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MALE ALTERNATIVE REPRODUCTIVE STRATEGIES IN A MARINE ISOPOD CRUSTACEAN (*PARACERCEIS SCULPTA*): THE USE OF GENETIC MARKERS TO MEASURE DIFFERENCES IN FERTILIZATION SUCCESS AMONG α-, β-, AND γ-MALES

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Abstract.—Three discrete male morphs coexist in *Paracerceis sculpta*, a marine isopod crustacean inhabiting the northern Gulf of California. Ornamented α-males establish themselves in the spongocoels of intertidal sponges, where females congregate to breed. Smaller β-males, resembling sexually mature females, enter spongocoels by deception, while tiny γ-males invade spongocoels by stealth. Isopods breed year-round, and the operational sex ratio fluctuates widely over short durations. When females are abundant, receptive females accumulate in spongocoels, and these spongocoels are preferentially invaded by β- and γ-males. To test the hypothesis that the density of receptive females affects relative fertilization success among male morphs, individual β- and γ-males, heterozygous for a dominant cuticular pigmentation allele, were placed in artificial spongocoels with an unmarked α-male and densities of one, two, and three unmarked, receptive females. The fertilization success of each male was determined by counting the number of marked and unmarked progeny each female produced. Alpha-males guard females effectively and sire nearly all young when one female is in a spongocoel. The success of β- and γ-males increases, however, and may even exceed the success of α-males when two or three females are present. The regular occurrence of more than one receptive female in the harems of α-males may contribute to the persistence of β- and γ-males in this species.

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Males in many animal species exhibit discontinuous variation in behaviors and morphologies 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; Clutton-Brock et al., 1982; Austad, 1984; Howard, 1984; Gross, 1982, 1985; Borowsky, 1985; Ra'anan and Sagi, 1985; Kuris et al., 1987). These alternative reproductive behaviors occur primarily in polygynous species in which variance in male mating success is high and, thus, in which sexual selection appears to be strong (Gadgil, 1972). Depending on the species, male alternative reproductive behaviors may represent discrete genetic differences among males, environmentally induced shifts in development or behavior that result in discontinuous male phenotypes, or some combination of environmental and genetic factors that produce recognizable categories of adult males (Austad, 1984; Dominey, 1984).

If male alternative reproductive behaviors are genetically distinct, the mean fitnesses of different male alternatives should be equal over time (Gadgil, 1972; Gross, 1985). If males employ condition-dependent reproductive alternatives, however, no genetic polymorphism need exist (Dawkins, 1980); males may simply make the best of their reproductive options given their body size, physical condition, and social standing. In such condition-dependent situations, mean fitnesses among different male alternatives need not be equal (Eberhard, 1982; Austad, 1984). Theoreticians argue that genetically distinct male reproductive alternatives should be vanishingly rare, either because genetic polymorphisms in sexual species should rapidly be invaded by modifier alleles that equalize fitnesses among the different morphotypes (Slatkin, 1979) or because natural selection should favor neural or developmental programming that permits males to respond appropriately to changes in their reproductive environments (Dawkins, 1980; Eberhard, 1982; Dominey, 1984). Seemingly in spite of these predictions, genetic (or apparently genetic) polymorphisms in male reproductive behavior and morphology do exist (van Rhijn, 1973;

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Hamilton, 1979; Cade, 1981; Kallman, 1983; Gross, 1985; Shuster, 1986), although, perhaps in accord with theoretical expectations, the hereditary basis for such intermale differences has been unambiguously demonstrated only once (in poeciliid fish, *Xiphophorus*; review in Kallman [1984]).

Due to the difficulty in documenting genetic differences among males, recent research on male alternative reproductive behaviors has concentrated mainly on documenting behavioral diversity among males or on examining circumstances that lead some males to employ alternative mating tactics. Therefore, most of what is known about the relative fitness of alternative male types is based on reports of differences in mating success among males (Clutton-Brock et al., 1982; Rubenstein, 1984; Gross, 1985; Finke, 1985; Greenfield and Shelley, 1985; but see Maekawa and Hino [1987]). Arnold and Wade (1984) have argued that the accuracy of studies that emphasize documentation of male mating success is limited for two reasons: 1) ejaculate competition and female control of syngamy are usually not considered when male reproductive success is equated with copulatory or ejaculatory success; and 2) differences in mating success measured over short durations or under a limited range of circumstances do not accurately reflect differences in lifetime reproductive success among males. Lacking the ability to conduct longitudinal analyses of relative fitness differences among individuals (Arnold and Wade, 1984), experiments examining male reproductive success must 1) identify factors or circumstances responsible for generating differences in success among males, 2) manipulate those factors or circumstances to produce a predictable shift in success among males, and 3) document reproductive success using numbers of progeny sired, rather than numbers of matings attempted by individual males. Such analyses provide the most accurate estimates of male fitness relative to differential reproductive success.

Genetically simple yet phenotypically distinct traits can serve as genetic "markers" in experiments measuring differential male fertilization success. Genetic markers have been used in paternity analyses in a variety of arthropod and nonarthropod species (Sassaman, 1978; Smith, 1979; Maekawa and Onozato, 1986; Maekawa and Hino, 1987; reviews in Smith [1984] and Ellstrand and Marshall [1986]) and have the advantage of documenting male reproductive success in terms of actual progeny sired rather than simply in terms of numbers of matings achieved. However, despite their extensive use in species with multiple insemination, genetic markers have only recently been used to document paternity in species employing alternative reproductive behaviors (Maekawa and Hino, 1987), and surprisingly, genetic markers have yet to be used in the study of male polymorphisms in arthropods.

Paracerceis sculpta is a sexually dimorphic, sphaeromatid isopod crustacean inhabiting intertidal and subtidal reefs in the northern Gulf of California (Brusca, 1980; Shuster, 1986, 1987*b*). Three distinct male morphs representing discrete male alternative reproductive behaviors coexist in this species (Shuster, 1987*a*): α-males possess enlarged uropods and telsons; β-males are smaller, lack ornamentation and resemble sexually receptive females; and γ-males, also unornamented, are smaller still (Fig. 1). All three male morphs are sexually mature, capable of inseminating females, and considerably different in their life histories and reproductive behaviors (Shuster, 1986, 1987*a*). In this paper, I identify three cuticular pigment patterns in *P. sculpta* that have their expressivities controlled by dominant alleles at autosomal loci. I demonstrate that these alleles have no deleterious effect on the fertility of individuals bearing them, and finally, by manipulating the density of sexually receptive females in artificial reproductive habitat in the laboratory, I document the effect of receptive-female density on the fertilization success of α-, β-, and γ-males, using the genetic markers to identify progeny sired by males of each type.

Cuticular Pigment Patterns in P. sculpta

Three distinctive cuticular pigment patterns are easily recognized in *P. sculpta*: CTRB individuals exhibit a red bar across the dorsal surface of their cephalons (head capsule) and telsons (abdomen), CTW individuals exhibit white areas covering their

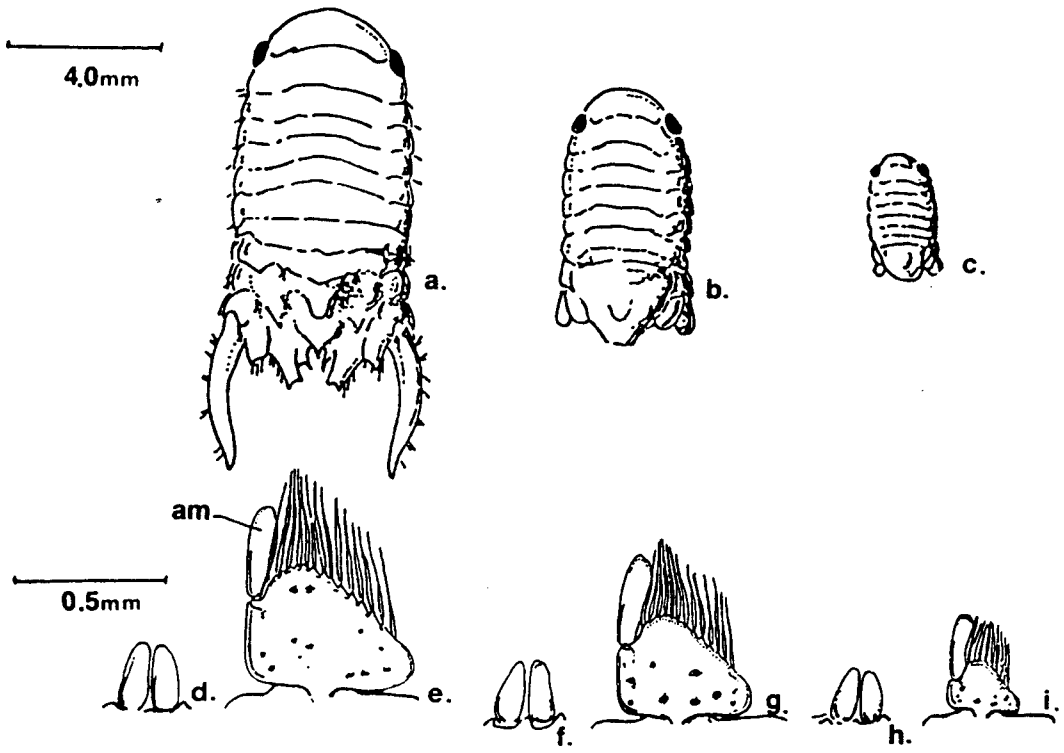

FIG. 1. Dorsal view of the three male morphs in *P. sculpta*. The anterior ends of males are directed toward the top of the page: a) α-male (elongated abdominal structures are uropods); b) β-male; c) γ-male; d) penes of α-male; e) 2nd pleopod of α-male (am = appendix masculina); f) penes of β-male; g) 2nd pleopod of β-male; h) penes of γ-male; i) 2nd pleopod of γ-male.

cephalons and telsons, and TS individuals exhibit a red spot on the crest of their telsons (Fig. 2). Genetic studies of pigmentation patterns in sphaeromatid isopods (review in Hedgecock et al. [1982]) indicate that nearly all such "markers" are controlled by dominant alleles of autosomal loci that occur at low frequencies in natural populations. The relative frequencies of CTRB, CTW, and TS among male and female *P. sculpta* collected from the northern Gulf of California are consistent with this explanation (Fig. 3). Moreover, preliminary crosses using field-caught marked and unmarked individuals suggest that nearly all marked individuals in nature are heterozygous for marker alleles (Shuster, 1986).

The Reproductive Biology of P. sculpta

After the adult molt, α-males leave feeding sites on subtidal coralline algae and establish themselves in the enlarged spongocoels of *Leucetta losangelensis*, a calcareous intertidal sponge that grows beneath rocks and ledges in the mid- and lower intertidal zones in the northern Gulf of California (Brusca, 1980; Shuster, 1986). Alpha-males position themselves at sponge oscula with their heads pointing into the spongocoel and with their uropods and telsons protruding outward. Females leave the feeding habitat shortly before their final molt and swim to sponges, where they are attracted to spongocoels containing α-males (Shuster, 1986). Females do not discriminate physical characteristics such as body size or uropod condition among α-males (Shuster, 1986), and sponge characteristics do not predict harem size (Shuster, 1986, 1987*b*), suggesting that female discrimination of reproductive habitat characteristics is minimal. Females do, however, prefer to enter spongocoels con-

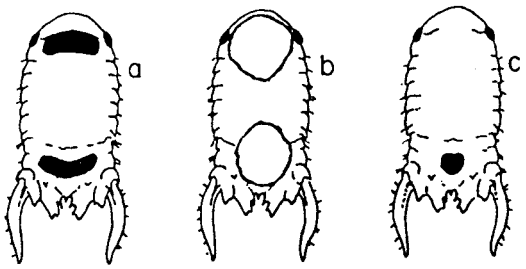

FIG. 2. Cuticular pigmentation markers in *P. sculpta*: a) CTRB individuals exhibit a red bar across the dorsal surface of their cephalons (head capsules) and telsons (abdomens); b) CTW individuals exhibit white areas covering their cephalons and telsons; c) TS individuals exhibit a red spot on the crest of their telsons (darkened areas represent red pigment).

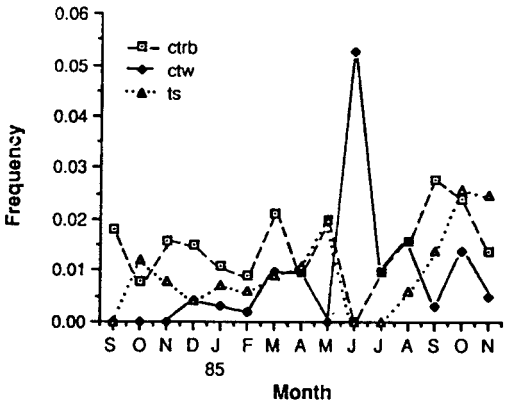

FIG. 3. Relative frequencies of CTRB, CTW, and TS phenotypes in collections of *P. sculpta* collected near Puerto Peñasco, Sonora, Mexico between February 1984 and December 1985.

taining gravid females, perhaps because these cavities represent established breeding sites (Shuster, 1986).

Females initiate courtship by moving directly to occupied spongocoels, where they begin pulling on the resident α-male's uropods with their mouthparts. Alpha-males are passive during this process and remain so until females move between the α-male's open uropods. Alpha-males respond by closing their uropods around the female, obtaining a firm grip, and rapidly shaking the female up and down by contracting and relaxing their dorsal musculature several times in succession. Alpha-males then release the female, who in nearly all cases moves further into the spongocoel and beneath the α-male. Alpha-males do not attempt to restrain females that move away from them, and females that enter a particular spongocoel do not leave that spongocoel to continue searching (N = 99; Shuster, 1986).

Alpha-males use their walking legs to grasp and hold females that enter their spongocoels. Females are evidently retained by α-males until they undergo a sexual molt (the molt that initiates female sexual receptivity; mean number of days between collection and molt = 5.21, SD = 2.91, N = 61). During the sexual molt, females first shed the posterior half of their cuticle and expose paired genital pores. Males deposit sperm into the female's oviducts, and females permit multiple matings (Shuster, 1986). Receptivity ends about 24 hours later when the female sheds the anterior half of her cuticle and shunts fertilized ova into a ventral brood pouch. Like many sphaeromatid isopods (Iverson, 1982), *P. sculpta* females lose functional mouthparts in their sexual molt and undergo considerable metabolic changes associated with providing nutrition for developing young (Holdich, 1971; Shuster, 1986). The female brood pouch forms an intimate, almost placental relationship with developing embryos, and resources stored by the female are evidently absorbed directly by young. Young develop in approximately four weeks and resemble miniature adult females when they leave the brood pouch (sexes are indistinguishable at this time). Young isopods leave spongocoels and disperse to intertidal and subtidal coralline algae to feed. Spent females are depleted of somatic resources, are incapable of feeding, and die within two weeks of parturition (Shuster, 1986, 1987*b*).

Alternative Reproductive Behavior in P. sculpta

Alpha-males use their uropods and telsons to defend their spongocoels and harems against other α-males. Alpha-males presumably attempt such take-overs because established harems are attractive to receptive females (Shuster, 1986). Fights usually consist of prolonged (up to 24 hours) bouts of grappling by resident and intruder α-males. Residents grip intruders with their uropods and periodically jerk forcefully in a dorsal direction in apparent attempts to

fling the intruder from the sponge. Intruders grasp residents with their walking legs, brace their uropods backward against the sponge, and attempt to pull the resident out (details in Shuster [1986]). Large α-males are more successful at cavity defense and take-over than are small α-males, and body size is more important than uropod condition in permitting α-males to retain or usurp spongocoels (Shuster, 1986). Alpha-males may accumulate up to 19 females in a single spongocoel (Shuster, 1987*a*), but many α-males are unsuccessful in acquiring mates (over 30% in most samples, Shuster, 1986, 1987*a*, 1987*b*). Thus, sexual selection among α-males is probably strong.

Beta-males enter spongocoels by deception. In addition to physically resembling receptive females (Shuster, 1987*a*), β-males mimic female courtship behavior to the closest detail (Shuster, 1986). Beta-males initiate oral contact with α-male uropods, solicit bouts of shaking, and enter spongocoels just like females. Female mimicry is apparently effective, as α-males rarely attempt to exclude β-males from their spongocoels (less than 2% of all trials; $N = 63$).

Gamma-males enter spongocoels by stealth. Using their small size and rapid movements, γ-males lurk near oscula and repeatedly attempt to rush around α-males and into spongocoels. Alpha-males vigorously resist such invasion attempts, either by blocking the osculum with their telsons, by extracting the tiny intruders from the spongocoel using their elongated uropods like forceps, or by grasping and flinging γ-males from the spongocoels with their walking legs. Despite this resistance by α-males, γ-males frequently invade spongocoels successfully and use their small size to sequester themselves deep within spongocoels and beyond the reach of α-males (Shuster, 1986).

In the field, β- and γ-males are most often found in spongocoels containing an α-male and one or more sexually receptive females (Shuster, 1986). Increasing numbers of receptive females in a spongocoel increase that spongocoel's probability of invasion by a β- or a γ-male (Shuster, 1987*a*). In the lab, β- and γ-males discriminate among females on the basis of reproductive condition. When given a choice between spongocoels containing low or high densities of receptive females, β-males prefer to enter artificial spongocoels containing multiple receptive females (Shuster, 1986). Preliminary laboratory data suggest that γ-males exhibit similar preferences for high densities of receptive females (Shuster, 1986).

Receptive-Female Density and Male Fertilization Success

Females reproduce year-round in *P. sculpta*, and the relative abundance of receptive females in the population varies widely over short durations (Fig. 4). The term "receptive" refers to unmolted females that enter spongocoels (i.e., sexually mature females that have not undergone a sexual molt and thus are virgins), as well as half-molted females that are capable of mating. When the proportion of receptive females in the population is low, unmolted and half-molted females in spongocoels are typically found clasped by the resident α-male. These females are evidently retained for the duration of their sexual receptivity and are repeatedly mated by the α-male (Shuster, 1986). When receptive females are more abundant, however, unmolted virgin females and mated (but still receptive), half-molted females are routinely found free in spongocoels (Shuster, 1987*a*), suggesting that α-males are unable to monopolize every female that enters their spongocoel at these times. The relationship between the number of receptive females in a spongocoel and its likelihood of invasion by β- and γ-males (Shuster, 1986) suggests that spongocoels containing high densities of sexually receptive females provide better mating opportunities for β- and γ-males than spongocoels containing few receptive females.

This "receptive-female density" hypothesis predicts that α-males should experience greater relative fertilization success when the density of receptive females in spongocoels is low, and that β- and γ-males should experience greater relative success when female density is high. Such consistent variation in fertilization success among male morphs associated with variation in the density of receptive females in spongocoels would indicate that the relative density of

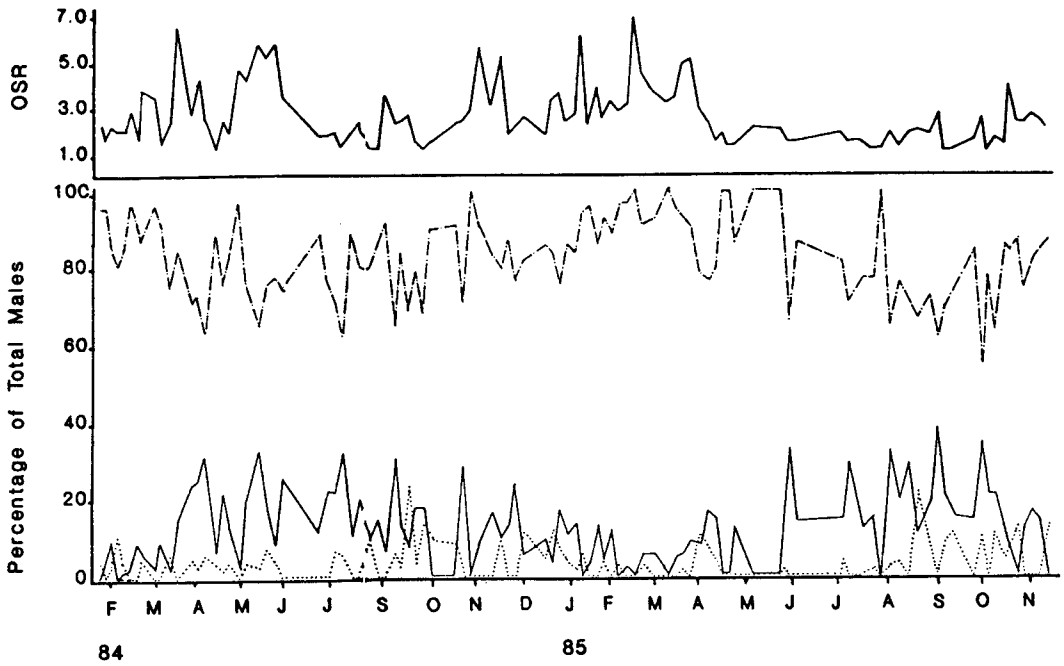

FIG. 4. Operational sex ratio (OSR = number of sexually mature males/number of sexually receptive females; upper solid line) and the frequencies of α- (line with alternating dashes and dots), β- (dotted line) and γ- (solid lower line) males for *P. sculpta* collected from spongocoels between February 1984 and December 1985 (number of individuals = 10,998, median sample size = 64, range = 6–204).

sexually receptive females plays a significant role in creating variance in fertilization success among α-, β-, and γ-males in nature.

MATERIALS AND METHODS

Collection of Paracerceis sculpta.—*Leucetta losangelensis* sponges grow abundantly year-round in tidepools on the coquina limestone reefs at Playa de Oro and at Station Beach, approximately three kilometers southeast of Puerto Peñasco, Sonora, Mexico (Shuster, 1986). Isopods used in experiments were obtained in collections of 6–204 individuals, made every 4–10 days between February 1984 and November 1985. Breeding aggregations of isopods were removed from spongocoels, placed in separate vials, and examined in the laboratory within 6 hours of collection. Virgin females were identified by their well-pigmented cuticles, unmetamorphosed mouthparts and possession of mature ovaries visible through the ventral cuticle. Such females are sexually mature and have not undergone a sexual molt (Shuster, 1986). Males were identified by the presence of external genitalia (Fig. 1) and were classified as α-, β-, or γ-males by their body size and external morphology. Further details of collection and animal-maintenance procedures, as well as details of male and female life histories, are available in Shuster (1986). All animals were returned to the Gulf of California after experiments were completed.

Interitance of Cuticular Pigmentation Patterns.—As mentioned above, nearly all field-caught individuals bearing the cuticular pigmentation patterns CTRB, CTW, and TS are heterozygous for that marker. Thus Mendelian inheritance of these pigmentation patterns was specifically tested in two types of crosses. In type-A crosses, field-caught marked individuals (symbolized CTRB/+, CTW/+ or TS/+) were mated to field-caught unmarked individuals (symbolized +/+). In type-B crosses, field-caught marked individuals were mated to field-caught individuals bearing the same marker (e.g., CTW/+ × CTW/+). If marked individuals were heterozygous for a dominant

marker allele, 50% marked and 50% unmarked progeny were expected from type-A crosses,and 75% marked and 25% unmarked progeny were expected from type-B crosses.

Individual sexually mature, unmolted (virgin) females were placed with their designated sire in 225-ml cups containing seawater. Females usually molted and mated within 24 hours. Males were removed after females became gravid, and females were maintained in covered cups with weekly water changes until they released young. Frequencies of marked and unmarked progeny were recorded and compared using heterogeneity G tests. In cases in which a male was crossed with more than one female, one female was randomly selected from among the dams and included in the analysis. Effects of dam identity on the expression of marker alleles contributed by marked males were examined by comparing the frequencies of marked and unmarked progeny among half-sibs using heterogeneity G tests.

To examine the effects of each marker on the fertility of males bearing them, the numbers of live young released by unmarked females mated to marked and unmarked males were compared using ANCOVA, with female body length as the covariate. Small sample sizes prevented specific analysis of interactions between marker and male morphology. Thus six groups of females were included in analysis and were identified by the following categories of sires: 1) unmarked α-males, 2) unmarked β-males, 3) unmarked γ-males, 4) CTRB marked males, 5) CTW marked males, and 6) TS marked males. Specific crosses are summarized in Table 1. To permit visual comparison of these relationships, the fecundities of females from crosses 4–6 (Table 1) were plotted against the regression of fecundity on female body length (with 95% confidence limits) for crosses 1–3. All values were log-transformed to meet assumptions of normality before analysis.

Construction and Use of Artificial Sponges.—Since natural *Leucetta* sponges are difficult to maintain in the lab and since isopods abandon dead or dying sponges, long-term experiments using natural sponges are impossible. I avoided this problem by using artificial sponges constructed of a synthetic polymer (FHP-3000, available from Dr. Joseph Bonaventura, Duke University, Biomedical Marine Laboratory; Shuster, 1986). When mixed with water, the prepolymer forms a rapidly setting foam, which may be poured into bottle caps to create life-sized sponge "colonies." Plastic-coated wire pushed into the setting foam creates spongocoels of any desired diameter, and when set, artificial sponges may be trimmed to a natural shape. These facsimiles simulate the physical characteristics of natural sponges, are inert, and are reusable. Furthermore, controlled choice experiments using natural sponges and artificial sponges indicate that isopods show only a slight initial preference for natural sponges (Shuster, 1986). Isopods adapt quickly to artificial sponges and assume apparently normal body positioning in sponge oscula. Courtship behavior on artificial sponges generates breeding aggregations that are indistinguishable from those found in nature (Shuster, 1986). Females that enter, mate, and rear young in artificial sponges suffer no decrease in fecundity compared to females that brood their young in 225-ml cups. Furthermore, females maintained under either of these conditions until all live young are released resemble spent females collected from the field in that they rarely contain undeveloped young in their brood pouches (Shuster, 1986).

Using Genetic Markers to Document Male Fertilization Success.—To measure differences in male fertilization success as a function of receptive-female density, a marked β- or γ-male, an unmarked α-male, and one, two, or three unmarked premolt females were placed in an artificial sponge of standardized dimensions (diameter = 20 mm; osculum diameter = 3 mm; spongocoel volume = 7.85 cm^3). Sponges containing these breeding aggregations were then submerged in individual 225-ml cups containing seawater.

One, two, or three females were introduced to males in three successive rounds. The order in which pairs of males experienced each female density was balanced, and each male was used in only one circuit of three female densities. Females were allowed to molt and to mate with marked and unmarked males within spongocoels over several days, and all isopods were removed

TABLE 1. Body lengths and fecundities of unmarked females crossed with genetically marked and unmarked males (SD in parentheses). ANCOVA: differences among adjusted means, $F_{[5, 42]} = 1.245$, $P > 0.25$; differences among slopes, $F_{[5, 37]} = 0.447$, $P > 0.75$.

Group	Marker	Male type	Number of crosses	Mean female length (mm)	Mean number of live young
1	(+)	α	12	5.25 (0.55)	80.25 (22.82)
2	(+)	β	14	5.34 (0.69)	77.79 (39.44)
3	(+)	γ	12	5.24 (0.83)	79.17 (39.08)
4	CTRB	α	4	5.05 (0.63)	59.40 (23.42)
		β	1	5.69	73
5	CTW	α	2	4.54 (0.33)	47.00 (25.46)
		γ	1	4.76	54
6	TS	α	1	4.92	23
		β	1	5.23	49
		γ	1	4.62	42

from each artificial sponge after every female in a particular trial had become gravid. That all females were gravid was determined by the presence of both halves of each female's cuticle outside the sponge osculum. Artificial sponges were rinsed in fresh water after each trial, and pairs of males were returned to their artificial sponge with the next density of receptive females. Gravid females were maintained in 225-ml cups containing seawater until they released young. At this time, the numbers of marked and unmarked progeny produced by each female were recorded. Five trials in which a marked γ-male and an unmarked α-male experienced all three female densities were completed. In the other 11 trials, the relative fertilization success of males could be reported for only one or two of the three female-density treatments because one of the males or one or more females mated at a particular density had died (death usually occurred when animals crawled onto the wall of the containers and desiccated). Despite these missing cases, the total numbers of cases analyzed for each female density were nearly equal, and the experimental design remained approximately symmetrical (see Table 6).

Fifty percent of a marked male's progeny should bear an autosomal marker allele; therefore, the fertilization success of a marked male was calculated as $2m/n$, where m = the number of marked progeny and n = the total number of progeny in the brood. Raw percentage data were arcsine-transformed using the modification for frequency data (Zar, 1974 p. 186). The fertilization-success scores of γ-males at the three female densities were compared using ANOVA, first considering only the five complete trials, and then considering all cases in which fertilization success could be recorded. As only one complete trial of this experiment was conducted using a marked β-male and an unmarked α-male, the fertilization successes of these individuals at the three female densities were compared using a G test.

RESULTS

Mendelian Inheritance of Cuticular Pigment Markers.—In heterogeneity G tests, all three markers met the predictions of Mendelian inheritance (CTRB type-A crosses: $G_{H[8]} = 4.462$, $P > 0.50$; CTRB type-B crosses: $G_{H[3]} = 1.176$, $P > 0.50$; CTW type-A crosses: $G_{H[4]} = 2.435$, $P > 0.50$; CTW type-B crosses: $G_{H[2]} = 0.040$, $P > 0.90$; TS type-A crosses: $G_{H[4]} = 2.950$, $P > 0.50$) (Table 2). Furthermore, all markers appear to be autosomal, as there was no heterogeneity among marked-male and marked-female crosses for any marker. Maternal genotype may influence the expression of a marker among progeny, as significant heterogeneity in marker expression among paternal half sibs occurred in two of 15 crosses (Table 3). In both cases in which effects of dam identity were apparent, however, there were fewer marked progeny than expected.

The Effect of Markers on the Fecundity of Parents.—In crosses involving unmarked females and unmarked α-, β- and γ-males,

TABLE 2. Mendelian inheritance of cuticular pigment patterns

Cuticular marker	Cross type		Sire	Dam	Dam body length (mm)	Progeny phenotype: Marker present	Progeny phenotype: Marker absent	N	Un-developed	G
CTRB	A		282α[a]	462	4.62	33	30	63	3	0.142
			533α[a]	667	4.92	27	30	57	0	0.157
			256α[a]	239	5.69	45	52	97	0	0.503
			952β[a]	951	5.69	34	39	73	12	0.340
			289α[a]	187	4.31	20	18	38	0	0.104
			211α	212[a]	4.77	23	24	47	0	0.021
			000α	657[a]	6.77	64	71	135	0	0.362
			852γ	250[a]	6.46	47	32	79	1	2.847
			347α	348[a]	4.46	17	17	34	0	0.000
		Total:				310	313	623		4.476
	B		244α[a]	008[a]	6.15	8	3	11	20	0.028
			000α[a]	869[a]	6.31	94	28	122	0	0.277
			083α[a]	099[a]	6.31	126	35	161	0	0.939
			475α[a]	605[a]	5.23	28	5	33	0	1.873
		Total:				256	71	327		3.117
CTW	A		374α[b]	368	4.31	12	17	29	1	0.852
			516α[b]	676	4.77	32	33	65	0	0.015
			407γ[b]	175	4.77	27	27	54	0	0.000
			528α	529[b]	4.62	27	31	58	5	0.274
			477γ	440[b]	5.39	52	41	93	0	1.297
		Total:				150	149	299		2.438
	B		793α[b]	002[b]	4.92	61	22	83	0	0.099
			682α[b]	747[b]	4.31	36	14	50	0	0.232
			662γ[b]	242[b]	4.62	26	10	36	0	0.143
		Total:				123	46	169		0.474
TS	A		354β[c]	201	5.23	20	29	49	0	1.646
			346γ[c]	692	4.62	24	18	42	0	0.850
			076α[c]	473	4.92	12	11	23	11	0.043
			429γ	443[c]	4.46	14	11	25	0	0.354
			—	912[c]	5.08	8	9	17	0	0.057
		Total:				78	78	156		2.950

[a] Bearing CTRB.
[b] Bearing CTW.
[c] Bearing TS.

no marked progeny were produced by unmarked parents. Furthermore, there were no significant differences in the adjusted means (ANCOVA, $F_{[5,42]} = 1.245$, $P > 0.25$) or in the slopes of the fecundities of females mated to marked or unmarked males (ANCOVA, $F_{[5,37]} = 0.447$, $P > 0.075$; Table 1). These data are graphically presented in Figure 5, in which the fecundities of females mated to marked males are plotted against the 95% confidence limits of the regression of fecundity on size for females mated to unmarked α-, β-, and γ-males (there were no significant differences in the adjusted means [$F_{[2,34]} = 0.544$, $P > 0.50$] or in the slopes of the fecundities for females mated to unmarked α-, β-, and γ-males [$F_{[2,32]} = 0.052$, $P > 0.75$]). The fecundities of eight of 11 females mated to marked males lie within the 95% confidence limits for the fecundities of females mated to unmarked males (Binomial test, $P = 0.113$); thus, there is no apparent effect of marker alleles on the fecundity of females mated to marked males.

Documentation of Differences in Male Fertilization Success as a Function of Female Density.—Three lines of evidence indicate that female density in spongocoels affects relative fertilization success among males in this species. First, a breeding aggregation collected from a spongocoel in November 1985 contained an unmarked α-male, three unmarked gravid females, and a CTRB β-male. Subsequent crosses (Shus-

TABLE 3. Effects of dam identity on the expression of marker alleles when marked males were crossed with unmarked females.

Marker	Sire	Dam	Dam body length (mm)	Progeny phenotype: Marker present	Progeny phenotype: Marker absent	N	Undeveloped	G value
CTRB	533α	848	4.92	52	47	99	1	0.251
		542	4.62	23	24	47	8	0.021
		899	4.46	15	34	49	0	7.468**
		667	4.92	27	30	57	0	0.157
	Total:			117	135	252		7.897
	952β	951	5.69	34	39	73	12	0.340
		374	5.54	26	32	58	2	0.626
		099	5.69	23	36	59	1	2.864
	Total:			83	107	190		3.820
CTW	374α	368	4.31	12	17	29	1	0.850
		622	4.46	30	30	60	0	0.000
	Total:			42	47	89		0.850
	516α	676	4.77	32	33	65	0	0.015
		748	4.92	48	35	83	0	2.032
		847	5.23	17	38	55	0	8.151**
	Total:			97	106	203		10.198**
TS	346γ	403	4.31	14	25	39	0	3.105
		—	4.62	30	30	60	0	0.000
		692	4.62	24	18	42	0	0.850
	Total:			68	73	141		3.955

** $P < 0.01$.

ter, 1986) showed this β-male to be heterozygous for CTRB, and since 26% of the field-caught females' young were CTRB, the β-male had sired at least 51% of the progeny produced in that spongocoel ($N = 94$, Table 4). The low frequency of CTRB in the population at the time of this collection (Fig. 3) minimizes the possibility that these females were inseminated by a CTRB-bearing male other than the marked β-male. Second, in a single complete trial of the female-density experiment described above, involving a heterozygously marked TS β-male and and unmarked α-male, the β-male sired more than 95% ($N = 50$), 24% ($N = 100$), and 67% ($N = 150$) of the progeny produced in a spongocoel at densities of one, two, and three females, respectively (Table 5). Third, in 16 trials of the female-density experiment using heterozygously marked γ-males and unmarked α-males and females, the fertilization success of the marked γ-males increased significantly (and at the expense of the fertilization success of α-males), as the number of receptive females in spongocoels increased (for five complete trials: ANOVA, $F_{[2,\ 12]} = 5.66$, $P < 0.025$; for all trials: $F_{[2,\ 27]} = 5.19$, $P < 0.025$; Table 6, Fig. 6). Furthermore, in three of 30 cases, marked γ-males sired 73%, 91%, and more than 95% of the progeny produced in a spongocoel (Table 6). There were no significant differences in the numbers of live young produced by individual females at the three densities of females in spongocoels (differences among adjusted mean body lengths: ANCOVA, $F_{[2,\ 50]} = 0.876$, $P > 0.25$; differences among size-fecundity slopes: $F_{[2,\ 48]} = 0.071$, $P > 0.75$).

DISCUSSION

The frequencies of CTRB, CTW, and TS phenotypes among the progeny of type-A and type-B crosses suggest that each of these cuticular pigment patterns is controlled by a dominant allele at an autosomal locus. None of these alleles appears to affect male fertility or female fecundity, and there are no apparent deleterious interactions between marker alleles and α-, β-, or γ-male genotypes. Backcrosses are impossible in this semelparous species, and low survivorship

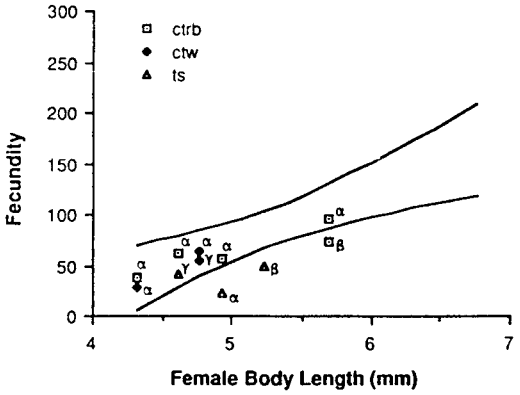

FIG. 5. The fecundities of field-caught females mated to marked α-, β-, and γ-males plotted against female body length. The 95% confidence limits for the regression of females mated to unmarked α-, β-, and γ-males ($Y = -181.72 + 7.863X$; $F_{[1,13]} = 14.4295$, $P < 0.005$) are indicated by the solid lines. Squares refer to sires bearing CTRB, circles refer to sires bearing CTW, and triangles refer to sires bearing TS. The adult phenotype of each sire is indicated beside each point.

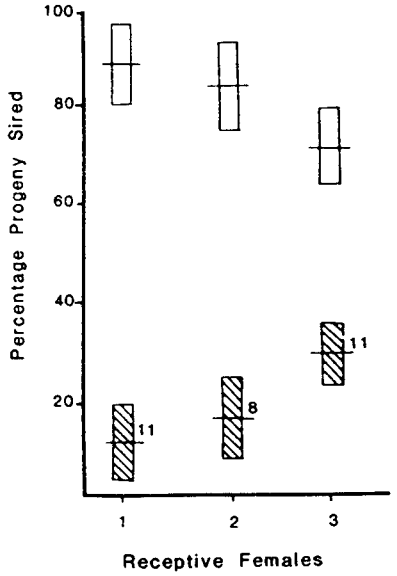

FIG. 6. Relative fertilization success of genetically marked γ-males and unmarked α-males in artificial sponges with densities of one, two, and three sexually receptive females. The relative fertilization success of γ-males increases, and the relative fertilization success of α-males decreases as the density of receptive females in the spongocoel increases ($F_{[2,27]} = 5.188$, $P < 0.025$). Horizontal lines represent means, bars represent one standard error, and numbers beside the means indicate the numbers of trials at that female density. Open bars represent α-males, and striped bars represent γ-males.

among progeny reared in the lab in 1985 (Shuster, 1986) prevented crosses of heterozygous F_1's to test for the expected 3:1 ratios of marked : unmarked F_2's characteristic of simple Mendelian loci. Despite the lack of these more definitive tests for Mendelian inheritance, the results presented above amply demonstrate that CTRB, CTW, and TS are suitable as genetic markers for examining variance in male fertilization success in *P. sculpta*. While the expression of marker alleles in progeny may occasionally be somewhat suppressed by maternal genotype, such suppression only makes estimates of male fertilization success in these experiments more conservative.

The density of receptive females in spongocoels evidently does influence relative fertilization success among α- and β-males, although the small sample sizes prevent explicit interpretation of this relationship. In both laboratory and field situations, β-males achieved at least some fertilizations with every female in the spongocoel, and contrary to predictions in the female-density experiment, the marked β-male sired

TABLE 4. Fertilization success of a field-caught (CTRB) β-male, heterozygous for CTRB. Overall fertilization success = 2(5 + 19)/94 = 0.51. Table entries are numbers of offspring with relative frequencies in parentheses.

Progeny phenotype	Female			Totals
	947	948	950	
CTRB	5 (0.14)	19 (0.33)	—	24 (0.26)
Other	29 (0.81)	39 (0.67)	—	68 (0.72)
Undeveloped	2 (0.05)	0 (0.00)	—	2 (0.02)
Totals:	36	58	0	94

TABLE 5. The fertilization success of a genetically marked β-male (TS) in a spongocoel containing an unmarked α-male and one, two, or three unmarked receptive females.

Number of receptive females	Number of marked progeny	Estimated number of progeny sired by β-male	Estimated number of progeny sired by α-male	Total number of progeny
1	26	50	0	50
2	12	24	76	100
3	50	100	50	150
Total:	98	174	126	300

$G = 92.051$, $d.f. = 2$, $P < 0.001$.

TABLE 6. A) Fertilization success of genetically marked γ-males in spongocoels containing an unmarked α-male and one, two, or three unmarked, sexually receptive females (proportions of progeny sired by γ-males are given in parentheses). B) Analysis of variance: fertilization success of γ-males.

A.

		One female			Two females			Three females		
γ-Male	Marker	Marked progeny	Progeny sired (proportion)	Total progeny	Marked progeny	Progeny sired (proportion)	Total progeny	Marked progeny	Progeny sired (proportion)	Total progeny
346	TS	0	0 (0.00)	55	15	30 (0.26)	115	22	44 (0.28)	157
344	CTRB	0	0 (0.00)	48	1	2 (0.02)	93	2	4 (0.06)	61
805	CTW	3	6 (0.13)	48	25	50 (0.68)	74	18	36 (0.22)	163
821	CTRB	0	0 (0.00)	65	0	0 (0.00)	110	24	48 (0.29)	166
973	CTW	0	0 (0.00)	86	4	8 (0.10)	78	17	34 (0.27)	124
963	TS	16	32 (0.91)	35	2	4 (0.03)	152	—	—	—
878	CTW	—	—	—	0	0 (0.00)	108	0	0 (0.00)	103
417	CTRB	6	12 (0.28)	45	—	—	—	11	22 (0.43)	51
049	TS	—	—	—	0	0 (0.00)	40	—	—	—
945	TS	0	0 (0.00)	53	—	—	—	81	162 (0.95)	170
091	CTW	0	0 (0.00)	84	—	—	—	—	—	—
535	CTRB	0	0 (0.00)	49	—	—	—	—	—	—
967	TS	0	0 (0.00)	65	—	—	—	—	—	—
172	CTRB	—	—	—	—	—	—	23	46 (0.36)	128
803	TS	—	—	—	—	—	—	1	2 (0.02)	115
969	TS	—	—	—	—	—	—	22	44 (0.22)	199
Weighted mean proportions of progeny sired:			0.079			0.151			0.307	

B.

Source	Sum of squares	*d.f.*	MS	*F*	*P*
All trials:					
Among treatments	386,449.115	2	193,224.600	5.188	<0.025
Within treatments	1,005,703.182	27	37,248.270		
First five trials:					
Among treatments	189,469.610	2	94,734.800	5.664	<0.025
Within treatments	200,721.161	12	16,726.760		

young most successfully when female density was low. Beta-males, however, are female mimics, and they enter spongocoels guarded by α-males with little difficulty. If α-males are unable to detect β-males that have invaded their spongocoels, α-males may release receptive females into their spongocoels before they become gravid, thus permitting matings by β-males. The fertilization success of β-males could be explained by female preference for such males, but other studies indicate that receptive females mate readily with any nearby male, regardless of his adult phenotype (Shuster, 1986).

The female-density experiment conducted with marked γ-males and unmarked α-males at three densities of receptive females produced the expected result. As the density of sexually receptive females increased, the fertilization success of γ-males increased significantly, at the expense of α-males (Table 6, Fig. 6). The relatively poor fertilization success of γ-males at low female density suggests that, unlike situations involving β-males, α-males may guard females more closely when γ-males are nearby. As expected, if α-males become less successful at guarding their mates with increasing female density, the fertilization success of γ-males increases as females in the spongocoel become more numerous.

The frequencies of marked and unmarked progeny produced in the female-density experiments indicate that, in several cases, both marked and unmarked males insem-

inated the same female. In three cases with apparent multiple insemination, the success of a β- or γ-male in a spongocoel equaled or exceeded the fertilization success of the resident α-male. Although little is known about patterns of sperm precedence in marine isopods, the potential for sperm competition in many species is probably high (Ridley, 1983). The oviducts of female sphaeromatid isopods such as *P. sculpta* are unmodified tubes leading directly from the vagina to the ovaries (Shuster, 1986). Sperm form a loosely coiled mass within the oviduct, and since sperm masses in multiply inseminated females appear to be homogeneous, sperm mixing undoubtedly occurs (Shuster, 1986). Beta- and γ-males devote proportionally more of their somatic mass to sperm production than do α-males (Shuster, 1987*a*) and probably compete with α-males and with each other via sperm competition. Beyond physical guarding of females, however, the response of α-males to this form of competition is unknown.

Male polymorphism involving three adult male types is known from diverse animal taxa (van Rhijn, 1973; Dominey, 1980; Gross, 1982; Kallman, 1984; Ra'anan and Sagi, 1985). The degree to which the three male morphs are distinct in *P. sculpta,* however, is unusually pronounced (Shuster, 1986, 1987*a*). Furthermore, the allelic variants of the electrophoretically detectable enzyme phosphoglucomutase (PGM) segregate with adult male phenotype. This suggests that the *Pgm* locus may be closely linked to genetic factors influencing male morphology and, thus, that α-, β-, and γ-males may be genetically as well as morphologically distinct (Shuster, 1986; Shuster and Sassaman, unpubl.). As mentioned, genetic polymorphisms in male reproductive behavior can be maintained only if the fitnesses of different male morphs are equal over time (Austad, 1984). Although equality of fitnesses was not demonstrated in this experiment, the influence of female density on fertilization success among males does suggest conditions that may allow multiple males in *P. sculpta* to persist.

Reproduction in this species occurs throughout the year, and overlapping generations of young isopods feed on subtidal coralline algae before moving to intertidal sponges to breed. In general, males live longer than females, and α-males, once established in spongocoels, accumulate potential mates as successive cohorts of females become mature and leave the algae. The harems of polygynous α-males typically consist of females in all stages of reproductive condition (Shuster, 1986). Algal abundance varies with mean water temperature and nutrient availability in the northern Gulf of California (Thomson and Lehner, 1976; M. Turk and R. Boyer, unpubl.), but algal abundance does not predict the relative abundance of sexually mature females (Shuster, unpubl.). Physical factors, however, such as extreme tides, sudden storms, and rapid changes in water temperature and salinity, for which the northern Gulf is well-known (Thomson and Lehner, 1976; Brusca, 1980), appear to exert a profound influence on the number of isopods that are able to reach maturity and successfully navigate the intertidal zone (Shuster, unpubl.). Female isopods must also risk predation by fish as they move from feeding habitat to breeding habitat in sponges. The combination of these stochastic events, whose influences on female abundance may interact, is likely to make the operational sex ratio extremely unpredictable at any particular time.

Theoretical models describing genetic polymorphisms typically assume nonoverlapping generations (O'Donald, 1980; Maynard Smith, 1982; Raper, 1983); such conditions do not apply in *P. sculpta* (Shuster, 1986). Circumstantial evidence suggests that environmental heterogeneity may be sufficient to maintain genetic polymorphisms in some species (Hedrick et al., 1976). More recent authors have argued, however, that such conditions are either seldom met (Maynard Smith and Hoekstra, 1980) or favor developmental plasticity rather than genetic heterogeneity (Via and Lande, 1985; Brockmann, 1986), particularly if cues predicting changes in the environment are somehow detectable. Nevertheless, Lively (1986) has shown that a genetic polymorphism can persist in a spatially heterogeneous environment if reliable cues predicting habitat type are unavailable (i.e., if the probability of finding one's self in an unfavorable habitat is less than 0.5). Similarly

unpredictable circumstances may exist for *P. sculpta* males attempting to secure mates in spongocoels.

The following conditions, then, may contribute to the persistence of male polymorphism in this species. When females are rare, α-males seem capable of guarding each female that enters their spongocoel. Beta-males may be capable of invading such spongocoels successfully; however, as female mimics, β-males are likely to be successful only when they occur in the population at low frequency. Thus, when females are rare, variance in male reproductive success is probably high and favors α-males. when females become more abundant, α-males become less effective at guarding females. Unmolted (unmated) as well as mated but still receptive females are released into the spongocoel, and these spongocoels are preferentially invaded by β- and γ-males (Shuster, 1986, 1987*a*). In species with condition-dependent alternative reproductive behaviors, mating success gained by satellite males appears to be marginal at best (reviews in Austad [1984], Waltz and Wolf [1984], and Thornhill and Alcock [1983]). Beta- and γ-males, however, obtain considerable fertilization success by invading spongocoels with high densities of receptive females. If such conditions occur frequently, variance in reproductive success among males may be substantially reduced. Seasonal cues predicting the availability of females might favor behavioral or developmental adaptations that permit males to capitalize on periods of female abundance and dearth (Eberhard, 1982). Such characteristics seem possible, however, only if cues predicting female abundance exist. The relative unpredictability of female abundance in this system may prevent the evolution of such plasticity in males.

Competitive interactions among β- and γ-males not examined in this experiment undoubtedly occur in the field, and the fertilization success of individual α-, β-, and γ-males clearly depends on the relative frequencies of other breeding males in the population. Nevertheless, the ability of individual β- and γ-males to outcompete α-males in their own spongocoels is significant and may enable the short-term fertilization success of β- and γ-males to approach that of α-males. A further increment to the overall success of β- and γ-males may then arise from life-history differences among the three male types. Gamma-males reach sexual maturity nearly twice as fast as α-males, with β-males maturing at an intermediate rate (Shuster, 1986). This difference in maturation rates is not sufficient to permit immature isopods to respond to changes in the operational sex ratio by becoming β- or γ-males (Shuster, 1986). It does, however, lead to a greater turnover rate for β- and γ-genotypes and to proportionally greater representation by β- and γ-males in the natural population than is indicated in Figure 5. Variance in male reproductive success among α-, β-, and γ-males may therefore be considerably less than is apparent from examinations of breeding aggregations alone (Shuster, 1986, 1987*a*, 1987*b*). Thus, by decreasing variance in reproductive success among males employing alternative reproductive strategies, unpredictable fluctuations in the abundance of sexually receptive females, as well as life-history differences among the three male morphs, may play substantial roles in maintaining male polymorphism in this marine isopod crustacean.

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