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The use of artificial sponges as breeding habitat by *Paracerceis sculpta* (Holmes) (Crustacea: Isopoda)

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Abstract: Artificial cavities constructed of a synthetic polymer, FHP-3000, were used as substitutes for calcareous sponges [*Leucetta losangelensis* (de Laubenfels)] normally used as reproductive habitat by *Paracerceis sculpta* (Holmes), a Gulf of California isopod crustacean. This paper demonstrates that: (1) artificial sponges adequately simulate natural sponges under laboratory conditions; (2) α -males in this species colonize spongocoels more readily than sexually receptive females; (3) isopods do not discriminate between artificial sponges containing and not containing a suspension of natural sponges; i.e., isopods may use cues other than waterborne chemicals produced by sponges to locate reproductive habitat; (4) α -males that have already occupied artificial sponges do not appear to recolonize artificial sponges more readily than naive α -males; (5) neither sexually receptive nor gravid (nonreceptive) females tend to form aggregations within spongocoels in the absence of α -males; and (6) α -males discriminate osculum diameter when colonizing spongocoels, i.e., they prefer oscula most closely matching their own body diameter, but do not discriminate sponge complexity or spongocoel volume. These results indicate that artificial sponges provide functional substitutes for this crustacean's natural reproductive habitat, and may facilitate experiments usually prevented for species that inhabit living substrata such as sponges or tunicates.

Key words: Artificial habitat; Colonization; Isopod; *Paracerceis*; Reproduction; Sponge

INTRODUCTION

Marine crustaceans commonly inhabit cavities in hard and soft substrata (Menzies, 1954; Caldwell & Dingle, 1976; Hatzios & Caldwell, 1983; Nash et al., 1984; Borowsky, 1985; Steger, 1987; Upton, 1987; Wada, 1987; Karnofsky et al., 1989; Christy & Salmon, 1991; Cowan, 1991). These structures variously provide protection against predators, surfaces for processing food, sites for courtship and mating, and nurseries for rearing young. For many species, competition for suitable cavities can be intense, and elaborate behaviors and specialized morphologies appear to have evolved specifically in the context of habitat utilization and defense (Caldwell & Dingle, 1975, 1976, 1979; Caldwell & Lamp, 1981; Caldwell, 1979, 1982; Shuster, 1987a; Adams & Caldwell, 1990; Christy & Salmon, 1991). Cavity-dwelling insects (Eberhard, 1979, 1987; Otronen, 1988) and fish (Marrors & Nursall, 1983; Hastings, 1988, 1991; Cote

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& Hunte, 1989; McGehee, 1989) exhibit suites of characters that are remarkably convergent with those observed in infaunal crustaceans. While cavity life appears to exert a prevailing influence on morphological, behavioral and life history evolution in these organisms, many of their specializations are poorly known: cavities shield their residents from the researchers as well as from attacks by predators or rivals. Organisms that inhabit living substrata such as sponges or tunicates, moreover, are particularly difficult to study because living substrata are often difficult to manipulate in nature and frequently do not survive well during laboratory experiments.

The purpose of this paper is to demonstrate the suitability of artificial cavities constructed of a synthetic polymer, as substitutes for the natural sponge habitat of *Paracerceis sculpta* (Holmes), a marine isopod crustacean inhabiting the northern Gulf of California. This paper describes: (1) the colonization preferences of isopods that were given a choice between artificial and natural sponges; (2) the colonization behavior of males, sexually receptive females and gravid females; and (3) whether isopods discriminate the physical characteristics of sponges when selecting sites for reproduction.

ASSOCIATION OF *PARACERCEIS SCULPTA* WITH *LEUCETTA LOSANGELENSIS* SPONGES

Like many members of the family Sphaeromatidae, *P. sculpta* exhibits conspicuous sexual dimorphism (Holmes, 1904; Hansen, 1905; Holdich, 1971; Iverson, 1982). Most males are larger than females and are equipped with robust pleotelsons and elongated uropods (Fig. 1). This species is nocturnal, and both sexes spend most of their prereproductive lives feeding on subtidal coralline algae (Shuster, 1991a). Following their adult molt, males with elongated uropods (α -males; Shuster, 1987b) swim from algae to the mid-intertidal zone where they establish breeding territories in the spongocoels of the calcareous sponge, *Leucetta losangelensis* (de Laubenfels) (Shuster, 1986, 1987a). α -males situate themselves in spongocoels with their uropods and telsons protruding from the spongocoel osculum.

Sexually mature females leave algae before their final molt and swim to sponges, where they are attracted to spongocoels containing α -males and other breeding females. Following a brief courtship (Shuster, 1990, 1992), females enter spongocoels, molt and mate. Females deposit embryos into ventral brood pouches (Shuster, 1991b), and remain within spongocoels during gestation. As successive females enter spongocoels and become gravid, individual α -males may accumulate aggregations of ≥ 19 females (Shuster, 1987b). 3–4 wk after females become gravid, young isopods (mancae) emerge from brood pouches, disperse from the spongocoel and settle on coralline algae to feed. Females reproduce once in their lives and die soon after parturition, thus, females in this species are semelparous (Shuster, 1991b).

The association of *P. sculpta* with a living reproductive habitat presents a number of problems for analysis of this isopod's reproductive behavior. *Leucetta* sponges require hard substrata for attachment, and isopods primarily inhabit sponges that are

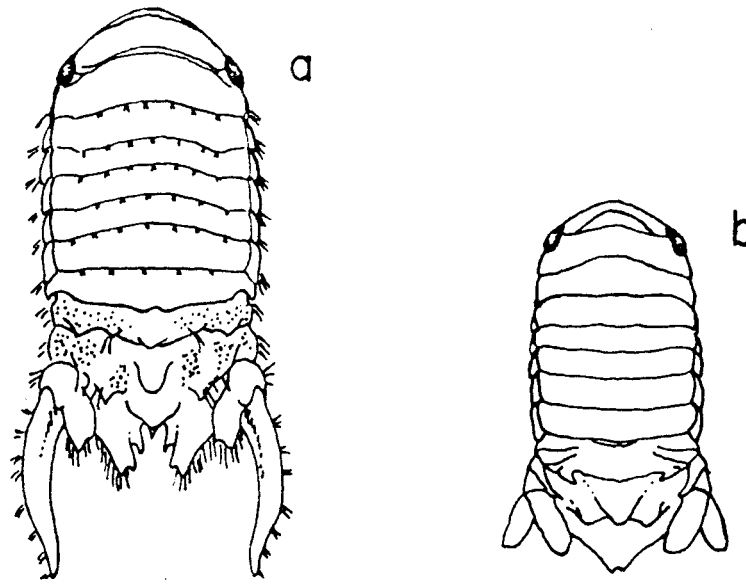


Fig. 1. *P. sculpta* adults: a. ♂-male; b. female; horizontal bar, 1 mm (redrawn from Brusca, 1980, and Shuster, 1990).

submerged in tidepools at low tide. Sponge distribution is therefore usually limited to sheltered areas in boulder fields or under ledges on the coquina limestone reef platform where sponges are nearly or completely obscured from view (Shuster, 1991a). It is a simple matter to remove sponges from rocks and transport them to the laboratory, but even with flowing seawater and a daily supply of suspended organic material as food, sponges are difficult to maintain in aquaria for long periods of time. Since isopods abandon dead or dying sponges, and since natural sponges deteriorate within a few days in the laboratory, long-term experiments using sponges are difficult or impossible. Moreover, since *Leucetta* sponges are highly irregular in shape, in size, and in spongocoel characteristics (Shuster, 1987b, 1991a), standardization of sponge characters for repeated analysis of behavior or colonization preferences using natural sponges is complicated and imprecise. Natural sponges are thus poorly suited for field and laboratory observations of isopod reproductive biology.

CONSTRUCTION OF ARTIFICIAL SPONGES

A synthetic polymer, FHP-3000, also called "Biosponge" by its inventors (J. Bonaventura and associates, Biomedical Marine Laboratory, Woods Hole, Massachusetts, and Duke University Marine Laboratory, Beaufort, North Carolina), simulates the color, texture and evidently even some of the water circulation characteristics of *L. losangelensis*. Shuster (1989b, 1990, 1991a, in press) and others (S. Palumbi,

pers. comm.) have successfully used this material to simulate natural sponges in field and in laboratory experiments. The prepolymer, a viscous, honey-like substance, when mixed with freshwater, forms a foamy material that may be molded into nearly any configuration. I constructed artificial sponges that closely resembled natural sponges by pouring the rapidly setting foam into small containers (bottle caps), pressing plastic-coated wire of the desired diameter or a spongocoel mold constructed of wax, into the foam to form "spongocoels", and then trimming the set foam into a natural shape. Artificial sponges constructed in this way were inert, reusable and standardized in shape and size for experiments in which sponge characteristics were held constant. Unless otherwise indicated, all sponges used in the experiments below were of standardized dimensions: diameter = 20 mm, osculum diameter = 3 mm, spongocoel volume = 7.23 cm³. Between experiments, artificial sponges were rinsed and squeezed out at least 10 times in freshwater. This procedure removes any evidence of residual scent left by previous residents.

EXPERIMENTAL ANIMALS

"Receptive" females in these experiments were females that had entered the spongocoels of α -males in the field, but had not yet undergone a reproductive molt (Shuster, 1990). Such females usually undergo their reproductive mounts 6–50 h after entering spongocoels (Shuster, 1991a). Isopod molts are biphasic (i.e., the cuticle is shed in two halves) and females become available for mating only after shedding the posterior portion of their cuticle in their final preadult molt (Shuster, 1991b). "Gravid" females in these experiments were females that had completed their reproductive molt and had deposited embryos into their brood pouches. Females in this condition can no longer be mated by males (i.e., they are nonreceptive).

EXPERIMENTS

COLONIZATION OF ARTIFICIAL SPONGES BY α -MALES AND RECEPTIVE FEMALES

Methods

Before using artificial sponges in laboratory experiments, it was necessary to determine: (1) whether males were more likely to colonize spongocoels than females; and (2) whether isopods discriminated among artificial and natural sponges. Collections of adults from *Leucetta* spongocoels suggest that α -males establish breeding territories and then are located and joined in spongocoels by females (Shuster, 1987a,b, 1990, 1991a). To test the hypothesis that α -males rather than receptive females colonize spongocoels, 50 α -males and 50 premolt females were individually released into 225-ml white plastic cups containing seawater and one artificial sponge. The positions of all isopods in cups were recorded 24 h later.

TABLE I

Comparison of artificial sponge colonization by α -males and sexually receptive females after 24 h.

	In	Out	N
α -Males	31	19	50
Receptive females	8	42	50
Totals	39	61	100

α -males colonize artificial sponges more readily than females ($G = 23.01$, $P < 0.001$).

Results

α -males entered artificial sponges significantly more readily than receptive females in 24 h (G test, $P < 0.001$; Table I). This result is consistent with the hypothesis that α -males rather than receptive females colonize spongocoels in the field (Shuster, 1990).

DISCRIMINATION OF NATURAL AND ARTIFICIAL SPONGES BY α -MALES

Methods

To determine whether α -males discriminate between artificial sponges and natural sponges, I first constructed experimental arenas that would permit natural sponges to be maintained in flowing seawater with artificial sponges. The arenas consisted of a Plexiglas grid with 144 $7 \times 7 \times 7$ -cm cells. The bottom of the grid was closed with a sheet of fine nylon mesh that was secured in place with a 60×60 -cm piece of 1.25-cm plastic egg crate material, and the entire grid was suspended in an 86-l flowing seawater table that circulated water within each cell. The sea table's turnover rate was 41 l/h, thus water bearing chemicals emitted by sponges was unlikely to pool substantially within experimental arenas. *Leucetta* sponges were removed from rocks in the intertidal zone and transported to the laboratory in ziplock bags containing seawater. These natural sponges were all ≈ 20 mm in diameter and possessed a single osculum ≈ 3 mm in diameter. One natural sponge and one artificial sponge were placed in each of 50 cells, and each of these experimental cells (NS + AS) was separated by at least one empty cell per full side (Fig. 2). One α -male was released in each of the experimental cells and the positions of α -males within cells were recorded 24 and 48 h later.

Because chemical cues emitted from natural sponges could influence α -male colonization of artificial sponges in the same cell, colonization behavior of α -males in experimental cells (NS + AS) was compared with colonization behavior of α -males in two controls: (1) in Control A, 50 α -males were allowed to choose between two natural sponges (NS + NS); (2) in Control B, 50 α -males were allowed to choose between two artificial sponges (AS + AS).

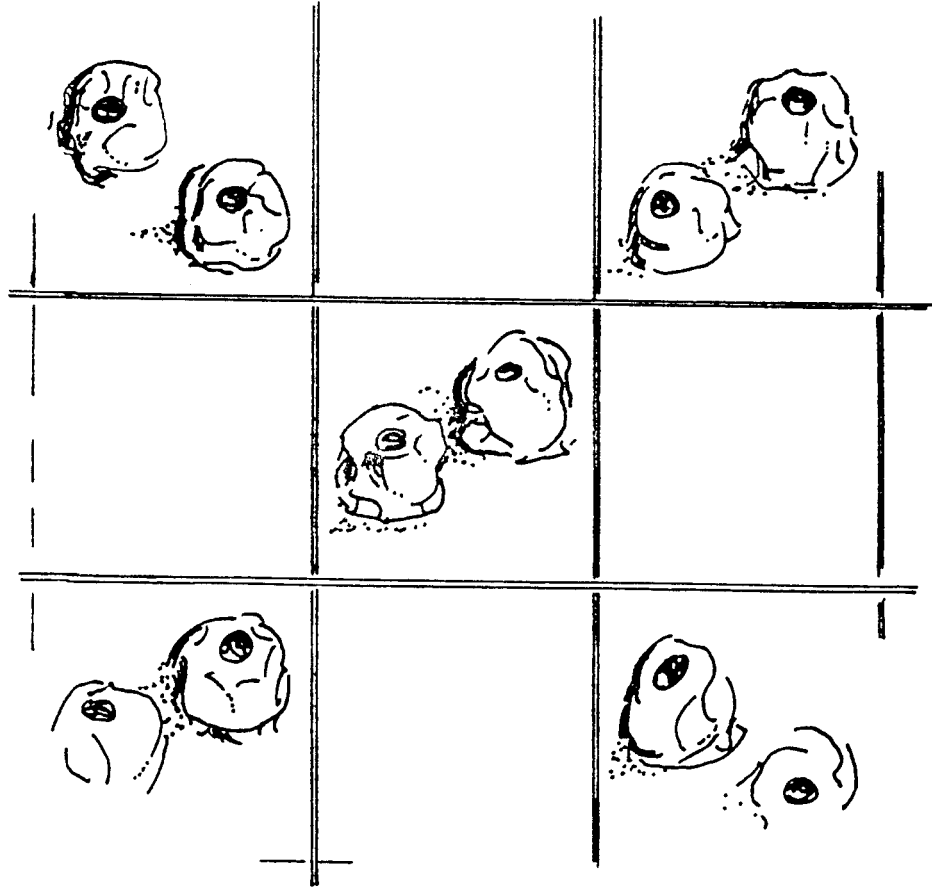


Fig. 2. Arrangement of sponges in cells of Plexiglas grid used to determine whether α -males discriminate between artificial and natural sponges. All cells containing sponges and isopods were separated from such cells by at least one empty cell per side.

Results

In cells containing one natural sponge and one artificial sponge (NS + AS), α -males colonized both types of sponges and showed no preference for natural sponge over artificial sponges in 24 or 48 h (Binomial test, $P = 0.61$, $N = 15$ and 0.82 , $N = 20$, respectively). When colonization rates for the experimental treatments were compared with colonization rates for Controls A (NS + NS) and B (AS + AS), α -male occupancy in Control B lagged behind Control A (but not behind the Experimental group) in 24 h (G test, $P < 0.01$, $N = 150$, 50 α -males/treatment; Table II). By 48 h, however, occupancy of the Experimental and both control treatments were equal (G test, $P > 0.20$; Table II). Natural sponges were still in good condition after 72 h in the flowing sea-

TABLE II
Sponge colonization by α -males: experimental and controls.

	24 h		48 h		N
	In	Out	In	Out	
Experimental (NS + AS)	15	35	20	30	50
Control A (NS + NS)	23	27	25	25	50
Control B (AS + AS)	9	41	26	24	50
Totals	47	103	71	79	150

Sponge occupancy among the three treatments was NOT EQUAL after 24 h ($G = 9.30$, $P < 0.001$); Occupancy among three treatments WAS EQUAL after 48 h ($G = 1.57$, $P > 0.20$); Experimental vs. Control A: NS in 24 h ($G = 2.69$, $P > 0.10$); Experimental vs. Control B: NS in 24 h ($G = 1.95$, $P > 0.10$); Occupancy between Controls A and B was NOT EQUAL after 24 h ($G = 9.08$, $P < 0.005$).

water table, and α -males which colonized natural sponges in 24 h showed no signs of abandoning their spongocoels even after 72 h.

SENSITIVITY OF α -MALES TO CHEMICAL CUES USING ARTIFICIAL SPONGES

Methods

To determine if chemical cues present in natural sponges could be simulated in artificial sponges, I ground up freshly collected natural sponge in seawater and mixed the slurry into the prepolymer used to make new artificial sponges. Each treated artificial sponge contained $\approx 1 \text{ cm}^3$ of natural sponge slurry. 42 α -males were placed in separate cells and allowed to choose between one treated artificial sponge and one same-sized, untreated artificial sponge. The positions of α -males were examined in 24 and in 48 h.

Results

The initial delay in colonization of artificial sponges in the first experiment (see above) suggests that isopods may use chemical cues to locate sponges. α -males, however, showed no preference for artificial sponges containing a suspension of natural sponge slurry over artificial sponges without the suspension in 24 or in 48 h ($G = 0.13$, $P > 0.50$, $N = 84$).

CONDITIONING OF α -MALES TO ARTIFICIAL SPONGES

Methods

To determine if α -males become conditioned to artificial sponges, i.e., if α -males colonize artificial sponges more readily after having already encountered and occupied

them. I removed 20 α -males from artificial sponges in which α -males had established themselves 48 h earlier. I placed these conditioned α -males into 225-ml cups containing seawater and a different artificial sponge than the one they previously occupied. As a control, I released 20 unconditioned α -males into cups containing seawater and an artificial sponge. The positions of conditioned and unconditioned α -males in cups were recorded 24 and 48 h later.

Results

α -males that had previously occupied artificial sponges did not enter novel artificial sponges more frequently than unexperienced α -males, thus α -males did not appear to become conditioned to artificial sponges ($G = 2.59$, $P > 0.10$, $N = 20$ and $G = 1.09$, $P > 0.10$, $N = 20$, for 24 and 48 h, respectively).

COLONIZATION OF ARTIFICIAL SPONGES BY RECEPTIVE AND GRAVID FEMALES

Methods

In nature, receptive and gravid females are occasionally found in spongocoels lacking α -males, either singly or in aggregations of up to 15 other gravid females (Shuster, 1986). To determine if receptive females will colonize artificial sponges and form aggregations with other females within spongocoels in the absence of α -males, (1) three sets of three receptive females were released into separate 225-ml cups containing seawater and three standard-sized artificial sponges, and (2) 50 sets of three gravid females each released into separate 225-ml cups containing seawater and three standard-sized artificial sponges. The positions of females in each cup and the frequencies of single- and group-occupancy by gravid females were recorded 24 and 48 h later.

Results

None of the three groups of receptive females aggregated in spongocoels within 24 or 48 h. In two cups, a single receptive female colonized one of the spongocoels, but colonization did not occur more frequently than expected by chance (binomial test, $P = 0.09$, $N = 9$). Thus, although the sample size is small, receptive females do not appear to aggregate in sponges in the absence of α -males.

Gravid females entered spongocoels and aggregations of two, but not three females, were observed. The distributions of gravid females in artificial spongocoels were not significantly different, however, from a Poisson distribution after 24 and 48 h ($\chi^2 = 1.08$, $P > 0.25$, $N = 144$, and 1.33 , $P > 0.25$, $N = 65$, respectively; Table III). Thus, while gravid females will move into empty spongocoels, they do not do so more frequently than expected by chance.

TABLE III
Sponge colonization by gravid females.

N females sponge	24 h	48 h
0	111	40
1	31	21
2	2	4
3	0	0
Totals	144	65

50 sets of three gravid females each were released into separate cups (one set of females cup) containing seawater and three artificial sponges. Distributions of females in sponges after 24 and 48 h were not significantly different from a Poisson distribution ($\chi^2 = 1.08$, $P > 0.25$, and 0.51 , $P > 0.50$, respectively).

DISCRIMINATION OF ARTIFICIAL SPONGE CHARACTERISTICS BY α -MALES: EFFECTS OF SPONGE COMPLEXITY, OSCULUM DIAMETER AND SPONGOCOEL VOLUME

Methods

To determine if α -males discriminate sponge complexity, 40 α -males were placed in individual cups and allowed to choose between a single- and a double-osculum artificial sponge. Both artificial sponges were of similar external dimensions, and all spongocoels were the same size. The positions of α -males were recorded in 24 and in 48 h.

α -males obtain a positional advantage against intruders in fights over spongocoel possession (Shuster, 1990). To determine, therefore, if α -males discriminate osculum diameter and if different-sized α -males prefer different-sized oscula, three body length classes of α -males (5.23–5.85 mm, $N = 24$; 6.0–6.61 mm, $N = 25$; 6.75–7.38 mm, $N = 25$) were allowed to choose from among three same-sized artificial sponges with small (2 mm), medium (3 mm) and large (4.5 mm) diameter oscula. The positions of α -males were examined in 24 and in 48 h.

Multiple regression analyses showed no correlation between spongocoel volume and the harem sizes of α -males in nature (Shuster, 1987b, 1991a), but a context for α -male discrimination of spongocoel volume does exist. If large spongocoels hold more females, α -males guarding large spongocoels could experience greater reproductive success than males guarding smaller spongocoels, thus favoring the ability to discriminate spongocoel volume among α -males. To determine, therefore, if α -males discriminate spongocoel volume, 30 similar-sized α -males ($\bar{x} \pm SD = 6.15 \pm 0.56$ mm) were allowed to choose from among three artificial sponges with similar external dimensions, but with small (41.89 mm³), medium (268.08 mm³) and large (575.96 mm³) spongocoel volumes. The positions of α -males were recorded in 24 and in 48 h.

Results

α -males showed no preference for complex (two oscula) artificial sponges over simple (one osculum) artificial sponges in 24 and in 48 h ($G = 0.00$, $P > 0.90$, $N = 40$ and

$G = 1.49$, $P > 0.10$, $N = 40$ for 24 and 48 h, respectively). α -males did, however, discriminate osculum diameter relative to their own body size (Spearman's $r = 0.280$, $P < 0.05$, Fig. 3). Consistent with observations of individuals in the field (Shuster, 1991a), smaller males preferred small oscula and larger males preferred larger oscula.

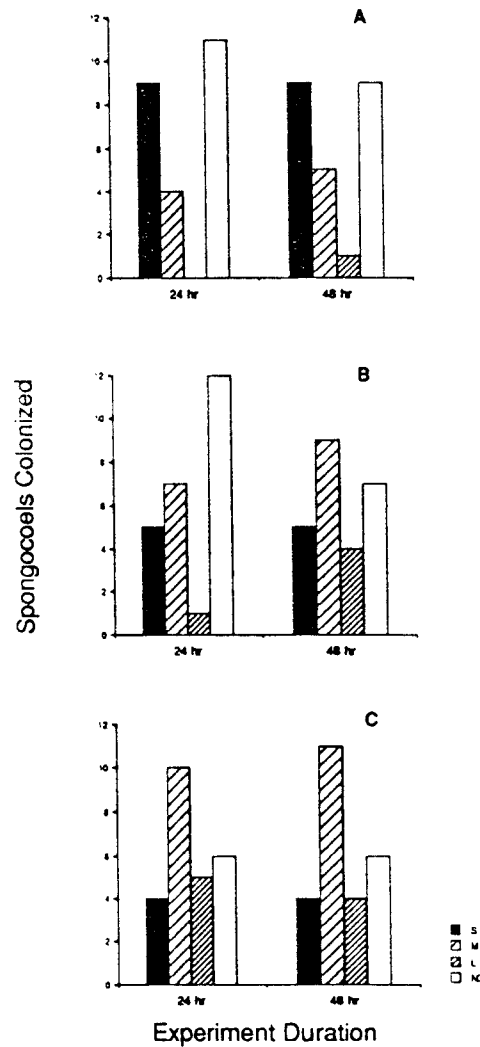


Fig. 3. Discrimination of osculum diameter in artificial sponges by: A, small α -males (5.23–5.85 mm in length); B, medium-sized α -males (6.00–6.61 mm in length); and C, large α -males (6.75–7.38 mm in length); histograms show number of α -males colonizing small (S, small osculum diameter = 2 mm, ■), medium-sized (M, medium osculum diameter = 3 mm, ▨) and large (L, large osculum diameter = 4.5 mm, ▩) diameter oscula (NC, no choice, □); relationship between α -male body length and osculum diameter is significant (Spearman's $r = 0.28$, $P < 0.05$).

TABLE IV
Artificial sponge colonization by α -males: discrimination of spongocoel volume.

	Spongocoel volume				N
	Small	Medium	Large	No choice	
24 h	7	3	2	18	30
48 h	11	2	1	16	30

α -males showed no significant preference for spongocoel volume after 24 h ($G = 3.49$, $P > 0.10$) but preferred small spongocoels (see text) after 48 h.

Interestingly, α -males showed no preference for large-volume spongocoels, and in fact appeared to discriminate against them. No preference for any sponge volume was clear after 24 h, but after 48 h, α -males preferred the smallest spongocoels ($G = 12.99$, $P < 0.005$, Table IV).

DISCUSSION

α -males showed no preference for natural sponges over artificial sponges in choice tests (NS + AS trials). Comparison of controls (NS + NS vs. AS + AS trials), however, suggested initial discrimination by α -males against artificial sponges, perhaps because artificial sponges lack certain chemical or tactile cues. Such cues are probably quite subtle, as artificial sponges treated with a suspension of natural sponge slurry were no more attractive than untreated artificial sponges.

Natural sponges remained in apparently good condition in sea tables for > 72 h. While inconspicuous deterioration of natural sponges in sea table chambers by 48 h could have caused isopods to leave natural sponges and move into artificial sponges, artificial sponges were occupied by isopods in high frequency, even in the presence of fresh, natural sponges. Moreover, α -males assumed apparently normal spongocoel guarding behavior in artificial sponge oscula (Shuster, 1989a, 1992). Thus, although not perfect, artificial sponges appear to adequately simulate the essential characteristics of natural sponges and spongocoels as far as α -males (and other reproductive individuals in *P. sculpta*, see Shuster, 1989b, 1990, 1991a; Shuster & Wade, 1991b) are concerned.

α -males entered spongocoels more readily than receptive females, substantiating the hypothesis that α -males establish breeding territories to which receptive females are attracted (Shuster, 1990, 1992; Shuster & Wade, 1991a,b). Although the sample size was small, receptive females showed no tendency to aggregate within spongocoels in the absence of α -males. Receptive females do, however, seem attracted to spongocoels containing α -males and several gravid females (Shuster, 1990; Shuster & Wade, 1991a).

Thus, aggregation behavior by receptive females appears to occur in the context of reproduction and does appear to represent "female copying (Wade & Pruett-Jones, 1990)", a form of mate selection in which females copy the mate selections of other females.

Gravid females colonized spongocoels singly, but showed no strong tendency to form aggregations similar to those found in spongocoels in the field (Shuster, 1986). Single, gravid females found in *Leucetta* spongocoels may represent females that left or were evicted from the spongocoels in which they were mated, and which later situated themselves in other spongocoels. Such females may also remain in spongocoels that α -males abandon or from which α -males have been removed by predators. That gravid females do not readily form aggregations in artificial sponges suggests that groups of gravid females found in *Leucetta* spongocoels without attending α -males (Shuster, 1990, 1991a) may also represent breeding aggregations from which α -males were removed by predators, or which α -males have abandoned.

As predicted by multiple regression (Shuster, 1987a, 1991a), α -males did not discriminate sponge complexity. α -males did, however, discriminate osculum diameter. This latter result is consistent with behavioral data indicating that resident α -males gain a positional advantage within spongocoels (Shuster, 1990, 1992). Steger (1985) has shown that the internal dimensions of cavities occupied by stomatopods (*Gonodactylus bredini*) strongly influence the ability of residents to defend them. Stomatopods are most successful at defending cavities 10% larger than their body volume and with slightly tapered entrances. If a similar relationship holds for α -males in *P. sculpta*, α -males may attempt to match their body size with an osculum from which they are less likely to be evicted.

That α -males did not prefer larger spongocoels is somewhat paradoxical given that larger spongocoels could contain larger harems and thus enhance male reproductive success. Large spongocoels, like large oscula, however, may be difficult to defend against the other male morphs that coexist with α -males in this species (β -males that mimic female behavior and morphology and γ -males that are tiny and inconspicuous (reviews in Shuster, 1991a, 1992) and which attempt to invade spongocoels containing receptive females. Moreover, at least within the range of harems sizes examined, increased female density within a spongocoel does not adversely affect female fecundity (Shuster, 1986). Thus, although tiny spongocoels place an upper limit on harem size, α -male reproductive success may not usually be limited simply by spongocoel volume.

Artificial sponges have proven useful for examining the behavior of males and females around sponges (Shuster, 1990, 1992). Furthermore, artificial sponges permit manipulation of densities of reproductive individuals in spongocoels to determine the affects of receptive female density and male-male competition on variation in male reproductive success (Shuster, 1989b; Shuster & Wade, 1991b). Artificial sponges allow correlational data on isopod distributions in the field to be substantiated by direct observation of discrimination behavior by isopods themselves, and the reusabil-

ity of artificial sponges permits repeatable manipulations of sponge and social variables that may influence isopod colonization characteristics. The suitability of artificial sponges for use in laboratory experiments, however, is best demonstrated by the fact that females gestating in artificial sponges suffer no discernible loss of fecundity (Shuster, 1986). Such subtle aspects of this species' reproductive biology would be difficult or impossible to conduct using natural sponges in the laboratory or in the field.

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REFERENCES

- Adams, E. S. & R. L. Caldwell, 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean, *Gonodactylus bredini*. *Anim. Behav.*, Vol. 39, pp. 706–716.
- Borowsky, B., 1985. Differences in reproductive behavior between two male morphs of the amphipod crustacean *Jassa falcata* Montague. *Physiol. Zool.*, Vol. 58, pp. 497–502.
- Brusca, R. C., 1980. *Common intertidal invertebrates of the Gulf of California*. University of Arizona Press, Tucson, Arizona, second edition, 513 pp.
- Caldwell, R. L., 1979. Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festai*: evidence for chemically mediated individual recognition. *Anim. Behav.*, Vol. 27, pp. 194–201.
- Caldwell, R. L., 1982. Interspecific chemically mediated recognition in two competing stomatopods. *Mar. Behav. Physiol.*, Vol. 8, pp. 189–197.
- Caldwell, R. L. & H. Dingle, 1975. Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften*, Vol. 62, pp. 214–222.
- Caldwell, R. L. & H. Dingle, 1976. Variation in agonistic behavior between populations of the stomatopod, *Haptosquilla glyptocercus*. *Evolution*, Vol. 31, pp. 220–223.
- Caldwell, R. L. & J. Dingle, 1979. The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. *Behaviour*, Vol. 69, pp. 255–264.
- Caldwell, R. L. & K. Lamp, 1981. Chemically mediated recognition by the stomatopod, *Gonodactylus bredini* of its competitor, the octopus, *Octopus joubini*. *Mar. Behav. Physiol.*, Vol. 8, pp. 35–41.
- Christy, J. H. & M. Salmon, 1991. Comparative studies of reproductive behavior in mantis shrimp and fiddler crabs. *Am. Zool.*, Vol. 31, pp. 329–337.

- Cote, I.M. & W. Hunte, 1989. Male and female mate choice in the redlip blenny: why bigger is better. *Anim. Behav.*, Vol. 38, pp. 78–88.
- Cowan, D.F., 1991. The role of olfaction in courtship behavior of the American lobster, *Homarus americanus*. *Biol. Bull.*, Vol. 181, pp. 402–407.
- Eberhard, W.G., 1979. The function of horns in *Podishnus agenor* (Dynastinae) and other beetles. In: *Sexual selection and reproductive competition in insects*, edited by M.S. Blum & N.A. Blum. Academic Press, New York, pp. 231–258.
- Eberhard, W.G., 1987. Use of horns in fights by the dimorphic males of *Ageopsis nigricollis* (Coleoptera, Scarabaeidae, Dynastinae). *J. Kansas Entomol. Soc.*, Vol. 60, pp. 304–309.
- Hansen, J.J., 1905. On the propagation, structure and classification of the family Sphaeromatidae. *Q. J. Microscop. Sci.*, Vol. 49, pp. 69–135.
- Hastings, P.A., 1988. Female choice and male reproductive success in the angel blenny. *Anim. Behav.*, Vol. 36, pp. 115–124.
- Hastings, P.A., 1991. Ontogeny of sexual dimorphism in the angel blenny, *Coralliozetus angelica* (Blennioidei:Chaenopsidae). *Copeia*, Vol. 1991, pp. 969–978.
- Hatzios, M.E. & R.L. Caldwell, 1983. Role reversal in courtship in the stomatopod, *Pseudosquilla ciliata* (Crustacea). *Anim. Behav.*, Vol. 31, pp. 1077–1087.
- Holdich, D.M., 1971. Changes in physiology, structure and histochemistry during the life history of the sexually dimorphic isopod, *Dynamene bideniata* (Crustacea:Peracarida). *Mar. Biol.*, Vol. 8, pp. 35–47.
- Holmes, S.J., 1904. Remarks on the sexes of the spheromids with a description of a new species of *Dynamene*. *Proc. Cal. Acad. Sci.*, Vol. 3, pp. 295–306.
- Iverson, E.W., 1982. Revision of the isopod family Sphaeromatidae (Crustacea:Isopoda:Flabellifera). I. Subfamily names with diagnosis and key. *J. Crust. Biol.*, Vol. 2, pp. 248–256.
- Karnoofsky, E.B., J. Atema & R.H. Elgin, 1989. Natural dynamics of population structure and habitat use of the lobster, *Homarus americanus* in a shallow cove. *Biol. Bull.*, Vol. 176, pp. 247–256.
- Marrors, C.H. & J.R. Nursall, 1983. The reproductive periodicity and behavior of *Ophioblennius atlanticus* (Pisces:Blenniidae) at Barbados. *Can. J. Zool.*, Vol. 61, pp. 317–325.
- McGehee, M.A., 1989. A method for studying egg masses in a benthic spawning fish. *Copeia*, Vol. 1989, pp. 201–202.
- Menzies, R.J., 1954. The comparative biology of reproduction in the wood-boring isopod crustacean, *Limnora*. *Bull. Mus. Comp. Zool. Harvard*, Vol. 112, pp. 361–388.
- Nash, R.D.M., C.J. Chapman & R.J.A. Atkinson, 1984. Observations on the burrows and burrowing behavior of *Calocaris macandreae* (Crustacea:Decapoda:Thalassinioidea). *J. Zool.*, Vol. 202, pp. 425–439.
- Otronen, M., 1988. Intra- and intersexual interactions at breeding burrows in the horned beetle, *Coprophanus ensifer*. *Anim. Behav.*, Vol. 36, pp. 741–748.
- Shuster, S.M., 1986. Reproductive biology of *Paracerceis sculpta* (Crustacea:Isopoda). Ph.D. dissertation, University of California, Berkeley, 278 pp.
- Shuster, S.M., 1987a. Male body size, not reproductive habitat characteristics predicts polygyny in a sexually dimorphic intertidal isopod crustacean, *Paracerceis sculpta* (Crustacea:Isopoda). In: *Mem. Simp. Biol. Mar. Univ. Auton. Baja Calif.*, Vol. 5, edited by G. Maligrino & H. Santoyo, Univ. Auton. Baja Calif. Sur, La Paz, B.C.S., Mexico, pp. 71–80.
- Shuster, S.M., 1987b. Alternative reproductive behaviors: Three male morphs in *Paracerceis sculpta*, an intertidal isopod from the northern Gulf of California. *J. Crust. Biol.*, Vol. 7, pp. 318–327.
- Shuster, S.M., 1989a. Female sexual receptivity associated with molting and differences in copulatory behavior among the three male morphs in *Paracerceis sculpta* (Crustacea:Isopoda). *Biol. Bull.*, Vol. 177, pp. 331–337.
- Shuster, S.M., 1989b. Male alternative reproductive behaviors in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among α -, β - and γ -males. *Evolution*, Vol. 34, pp. 1683–1698.

- Shuster, S. M., 1990. Courtship and female mate selection in a semelparous isopod crustacean (*Paracerceis sculpta*). *Anim. Behav.*, Vol. 40, pp. 390–399.
- Shuster, S. M., 1991a. The ecology of breeding females and the evolution of polygyny in *Paracerceis sculpta*, a marine isopod crustacean. In, *Crustacean sexual biology*, edited by R. Bauer & J. Martin, Columbia University Press, pp. 91–111.
- Shuster, S. M., 1991b. Changes in female anatomy associated with the reproductive molt in *Paracerceis sculpta* (Holmes), a semelparous isopod crustacean. *J. Zool. London*, Vol. 225, pp. 1–15.
- Shuster, S. M., 1992. The reproductive behaviour of α -, β -, and γ -males in *Paracerceis sculpta*, a marine isopod crustacean. *Behaviour*, Vol. 121, pp. 231–250.
- Shuster, S. M. & M. J. Wade, 1991a. Female copying and sexual selection in a marine isopod crustacean. *Anim. Behav.*, Vol. 42, pp. 1071–1078.
- Shuster, S. M. & M. J. Wade, 1991b. Equal mating success among male reproductive strategies in a marine isopod. *Nature*, Vol. 350, pp. 606–661.
- Steger, R., 1985. The behavioral ecology of a Panamanian population of the stomatopod, *Gonodactylus bredini* (Manning). Ph.D. dissertation, University of California, Berkeley, 114 pp.
- Steger, R., 1987. Effects of refuges and recruitment on gonodactylid stomatopods, a guild of mobile prey. *Ecology*, Vol. 68, pp. 1520–1533.
- Steger, R. & R. L. Caldwell, 1983. Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods (Arthropoda:Crustacea). *Science*, Vol. 221, pp. 558–560.
- Upton, N. P. D., 1987. Asynchronous male and female life cycles in the sexually dimorphic, harem forming isopod, *Paragnatha formica* (Crustacea:Isopoda). *J. Zool.*, Vol. 212, pp. 677–690.
- Wada, K., 1987. Neighbor burrow-plugging in *Ilyoplax pusillus* (Crustacea:Brachyura:Ocypodiidae). *Mar. Biol.*, Vol. 95, pp. 299–303.
- Wade, M. J. & S. G. Pruett-Jones, 1990. Female copying increases the variance in male mating success. *Proc. Natl. Acad. Sci. U.S.A.*, Vol. 87, pp. 5749–5733.