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Relationship Among Reproductive Traits and Brood Production Pattern of Caridean Shrimp, *Palaemon gravieri* (Decapoda: Caridea: Palaemonidae)

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Reproductive traits of *Palaemon gravieri* such as embryo size, number of embryo (fecundity), incubation period, larval development mode, larval development period, larval survival and larval growth were described and compared to analyze the correlation among those traits. Embryo volume is a primary factor determining other ensuing reproductive features. Egg volume was 0.042 mm^3 in the first developmental stage. Embryo volume in *P. gravieri* was comparatively small which is indicative of great number of embryo (y = 3.0161x + 0.0185 R^2 = 0.74 positive isometric relationship) and relatively long incubation period. Larvae survived from zoea 1 to post-larvae and it took 45 days at 22°C. Survival rate of the larvae was rather great in the early stage and thereafter steadily decreased. Daily growth rate of larvae in *P. gravieri* at 22°C was 0.0195 mm on average. They grew steadily as time went by. Incubation period was between 10-14 days at 22°C. Larval development mode was almost complete planktotrophic. PNR (point of no return) appeared to be the third day on average. Survival rate of larvae without feeding declined rapidly between 3 and 4 days. Larval development period and stage frequency were 23-30 days and 11 stages which imply prolonged larval period and high mortality. The pattern of brood production followed fast successive partarial pattern. Most ovigerous female had mature ovary when they performed parturial molt soon after hatching (larval release).

Keywords: Reproductive traits, Palaemon gravieri, Blood production pattern

Introduction

Palaemon gravieri (Yu) is distributed around coastal region of the Yellow Sea and Southern Sea of Korea (Holthuis, 1950; Kim 1977). The species is also commercially used as food for human and fish bait (Kim, 2005).

Reproductive traits of the life history characters in marine organisms are crucial components to influence other traits. And generally growth and reproduction were known to be a trade-off in the energy diversion in the individual organism (Kim and Hong, 2004). Thus, in the marine organisms embryo (egg) size is the primary component to influence the property of other traits, and, fecundity and larval development mode (period) are highly correlated factors with embryo size among reproductive traits. Vance (1973a) also suggested that nutritional mode of the larvae is obviously correlated with the embryo size, and earlier embryo size is the conspicuously important and determinant factor affecting other reproductive traits such as incubation period and larval development pattern. The larvae of marine invertebrates generally differ from those of other taxa with complex life cycles and dispersing stages in their ability to feed in their dispersal medium, water (Strathmann, 1990). This ability has generated a wealth of diversity in larval form and function. Most marine invertebrates produce offspring that obtain nutrition during development either from the parent or from external food sources.

Thorson (1946) made a classification for larval development modes that is widely used today, despite subsequent revision (Miliekovsky, 1971; Chia, 1974; McEdward and Janies, 1993). Thorson (1950) classified larvae into several categories based largely on nutritional mode and length of their planktonic phase. Subsequently Mileikovsky (1971) reviewed developmental patterns in various taxa and proposed four developmental types a) pelagic development b) demersal development c) direct development and d) viviparity.

Thorson (1950) noted a trend toward increased egg size and non- planktonic, non-feeding development along gradients of increasing latitude and water depth. He attributed these trends to restricted availability of food and slow development associated with cold temperatures. However, some work on Antartic and deep-sea invertebrates have revealed many exceptions to Thorson's idea (Pearse et al., 1991). The evolution of direct development involves dramatic increase in egg size (Emlet et

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al., 1987; Wray and Raff, 1991). Which indicates that smaller eggs usually undergo planktotrophic development while species with larger, more yolky eggs are likely to have lecithotrophic development.

The pattern of brood production is related with ovarian development cycle, embryonic development cycle and molting cycle (Bauer, 2004). It indicates interspawn period, incubation period (embryonic development period), molting time after hatching, molting frequency and ovulation time after hatching. And the pattern of brood production was described as three different types; slow successive parturials, fast successive parturials, alternate parturials (Bauer, 2000).

Caridean shrimps generally undergo larval development period as a complete plankton stage in the water from zoea to postlarvae before settlement (Bauer, 2004). Thus, during planktonic period after hatching the zoeal nutritional mode must have been selected as planktotrophic which is supposed to be highly correlated with egg size and number of eggs.

P. gravieri has been reported to inhabit warm temperate waters and coastal regions of 25-30 m in depth (Kim and Hong, 2004) Thus, the larvae of *P. gravieri* is hypothesized to be obligate planktotrophic as are other caridean larvae which may link to relatively small egg size, shorten incubation period, high fecundity and prolonged larval development duration.

The objective of this study is to describe reproductive traits, brood production pattern and analyze relationships among those reproductive traits of *P. gravieri*.

Materials and Methods

Ovigerous females of *P. gravieri* were collected around coastal areas of Namhae in May, 2004 to carry out the analysis of reproductive traits. Some of samples collected were lively transferred to the laboratory and maintained at temperature 22°C, 30-32‰ and at 12: 12 (L:D) light and dark cycle to know incubation period, larval development mode, larval development period and pattern of brood production. Sufficient artificial foods such as chopped clams and squids for ovigerous females were supplied everyday. Sea water in the container was exchanged every other day, and detritus and excreted materials from the shrimp were siphoned off the container. The ovigerous females were sorted out into newly spawned females (first stage of embryonic development) to experiment the incubation period until hatching of the larvae. Individuals out of larvae hatched from ovigerous females were individually transferred to each glass bottle and maintained with the same environmental conditions. Seawater in the glass bottle was exchanged with filtered sea water everyday. Ovarian developmental stages were divided into three stages on the following morphological criteria: stage 1, immature- ovary thin and translucent; stage 2, intermediate-green ovary filling one-half of the cephalothorax volume; stage 3, mature-ovary filling almost all of the cephalothorax, prespawning stage. Larvae were sufficiently fed with newly hatched *Artemia* nauplii. The period of larval development was observed. Survival rate of zoea without any nutrition measured by another controlled experiment to know PNR (point of no return). And also incubation period and spawning frequency were obtained. Carapace lengths of the female adult and larvae were measured from the posterior rim of the eye socket to the posterior lateral edge of the carapace. Fecundity (number of eggs) was determined by the equation of log-transformed number of eggs on carapace length at non-eyed embryos of ovigerous females. Embryos were subsampled to calculate embryo volume. These were measured along the major and minor axes using stereomicroscope by the formula: $4/3\pi\ r_1 r_2^2$ where r_1 is half the major axis and r_2 is half the minor axis.

Results

Larval development experiment to know the development mode displayed that larval development mode (nutritional mode) was close to obligate planktotrophic.

The larvae endured 2 or 3 days without food on average. Most of them after this period died without food. Survival rate of the larvae reared at 22°C was 97-100% (Fig. 1A) The survival of the larvae maintained high until 4 instar, and then decreased steadily as the instar proceeded. The larvae underwent 11 instar before they reached post-larvae, Molt frequency in the larvae seemed to be comparatively more than other palaemonid larvae. Larvae survived from zoea 1 to post-larvae during 45 days which was the larval development period. Sixteen% of the larvae reached post-larvae. Daily growth rate of the larvae in *P. gravieri* at 22°C was 0.0195 mm on average (Fig. 1B). Without nutrition the survival rate of the larvae was not high. PNR was second day after hatching (Fig. 2). They could return from the first day and second day but never return to survival, if feeding them, after this period. The relationship between number of eggs and carapace length was expressed as the equation (fecundity): $y = 3.0161x + 0.0185$ $R^2 = 0.74$ (Fig. 3A). The relationship between carapace length

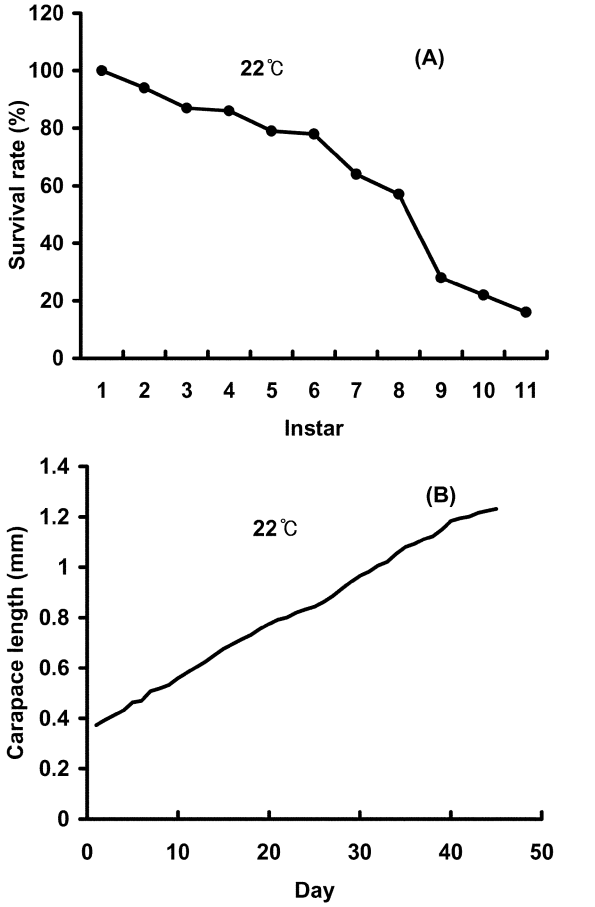

Fig. 1. *Palaemon gravieri.* Survival rate (%) per instar of the larvae reared at 22°C (A) Growth (%) per day at 22°C (B).

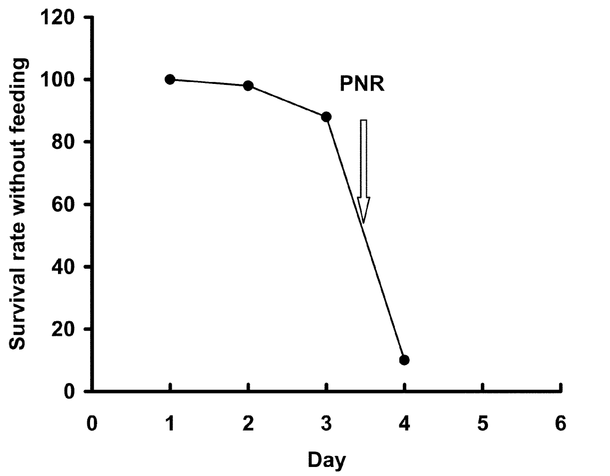

Fig. 2. *Palaemon gravieri.* Survival rate (%) without feeding per day of the larvae reared at 22°C and PNR.

and number of embryo was positive and the slope showed about 3 which implies isometric relationship. The embryo volume increased as embryo development proceeded from stage 1 to stage 5 (Fig. 3B). The embryo volume increase in

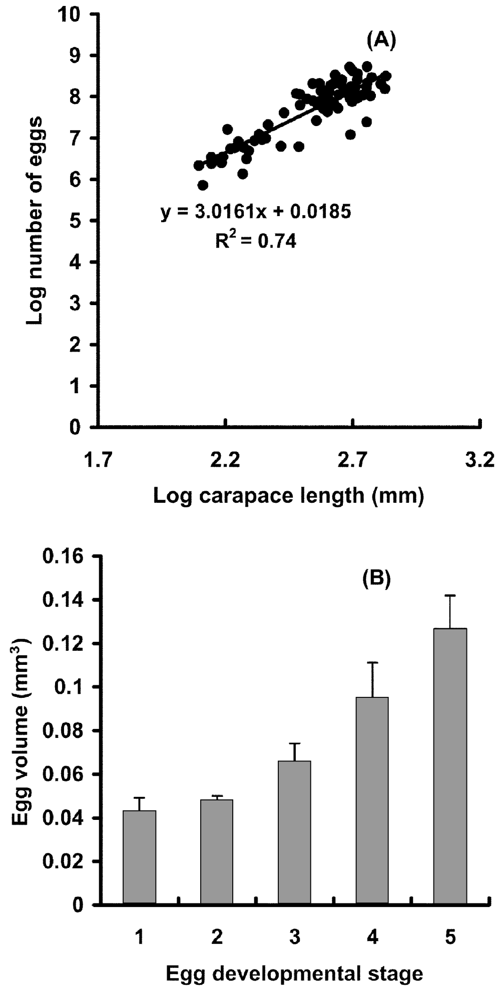

Fig. 3. *Palaemon gravieri.* Relationship between log carapace length (mm) and log number of embryos (A) and embryo volume increment with embryo developmental stages (vertical bar, standard deviation) (B).

the first and second stage was small but it started to increase more at the third stage. The increment percentage in embryo volume was 160% from stage 1 to 5. ANOVA test showed mean embryo volume was significantly different between the embryonic developmental stages ($P<0.05$). Embryo volume was 0.042 mm^3 in the first stage which was comparatively small. Embryo volume increased a little bit between stage 1 and 2, and greatly between stage 2 and 3 and then steadily between stage 3 and 5. Incubation period was between 7-12 days at 22°C. The pattern of brood production showed fast successive parturials (Fig. 4A). Ovarian development in the laboratory experiment showed that most of ovigerous females had a mature ovary when they release the larvae (hatching-out) after incubation period (Fig. 4B). Relationship among reproductive traits showed that each trait was highly correlated (Table 1).

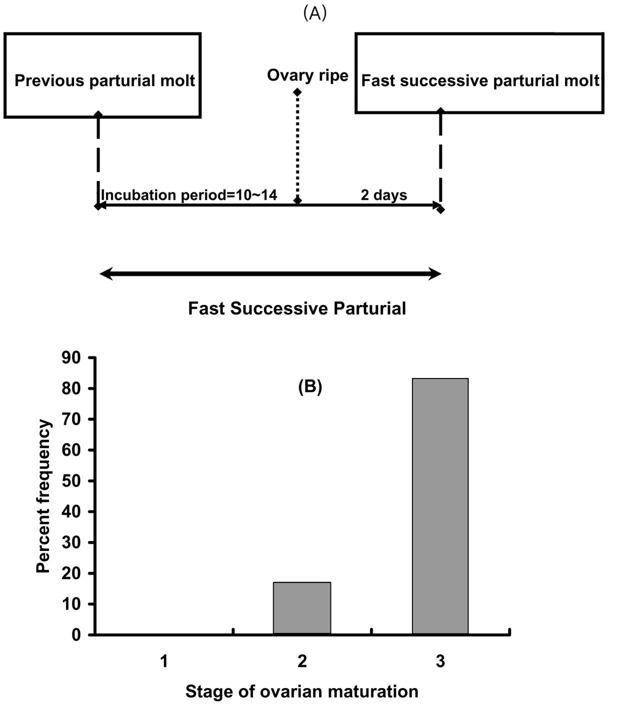

Fig. 4. *Palaemon gravieri*. Pattern of brood production, schedule of molting, spawning, embryo incubation, hatching, ovarian maturation (A). Stage of ovarian maturation of laboratory females upon hatching of brooded embryos (B).

Discussion

The relationship between embryo volume and fecundity can be explained as trade-off in the energy allocation of the female (Kim and Hong, 2004). Thus, from the evolutionary perspective embryo volume could be selected by diverse life history traits and environments surrounding the species such as growth, fecundity, incubation period, spawning frequency, larval development period, mortality, larval dispersal period and abiotic factors (Bauer, 2004). If egg volume was relatively small which is indicative of determining the property of other traits, therefore, there should be great number of embryos (high fecundity), rather short incubation period and long larval development period (many larval development stages). Those were consistent with the results of the current research. Long larval development period indicates long larval period and high larval mortality rate. In *P. gravieri* adult mortality was relatively small (Kim, 2005) and adult growth was rather faster (Kim, 2005) but larval growth was rather slow (Kim, 2005). Egg volume was relatively small compared to other palaemonid species such as *Palaemon northropi* (Rankin, 1898) (0.200 mm^3); *Palaemonetes intermedius* Holthuis, 1949 (0.294 mm^3); *Leander tenuicornis* (Say, 1818) (0.163 mm^3); and *Macrobrachium ohione* (Smith, 1874) (0.080 mm^3) (Corey and Reid, 1991), which is related with high fecundity that leads to short incubation period, long larval development period (obligate planktotrophic) and high larval mortality.

Some authors have noted the costs and benefits of producing many small, energetically inexpensive eggs versus producing fewer, larger eggs which are stored with more yolk (Grahame and Branch, 1985; Strathmann, 1985). This trade-off was first assessed analytically by Vance (1973a, b), who created a simple model to investigate the relationship between planktonic mortality, egg size and development time, and egg number. And he suggested inverse relationship between number of eggs and egg size. Vance model showed the outcome that under some combinations of growth and mortality rates, selection would favor large eggs and small egg simultaneously. Christiansen and Fenchel (1979) presented a modified model which included sigmoid larval growth and size-dependent mortality (decreasing mortality with increasing size). Both Vance (1973a, b) and Christiansen and Fenchel (1979) used the correlation between egg size and larval type to infer that the evolutionary stability of the extremes of egg size indicated that only the extreme of developmental type would be stable, i.e. selection should favor feeding larvae or non-feeding larvae, but not intermediate forms. As suggested above for *P. gravieri* high correlations among reproduction, growth and mortality traits were produced.

Meanwhile, many caridean females are continuous or successive breeders (Bauer, 1976, 1979, 2004), *P. gravieri* was also fast successive breeder, thus, continuous breeders, females which are carrying embryos near hatching have a mature, prespawning ovary and then carry out parturial molt within one or two days. Continuous (fast successive) breeding has been reported in females of many caridean species, *Heptacarpus sitchensis*, *H. palundicola* (Bauer, 1976, 1979, 2004),

Table 1. Correlation among reproductive traits out of life history traits

Embryo volume	Fecundity	IP	LT	LG	LM	LDP
small	high	long	Planktotrophic	fast	high	long
large	low	short	Lecithotrophic	slow	low	short

(IP: Incubation period, LT: Larval type, LG: Larval growth, LM: Larval mortality, LDP: Larval developmental period).

Macrobrachium rosenbergii (Wickins and Beard, 1974).

In conclusion the larvae of *P. gravieri* showed pelagic development (planktotrophic) and egg volume was the most crucial factor. And it was highly correlated with number of embryo, larval type, period and rate of other traits through the evolution associating with the components in the life history.

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