. *Crustaceana*, *87*(7), 814-826.

Sardà, F., Lleonart, J., & Cartes, J. E. (1998). An analysis of the population dynamics of *Nephrops norvegicus* (L.) in the Mediterranean Sea. *Scientia Marina*, *62*(S1), 135-143.

Sastry, A. N., Vernberg, F. J., & Vernberg, W. B. (1983). Ecological aspects of reproduction. *The biology of Crustacea*, *8*, 179-270.

Severino-Rodrigues, E., Hebling, N. J., & da Graça-Lopes, R. (2018). Biodiversidade no produto da pesca de arrasto-de-fundo dirigida ao lagostim,. *Metanephrops rubellus* (Moreira, 1903), desembarcado no litoral do Estado de São Paulo, Brasil. *Boletim do Instituto de Pesca*, *33*(2), 171-182.

Smith, R. S. M. (1987). The biology of larval and juvenile *Nephrops norvegicus* (L.) in the Firth of Clyde (Doctoral dissertation, University of Glasgow).

Sparre, P. (1998). Introduction to tropical fish stock assessment. Part 1. Manual. *FAO Fisheries Technical* Paper, *306*(1), 1-407.

Talbot, P., & Harper, R. (1984). Abnormal egg stalk morphology is correlated with clutch attrition in laboratory-maintained lobsters (*Homarus*). *The Biological Bulletin*, *166*(2), 349-356.

Talbot, P., Thaler, C., & Wilson, P. (1984). Spawning, egg attachment and egg retention in captive lobsters (*Homarus americanus*). *Aquaculture*, *37*(3), 239-249.

Thomas, H. J. (1964). The spawning and fecundity of the Norway lobsters (*Nephrops norvegicus* L.) around the Scottish coast. *ICES Journal of Marine Science*, *29*(2), 221-229.

Ulmestrand, M., & Eggert, H. (2001). Growth of Norway lobster, *Nephrops norvegicus* (Linnaeus 1758), in the Skagerrak, estimated from tagging experiments and length frequency data. *ICES Journal of Marine Science*, *58*(6), 1326-1334.

Wallner, B.G. and Phillips, B. F. (1995). Development of a trawl fishery for deepwater metanephropid lobsters off the northwest continental slope of Australia: designing a management strategy compatible with species life history. *ICES Marine Science Symposia, 199,* 379-390.

Warner, G. F. (1977). *The biology of crabs.* London: Elekscience.

Wear, R. G. (1976). Studies on the larval development of *Metanephrops challengeri* (Balss, 1914) (Decapoda, Nephropidae). *Crustaceana*, *30*(2), 113-122.

Yamada, U., Takagawa, M., Kishida, S., & Honjo, K. (1986). *Fishes of the East China Sea and the Yellow Sea*. Nagasaki: Seikai Regional Fisheries Research Laboratory.