ALTERNATIVE REPRODUCTIVE BEHAVIORS: THREE DISCRETE MALE MORPHS IN *PARACERCEIS SCULPTA,* AN INTERTIDAL ISOPOD FROM THE NORTHERN GULF OF CALIFORNIA

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ABSTRACT

Paracerceis sculpta breeds in intertidal sponges, *Leucetta losangelensis,* where males employ 1 of 3 discrete alternative reproductive behaviors. Elaborate alpha-males attract females to spongocoels where mating and brooding of young by females occurs. Variance in the number of females per alpha-male is high ($N = 0$–11). Smaller beta-males, resembling females, and tiny gamma-males, resembling juveniles, invade spongocoels containing alpha-males and sexually receptive females. Alpha-, beta-, and gamma-males maintained in the laboratory do not molt or grow, and the 3 morphs differ in the relative amounts of energy they invest in somatic versus gonadal tissue (gamma > beta > alpha). Alternative male reproductive behaviors may have evolved in *P. sculpta,* since intensifying sexual selection on alpha-males allowed only the most competitive alphas to mate. Males that obtained mates by avoiding direct competition with alphas (e.g., mimicking females or stealing mates) may have persisted, despite their reduced fitness, because they experienced greater fitness than competitively inferior alphas. Similar selective pressures and thus similar male polymorphisms probably exist in other Crustacea.

Males in many animal species exhibit discontinuous variation in behaviors and morphologies that are associated with reproduction (Parker, 1970; van Rhijn, 1973; Alcock, 1979; Hamilton, 1979; Perrill *et al.,* 1978; Dominey, 1980; Gross and Charnov, 1980; Cade, 1981; Thornhill, 1981; Eberhard, 1982; Gross, 1982; Clutton-Brock *et al.,* 1982; Austad, 1984; Howard, 1984; Gross, 1985). These alternative reproductive behaviors (ARBs) occur primarily in polygynous species in which variance in male mating success is high and thus in which sexual selection is strong (Gadgil, 1972). "Behaviors" are emphasized in this terminology, since male reproductive alternatives involving only facultative shifts in reproductive tactics are by far the most common, while ARBs involving morphological differences between males are comparatively rare. Moreover, differences in reproductive morphology are usually associated with specific differences in mating behavior (Austad, 1984). Reports of ARBs are few or nonexistent for the Crustacea. This is unexpected, since many crustaceans are polygynous (Salmon, 1984) and sexual selection has been demonstrated in a variety of species (Holdich, 1968, 1971; Stein, 1976; Knowlton, 1980; Shuster, 1981; Christy, 1983; review in Salmon, 1984). The exemption of the Crustacea from what now seems a common evolutionary response to male sexual selection bears further investigation.

Glynn (1968) described two male morphs in a Caribbean isopod, *Dynamenella perforata,* that inhabits the pallial grooves of intertidal chitons. He found small, "intermediate" males within isopod aggregations consisting primarily of females and of larger and ornamented "adult" males. Although intermediates possessed penes, no reproductive activity was associated with these individuals because they lacked mature appendices masculinae and did not exhibit the enlarged uropods and elaborate telsons possessed by adult males. Glynn maintained intermediates and undifferentiated individuals in a common container, and reported that some of these individuals grew into adult males after several days. The fact that intermediates lacked fully developed appendices masculinae argues in favor of Glynn's
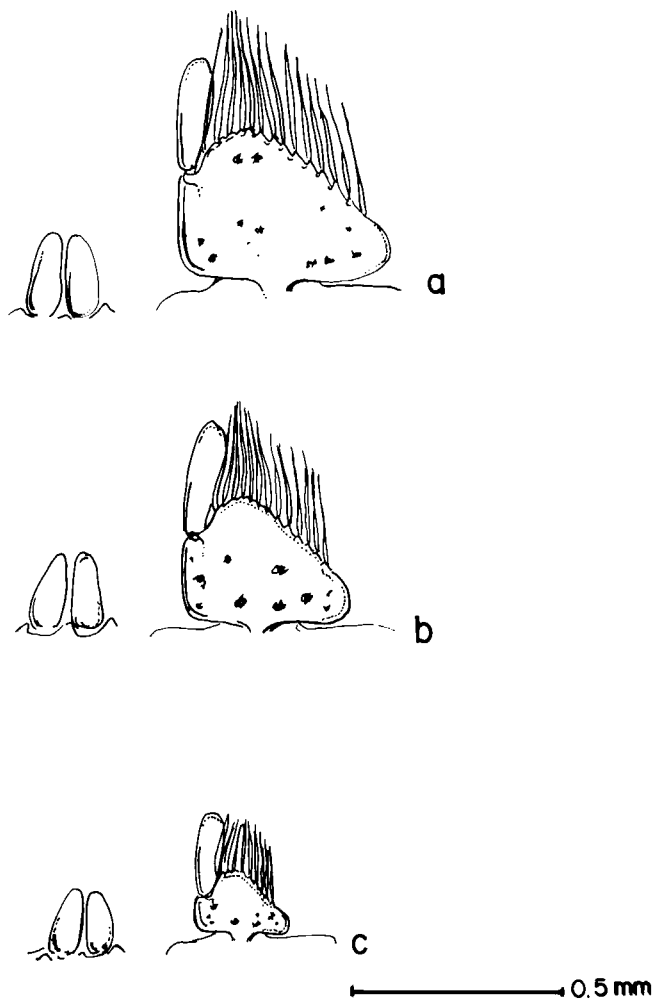
Fig. 1.   Penes and second pleopod endopodites (showing appendices masculinae on the upper medial aspect) of (a) alpha-, (b) beta-, and (c) gamma-males in *Paracerceis sculpta.*

classification of these individuals as immature. Whether undifferentiated individuals or intermediates gave rise to adults, however, was unclear, and whether intermediates possessed mature sperm-producing organs remains uncertain.

   Paracerceis sculpta is a sphaeromatid isopod inhabiting intertidal zones throughout the northern Gulf of California (Brusca, 1980). Like many sphaeromatids, the taxonomically recognized males in this species possess enlarged, rugose telsons and elongated uropods (Hansen, 1905; Iverson, 1982). I have recently discovered that two other types of males coexist with the elaborate males in this species. This paper (1) documents the existence of three discrete morphs in *P. sculpta,* (2) demonstrates that the three morphs are sexually mature and exhibit three apparently distinct reproductive behaviors, and (3) describes differences in reproductive anatomy that suggest differential energy investment toward somatic versus sperm-producing tissue among the three male morphs.
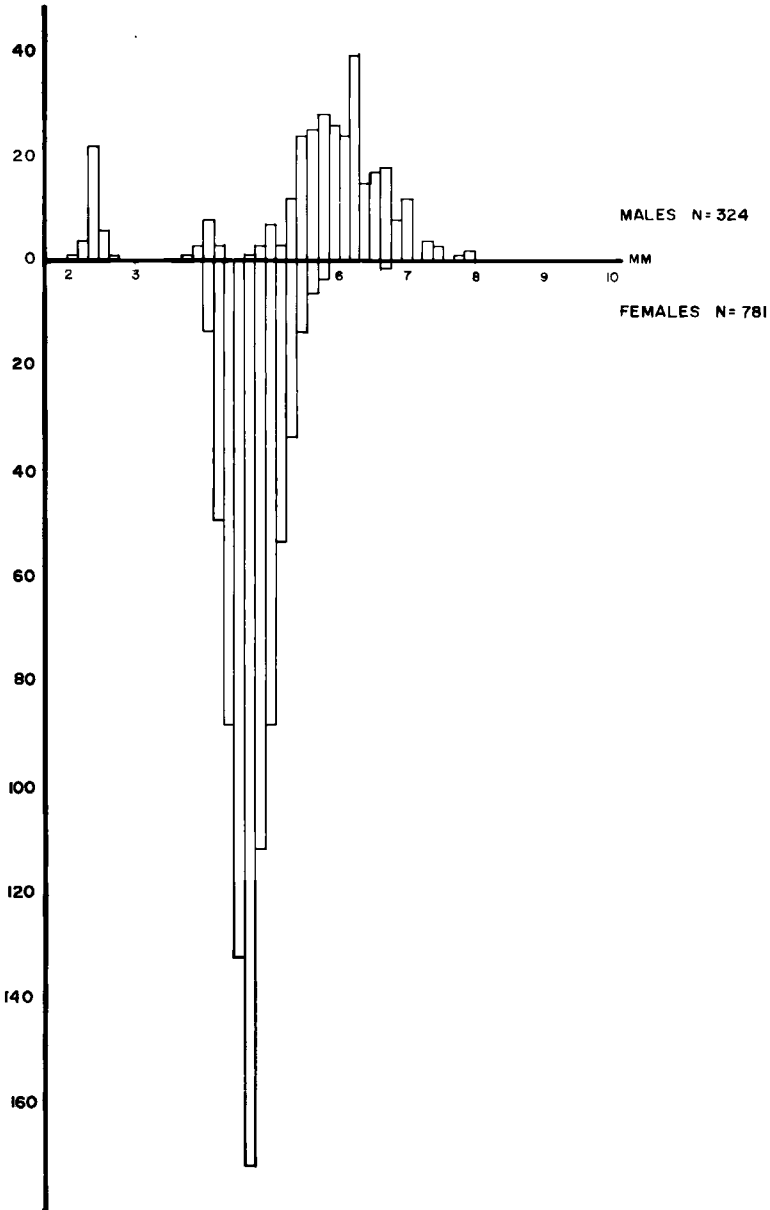
Fig. 2. Size-frequency histogram for *Paracerceis sculpta* collected from spongocoels of *Leucetta losangelensis* between October and December 1983. Upper histograms represent males and lower histograms represent females. Body lengths are in mm. For males the smallest mode represents gamma-males, the intermediate mode represents beta-males, and the largest mode represents alpha-males.

The Breeding Ecology of *Paracerceis sculpta*

The elaborate males in *P. sculpta* establish themselves in the spongocoels of a common calcareous sponge, *Leucetta losangelensis* (in Shuster, in press, and in preparation). Males position themselves at the spongocoel osculum with their

Fig. 3. The three male morphs in *Paracerceis sculpta*. Left to right, gamma, beta, alpha.

telsons and uropods protruding outward. Females are attracted to and enter these occupied spongocoels, and, once inside, undergo a molt that initiates their sexual receptivity. Mating occurs within the spongocoel and females remain therein to brood their young. Females reproduce only once, but males established in spongocoels evidently remain in the same location for several female gestations. Sponges serve only as a reproductive habitat, since males do not feed within the sponge and females lose their mouthparts in their sexual molt. Females thus provide nutrition for their developing young with stored resources alone. After emerging from females, juveniles leave the sponge to begin feeding on intertidal algae.

MATERIALS AND METHODS

Leucetta losangelensis grows abundantly in tide pools near Puerto Peñasco, Sonora, Mexico. Isopods were collected from these sponges between October and December 1983 by opening spongocoels with a sharp knife and placing each isopod breeding aggregation in a separate vial for transport to the laboratory and examination. Isopods contained in spongocoels that were damaged during collection were included in population analysis, but were excluded from breeding aggregation analysis. Mature males were identified by well-formed external genitalia (penes and appendices masculinae, Fig. 1) and seminal vesicles visible through the ventral cuticle. The body lengths of all individuals were measured to the nearest 0.15 mm using an ocular micrometer.

Fifty-five males were removed from samples and maintained in 8-ounce (227-g) plastic cups until they died. Cups were equipped with ventilated lids to minimize evaporation, and isopods were provided with algae as food (*Amphiroa* sp.) and with weekly water changes.

An additional 50 males were placed in a freezer for 10 min and then dissected in physiological saline under a stereomicroscope. The androgenic glands and seminal vesicles of each individual were exposed within the body cavity using fine forceps, and seminal vesicles were measured to the nearest 0.15 mm using an ocular micrometer.

RESULTS

The size distribution of females collected from sponges was unimodal, and all females shared the same external morphology (Fig. 2). Males, however, fell into
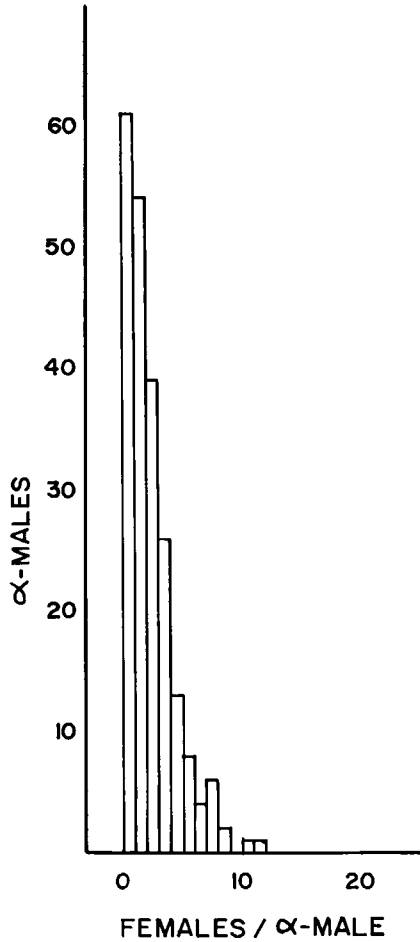
Fig. 4. Variation in the number of females per alpha-male in *Paracerceis sculpta*. *N* alpha-males = 215, median females/male = 1.

three distinct classes that differed significantly in body size and in their external morphology (Fig. 3, Table 3). Large males possessing elongated uropods and sculptured telsons were named "alpha." Intermediate-sized males lacking ornamentation and resembling females were named "beta," and the smallest males, resembling immature individuals, were named "gamma." Most occupied spongocoels contained an alpha-male and 0–11 females (215 of 404, 53%, median of females/male = 1, Fig. 4). Twenty-eight per cent of these spongocoels ($N = 61$) contained a single, unmated alpha-male. Such high variability in the number of females per alpha-male suggests that sexual selection in *P. sculpta* is extreme (Wade and Arnold, 1980). Six spongocoels contained two alpha-males. In four of these cases, spongocoels contained at least one receptive female, and in all cases, both alphas were wedged tightly together at the osculum of the spongocoel. Although I have found significant relationships between male body size and the number of females per male in two earlier years (Shuster, in press), there was no relationship between alpha-male body size and the number of females per male in this sample ($F > 0.25$, $r^2 < 0.01$).

Table 1.   Distribution of beta- and gamma-males of *Paracerceis sculpta* in spongocoels of *Leucetta losangelensis* with respect to the presence or absence of alpha-males and the reproductive condition of females. Beta- and gamma-males are most frequently found in spongocoels containing 1 alpha-male and 1 or more receptive females (median receptive females/spongocoel = 1, range = 1–4, N = 92). Total numbers of alpha-males and females collected from spongocoels are reported on pp. 322–323 and in Fig. 4. + = present; − = absent.

			Other spongocoel occupants	
Betas	Gammas	Alpha	Females	N cases
11	11	+	receptive	97
5	6	+	recently receptive	54
2	0	+	nonreceptive	35
0	2	+	−	61
0	0	−	receptive	9
0	1	−	recently receptive	7
0	1	−	nonreceptive	132
1	3	−	−	3
Total 19	24			398

Nine per cent of occupied spongocoels (N = 35) contained beta- and/or gamma-males. Both beta (N = 19)- and gamma (N = 26)-males were most frequently found in spongocoels occupied by an alpha-male and at least one sexually receptive female (Table 1). Beta- and gamma-males were also frequently found in spongocoels containing females that had recently (<36 h, Shuster, unpublished) been sexually receptive. In most cases, only one beta- or one gamma-male was present in a spongocoel, but multiple betas and gammas were also encountered (N = 7, range = 2 or 3). There was no apparent tendency for betas to associate with other betas, for gammas to associate with other gammas, or for betas to associate with gammas. Thirty-three per cent of occupied spongocoels contained only females that were gravid, were releasing offspring, or were spent (N = 132, Table 1) and less than 5% of spongocoels contained only receptive or recently receptive females.

Field-caught alpha (N = 21)-, beta (N = 13)-, and gamma (N = 19)-males maintained in the laboratory showed no significant differences in survival rates (Table 2). Moreover, in no case did males of any of the three morphs molt or grow into a different male morph.

Dissected alpha (N = 20)-, beta (N = 11)-, and gamma (N = 19)-males possessed mature androgenic glands and seminal vesicles filled with sperm. The ratio of seminal vesicle length : male body length was significantly different among the three male morphs (Kruskal-Wallis test, P < 0.001, Table 3). I split the seminal vesicles of several males of each type and teased the contained sperm onto a petri dish with a drop of physiological saline. I observed no apparent differences in the sperm borne by alpha-, beta-, or gamma-males. In all cases sperm were long (about 650 μm) and nonmotile.

DISCUSSION

In *P. sculpta,* the coexistence of three discrete male reproductive alternatives is clear. Alpha-, beta-, and gamma-males differ significantly in size and morphology, yet all three morphs possess well-formed external genitalia and mature sperm-producing organs. The three male morphs employ different reproductive behaviors, and I have demonstrated elsewhere that alpha-, beta-, and gamma-males do not differ in their ability to inseminate females or in their ability to sire viable offspring (Shuster, 1986).

Table 2. Survivorship of 3 male morphs (field-caught) of *Paracerceis sculpta* under laboratory conditions. *No significant differences (Kruskal-Wallis test, $P > 0.10$).

	Alpha	Beta	Gamma
N	21	13	21
Median days survived*	92	63	68
Range	45–141	10–133	6–129

Alphas station themselves at the osculum of spongocoels and attract females. Betas and gammas associate most frequently with alpha-males possessing still receptive females in their spongocoels. If females that have only recently become nonreceptive are included in this analysis, the relationship is even stronger (Table 1). How beta- and gamma-males enter spongocoels is unknown, but beta-males, resembling sexually mature females, may be "female mimics" and gain access to spongocoels by deceiving alpha-males. Female mimicry by males occurs in vertebrates and in insects (Morris, 1951; Dominey, 1980; Gross, 1982; Thornhill, 1981). Gamma-males were most often found in small depressions or in tight passageways within spongocoels. This behavior combined with their comparatively small size suggests that gammas may attempt to be inconspicuous to alpha-males, and may "sneak" into spongocoels. Sneak or satellite male behavior is common in many animals (Parker, 1970; van Rhijn, 1973; Perrill *et al.*, 1978; Alcock, 1979; Dominey, 1980; Cade, 1981; Gross, 1982; Clutton-Brock *et al.*, 1982; Fairchild, 1984; Howard, 1984; Waltz and Wolf, 1984; Gross, 1985).

Austad (1984: 309) has proposed a taxonomy for ARBs which "classifies reproductive alternatives according to whether they represent genetic differences between individuals (genotypic vs. phenotypic alternatives), whether the alternatives can be expected to manifest equal or unequal fitnesses (isogignous vs. allogignous alternatives) and whether individuals may switch back and forth between alternatives (reversible vs. irreversible alternatives)." Precisely how *P. sculpta*, or for that matter how most species studied to date fit into this scheme, remains unclear. Data on genetic as well as on fitness differences between male ARBs are available for only a fraction of the species in which they are known. Austad's elegant framework does, however, show that future research on ARBs must include analyses of genetic and/or fitness differences between individuals. Using Austad's last category, the three male morphs in *P. sculpta* are evidently irreversible. Growth in males seems to end after sexual maturity is reached. Determinate growth is common among the dynamenine Sphaeromatidae (Holdich, 1971; Iverson, 1982).

Table 3. Body length, seminal vesicle length (SVL), and seminal vesicle (SV) : body length (BL) ratio for three male morphs of *Paracerceis sculpta*. ***Kruskal-Wallis $H = 43.58$, $P < 0.001$. **Kruskal-Wallis $H = 8.72$, $P < 0.01$. *Kruskal-Wallis $H = 37.04$, $P < 0.001$.

	Alpha	Beta	Gamma
N	21	11	**18**
Median body length (mm)***	5.85	4.15	2.31
Range	5.05–6.92	3.60–4.77	2.15–2.46
Median SVL (mm)**	1.89	1.78	1.94
Range	1.56–2.50	1.38–1.94	1.38–2.22
Median SV:BL ratio*	0.34	0.43	0.82
Range	0.25–0.41	0.33–0.49	0.60–0.96

The differences in relative seminal vesicle size (and thus in the relative amount of sperm produced) between the three male morphs suggest that gamma-males invest the most energy, beta-males invest intermediate energy, and alpha-males invest the least energy in sperm production. Increased sperm production suggests that beta- and especially gamma-males may engage in ejaculate competition with alpha-males and with each other (Dominey, 1980). The relative energy cost involved with the production of abundant sperm compared to the cost of elaborate somatic structures is unknown, but the enormous size of sperm in this species suggests that sperm competition (as for beta- and gamma-males) need not be less expensive than direct male-male competition (as for alpha-males).

How three male morphs may have evolved in this species is open to speculation. Evolutionary mechanisms provided by Gadgil (1972) and by Eberhard (1982), however, seem appropriate for *P. sculpta.* The elaborate posteriors and large body size of alpha-males seem to have arisen, at least in part, as a result of competition among alpha-males for access to females. Alpha-males were observed attempting to force their way into spongocoels containing other alphas and their harems, and although no relationship was indicated in this sample, harem size has correlated with alpha-male body size in other samples (Shuster, in press). An evolutionary history favoring large and elaborate males would have placed small males with alpha morphology at increasingly severe reproductive disadvantage. Intensifying male-male competition may have favored males capable of obtaining mates in ways not involving direct competition with large alpha-males (Gadgil, 1972), and since the fitness of these non-alphas would probably have exceeded that of the smallest alpha-males, even marginal success by non-alphas would have been sufficient to establish them in the population (Eberhard, 1982). How three morphs are presently maintained in *P. sculpta* depends on whether the differences between males are genotypic or phenotypic. This, as mentioned, is still unknown.

Gadgil (1972) predicted that two male types would arise in species under intense sexual selection; *P. sculpta* exhibits three. Three male morphs also occur in sunfish (*Lepomis* sp.) (Dominey, 1980; Gross, 1982; Gross and Charnov, 1980) and in ruffs (*Philomachus pugnax*) (van Rhijn, 1973). In sunfish, however, sneaks grow into female mimics; thus the male alternatives are reversible (sensu Austad, 1984). In ruffs, males exhibit plumage differences, but all males are approximately the same size. Furthermore, one of the morphs, being intermediate in color between the other two morphs, switches between display and sneak behaviors as different mating opportunities arise (van Rhijn, 1973); thus male reproductive alternatives are reversible in this species as well. The three discrete behaviors and morphologies exhibited by males of *P. sculpta* are evidently unique.

If sexual selection has produced elaborate males in *P. sculpta,* and then has produced males that seem inconspicuous to these elaborate males, there is good reason to expect intrasexual deception to have evolved in at least some other polygynous crustaceans. Males employing reproductive alternatives, however, are not likely to resemble the elaborate (and probably most abundant) males in these species. Thus the apparent rarity of ARBs in the Crustacea may simply be the result of intrasexual deception being effective on researchers as well as on elaborate males. A closer look at sexually dimorphic crustaceans may show that alternative reproductive behaviors in this group are as numerous and diverse as they are in other animal taxa.

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ANNOUNCEMENT

"Decapod crustaceans from continental shelf and slope around Japan" by Keiji Baba (Kumamoto University), Ken-Ichi Hayashi (Shimonoseki University of Fisheries), and Masahiro Toriyama (Nensei Regional Fisheries Research Labo-ratory) has been published (1986) by the Japan Fisheries Resource Conservation Association. This book of 336 pages reports the results of intensive research of unexploited fishery resources on continental slopes during 1977–79 in waters within 200 nautical miles of Japan. For the 176 species included, colored illus-trations and descriptions in both Japanese and English are provided. The decapods comprise 114 species of shrimps and lobsters, 46 species of anomurans, and 16 species of brachyurans. The following six new species are described: *Cryptopenaeus brevirostris* Hayashi, *Periclimenes granuloides* Hayashi, *Pandalopsis miyakei* Hay-ashi, *Plesionika chacei* Hayashi, *Munidopsis plana* Baba, and *Pagurus miyakei* Baba.

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