

**Changes in female anatomy associated with the reproductive moult in  
*Paracerceis sculpta*, a semelparous isopod crustacean**

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(With 9 figures in the text)

*Paracerceis sculpta* (Holmes) is a sexually dimorphic sphaeromatid isopod crustacean inhabiting intertidal zones in the northern Gulf of California. Adult females in this species undergo a biphasic moult that initiates their sexual receptivity. Coincident with this moult, females experience anatomical changes associated with oviposition and gestation of young within the female marsupium. These modifications restrict female mobility, prevent females from feeding, and ultimately result in obligate female semelparity. In this paper, I describe the external and internal anatomy of premoult, half-moulted and postmoult females collected from breeding aggregations in intertidal sponges. Field-collected premoult females possessed hard, lustrous cuticles, and did not contain sperm. Females in half-moulted condition contained sperm masses in both oviducts. Postmoult females contained developing embryos in internal brood pouches, and possessed cuticles that were pliable, translucent and setose. Embryos completed their development within postmoult females and dispersed from their mothers as mancae. Gestation duration decreased with increasing ambient temperature, from a maximum of 75 days at 12 °C to a minimum of 13 days at 35 °C. Female fecundity correlated positively with female body length. Spent females, depleted of lipid stores and muscle mass, died within two weeks of releasing mancae. 'Female metamorphosis' is considered a taxonomic character in certain sphaeromatid species descriptions. Anatomical changes in reproductive females similar to those in *P. sculpta* may occur in these species as well.

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### Introduction

Female sexual receptivity is often associated with moulting in crustaceans (reviews in Wickler & Seibt, 1981; Ridley, 1983; Shuster, 1989*b*). The duration of this 'reproductive moult' determines the length of time individual females are capable of mating, as well as the opportunity females have for mating more than once (either with a single male or with many males in succession). The spatial distribution of females undergoing reproductive moults, as well as the relative synchrony with which receptive females appear in the population, constrain the mate-acquisition abilities of males (Knowlton, 1979; Wickler & Seibt, 1981; Shuster & Caldwell, 1989). Thus, the details of the female reproductive moult cycle: (1) provide clues to how natural selection may have shaped female life-history characteristics (Strong, 1973; Shuster, 1991); and (2) permit investigation of the nature of, and the opportunity for sexual selection on, crustacean males (Shuster, 1990).

Oviposition and care of the young often follow reproductive moulting in female Crustacea (Menzies, 1954; Ridley, 1983). In most iteroparous species, females undergo minor anatomical changes associated with the movement of ova through oviducts, or with producing structures necessary for attaching embryos to the body. These modifications are usually lost in subsequent nonreproductive moult cycles (review in Nelson, Hedgecock & Borgeson, 1988). Females in many sphaeromatid Isopoda, however, undergo extensive morphological changes during reproductive moulting and gestation of young (Harrison, 1984). These changes coincide with the appearance of elaborate anatomical and physiological mechanisms that permit females to provide nutrition to their developing embryos (Holdich, 1968, 1971), and evidently result in obligate female semelparity in certain species (see Discussion and Shuster, 1991).

Most female isopods brood their young beneath oostegites (expanded pereopodal structures) that appear at the base of the walking legs after the reproductive moult. Depending on the species, these structures overlap to various degrees along the ventral body midline and form a brood pouch that contains developing embryos (see Ridley, 1983). In most species, embryos are deposited directly into the pouch. However, in over one-third of sphaeromatid genera in which marsupial structures are described (23/63, Harrison, 1984), females develop membranous invaginations within the brood pouch that place embryos within the female body cavity. This intimate arrangement appears to permit mothers to provision their developing young with nutrients circulated in blood or in other bodily fluids (Menzies, 1954; Holdich, 1968, 1971; Harrison, 1984).

The mouthparts of most of these females (21/63 genera, Harrison, 1984) either become modified to circulate water beneath the oostegites, or cease to function altogether and become fused to the cephalon. Females in these genera are unable to feed while brooding, and lose much of their prereproductive cuticular pigmentation while gravid (Holdich, 1971; Shuster, 1986). The overall degenerate condition of brooding sphaeromatid females is so obvious that it is considered an important taxonomic character by many sphaeromatid systematists (review in Harrison, 1984).

Despite evidence for interspecific variation in female parental care among the Sphaeromatidae,

the sequence of anatomical changes females undergo while moulting, brooding and provisioning young have been documented in relatively few species (Holdich, 1968, 1971; Shuster, 1981; Harrison, 1984). In this paper, I describe this process for females in *Paracerceis sculpta*, a sphaeromatid isopod crustacean inhabiting the northern Gulf of California. Since female oostegites are transparent in this species, I present a scheme for classifying brooding females based on changes in female anatomy and in the developmental condition of embryos visible through the marsupium. I also describe the relationships between ambient temperature and gestation duration, and between female body length and fecundity, as well as the length of time females survive after releasing their broods.

#### The reproductive biology of *Paracerceis sculpta*

*Paracerceis sculpta*, like many sphaeromatid isopods (Iverson, 1982), exhibits conspicuous sexual dimorphism (Fig. 1). Most adult males (' $\alpha$ -males', approximately 82%, Shuster, 1987a) are larger than females, and possess enlarged, rugose pleotelsons, with elongated, forceps-like uropods. These structures are unmodified in females.

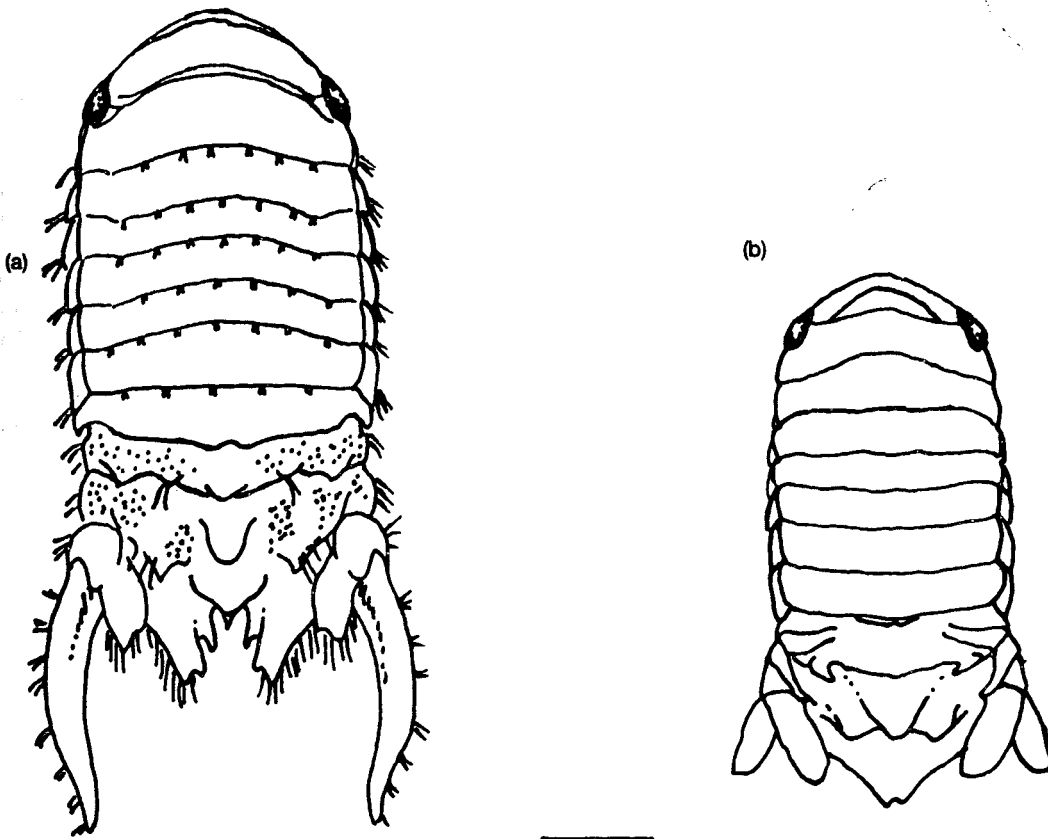


FIG. 1. Sexual dimorphism in *Paracerceis sculpta*. (a)  $\alpha$ -male; (b) adult female. Scale bar represents 1 mm. Redrawn from Shuster, 1991.

Alpha-males establish breeding territories in the spongocoels of calcareous intertidal sponges (*Leucetta losangelensis*), and females are attracted to spongocoels containing other breeding conspecifics (Shuster, 1990). Females undergo their reproductive moults within 3–5 days of entering spongocoels, and mate repeatedly for 24–48 hours until moulting is completed. Inseminated females oviposit into a ventral brood pouch, and embryos develop over the next 2–9 weeks, depending on water temperature (see below). During this time, additional females may enter the spongocoel, and aggregations of up to 19 females ( $\bar{x} \pm \text{S.D.} = 1.73 \pm 3.56$ ,  $N = 212$ ; Shuster, 1987a) may accumulate with a single  $\alpha$ -male. After emerging from the marsupium, mancae disperse from the sponge and settle on subtidal coralline algae (*Amphiroa* or *Corallina* sp., Shuster, 1991) to feed.

Adult male isopods are rarely found in algal samples (Shuster, 1986). This suggests that males leave algae before or shortly after their adult moult, and migrate to sponges in the mid- to upper intertidal zone. Females with mature or nearly mature ovaries are often found in algal samples. Migration from algae to sponges by females, therefore, appears to occur only a few days before females enter spongocoels and become sexually receptive (Shuster, 1990, 1991). Further details of the life history and mating system of *P. sculpta* are available in Shuster (1986, 1987a, b, 1989a, b).

### Methods

Isopod breeding aggregations were collected from spongocoels between October 1983 and November 1985 as described in Shuster (1987a and 1991). Females were separated from samples, measured to the nearest 0.15 mm using a stereomicroscope, and classified by reproductive condition using the following criteria: (1) the relative stage in the sexual moult cycle [pre-moult, half-moulted, post-moult]; (2) the distribution and relative condition of cuticular pigmentation; (3) the relative size and appearance of the hepatopancreas; and (4) the condition of ovaries and/or developing young.

To permit examination of the internal structures of females, 20 pre-moult females, 10 newly inseminated half-moulted females, and 6 post-moult females that had transported ova into their brood pouches, were removed from samples, chilled in a freezer for 10 min and dissected in physiological saline under a stereomicroscope. To permit examination and description of upper and lower aspects of the reproductive organs, the body cavities of half of the females of each type were opened from a dorsal aspect; the remaining females were opened ventrally. The gut of each individual was examined for ingested material, and the length and relative condition of the hepatopancreas, as well as the position and relative maturity of the oviducts, ovaries and marsupial structures were recorded. The position, amount and activity of sperm in the female reproductive tract were also recorded for each female. Eight stages of female reproductive condition are summarized in Table I.

Live females were maintained in covered 225 ml plastic cups containing sea water at ambient air temperature with *Amphiroa* thalli provided as food. Sea water and algae in cups were changed every 3–7 days. Other details of isopod maintenance are available in Shuster (1986). To determine the relationship between ambient air temperature and gestation duration, the number of days between the reproductive moult and the release of mancae from the brood pouch was plotted for 100 newly mated females, against the mean of the midday air temperatures recorded during gestation. To determine the relationship between female body size and fecundity, the number of young released by 120 field-collected, gravid females was plotted against female body length.

To determine whether females are capable of repeated reproduction, 76 females that had released their broods in the laboratory were maintained in covered 225 ml cups containing sea water and *Amphiroa* thalli until they died. Water and food were changed as described above. The survival and feeding of these females was compared with 10  $\alpha$ -males and 20 immature individuals maintained under similar conditions.

TABLE I  
*Female reproductive condition: Stages S<sub>1</sub>-S<sub>7</sub>*

Stage	Description
S <sub>1</sub>	Female unmoulted; cuticle well-pigmented; mouthparts dark, well-formed, movable; hepatopancreas dark, extending to 5th segment; ovaries orange, filling pereon body cavity dorsal to digestive structures; oostegites absent.
S <sub>2</sub>	Female half-moulted, other characters as above.
S <sub>3</sub>	Female fully moulted, new cuticle dull in colour, setose at segment margins; mouthparts metamorphosed, fused to cephalon; hepatopancreas dark, compressed into 1st segment; brood pouch filled with orange, subspherical, undifferentiated embryos.
S <sub>4p</sub>	Hepatopancreas reduced and confined to 1st pereon segment; embryos elongate, orange, but slightly greenish at margin; eyespots absent.
S <sub>4c</sub>	Hepatopancreas indistinct; embryos elongate, only faintly orange or green, eyespots apparent.
S <sub>5</sub>	Mantae well-developed, segmentation clearly visible, movements apparent.
S <sub>6</sub>	Mantae fully developed, dispersing from brood pouch.
S <sub>7</sub>	Brood pouch empty, female spent.

## Results

### *Population samples*

Unlike males, *P. sculpta* females showed no evidence of morphological polymorphism (Shuster, 1987a). The distribution of adult female body lengths (post reproductive moult) was essentially unimodal ( $\bar{x} \pm \text{S.D.} = 5.34 \pm 0.66$  mm,  $N = 3269$ , Fig. 2), and females possessed no conspicuous variation in cuticular morphology similar to that possessed by adult males (Shuster, 1987a). The composition of breeding aggregations collected in these samples is reported in detail in Shuster (1987a, 1989b, 1990).

### *Premoult females*

#### *External anatomy*

Sexually mature females (with mature ovaries, see below) that had not undergone a reproductive moult (premoult females) were classified as S<sub>1</sub> (Fig. 3a). These individuals possessed lustrous cuticles with uniformly distributed ground pigmentation. In most cases, ground pigmentation was dark purple or dark green. A wide variety of mottling and banding patterns observed was among females (as well as among males) that appeared similar to those reported in other sphaeromatid species (review in Hedgecock, Tracey & Nelson, 1982). As in these other species, the inheritance of most major pigmentation patterns in *P. sculpta* appears to be controlled by dominant alleles at relatively few genetic loci (Shuster, 1989a, unpubl. data).

Premoult females possessed well-formed and functional mouthparts that differed little from those of juveniles or mature males (Fig. 4a, d). The ventral pereon of premoult females was slightly convex, and no oostegites were visible on the ventral cuticles of unmoulted females. As the ventral

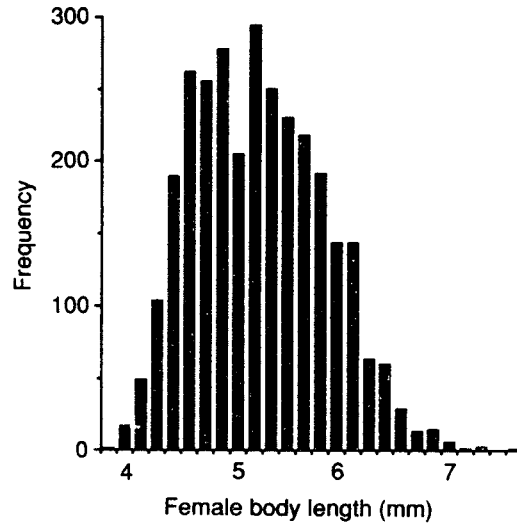


FIG. 2. Distribution of female body lengths for females collected in *Leucetta losangelensis spongocoeh*.  $\bar{x} \pm S.D. = 5.43 \pm 0.66$  mm,  $N = 3269$ .

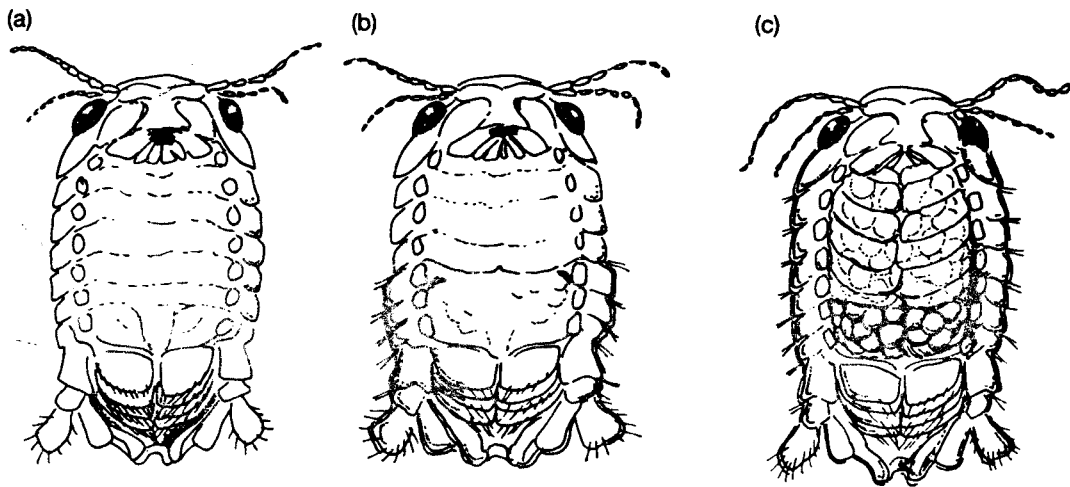


FIG. 3. (a) Premoult, (b) half-moulted and (c) postmoult females. Redrawn from Shuster, 1989b.

cuticle was transparent, the gut, which was usually filled with ingested material, and the dark branches of the hepatopancreas, were conspicuous against the bright orange or yellow ovaries, located dorsal to the digestive structures. Also visible from a ventral aspect were the unfilled pouches of the marsupium, appearing as four pairs of round, hyaline structures situated along either side of the midline of pereonites 1-4 (Fig. 5).

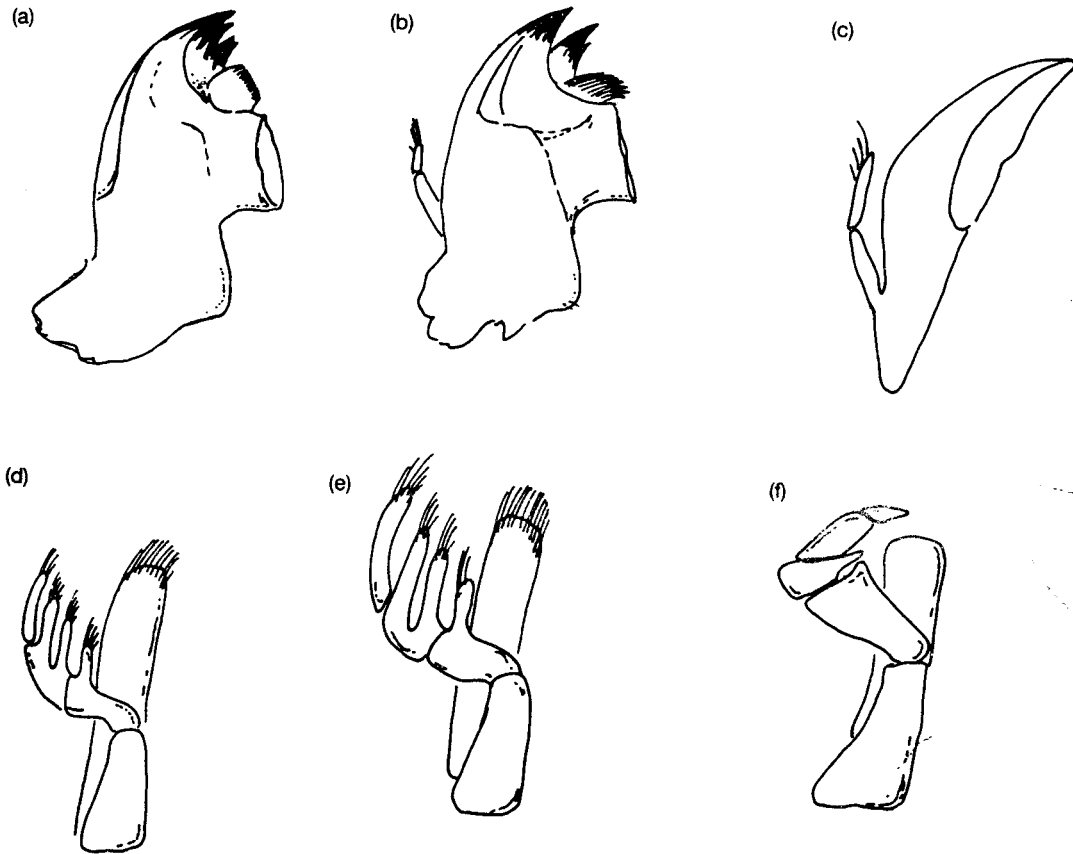


FIG. 4. Mouthparts of  $\alpha$ -male (a, d), premoult female (b, e) and postmoult (and gravid) female (c, f). Mandibles (a,b,c); 1st and 2nd maxillipeds (d,e,f).

#### *Internal anatomy*

The guts of 15 of 20 premoult females were filled with finely divided brown or purplish material, presumably the masticated cells of coralline algae. Bits of crustacean cuticle were found in the guts of five of 20 females, suggesting that females had ingested their own exuvia, or, like early stage juveniles, were facultatively carnivorous (Shuster, 1986).

The hepatopancreas of premoult females consisted of 4–6 dark, turgid branches that presumably contained stored lipids (Holdich, 1968). The ovary was H-shaped and filled with orange, subspherical ova (Fig. 6a). An oviduct led away from each of the ovary's midventrolateral margins, and terminated near the base of each 5th pereopod. A depression in the outer cuticle suggested the location of the future genital pore, but no external opening was visible, and premoult females did not contain sperm. A lateral duct leading away from the oviduct toward the brood pouches was identifiable in most females (Fig. 6d). In premoult females this structure resembled a ligament or other supportive structure. After ova were transported to brood pouches, however, the lateral duct structure was more obvious (see below).

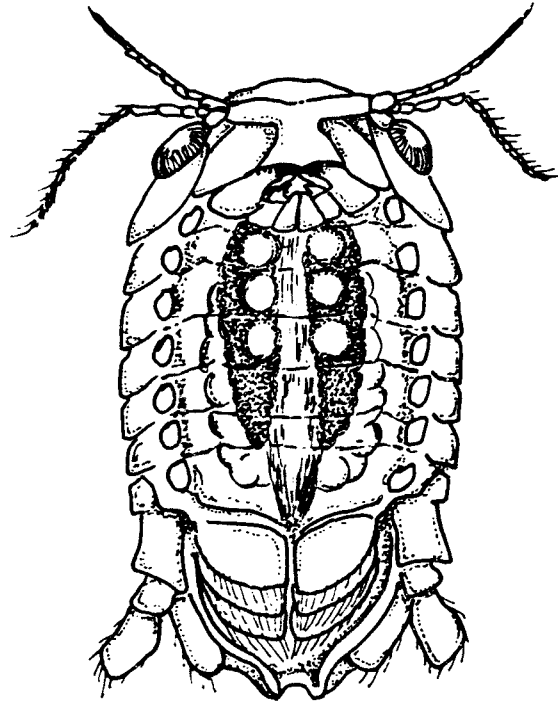


FIG. 5. Ventral view of a premoult female. Pereopods are removed at their bases. Note unmetamorphosed mouthparts and unfilled brood pouches in pereonal segments 2-4. Brood pouches in segment 1 are obscured by the mouthparts. Dorsal to the brood pouches are the dark branches of the hepatopancreas, which are ventral to the mature ovaries. The gut is located along the body midline between the hepatopancreas branches.

### *Half-moulted females*

#### *External anatomy*

Half-moulted ( $S_2$ ) females had shed the posterior portion (below the 4th pereonal segment) of their cuticles. The cuticular textures of premoult and gravid females were easily compared in half-moulted females because the posterior half of their bodies had expanded, while the anterior half was still constrained by the unshed anterior portion of the cuticle (Fig. 3b). While premoult females possessed hard, lustrous and well-pigmented cuticles, those of moulted females were softer, less densely pigmented, somewhat translucent and setose.

#### *Internal anatomy*

The relative positions of the ovaries, oviducts, hepatopancreas and brood pouches of half-moulted females did not differ substantially from those of premoult females. The genital pores of half-moulted females, however, had become relatively large, conspicuous openings. A pliable flap of cuticle partially closed each genital pore, but the flap was easily retracted and the genital pore communicated directly with the oviduct. Females that had undergone reproductive moults in the field usually possessed a whitish sperm mass in each oviduct (Fig. 7, Shuster, 1989b).



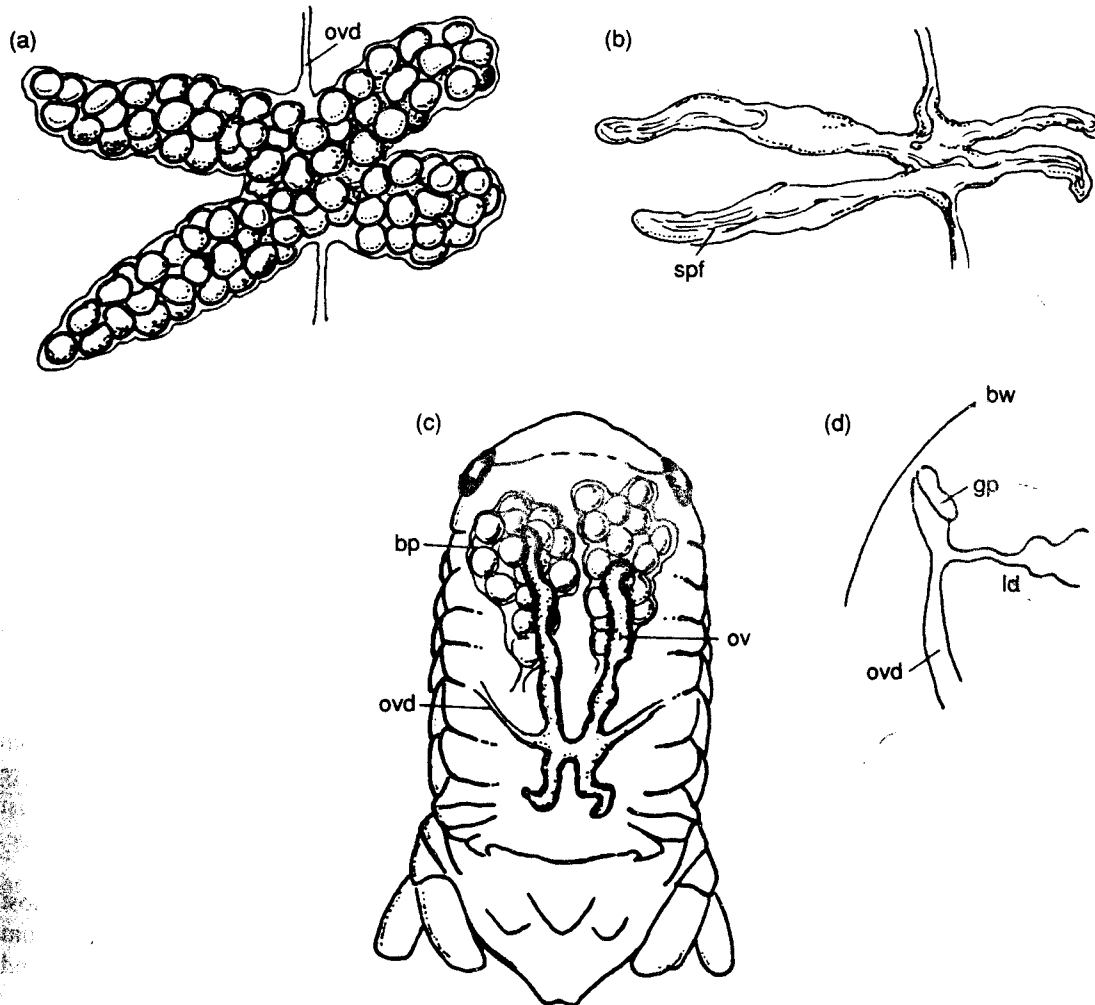


FIG. 6. Ovaries of (a) a premoult female; (b) spent ovaries of a gravid female containing sperm pseudoflagellae; (c) dorsal view of spent ovaries overlying the filled pouches of a gravid ( $S_3$ ) female; (d) schematic diagram of the vagina, the oviduct and the lateral duct leading to the brood pouch of a postmoult female; bp = brood pouch; bw = body wall; ld = lateral duct; ov = ovary; ovd = oviduct; spf = sperm pseudoflagella; gp = genital pore.

As females in this species possess no sperm storage organs, the sperm masses of inseminated females were located directly within the oviduct lumen, about 0.25 mm from each of the genital pores. A constriction in the oviduct appeared to prevent the sperm mass from contacting the ovary (Fig. 7). Individual spermatozoa were macroscopic (1.5 mm, Shuster, 1989b), and sperm found in the reproductive tracts of females were identical to sperm found in the seminal vesicles of  $\alpha$ -,  $\beta$ - and  $\gamma$ -males (Shuster, 1987a). Both in the reproductive tracts of half-moulted females and in the seminal vesicles of males sperm were nonmotile.

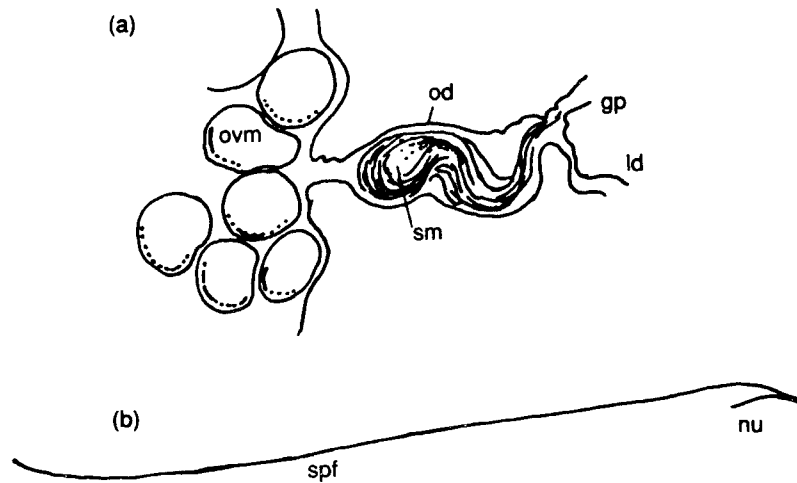


FIG. 7. Sperm mass in the oviduct of a half-moulted female; gp = genital pore; ld = lateral duct; nu = sperm nucleus; od = oviduct; ovm = ovum; sm = sperm mass; spf = sperm pseudoflagella. Redrawn from Shuster, 1989b.

### *Postmoult females*

#### *External anatomy*

Newly moulted ( $S_3$ ) females shed the anterior portion of their cuticles and transported ova from their ovaries to the internal pouches (Fig. 3c). The hepatopancreases of postmoult females were pushed anteriorly within the pereonal cavity during oviposition, and formed a dark mass just posterior and internal to the maxillipeds. The brood pouches were filled with bright orange, subspherical embryos that were visible posterior to the hepatopancreas.

Like many dynamenine sphaeromatids (Harrison, 1984), postmoult *P. sculpta* females lost functional mouthparts when they shed their anterior cuticles. The vestigial maxillipeds that remained, while weakly movable, were nearly devoid of setae. The mandibles lacked molar and incisor processes, and were fused to the head (Fig. 4c, f).

#### *Internal anatomy*

Transport of zygotes from the ovaries, through the oviduct, and into the brood pouches, occurred 6–12 h after females shed their anterior cuticles (Shuster, 1989b). After zygote transport, the ovaries, from a dorsal view, appeared as a thin, H-shaped bag overlying the filled brood pouches (Fig. 6b). The pseudoflagellae of sperm were distributed throughout the spent ovaries, suggesting that females moved sperm into the ovaries for fertilization, or that sperm became activated and somehow moved into the ovaries near the time that females completed their moult. Fertilization evidently did not, as has been suggested for some isopods (Ridley, 1983), occur in either the marsupium or in the oviduct itself.

After zygotes were transported, the duct leading from the oviduct to the brood pouch was more conspicuous (Fig. 6c, d), and led toward an area beneath the oostegites from which the brood pouches invaginate the body wall. When filled, the brood pouches occupied nearly all available

space within the body cavity, pushing the remains of the gut against the dorsal body wall, and extending into the cephalon.

### *Gravid females*

#### *The developmental condition of embryos*

Three successive stages based on the relative development of embryos in the brood pouches were distinguishable in gravid females. Early stage gravid females ( $S_{4p}$ ) possessed elongate, ovoid embryos which, while still orange, appeared somewhat green at the margins. Embryos at this stage lacked eyespots. The brood pouches of middle stage gravid females ( $S_{4e}$ ) contained embryos with eyespots. These embryos were still greenish orange and were not clearly segmented, but dark eyespots were conspicuous, and slight movement was detectable. Late stage gravid females ( $S_5$ ) had fully developed mancae in their internal pouches.

During development, embryos appeared to increase in size, such that by  $S_5$ , the ventral aspects of most females were markedly distended. Mancae contained little or no orange yolk, and cuticular pigmentation patterns were usually visible. Mancae at this stage were clearly segmented, well-formed and moving. Females in the process of releasing young were classified as  $S_6$ . Mancae were contained mainly within internal pouches, but also had begun to slip out between the oostegites. Offspring release occurred in most females over 1–3 days.

### *Spent females*

Spent females ( $S_7$ ) had released all of their young, and possessed cuticles that were pale or occasionally white. While capable of movement, spent females were typically sluggish and swam only with apparent difficulty. With their oostegites spread and what was left of their viscera pushed far into the cephalon or against the dorsal body wall, spent females appeared devoid of nearly all of their prereproductive viscera and muscle mass.

### *Ambient temperature and gestation duration*

Ambient air temperatures in Puerto Peñasco, Sonora, Mexico during the course of this experiment ranged from 10 to 35 °C. As isopods were maintained in 225 ml cups, these temperatures were translated directly to females. The relationship between ambient temperature and gestation duration was curvilinear, with a maximum duration of 75 days at 12 °C, and a minimum of 14 days at 35 °C (Fig. 8). Although daily variation in ambient temperature was not controlled in this experiment, the data closely fit a negative exponential curve ( $r^2 = 0.891$ ).

### *Female body length and fecundity*

Female body length and fecundity were positively correlated ( $r^2 = 0.862$ ,  $P < 0.001$ ,  $N = 120$ , Fig. 9).

### *Female survival after manca release*

All premoult females maintained in cups with algae fed frequently and produced faecal pellets.

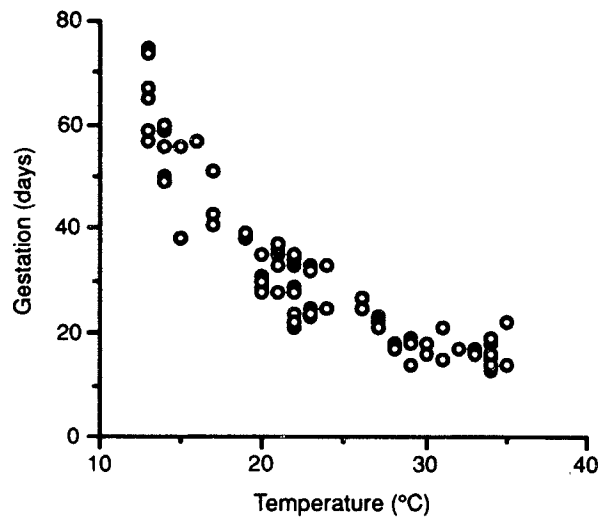


FIG. 8. Relationship between ambient air temperature and gestation duration ( $r^2=0.891$ ,  $P<0.001$ ,  $N=100$ ).

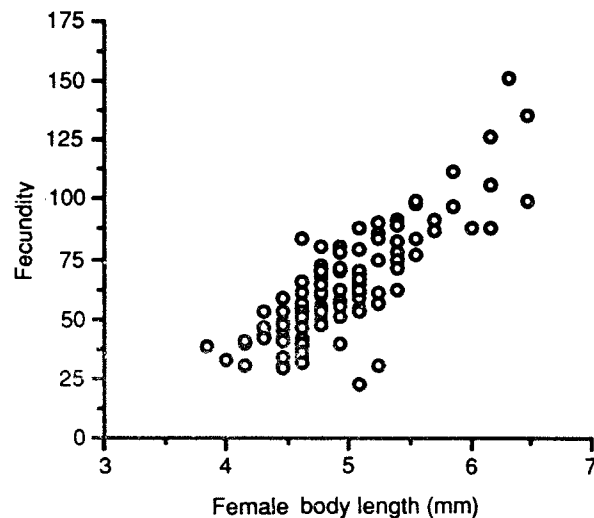


FIG. 9. Relationship between female body length and fecundity ( $r^2=0.862$ ,  $P<0.001$ ,  $N=120$ ).

Only one premoult female could be maintained in each container because females that initiated their reproductive moults were often cannibalized by other premoult females. Half-moulted females were not observed to feed or defecate. Gravid females also did not feed, and no faecal pellets were found in the bottom of their containers.

Spent females neither fed nor moulted, despite the availability of food in their containers and, at ambient temperatures, died within two weeks of releasing their broods ( $\bar{x} \pm S.D.$  days survived =  $13.06 \pm 0.68$ ,  $N=76$ , Table II). All immature individuals and nine of 10  $\alpha$ -males fed and

TABLE II  
*Laboratory survivorship of  $\alpha$ -males, immatures and spent females*

	N	Fed	Moulted	Died	Days survived
$\alpha$ -Males	10	9	0	0	25+
Immatures	20	20	10	0	25+
Spent females	76	0	0	76	13.06+0.68 ( $\bar{x}$ +S.D.)

defecated over the 25 days they were observed. Although none of the  $\alpha$ -males moulted during this time (substantiating earlier observations that growth in adult males is determinate: Shuster, 1986, 1987a), 10 of 20 immatures moulted and grew over the 25 days of observation. None of the immatures or  $\alpha$ -males died.

### Discussion

Premoult females were voracious feeders. This is not surprising given that females must travel from algae to sponges to reproduce, and may rely on stored energy while locating breeding sites. Of potentially greater significance to female feeding patterns, however, particularly with respect to the cannibalistic tendencies of premoult females, is the fact that ovarian maturation occurs primarily during the last half of females' penultimate intermoult (S. M. Shuster, unpubl. data). Volume feeding on high quality food (such as other isopods) by premoult females may speed yolk deposition and enhance offspring survival.

In nature, premoult females are attracted to spongocoels containing breeding aggregations of conspecifics, and engage in courtship behaviour with  $\alpha$ -males at the spongocoel osculum (Shuster, 1990). Thus, premoult females are *behaviourally* receptive (Shuster, 1989a). Actual sexual receptivity and copulation, however, occur only in half-moulted females (Shuster, 1989b). Females shunt their ova almost immediately after shedding their anterior cuticles, and are sexually receptive until moments before completing their moults (Shuster, 1989b). Fertilization evidently occurs in the ovary, as sperm pseudoflagellae, minus their nuclei, were abundant within the spent ovarian lumen.

How sperm move from the oviduct to the ovary remains unclear since sperm pseudoflagellae in this species, like those in other isopods (Fain-Maurel, Reger & Cassier, 1975), appear structurally incapable of generating movement (Shuster & Kooda, unpubl. data). Some sperm movement may occur in an acrosome reaction chemically induced by females (P. Talbot, pers. comm.), or females may have contractile tissues in their oviducts that facilitate sperm transport to ovaries (Shuster, 1986). The likelihood that ova would flush sperm out of the oviduct during transport and the abundance of sperm pseudoflagellae in the spent ovary, however, make oviducal fertilization unlikely.

Gestating females were maintained at ambient air temperature, thus daily thermal variation and its likely effect on gestation duration was uncontrolled. Despite this potential source of variance, gestation duration decreased smoothly with increasing temperature ( $r^2 = 0.891$ , Fig. 8). Moreover, the asymptotic decline in gestation duration with increasing ambient temperature suggests that, while the rate of embryonic cell division is sensitive to temperature, certain complexities of development are unable to occur in less than two weeks. Presumably, decreases in temperature

below 10 °C would result in increased gestation duration, but prolonged cold (or heat) seem likely to affect the survival of females as well as their embryos. The relationship between female body length and fecundity in this species is similar to that observed for most Crustacea (review in Ridley, 1983).

The rapid deterioration of cuticular pigmentation, the depletion of hepatopancreatic tissue and the loss of muscle mass in gravid females appears too extreme to be explained simply by senescence. Gestating *P. sculpta* females thus appear to provision their broods during pregnancy in a way similar to that documented in another dynamenine species (*Dynamene bidentata*, Holdich, 1968, 1971). The narrow range in female body size, the loss of functional mouthparts by gravid females, the fact that uninseminated females do not resorb ova (Shuster, 1989b), and the death of females shortly after progeny are released, indicate that semelparity is the rule for females in *P. sculpta*. Obligate semelparity may be the rule for other sphaeromatid species with similar female gestational histories.

Semelparity has evidently had considerable influence on the evolution of reproductive behaviour in *Paracerceis sculpta*, and perhaps in other related sphaeromatids as well (Shuster, 1991; Shuster & Wade, 1991). Females seem likely to have begun associating with protected habitats while brooding to escape predation (Shuster, 1991). Risks associated with repeated trips to and from feeding and breeding habitats may have favoured increased emphasis by females on a single reproductive event (Bell, 1980; Shuster, 1990, 1991). Intensifying selection for semelparity may have forced ancestral females to become more sedentary during gestation, thus favouring females that situated themselves in predictably available breeding habitats (such as sponges) while brooding young (Shuster, 1990). The association of females with sponges, in turn, may have favoured males that attempted to monopolize locations preferred by females (Parker, 1978). Sexual selection in this context may have favoured physical or behavioural attributes of males that enhanced their ability to defend spongocoels, such as large body size and uropod and pleotelson modifications useful in spongocoel defence and takeover (Shuster, 1989a, In prep.). Similar circumstances may have led to the co-occurrence sexual dimorphism and extreme polygyny in other isopod Crustacea (Menzies, 1954; Ridley, 1983; Upton, 1987).

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#### REFERENCES

- Bell, G. (1980). The costs of reproduction and their consequences. *Am. Nat.* **116**: 45–76.
- Fain-Maurel, M.-A., Reger, J. F. & Cassier, P. (1975). Le gamete mâle des schizopodes et les analogies avec celui des autres peracarides. 1. Le spermatodoïde. *J. Ultrastruct. Res.* **51**: 269–280.
- Harrison, K. (1984). The morphology of the sphaeromatid brood pouch (Crustacea: Isopoda: Sphaeromatidae). *Zool. J. Linn. Soc.* **82**: 363–407.

- Hedgecock, D., Tracey, M. L. & Nelson, K. (1982). Genetics. In *The biology of Crustacea 2. Embryology, morphology and genetics*: 284–403. Abele, L. G. (Ed.). New York: Academic Press.
- Holdich, D. M. (1968). Reproduction, growth and bionomics of *Dynamene bidentata* (Crustacea: Isopoda). *J. Zool., Lond.* **156**: 137–153.
- Holdich, D. M. (1971). Changes in physiology, structure and histochemistry occurring during the life cycle of the sexually dimorphic isopod, *Dynamene bidentata* (Crustacea: Peracarida). *Mar. Biol., Berlin* **8**: 35–47.
- Iverson, E. W. (1982). Revision of the isopod family Sphaeromatidae (Crustacea: Isopoda: Flabellifera). 1. Subfamily names with diagnoses and key. *J. Crust. Biol.* **2**: 248–256.
- Knowlton, N. (1979). Reproductive synchrony, parental investment and the evolutionary dynamics of sexual selection. *Anim. Behav.* **27**: 1022–1033.
- Menzies, R. J. (1954). The comparative biology of reproduction in the wood-boring isopod crustacean *Limnoria*. *Bull. Mus. comp. Zool. Harv.* **112**: 361–388.
- Nelson, K., Hedgecock, D. & Borgeson, W. (1988). Effects of reproduction upon molting and growth in female American lobsters (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* **45**: 805–821.
- Parker, G. A. (1978). Evolution of competitive mate searching. *A. Rev. Ent.* **23**: 173–196.
- Ridley, M. (1983). *The explanation of organic diversity: the comparative method and adaptations for mating*. Oxford: Oxford Science Publications.
- Shuster, S. M. (1981). Sexual selection in the Socorro isopod, *Thermosphaeroma thermophilum* (Cole and Bane) (Crustacea: Peracarida). *Anim. Behav.* **29**: 698–707.
- Shuster, S. M. (1986). *The reproductive biology of Paracerceis sculpta* (Crustacea: Isopoda). PhD thesis, University of California, Berkeley.
- Shuster, S. M. (1987a). Alternative reproductive behaviours: three discrete male morphs in *Paracerceis sculpta*, an intertidal isopod from the northern Gulf of California. *J. Crust. Biol.* **7**: 318–327.
- Shuster, S. M. (1987b). Male body size, not reproductive habitat characteristics predicts polygyny in a sexually dimorphic intertidal isopod crustacean, *Paracerceis sculpta* (Crustacea: Isopoda). In *Memorias del V Simposium Biologia Marina*: 71–80. Maligrino, G. & Santoyo, H. (Eds). Universidad Autonoma de Baja California Sur, La Paz, B.C.S., Mexico.
- Shuster, S. M. (1989a). Male alternative reproductive strategies in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among  $\alpha$ -,  $\beta$ - and  $\gamma$ -males. *Evolution* **43**: 1683–1698.
- Shuster, S. M. (1989b). Female sexual receptivity associated with molting and differences in copulatory behavior among the three male morphs in *Paracerceis sculpta* (Crustacea: Isopoda). *Biol. Bull. mar. biol. Lab. Woods Hole* **177**: 331–337.
- Shuster, S. M. (1990). Courtship and female mate selection in a semelparous isopod crustacean, *Paracerceis sculpta*. *Anim. Behav.* **40**: 390–399.
- Shuster, S. M. (1991). The ecology of breeding females and the evolution of polygyny in *Paracerceis sculpta*, a marine isopod crustacean. In *Crustacean sexual biology*: 91–110. Bauer, R. & Martin, J. (Eds). Columbia University Press.
- Shuster, S. M. & Caldwell, R. L. (1989). Male defense of the breeding cavity and factors affecting the persistence of breeding pairs in the stomatopod, *Gonodactylus bredini* (Manning) (Crustacea: Hoplocarida). *Ethology* **82**: 192–207.
- Shuster, S. M. & Wade, M. J. (1991). Female copying and sexual selection in a marine isopod crustacean (*Paracerceis sculpta*). *Anim. Behav.* **42**: 1071–1078.
- Strong, D. R., Jr (1973). Amphipod amplexus, the significance of ecotypic variation. *Ecology* **54**: 1383–1388.
- Upton, N. P. D. (1987). Asynchronous male and female life cycles in the sexually dimorphic, harem-forming isopod *Paragnathia formica* (Crustacea: Isopoda). *J. Zool., Lond.* **212**: 677–690.
- Wickler, W. & Seibt, U. (1981). Monogamy in Crustacea and man. *Z. Tierpsychol.* **57** (3–4): 215–234.