

## Comparative study on reproductive effort and spawning frequency of the two palaemonid prawns (*Exopalaemon modestus* and *Palaemon gravieri*) with different habitats

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Reproductive effort and spawning frequency of the two palaemonid prawns, *Exopalaemon modestus* and *Palaemon gravieri*, were investigated. In both embryos of the two species, egg size was larger in *E. modestus* than in *P. gravieri* but for a given size, number of eggs (EN) was fewer in *E. modestus*. The statistical results revealed that there were significant differences in egg size and EN between the two species. *E. modestus* living in freshwater environments had larger and fewer offspring than *P. gravieri* inhabiting marine environments. These findings are consistent with predictions from *r*- and *K*-selections models. Reproductive effort (RE) also was higher in *E. modestus*, suggesting the possibility for *E. modestus* to invest larger amount of energy per individual offspring. In the two prawns the ovarian dry weight of females with eyed eggs was significantly higher than those with non-eyed eggs. This indicates that the ovarian maturation occurs during the period between the two embryonic stages, suggesting females being potentially of continuous breeding within a single reproductive period. In the both species brood loss did not occur during the incubation period.

Key words: *Exopalaemon modestus*, *Palaemon gravieri*, reproductive effort, spawning frequency, egg size, fecundity, brood loss.

### Introduction

Crustaceans are remarkably successful groups, both in number of living species and in colonization of different habitats in freshwater, brackish and marine environments. This is reflected in highly diversified reproductive patterns and the reproductive strategies (Sastry, 1983; Hartnoll, 1985). Thus studies on the reproductive biology of decapod crustaceans are essential information for understanding of their reproductive pattern and strategies. These variations in reproductive aspects lead to the diversity of life history pattern necessary for the success of reproduction and growth (Hartnoll, 1985).

The Siberian prawn *Exopalaemon modestus* (Heller, 1862) and the Chinese ditch prawn *Palaemon gravieri* (Yu, 1930) occur in Indo-west pacific, Korea and

China (Holthuis, 1980). In Korea the former occurs in the fresh waters of southwest areas and the latter in the western coastal waters of Yellow Sea (Kim, 1977). The palaemonid prawns play ecologically important role as omnivores in freshwater, estuarine and marine environments. They feed on algae, detritus and aquatic insects, crustaceans, and meiofauna (Bell and Coull, 1978) and in turn, are preyed by fishes and other predators (Fresi et al., 1984; Lowe and Provenzano, 1990). The two prawns also have been commercially exploited in China and Korea (Holthuis, 1980).

Because the palaemonid shrimps display a variety of distribution pattern by adapting to a wide range of environmental conditions, it is an ecologically interesting subject to contrast reproductive variables between palaemonid species inhabiting two extreme environments. Previous studies have attracted the effects of environmental factors (temperature, salinity) on reproductive success, fecundity, and survival of

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palaemonid shrimps in the field (Dobkin and Manning, 1964; Berglund, 1980, 1984, 1985). Berglund (1985) reported that the different estuarine distributions of *Palaemon adspersus* and *P. elegans* led to inter-specific differences in reproductive success due to changes in salinity. Similar effects of salinity have been addressed for *Palaemonetes paludosus* in the laboratory (Lowe and Provenzano, 1990).

The present study is to test the hypothesis that there are differences in reproductive effort between the freshwater prawn *E. modestus* and the marine prawn *P. gravieri* by investigating 1) difference in fecundity and egg length and volume, and 2) difference in reproductive effort. We also examined the spawning frequency of the two palaemonid prawns by comparing the regressions between carapace length and ovarian dry weight for females with non-eyed egg stage and eyed egg stage. This will provide insight on the reproductive strategies and spawning frequency of the two shrimps with differing habitats.

## Materials and Methods

### Sampling

Samples of *E. modestus* were collected from Young-am Lake (34°45'N; 126°35'E), Chonnam, Korea, between March and November 1999. Sampling was carried out with hand push nets with fine mesh size (3×3 mm). *P. gravieri* were obtained from by-catches in one of *Acetes* fishery areas using 'single-walled tangle nets' (10×10 mm) on the western coast of Korea (34°53'N; 125°54'E) during the period from April and August 2000. Samples were fixed in 4% neutralized formalin for a day and then transferred to 70% alcohol for storage.

In Young-am lake water temperature varied in the range from 13.5°C in March to 29.5°C in August and salinity in the range from 0.4 ppt to 0.7 ppt. In *Acetes* fishery areas temperature ranged from 12.1°C to 20.9°C and salinity from 30.8 ppt to 32.1 ppt. This showed that the two prawns inhabited environments of two extremes in salinity.

### Sample analysis

Sex of all shrimps was determined by morphological examination (the shape of the endopod of the first pleopods and the presence or absence of the appendix masculina) and reproductive organ

under a dissecting microscope where obscure. Carapace length (CL), the shortest distance between the posterior margin of the orbit and the middorsal posterior edge of the carapace was measured with an ocular micrometer equipped with the microscope.

### Fecundity and reproductive effort (RE)

The embryonic development of ovigerous females was broadly divided into two categories: non-eyed egg stage and eyed egg stage. Eggs were carefully stripped using fine forceps and any setal material or extraneous matter was removed. All of eggs removed are counted directly to minimize the bias, which might be caused by indirect methods. For fecundity-carapace length relationship and RE estimation only females with non-eyed embryonic stage were used. The female and egg mass dry weight were dried at 60°C for 48 h and weighed to the nearest 0.0001 g using the electronic digital balance. Similarly, ovary dry weight was determined. Gonadosomatic index (GSI) was determined as follows:

$$\text{GSI} = \left( \frac{\text{Ovarian dry weight}}{\text{Dry weight of female}} \right) \times 100$$

Reproductive effort (RE) was estimated by dry weight by applying the formula adapting to Clarke et al. (1991):

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

For egg volume calculation, 10 eggs were subsampled before drying. These were measured along the major and minor axes (including the chorionic membrane tightly adhering to the egg surface), using the ocular micrometer. Eggs were treated as ellipsoids and volume quantified by the formula:

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

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

### Statistical analysis

Linear regressions of  $\log_e$  transformed data were determined for number of egg (EN) on carapace length (CL) and ovarian dry weight (Odw) on carapace length (CL). For two factors (species and egg stage) the differences in egg length and volume and reproductive effort (RE) were tested using two-way analysis of variance (ANOVA). Prior to

ANOVA, assumptions of ANOVA were examined using Bartlett's test. Where necessary, the data were log-transformed in order to produce acceptable homogeneity of variance and distribution of residuals. Regressions between ovary dry weight and carapace at non-eyed and eyed egg stage were tested for two regression lines and elevations using an analysis of covariance (ANCOVA) (Zar, 1984). When individual slopes were not significantly different, a common slope was computed and the recalculated elevations tested.

**Results**

**Fecundity and reproductive effort (RE)**

The number of eggs per brood ranged from 254~1,702 for female *Exopalaemon modestus* ranging in size of CL from 7.69~16.61 mm CL and 212~3,989 for *Palaemon gravieri* ranging in size of CL from 9.97~19.78 mm CL. In both species the regression analysis of each embryonic stage between log number of eggs per brood (EN) and log CL are shown in Table 1. For all stages of the two species the regressions were highly significant (Table 1, Fig. 1). Table 1 shows that for non-eyed embryonic stage, the number of eggs per brood negatively allometric function of female size for *E. modestus* and isometric function of the size for *P. gravieri* at 95% confidence level.

An analysis of covariance (ANCOVA) was used to examine whether the relationship between EN and CL differed between non-eyed egg stage of the two species (Fig. 2). The regression slopes did not differ significantly between the two species ( $F=1.19$ ,  $df=1, 95$ ,  $P>0.2$ ). However, after recalculating to a common slope ( $bc=2.289$ ) were significant differences in elevations ( $F=215.51$ ,  $df=1, 96$ ,  $P<0.001$ ).

Table 1. Details of linear regressions for ovigerous females of *Exopalaemon modestus* and *Palaemon gravieri* with the non-eyed eggs and the eyed eggs. Log<sub>e</sub> egg number (EN) is regressed on log<sub>e</sub> carapace length (CL)

Species	Egg stage	Regressions	±slope	n	r <sup>2</sup>
<i>E. modestus</i>	The Non-eyed	lnEN=2.081 lnCL+0.097	0.628	83	0.68***
	The Eyed	lnEN=2.342 lnCL-0.601	0.781	80	0.64***
<i>P. gravieri</i>	The Non-eyed	lnEN=2.498 lnCL+0.070	0.897	16	0.72***
	The Eyed	lnEN=1.721 lnCL+1.940	0.365	20	0.84***

\*\*\*  $P<0.001$

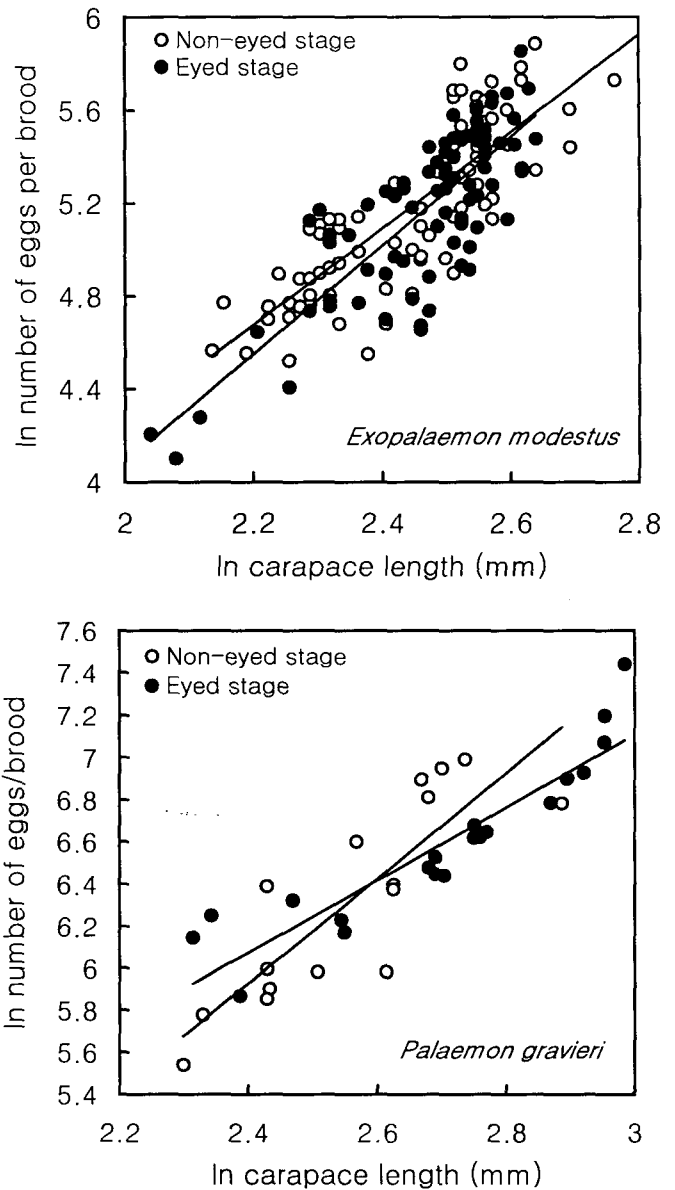


Fig. 1. Log<sub>e</sub> number of eggs per brood plotted against log<sub>e</sub> carapace length for *Exopalaemon modestus* and *Palaemon gravieri* with the non-eyed eggs and the eyed eggs.

This indicates that *E. modestus* had significantly more numerous in number of eggs than *P. gravieri*.

Reproductive effort (RE) ( $\pm$ SE) was determined from the individual value for females as 12.74 ( $\pm$ 6.57) for *P. gravieri* and 17.45 ( $\pm$ 8.56) for *E. modestus*. An analysis of variance (ANOVA) revealed that there was a higher reproductive effort in *E. modestus* ( $F=6.13$ ,  $df=1, 99$ ,  $P<0.05$ ).

To investigate the occurrence of brood mortality in the both species, the regressions between EN and

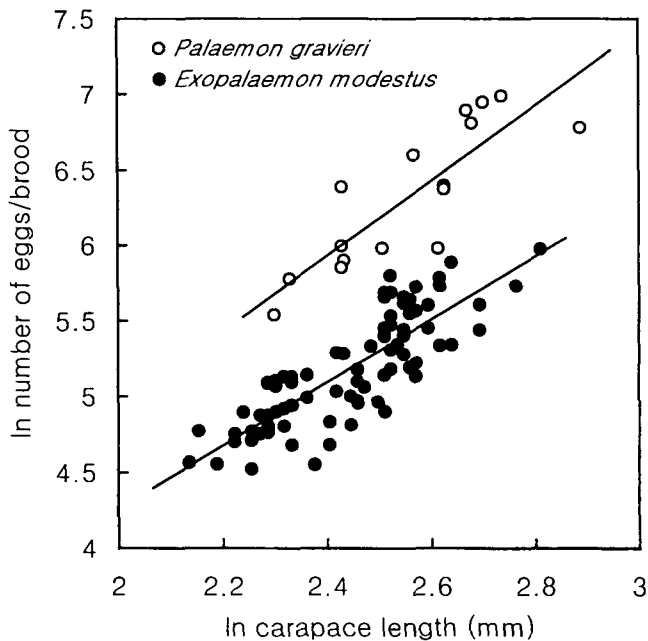


Fig. 2.  $\log_e$  number of eggs per brood plotted against  $\log_e$  carapace length for *Exopalaemon modestus* and *Palaemon gravieri* with the non-eyed eggs.

CL for both egg stages of each species were compared. All regressions were significant (Table 1, Fig. 1). In *E. modestus* ANCOVA revealed that the slopes of the regressions were not significantly different between the two egg stages ( $F=1.08$ ,  $df=1$ , 159,  $P>0.3$ ), nor was the elevations ( $F=3.08$ ,  $df=1$ , 160,  $P>0.05$ ). Similarly, in *P. gravieri* ANCOVA revealed that the slopes of the regressions were not significantly different between the two egg stages ( $F=3.64$ ,  $df=1$ , 32,  $P>0.06$ ), nor was the elevations ( $F=0.02$ ,  $df=1$ , 33,  $P>0.8$ ). These statistical analyses indicate that in the two palaemonid prawns brood loss did not occur during the incubation time.

For two embryonic stage of the both species the mean and standard deviation of egg length and volume are shown in Fig. 3. The mean egg length increased by 10% from 1.321 ( $\pm 0.075$ ) mm in non-eyed egg stage to 1.452 ( $\pm 0.119$ ) mm in eyed egg stage in *E. modestus* and by some 18% from 0.615 ( $\pm 0.070$ ) mm in non-eyed egg stage to 0.730 ( $\pm 0.065$ ) mm in eyed egg stage in *E. modestus*. A two-way ANOVA revealed that there were significant differences between species ( $F=458.31$ ,  $df=1$ , 84,  $P<0.001$ ), between egg stages ( $F=13.65$ ,  $df=1$ , 84,  $P<0.001$ ) and no interaction ( $F=0.060$ ,  $df=1$ , 84,  $P>0.8$ ).

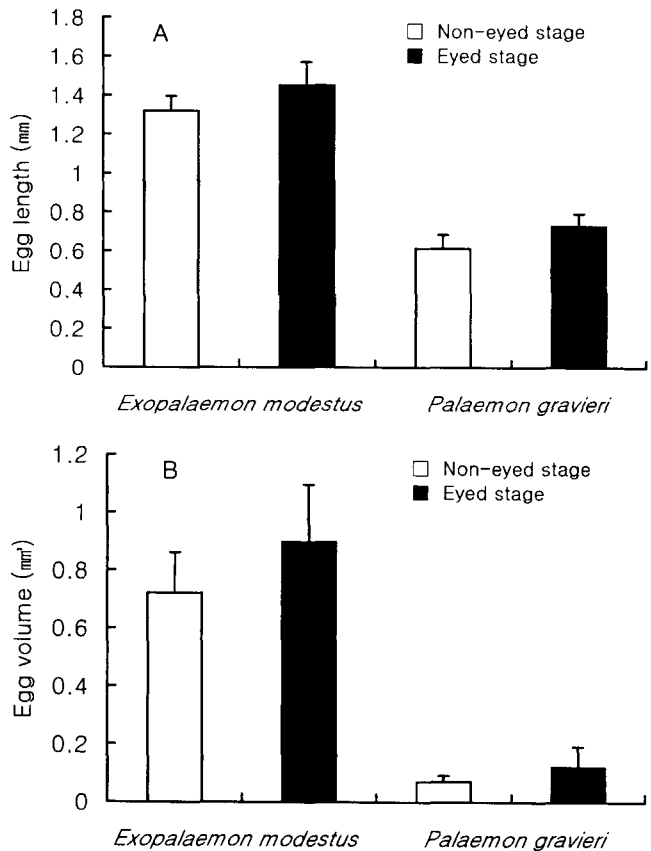


Fig. 3. Mean egg length (A) and volume (B) in the two embryonic stages of *Exopalaemon modestus* and *Palaemon gravieri*.

Mean egg volume increased by 24% from 0.722 ( $\pm 0.139$ ) mm<sup>3</sup> in non-eyed egg stage to 0.897 ( $\pm 0.199$ ) mm<sup>3</sup> in eyed egg stage in *E. modestus* and by 57% from 0.071 ( $\pm 0.020$ ) mm<sup>3</sup> in non-eyed egg stage to 0.112 ( $\pm 0.072$ ) mm<sup>3</sup> in eyed egg stage in *E. modestus* (Fig. 3). A two-way ANOVA revealed that there were significant differences between species ( $F=161.92$ ,  $df=1$ , 84,  $P<0.001$ ), between egg stages ( $F=4.02$ ,  $df=1$ , 84,  $P>0.05$ ) and no interaction ( $F=1.273$ ,  $df=1$ , 84,  $P>0.2$ ). These results indicate that *E. modestus* had larger eggs in both egg stages than *P. gravieri* and there was an increase in egg size during incubation time.

#### Spawning frequency

In all egg stages of the two species ovarian dry weight was significantly correlated with carapace length (Table 2; Fig. 4). To determine whether the relationship between ovarian dry weight (Odwt) and carapace length (CL) differed between females with

Table 2. Details of linear regressions for females of *Exopalaemon modestus* and *Palaemon gravieri* with non-eyed eggs and eyed eggs. Log<sub>e</sub> ovarian dry weight (Odwt) are regressed on log<sub>e</sub> carapace length (CL)

Species	Egg stage	Regressions	±slope	n	r <sup>2</sup>
<i>E. modestus</i>	The Non-eyed	lnOdwt=2.38 lnCL-11.21	1.81	81	0.26***
	The Eyed	lnOdwt=3.50 lnCL-13.17	1.97	78	0.22***
<i>P. gravieri</i>	The Non-eyed	lnOdwt=3.84 lnCL- 8.37	2.11	16	0.33*
	The Eyed	lnOdwt=1.73 lnCL- 0.87	0.89	35	0.32***

\* P<0.05, \*\*\* P<0.001

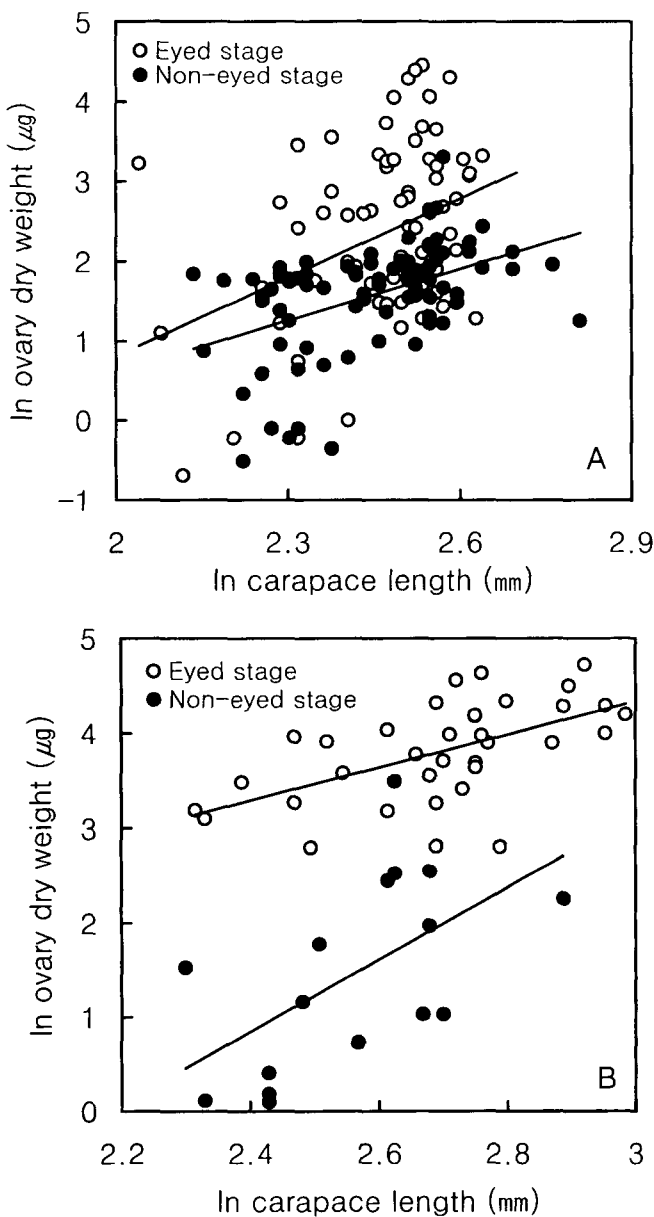


Fig. 4. Regressions of ovarian dry weight on carapace length of female *Exopalaemon modestus* (A) and *Palaemon gravieri* (B).

non-eyed egg stage and eyed egg stage for each species, the two regressions were tested for difference in regression slope and elevation. In *P. gravieri* the slopes did not differ between the two egg stages (ANCOVA:  $F=3.24$ ,  $df=1$ ,  $47$ ,  $P>0.07$ ), but intercepts, after determining a common slope (2.786), were significantly different (ANCOVA:  $F=18.85$ ,  $df=1$ ,  $48$ ,  $P<0.001$ ). Similarly, in *E. modestus* the slopes was not different between the two egg stage (ANCOVA:  $F=1.68$ ,  $df=1$ ,  $155$ ,  $P>0.1$ ), but intercepts, assuming a common slope (2.786), did significantly differ (ANCOVA:  $F=59.81$ ,  $df=1$ ,  $156$ ,  $P<0.001$ ). Mean GSI also was higher in later egg stage in both species (Fig. 5). ANOVA revealed that significant difference in mean GSI between the two egg stages was found for both *P. gravieri* ( $F=11.15$ ,  $df=1$ ,  $49$ ,  $P<0.01$ ) and *E. modestus* ( $F=20.04$ ,  $df=1$ ,  $153$ ,  $P<0.001$ ). These results showed that in the two palaemonid prawns there was a significant increase in ovarian dry weight from non-eyed egg to eyed egg stage, indicating consecutive breeders, capable of multiple spawning within a single reproductive season.

### Discussion

Brood weight averaged 12.7% of female body weight of *P. gravieri* and 17.5% that of *E. modestus*. The reproductive effort (RE) of the palaemonid shrimps ranged from 12% to 22%, and that of the other caridean shrimps from 9% to 20% (Table 3).

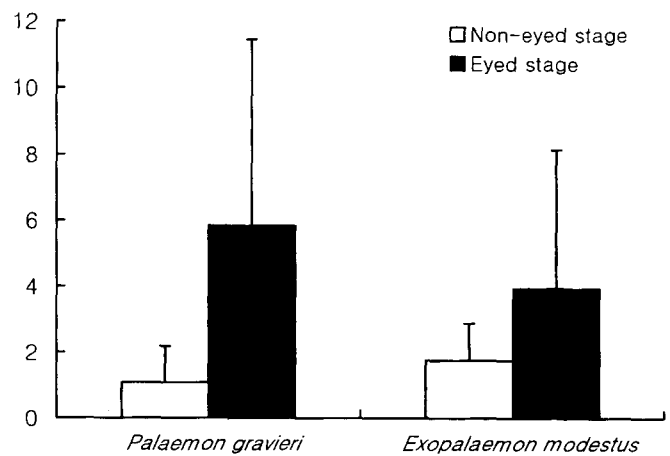


Fig. 5. Mean gonadosomatic index (GSI) in the two embryonic stages of *Exopalaemon modestus* and *Palaemon gravieri*.

Table 3. Comparison of reproductive effort (RE) for a variety of caridean shrimps

Family	Species	RE	Source
Crangonidae	<i>Crangon crangon</i>	17%	Clarke, 1987
	<i>Philocheas trispinosus</i>	24%	Oh & Hartnoll, 1999
	<i>Sabina septemcarinata</i>	14%	Clarke, 1987
	<i>Notocrangon antarcticus</i>	12%	Clarke, 1987
Pandalidae	<i>Pandalus montagui</i>	20%	Clarke, 1987
Alpheidae	<i>Betaeus emarginatus</i>	9%	Lardies & Wehrtmann, 1997
	<i>B. truncatus</i>	13%	Lardies & Wehrtmann, 1997
	<i>Synalpheus spinifrons</i>	17%	Lardies & Wehrtmann, 1997
Palaemonidae	<i>Palaemon northropi</i>	14%	Anger & Moreira, 1998
	<i>P. pandaliformis</i>	19%	Anger & Moreira, 1998
	<i>Macrobrachium olfersii</i>	22%	Anger & Moreira, 1998
	<i>M. acanthurus</i>	19%	Anger & Moreira, 1998
	<i>Exopalaemon modestus</i>	17%	This study
	<i>Palaemon gravieri</i>	12%	This study

In this study the freshwater shrimps *E. modestus* showed about 5% higher reproductive effort than the marine species *P. gravieri*. Similar examples are found in the observations on the four palaemonid shrimps by Anger and Moreira (1998). In general, the freshwater palaemonid shrimps (*Palaemon northropi* and *Exopalaemon modestus*) show higher reproductive effort than the marine species (Table 3). This suggests that the higher RE of palaemonids living in freshwater habitats could be the reproductive traits of the family Palaemonidae. According to Hines (1982, 1988, 1991, 1992) brood weight in brachyurans crabs is generally constrained to 10% of the female body weight. This study shows RE rather higher than that value, which seems to be a general phenomenon in carideans. The differences in RE available for one spawning and in egg size, between the two species, give rise to the varied clutch sizes and subsequently lead to changes in annual egg production.

There is substantial evidence to suggest that when removing the variability in the female size *E. modestus* had significantly larger and fewer eggs per brood and higher reproductive effort (RE) than *P. gravieri*. This was clearly indicated by difference in regression lines between number of eggs and carapace length of female with non-eyed eggs and differences in mean egg size. This means that reproductive investment between the two species is differently allocated, suggesting the possibility for *E. modestus* to invest larger amount of energy per individual

offspring.

The effect of egg size on incubation period and survival differ between species, which leads to different reproductive strategies. In this study *E. modestus* living in freshwater was significantly larger egg size than *P. gravieri* inhabiting marine environments. Mashiko (1990, 1992) reported that the small egg population of *Marcobrachium nipponense* was found in brackish waters. He suggested that the specific environmental difference between small egg and large egg population was whether the water body as their habitat is entirely open to the sea or not. Depending on hydrographic features of habitats, intraspecific variations of egg size also have been well addressed for *Marcobrachium nipponense*. In crustaceans this is linked with the increase of adaptive value for the environmental conditions (Sastry, 1983; Clarke, 1993). Larger egg size in freshwater invertebrates could be advantageous when necessary for long incubation time and better survival of planktonic larvae, while relatively small-sized eggs of marine decapod crustaceans develop within a short period of time and few survive to adults (Thorson, 1950; Barnes and Barnes, 1965; Vance, 1973; Wear, 1974). These findings are consistent with predictions from *r*- and *K*-selections models (Pianka, 1970). Therefore, compared with the two species living at two extreme environments, it is likely to conclude that *P. gravieri* are in *r*-selected continuum and *E. modestus* in *K*-selected continuum.

The two palaemonid prawns can produce more than one batch of eggs within a single reproductive period, probably sequentially immediately after moulting. In the both palaemonid prawns females with late embryos were significantly higher in ovarian weight than those with early embryo when removing the variability in the female size. According to Pillay and Nair (1971), this could be interpreted as an indication of the potential to produce another brood within a single breeding period. Various decapod crustaceans display the same reproductive pattern (Hartnoll, 1982). Guerao et al. (1994), working on the reproduction of *Palaemon xiphias* in Alfacs bay on the Spanish Mediterranean coast, reported that the number of spawning by each female *P. xiphias* was minimum of 2, and 5 or 6 spawnings were possible. Oh and Hartnoll (1999) found that the

dominant reproductive pattern found in *Philocheras trispinosus* is of continuous reproduction throughout the breeding season. However, *P. serratus* had up to 3 spawnings on French coasts, while in the colder Irish and Welsh waters spawning occurred only once a year (Cole, 1958). Thus in the palaemonid shrimps the multiple spawning does not seem to be species-specific reproductive traits. It is likely that the spawning frequency of the palaemonid shrimps was determined by temperature, the most important single factor associated with spawning, which could be attributed to appropriate energy allocation for the success of reproduction.

In this study an attempt has been made to find whether brood loss occurs in the two species. The results showed that in the both species no brood loss occurred during incubation time. Based on the laboratory experiments, the only one study on the brood mortality of palaemonid shrimps has estimated 38% for *Palaemon serratus* (Reeve, 1969). The difference in observations of brood loss between the two studies may be attributed to the physical stress of ovigerous females in captivity or possibly, the occurrence of some error in categorizing the embryonic stage of berried females in this study.

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