Courtship and female mate selection in a marine isopod crustacean, *Paracerceis sculpta*

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Abstract. Females are semelparous in *Paracerceis sculpta*, a harem polygynous isopod that breeds in intertidal sponges in the northern Gulf of California. Reproductive females locate males established in spongocoels, and initiate courtship, which involves oral contact of males by females, and lifting and shaking of females by males. Despite this apparent assessment, females do not discriminate among males that differ by 10% in body length, by 30 days in age, or that lack appendages used in courtship. In most cases, females pair with the first male they encounter. Males, moreover, show no reluctance to pair with any female that approaches their spongocoel. Females as well as males are attracted to spongocoels occupied by multiple gravid females. Males attempt to control such sites, and body size confers an advantage in spongocoel takeover. Predation risks incurred by females while searching for spongocoels may favour individuals responding to chemical cues that reliably indicate breeding site quality, e.g. those emanating from established breeding aggregations. That sponges containing gravid females attract unmated females may explain why males attempt to monopolize these sites.

Mate selection criteria for females in iteroparous species may vary with a female's age, her previous breeding experience and the environment in which she attempts to reproduce (Wittenberger 1981). Females in semelparous species are often unable to use such criteria when selecting mates because a semelparous female's first mate may also be her last. Variations in reproductive habitat or male quality seem certain to influence lifetime fitness, regardless of the number of times a female breeds. Thus, lacking the ability to compare previous mates or reproductive habitats, mate selection criteria used by semelparous females are likely to consist of condition-independent cues about male or breeding site quality, that have correlated with female fitness over evolutionary time. To explore this possibility, and to examine the behaviour of males in response to female breeding decisions, I will describe the details of courtship and mate selection in *Paracerceis sculpta*, an isopod crustacean in which females reproduce only once.

Paracerceis sculpta is a marine sphaeromatid isopod inhabiting the northern Gulf of California (Brusca 1980; Shuster 1986). Males in this species occur as three morphologically distinct types that represent alternative reproductive strategies. Alpha-males (a-males) possess enlarged pleotelsons

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and elongated uropods (Fig. 1). Beta-males (β-males) are smaller than a-males, lack ornamentation and resemble sexually receptive females in their behaviour and morphology. Gamma-males (γ-males) also lack ornamentation, are smaller than β-males, and use their small size and rapid movements to slip around a-males and into spongocoels (Shuster 1987a, 1989a). While the three male morphs differ in their reproductive behaviour (Shuster 1989a, b, in press), they do not differ in their abilities to sire young successfully when isolated with females (Shuster 1986, 1987a). Moreover, relative fertilization success among males in spongocoels varies with the density of receptive females, and evidently with the relative frequency of other male types in the population (Shuster 1989a). The influence of β- and γ-males on the behaviour of a-males and females is described in further detail elsewhere (Shuster 1986, 1989a, b, in press).

Most males in the northern Gulf of California population are a-males (82%; Shuster 1987a). a-Males establish breeding sites within the spongocoels of calcareous intertidal sponges, *Leucetta losangelensis* (Shuster 1987b). Females are attracted to these sites, and polygynous breeding assemblages form that may include up to 19 females per a-male ($\bar{X} \pm$ SD = 1.90 ± 2.22, $N = 1122$). Shortly after entering spongocoels, females undergo a moult that initiates their sexual receptivity (Shuster
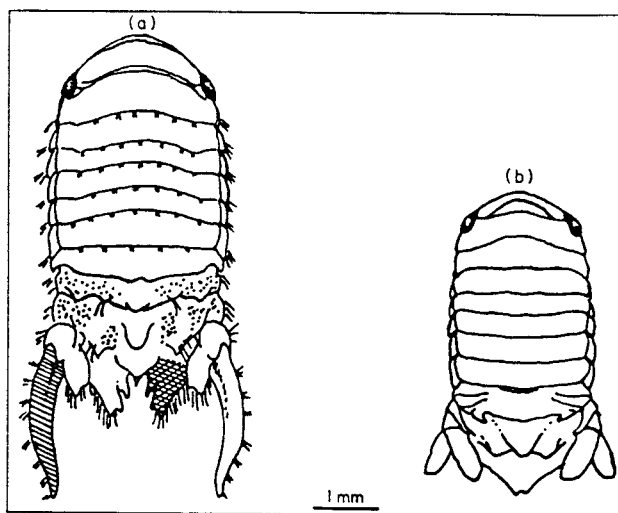
Figure 1. a-Male (a) and premoult adult female (b) *Paracerceis sculpta* (redrawn from Brusca 1980). Hatched lines indicate areas amputated on a-males used in mate choice experiments. Single hatching: uropod; crossed hatching: pleotelson apex.

(1989b). Females mate in spongocoels at this time and begin brooding their embryos in a ventral brood pouch.

The reproductive moult is a terminal moult in *Paracerceis sculpta* because post-moult females lose functional mouthparts and cease to feed after they become gravid. The dramatic physical deterioration of gravid females during gestation, moreover, suggests that metabolic changes associated with providing nutrition to developing embryos, as described for a related sphaeromatid *Dynamene bidentata* (Holdich 1971), may occur in *P. sculpta* females. Young isopods (mancas) emerge from females approximately 4 weeks after mating, depending on water temperature. All females die within 2 weeks of parturition (Shuster 1986). Thus, females in this, and evidently in at least 16 other sphaeromatid genera (Harrison 1984), are obligately semelparous (or uniparous, sensu Kirkendahl & Stinseth 1985).

The observed distribution of harem sizes within spongocoels differs significantly from a Poisson distribution: unmated a-males, and a-males mated to five or more females occur more frequently than expected by chance (Shuster 1987a). Multiple regression of harem size on the physical characteristics of a-males and of the sponges in which harems are found, indicates that only male body length consistently explains significant variance in harem

size (two of three independent regression analyses, Shuster 1987b, in press). Thus, despite considerable variation in sponge morphology, females evidently do not use the physical characteristics of sponges to select breeding sites.

The details of courtship behaviour are presently undescribed for most sphaeromatid isopods, including *Paracerceis sculpta*. Moreover, because males and females in this species are active primarily at night, water-borne cues may be important in the identification of conspecifics, as in many other crustaceans (see reviews in Caldwell 1979, 1982). The multivariate results described above indicate that while females in this species evidently do not discriminate between reproductive habitat characteristics, they may discriminate certain physical attributes of males, particularly those related to male body size. However, while the context for discrimination of male characteristics by females may exist, it is also possible that females use the breeding decisions of other females to assess variation in male or habitat attributes, as has been suggested for certain lizards, birds and fish (Kiester 1979; S. G. Pruett-Jones and C. W. Petersen, personal communications).

To address these topics, I describe below the precopulatory behaviour of sexually mature females and established a-males, including the apparent ability of females to detect a-males in spongocoels

using water-borne cues. I also examine female mate discrimination based on α-male body size, age and uropod condition, and whether female mate selection is influenced by the presence of gravid females in spongocoels. To explore male behaviour in response to female mating decisions, I examine α-male discrimination among empty spongocoels and spongocoels containing gravid females, as well as the relationship between α-male body length and success in spongocoel takeover. Finally, I describe the relationship between harem size and the reproductive condition of females collected from the field to determine whether females tend to enter established spongocoels in nature.

METHODS

Collection and Identification of Experimental Animals

Isopods were collected from *L. losangelensis* spongocoels and maintained in the laboratory as described in Shuster (1987a). Individual α-males were identified by their relative size, their age (the relative amounts of pigment remaining in the dorsal cuticle and of algae encrusting the pleotelson, Shuster 1986), and by unique pigmentation patterns on their dorsal cuticles. Individuals that had been maintained in the laboratory for over 2 weeks were examined and rescored before being used in behavioural experiments. No individual was used more than once in the same experiment.

The Use of Artificial Sponges

Natural *Leucetta* sponges are difficult to maintain in the laboratory, and isopods abandon dead or dying natural sponges. To avoid this problem, I constructed artificial sponges from a synthetic prepolymer (FHP-3000, made available to me by J. Bonaventura, Duke University Marine Laboratory, details in Shuster 1986). The prepolymer, when mixed with fresh water, forms a rapidly setting foam. The foam was poured into bottle caps, a small length of coated wire was inserted into the foam to form a spongocoel, and the sponge was trimmed to a natural shape after the foam had set.

Choice experiments using natural and artificial sponges indicate that isopods show only a slight initial preference for natural sponges. Isopods adapt quickly to artificial sponges, however, and assume normal body positioning in artificial sponge oscula. Isopods form breeding aggregations

within artificial sponges that are indistinguishable from those found in nature, and females that enter, mate and rear young in artificial sponges suffer no decrease in fecundity compared to females that have brooded their young in natural spongocoels. Artificial sponges thus simulate the physical characteristics of natural sponges, yet are chemically inert, can be standardized in size and are reusable (details in Shuster 1986).

Conditions for Behavioural Observations

All isopods used in these experiments were collected from the intertidal zone between Playa de Oro Trailer Park and Station Beach, approximately 3 km southeast of Puerto Peñasco, Senora, Mexico (details in Shuster 1987a, in press). Behavioural observations were conducted at the Center for the Study of Deserts and Oceans (CEDO) in Puerto Peñasco, between February and June 1985. Although *P. sculpta* breeds throughout the year, this interval corresponds to the annual peak in reproductive activity for this species (Shuster, in press).

Artificial sponges used in experiments were of standardized dimensions (diameter = 20 mm; osculum diameter = 3 mm; spongocoel volume = 7.85 cm^3) and were rinsed in tap water between uses. Isopods show no preference for previously occupied artificial sponges that have been rinsed into tap water over new constructed sponges (Shuster 1986), indicating that rinsing removes any significant residual scent left by previous spongocoel occupants.

Cylindrical plastic 225-ml cups containing seawater served as arenas for all behavioural experiments. The shape of the arena prevented possible position effects among sponges used in choice tests. All behaviour was observed under red light between 1900 and 0200 hours, and unless otherwise stated, the behaviour of individuals in cups was recorded for 2 h on tape after each trial was begun. This interval allowed individuals sufficient time to assess conditions within each cup, but limited the number of behavioural interactions possible for each trial, thus minimizing the possibility that a few individuals could inflate the number of certain behavioural acts. Taped observations confirmed that such redundancy was not a problem. When behavioural observations were completed, each trial was examined 12 h later and the positions of individuals within each cup were recorded. All trials were terminated at this time.

Interactions Among Females and α-Males

The following procedure was used to examine how females locate α-males, and to describe interactions among premoult females and α-males established in spongocoels. α-Males were first placed into individual 225-ml cups containing an artificial sponge and seawater. These males were allowed to establish themselves in sponges and were left undisturbed for 24 h. Each established α-male was then transferred, while still in his sponge, to a separate arena containing fresh seawater and an unoccupied artificial sponge of standard size. After 15 min, a premoult female was introduced to each arena between the two sponges using a large pipette. Behaviour was observed as described above for 40 trials. As a control, the settlement patterns of 20 premoult females introduced to arenas containing two unoccupied artificial sponges were also recorded. Breeding site choice was considered to have occurred when a female entered and remained in a spongocoel for more than 60 s. After selecting a spongocoel containing a male, females were never observed to leave (see below).

Female Discrimination of α-Male Characteristics

Male body length

To determine whether females discriminate α-male body length, individual premoult females were allowed to choose between two α-males, each established in separate, standardized artificial sponges as described above. α-Males were of similar age and physical conditions, but differed by 10% in body length. A body size difference of 10% or less is recognizable by many animals (Wallace 1987). A total of 70 trials were conducted.

To determine whether females tend to discriminate α-male body size when more than one α-male is present on the same sponge, 10 premoult females were allowed to choose between larger and smaller α-males occupying different spongocoels on the same sponge.

Male age

To determine whether females discriminate α-male age, 20 premoult females were allowed to choose between two α-males, each established in separate standardized artificial sponges as described

above. The two α-males were the same size, but differed in age by three pigment/algae ranks (Shuster 1986). This difference is equivalent to 6–8 weeks for adult male isopods (unpublished data).

Male uropod condition

During precopulatory behaviour, α-males use their uropods to lift and shake females before allowing them to enter their spongocoels (see below). The following procedure was used to determine whether α-males that lack one uropod, and thus are incapable of normal courtship, are as attractive to females as intact α-males. α-Males with damaged uropods comprise 1–5% of the α-male population at any time (unpublished data).

Twenty pairs of α-males were standardized for body length and age. The right uropod of one α-male in each pair was removed at the basis. The left pleotelsonic apex of the other male was removed as a control (Fig. 1). Males were allowed 24 h to recover from this procedure and no males died from appendage removal. The males were established in separate, standardized artificial sponges, and introduced to arenas as pairs following the procedure described above. A premoult female was then placed into each arena and allowed to choose between the α-males.

Presence of other females in spongocoels

The following procedure was performed to determine whether females prefer spongocoels containing α-males and their harems, over spongocoels containing only α-males. To create spongocoels into which harems of standard size could be introduced, modified artificial sponges were constructed as shown in Fig. 2. Sponge modification involved casting an artificial sponge around a spongocoel mould that created anterior and posterior spongocoel compartments, separated by a constriction. The constriction was closed by a fine mesh screen, secured in place with cyanoacrylate glue. An opening toward the rear of the posterior compartment permitted introduction of isopods into the posterior compartment, and a small piece of artificial sponge was used as a plug to close the rear opening.

Twenty premoult females were allowed to choose between pairs of modified artificial sponges. One sponge contained three gravid females in the
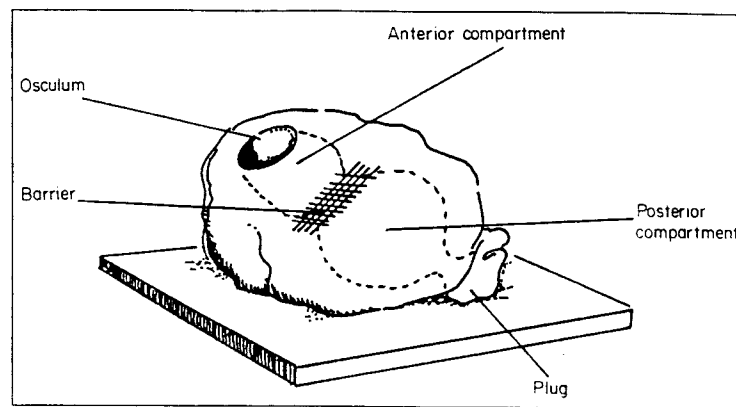
Figure 2. Artificial sponge with anterior and posterior compartments separated by a fine-mesh screen. The screen retains isopods in the posterior compartment, but permits water-borne substances to escape through the sponge osculum.

posterior compartment; the other sponge contained no females in the posterior compartment. Both sponges contained a size- and age-matched a-male established in the anterior compartment.

a-Male Discrimination of the Presence of Females in Spongcoels

To determine whether a-males discriminate among empty spongocoels and spongocoels containing aggregations of females, 44 a-males were allowed to choose between pairs of modified artificial sponges as follows. One sponge in each pair contained three gravid females in the posterior compartment. The other sponge contained no females. Pairs of sponges were placed into arenas as described above, and an a-male was introduced to each arena between the sponges using a large pipette. The behaviour of a-males was recorded as described above for females.

The Effect of a-Male Body Size on Spongocoel Takeover Success

To determine the effect of body size on competitive interactions among a-males, three sets of 20 a-males were established in sponges and were each allowed to pair with one receptive female as described above. Size- and age-matched a-male intruders were introduced to the first set of residents. Age-matched intruders that were 10% smaller in body length than residents were introduced to the second set of a-males, and age-matched intruders that were 10% larger than residents were introduced to the third set of a-males. The positions of residents and intruders were recorded after 12 h.

The Relationship Between Harem Size and Female Reproductive Condition

The reproductive condition of females brooding developing embryos can be classified into eight distinct stages defined by the relative condition of the female's mouthparts, cuticle, reproductive organs and the developmental stage of her embryos. All characteristics are visible under low power using a stereomicroscope (Shuster 1986). The range of this scale is defined by newly arrived, premoult females (designated S_1) possessing unmetamorphosed mouthparts, well pigmented cuticles and mature ovaries, and by post-moult females possessing metamorphosed mouthparts, faded cuticles, spent ovaries and mancas emerging from the brood pouch (designated S_7; stage 4 is divided into early and late substages determined by the presence or absence of eyespots on embryos). The approximate gestation time for developing isopods at 25°C is 4 weeks.

Females collected from *Leucetta* spongocoels between October and December 1983 (details in Shuster 1987a, $N = 156$ spongocoels, 410 females) were ranked on the above scale. Each rank was transformed as $\log(x_i + 1)$, and the relationship between harem size and mean reproductive condition of harem members was determined using ANOVA.
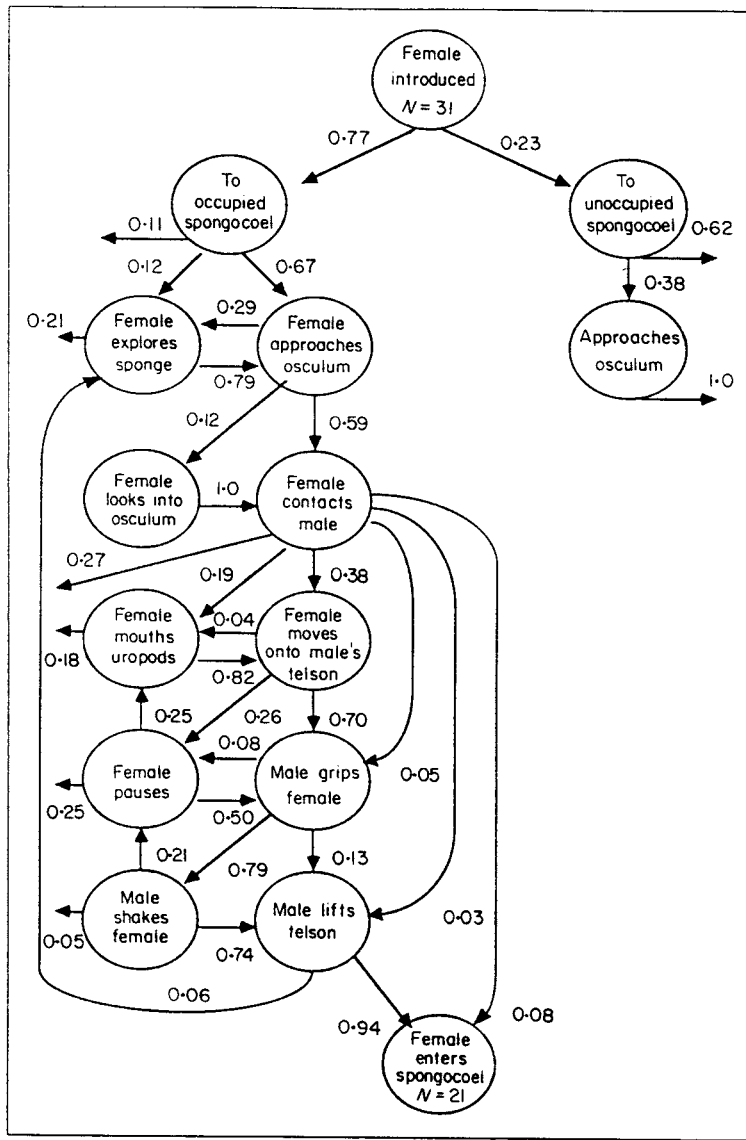
Figure 3. Interactions among premoult females and a-males in artificial sponges. Arrows pointing horizontally indicate individuals leaving the sponge. The frequency of transition is indicated beside each arrow.

RESULTS

Interactions Among Females and a-Males

Unmoulted females evidently locate a-males in spongocoels from some distance, perhaps using a water-borne substance as a cue. When allowed to choose between an artificial sponge occupied by an a-male and an empty artificial sponge, females moved directly onto the occupied sponge (24 of 31

cases, $G = 8.01$, $P < 0.005$; no behaviour was observed in 9 of 40 cases). When no a-males were present, females settled on artificial sponges randomly (12:8, binomial test, $N = 20$, $P = 0.25$).

When investigating sponges occupied by a-males (Fig. 3), females usually climbed to the top of the sponge and began spiralling downward. Occasionally, upon reaching the sponge osculum, females walked around the osculum perimeter and briefly
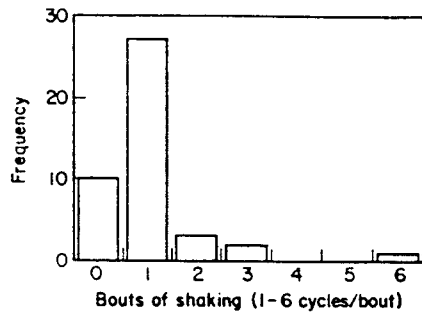
Figure 4. Bouts of mate-shaking by a-males, $N=43$.

contacted the a-male's uropods before moving on ($N=7$). Several females ($N=3$) performed this sequence at least three times in succession. More frequently, however, females moved directly to the osculum and initiated oral contact with the a-male's uropods for at least 30 s ($N=22$), occasionally pulling on the male's uropods with their mouthparts. Although some a-males moved their uropods or rotated within their spongocoels at this time ($N=5$), most a-males were passive throughout this process.

After mouthing the a-male's uropods, females moved down into the spongocoel and between the a-male's open uropods ($N=14$). a-Males responded to this behaviour by closing their uropods around the female, obtaining a firm grip and then rapidly and forcefully shaking the female for one to six cycles (Fig. 4). Males then released the female, who either moved away from the male ($N=5$), remained in place for more shaking (up to six successive bouts were observed) or moved further into the spongocoel, beneath the a-male ($N=21$). a-Males made no attempt to restrain females that moved away from them ($N=5$), and females that entered a particular spongocoel did not leave that spongocoel to continue searching ($N=21$ for this experiment, $N=99$ all other observations, Shuster 1986).

Female Discrimination of α-Male Characteristics

Male body length

Females did not discriminate a-male body length ($G=0.91$, $N=70$, $P>0.25$). In most cases, females moved directly to one male and paired immediately (29 of 43 trials in which pairing was observed, $G=5.29$, $P<0.025$). Females first encountered large and small a-males with equal frequency ($G=0.31$, $N=29$, $P>0.50$), and females not pairing with the first male encountered, i.e. females that appeared to

assess both males before making a choice, paired as frequently with large a-males as they did with small a-males (binomial test, $N=14$, $P=0.38$). Females also did not discriminate a-male body size when both males occupied spongocoels on the same sponge (binomial test, $N=10$, $P=0.623$).

Male age

Females did not discriminate a-male age (binomial test, $N=20$, $P=0.412$). As in the body length choice test, females showed little tendency to assess both males, and usually paired with the first male encountered.

Male uropod condition

Females also did not discriminate uropod condition among a-males (binomial test, $N=20$, $P=0.588$). Females pairing with a-males missing uropods simply omitted the shaking phase of courtship and moved directly into the a-male's spongocoel.

Presence of other females in spongocoels

Females did, however, prefer spongocoels already containing an a-male and three females (i.e. mated males), over spongocoels containing an a-male alone (i.e. singleton males; 12/16 trials, binomial test, $P=0.038$). In 4 of 20 trials, singleton males left their spongocoel before females had approached either sponge. These cases were discarded. In the remaining 16 trials, five singleton a-males left their spongocoels within 2 h after premoult females had paired with mated a-males. During this interval, all five singleton a-males attempted at least once to usurp spongocoels occupied by mated a-males and their females. None of these attempts was successful in 24 h.

α-Male Discrimination of the Presence of Females in Spongocoels

a-Males preferred spongocoels containing three gravid females over spongocoels containing no females in 23 of 32 cases ($G=6.34$, $P<0.025$). Twelve of 44 a-males showed no preference among the spongocoels and were found free in the container after 12 h.

The Effect of α-Male Body Size on Spongocoel Takeover Success

Resident a-males defended their spongocoels against same-sized intruders in 16 of 20 trials. Residents with a 10% size advantage over intruders were

Table I. The effect of α-male body size on spongocoel defence

Treatment	R retains spongocoel	R evicted from spongocoel	N
R = I (control)	16	4	20
R > I	16	4	20
R < I	7	13	20

R: resident; I: intruder. Large intruders are more successful at usurping spongocoels than same-sized or smaller intruders ($G = 8.63$, $P < 0.01$).

no more successful at defending their spongocoels than size-matched controls. Residents were displaced in 13 of 20 trials, however, by intruders with a 10% size advantage ($G = 8.63$, $P < 0.01$, Table I). Thus, body size confers a significant advantage in permitting α-males to usurp spongocoels from residents.

Harem Size and Female Reproductive Condition

The relationship between harem size and the mean reproductive condition of females in spongocoels was significant and positive ($F_{9, 400} = 5.13$, $P < 0.001$). Larger harems contained females with embryos in more advanced states of development than smaller harems. Furthermore, the untransformed data with two standard errors plotted in Fig. 5 indicate that variance in female reproductive condition within harems becomes larger with increased harem size. Thus, larger harems contain newly arrived females as well as females in advanced reproductive condition. Smaller harems consist primarily of females in early stages of reproductive condition.

DISCUSSION

Although females engage in brief courtship with α-males, females do not appear to discriminate among α-males on the basis of body size, age or uropod condition. Females simply move into the spongocoel of the first male they encounter. The direct movement of females to spongocoels containing α-males suggests that females use waterborne cues to locate α-males, especially since reproductive behaviour occurs at night (Shuster
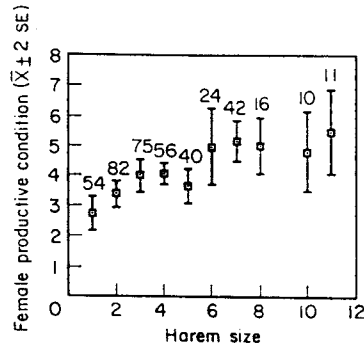

Figure 5. The relationship between harem size and the mean reproductive condition of females in spongocoels. Larger harems contain newly-arrived females as well as females in advanced reproductive condition. Smaller harems contain primarily females in early stages of reproductive condition. Numbers above error bars represent the total number of females examined at each harem size.

1989b). Whether females use this putative substance to obtain information about individual α-males, however, remains unclear.

The significance of mate-shaking by α-males is also uncertain. Males in other isopod species lift females during courtship and evidently discriminate female body size (Bowman & Kuhne 1974; Shuster 1981; Ridley 1983). No discrimination of female characteristics, however, was apparent among α-males, as all females approaching spongocoels were permitted to enter. Females occasionally solicited several bouts of shaking by α-males and may use this behaviour to assess male vigour (Kodric-Brown & Brown 1984). Females may also obtain information on some aspect of male quality through oral contact with α-male uropods. Females, however, did not discriminate against young α-males, small α-males or α-males missing uropods. Thus, if females do assess variation among α-males through shaking or oral contact, male characteristics important in female choice evidently do not covary with α-male age, size or uropod condition.

That females prefer spongocoels containing α-males with harems over spongocoels containing unpaired α-males suggests that α-males may provide some resource to females such as parental care (Downhower & Brown 1980). However, females maintained in artificial sponges with and without α-males do not differ in fecundity (Shuster 1986). Moreover, female fecundity does not diminish with increasing harem size, as expected if males provide parental care that is somehow limited in quality or

in quantity (Garson et al. 1981; Shuster 1986). Spongocoels containing a-males may be safer from predators than spongocoels lacking a-male residents, but I have found no evidence that fish or other large predators attack groups of isopods in sponges. Furthermore, I have found no clear evidence of predation by polychaete worms or other predators that could directly invade spongocoels.

The mere existence of a spongocoel containing multiple gravid females may demonstrate its quality as a potential breeding site. Indeed, the relationship between harem size and the mean reproductive condition of females in spongocoels indicates that larger harems are older than smaller harems, i.e. larger harems have a history of success as breeding sites. Without a demonstrated benefit to females that associate with established spongocoels, however, the simplest explanation for the attraction of premoult females to breeding aggregations is that such spongocoels are simply more conspicuous than empty spongocoels or spongocoels occupied by a single a-male. This explanation is consistent with results suggesting that isopods recognize conspecifics using water-borne cues.

Females migrating from feeding sites in algae to breeding sites in spongocoels evidently face considerable predation pressure from fish (Shuster, in press). The probability of successful multiple trips from feeding habitat to breeding habitat therefore appears small. Obligate semelparity is thought to evolve if prolonged adult survivorship provides minimal returns in fecundity (Bell 1980), as is likely if predation risks to females attempting iteroparity are substantial. Bell's principle thus seems well illustrated by the obligate semelparity of *Paracerceis sculpta* females and their sphaeromatid relatives (Holdich 1971; Harrison 1984). In these coastal marine species, semelparity appears correlated with a spatial separation of feeding and reproductive habitats (Shuster, in press).

Like premoult females, a-males are attracted to established spongocoels. a-Males fight for access to spongocoels containing females, moreover, and body size confers an advantage in spongocoel takeover. If premoult females are attracted to established spongocoels, a-males that locate and can successfully monopolize such sites are likely to experience greater reproductive success than less capable a-males (Parker 1978). Such circumstances are likely to have favoured large size and elongated uropods among ancestral a-males (Shuster 1987b, 1989a, in press).

In *Paracerceis sculpta*, natural selection responsible for shaping female life histories appears to influence the evolution of specific patterns of female mate selection. The reproductive behaviour of females in turn, exerts a fundamental influence on the nature and intensity of sexual selection on males. Evolutionary analyses of animal mating systems logically begin, therefore, with investigations of how female life history is shaped by natural selection. An understanding of these female attributes may thus provide a predictive framework for examining the evolution of male reproductive behaviour.

ACKNOWLEDGMENTS

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