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Reproductive Pattern of the Epifaunal Amphipod *Pontogeneia rostrata* (Crustacea) on Dolsando Sandy Shore in Korea

Ok Hwan Yu^{1*}, Seung Jin Jeong², and Hae-Lip Suh³

¹Marine Living Resources Research Department, KORDI, Ansan P.O. Box 29, Seoul 425-600, Korea ²Department of Biology, Pusan National University, Busan 609-735, Korea ³Department of Oceanography, Chonnam National University, Gwangju 500-757, Korea

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Abstract - Reproductive patterns of an epifaunal amphipod, Pontogeneia rostrata, were studied on Dolsando sandy shore in Korea. The life history pattern was iteroparous, with recruitment mainly occurring from winter to spring. The sex ratio was malebiased, especially during breeding periods. The mean body length of females was significantly larger than that of males. Brood size and egg volume were positively related to the body length of ovigerous females. There was no significant difference in brood size between successive breeding periods, but egg volumes were significantly higher in early winter (December) than in late spring breeding (May and June), increasing the probability of survival to hatching. These traits contribute to more reproductive potential in early winter than in late spring breeding. The mean brood size of epifaunal P. rostrata was larger but the mean egg volume smaller than that of infaunal amphipods in this sampling area. We suggest that reproductive effort for epifaunal species may be proportionally greater than for infaunal species in risky environments.

Key words – *Pontogeneia rostrata*, life history, reproduction, epifaunal amphipod, sandy shore, recruitment, free-swimmer

1. Introduction

The eusiroid amphipod *Pontogeneia rostrata* Gurjanova, 1938 is an epifaunal nestler that occurs mainly along the west and east coasts of the North Pacific Ocean (Kim 1991; Hirayama 1985), and is distributed widely from warm temperate to arctic waters at depths of 0-220 m (Barnard and Karaman 1991). In the sandy shore surf zone of Dolsando,

*Corresponding author. E-mail: ohyu@kordi.re.kr

an island in the southern part of South Korea, *P. rostrata* is one of the most dominant amphipods and migrates according to diel and tidal rhythms with a maximum density on the bottom at a depth of 1 m (Suh and Yu 1997). As *P. rostrata* is a dominant epifauna in the sandy shore, it may play an important role in energy flow of the habitat. Thus, the understanding of its spatial distribution, biomass, and reproduction is fundamental in extending our knowledge of its share in energy distribution. However, little information is available concerning the reproductive biology and population dynamics of this species.

Sainte-Marie (1991) reviewed the life history traits of gammaridean amphipods having various lifestyles. Eusiroid amphipods have few broods, large eggs, and a low reproductive potential, reflecting a greater mortality risk for adults from predation. Eusiroid amphipods also exhibit an epibenthic or suprabenthic lifestyle and produce the largest eggs relative to body size. Reproductive patterns generally appear to be more specific within amphipod family groupings because of their habitat specificity (Nelson 1980). Water temperature is believed to be most responsible for this variation in life history traits. Reproductive effort in the eusiroid Calliopius laeviusculus (Krøyer 1838) tends to be greater in polar than in boreal or temperate populations (Steele and Steele 1975). Studies of the reproductive biology in eusiroid amphipods are restricted to cold regions (reviewed by Sainte-Marie 1991) and have not been undertaken in warm temperate waters. We hypothesized that reproductive patterns differ between cold and warm temperate regions. The aim of this

study is to analyze the reproductive biology of P. rostrata on a warm temperate sandy shore and to compare the results to data on amphipods with various lifestyles.

2. Materials and Methods

Specimens of Pontogeneia rostrata were collected monthly from July 1996 to June 1997, from the bottom (1 m depth) at spring tide low water situated on Dolsando (34°37'39", 127°47'44"E) in southern Korea. A detailed description of environmental characteristics of Dolsando has been given elsewhere (Suh and Koo 1997). Annual water temperature and salinity ranged from 5.3 °C to 26.2 °C and from 32.6 to 34.8 psu, respectively. Five replicate samples were taken with a sledge net $(12 \times 30 \text{ cm opening}, 330 \text{-}\mu\text{m})$ mesh) over a distance of 20 m parallel to the shoreline at a speed of approximately 1 m s⁻¹. A sledge net with a chain was modified to collect the nestling and shallow burrowing species (Suh et al. 1995). Samples were fixed immediately in 5% buffered formalin in seawater.

Specimens were sorted and counted under a dissecting microscope in the laboratory. Using an image analysis system (Image Pro Plus 2.0), the curved dorsal outline of the amphipod was measured from the tip of the rostrum to the end of the telson. All species were sexed and divided into four categories: juveniles, males, females, and ovigerous females with eggs or juveniles (Donn and Croker 1986).

Reproductive output was estimated by the ratio of brood volume (brood size \times egg volume) to female body length (Sainte-Marie 1991). Egg volumes were treated as ellipsoids and were quantified by the formula

 $V = 4/3\pi r_1 r_2^2$

where r_1 is half of the longest dimension of the egg, and r_2 is half of the broadest dimension perpendicular to r_1 .

Prior to statistical analysis, the data were tested for homoscedacity and normality by Bartlett's test (Statistica version 5.1, Statsoft Inc., 1984-1996). Normally distributed data were tested with parametric methods; otherwise nonparametric methods were used. Abundance data were analyzed for significant temporal variability by one-way analysis of variance (ANOVA; SPSS version 8.0, SPSS Inc., 1997). Differences in density between adjacent sampling periods were tested by Scheffé post hoc comparisons. We used a χ^2 test to ascertain differences in the occurrence of males and females. Size differences between males and females

were assessed using the Kolmogorov-Smirnov two-sample test. Differences in egg volume between seasons and developmental stages were tested with two-way ANOVA. The relationships of brood size or of egg volume against body length were determined by the equation.

 $\log y = a + b \log x$

where y is the brood size (number of embryos per brood) or the egg volume (mm³), x the body length (mm) of ovigerous females, a the intercept of the equation, and b the slope. To determine whether differences in the slope occurred between two breeding seasons, analysis of covariance (ANCOVA) was used to compare regression slopes and elevations (Zar 1984). To determine the relationship between brood size or egg volume and body length, only ovigerous females with stage I embryos were used (see Rajagopal et al. 1999). The determination of five egg developmental stages in ovigerous females was followed by that of Fish (1975).

3. Results

Annual variation in density

The population density of P. rostrata varied significantly throughout the year (Kruskal-Wallis test; H = 53.38, P <0.001; Fig. 1). Multiple comparisons revealed no significant difference in density between successive sampling months except for November to December (Tukey test, P < 0.05). Total population densities ranged from 22.0 individuals m⁻² in March to 0.03 individual m⁻² in November. Juveniles constituted the major proportion (>50% of the total

10.0 0.0 I 2Aug 12Sep 25Oct 27Nov 13Dec 24Jan 24Feb 24Apr 20Mav 2Jul 24Mar 19Jun Fig. 1. Temporal variation in density of Pontogeneia rostrata. Aster indicates that a significant difference in density occurs between two adjacent months (P < 0.05, Tukey

test). Error bars show \pm SE.





Fig. 2. Proportion (%) of life stages of *Pontogeneia rostrata* during the sampling periods.

population) in all months. By contrast, adult individuals never accounted for more than 50% of the total population, except in July and May (Fig. 2). The frequency of juveniles increased monthly from August to December in 1996, but decreased from March to May in 1997. The largest proportion of ovigerous females, more than 6% of the total population, occurred in June, but this group comprised less than 3% of the total population in most sampling periods (Fig. 2).

Recruitment

Pontogeneia rostrata showed two annual peak periods of breeding: the main breeding period extended from February to June, and a small breeding peak appeared in December (Fig. 1). Main recruitment events appear to occur from early winter to spring (Fig. 3). Most juveniles that hatched in early winter periods decreased during winter periods. Those surviving the winter began to reproduce in March, and most large individuals decreased after breeding. Cohorts born in the spring began to reproduce in early winter (Fig. 3).

All stages of amphipods occurred in December 1996 and from February to June 1997 (Table 1). *Pontogeneia rostrata* showed a bi-modal pattern of greater breeding periods: in December and from March to May. Population densities were very low between July and November 1996, and ovigerous females did not occur in these periods. The mean body length of juveniles, nonbreeding females, and males in July was 1.56 mm, 4.94 mm, and 4.53 mm, respectively, and their body lengths increased until October 1996 (Table 1). In December, the proportion of juveniles was high, more than 85%, and that of ovigerous females was 0.26%.



Fig. 3. Size-frequency distribution of *Pontogeneia rostrata* at Dolsando from July 1996 to June 1997. The distribution for each sampling period represents pooled data of five replicates.

Juveniles increased in the body length and the mean body length of ovigerous females was highest, 8.46 mm, in December. The proportion of males and nonbreeding females continued to increase during winter periods while that of juveniles decreased after early winter periods (Table 1). No ovigerous females appeared in January 1997. The proportion of newly hatched juveniles (<1.3 mm) increased to more than 88.8% of the total population in March 1997, but decreased in April and May 1997. The proportion of ovigerous females was less than 2% in March 1997. During April and May, the proportion of ovigerous females and males increased. In June, the proportion of juveniles increased to 50.63% of total population again while the proportions of the other stages were very low (Fig. 2). Yu, O.H. et al.

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Sex composition (%) Length (mm) Sex ratios Date Total Non-breeding Ovigerous Non-breeding Ovigerous Juveniles Males [m/(m+f)]Juveniles Males females femals females females 13 Jul 1996 25.0 25.0 50.0 0.0 0.33 4.5±0.0 4.9±1.8 4 _ _ 50.0 0.0 2 12 Aug 0.0 50.0 0.00 1.6 ± 0.0 _ 5 12 Sep 80.0 20.0 0.0 0.0 1.00 1.8±0.3 3.3±0.0 _ 12 25 Oct 50.0 25.0 25.0 0.0 0.50 2.1±0.4 4.8±0.6 5.3±1.5 27 Nov 100.0 0.0 0.0 0.0 1 13 Dec 85.5 9.6 4.7 0.3 0.66* 2.1±0.6 4.6±1.3 4.1±0.6 8.5±0.0 386 0.86** 24 Jan 1997 52.3 40.9 6.8 0.0 2.4±0.6 4.4 ± 0.8 4.3±0.6 44 _ 24 Feb 52.1 25.0 18.8 4.2 0.52 2.4±0.7 5.2±1.7 5.8±2.2 7.7±0.3 48 24 Mar 88.8 6.4 3.3 1.5 0.57 2.2±0.4 5.1±1.5 5.4±1.5 7.9±1.1 661 24 Apr 63.9 17.8 18.2 0.2 0.49 2.5±0.7 4.2 ± 1.0 4.3±1.1 8.3±0.0 584 20 May 47.3 31.8 18.6 2.3 0.60 2.4±0.7 4.1±1.2 4.3±1.1 8.4±1.5 129 16 Jun 50.6 23.3 17.6 8.5 0.47 1.9±0.6 4.3±1.0 3.9±0.9 5.9±0.9 318

Table 1. Monthly population composition and length of Pontogeneia rostrata. The χ^2 statistics are significant (*, P < 0.05; **, P < 0.01)

Length = mean±SD

Sex ratio

The sex ratio (male/[male + female]) was >0.5 during the breeding periods (Table 1). The lowest sex ratio (0.33) occurred in July 1996. Males were more abundant than females in December and January, whereas in June and July, the abundance of females was higher than that of males (Table 1). Overall during the study period, the total number of males was higher than that of females ($\chi^2=18.47$, *d.f.=7*, *P*<0.01).

Size of stages

The maximum body lengths of females and males were 10.10 mm and 9.43 mm, respectively. Males and females were distinguishable when the body length was larger than 2.3 mm. The smallest and largest breeding females were 4.86 mm and 10.10 mm in length, respectively. Most ovigerous females were between 5.57 mm (lower quartile) and 7.92 mm (higher quartile). The average body length of females and males was 4.72 ± 1.48 mm (SD) and 4.39 ± 1.17 mm (SD), respectively, and the body length of females was larger than that of males (Kolmogorov-Smirnov test, d=0.11, P<0.05). After March, there was a decrease in the body length of males (Kolmogorov-Smirnov test, d=0.34, P<0.01) and nonbreeding females (Kolmogorov-Smirnov test, d=0.34).

Fecundity

There was a significant relationship between the brood sizes and body length of stage I egg-bearing females (Student's



Fig. 4. Seasonal variation of body length (mean ± SE) of males (A), non-breeding females (B) and ovigerous females (C) of *Pontogeneia rostrata*.

t-test; t = 6.53, P < 0.001), and the correlation coefficient (r^2) was high at 0.87 (P < 0.05) (Fig. 5). A positive linear



Fig. 5. The relationship between stage I brood size (y) and body length (x) of *Pontogeneia rostrata*: $\log y = -1.43 + 3.20 \log x (r^2 = 0.87, p < 0.05, n = 16).$

relationship was found between the female body length (*x* in mm) and the numbers of stage I eggs (*y*): log $y = -1.43 + 3.20 \log x$ (n = 16). The number of stage I eggs decreased with decreasing body length of ovigerous females from March to June 1997 (ANOVA, F = 3.87, df = 2, 12, P < 0.05). The mean brood size of ovigerous females was 36.50 ± 33.23 (SD) in March and 12.90 ± 7.82 (SD) in June. The maximum brood size of *Pontogeneia rostrata* in the study was 60 and the mean brood size was 18.38 ± 15.40 (SD).

Egg volume

There was a positive relationship between the volume of stage I eggs and the length of ovigerous females (t = 3.06, P < 0.01; Fig. 6). The egg volume (y in mm³) and body length (x in mm) were related by the following equation: $\log y = -2.54 + 1.04 \log x$ (n = 24). There was no significant relationship between egg volume and brood size (ANOVA,



Fig. 6. The relationship between egg volume (mm³) (y) and body length (x) of *Pontogeneia rostrata*: log y = -2.54 + 1.04log x (r² = 0.55, p < 0.01, n = 24).



Fig. 7. Seasonal variation of egg volume (mm³) of *Pontogeneia rostrata* during breeding months.

F = 0.22, d.f. = 1, 22, P > 0.6), but mean egg volume was typically large in the case of both large body length and brood size.

The mean volume of stage I eggs at laying varied seasonally (Fig. 7) and differed between months (Kruskal-Wallis test, H = 115.68, P < 0.001). During the winter, mean egg volume ranged from 0.03 to 0.04 mm³, but suddenly decreased to 0.01 mm³ in May and June 1997. There was a difference in mean egg volume between the two periods (Mann-Whitney *U*-test, H = 112.04, P < 0.001).

Egg volume increased with development from stage to stage (ANOVA, F=79.83, df=2, 128, P<0.001). Egg volume increased from 0.02 mm³ at egg stage II to 0.03 mm³ at egg stage V (Scheffé test, P < 0.001). The increase in egg volume was large in the latter stages of egg maturation.

4. Discussion

Several studies revealed that the highest density of amphipods was related to the recruitment of species (Sudo and Azeta 1996; Gouvis *et al.* 1997; Kevrekidis 1997; Beare and Moore 1998a). In Fig. 2, fluctuations in the density of juveniles of *P. rostrata* exhibited a pattern similar to those in the total population, indicating that recruitment was the factor determining total population abundance. In general, eusiroid amphipods are epibenthic and powerful free-swimmers (reviewed by Sainte-Marie 1991). Epifaunal amphipod species have been shown to be generally more subject to mortality due to predation than infaunal species in soft-bottom habitats (Nelson 1979). The swimming behavior of the amphipods decreased the population density in bottom (Sudo and Azeta 1996; Beare and Moore 1998b). In the sandy shore surf zone, *P. rostrata* is an epifaunal nestler and active swimmer (Suh and Yu 1997). The distribution of *P. rostrata* was affected by tidal and diel variation. In addition, *P. rostrata* showed a seasonal vertical movement from the bottom to the surface (Yu *et al.* 2002a). Thus, swimming behavior may increase exposure to predation in the water column, leading to an increase in mortality. After breeding, the adult population decreased and most of the population consisted of juveniles (Fig. 2). This may be due to the death of breeding individuals. Thus, as a consequence of predation and the death of breeding individuals, the heavy mortality of the population may also be a principal factor regulating the population density.

Although the interpretation of the life cycle is less convincing, the life cycle of *P. rostrata* may be one year because large adults did not occur after the spring breeding period. A similar pattern showed in *P. rostrata* on a seagrass bed (Jeong 2007). Ovigerous females occurred from February to June. Subsequently, the proportion of juveniles was lower in summer than in other seasons. This result indicates that *P. rostrata* in a sandy shore does not show year-round breeding activity.

In this study, the sex ratio of *Pontogeneia rostrata* was more strongly male-biased than the female-biased ratios reported for other gammarideans (Fincham 1971; Moore 1981; Beare and Moore 1996, 1998b; Sudo and Azeta 1996). Although the mechanisms generating male-biased sex ratios are not known, some advantages to populations of a male-biased sex ratio may be obvious. In gammarideans, mating almost certainly involves the male engaging in amplexus with the female by grasping her with his gnathopods. Males of *P. rostrata* have long second antennae with sensory organs for receiving female pheromones. During breeding periods, a larger number of males may increase the chances of encountering females, thus increasing breeding success.

The life history patterns of amphipods markedly differ according to geographic region; amphipods in cold water are characterized by univoltinism, large body size, large longevity, large embryos, and small brood sizes (Steele and Steele 1975; Sainte-Marie 1991). The opposite set of traits tends to typify warm-water populations. At a body length of 10.1 mm, ovigerous female *P. rostrata* showed a maximum brood size of 60. This value was much higher than those reported for *Pontogeneia* species living in cold regions (reviewed by Sainte-Marie 1991). Van Dolah and Bird

(1980) presented evidence that the brood size of amphipods increases from high to low latitudes. Thus, the higher brood size and smaller egg volume of *P. rostrata* in warm temperature zones than in colder regions may result from its short life span due to higher temperatures. Also, the reproductive potential of *P. rostrata* in this region may be much greater than in cold regions because of the larger brood size and shorter life span.

In the same size group and geographic region, epifaunal amphipods have substantially larger brood sizes and smaller egg sizes than infaunal species (Nelson 1980; Van Dolah and Bird 1980). In this study, the mean brood size of Pontogeneia rostrata was 18. This is large compared to infaunal amphipods in this sampling area. For example, the brood size of Synchelidium lenorostralum Hirayama, 1986 and S. trioostegitum Jo, 1990 was 14 and 4.9, respectively (Yu et al. 2002b; Yu and Suh 2006). Moreover, mean egg volume of *P. rostrata* (0.02 mm³) was smaller than that of the infaunal S. lenorostralum and S. trioostegitum in the same sampling area. Epifaunal amphipods are generally subject to greater mortality due to predation than infaunal species in at least one habitat examined (Nelson 1979). Producing small eggs increases the number of eggs that a female can brood at one time (Steele and Steele 1975). This can be advantageous when the risk of adult and/or juvenile mortality is high (Price 1974; Van Dolah and Bird 1980). Moreover, greater reproductive effort is indicated by the greater brood size per unit body length of epifaunal versus infaunal species (Nelson 1980). P. rostrata is a powerful free swimmer (Suh and Yu 1997; Yu et al. 1998) that encounters a high-risk environment. Therefore, reproductive effort for epifaunal species may be proportionally greater than for infaunal species in risky environments.

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