

REPETITIVE COPULATION AND VARIABLE SUCCESS OF INSEMINATION IN THE MARINE SHRIMP *SICYONIA DORSALIS* (DECAPODA: PENAEOIDEA)

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A B S T R A C T

Copulation was observed in 18 of 25 mating pairs of *Sicyonia dorsalis* whose activities were recorded with a time-lapse video system, and mating behavior was described. Male success in inseminating females was determined by examination of female seminal receptacles for the presence of sperm. A male must copulate at least once from each side of the female in order to fill both seminal receptacles, but multiple copulations by the male on each side of the female were often observed. However, in several pairs, one of the two female receptacles remained empty in spite of often repeated copulations by the male on the unfilled side. In three pairs, the male copulated several times only on one side of the female, filling only the receptacle of that side. All females collected from the field which had mated previously had sperm in both seminal receptacles. One interpretation of these results is that in nature at least some females may mate with and be inseminated by more than one male. Multiple paternity might increase the genetic diversity of a female's spawns, which may enhance survival of dispersed planktonic larvae that settle in a mosaic or heterogeneous benthic environment.

Sexual behavior and mating systems of marine crustaceans have received increased attention in recent years (Hazlett, 1975; Wickler and Seibt, 1981; Ridley, 1983; Salmon, 1983; Atema, 1986; Caldwell, 1991; Diesel, 1991; Morin and Cohen, 1991; Shuster, 1991). However, basic information necessary for the analyses of sexual systems (such as pre- and postmating interactions between male and female, copulatory behavior, and success of insemination) is still sparse for most crustaceans, especially compared to that known for terrestrial vertebrates and arthropods (Parker, 1970; Trivers, 1972; Emlen and Oring, 1977; Borgia, 1979; Wittenberger, 1981; Thornhill and Alcock, 1983; Smith, 1984; Kirkpatrick, 1987). This is especially true of the dendrobranchiate shrimps, Penaeoidea and Sergestoidea, marine decapods that release eggs, fertilized just after spawning, into the water column for planktonic development.

Mating behavior and insemination in penaeid shrimps have been briefly described by De Saint-Brisson (1985), Brisson (1986), Hudinaga (1941), and Primavera (1979). Yano *et al.* (1988) have reported on mating in *Penaeus vannamei* in greater detail. Studies on the morphology of male and female genitalia of *Sicyonia* spp. have been performed by Heldt (1938), Pérez Farfante (1985), and Bauer (1986, 1991). Palombi (1939) first described copulation in a sicyo-

niid penaeoid, *Sicyonia carinata*. In this species, males were observed mating repeatedly with females with which they were paired. Bauer (1991) briefly characterized mating and patterns of insemination in *S. parri* and *S. laevigata*. Preliminary experiments on copulation in the latter pair of species indicated that males can inseminate only one of the paired seminal receptacles with a single copulation. In a few apparently "normal" copulations, insemination of the seminal receptacles did not occur, indicating variability of insemination success among males.

In this study, extended observations were made with time-lapse video on male/female pairs of *Sicyonia dorsalis* in order to (1) describe copulatory behavior, (2) determine if repetitive copulation occurs in this species, and (3) report on variation in male success in insemination of the female.

MATERIALS AND METHODS

Individuals of *Sicyonia dorsalis* were taken live in night trawls over sand/mud bottom on the north side of Horn Island, Mississippi, on 22 September, 14 November, and 14 December 1989. Shrimps were transported to the laboratory in plastic bags filled with ambient sea water that was saturated with oxygen. Females used in matings were isolated in plastic containers on a recirculating water table at a water temperature of 23–26°C and a salinity of 25–28 ppt. Mixed populations of males and females were maintained in recirculating aquaria under similar conditions of water temperature and salinity. Preliminary observations on the

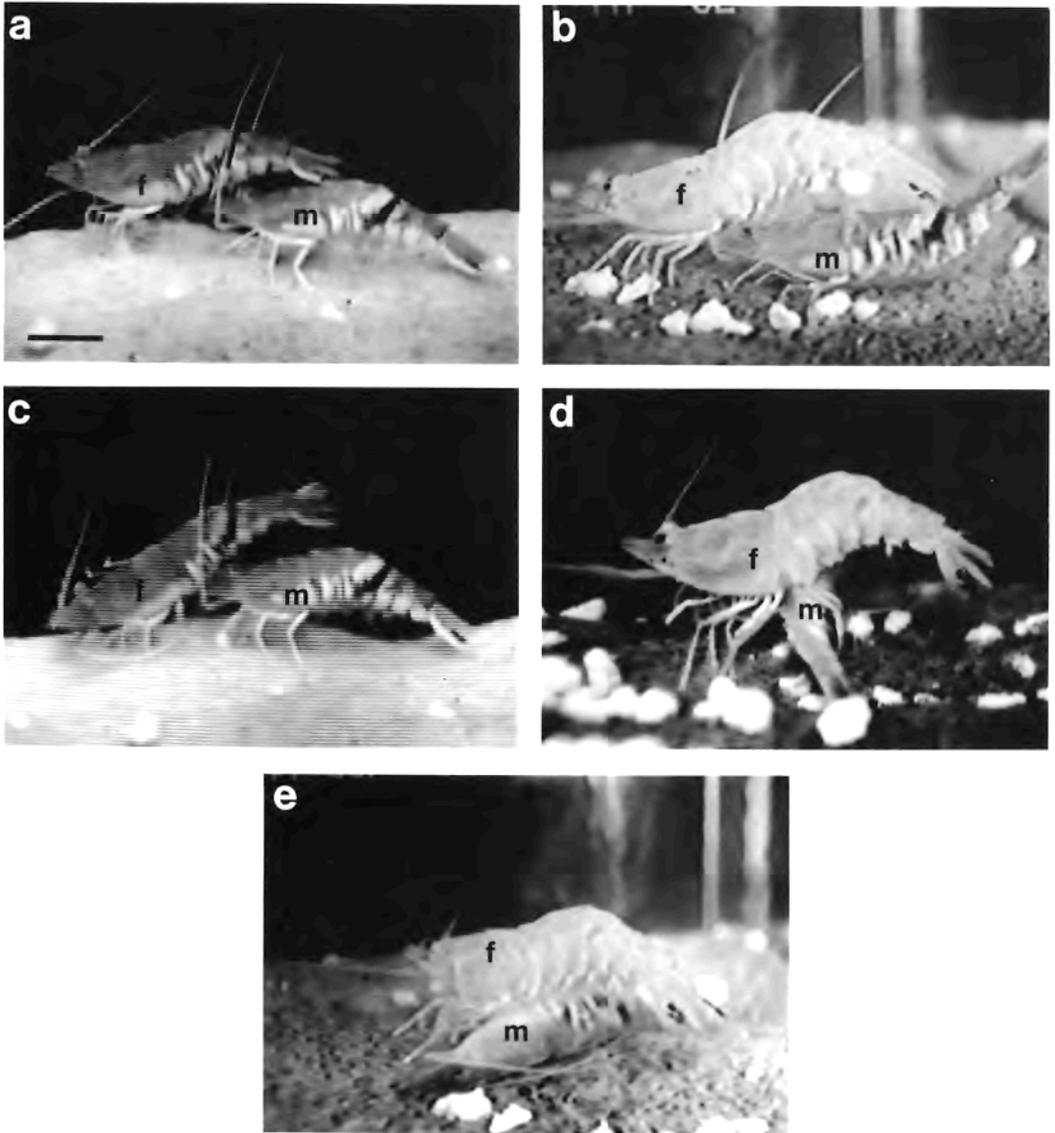


Fig. 1. Video images of mating and copulation in *Sicyonia dorsalis*; m = male, f = female. a, male follows female, with an antennal flagellum on each side of the female's abdomen; b, male probes female's genital area; c, female's body tilted upward by male; d, copulatory position, with male mating from female's right side, male body perpendicular to that of female; e, male copulating from left side of female, male body oblique to that of female. Scale bar in (a) represents 10.3 mm in (a), 9.3 mm in (b) and (d), 11.3 mm in (c), and 10.8 mm in (e).

mixed populations indicated that mating occurred after the female molt, as in *S. laevigata* and *S. parri* (see Bauer, 1991) and other penaeoid species with females storing sperm in seminal receptacles (e.g., Hudinaga, 1942; Pérez Farfante, 1969; De Saint-Brisson, 1985; Brisson, 1986; Primavera, 1979). Females were checked once a day for molting, at which time they are receptive to mating. Time between molting of the the female and its use in mating experiments varied from 1–5 days (1 day, $N = 16$; 2, 3, and 5 days, $N = 2$ each; 4 days, $N = 3$). Because isolated females were examined once a day, a given female could have molted at any time

from just after being observed up to just before being checked again. Thus, "1" day between molting of the female and its use in a mating observation could actually be from a few minutes to 1 full day, "2" days from 1–2 days, and so "n" days from $n - 1$ to n days.

A small aquarium (30 cm length \times 10 cm width \times 16.5 cm water depth) was used as a mating arena. Fine sand covered the bottom of the aquarium, and the sea water was aerated and heated. Temperature and salinity of aquarium water were kept within the same limits as those of water tables and aquaria that were used for maintaining males and females. A male and a female

Table 1. Number and pattern of copulations and success of insemination in 18 pairs of male and female *Sicyonia dorsalis* in which at least one copulation was recorded. The number of copulations with the male on the female's left and right side is given. Insemination is scored by the presence (+) or absence (-) of a sperm mass in the female's left and/or right seminal receptacle. The duration of observation of each pair by video time-lapse camera is given in hours. The time spent by the male in the copulatory position was measured for all copulations, and the median and range are given in seconds.

Pair number	Duration of observation (h)	Number of copulations		Presence of sperm in seminal receptacles		Duration of copulation (s)	
		Left side	Right side	Left side	Right side	Median	Range
1	18.0	0	9	-	+	3	3-5
2	14.8	7	0	-	-	5	1-9
3	16.5	5	0	-	-	7	2-11
4	18.5	7	1	-	-	6	3-9
5	16.5	1	2	-	-	3	1-5
6	14.0	3	3	-	-	6	3-9
7	20.5	4	1	-	-	12	9-15
8	20.0	6	4	-	+	3	1-5
9	19.5	7	22	-	+	10	3-46
10	17.0	8	5	-	+	17	7-93
11	0.5	1	1	-	+	5.5	5-6
12	18.0	5	1	-	+	3.5	2-8
13	24.5	7	8	+	+	5	2-13
14	22.0	7	5	+	+	6	2-13
15	23.0	9	6	+	+	6	2-28
16	22.0	2	3	+	+	11	5-27
17	17.2	13	7	+	+	8	1-47
18	24.0	1	1	-	-	7.5	7-8

were paired in the aquarium, which was isolated in a small room, and mating observations were recorded on videotape. Activities of the pair were observed and recorded through a 12.5-mm lens on a video camera attached to a time-lapse video cassette recorder. After being placed in the aquarium, mating pairs were taped at the 24 h time-lapse mode (5 pictures or fields/s) for a period of 14-25.4 h ($N = 4$, median = 18.5 h). Observations on one other mating pair, for which the pattern of insemination is reported, were terminated after the male had copulated once from each side of the female (duration of observation, 0.5 h; recorded at 60 fields/s). The male and female of all mating pairs were anesthetized by chilling and preserved in 10% sea-water Formalin at the end of the video observation period. The number of copulations, their duration, and the position of the male relative to the female during copulation were determined by viewing video recordings of mating pairs.

Insemination in females was determined by examination of their seminal receptacles. The area of the ventral cephalothorax with the seminal receptacles (Pérez Farfante, 1985; Bauer, 1991) was dissected out of females preserved in 10% sea-water Formalin. Presence or absence of sperm masses in the receptacles was observed with a stereomicroscope, using reflected light. The receptacles were also mounted on slides and examined with a compound microscope using transmitted light.

RESULTS

Description of Mating Behavior

Receptive, recently molted females did not noticeably interact with males placed

with them until mating behavior began. In a typical sequence, precopulatory behavior was initiated when the male and female made physical contact while moving about the aquarium. If the male was behind the female when first contact was made, it immediately began to push under the female with its cephalothorax. If first contact was made from any other position, the male moved behind the female before pushing below it. The male then followed behind the female, and grasped or contacted the female's abdomen with its long antennal flagella, which quivered or vibrated during this "following" behavior (Fig. 1a). During following behavior, the dorsal cephalic region of the male, with the rostrum, eyes, and antennules, touched and prodded the female's genital area or thelycum, where the apertures to the female's seminal receptacles are located (Fig. 1b). Next, the male pushed upwards, tilting the female's body forward so that the genital region on the posteroventral cephalothorax was lifted well off the substratum (Fig. 1c). The male assumed the copulatory position by rolling upside down below the female, with the male's body perpendicular or slightly oblique to that of the female (Fig. 1d, e). In

the copulatory position, the genital regions of the male and female were opposed. Median duration of the copulatory posture varied from 3–17 s (overall median = 6 s) in the 18 pairs in which mating was observed (Table 1).

Copulation usually terminated when the male rolled back to an upright position and backed away slightly from the female, although the female sometimes broke off the copulation with sudden retrograde swimming by rapid abdominal flexion. After a copulation, the male frequently initiated following behavior again, although numerous and sometimes extensive bouts of following behavior often did not result in copulation. Between bouts of mating behavior, the male and female separated in the narrow confines of the mating chamber without obvious indications of association or recognition.

Pattern and Success of Insemination

Seminal receptacles of isolated females that molted were empty, because the receptacles are cuticular and are cast off, along with any sperm that they may have contained from a previous copulation (Fig. 2a,b). Stored sperm were observed in both the left and right seminal receptacles of exuviae from all females collected during September and November which molted after capture ($N = 45$), 21 of which were used in the mating observations. Exuviae of females collected in December ($N = 7$), four of which were used in mating observations, did not contain sperm in either seminal receptacle, showing that they were not inseminated when captured.

Copulations were observed in 18 of 25 pairs with newly molted females (Table 1). In these 18 pairs, the number of copulations per pair varied from 2–29 (median = 7.5); the number of copulations per h of observation period in 17 pairs kept together for comparable times (14–24.5 h) ranged from 0.1–1.5 (median = 0.5 per h). The male copulated only on one side of the female (5–9 times) in 3 of the 18 pairs, while in the other 15 pairs the male mounted the female from both sides one or more times (Table 1).

In two pairs, the female was mounted by the male from only the left side (5 and 7 times), and only the left seminal receptacle was inseminated (Fig. 2c). In another pair,

the male copulated with the female nine times on her right side only, and only the right receptacle contained sperm (Fig. 2d). In the 15 pairs in which males copulated one to several times on both sides of the female, both seminal receptacles were inseminated in seven females (Table 1, Fig. 2e). In one pair, the male filled both receptacles with a single copulation on each side of the female. In seven other females, only one of the two seminal receptacles contained sperm, in spite of often repeated matings on the unfilled side (Table 1, Fig. 2f). One male failed to transfer sperm to any receptacle with a single copulation on each side of the female.

DISCUSSION

All investigators who have observed mating in penaeoid species in which sperm is stored in enclosed seminal receptacles ("closed thelycum" species) have reported that copulation takes place in a period (minutes to a few days) after the female molts (Hudinaga, 1942; Brisson, 1986; Primavera, 1979; Bauer, 1991). Although intermolt mating cannot be ruled out without careful monitoring of females between molts (cf. the American lobster *Homarus americanus*; Waddy and Aiken, 1991), qualitative observations on mixed male and female populations of *Sicyonia dorsalis* indicated that mating only takes place within a few days after the female molts. Females cast off the old cuticular linings of the seminal receptacles along with sperm masses contained within these structures. Mating must occur to replenish the sperm supply of the female.

The precopulatory following behavior observed in *Sicyonia dorsalis* and other *Sicyonia* spp. (Palombi, 1939; Bauer, 1991) is similar to that of *Penaeus japonicus* (see Hudinaga, 1942), *P. monodon*, and *P. vannamei*, in that there is a variable period of precopulatory following of the female by the male. In the latter two species, the following behavior involves swimming in which the male swims below and parallel to the female before turning upside down so that male and female ventral surfaces oppose for copulation. I have also observed this kind of precopulatory swimming in male-female pairs of *Trachypenaeus similis* just after the female molts and prior to copulation. The lack of off-the-bottom swimming during

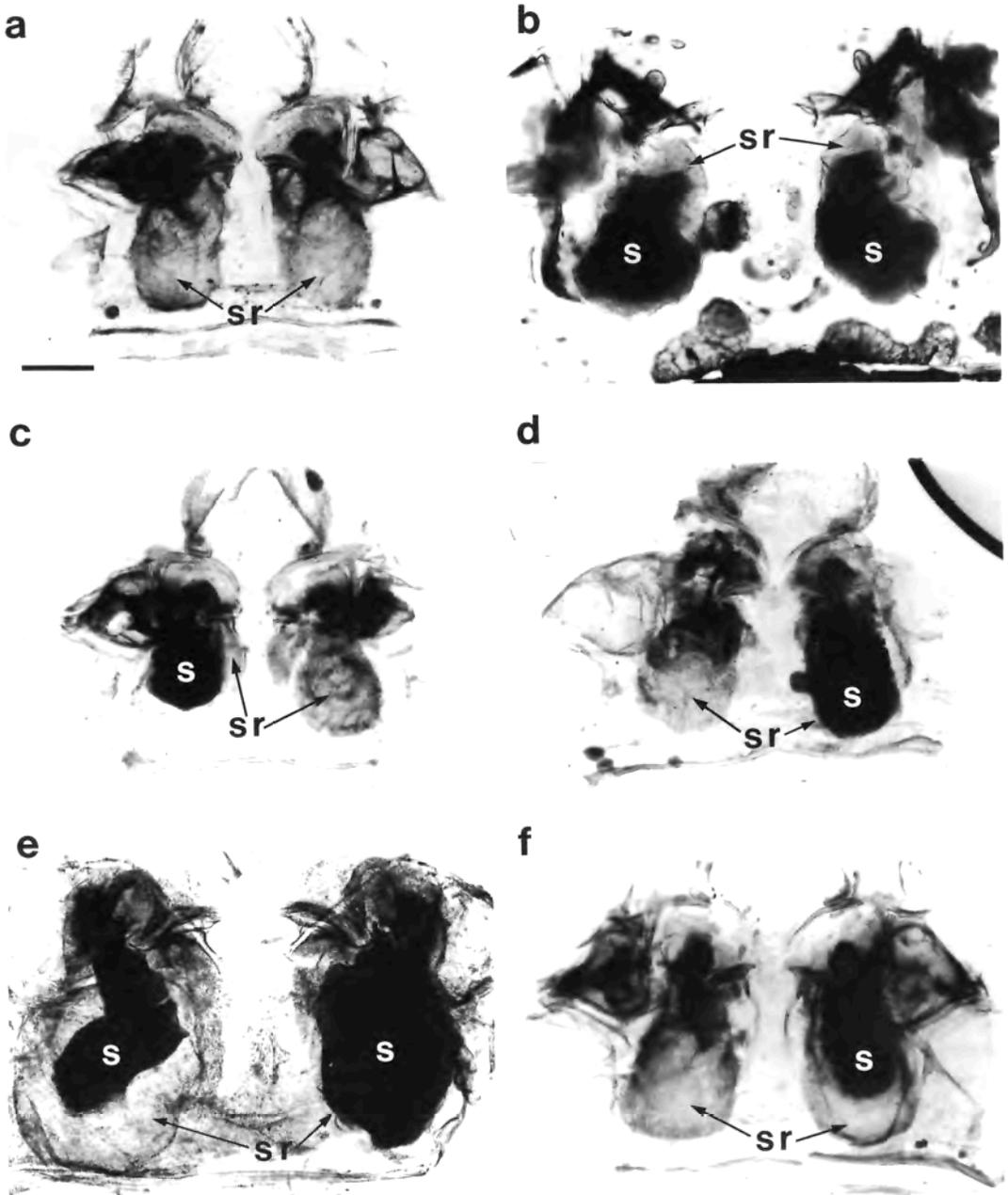


Fig. 2. Variation in insemination of female seminal receptacles of *Sicyonia dorsalis*; s = sperm mass; sr = sperm receptacle. a, empty receptacles from recently molted, unmated female; b, receptacles, filled with sperm, from castoff molt skin of previously inseminated female; c, receptacles of female copulated by male (7 times) from female's left side only. Note filled left and empty right receptacle (posterior end of left receptacle torn off during specimen preparation, sperm mass undisturbed); d, receptacles of female mated (9 times) from its right side only. Note empty left and filled right receptacle; e, sperm masses in both receptacles from matings from both left (7 times) and right (8 times) sides; f, receptacles of female mated 8 times from left side and 5 times from right, with sperm deposition only in right receptacle. Scale bar in (a) represents 0.83 mm in (a), (c), (d), and (f), and 0.35 mm in (b) and (e).

following behavior of *Sicyonia* spp. may simply reflect the relatively reduced forward swimming abilities of these highly benthic shrimps, with their heavily calcified exoskeletons (common name, "rock shrimp") and the reduction of natatory adaptations in their general body morphology. Precopulatory behavior of *Sicyonia* spp. does seem to be unique among penaeoid species in the extent to which the male contacts (possibly investigating or stimulating) the female genital region prior to copulation. This may reflect major differences among penaeoid spp. in the specific characteristics that stimulate males to copulate or in the way males stimulate females to accept copulation.

Although the precopulatory following behavior of males of *Sicyonia dorsalis* appears similar to that observed in the mating of other *Sicyonia* spp. (Palombi, 1939; Bauer, 1991), the pattern of copulations in pairs of *S. dorsalis* is quite different from that reported for *S. laevigata* and *S. parri* (see Bauer, 1991). In those species, males copulated first from one side and then immediately switched over to mount the female from its other side, after which a mating bout usually terminated, although long-term observations of a single pair were not made as in this study. In contrast, immediate switching of the male from one side of the female to the other side for the next copulation was not observed in *S. dorsalis*. The pattern of copulation was quite variable in *S. dorsalis*, with males sometimes mating a single time on both sides, sometimes several times on both sides, and, in three pairs, copulating several times from one side of the female but never on the other.

Results from this study show that, as in *Sicyonia laevigata* and *S. parri*, the paired seminal receptacles of females of *S. dorsalis* are filled individually from separate copulations in which the male deposits sperm in the receptacle on the same side on which he is mounting the female. Thus, females must be mated at least once on each side of the body by the male in order to be completely inseminated.

Females of *Sicyonia dorsalis* can copulate with males without being inseminated. In seven pairs in this study, a male copulated on a given side of the female, sometimes several times, without transferring sperm to the seminal receptacle of that side. The male-

female behavior of these copulations was indistinguishable from those observed in matings in which insemination was successful. Copulations without insemination, such as those observed in this study, may occur routinely in field populations of *S. dorsalis*. Normal copulatory behavior without sperm transfer is not unusual in animals (Eberhard, 1985). However, all females of *S. dorsalis* taken from the field which had been previously inseminated had sperm in both seminal receptacles. This was also true of field populations of *S. laevigata* and *S. parri* (Bauer and Rivera Vega, personal observations). In more limited observations on laboratory mating in these latter species, Bauer (1991) also reported the occurrence of copulation without insemination.

These observations suggest the hypothesis that females of *S. dorsalis* may often be mated and inseminated in their natural habitat by more than one male. One interpretation of the results on variable insemination in these laboratory matings is that a female may allow copulation but prevent or withhold insemination. An alternative explanation is that males vary in their mechanical ability to inseminate females. The details of sperm transfer during copulation are still unknown although likely to be complicated, given the complexity of the male genitalia (Pérez Farfante, 1985; Bauer, 1991). Males may have to place the petasma in some exact way during the brief period of copulation in order to successfully transfer sperm. A third alternative is that the success of insemination in laboratory matings is less than that in nature because of some unknown laboratory artifact. However, there is nothing from the observations made in this study to suggest what that artifact might be.

Assuming that success of insemination in nature is as variable as it is in laboratory matings, the evidence suggests that each seminal receptacle of the female could be inseminated as a result of copulations by a separate male. It is also possible that more than one male could be inseminating each seminal receptacle. Male sicyoniids do not deliver sperm in discrete packets, or spermatophores, as do most male penaeoids (Bauer, 1991), but rather as a cord of sperm in a matrix that quickly becomes fluid. Sperm addition and mixing with sperm pre-

viously deposited in the seminal receptacle may occur. In the laboratory, newly molted females introduced into aquaria with males are often surrounded by several of them that then attempt the following behavior that is a prelude to copulation. Insemination of a female by two or more males needs to be confirmed by further laboratory observations and experiments.

I suggest an adaptive advantage for the hypothesized polyandry of females of *Sicyonia dorsalis* and other *Sicyonia* spp., penaeoid species in which fertilized eggs are broadcast directly into the plankton for embryonic and larval development. Females may spawn more than once between molts, when mating and insemination occur. Anderson *et al.* (1985) showed in *Sicyonia ingentis* that the seminal receptacles of a female contained enough sperm to fertilize multiple spawns. With insemination by more than one male, a female would not commit multiple spawns to the same male. Multiple paternity of female spawns would likely increase the genetic variability of offspring. Increased genetic diversity of broods might be an advantage in that the planktonic larvae are subject to long distance dispersal by currents and the subsequent vagaries of encountering suitable habitat for settlement in a mosaic or heterogenous benthic environment ("lottery analogy" of Williams, 1975; discussed by Thornhill and Alcock, 1983).

In laboratory populations of males and premolt females, there was no qualitative indication of precopulatory mate guarding, at least not the obvious kind seen in many crustaceans (*Hymenocera picta*, Wickler and Seibt, 1981; many examples, Ridley, 1983; *Macrobrachium rosenbergii*, Ra'anan and Sagi, 1985; *Callinectes sapidus*, Gleason, 1991). There were no apparent signs of postcopulatory guarding of the female in laboratory populations. Quantitative studies on interactions are needed to verify these assertions about pre- and postcopulatory mate guarding in *S. dorsalis*. Although repetitive copulation by males might insure complete insemination of a female, it may also represent an indirect form of postcopulatory mate guarding in which males prevent mating and insemination of the female by other males. Males appear to be polygynous, attracted only to newly molted, receptive fe-

males, and may engage in "scramble competition" (Thornhill and Alcock, 1983) for such females. The evidence from this study suggests that at least some females are polyandrous.

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