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# The Reproductive Biology of Some Serolid Isopods from the Antarctic

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**Summary.** Several species of serolid isopod from Signy Island, South Orkney Islands and also from South Georgia were studied, and aspects of their reproductive behaviour and associated morphology are discussed. In *Serolis polita* Pfeffer egg-laying took place at a mean age of 28 months, and the eggs were then incubated in a ventral marsupium for a period of 20 months before the release of juveniles in the spring. The mean egg dry weight at spawning was 0.68 mg for *S. polita* and 3.35 mg for *Serolis cornuta* Studer. The egg weight increased during marsupial development due to the uptake of minerals, but the total calorific content fell. Within each species brood size was linearly related to female size and the mean number of eggs varied from 40 for *S. polita* to 232 for *Serolis pagenstecheri* Pfeffer. There was no detectable marsupial mortality. *S. polita* appeared to breed repeatedly at two-year intervals, but *S. cornuta* probably only breeds once. The reproductive biology of Antarctic serolids is compared with that of temperate isopods, and it is shown that they produce larger young which is related to their larger adult size. The extremely protracted period of marsupial incubation is associated with the need to synchronize reproduction with the seasonal nature of Antarctic primary production.

## Introduction

Antarctic marine invertebrates show many striking adaptations which can be attributed to the polar environment, particularly in their reproductive biology. Thorson (1950) discussed the occurrence of large yolky eggs and the high incidence of brooding, and White (1977) has shown how the reproductive cycles are often synchronized with the cycle of primary production. Unfortunately there is a paucity of good data with which to examine these theories, and some important groups of invertebrates remain almost unstudied.

Isopods are prominent constituents of the Antarctic benthic fauna and the Serolidae are a widespread and significant component. This family is almost entirely confined to the southern hemisphere, and about 25 species are found over a wide depth range in the seas surrounding the Antarctic Continent (Sheppard 1933; Kusakin 1967). Little is known of their biology (Bastida and Torti 1970; Moreira 1973a) and in this investigation some antarctic members of the genus have been studied for the first time. All are characteristic of soft substrates and are predatory on a variety of smaller invertebrates.

The majority of this work was carried out on two species, *Serolis polita* Pfeffer and *Serolis cornuta* Studer, from Signy Island, South Orkney Islands (60°43′S, 45°38′W), but additional material of *Serolis septemcarinata* Miers from South Georgia (54°26′S, 36°40′W) and *Serolis pagenstecheri* Pfeffer was examined.

The mean monthly sea temperatures at 10 m depth at Signy Island fluctuate between −1.7 °C and +0.4 °C (BAS unpublished records), and fast-ice covers the inshore areas for an average of 149 days a year with pack-ice for much of the remaining time (White 1977).

In this paper observations on the sexual morphology and reproductive biology of the genus are presented, and discussed in the light of existing theories of Antarctic reproductive patterns.

## Materials and Methods

The shallow water population of *S. polita* was sampled at monthly intervals for two years from sites within Borge Bay, Signy Island, using a diver-operated suction sampler (Luxmoore, in press). Samples of *S. cornuta* were taken at roughly bimonthly intervals from deeper water (30-50 m) off the mouth of the bay using a 75-cm rectangular dredge. A collection of *S. pagenstecheri* was made by divers in Cumberland Bay, South Georgia, at depths of 7 – 16 m, and preserved in 4% formal saline. Further preserved specimens of *S. septemcarinata* were obtained from samples taken during the South Georgia Benthic Survey from 40 m depth in the Bay of Isles, South Georgia (White and Maxwell 1973).

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All adult females were measured and the contents of their marsupia removed. The broods were assigned to one of five developmental stages as follows:

A. Simple yolky embryos; no embryonic tissue visible.
B. Traces of embryonic tissue visible; eyes, if formed, still unpigmented.
C. Embryos with pigmented eyes visible through egg membrane
D. Main egg membrane ruptured, and embryos free within the marsupium; no setae present on limbs, and body pigmentation absent.
E. Embryos well developed; setae and body pigmentation visible. Some juveniles may have assumed flattened adult form and have calcified cuticles, ready for release from the marsupium; this is identical to the first post-marsupial moult class (Luxmoore, 1982).

Adult females with fully formed oostegites but empty marsupia were classified as 'spent'. These stages correspond roughly to those described for *Dynamene bidentata* by Holdich (1968). When some embryos were slightly further developed than others, the brood was classified on the basis of the most advanced embryo present. Embryos in the same marsupium were never found to be separated by more than one developmental stage. Fresh broods were counted, rinsed in isotonic ammonium formate and transferred to porcelain crucibles. Dry and ash weights were determined after drying at 60 °C – 65 °C for 24 h and ignition at 500 °C – 550 °C for 6 h respectively. Selected broods were pelleted after drying and calorimetric determinations made in a micro-bomb calorimeter. Pellet weights ranged from 10 – 45 mg, and the system was calibrated with benzoic acid.

Some females of all ages were dissected and their ovaries examined. The maximum diameter of the developing oocytes or ova was measured with a microscope eyepiece graticule, and the animals were aged by the criteria described in Luxmoore (1982).

Observations of behaviour were made on animals maintained in aquaria and comparative information was also drawn from the literature.

## Results

### *Morphology*

The reproductive process in *S. polita* and *S. cornuta* was observed both in wild animals and specimens kept in aquaria. Males carried sub-adult females in amplexus by grasping the front of the female's cephalon with the modified second pereopods as described by Moreira (1973a). In addition, the dactylus of the male's 7th pereopod was hooked round the posterior-edge of the female's coxal plates, thus securing him to the female by four points of attachment. The precopulative association lasted until after the female's parturial moult (the moult at which fully adult morphology is attained) and the eggs had been laid into the marsupium.

Several morphological features seem to be associated with this precopulatory behaviour, and appear in adult males of a variety of species as secondary sexual characteristics. Of these the most obvious and universal is the subchela of the 2nd pereopod which is used as the main clasping organ. Other secondary sexual characteristics are the scattered patches of setae which show great interspecific variation but which can be classified into seven main types as illustrated in Fig. 1:

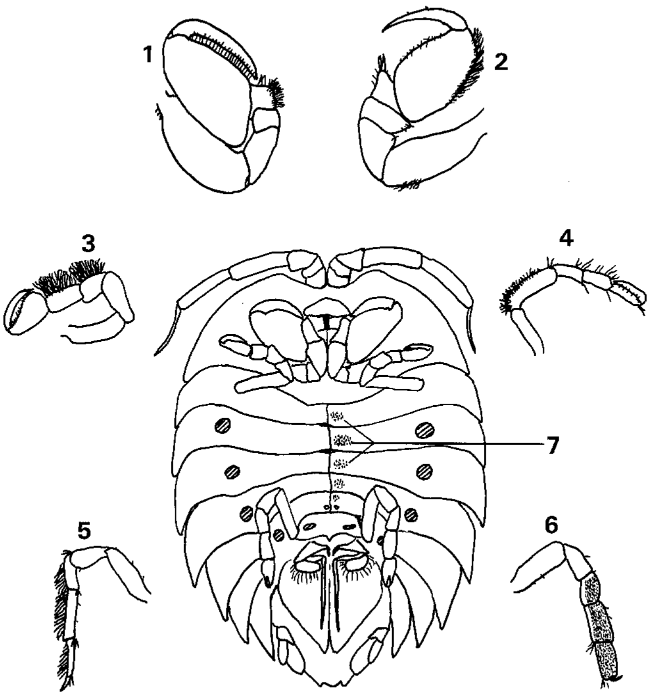

**Fig. 1.** A generalized male serolid showing secondary sexual characters: pereopods 4 – 7 and 1st pleopod removed; numbers 1 – 7 refer to positions of the setae mentioned in the text

1. A dense patch of long setae on the inner margin of the carpus of the 1st pereopod; e. g. *Serolis marplatensis, Serolis convexa, Serolis gaudichaudi, Serolis laevis, Serolis similis* (Bastida and Torti 1970; Sheppard 1933; Bastida and Torti 1970; Moreira 1971; Moreira 1974b).
2. Long setae on the outer margin of the propodus of the 1st pereopod; e.g. *Serolis exigua, Serolis uaperta, Serolis inermis, Serolis arcuata, Serolis completa* (Nordenstam 1933, Moreira 1971; Moreira 1974a; Moreira 1977; Moreira 1971).
3. Long setae on the inner margins of the merus and carpus of the 2nd pereopod; e.g. *Serolis polita, Serolis neaera* (this study; Beddard, 1884).
4. Long setae on the inner margin of the ischium of the 2nd pereopod; e.g. *Serolis sheppardi, Serolis veaperta, Serolis tropica* (Bastida and Torta 1969; Moreira 1971; Glynn 1976).
5. Patches of long setae on the 7th pereopods; e.g. *Serolis marplatensis, Serolis gaudichaudi, Serolis kempi* (Bastida and Torti 1970; Sheppard 1933).
6. A fine velvety mat of setae on the lower surface of the 7th pereopods; e.g. *Serolis pagenstecheri, Serolis septemcarinata, Serolis ovata* (this study; White 1972).
7. Velvety patches of setae on the pereon; e.g. *Serolis convexa, Serolis gaudichaudi, Serolis laevis* (Beddard 1884; Bastida and Torti 1970; Moreira 1971).

One common factor relating all these different patches of setae is that they all come into contact with the dorsal surface of the female during amplexus, and thus three possible functions can be inferred from this morphological evidence. Firstly, sensory: the male may receive stimulation from the female via the setae.

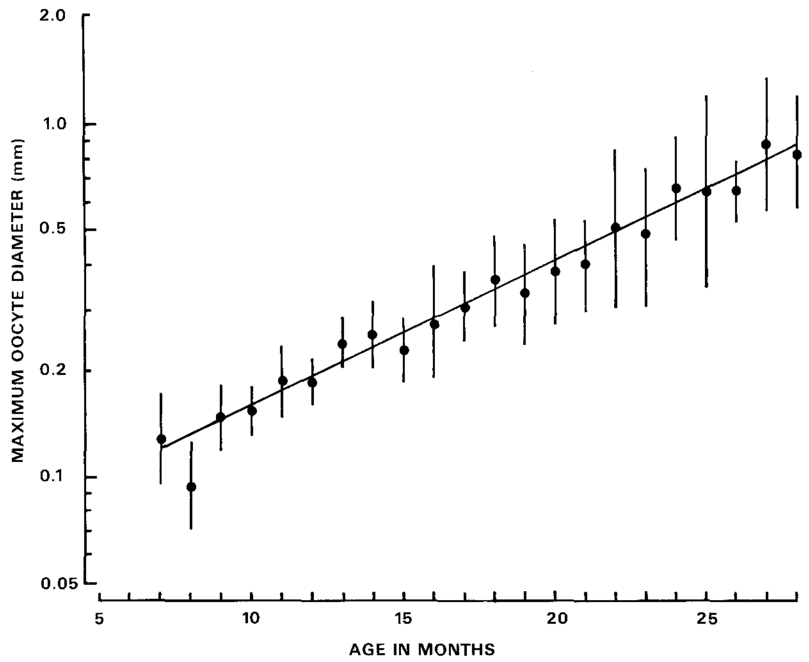

**Fig. 2.** Oocyte enlargement within the ovaries of *Serolis polita;* the circles represent mean oocyte diameters ± standard deviation (vertical lines)

Secondly, stimulatory: the male may stimulate the female with the setae. And thirdly, physical: the setae may form a protective cushion at points of contact between the two bodies, or assist the male in maintaining a grip, as Naylor (1955) suggested for *Idotea emarginata.* Whatever their function, it is certain that these morphological features are in some way associated with copulatory behaviour. Wide interspecific variation also suggests that they may serve to maintain specific isolation by preventing interbreeding.

### Reproductive Behaviour

Egg laying took place shortly after the female's parturial moult while the cuticle was still soft, eggs passing out of the oviducts directly into the marsupium via openings in the 5th pereonal sternites. Embryos were brooded in the marsupium and after hatching, young emerged through the opening behind the 4th pair of oostegites. Three female *S. cornuta* were observed releasing young in an aquarium, and it was found that the release of the entire brood took from 18 to 33 days. In each female young were released at fairly regular intervals, with no evidence of any period of increased release activity. In well developed class E broods, only a few juveniles at any one time were unfurled into the flattened adult shape, having calcified cuticles. This is presumably because of restricted space in the marsupium, and as a result, it would be impossible for the whole brood to be released simultaneously.

Spent females of *S. polita* were also found in amplexus and on two occasions were observed to moult and lay eggs. This, together with the evidence that the majority of incubating females had developing eggs in their ovaries, indicates that females can survive to breed for a second time. All incubating *S. cornuta* examined had degenerate ovaries, suggesting that this species only breeds once.

The act of sperm transfer has never been observed in *Serolis.* In spite of over two years of continual observation in aquaria, males in amplexus were never seen to quit their position on the dorsal surface of the female, as has been reported for other isopods during copulation (White 1970; Sutton 1972). On all occasions the male left the female within one day of egg-laying, and it can therefore be assumed that mating occurs in the brief period from the parturial moult until shortly after the eggs have passed into the marsupium.

### Development of the Ovary

On dissection ovaries were visible in females of the first postmarsupial moult class, even before the sexes were externally distinguishable, and the diameter of developing oocytes could be measured from about the third moult class onwards. The maximum oocyte diameter of *S. polita* was plotted against the age of the female (Fig. 2), and a regression line was calculated as:

$$\ln(\text{oocyte diameter, mm}) = 0.0938\,(\text{age in months}) - 2.769$$
$$(n = 181,\ r^2 = 0.694).$$

As oocytes are geometrically simple shapes it can be assumed that the weight is proportional to the cube of the diameter; and therefore the slope (b) in the equation

$$\ln(\text{total oocyte weight, mg}) = (\text{age in months}) + c$$

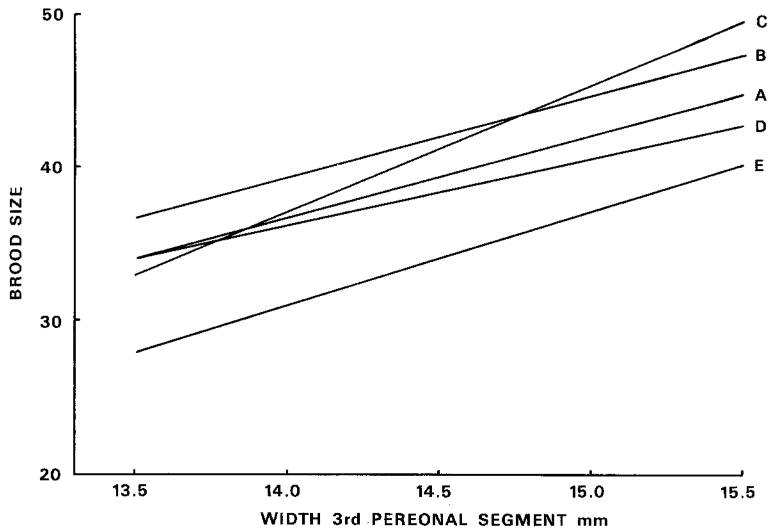

**Fig. 3.** Regression lines relating brood size to width of female for the five embryonic development stages in *Serolis polita*

can be approximated by

$$0.0938 \times 3 = 0.2814$$

Since at egg-laying (i.e. an age of 28 months) the mean brood weight is the mean brood size (40.2) times the mean weight of class A eggs (0.682 mg), the intercept (c) can be calculated as

$$\ln (40.2 \times 0.682) - (0.2814 \times 28) = -4.568$$

From this it can be shown that 75% of the weight of the brood of eggs is accumulated in the ovary during the final summer (October – March) before egg-laying.

The ovaries of ovigerous females were also examined and it was found that spent females, and those incubating class E embryos, mostly had well-developed ova. This suggests that having released one brood in the spring some females are capable of laying another brood of eggs in the following autumn. At any one time there was only one set of eggs in the ovary, and so the second

**Table 1.** Gravimetric and calorimetric data for embryos of three species of *Serolis*; columns 1 – 4 are the means of a number (*n*, in brackets) of determinations of whole broods of embryos (± standard deviation); column 5 is the product of columns 1 and 4

| Embryo developmental stage | 1 Dry wt. per embryo (mg) | 2 Ash-free dry wt. per embryo (mg) | 3 Ash content (% of dry wt.) | 4 Calorific value (J/mg dry wt.) | 5 Total calorific content per embryo (J) |
|---|---|---|---|---|---|
| *Serolis polita* | | | | | |
| A | 0.682 ± 0.127<br>(167) | 0.667 ± 0.076<br>(106) | 4.7 ± 2.3<br>(106) | 25.18 ± 1.04<br>(23) | 17.18 |
| B | 0.674 ± 0.072<br>(88) | 0.637 ± 0.066<br>(66) | 4.3 ± 2.2<br>(66) | 24.44 ± 1.73<br>(21) | 16.48 |
| C | 0.708 ± 0.082<br>(77) | 0.671 ± 0.072<br>(65) | 5.7 ± 2.7<br>(65) | 23.78 ± 1.02<br>(11) | 16.84 |
| E | 0.726 ± 0.097<br>(35) | 0.607 ± 0.065<br>(25) | 15.4 ± 9.9<br>(25) | 20.66 ± 0.77<br>(11) | 12.54 |
| *Serolis cornuta* | | | | | |
| A | 3.35 ± 0.33<br>(92) | 3.19 ± 0.33<br>(77) | 4.6 ± 2.3<br>(77) | 25.24 ± 0.67<br>(10) | 84.56 |
| B | 3.37 ± 0.31<br>(19) | 1.15 ± 0.32<br>(19) | 6.69 ± 3.18<br>(19) | 24.70 ± 0.52<br>(10) | 83.23 |
| C | 4.50 ± 0.56<br>(6) | 4.15 ± 0.52<br>(6) | 7.7 ± 1.1<br>(6) | 23.38 ± 0.74<br>(2) | 105.22 |
| D | 4.36 ± 0.28<br>(3) | 3.84 ± 0.29<br>(3) | 12.2 ± 1.2<br>(3) | | |
| E | 7.27 ± 0.09<br>(2) | 2.89 ± 0.42<br>(2) | 20.5 ± 9.5<br>(2) | 19.12 ± 0.73<br>(5) | 69.59 |
| *Serolis pagenstecheri* | | | | | |
| All | 0.913 ± 0.154<br>(5) | | | | |

set of ova cannot start developing until after the first set has passed into the marsupium. They must therefore develop in 24 months rather than the 28 months inferred for the first set.

### *Embryonic Development*

The mean dry weight and ash percentages of embryos at different stages are given in Table 1, together with the calculated calorific content per embryo. In *S. polita* the dry weight increased during development, owing largely to an increase in ash content; and the ash-free dry weight decreased slightly. The total calorific content fell as nutrient stores were utilized, but mineral ash content per embryo increased particularly during the later stages of development indicating uptake of inorganic ions from the external medium. These findings are similar to those of Holdich (1971) for *Dynamene bidentata*. *S. cornuta* shows a similar pattern although few data are available for stages C to E.

### *Brood Size*

At all developmental stages in *S. polita* the number of embryos was positively correlated with female size (Fig. 3). Analysis of variance showed that the slopes of all the regression lines were not significantly different ($F = 0.8$; 4,422 d. f.) but that there was a difference between the intercepts ($F = 8.8$; 4,430 d. f.). Removing the line for class E from the analysis halved the variance ratio for intercepts but the intercepts of the remaining four lines were still significantly different ($F = 4.2$; 3,388 d. f.). The level of the line for class E was significantly lower than the earlier stages (Fig. 3), and this can be attributed to release from the marsupium which occurs during this stage. The intercepts of lines A to D were ranked in increasing order C, A, B, D which indicates that there was no reduction in brood size during the course of incubation and therefore no detectable marsupial mortality. Consequently a common regression line was calculated for all stages A – D (Table 2). The mean width of adult female *S. polita* was 14.45 mm (Luxmoore, 1982), and this value was substituted into the combined A – D regression equation to show that the mean brood size was 40.2 ± 15.7 (95% confidence limits).

**Table 2.** The relationship between brood size and the size of the female for species of *Serolis*. Parameters of the least squares regression equation: Brood size = b (Width of female, mm) + c. In all cases the data for the embryo development stages A – D were combined

| | *c* | *s. e. b.* | *c* | $r^2$ | *n* | *p* |
|---|---|---|---|---|---|---|
| *S. polita* | 5.93 | 7.98 | −45.6 | 0.168 | 393 | $10^{-11}$ |
| *S. cornuta* | 7.31 | 22.73 | −228.4 | 0.537 | 94 | $10^{-11}$ |
| *S. septemcarinata* | 11.34 | 6.16 | −69.5 | 0.452 | 56 | $10^{-8}$ |
| *S. pagenstecheri* | 13.44 | 32.88 | −261.9 | 0.654 | 14 | $10^{-4}$ |

The treatment for *S. cornuta* was similar, and as no marsupial mortality was apparent, the combined regression equation for stages A – D is given in Table 2. From this the mean brood size of a female of width 47.5 mm was calculated as 105.8 ± 45.5 (95% confidence limits).

Preserved specimens of *S. pagenstecheri* and *S. septemcarinata* were also analysed and the corresponding regression equations are given in Table 2. Using mean female widths of 37.1 mm and 9.3 mm, mean brood sizes can be calculated from these equations as 232 and 30 for the two species respectively, however because some loss of embryos usually occurs on preservation these may be slightly lower than the true values.

### *Duration of Incubation*

A study of the growth pattern in *S. polita* indicated that the female's parturial moult occurred mostly in March (Luxmoore 1982). As egg – laying accompanies this moult it, too, must reach a peak in March. The end of incubation is signified by the release of juveniles into the environment, predominantly in November (Luxmoore, in press). This might suggest a duration of 8 months for incubation, however embryos are found in the marsupia all year round indicating that incubation must last for

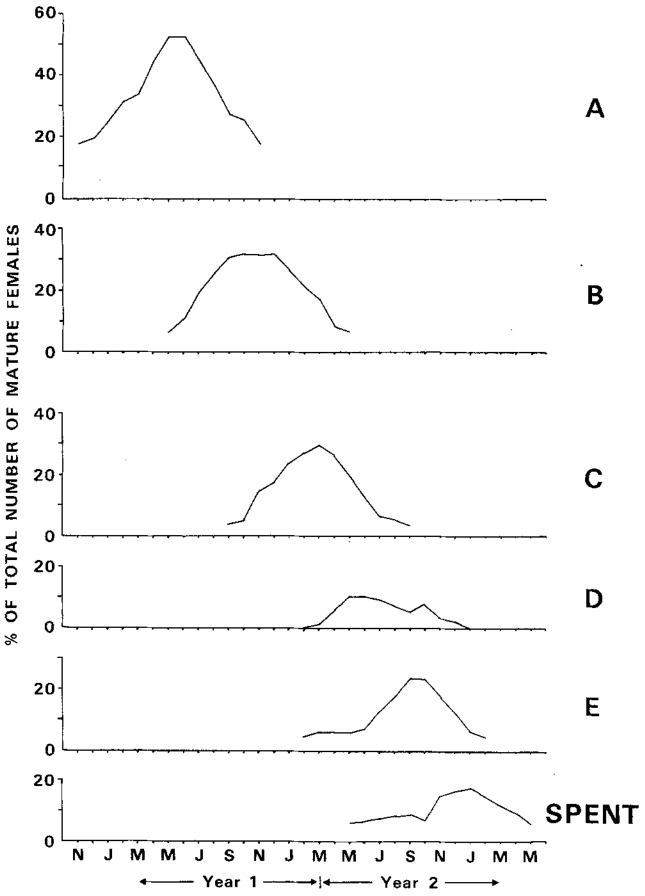

**Fig. 4.** The relative abundance of embryo developmental stages of mature female *Serolis polita;* three-monthly running means averaged over two years

more than one year, probably 20 months. The full course of incubation can be shown by a study of the relative proportions in the population of broods at each of the five developmental stages. At each sampling date the number of broods at each stage was expressed as a percentage of the total number of adult females caught. Data for the two years were pooled, and three-monthly running means were calculated and plotted (Fig. 4). The peak abundance of class A was in May-June, which agrees with a mean egg-laying date in March. The peaks for classes B – E then sequentially span a further 20 months before release in November, which can be seen to occur between the peaks for class E and spent females (i.e. those which have just released young). This confirms that in *S. polita* incubation lasts for 20 months: eggs are laid in the autumn, develop for one and a half years, and are released in the spring.

### *Sex Ratio*

Determination of the true sex ratio at birth from samples of adults is complicated by many factors, such as differential migration or differential mortality between the sexes (Wenner 1972); however with care all these can be circumvented. Sex is externally distinguishable from the second and third post-marsupial moults onwards in *S. polita* and *S. cornuta* respectively, and females live longer than males (Luxmoore, 1982). Females therefore predominate in the older age classes but this differential mortality is considered to take place only after mating has occurred (i.e. at a mean age of 28 months in *S. polita*). In *S. polita* sex ratio can therefore be calculated reliably from the second moult until an age of 28 months. Population data for two years were analysed and the mean sex ratio in this age range was found to be 0.75 females : 1 male, which was significantly different from 1 : 1 ($p < 0.001$). This value varied between months but did not show any consistent fluctations with time. As differential mortality is unlikely to affect eggs or very young juveniles it must be assumed that the preponderance of males was present at release from the marsupium. A similar treatment for *S. cornuta* revealed a mean sex ratio of 1.01 females : 1 male.

## Discussion

The reproductive behaviour of some species of *Serolis* has been described by Moreira (1973a) and Bastida and Torti (1970). The observations made in this study largely agree with these previous reports, although the use of the 7th pereopods in amplexus has not been noted before.

White (1970) found that amplexus in *Glyptonotus antarcticus* could last for up to 190 days. In contrast Moreira (1973a) reported only four days for *Serolis polaris*, and the flabelliferan isopod, *Cirolana hardfordi* has no lengthy procopulatory pairing (Johnson 1976). In this study the majority of females in the final sub-adult moult class were found to be in amplexus, which suggests that this association can last for the whole duration of the inter-moult period (an average of 90 days in *S. polita*).

In *S. polaris* and *S. laevis* neither males nor females were found to eat during the breeding period (Moreira 1973a). However examination of gut contents showed that all species in this study continued to eat throughout the life-cycle.

The mean duration of incubation in *S. polita* (about 600 days) is second among isopods only to that reported for another Antarctic species *Glyptonotus antarcticus* (up to 626 days: White 1970). White (1977) suggested that the reproductive cycle of many Antarctic invertebrates was synchronized with the seasonal pattern of the primary productivity, which is very high for a short period in the summer and very low all winter, although he pointed out that for some benthic organisms this seasonality might not be so extreme. To take advantage of this, young must be released at the beginning of the summer, and this is clearly the case with *S. polita* and *S. cornuta*. Sheppard (1933), on the basis of examining a limited number of museum specimens, stated that breeding was non-seasonal in *Serolis*, since broods at all stages of development could be found all year round. However the data in Fig. 4 show that a 20-month incubation period, combined with a fair degree of synchrony of spawning and release, will also explain these observations.

The period of maximum energetic drain on the female occurs when the yolk reserves for the eggs are laid down in the ovary, White (1977) suggested that this too should coincide with the season of maximum food availability. In *S. polita* 75% of the weight of eggs was accumulated in the summer, and incubation then commenced following spawning in the autumn. It thus seems that the beginning and the end of incubation are determined by the pattern of food availability, and if embryonic development cannot be completed within 8 months it must continue for a further year, making a total of 20 months. The large egg size and low temperatures probably play an important role in determining the lengthy incubation period as both are thought to increase development time (Van Doolah and Bird 1980) although Corkett and McLaren (1978) showed that, of the two, egg size had the greater effect in copepods. Bregazzi (1972) found a marked correlation between brood development time and latitude in amphipods, and suggested that this could be attributed to temperature, but failed to allow for the effect of increasing egg size. A similar phenomenon of protracted incubation in two temperate crustacea *Hyas coarcticus* and *Corystes cassivelaunus*, was reported by Wear (1974) who also suggested that it was related to a seasonal pattern of food availability.

Sheader (1977) and Jones (1970) both suggested that there was a reduction in the rate of oocyte enlargement in *Idotea pellagica* and *Eurydice affinis* respectively during the winter period, as would be expected if food supply were reduced. No such interruption was found in the development of *S. polita* oocytes, but this may be because of the method of calculation: all animals in the same moult were assumed to be exactly the same age, and as this is not strictly true it would tend to reduce any monthly fluctuations.

The brood size of many species of isopod has been reported to be related to the size of the female; in some species this relationship was found to be linear (Jones and Naylor 1971; Johnson 1976; Strong and Daborn 1979; Koop and Field 1980; Shafir and Field 1980), while in others an exponential relationship gave a better correlation (Jensen 1955; Holdich 1968; Moreira and Pires 1977). In this study, linear relationships gave slightly higher correlation coefficients in all cases, but the size range of breeding females was so small that there was little difference between the two relationships. In *S. septemcarinata* and *S. cornuta* the correlation between size and brood size was strong, and the regression accounted for 45.2% and 53.7% of the variance respectively. In *S. polita* it only accounted for 16.8% of the variance, showing a much weaker correlation, and suggesting that some factors other than the size of the female may be important in determining the brood size. An obvious possibility might be the nutritional state or stored food reserves of the female. One implication of this is that, given good feeding conditions, *S. cornuta* can best increase its reproductive output by investing more energy in increasing its body size. *S. polita,* on the other hand, may be able to increase its reproductive output independantly from body size. It is interesting to note that there were marked variations in the size of adult *S. cornuta* from year to year, while the size of *S. polita* remained more or less constant (Luxmoore, 1982).

Within some isopod species there is also a correlation between body size and egg size (Moreira and Pires 1977), but in *S. polita* and *S. cornuta* the two were found to be independant ($p \geqslant 0.1$). This means that brood size alone gives an adequate estimate of reproductive output.

The sex ratio of most marine isopods is strongly biased towards the females (Holdich 1968; Fish 1970; Jones and Naylor 1971; Johnson 1976; Salemaa 1979; Shafir and Field 1980), and it is assumed that each male can impregnate more than one female (cf. Sutton 1972). White (1970), however found a ratio of 1.2 males : 1 female in *Glyptonotus antarcticus* from Signy Island. It is possible that, because of the long duration of amplexus, an adequate number of males to ensure fertilization of all the females in the brief period after their parturial moult requires a ratio of nearer 1 : 1 as is found in *S. cornuta.* The excess of males in *S. polita* and *G. antarcticus* may be owing to the fact that females of both can breed more than once, and males must therefore be

**Table 3.** The relative size of newly released juveniles as a function of female size for several species of isopod. The mean length is quoted unless only a range was given, in which case the median value was used to calculate the size ratio

| | Female length (mm) | Juvenile length (mm) | (Juv. length) / (Female length) | Source |
|---|---|---|---|---|
| 1. *Glyptonotus antarcticus* | 78 – 108[a] | 9.1 | 0.098 | White (1970)[b] |
| 2. *Serolis cornuta* | 53.1[a] | 10.9 | 0.205 | Luxmoore (1982)[b] |
| 3. *Serolis pagenstecheri* | 44.6[a] | 6.2 | 0.137 | Luxmoore (1982)[b] |
| 4. *Serolis polita* | 19.0[a] | 5.5 | 0.289 | Luxmoore (1982)[b] |
| 5. *Idotea baltica* | 17.6 | 2.17 | 0.123 | Strong and Daborn (1979) |
| 6. *Serolis ovata* | 16.0[a] | 4.3 | 0.268 | Luxmoore (1982)[b] |
| 7. *Idotea baltica* | 13.6 | 2 | 0.147 | Salemaa (1979) |
| 8. *Idotea emarginata* | 7 – 17 | 2.0 – 2.3 | 0.179 | Naylor (1955) |
| 9. *Serolis septemcarinata* | 11.8[a] | 3.7 | 0.313 | Luxmoore (1982)[b] |
| 10. *Idotea chelipes* | 10.2 | 2 | 0.196 | Salemaa (1979) |
| 11. *Cirolana hardfordi* | 9 – 11 | 2.5 – 3 | 0.275 | Johnson (1976) |
| 12. *Cirolana imposita* | 7 – 11 | 2.2 – 2.8 | 0.278 | Shafir and Field (1980) |
| 13. *Idotea pelagica* | 6.5 | 1.5 – 2.0 | 0.269 | Sheader (1977) |
| 14. *Eurydice pulchra* | 5.9 | 1.8 | 0.305 | Jones (1970) |
| 15. *Serolis vemae* | 5.7 | 2.3 | 0.404 | Hessler (1967) |
| 16. *Dynamene bidentata* | 5.32 | 1.4 | 0.263 | Holdich (1968) |
| 17. *Eurydice pulchra* | 5.0 | 1.9 | 0.380 | Fish (1970) |
| 18. *Serolis menziesi* | 4.4 | 1.8 | 0.409 | Hessler (1970) |
| 19. *Eurydice affinis* | 3.9 | 1.5 | 0.385 | Jones (1970) |
| 20. *Jaera ischiosetosa* | 3.9 | 0.78 | 0.200 | Steele and Steele (1972) |
| 21. *Jaera forsmani* | 3.5 | 0.92 | 0.263 | Jones and Naylor (1971) |
| 22. *Serolis completa* | 3.10 | 1.49 | 0.481 | Moreira (1973b) |
| 23. *Jaera ischiosetosa* | 3.1 | 0.70 – 0.88 | 0.287 | Jones and Naylor (1971) |
| 24. *Jaera albifrons* | 3.0 | 0.78 – 0.87 | 0.268 | Jones and Naylor (1971) |
| 25. *Jaera praehirsuta* | 2.8 | 0.70 – 0.97 | 0.298 | Jones and Naylor (1971) |

[a] Antarctic species

[b] In these species length was calculated from the quoted width by multiplying by the appropriate factor

present to inseminate females of previous generations as well as their own.

Thorson (1950) pointed out that there was a tendency for direct lecithotrophic development in benthic invertebrates in polar regions, in contrast to the pelagic, planktotrophic development prevalent in lower latitudes. He further showed that the Antarctic fauna differed from that of the Arctic in having a greater incidence of brood protection and still larger, yolky eggs. This observation has received widespread confirmation in more recent studies (Arnaud 1974; Clarke 1979; Picken 1980). All free-living species of isopod brood their young in a marsupium, and so this feature cannot therefore be considered to have evolved as an adaptation to the Antarctic environment, but it may, in a sense, have preadapted the order to colonization of the Antarctic region (Dell 1972; Arnaud 1974), and thus explain the prevalence of isopods in the fauna.

Thorson's generalization also suggests that polar invertebrates should have larger eggs than their temperate counterparts. Data on the egg size of isopods are scarce, but the size of newly released juveniles is better documented and probably gives a reasonable approximation. If these data are considered (Table 3) it can be seen that Antarctic species do, indeed, tend to have larger young. But it was shown (Luxmoore, 1982) that the adult size of serolids is also greater in higher latitudes, and, as juvenile size tends to be correlated with adult size (Nelson 1980), it is hardly surprising that the polar species should also have large young. If, instead of considering the absolute size of young, their relative size is used (Juvenile size / adult size), exactly the opposite trend is found: polar species of *Serolis* tend to have relatively smaller young than the temperate species. This comparison was analysed for all the species of isopod in Table 3, and there is a clear negative correlation (Spearman's rank correlation coefficient. $R_S = -0.548$. $0.01 > p > 0.001$): small isopods have relatively larger young. A re-examination of both Nelson's (1980) and Thurston's (1972) data shows that there is a similar situation in amphipods, and that the relative size of eggs is inversely correlated with female size. No explanation has been found for this observation, but it may be due to some physical constraint connected with the size of the marsupium, and be entirely unrelated to the factors which determine the absolute size of adults.

It has been argued (Luxmoore, 1982) that seasonal food shortage in the Antarctic marine ecosystem selected for increased body size, but this, apparently, automatically entails a decrease in the relative size of young. Thus, although Thorson's generalization is upheld in serolids, there are many complicating factors to be considered: egg size is correlated with parent size, which in turn is correlated with latitude. Thus it is not possible to say whether the large egg size found in high latitudes is due to a direct selection pressure, or to indirect selection for large adult size which entails an increase in egg size.

The chief adaptation to the Antarctic environment exhibited by the reproductive strategy of serolids is therefore in the seasonal synchronization of the breeding cycle. This, in conjunction with the slow development, probably caused by large egg size and low temperatures, results in a very protracted marsupial development period, which is one of the longest recorded for any invertebrate.

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