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Female reproductive success in artificial sponges in  
*Paracerceis sculpta* (Holmes) (Crustacea: Isopoda)

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## Female reproductive success in artificial sponges in *Paracerceis sculpta* (Holmes) (Crustacea: Isopoda)

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### Abstract

*Paracerceis sculpta* (Holmes), a sphaeromatid isopod crustacean, breeds in the spongocoels of intertidal sponges (*Leucetta losangelensis* de Laubenfels) in the northern Gulf of California. In the laboratory, *P. sculpta* adults readily colonize and inhabit artificial sponges constructed of a synthetic polymer (FHP-3000). To examine the effect of artificial sponges on female fecundity, I compared the numbers of live manca and undeveloped embryos produced by females that had completed their gestations (1) without sponges in 225 ml cups, (2) within artificial sponges at densities of one, three and five females per sponge, and (3) within natural sponges in the field. Females that completed their gestations in 225 ml cups released the most live mancas, whereas females that completed their gestations in the field released the fewest live mancas. Although differences among female groups in numbers of undeveloped embryos were found, the majority of females in all groups produced no undeveloped progeny, thus the significance of these differences is uncertain. There were no differences in numbers of live mancas released, or in numbers of undeveloped embryos remaining in the brood pouches among females that completed their gestations in artificial sponges at different densities. Thus, neither female aggregation nor gestation in artificial sponges appear to deleteriously affect female fecundity. These results corroborate earlier experiments indicating that artificial sponges provide suitable substitute reproductive habitat for laboratory studies of *P. sculpta*, and suggest that selection in other contexts (perhaps predation) maintains the tendency for females to complete their gestations in protected locations.

**Keywords:** Artificial habitat; Female reproductive success; Isopoda; Paracerceis; Sponge

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### 1. Introduction

Many species of marine crustaceans reproduce in cavities (reviews in Christy & Salmon, 1991; Shuster, 1992a). These infaunal organisms are diverse, abundant,

and frequently possess short generation times, characteristics that facilitate behavioral, life history, and genetic investigations. Despite these experimental advantages, the reproductive biology of most cavity-dwelling species is poorly known because manipulations of natural breeding sites can be difficult and imprecise. Artificial habitats can be used to solve this problem (Caldwell, 1982; Steger, 1987; Shuster, 1992a), but since not all facsimiles adequately approximate the physical characteristics of natural habitats, the effects of artificial cavities on the fitness of their potential inhabitants should be assessed before these structures are used for experimental manipulations.

*Paracerceis sculpta*, a sphaeromatid isopod inhabiting the northern Gulf of California, breeds in the spongocoels of intertidal sponges (*Leucetta losangelensis* de Laubenfels; Brusca, 1980; Shuster, 1991a). Most males in this species ( $\alpha$ -males:  $\approx 82\%$  of all males) are larger than females and possess elongate uropods that are used to defend the spongocoels against conspecific male intruders. Alpha-males are morphologically and genetically distinct from the two other male morphotypes that coexist in this species;  $\beta$ -males (14% of all males) mimic female behavior and morphology;  $\gamma$ -males (4% of all males) are small and inconspicuous (Shuster, 1987, 1992b; Shuster & Wade, 1991a). Whereas  $\beta$ - and  $\gamma$ -males inhabit spongocoels and compete for matings with  $\alpha$ -males, these smaller males do not colonize spongocoels or establish breeding assemblages to any recognizable degree (Shuster, 1992b). Thus, all *P. sculpta* males used in the present study were  $\alpha$ -males.

Like many other sphaeromatid isopods (Harrison, 1984), females in this species are semelparous (Shuster, 1991a). After their ovaries mature, females are attracted to established males in spongocoels and can form aggregations of up to 25 individuals, although the average number of females per spongocoel is usually much smaller ( $\bar{x} \pm SE = 1.47 \pm 1.56$ ,  $N = 387$ ; Shuster, unpubl. data). After entering spongocoels, *P. sculpta* females undergo a sexual molt and mate while in half-molted condition. Females then oviposit and brood their developing embryos within a ventral marsupium. Gravid females remain within spongocoels and release manca after 2 to 4 wk. Females lose functional mouthparts in their sexual molt, and presumably because they are unable to feed during gestation and after parturition, females die within 2 wk after releasing manca. Males do not undergo a similar molt, but they seldom feed after reaching adulthood (Shuster, 1991a).

Although spongocoels provide shelter for gravid females, the structural characteristics of sponges do not appear to influence female reproductive success (Shuster, 1991a). Moreover, male characteristics are not involved in female mate choice (Shuster, 1990). Instead, the relative size of the existing breeding aggregation appears to be the most important component of spongocoel attractiveness (Shuster, 1990, 1991a), suggesting that females may benefit by locating and/or associating with other females. Note that whereas the average size of female aggregations attended by  $\alpha$ -males is small, variance in harem size is quite large, indicating that gravid females aggregate in sponges in nature.

Shuster (1989, 1990, 1992b) has shown that *P. sculpta* adults will colonize and inhabit artificial sponges constructed of a synthetic polymer (FHP-3000; J.

Bonaventura. Duke University Marine Laboratory, Beaufort, NC, USA) in the laboratory. Choice tests show that artificial sponges adequately simulate natural sponges for such experiments, and that females will form aggregations similar to those found in nature within artificial sponges. These experiments suggest that artificial sponges provide suitable substitutes for natural reproductive habitat in behavioral experiments. However, these results do not demonstrate the effects artificial sponges or aggregations of isopods within spongocoels may have on the fecundity of females that brood their progeny therein.

The purpose of this paper is to compare the fecundities of female *P. sculpta* when allowed to complete their gestations within natural sponges, within artificial sponges, and without sponges. The effect of the density of females within artificial spongocoels on female fecundity is also assessed (density = one, three and five females). The results reported here corroborate those of earlier studies, and confirm the suitability of artificial sponges as substitute reproductive habitats for laboratory studies of this species (Shuster, 1989, 1992a). These results also suggest that (a) males in this species do not provide parental care essential to the survival of developing progeny (at least in the laboratory), and (b) selection favoring female aggregation operates before, rather than after females enter spongocoels.

## 2. Methods

### 2.1. Collection and maintenance of adult isopods

Isopods were collected from the spongocoels of *L. losangelensis* (de Laubenfels) sponges 5 km southeast of Puerto Peñasco, Sonora, Mexico. Breeding biology and collection procedures for *P. sculpta* are described in detail elsewhere (Shuster, 1989, 1991a, 1992b). Since adult isopods do not feed, collected animals were simply maintained in loosely covered 225 ml plastic cups containing seawater that was changed weekly.

### 2.2. The effect of artificial sponges on female fecundity

The construction of artificial sponges from the synthetic polymer, FHP-3000, and their use in laboratory experiments with *P. sculpta* are described elsewhere (Shuster, 1990, 1992a). To assess the effect of artificial sponges on the fecundity of brooding *P. sculpta* females (Treatment 1), 24 identical artificial sponges (diameter = 20 mm; osculum diameter = 3 mm; spongocoel volume = 7.23 cm<sup>3</sup>) were placed in separate 225 ml cups containing seawater. One male was released into each cup and allowed to establish himself in the sponge osculum (Shuster, 1992b). All males used in this experiment were approximately the same body length (Table 1).

The following evening, an unmolted (i.e., sexually receptive; Shuster, 1991a) adult female was placed into each cup and allowed to pair with the resident male. Successful pairings were determined by noting the presence of both halves of each

Table 1  
Body sizes and fecundities for male and female *P. sculpta* by treatment

Treatment	Male body length			Female body length			Live mancas			Undeveloped embryos		
	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N
T1	6.19	0.04	24	5.13	0.09	24	66.17	3.17	24	2.50	0.78	24
C1	–	–	–	5.40	0.12	30	88.00	3.86	30	0.33	0.12	30
C2	–	–	–	4.85	0.09	30	54.77	3.15	30	–	–	–
T2	6.35	0.12	7	4.91	0.06	21	57.33	5.99	7	0.14	0.38	7
T3	6.04	0.10	4	5.10	0.07	25	62.04	3.05	5	0.72	0.46	5

T1: Females paired with a male in an artificial sponge and allowed to complete gestation; C1: females mated by a male and maintained in 225 ml cups containing seawater for the duration of their gestation; C2: females collected from natural sponges (*L. losangelensis*) less than 2 days before manca release; T2: females maintained in artificial spongocoels with a male and two other gravid females; T3: females maintained in artificial spongocoels with a male and four other gravid females.

female's shed cuticle outside of the osculum of the artificial sponge, indicating that the sexual molt and mating had occurred (Shuster, 1990). All females used in this treatment (T1) were approximately the same body length (Table 1).

Cups were examined every other day and water changes were performed as described above. At parturition, mancas emerged from females, exited the spongocoel and swam about in cups. Newly-released mancas were removed from each cup using a Pasteur pipette and were counted once daily until no mancas were observed in the cup for three successive days. The females were then removed from the artificial sponge and examined for undeveloped embryos.

Two controls were conducted: For Control 1 (C1), 30 sexually receptive females were mated to males and maintained in individual 225 ml cups containing seawater with no artificial sponge for the duration of their gestations. For Control 2 (C2), 30 field-collected females that had spent all but 2 days of their gestations in natural *L. losangelensis* sponges were maintained in 225 ml cups containing seawater for the final day of their gestations [females that enter spongocoels to mate and brood young rarely leave them (Shuster 1990); thus females from male-occupied spongocoels that released mancas the day after collection were assumed to have spent all of their gestation within that spongocoel]. At parturition, newly-released mancas were removed from each cup as described above. Females in Control 1 were examined for undeveloped embryos; the number of undeveloped embryos for Control 2 females was not recorded.

### 2.3. The effect of female density in spongocoels on female fecundity

To assess the effect of female density in spongocoels on the fecundity of females, 12 identical artificial sponges (sponge diameter = 20 mm; osculum diameter = 3 mm; spongocoel volume = 7.85 cm<sup>3</sup>) were placed into individual 225 ml cups containing seawater. One male was introduced to each cup and was allowed to establish himself in a sponge. All males were approximately the same

body length (Table 1) and were not significantly different in size from males used in the previously described treatments ( $F_{[2,35]} = 2.58$ ,  $p = 0.09$ ).

Two treatments were performed for comparison with Treatment 1, and with Controls 1 and 2 above. For Treatment 2 (T2), three unmolted females were released into each of seven cups containing artificial sponges and allowed to pair with the established male (total T2 females = 21). For Treatment 3 (T3), five unmolted females were released into each of the five remaining cups and allowed to pair with the male (total T3 females = 25). All females entered spongocoels and mated with males within 30 h. Females established in spongocoels were maintained as described above, and at parturition, mancas were removed from cups and counted as previously described. Since the fecundity of individual females could not be established for Treatments 2 and 3, the average body length and average fecundity per female was calculated for each case in each treatment. This procedure established seven and five independent values for female size and fecundity, for T2 and T3, respectively. Specific methods for comparison of female fecundity among groups are described in the Results below. All variables were log-transformed before analysis to meet assumptions of normality (Sokal & Rohlf, 1981).

### 3. Results

#### 3.1. Differences among female groups

Among the treatment and control groups, I found significant differences in (a) female body length ( $F_{[4,95]} = 4.29$ ,  $p < 0.005$ ), (b) the number of live mancas per female ( $F_{[4,95]} = 12.87$ ,  $p < 0.001$ ), and (c) the number of undeveloped embryos per female ( $F_{[3,65]} = 5.45$ ,  $p < 0.003$ ). While (b) and (c) suggested that female fecundity was influenced by the conditions females faced during their gestations, these results were confounded by differences in female body size among the female groups, as well as by the correlation of fecundity with female body size in this species (Shuster, 1991a). These relationships necessitated adjustment of average fecundity among females using female body length as a covariate, but only if significant relationships between female body length and the measures of female fecundity were first identified (Sokal & Rohlf, 1981).

#### 3.2. Differences in undeveloped embryos numbers among female groups

Individual regressions of undeveloped embryo numbers on female body length for Treatments 1–3 and for Control 1 were nonsignificant in each case (T1:  $F_{[1,23]} = 2.10$ ,  $p > 0.16$ ; C1:  $F_{[1,29]} = 0.62$ ,  $p > 0.43$ ; T2:  $F_{[1,6]} = 0.13$ ,  $p > 0.73$ ; T3:  $F_{[1,4]} = 5.89$ ,  $p > 0.09$ ), indicating that no significant relationship existed between female body length and number of undeveloped embryos per female. Although on average, more undeveloped embryos were produced by females in Treatment 1

than in the other female groups (Table 1), the majority of females in this group, as well as in the other female groups, produced no undeveloped progeny whatsoever (note the large standard errors for numbers of undeveloped embryos in Table 1). Thus, while differences in this aspect of female fecundity appear to exist, the importance of these differences is uncertain.

### 3.3. The effect of female density in spongocoels on female fecundity

Individual regressions of live manca numbers on female body length were significant for Treatment 1 and for both controls (C1:  $F_{[1,29]} = 17.80$ ,  $p < 0.001$ , Fig. 1a; T1:  $F_{[1,23]} = 11.93$ ,  $p < 0.005$ , Fig. 1b; C2:  $F_{[1,29]} = 34.37$ ,  $p < 0.001$ , Fig. 1c). However, similar regressions were not significant for Treatments 2 and 3. (T2:  $F_{[1,6]} = 0.003$ ,  $p > 0.95$ , Fig. 1d; T3:  $F_{[1,4]} = 0.18$ ,  $p > 0.69$ , Fig. 1e), perhaps because

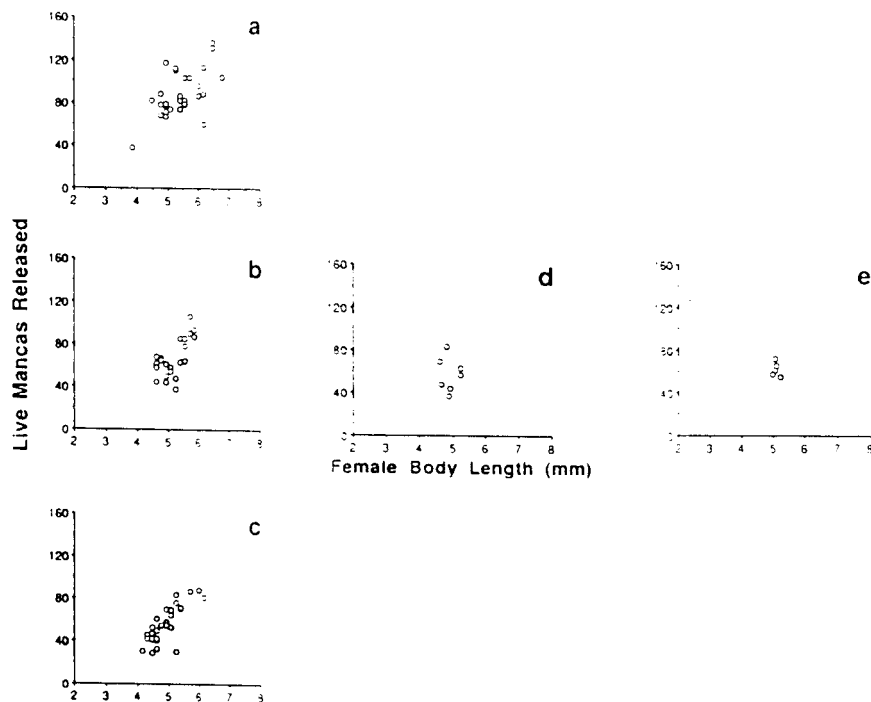


Fig. 1. Relationship between female body length and numbers of live mancas released; (a) C1: Females mated and maintained in 225 ml cups containing seawater for the duration of their gestation; (b) T1: Females paired with a male in an artificial sponge and allowed to complete gestation; (c) C2: Females collected from natural sponges (*L. losangelensis*) less than 2 days before manca release; (d) T2: Females maintained in artificial spongocoels with a male and two other gravid females; each point represents the average body lengths and average fecundities for three females maintained in the same sponge; (e) T3: Females maintained in artificial spongocoels with a male and four other gravid females; each point represents the average body lengths and average fecundities for five females maintained in the same sponge.



live manca numbers were averaged across three females in T2, and across five females in T3. Since there were no differences in female body length among females in T1–3 ( $F_{[2,35]} = 0.89$ ,  $p > 0.42$ ), and no differences in the numbers of live mancas produced by females in these treatments ( $F_{[2,35]} = 0.90$ ,  $p > 0.41$ ), I concluded that there was no effect of female density in spongocoels on the number of live mancas females produced, and pooled these data for comparison with the controls.

#### 3.4. The effect of artificial sponges on female fecundity

Analysis of female fecundity among T1–3, C1 and C2 using female body length as the covariate, showed (a) a significant common slope for the pooled regression ( $F_{[1,95]} = 58.18$ ,  $p < 0.001$ ), and (b) no significant interaction between slopes among the female groups ( $F_{[2,95]} = 2.43$ ,  $p > 0.09$ ). These results indicate that the slopes describing the relationship between live manca numbers and female body length were indistinguishable among the treatment and control groups. After adjusting the female group means for the effects of female body length on fecundity among the treatment and control groups, the Y-intercepts of these slopes were found to be heterogeneous ( $F_{[2,95]} = 14.72$ ,  $p < 0.001$ ). Thus, the adjusted average fecundity of females who completed their gestations in cups without sponges (C1 females) exceeded that of females who completed their gestations in artificial sponges (T1–3 females), and both of these female groups produced more live mancas than females who completed their gestations in natural sponges (C2 females).

#### 4. Discussion

Three general conclusions are possible from these results: (1) females completing their gestation in artificial sponges release more live mancas than females completing their gestation in natural sponges in the field. These results indicate that female fitness in artificial sponges equals or exceeds female fitness in natural sponges, and substantiates the use of artificial sponges in studies of this species' breeding biology (Shuster, 1992a).

(2) Female density in spongocoels evidently has no effect on female fecundity. Although the sample was relatively small, these results suggest that fitness variation among females within breeding aggregations may be low, especially since the maximum female density in this experiment exceeded the average density of females in natural spongocoels nearly 4-fold (Shuster & Wade, 1991a). Aggregations of females in spongocoels do not mutually deplete food resources because, like many sphaeromatid species, gravid *P. sculpta* females cannot feed (Harrison, 1984; Shuster, 1991b). Moreover, the nature of food capture by sponges in which a current of water is continuously circulated through the spongocoel (Brusca & Brusca, 1990) makes anoxic conditions for spongocoel residents unlikely. Since females in this species generally do not transport

unfertilized ova to their marsupia (Shuster, 1992a), and since all undeveloped embryos identified in these experiments were found in this location, differences in numbers of undeveloped embryos among females are unlikely to have arisen from differential fertilization success among the female groups.

(3) The fecundity of females gestating embryos in cups exceeds that of females gestating embryos in spongocoels. This potential fitness difference is probably seldom realized in nature since to date, gravid females in this species have been collected only from natural spongocoels in the field (Shuster, pers. obs.). However, the depressed fitness of females gestating in spongocoels, combined with the apparent necessity of spongocoels for female reproduction in nature, suggests that other selection, such as predation, maintains the tendency for females to brood their embryos in protected locations.

Predation on *P. sculpta* by visual predators is evidently intense. Not only are individuals cryptically pigmented (Shuster, 1991b), but preliminary experiments show that exposed females are easy prey for reef fish and octopods (Shuster & Voight, unpubl. data). If female fitness varies little once females join a breeding aggregation, but is near zero if one is not found, selection may act primarily on female abilities to accurately locate secure breeding sites. Females in this species do not appear to be attracted to male or sponge characteristics, but they are attracted to breeding aggregations, usually consisting of a male and several females (Shuster, 1990; Shuster & Wade, 1991b; Shuster et al., in review). Perhaps the scent produced by aggregations of already-breeding isopods reliably indicates the location of long-standing, and thus relatively secure sites in which to mate and brood progeny. Olfactory location of breeding sites may explain these females' tendency to be attracted to and aggregate within spongocoels containing assemblages of other breeding isopods even though aggregation itself may have little effect on female fecundity.

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