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# MATING BEHAVIOR AND SPAWNING OF THE BANDED CORAL SHRIMP *STENOPUS HISPIDUS* IN THE LABORATORY

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ABSTRACT

Mating behavior and relative fecundity, egg weight, and egg volume were investigated in the banded coral shrimp *Stenopus hispidus*. The effect of fluctuating temperature (4–6°C and 1.5–2°C difference between day and night) on fecundity was also tested. The relative fecundity was 1,229 ± 467 (mean ± SD) eggs/brood/g of female (wet body weight, WBW); egg volume was 0.0628 ± 0.0050 $mm^3$ (mean ± SD); and dry egg weight was 35.1 ± 2.9 μg/egg (mean ± SD). Linear relationship between total length of the shrimp and relative fecundity was significant ($P = 0.01$), and there was a significant negative relationship between egg volume and relative fecundity ($P = 0.03$). High temperature fluctuation (4–6°C) resulted in lower dry egg weight ($P = 0.0079$).

Mating behavior in *Stenopus hispidus* is described for the first time. It occurs in the following sequence: antennule contact, erection of female body, grasping, mating, and spawning. Females can mate successfully within 24 h after molting.

Cleaner shrimps remove and consume parasites, injured tissue, and possibly considerable food particles from fishes, such as the white-spotted moray and blue tang in coral reef systems (Limbaugh *et al.*, 1961; Jonasson, 1987), and thus play a vital role in the system. Because of their colorful body and the relative ease with which they can be maintained in a marine aquarium environment, adult cleaner shrimps are popular in the marine aquarium industry. However, removal of cleaner shrimps from the natural environment will result in a reduction of reef fish abundance and a high incidence of fishes with frayed fins and ulcerated sores (Limbaugh *et al.*, 1961; Glynn, 1983).

The banded coral shrimp is one of the most popular cleaner shrimps among aquarists due to its strikingly colorful body. It is distributed throughout the Indo-Pacific region from the Red Sea and South Africa to the Hawaiian and Tuamotu Islands. In the western Atlantic, it is found from Bermuda and off the coast of North Carolina, Gulf of Mexico, and south Florida to the north coast of South America (Holthuis, 1946; Kruczynski and Jenner, 1969; Lukens, 1978). Pairs have been observed in shallow water where fishes are abundant. It usually occurs at depths of 2–4 m (Limbaugh *et al.*, 1961). Most studies have concentrated on its distribution, cleaning (Limbaugh *et al.*, 1961; Jonasson, 1987), and pairing behaviors (Johnson, 1969, 1977). Little information on its reproductive biology has been reported. After the female molts, she usually mates with the paired male, and a mass of eggs is deposited on the swimmerets under the abdomen (spawning). The eggs first appear as a greenish mass and gradually become transparent with darkly pigmented eyes. The larvae hatch about 16 days later at 28°C (Young, 1979).

Temperature is one environmental factor that affects reproduction of crustaceans. Many studies have been conducted on the relationship between temperature and egg production in copepods (e.g., Runge, 1984: Hirche, 1990, 1997; White and Roman, 1992), and to a much lesser extent in decapods. The studies have mainly focused on the influence of temperature on egg quality, such as biochemical composition (Efford, 1969; Clark *et al.*, 1991; Clark and Gore, 1992; Clarke, 1993).

In the present paper, we characterize and test the effects of temperature on the major reproductive parameters of *Stenopus hispidus* (Olivier), including fecundity and egg size, and describe for the first time mating behavior and spawning in the laboratory.

## MATERIALS AND METHODS

The study was conducted at the Harbor Branch Oceanographic Institution, Inc., U.S.A., between July and October, 1996.

*Ovigerous female.*—Males and ovigerous females were purchased from local pet shops (collected from the wild 1–2 days prior to our purchase) and maintained in a recirculating sea-water system under 14 h light : 10 h dark. Two fluctuating temperature regimes (4–6°C and 1.5–2°C difference between day and night) were used to test the

Table 1. Standard deviation (SD) and range (Max = maximum, Min = minimum) of egg volume (EV, $mm^3$), egg dry weight (EDW, µg), and relative fecundity (RF, egg/brood/g WBW) of the 30 *Stenopus hispidus* examined.

| | Mean | SD | MAX | Min |
|---|---|---|---|---|
| EV | 0.0628 | 0.0050 | 0.0742 | 0.0545 |
| EDW | 35.1 | 2.9 | 42 | 30 |
| RF | 1,229 | 467 | 2,320 | 409 |
| TL | 4.3 | 0.4 | 3.2 | 4.8 |
| WBW | 1.36 | 0.32 | 0.52 | 2.09 |

effect of temperature on fecundity and egg size. Each pair (1 female and 1 male) was cultured in 25-l plastic tanks in a greenhouse or in 75-l tanks inside a temperature controlled room (indoors). In the greenhouse, water temperature fluctuated 4–6°C day and night (between 26 and 32°C during the 3-month study period); in the indoor tanks temperature fluctuated from 1.5–2°C day and night (between 26 and 29.5°C during the 3-month study period). Due to evaporation, the salinity in the greenhouse tanks (33–35 ppt) was higher than that in the indoor tanks (28–30 ppt) during the 3-month study period. The shrimps were fed in excess with frozen *Artemia* or squid once a day. Thirty pairs of shrimp were used for the study.

*Fecundity.*—The following parameters were measured: relative fecundity (egg weight/wet body weight (WBW) of the spawned female), total length (TL) from the end of telson to the tip of rostrum of a berried female, egg size, dry weight of the egg mass, and dry weight per egg. About 24 h after spawning, the complete egg mass was removed gently from each female with small forceps, dried on blotting paper, and air dried for 10 min before being weighed using a digital balance. Dry egg mass was estimated by removing 100 eggs, and drying them at 70°C for 48 h. The rest of the eggs were dried at the same time. Mean dry weight per egg was calculated. Diameters of 30 eggs randomly selected were measured under a microscope with an ocular micrometer. Egg volume was calculated from egg diameters using the formula $V = 1/6(\pi d^3)$ for spherical eggs, where d is the egg diameter; the formula $V = 1/6(\pi d1 \times d2^2)$ for prolate spheroids, where d1 is the least diameter and d2 is the greatest diameter.

The spawned female was dried on blotting paper, its TL (to the nearest 1 mm) and WBW (to the nearest 0.0001 g) were measured.

*Mating Behavior.*—Females that were about to hatch were moved to individual 270-l conical fiberglass tanks equipped with an internal standpipe with 53-µm mesh. Eight to 10 h (around 0800) after a female had hatched and molted, it was taken to a tank with the original male for observation of mating behavior. Water temperature was 26–28°C. Photographs were taken using a 35-mm camera with a standard 50-mm lens. Soon after mating, 3 females were observed under a dissecting microscope for the presence of spermatophores. To determine how long after the molting females can still mate successfully, the females were separated from the paired males immediately after molting for 12 h (5 pairs), 24 h (5 pairs), and 36 h (4 pairs) before being returned to the original males. Mating success (indicated by subsequent spawning) was assessed.

Student's *t*-test was used to compare the difference of means of relative fecundity, egg size, and dry egg weight, respectively, between those from the greenhouse and in-



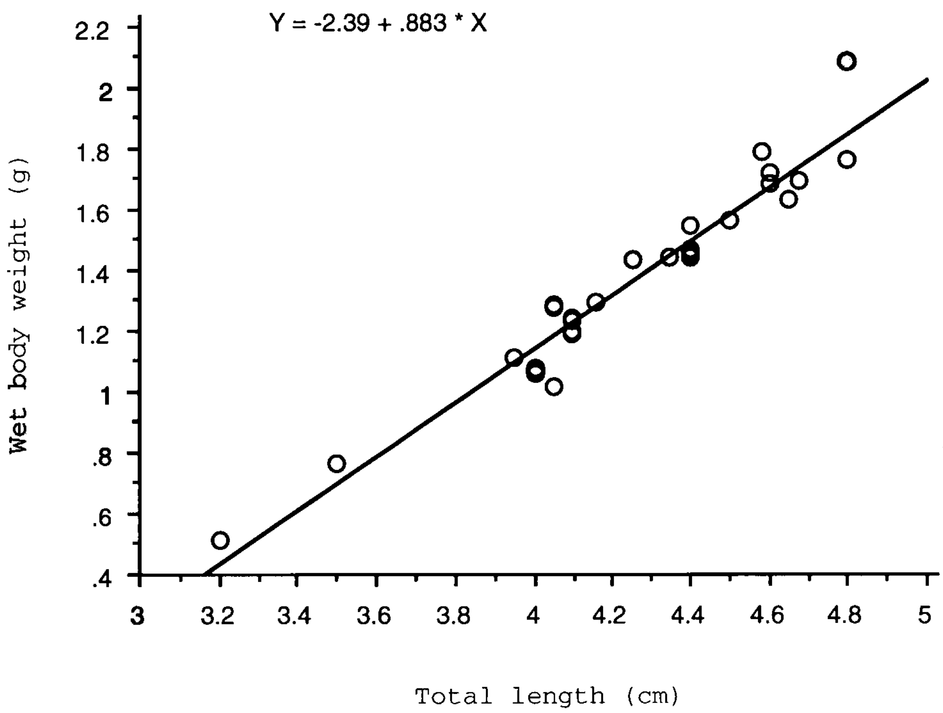


Fig. 1. Linear regression of total length (cm) on wet body weight (g) in the banded coral shrimp *Stenopus hispidus* ($P < 0.001$, $R^2 = 0.937$).

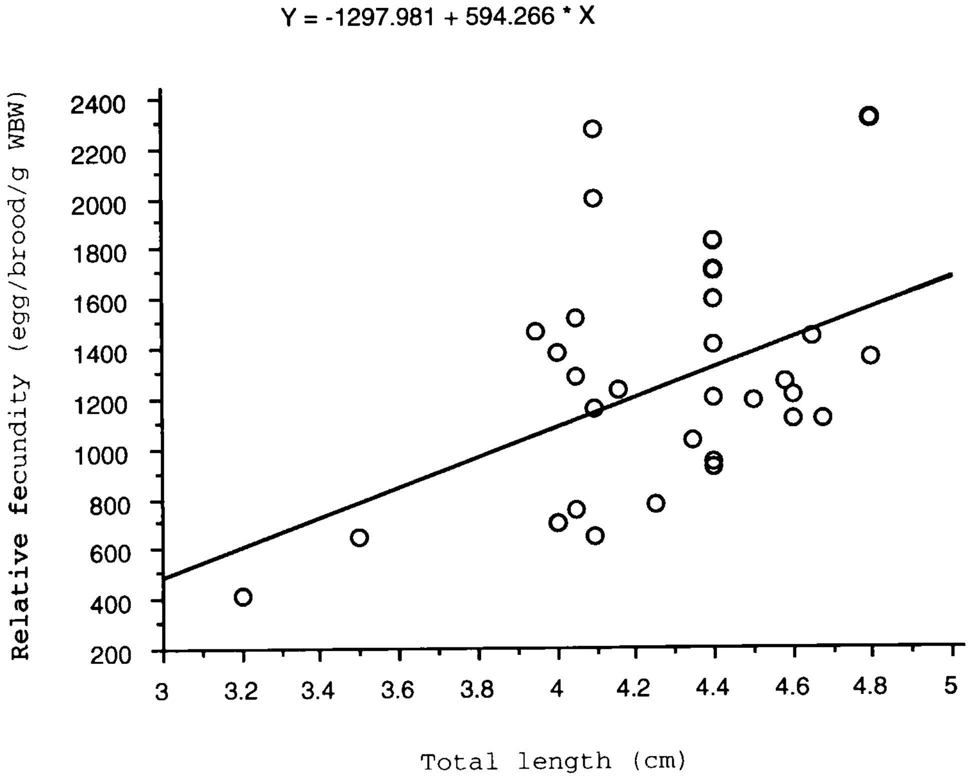


Fig. 2. Linear regression of total length (cm) on relative fecundity in the banded coral shrimp *Stenopus hispidus* ($P = 0.01$, $R^2 = 0.197$).

door tanks. Linear regression was used to correlate the relationships between the parameters.

## RESULTS

### Fecundity

Thirty-two data sets were collected from 30 females, of which three data sets were from one female over time. For this female, the first (3.2-cm TL), second (3.5-cm TL), and fifth (4.0-cm TL) spawning produced 211, 491, and 1,630 eggs, respectively. The average TL and WBW of the females used in the study was 4.3 ± 0.4 cm and 1.36 ± 0.32 g (mean ± SD), respectively (Table 1). A highly significant ($P < 0.001$) and strong linear relationship ($R^2 = 0.937$) existed between TL and WBW (Fig. 1). Relative fecundity (RF) varied substantially among the females. The average (and standard deviation) was 1,229 ± 467 eggs/brood/g WBW, (Table 1). There was a significant ($P = 0.01$), but weak relationship between RF and TL ($R^2 = 0.197$) (Fig. 2).

The egg is usually oval and the mean egg volume (EV) is 0.063 $mm^3$. There are large variations in EV within an egg batch. The average coefficient of variation in EV within an egg batch was 7.2 ± 2.7% (range 3.8–15.2%, $N = 32$). There was no significant relationship between EV and TL ($P = 0.683$), or between EV and WBW ($P = 0.739$). A significant ($P = 0.03$), but weak negative linear relationship ($R^2 = 0.146$) was found between EV and RF (Fig. 3).

Egg dry weight (EDW) was 35.1 ± 2.9 µg/egg (mean ± SD, range 30–42, $N = 32$) (Table 1). There was no significant relationship between EDW and TL ($P = 0.114$), EDW and WBW ($P = 0.074$), EDW and RF ($P = 0.557$), or EDW and EV ($P = 0.075$).

All parameters of the eggs from the indoor tanks tended to be higher than those from the greenhouse tanks. EV, EDW, and RF of the eggs from the greenhouse tanks were 0.0627 $mm^3$, 34.2 µg, and 1,198 eggs/brood/g WBW, respectively; compared to 0.0632 $mm^3$, 37.1 µg, and 1,307 eggs/brood/g WBW, respectively, from the indoor tanks. However, the difference is significant ($P = 0.0079$) only for EDW (Table 2).

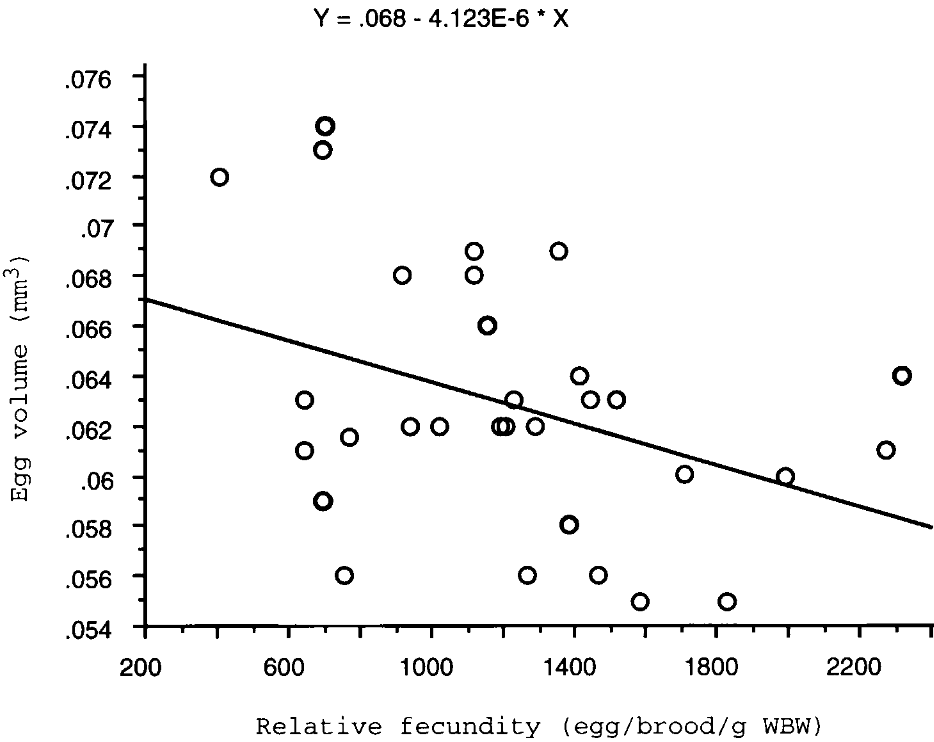


Fig. 3. Linear regression of relative fecundity on egg volume in the banded coral shrimp *Stenopus hispidus* ($P$ = 0.03, $R^2$ = 0.146).

## Mating Behavior

In general, a female molts between 2230 and 2400. Recently molted females with ripe ovaries are receptive to mating and attractive to males. *Stenopus hispidus* is a multiple brooder; the female carries both developing embryos and ovaries. Molting occurs hours to one day after hatching. Molting removes the attached egg membranes of hatched larvae and the few unhatched embryos.

Table 2. Comparison of mean egg volume (EV, $mm^3$), mean dry egg weight (EDW, μg), relative fecundity (RF, egg/brood/g WBW) of the *Stenopus hispidus* cultured in the greenhouse and in indoor tanks. The difference is significant ($P < 0.01$) only for EDW.

| | Mean | SD | MAX | Min | *N* |
|---|---|---|---|---|---|
| Greenhouse | | | | | |
| EV | 0.0627 | 0.0055 | 0.0742 | 0.0545 | 23 |
| EDW | 34.2 | 2.6 | 42 | 34 | 23 |
| RF | 1,198 | 486 | 2,270 | 409 | 23 |
| Indoors | | | | | |
| EV | 0.0632 | 0.0037 | 0.0563 | 0.0692 | 9 |
| EDW | 37.1** | 2.4 | 39 | 30 | 9 |
| RF | 1,307 | 432 | 2,320 | 770 | 9 |

The females are more attractive to the males within the first 24 h after molting and all matings at 12 h and 24 h after molting were successful. At 36 h after molting, only one out of four pairs mated successfully. Mating behavior can be divided into the following five discrete steps:

(1) Antennule contact: After the female was put into the observation tank, the male slowly approached the female. Then the male and female established attennule contact (Fig. 4) and at times the male and/or female gently waved their large claws (the third pair of walking legs) at each other (chelipeds surround; Johnson, 1969). This process lasted for 10 min to 6 h. The female was not always passive and sometimes resisted the approach of the male, but fighting rarely occurred.

(2) Erection of the female body. Following step 1, the female turned around with abdomen raised (Fig. 5).

(3) Grasping: Once the female stood with abdomen raised, the male rapidly approached the female, also with abdomen raised (Fig. 5). The male then held the female abdomen to abdomen.

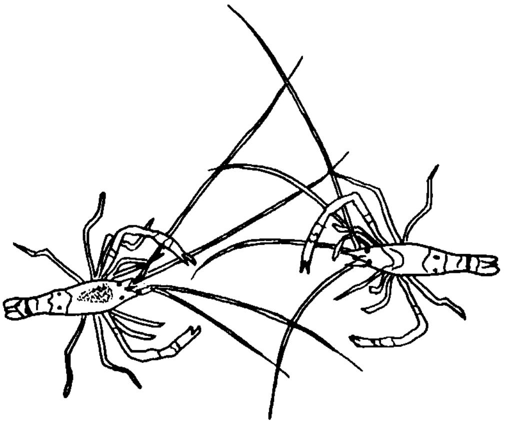

Fig. 4. Mating in *Stenopus hispidus*. Step 1: antennule contact (the male is on the right).

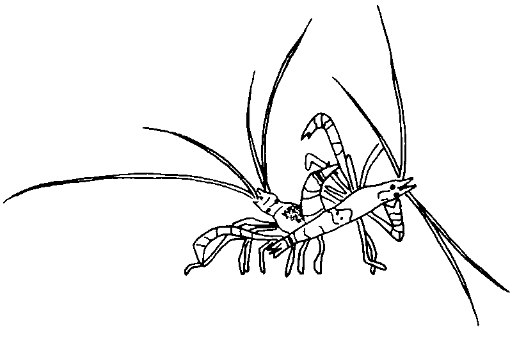

Fig. 6. Mating in *Stenopus hispidus*. Step 4: mating (the male is on the right).

(4) Mating: After grasping the female, the male turned rapidly (150–180°) to face the female abdomen to abdomen and head to tail (Fig. 6). Copulation then occurred, lasting for about 10 s.

(5) Spawning: After successful mating, the male left the female. The female began spawning in 15–25 min. The spawning lasted for about 10 min. On three occasions, the females were inspected for the presence of spermatophores after mating, and no spermatophores were found. These three females failed to spawn, but resumed spawning after the following molt and mating.

## Discussion

### Fecundity and Egg Size

In copepods, egg production increases linearly or exponentially with increasing temperature in a certain range (Runge, 1984; Hirche, 1990, 1997; White and Roman, 1992). Egg size is negatively correlated with temperature in the copepod *Pseudocalanus* (see McLaren, 1965). Egg size has also been found to be inversely correlated with water temperature in crabs (Efford, 1969; Amsler and George, 1984). In the present study, temperature fluctuation affected several parameters of the eggs. Egg size, egg dry weight, and relative fecundity were higher at a 1.5–2°C (26–29.5°C ) fluctuation than those at a fluctuating temperature of 4–6°C (between 26 and 32°C), but a significant effect was only found in egg dry weight (Table 2). Egg dry weight is significantly related to egg organic content in crustaceans (e.g., Clarke, 1993). Therefore, relatively constant (fluctuating between 1.5 and 2°C day and night) and lower temperature may improve energy accumulation in the eggs and increase brood size in the shrimp. Embryos of the crab *Callinectes sapidus* Rathbun spawned at 16°C have initially greater lipid levels than those spawned at 26°C (Amsler and George, 1984), and the mean brood size of *Ceriodaphnia dubia/affinis* (J. Richard and Lilljeborg) is somewhat larger at the lower temperature (Cowgill *et al.*, 1985).

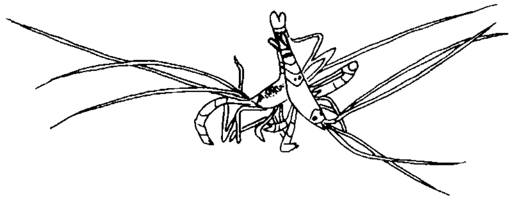

Fig. 5. Mating in *Stenopus hispidus*. Step 3: grasping (the male is on the right).

Salinity may affect ovarian development. Since the shrimp lives in a natural environment of 33–35 ppt, the salinity in the greenhouse tanks (33–35 ppt) may be better for ovarian maturation than that in the indoor tanks (28–30 ppt). However, the higher brood size and egg weight of females cultured in the indoor tanks show that temperature, rather than salinity, mainly affects ovarian development.

The positive relationship between fecundity and female size is consistent with observations made for other species of crustaceans (e.g., Hines, 1988; Corey and Reid, 1991; Carsen *et al.*, 1996; Stella *et al.*, 1996). Our study shows that TL is a good predictor of fecundity in *S. hispidus*.

The egg volume of crustacean species is

partly under genetic control (Raven, 1961). It shows a general pattern of interspecific variation that larger-sized species of crustaceans have larger eggs (e.g., Nelson, 1980; Corey, 1981; Luxmoore, 1982; Mauchline, 1988; Corey and Reid, 1991). Egg size also increases within a species with increasing adult size in some species (Clarke, 1993), but not in others (Hines, 1991). In the banded coral shrimp *S. hispidus*, the egg volume did not show a significant relationship ($P = 0.683$) with body size (TL). The other important factor influencing egg size is fecundity. A negative relationship between egg size and fecundity in shrimps within a genus has been found (Corey and Reid, 1991), but little is known, however, of intraspecific variation. Results presented here show that there is a significant ($P = 0.03$) negative relationship between egg volume and relative fecundity in *S. hispidus*. Higher fecundity with smaller eggs may be a pervasive phenomenon in crustaceans.

Larger eggs normally contain more yolk in invertebrates and fish (e.g., Strathmann and Vedder, 1977; Shakuntala and Reddy, 1982; Quattro and Weeks, 1991). This is considered to be linked with reproductive strategy (Herring, 1974). Weight of the dry egg mass is significantly correlated with egg volume in some species (e.g., Clarke, 1993). The present study shows that there was a relationship between dry egg weight and egg volume that approached significance ($P = 0.075$).

### Mating Behavior

The courtship behavior of *S. hispidus* during pairing has been described by Johnson (1969). It includes cleaning, antennae entwined, chelipeds surround, and dance. Dance was not observed in the present study.

In most shrimps, mating occurs soon after the female molts, when she is attracted to males for periods ranging from several hours to several days (see a review by Salmon, 1983). In the banded coral shrimp, the mating occurred successfully within 24 h after the female molted. At 36 h after molting the rate of successful mating decreased to 25%.

The basic pattern of mating in *S. hispidus* is the same as in other shrimps. In penaeid and many caridean species, the female is more passive, and the male holds the female and flexes his abdomen under that of the female (e.g., Bauer, 1976; Berg and Sandifer, 1984; Misamore and Browdy, 1996). In *S. hispidus*, after antennule contact, the female stands with abdomen raised, the male rapidly embraces the female abdomen to abdomen, then the male turns 150–180° to mate. The male does not bend around the body of the female. The courtship time ranges from 10 min to 6 h in the present study, probably depending upon the separation time of the female and male. *Stenopus hispidus* is territorial and found in male-female pairs in the natural environment (Limbaugh *et al.*, 1961). In the present study, because male and female shrimps were separated for 8–10 h before mating observations, a recognition time may be needed. The separation was necessary to conduct observation and photography during the daytime, since females generally molt at night. An identical mating pattern was observed one night for a pair of shrimps that were not separated; they mated about 2 h after the female molted (D. Zhang, personal observation).

In many crustacean species, especially in carideans, spermatophores are externally deposited and carried by the female until fertilization (Bauer, 1986; Subramoniam, 1991, for reviews). Stenopodid shrimps are on a similar level of sperm transfer complexity as that of carideans. Balss (1944) reported that a spermatophoric mass adheres to the ventral surface of the female. However, in our study, no spermatophore was found in the females of *S. hispidus* after mating. The spermatophore may be pushed into the genital pore of the female, and fertilization occurs internally as in the shrimp *Crangon crangon* (L.) (see Boddeke *et al.*, 1991). Future study is needed to investigate sperm transfer and storage.

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