

Growth, Fecundity, Egg Size and Recruitment of *Palaemon serrifer* (Decapoda: Caridea: Palaemonidae)

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ABSTRACT: Growth and reproduction of *Palaemon serrifer* were described and analyzed in a population inhabiting tide pools in warm temperate waters in Korea. The water temperature varied greatly in the tide pools, ranging from 8°C to 27.8°C. Population structure and growth were investigated using size frequency distribution data collected from January to December 2003. Sex ratios fluctuated, but were almost equal during the breeding period. Growth was continuous and size increased gradually throughout the year. Adult females were larger and grew faster than males. von Bertalanffy growth parameters for a one-year sample of females and males were estimated as $L_{\infty} = 11.32$, $K = 0.311$, $t_0 = -0.4115$ and $L_{\infty} = 8.36$, $K = 0.228$, $t_0 = -0.9693$ respectively. Breeding was seasonal, starting in May, peaking in August, and finishing by the end of August. The species showed continuous production of successive broods. Laboratory observation showed that females with embryos near hatching had ovaries filled with vitellogenic oocytes ready for spawning. The reproductive output (effort) of each female (mean number of eggs: 552–1355) was not high. The mean embryo volume, 0.078 mm³, is relatively small, indicative of low energy allocation to each embryo. Recruitment of juveniles was closely linked to the breeding period, beginning in September.

Key words: Grass shrimp, Growth and reproduction, *Palaemon serrifer*, Sex ratio

INTRODUCTION

The grass shrimp, *Palaemon serrifer*, is distributed in Korea around the Yellow and Southern Seas (Kim 1977). This species usually occurs in the intertidal area and is occasionally restricted in tide pools.

Growth, reproduction, and recruitment of caridean shrimps in the tide pools of intertidal areas can be influenced by environmental factors such as temperature (Bauer 1992a, Kim and Hong 2004). The environment in a tide pool can be harsh due to rapid change of temperature. Growth and year classes of decapods have been estimated using analysis of length-frequency data (LFD) and their average growth curves appear to fit the von Bertalanffy growth functions (VBGF) (Beverton and Holt 1957, Ricker 1975), applied to the mean lengths of year classes in relation to their ages (Parrack 1979, Garcia and Le-Reste 1981, Frechette and Pearsons 1983, Roa and Ernst 1996, Tuck et al. 1997).

The durations of breeding periods for marine animals have been reported to depend on the latitude (Orton 1920, Thorson 1950). Breeding is limited to spring and summer in temperate regions, and summer in polar regions, but occurs almost year-round in tropical regions (Bauer 1989). Temperature is known to be the most impor-

tant proximate factor affecting the breeding period (Orton 1920, Thorson 1950, Bauer 1992a). Reproductive output can be described as the number of eggs produced, which reflects energy allocation to reproduction (Tinkle and Hadley 1975, Clarke 1987). The relationship between reproductive output and body size is generally measured using regression equations (Gould 1966, Hines 1982, Hartnoll 1985, Bauer 1991). Embryo size is an important and determinable factor affecting various life history traits, and is highly correlated with growth rate and reproductive output. In general, embryo size is relatively large in polar and deep sea benthic regions, which have relatively constant environments, and in terrestrial and freshwater regions (Mauchline and Fisher 1969, Omori 1974).

P. serrifer inhabit tide pools in intertidal areas of warm temperate waters. Tide pools are highly variable in environmental conditions. Thus, growth of *P. serrifer* fluctuates seasonally and its reproduction and recruitment should be seasonal, coinciding with periods of high temperature, in warm temperate waters.

The main objective of this study is to describe growth, reproduction, and recruitment patterns in *P. serrifer* from Korean waters.

MATERIALS AND METHODS

P. serrifer were collected monthly from January to December

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2003 using a dip net of 1 mm mesh size in tide pools on Dongback Island in Korea (34° 49' N, 127° 48' E). Sampling was carried out at neap tide, during which the tide pools were completely exposed and separated from the shore.

All samples including ovigerous females were collected and fixed with 10% neutral formalin in the laboratory and then preserved in 70% alcohol solution in a plastic container. The water temperature was measured at the time of sampling. Sex was determined by the presence (males) and absence (females) of an appendix masculina on the second pleopod. Carapace length of the shrimp was measured from the posterior rim of the eye socket to the posterior lateral edge of the carapace. Carapace length frequency distributions for females and males were determined for both sexes. Growth parameters were estimated using carapace length frequency distributions with 1 mm length intervals using the von Bertalanffy growth function (Beverton and Holt 1957) as follows: $L_t = L_{\infty} (1 - \exp(-K(t-t_0)))$. Growth curves were then created using the parameters estimated. Females with developing gonad and ovigerous females were examined to measure ovarian and embryonic development. Ovarian development was divided into three stages using the following morphological criteria: stage 1, immature- ovary thin and translucent; stage 2, intermediate- green ovary filling half of the cephalothorax volume; stage 3, mature-ovary filling almost the entire cephalothorax in the prespawning stage. Embryonic developmental stages were categorized as described by Omori and Chida (1988): stage 1, from fertilization to the advent of the blastodisc; stage 2, from the end of stage 1 to the advent of the maxilliped rudiment (the end of the embryonic nauplius stage); stage 3, from the end of stage 2 to the pigmentation of compound eyes; stage 4, from the end of stage 3 to the point at which the tip of the telson reaches the dorsofrontal margin of the compound eyes; stage 5, development subsequent to the end of stage 4. Live females collected from the field were individually and collectively maintained in the laboratory at 20~22°C in an isolated aquarium (65 × 45 × 35 cm) and plastic containers (20 × 15 × 10 cm) with sufficient aeration to observe brood production. The water in the aquarium and in the plastic container was filtered, recirculated and changed daily. Fecundity of ovigerous females was described as reproductive effort (number of embryos). The relationship between the log-transformed number of eggs or non-eyed embryos (dependent variable) and the log-transformed carapace length (independent variable) was examined using regression. Embryos were subsampled and measured along the major and minor axes using a stereomicroscope. Embryo volume was then calculated using the formula: $V = 4/3 r_1 r_2^2$ where r_1 is half the major axis and r_2 half the minor axis (Corey and Reid 1991, Kuris 1991).

RESULTS

Environmental Factor and Sex Ratio

The water temperature displayed substantial variation at the sampling site (Fig. 1). The sex ratio also oscillated during the sampling period, generally being more female-biased in the winter than in the spring and summer. However, the lowest number of females appeared in September and the highest in October (Fig. 2).

Size Frequency Distribution and Growth

The size-frequency distribution showed that the population was composed of two year-classes (Fig. 3). The population began to recruit in September, but members of the previous generation coexisted with the new generation, with a few older individuals surviving to December. The growth parameters for females and males were estimated using the von Bertalanffy growth parameters using a one-year sample as $L_{\infty} = 11.32$, $K = 0.311$, $t_0 = -0.4115$ and

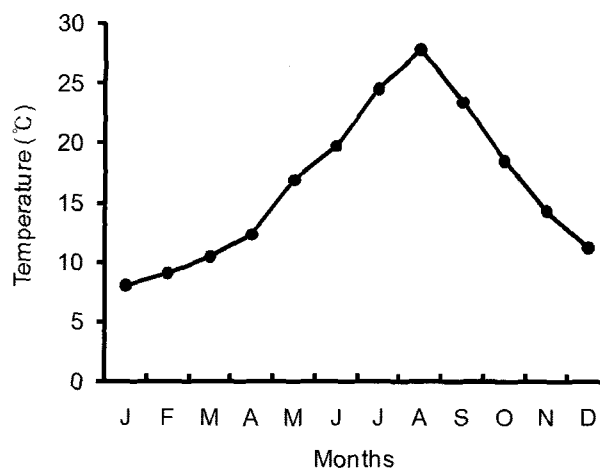


Fig. 1. Seasonal changes in water temperature in the sampling site.

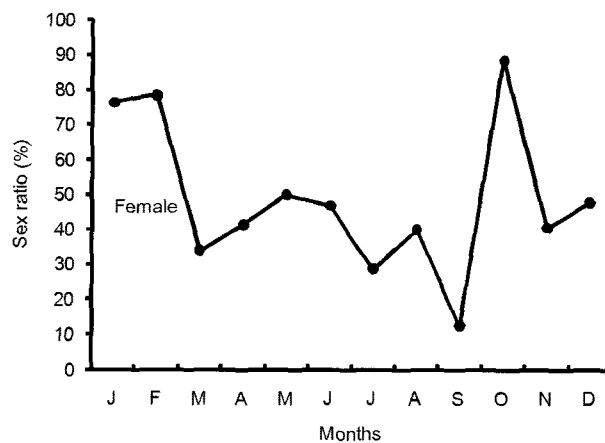


Fig. 2. Sex ratio of the *P. serrifer* population in each study month.

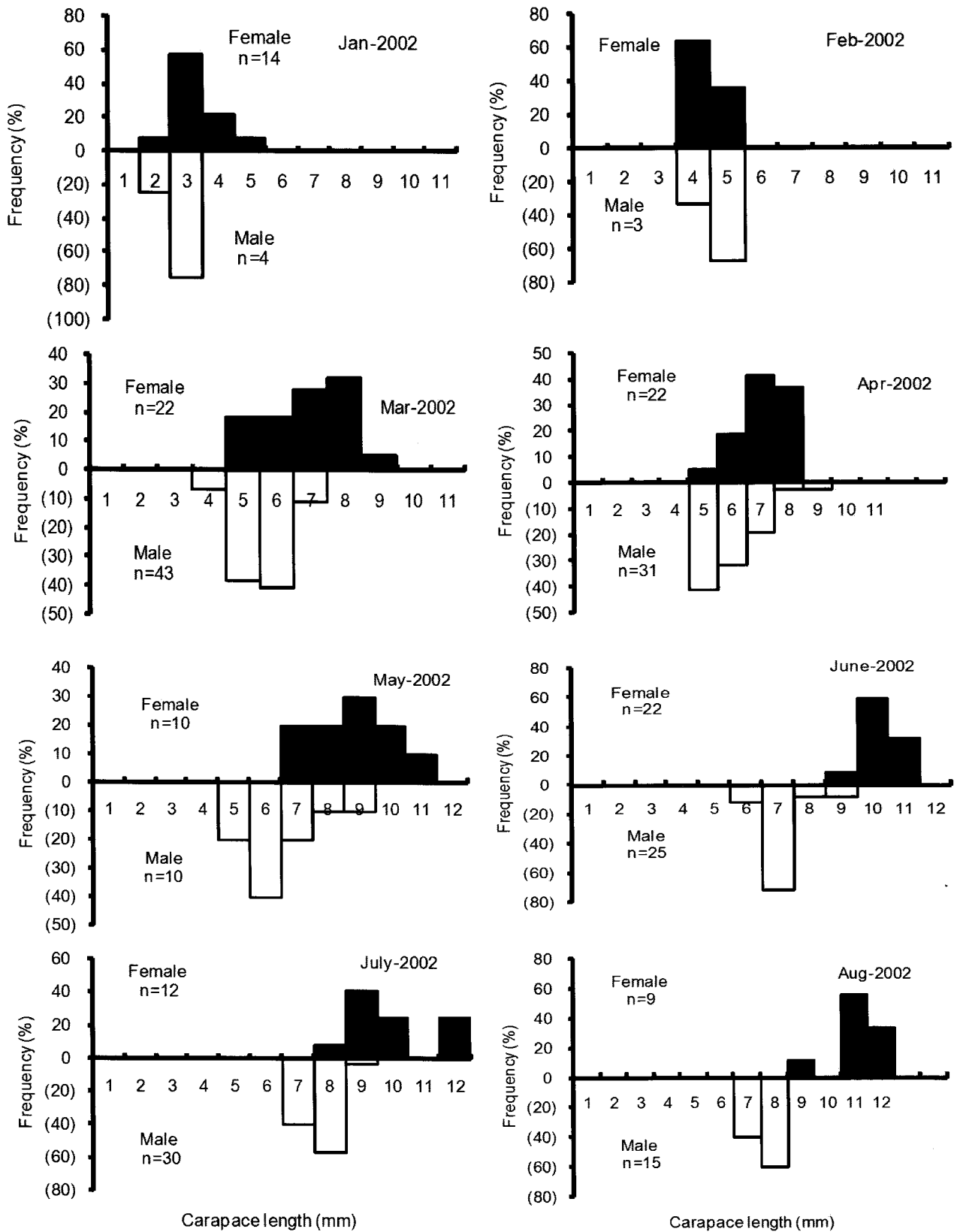


Fig. 3. Size frequency distribution of *P. serrifer* for each study month.

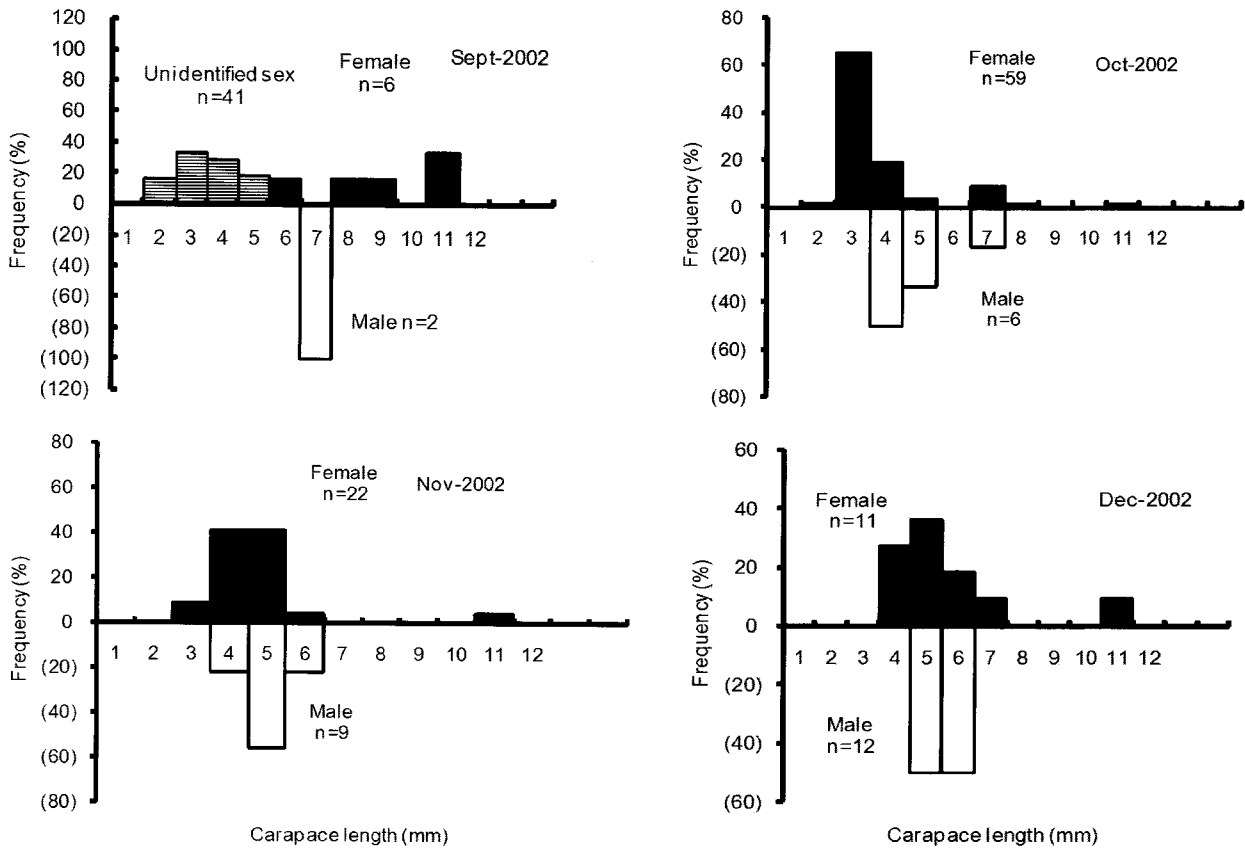


Fig. 3. Continued.

$L_{\infty} = 8.36$, $K = 0.228$, $t_0 = -0.9693$, respectively (Fig. 3). Growth occurred year-round and was faster in summer than in winter. Females grew somewhat faster and to a larger size than males (Fig. 4). The size frequency distribution data suggest a life span for the species of about 15~18 months. The maximum and minimum carapace lengths recorded for females were 12.47 mm and 2.12

mm, respectively, and the maximum and minimum for males were 2.52 mm and 7.76 mm, respectively.

Breeding Period and Reproductive Output (Fecundity)

The breeding period was seasonal, occurring in late spring and early summer. Breeding started in June, peaked in August, and

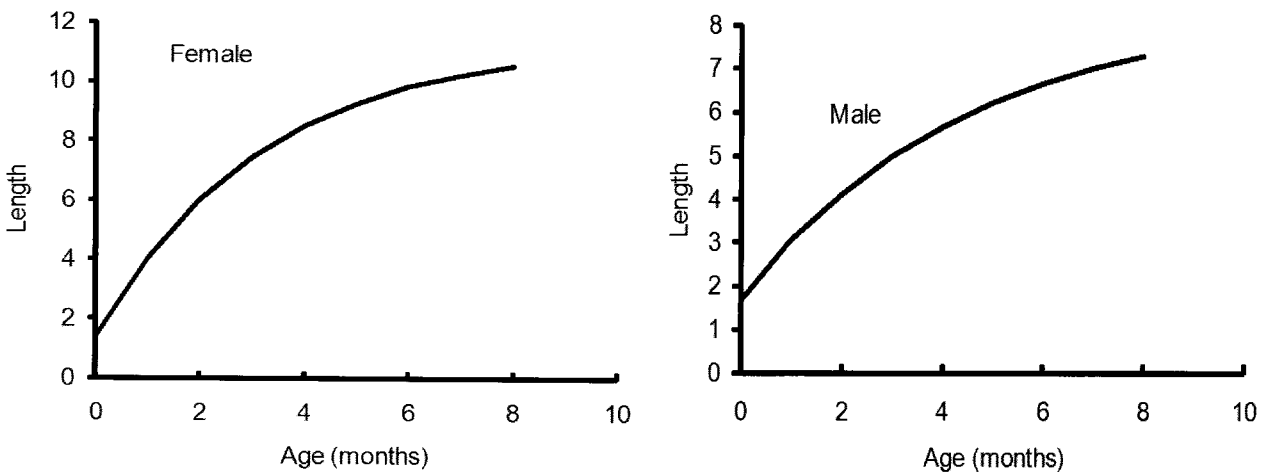


Fig. 4. Growth curves of female and male *P. serrifer*.

ended in September (Fig. 5). Laboratory observations showed that females carrying embryos almost ready to hatch also had ovaries filled with large vitellogenic oocytes, demonstrating that ovigerous females can spawn twice or more during the breeding season. After a brood of embryos hatched, the females molted within a day or two, after which the females spawned new broods. Ovarian development and embryonic development seemed to proceed simultaneously. Regression analysis of log-transformed variables demonstrated that reproductive output was significantly positively related to body size (Fig. 6), with regression equation $y = 2.7744x + 0.208$ $R^2 = 0.7961$. The slope of the equation is close to 3.0, which suggests an isometric relationship between carapace length and number of embryos ($P < 0.05$).

Embryo Volume and Recruitment Pattern

The mean embryo volume gradually increased as embryonic de-

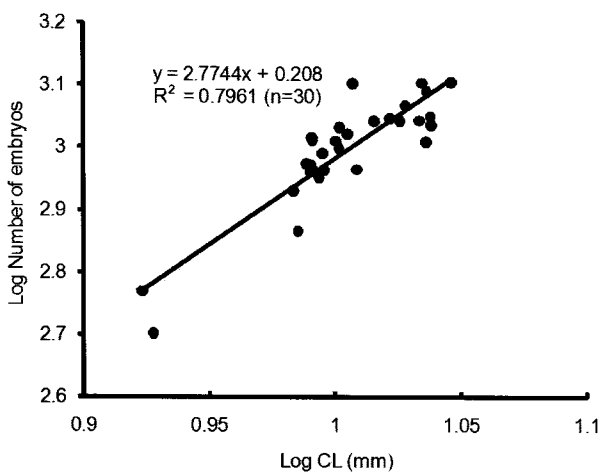


Fig. 5. Log-log plot of embryo number vs. carapace length in *P. serrifer*.

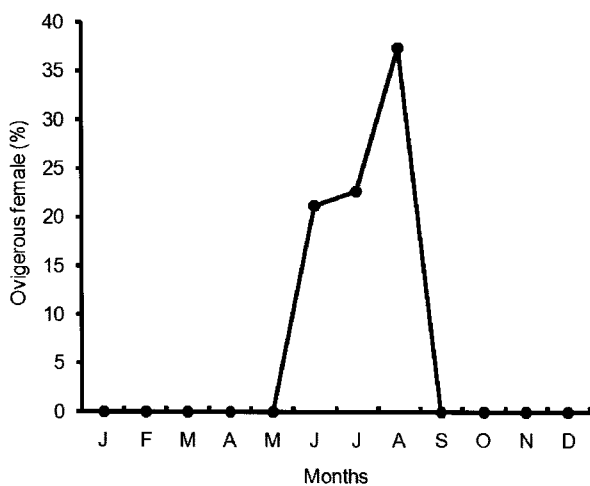


Fig. 6. Percentage of *P. serrifer* females ovigerous in each study month.

velopment progressed from stage 1 through stage 5 (Fig. 7). The increment of the embryo volume between stage 1 and 2 was comparatively small, but from the third stage to the fifth it increased steadily. Mean embryo volume differed significantly in different stages of embryonic development (analysis by ANOVA, $P < 0.001$). The recruitment pattern was seasonal, with juveniles appearing in September.

DISCUSSION

Sex Ratio and Size Frequency Distribution and Growth

The sex ratio fluctuated dramatically, but was almost equal during the breeding period. The growth rate of *P. serrifer* females was higher than that of males, which indicates lower energy investment in growth for males than females. Those results were concordant with studies of other *Palaemon* species (Berglund 1981, Guerao et al. 1994). There was little difference in the K values of females and males, indicating that females are larger and grow a little faster than males.

Breeding Period

Females of *P. serrifer* with mature ovaries indicative of imminent spawning were only found from June to August, which indicates that breeding is seasonal. Mature females displayed simultaneous cycles of ovarian and embryonic development, and each female apparently spawned twice or more in a breeding period. Females carrying their first brood of embryos displayed evidence of maturing ovaries when their embryos were ready to hatch, and laboratory experiments also suggested that after a brood hatched, the females performed a parturial molt and produced a new brood. This pattern is also common in other *Palaemon* spp. (Guerao et al. 1994, Guerao and Ribera 1995, Kim and Hong 2004).

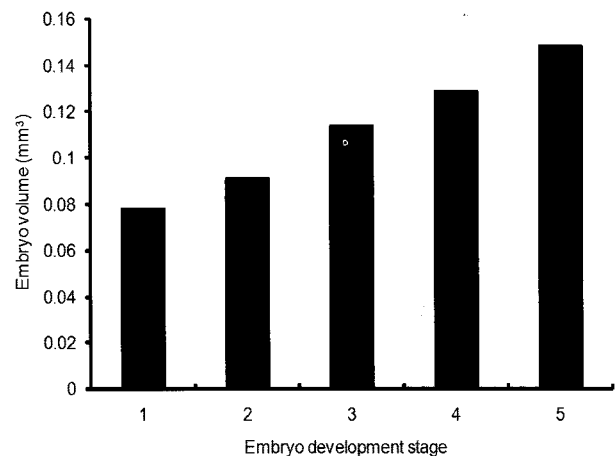


Fig. 7. Mean *P. serrifer* embryo volume in each developmental stage.

Water temperature is a proximate factor affecting spawning patterns of caridean shrimps (Kikuchi 1962, Allen 1966, Bauer 1992a). In this study, the number of ovigerous females and mature ovaries was positively correlated with water temperature, which is a common pattern among carideans (Bauer 1992a, Kim and Hong 2004). However, several species, such as *Spirontocaris* spp., *Pontophilus spinosus* Letch, 1815 and *Caridion gordonii* Bate, 1858 (Allen 1966), display a different pattern, spawning in winter (November or December) and hatching in spring. Thus, the hypothesis proposed by Orton (1920), Thorson (1950), and Bauer (1992a) that water temperature is a crucial factor driving the breeding process appears to be supported for *Palaemon serrifer* inhabiting warm temperate waters.

Reproductive Output and Fecundity

The relationship between brood size and female size (carapace length) suggests selective pressure operating on reproductive output in this species (Reaka 1979, Hines 1982, Bauer 1991). This allometric relationship can be generally expressed by linear regression of brood size and female size. Gould (1966) suggested that brood size is a simple volumetric function of female size, and decapod species generally display isometric relationships between female size and brood size, although there are some exceptions (Hines 1982, Bauer 1991, Corey and Reid 1991). In *P. serrifer*, the relationship between brood size and female size was isometric (Jensen 1958). The total reproductive output of *P. serrifer* is relatively low. Variation in reproductive output among crustacean species is affected by differences of the female body size. However, egg size, latitudinal, seasonal variation (Boddeke 1982), and habitat adaptation (Mantelatto and Fransozo 1997) may also influence reproductive output. Clarke et al. (1991) found that reproductive output in *Pandalus borealis* Krøyer, 1838 differs from site to site, but is not correlated with either latitude or embryo size. Restriction of reproductive output by female carapace length would result in determination of embryo size.

Embryo Volume and Recruitment

Selection acts on embryo size over evolutionary time scales via the effects of feeding conditions experienced by newly-hatched young, whereas female investment is dictated by feeding conditions experienced by the adult as her ovary matures (Clarke et al. 1985). Embryo size is a primary characteristic determining other life history traits. Reproductive patterns and life history traits can be determined by the mode of energy allocation to either single embryos or broods (Vance 1973a, 1973b, Christiansen and Fenchel 1979, Clarke 1993). *P. serrifer* retains a relatively small embryo volume (0.078 mm³) compared to other palaemonid spp. such as

Palaemon northropi Rankin, 1898 (0.200 mm³), *Palaemonetes intermedius* Holthuis, 1949 (0.294 mm³), and *Leander tenuicornis* Say, 1818 (0.163 mm³) (see Corey and Reid 1991). Recruitment was periodic and seasonal, and showed patterns similar to those of other palaemonid shrimps (Kim and Hong 2004).

In conclusion, the trade-off between growth and reproduction is a common phenomenon in crustaceans (Hartnoll 1985). *P. serrifer* grows fast, reaches maturity early, and is iteroparous, all of which are predicted for r-selected species. Consequently, *P. serrifer* invests large amount of energy initially in growth, and then allocates the rest of its energy to reproduction.

ACKNOWLEDGMENTS

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