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On the Reproductive Biology of *Ceratoserolis trilobitoides* (Crustacea: Isopoda): Latitudinal Variation of Fecundity and Embryonic Development

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Summary. The embryonic development of *Ceratoserolis trilobitoides* (Crustacea: Isopoda) is described. It is estimated that breeding lasts nearly 2 years. In comparison with non-polar isopods 3 causes for the retardation of embryonic development are discussed: genetically fixed adaptations to the polar environment, the physiological effect of temperature and the effect of egg size. The latter seems to be of minor importance. Intraspecific variations of fecundity are found in populations from the Weddell Sea, the largest eggs occur in the coldest region. The distribution of physiological races corresponds to the distribution of morphotypes.

Introduction

An increasing number of data supports the suspicion that in spite of having high biomasses the populations of the Antarctic benthos show a low productivity (i.e. Clarke 1985; Hempel 1985). One of the causes, for which we have some studies on metabolism (summary in Clarke 1985; Maxwell and Ralph 1985) and very few field observations on population dynamics, is the retardation of growth of all developmental stages. For the calculations of the rate of reproduction (in the sense of number of female offsprings per female per time) we need information on population structure, growth, and age at maturity, the number of eggs and of released larvae. An important factor that prolongates the life of Antarctic invertebrates is the embryonic period. In the present study new observations on the embryonic development and the number of eggs of *Ceratoserolis trilobitoides* (synonyms: *Serolis trilobitoides* and *Serolis cornuta:* Wägele, in press) are presented. This isopod is one of the large and frequent Antarctic crustaceans, with a wide distribution in the Weddell Sea (see Wägele, in press). For this species several observations on biology and reproduction already exist (Luxmoore 1982 a, b).

Material and Methods

During the expedition "Antarktis III" of *RV Polarstern* several samples were taken in the area of the Antarctic Peninsula, South Shetlands, South Orkneys and the Eastern and Southern Weddell Sea by means of an Agassiztrawl (localities with *C. trilobitoides*: see Wägele, in press).

Females used for the study of latitudinal variations of fecundity and egg size (Fig. 6) were collected from the following sites: 62°8.89′S 58°0.46′W, 449 m (King George Island); 60°42.40′S 45°33.07′W, 86 m (Signy Island); 73°39.7′S 20°59.76′W, 100 m (off Riiser-Larsen Ice Shelf, near Camp Norway); 72°30.35′S 17°29.88′W, 250 m (off Riiser-Larsen Ice Shelf); 73°23.36′S 21°30.37′W, 470 m (off Riiser-Larsen Ice Shelf); 77°18.42′S 41°25.79′W, 650 m (Gould Bay); 77°28.85′S 41°25.92′W, 690 m (Gould Bay); 77°31.67′S 42°12.42′W, 620 m (Gould Bay); 77°7.5′S 48°35.8′W (Gould Bay area).

To keep the animals alive they were immediately sorted out on deck and transferred to aquaria, where they were kept at $-1\,°C \pm 1$. After 3 months the material was transported to Germany in a temperature-controlled container, where the in vitro experiments were continued for another 7 months.

The contents of the marsupium of those females, which were injured during catching (about 80%!) were extruded, eggs and embryos were counted and then kept in filtered sea-water. In vitro development was only successful when few eggs (about 20) were kept in small aerated glasses (100 ml). As we did not work under sterile conditions, several batches died from bacterial and fungal infections. Broods of 48 females were cultured. Samples from developing batches were fixed in formaline at 4 weeks' intervals. Before fixation the general features of the stages were noted.

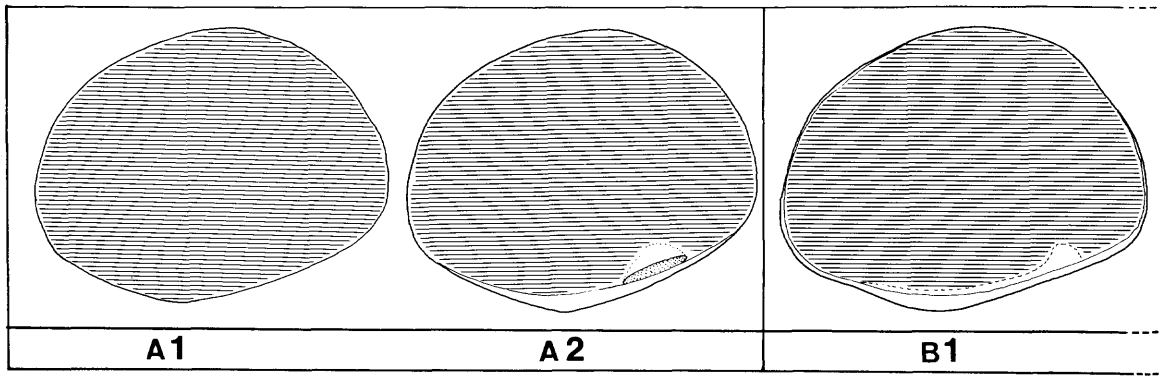
The embryonic membranes were later removed and the stages were drawn with the help of a camera lucida. For the observation of the smallest germs, yolk was removed with the help of fine needles and the germ bands were embedded in caedax. Cleavages were not studied.

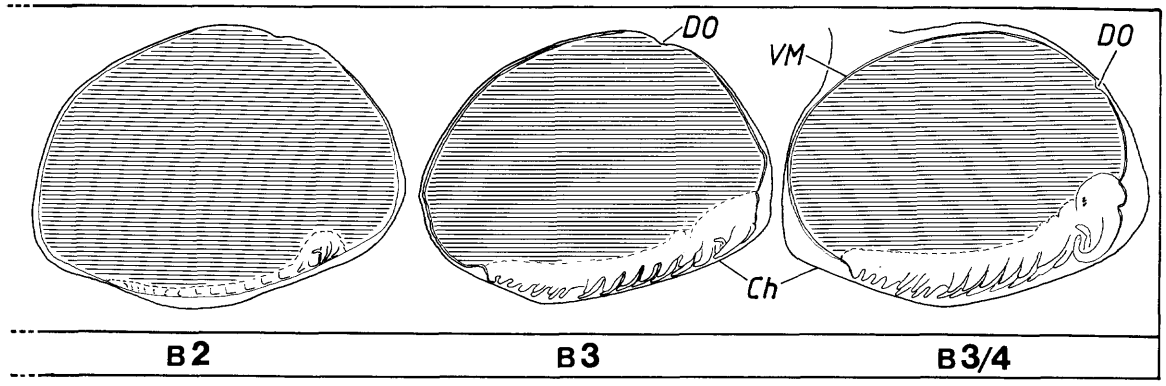
To count the ommatidia the embryonic eyes were drawn after removing of the embryonic membranes. Only pigmented ommatidia were considered.

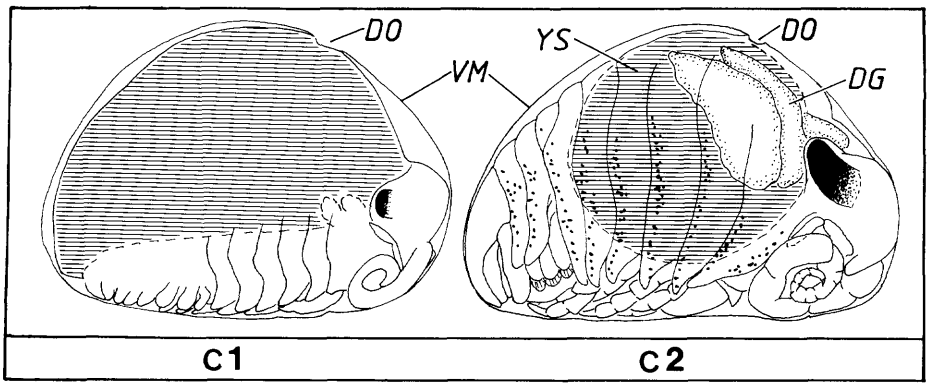
Results

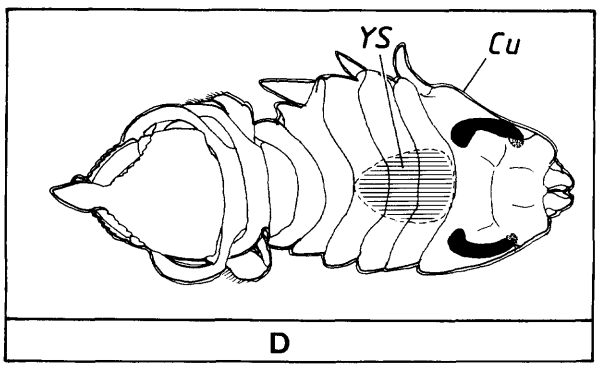
Embryonic Stages

Following the classification of Holdich (1968); Luxmoore (1982 b) discerned in *Serolis* 5 embryonic stages (*A*: yolky embryos; *B*: traces of embryonic tissue visible; *C*: pigmented eyes visible; *D*: main egg membrane ruptured;









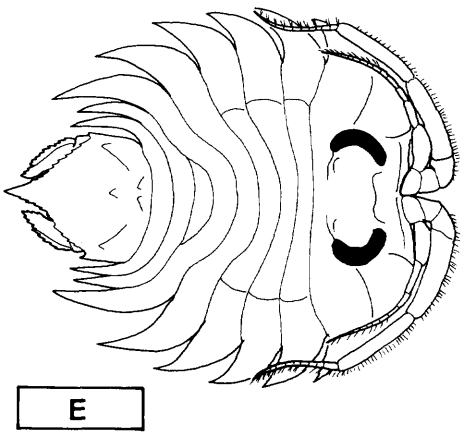


Fig. 1. Schematic representation of the embryonic stages (A 1 to E) of *Ceratoserolis trilobitoides* (not according to scale). D = premanca, E = manca. Hatched area = yolk. For symbols see list of abbreviations.

Abbreviations: An 1,2 = antenna 1,2; *Ch* = chorion; *CPr* = cephalic projection; *CP 1–6* = coxal plates of pereopods 1–6; *Cu* = cuticle of premanca stage; *DG* = digestive gland; *DO* = dorsal organ; *E* = eye; *En* = endite of maxilliped; *Ep 2,3* = epimeral plates of pleonites 2,3; *Ex* = exopod; *Md* = mandible; *MdP* = mandibular palp; *Mx 1,2* = maxilla 1,2; *Mxp* = maxilliped; *P 1–6* = pereopods 1–6; *Plp 1–5* = pleopods 1–5; *Pr* = proctodaeum; *St* = stomadaeum; *T8* = 8. thoracic segment (pereonite 7); *Tel* = telson; *Urp* = uropod; *VM* = vitelline membrane; *YS* = yolk sack

E: embryos ready for release from marsupium). This classification can be accepted for the most part, as it is based on some events which are perceptible steps in an otherwise continuous development. These stages can be further subdivided with the arguments of Sømme (1960), to set a better determination of the embryos' age. Figure 1 shows schematically these stages of *Ceratoserolis trilobitoides*:

Stage A1: Eggs show no differentiation (cleavages are not visible).
Stage A2: Formation of blastodisc at presumptive anteroventral part of embryo and gastrulation.
Stage B1: Embryonal tissue visible macroscopically, formation of germ band.
Stage B2: Segmentation of germ band and growth of naupliar appendages.
Stage B3: All appendages, epimeral and coxal plates are visible.
Stage B4: Elongation of appendages, beginning of enrollment of antenna 2, first pigments of eyes appear. At the end of this phase the chorion is shed.
Stage C1: Early phase of development within vitelline membrane: eyes small, yolk filling most part of the embryo.
Stage C2: Late phase of development within vitelline membrane: yolk mass shrinking within yolk sack, segmentation completing on dorsal part of embryo, eye approaching final form, first chromatophores appear. The stage ends with the rupture of the vitelline membrane.
Stage D: Premanca-phase: embryo with cirolanid-like form, covered by embryonal cuticle. Pleopods 1–3 with long, free setae. The phase ends with the embryonal one-stage moult.
Stage E: Manca, ready to leave marsupium.

The yolk of *C. trilobitoides* has a light yellow to orange colour, depending on the locality. Within the embryonic digestive glands the colour deepens.

Figures 2–4 show further details of the embryonic stages. The first stage in Fig. 2 (B1/2) is a germ band with distinct segmentation in the thoracic area. Segments of pleon are beginning to form, the medial segmental portions of tissue are the rudiments of the ganglia. Appendages are present on the cephalic lobes (antenna 1 to maxilla 2). Stomodaeal and proctodaeal invaginations can be seen. In early stage B3, rudiments of the remaining appendages are formed, the mouthparts, especially the mandibles, are relatively large. While coxal plates become visible on thoracopods 2 to 7, the first thoracopod (presumptive maxilliped) shows a small lateral lobe which evolves to the maxillipedal epipod. Thoracopod 8 is lacking. In the second and third pleonites laterally to the pleopodal insertions small lobes emerge, which grow to become epimeral plates. The medioventral line of the embryo has a deep groove which forms during delamination of the ventral nerve cord (for summary of early development in isopods see Strömberg 1972).

During the stage B3 the appendages grow until the seventh thoracopod reaches the first pleopod. Close to the antenna 2 a lateral pair of lobes grows on the cephalothorax (Figs. 2, 3: CPr), which can be traced to stage D, where they become the frontolateral cephalic lobes which unite with the frontal part of the first coxal plate (Fig. 4, stage E: CPr). During elongation the second antennae enroll and grow covering the mouthparts, of which finally only the mandibular palp can be seen. The germ band covers nearly 1/3 of the egg's circumference at stage B4 and stretches a little, a process not so conspicuous as in other isopods due to the large yolk mass. At the end of this phase the chorion bursts. The dorsal organ, which appears in the course of stage B, is not shed together with the chorion. At this stage the small eyes have their first pigments and 20 to 50 immature, pigmented ommatidida can be counted.

The C-embryos are only covered by the more elastic vitelline membrane. They experience a number of important continuous changes; the anatomy is completed and segmentation proceeds to the dorsal part of the embryo. Already in early stage C the digestive glands start to grow in the region behind the eyes (for description of embryonal gut of isopods see Bullar 1878; Strömberg 1967). The glands are filled with an oily orange substance, the liquefield yolk. The 3 pairs of digestive glands grow while the yolk sack shrinks. The appendages are subdivided into articles, the propodus of pereopod 1 enlargens and becomes very prominent. While the coxal plates grow, the insertions of the pereopods drift laterally until the first articles of the legs are covered by the coxal plates. The pleopods, subequal until stage B3, differentiate into shorter anterior pleopods (1 to 3, with long, slender sympods) and large posterior pleopods (4 to 5). The only setae growing freely on the embryo are those of pleopods 1–3, which in stage D start to ventilate. The telson, raised during stage B, inclines frontally, covering the anus and getting an acute distal point.

The development of stage C lasts a long period but shows no distinct demarcations that could be useful to find a clear subdivision. To compare the different phases during stage C the number of ommatidia turned out to be a good tool. This number increases to about 280 in stage D (ommatidia have been used before to characterize postembryonal stages: Kuers 1961; Schneider and Nauroz 1972).

In late stage C under the vitelline membrane the embryonal cuticle, the envelope of stage D, detaches from ventral parts of the embryo and is clearly discernible. This cuticle does not participate in the formation of the cuticular lenses of the ommatidia (Fig. 5). Shortly before the rupture of the vitelline membrane the first chromatophores appear on coxal plates and tergites.

Stage D is the phase between the shedding of the vitelline membrane and the embryonic moult, it can be termed "premanca stage". It still bears the dorsal organ (Fig. 5). First the premancas are bent as in stage C, but then they slowly stretch along the longitudinal axis. The

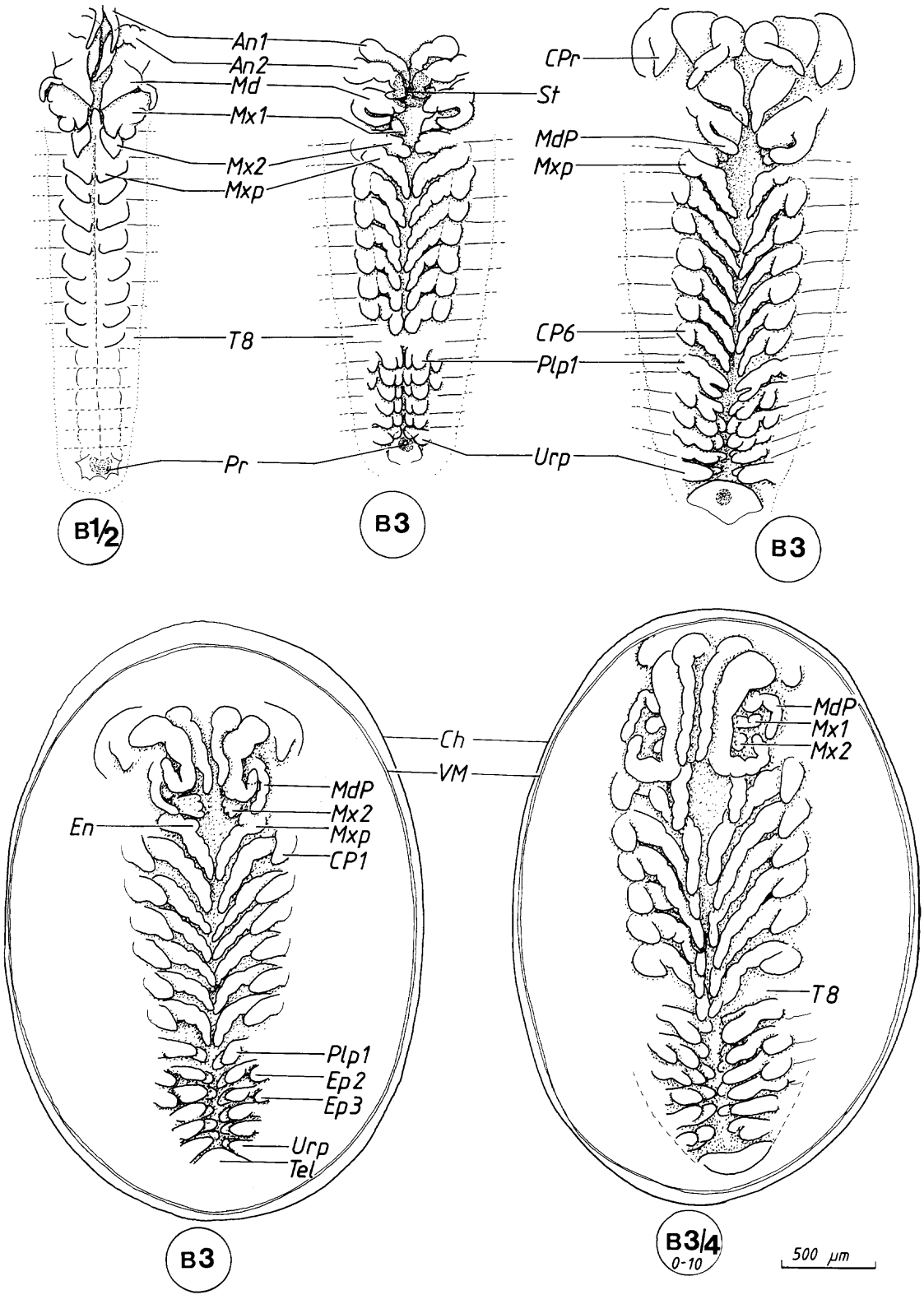


Fig. 2. Embryonic stages of *Ceratoserolis trilobitoides*. Stage denomination (*in circles*) equivalent to Fig. 1. *Small numbers* within circle = number of ommatidia of embryonal eye. For symbols see list of abbreviations

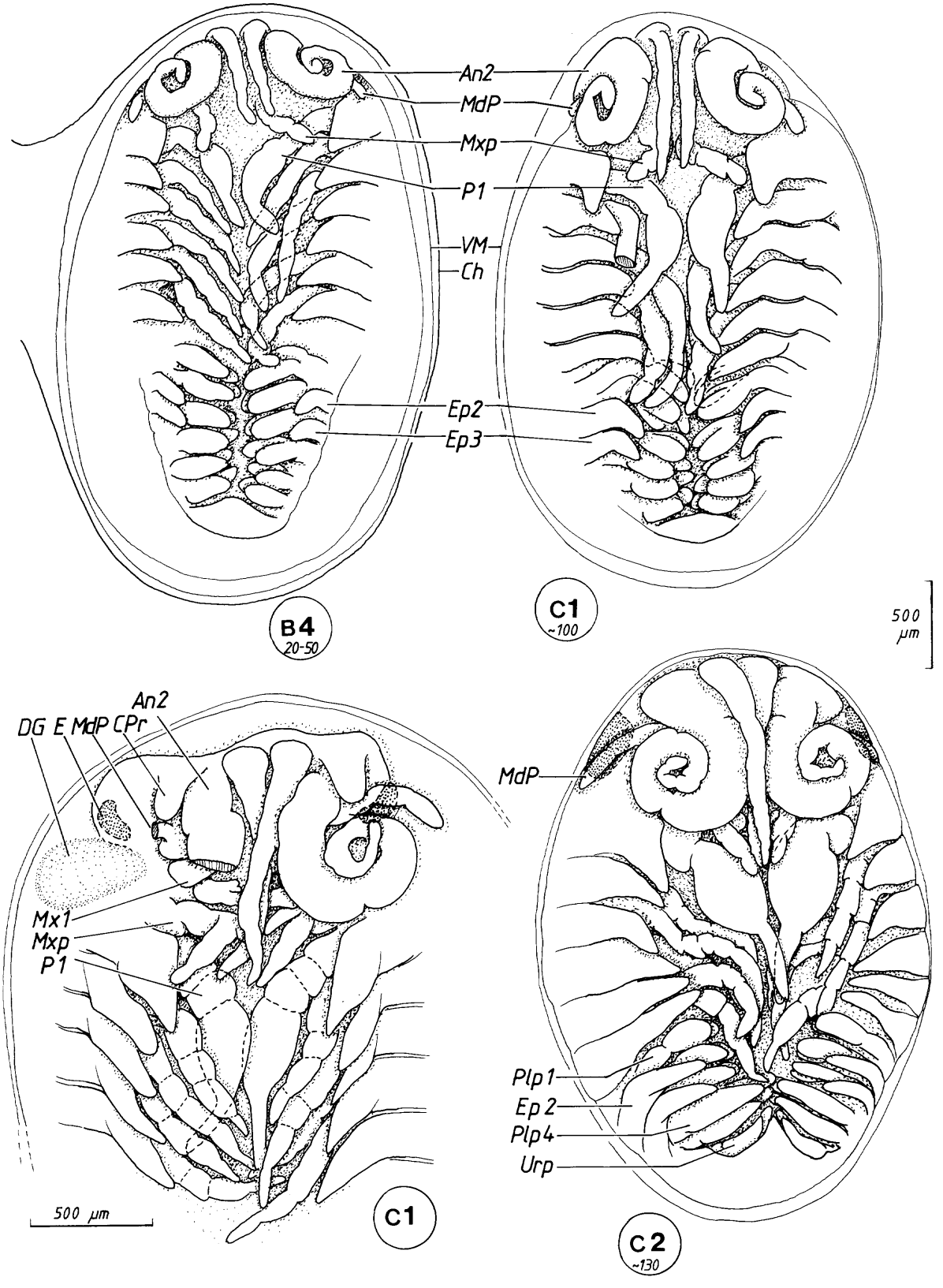


Fig. 3. Embryonic stages of *Ceratoserolis trilobitoides. In circles:* stage denomination and number of ommatidia of the drawn stage. Of C 1 an enlarged portion of the anterior ventral germ is shown (*below, left*), the right antenna 2 (*An 2*) has been cut off

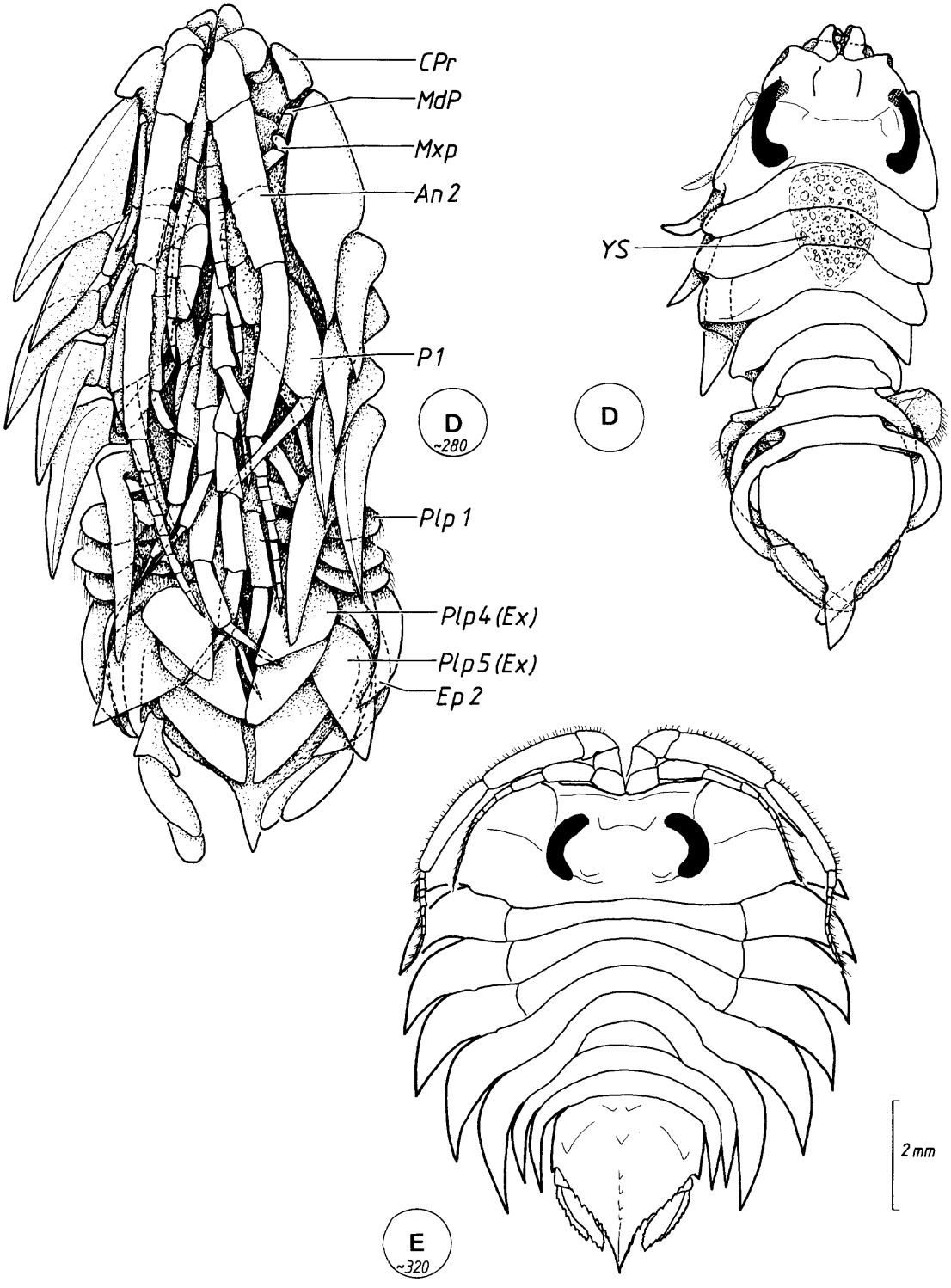


Fig. 4. Embryonic stages of *Ceratoserolis trilobitoides*. Symbols as in Fig. 3. Stage D is shown in ventral (*left*) and dorsal view (*right*)

first coxal plates start to bend dorsally, then the movement is followed by the more posterior coxal plates and finally by the epimeral plates of the pleon, until the cirolanoid embryo has adopted the serolid habitus. During the cirolanid phase muscular contractions begin, especially in the pleopods, later the pleopods 1–3 beat slowly at intervals, probably for respiration. The cuticle of the premanca is shed in one piece (the act could not be observed) and the manca (stage E) appears with its complete set of setae and a small reserve of yolk in gut and digestive glands. This stage stays in the marsupium for some weeks.

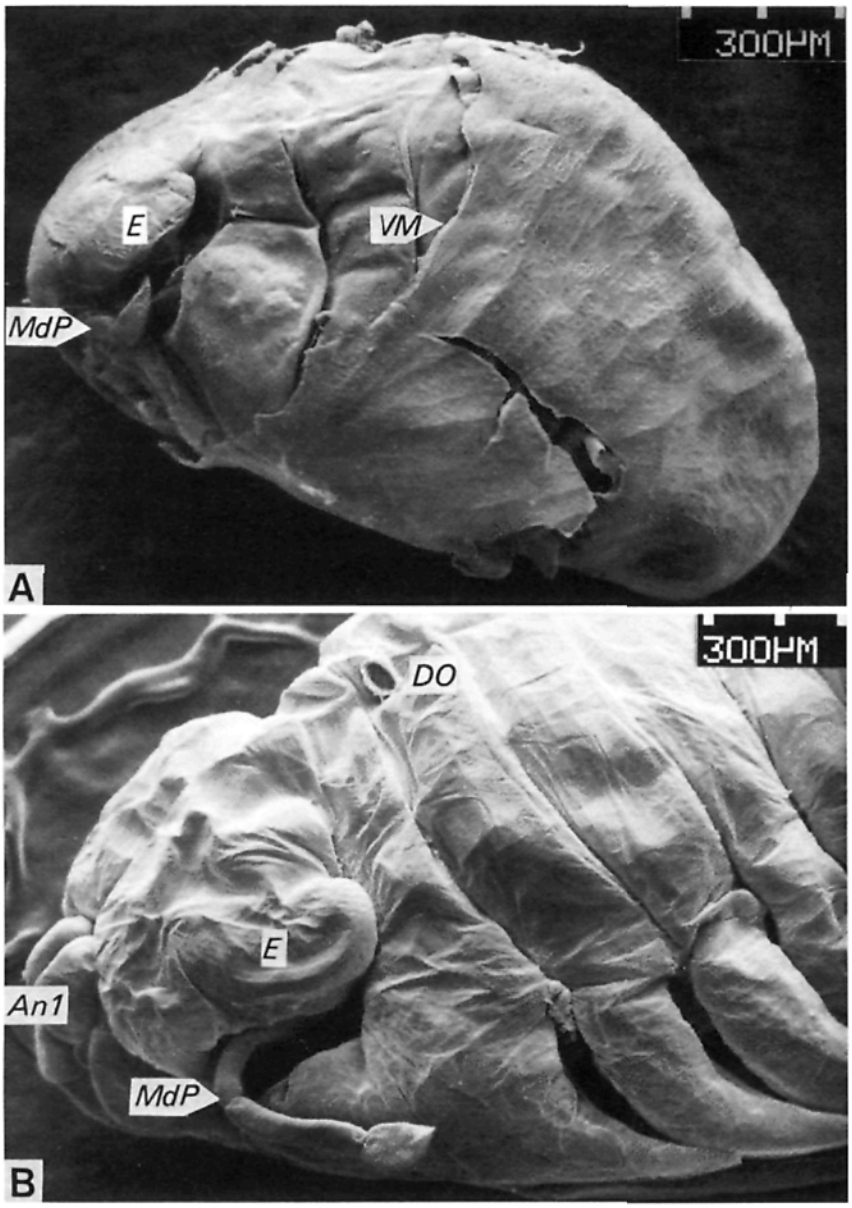


Fig. 5 A, B. SEM-pictures of embryonic stages of *Ceratoserolis trilobitoides*. **A** stage C 2; vitelline membrane (*VM*) removed from anterior part of embryo, to show the eye (*E*), covered by the embryonal cuticle (MdP = mandibular palp). **B** late premanca (stage D) just before moult. Dorsal organ (*DO*) still present, embryonal cuticle covering eye (*E*). Mandibular palp (*MdP*) projecting from the still open gap between cephalothorax and first coxal plate. *An 1* = antenna 1

Duration of Embryonic Development

For the calculation of the duration of development only material from the Antarctic Peninsula and from the neighbouring archipelagos was used. These "northern" broods survived laboratory conditions better than material from southern samples. Furthermore the southern eggs are larger (see below) and therefore might have a slower developmental rate.

The in vitro observations are not complete, as for all samples the exact time of spawning is not known and some stages (B1) were not found. Some insecurity raises from the fact that late embryonic stages do not develop synchronically; differences equivalent to about 4 weeks of development were frequently found.

Only few batches of stage A could be observed for some weeks before they died. A period of 8–9 weeks elapses from yolky eggs without visible tissue (A1) to gastrulation (A2), which is discernible macroscopically by a depression of the anterior ventral embryo (Fig. 1). From stage A2 to the beginning of the formation of a germ band (B1) another 8 weeks pass. As the time of spawning is not known and most eggs probably were already some weeks old when they were collected it seems to be realistic to assume that stage A lasts for about 5 months. This period is equivalent to about 1/4 of the total development (see below), a normal proportion in comparison with the development of temperate isopods and of *Serolis polita* (Table 3).

For the early stage B the following periods could be observed: embryos in early stage B2 needed 16 weeks (!) to reach stage B4. From stage B3 (Fig. 2: below) to the first appearance of eyes (B3/4) 8 weeks passed, another 8 weeks later the chorion was shed (stage B4/C1). Summing up, stage B lasts about 22 weeks, if we assume that

Table 1. Observations on the increase of the number of pigmented ommatidia in embryos of *Ceratoserolis trilobitoides* (taken from batches cultured in vitro)

n_1 = number of ommatidia at time t_1	n_2 = number of ommatidia at time t_2	transcurred time (t_2-t_1) (days)	$\frac{(n_2-n_1)}{(t_2-t_1)}$
3	47	39	1.128
13	59	35	1.314
13	42	35	0.829
17	95	63	1.238
23	89	63	1.048
23	60	29	1.276
38	77	39	1.000
42	81	40	0.975
47	80	72	0.458
51	93	39	1.077
60	95	35	1.000
63	87	23	1.043
72	110	23	1.652
80	122	40	1.050
81	118	39	0.949
89	233	79	1.823
95	128	40	0.825
112	134	23	0.957
128	244	81	1.432
128	143	39	0.538
138	179	22	1.864
183	230	40	1.175
244	284	57	0.702

B1, the phase that could not be studied, needs a minimum of 4 weeks.

Better documented is the development of stages C and D. If we follow the increase of the number of ommatidia per unit of time over the different stages, a mean increase of about 1.1 ($\pm$0.35) (Table 1) ommatidia per day is obtained. This number, of course, is only an approximation. We do not know what effect laboratory conditions might have, also the effect of age on the growth rate of the eye was not studied, in older stages the process seems to be slower. Anyway the developmental stage of the eye proved to be very useful to compare the different batches.

From B3/4 to the embryonic moult of the premanca about 320 ommatidia are formed. This is equivalent to 352 days, nearly 1 year. In stages C and D the number of ommatidia increases from 20–50 to about 280 in 10 months.

A female caught off Signy Island (depth: 86 m) on January 13th, 1985 with eggs in stage B1/B2 was controlled 8.5 months later: the embryos were in stage C1. After 2 months the eyes had increased in size, a sample from the female's marsupium contained embryos in stage C2 and 4 months later in stage D, i.e. 15.5 months elapsed from B1/B2 to D. This continuous observation confirms the above calculations obtained from the study of samples from the in-vitro experiments.

We do not know exactly how long stage E stays in the marsupium. In one female it took 4 weeks from the birth of the first manca to the hatching of most of the young, but the last stayed 9 weeks in the marsupium. These belong to those young which at the beginning of the hatching process still were in a late cirolanoid stage (D); they lay farthest from the last pair of oostegites, where the first mancas leave the brood pouch. So a time of 9 weeks can be assumed for the period between stage D/E and hatching.

Though these estimations of the developmental time obtained by in vitro experiments are not exact, it is clear, which order of magnitude must be considered. For *Ceratoserolis trilobitoides* we obtain a total time of about 23 months, a number very similar to hitherto published observations on embryonic development of Antarctic isopods: *Serolis polita* and *Glyptonotus antarcticus* need about 20 months (Luxmoore 1982 b; White 1970).

It is astonishing that the much larger *Ceratoserolis* with its voluminous eggs (dry weight: 3.34$\pm$0.33 mg; Luxmoore 1982 b) needs about the same time for embryonic development as the small *Serolis polita* (dry weight of egg: 0.682$\pm$0.127 mg; Luxmoore 1982 b).

Seasonality of Reproduction

For many species of Antarctic benthos it is suspected that they release their larvae at a certain time of the year, namely the short summer (Pearse 1965; Pearse and Giese 1966; Rakusa-Suszczewski 1972; Bregazzi 1972; Maxwell 1977; Clarke 1977, 1980 and 1982; White 1977 and 1984; Picken 1980; Luxmoore 1982 a). The necessity for this seasonality can be seen in the exploitation of the short phytoplankton bloom, essential for planktivor or detritivor species or for species with planktivor larvae, but in carnivor or omnivor species seasonality (discussed for *Glyptonotus* in White 1977, for prosobranch gastropods with brood protection by Picken 1980) needs a moore careful explanation (see "Discussion"). The ques-

Table 2. Frequency of embryonic stages of *Ceratoserolis trilobitoides* in January/February samples

Stage:	A1	A1/2	A2	A2/B1	B1	B1/2	B2	B2/3	B3	B3/4	B4	B4/C1	C1	C1/2	C2	D	D/E	E
Region:																		
Antarctic Peninsula		3	1	2		1		2		2	1		1		2	6	1	
Camp Norway		2										1	2	3		2		
Gould Bay		4	11	3			1	1	2	1			1	3	2		1	

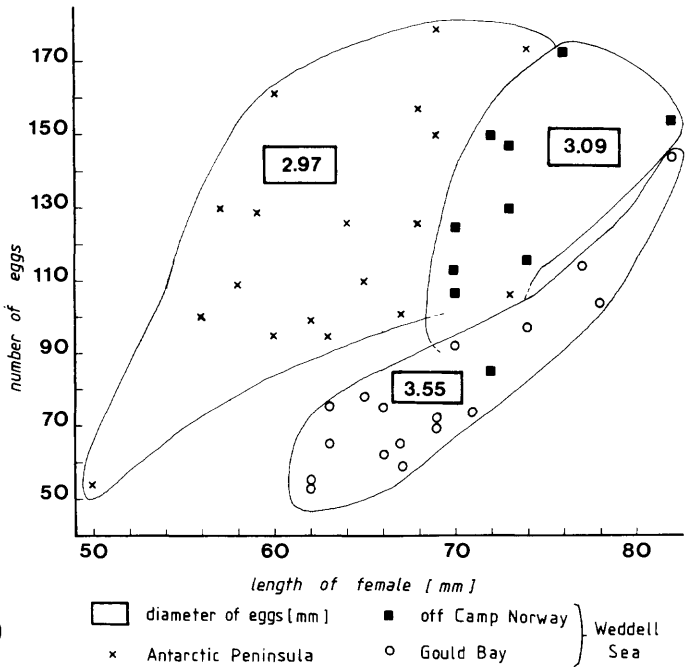


Fig. 6. Contents of brood pouches of *C. trilobitoides* from 3 different regions (Antarctic Peninsula and adjacent archipelagos, area off Camp Norway, Gould Bay; off Camp Norway = area off Riiser-Larsen Ice Shelf between 21°W and 17°W, i.e. around Vestkapp)

tion arose whether the carnivorous serolids, which show seasonality at Signy Island (Luxmoore 1982 b), do also have a distinct spawning period (release of eggs into marsupium) in the southern Weddell Sea. Table 2 shows the number of broods found in the samples and the corresponding embryonic stages. The number of samples is too small in all 3 regions (Antarctic Peninsula to South Orkneys, area off Camp Norway, Gould Bay) for a clear statement, but it is possible that even in the coldest area (Gould Bay) a spawning period exists (60% of the broods of the samples from January and February were in stage A1 to B1). Most eggs were probably produced around October/November of the preceding year.

Number and Size of Eggs

Differences in the size of eggs of females from different regions of the Weddell Sea are already conspicuous to the naked eye, the more southern populations obviously having larger eggs. To complete these observations the number of early stages (A1 to B1) in the brood pouch were counted and correlated with the length of the females. The result is shown in Fig. 6: Combining all samples a correlation between length of female and clutch size is not found. But this impression changes when the samples are divided into geographic regions or into the equivalent morphotypes described by Wägele (in press), namely the northern "cornuta"-forms from the South Orkneys and from neighbouring sites (South Shetlands; similar populations also in Bransfield Strait), the yellowish and brown forms from off Camp Norway (Riiser-Larsen Ice Shelf) and the dark grey forms from Gould Bay. After this partition we obtain a clearer result, though the points in Fig. 6 are still rather scattered, because many (not all) females lose eggs during trawling and sorting, so that mean values for egg numbers calculated with these data would be too low. Nevertheless it can be seen that the usual correlation between body size and egg number exists in all 3 regions. More interesting is the fact that the correlation egg number/female size differs clearly in the studied areas. Females from the northern sites have a larger clutch size and smaller eggs (size = length of longest axis of the oval egg), in the south, egg size is larger and the number of eggs is smaller.

The data were obtained by measuring eggs of stage A1 – B1 from samples of the cultured batches; 226 eggs from 24 females were available. Mean egg sizes from the northern populations (2.97 ± 0.18 mm), the area around Camp Norway (3.09 ± 0.19 mm) and from the Gould Bay (3.55 ± 0.24) differ from each other significantly with a probability of at least 95%.

So we find on the intraspecific level a phenomenon well documented in interspecific comparisons: with decreasing temperature the number of eggs also decreases but size of eggs grows. This result can possibly imply that the time for embryonic development is longer in the southern Weddell Sea than in the smaller embryos studied, but this must not necessarily be so (see above: comparison of *S. polita* and *C. trilobitoides*).

The different size of eggs indicates that in the southern Weddell Sea not only different morphotypes can be found, but also physiological races (see also Wägele, in press). That serolids may have regionally differing physiological races is also implied by Luxmoore (1982 a) in his description of the differences in the number of moults needed to reach maturity in populations of *S. pagenstecheri* from South Georgia and Signy Island.

Discussion

Leaving aside the formation of typical serolid features (i.e. large epimeral and coxal plates) the ontogeny of *C. trilobitoides* resembles that of boreal isopods (review in Strömberg 1972). Cleavages and histology of germ layers were not studied. A dorsal flexure is lacking as in all isopods that produce large eggs. A conspicuous feature of embryonic development of *C. trilobitoides* is the slowness of the process, which is also typical for other polar crustaceans (i.e. Amphipoda: Bregazzi 1972; Mysidacea: Wittmann 1984). The length of this first period of the animals' life has an important influence on the calculation of fertility (offsprings per unit of time): in *Ceratoserolis* it occupies probably about 1/3 to 1/4 of the lifetime needed to reach maturity (maturity is probably reached after 4 years of postembryonic growth at Signy Island: Luxmoore 1982 a).

Table 3 compares the duration of embryonic stages in several isopods; unfortunately in most studies embryonic

Table 3. Comparison of the duration of embryonic stages in temperate isopods and antarctic serolids (d = days, w = weeks, m = months)

Author	Species	Stage									
		A1	A2	B1	B2	B3	B4	C1	C2	D	E
Jones (1970)	*Eurydice affinis*	8d		13d						10d	5.5d
Jones (1970)	*Eurydice pulchra*	13d		19.5d						14d	8.5d
Betz (1980), Jensen (1955)	*Sphaeroma rugicauda*	15–16d						6d		10d	18d(?)
Daum (1954)	*Caecosphaeroma burgundum*	12–14w						15w	8w(?)	15w(?)	3w
Sømme (1940)	*Limnoria lignorum*	17–23d						8–10d		11–13d	
Sheader (1977)	*Idotea pelagica*	8d						6–12d		5–8d	3–6d
Henry (1976)	*Proasellus cavaticus*	45–50d								30d	
Forsman (1944)	*Jaera albifrons*	3d		1d				2–3d		2–3d	hours
Luxmoore (1982)	*Serolis polita*	5m(?)		5m				4m		2m	3–4m
Present study	*Ceratoserolis trilobitoides*	5m(?)		$5^1/_2$m				10m(?)			$2^1/_2$(?)

stages were not defined exactly or were not considered at all. Table 4 summarizes data on egg sizes and durations of the complete embryonic development [several data on egg sizes can be found in Strömberg 1972, data for *Cyathura carinata* from the author's own measurements; Anderson's data (1969) combined from 2 Swedish localities; *Proasellus cavaticus* (Henry 1976) from different caves].

It seems that most studies are not precise enough to calculate a mean duration of embryonic stages, variations are great. From the data of Table 3 it appears that stage A may need 15–25%, stage B 15–25%, stage C 15–37% (most about 25%) and stage E 14–30% of the total marsupial phase. It is remarkable that the first stage (cleavage, gastrulation) lasts so long. More exact observations at constant temperatures would be useful for the ecologist who wants to calculate the spawning time.

In Table 4 there also exists some uncertainty (exact temperature, duration of incubation), also a comparison of data is critical as some are based on in-vitro experiments, some on field observations, but the order of magnitude is reliable. Daum (1954) for example presents some data on the duration of single embryonic stages of *Caecosphaeroma* (see Table 3) adding up to 53 to 55 weeks, but finally states that the development lasts about 11–12 months (Table 4).

The Antarctic isopods (*Ceratoserolis, Glyptonotus, Serolis*) have the slowest development. To discuss the causes for this retardation 3 important factors must be considered: the physiological effect of temperature, the evolutionary adaptation to the environment of a locality, and the size of the eggs. In Table 4 and Fig. 7 we find examples for the influence of each of these factors. The influence of the quality of the females' food during oocyte growth on the quality of embryonic development has not been studied so far in isopods, though postembryonic growth clearly depends on the nutrition (i.e. Økland 1978).

Temperature is of course the outstanding factor influencing the duration of embryonic development. *Asellus aquaticus* needs more than 134 days for incubation at 4.5 °C (Andersson 1969). At low temperatures development slows down, and it stops at too low (as at too high) temperatures, as shown for *Dynamene bidentata* (Holdich 1968) or for species of *Limnoria* (Eltringham 1967); the fact that Antarctic species can reproduce at −1 °C is a remarkable adaptation.

But the temperature alone cannot be used as a factor to explain all observations. *Proasellus cavaticus*, a stygobiont species, has eggs which are slightly smaller than those of *Asellus aquaticus*, but nevertheless their development is, at the same temperature (11 °C), 2.5 times lon-

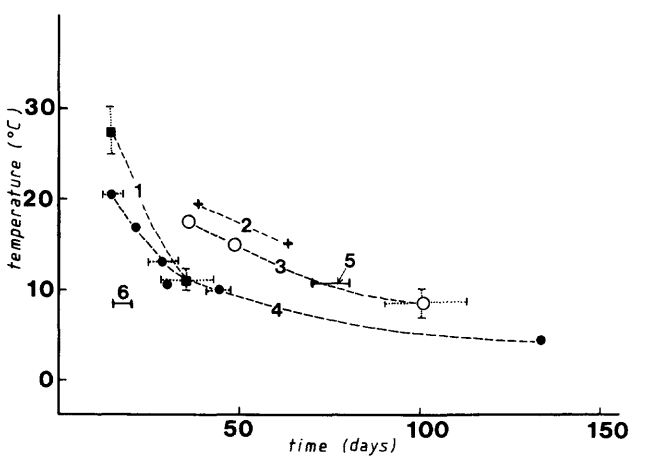


Fig. 7. Illustration of the effect of temperature on incubation time of temperate isopods (see also Table 4) (*vertical lines*: range of temperature; *horizontal lines*: range of developmental time). 1 = *Limnoria lignorum*; 2 = *Sphaeroma hookeri*; 3 = *Dynamene bidentata*; 4 = *Asellus aquaticus*; 5 = *Proasellus cavaticus*; 6 = *Clypeoniscus hanseni* (using data of the following authors: 1: Henderson 1929; 2: Jensen 1955; 3: Holdich 1968; 4: Andersson 1969, Henry 1976; 5: Henry 1976; 6: Sheader 1977)

Table 4. Duration of the embryonic development of isopods (d = days, w = weeks, m = months), temperature (at which development took place), egg diameter and latitude (of the locality from which the species were collected)

Species	Author	Time	Temperature	Egg diameter	Latitude
Cyathura carinata	Wägele (1979)	4 w	15–20 °C	480 µm	54.3°N (9.9°E)
Eurydice affinis	Jones (1970)	37 d	>12 °C	?	51.5°N (4.1°W)
Eurydice pulchra	Fish (1970)	12–35 d	15–20 °C	600 µm	52.2°N (4°W)
Eurydice pulchra	Jones (1970)	57 d	>10 °C	600 µm	51.5°N (4.1°W)
Caecosphaeroma burgundum	Daum (1954)	11–12 m	11.5 °C	750 µm	49°N (6°E)
Dynamene bidentata	Holdich (1968)	36 d	17.5 °C	500 µm	51.8°N (5.1°W)
Dynamene bidentata	Holdich (1968)	48 d	15 °C	500 µm	51.8°N (5.1°W)
Dynamene bidentata	Naylor and Quenisset (1964)	4–5 w	15–16 °C	500 µm	South Wales ~51.5°N 4°W)
Dynamene bidentata	Holdich (1968)	90–110 d	7–10 °C	500 µm	51.8°N (5.1°W)
Sphaeroma hookeri	Jensen (1955)	38 d	19.5 °C	500 µm	55.6°N (12.5°E)
Sphaeroma hookeri	Kinne (1954)	~4 w	15–24 °C	500 µm	54.3°N (10.1°E)
Sphaeroma hookeri	Jensen (1955)	63 d	15 °C	500 µm	55.6°N (12.5°E)
Sphaeroma rugicauda	Betz (1980)	40–50 d	15–25 °C	?	54.5°N (9.7°E)
Sphaeroma serratum	Charmantier (1974)	4 w	15–25 °C	?	43.4°N (3.6°E)
Limnoria lignorum	Henderson (1924)	2 w	25–30 °C	400 µm	45.1°N (67°W)
Limnoria lignorum	Henderson (1924)	4–6 w	10–12 °C	400 µm	45.1°N (67°W)
Limnoria lignorum	Sømme (1940)	37 d	10–16 °C	400 µm	60.6°N (4.9°E)
Limnoria lignorum	Sømme (1949)	3 m?	6 °C	400 µm	60.6°N (4.9°E)
Idotea emarginata	Naylor (1955)	30 d	9 °C	700 µm	54.2°N (4.2°W)
Idotea neglecta	Kjennerud (1950)	38–55 d	?	525 µm	60.4°N (5.3°E)
Idotea pelagica	Sheader (1977)	34 d	8–9 °C	500–580 µm	55.0°N (1.4°W)
Idotea baltica	Strong (1978)	6 w	11–14 °C	488 µm	45.2°N (64.3°W)
Glyptonotus antarcticus	White (1970)	20 m	−1 °C	3000 µm	66.7°S (45.6°W)
Asellus aquaticus	Steel (1961)	16–18 d	?	300–400 µm	51.4°N (0.9°W)
Asellus aquaticus	Andersson (1969)	13–17 d	20.5 °C	300–400 µm	59.8°N (18.6°E) and 59.9°N (17.7°E)
Asellus aquaticus	Henry (1976)	21 d	16 °C	300–400 µm	France
Asellus aquaticus	Henry (1976)	30 d	11 °C	300–400 µm	France
Asellus aquaticus	Andersson (1969)	25–32 d	13.5 °C	300–400 µm	59.8°N (18.6°E) and 59.9°N (17.7°E)
Asellus aquaticus	Andersson (1969)	41–48 d	10 °C	300–400 µm	59.8°N (18.6°E) and 59.9°N (17.7°E)
Asellus aquaticus	Andersson (1969)	>134 d	4.5 °C	300–400 µm	59.8°N (18.6°E) and 59.9°N (18.6°E)
Proasellus cavaticus	Henry (1976)	70–80 d	11 °C	300 µm	France

(continued overleaf)

Table 4 (continued)

Species	Author	Time	Temperature	Egg diameter	Latitude
Ligia oceanica	Besse et al. (1975)	40 d	summer	?	Charente Maritime 45.6–46.2°N (1.2°W)
Ligia oceanica	Saudray and Lemercier (1960)	6–8 w	14–20 °C	?	Calvados 49.3°N (0–1°W)
Ligia oceanica	Besse et al. (1975)	90 d	winter	?	Charente Maritime 45.6–46.2°N (1.2°W)
Porcellio laevis	Nair (1984)	24	28–33 °C	?	28.6°N (77.2°E)
Jaera albifrons	Forsman (1944)	9–11 d	18–20 °C	260 µm	58.3°N (11.5°E)
Clypeoniscus hanseni	Sheader (1977)	15–20 d	8–9 °C	120–126 µm	55.0°N (1.4°W)
Serolis polita	Luxmoore (1982 b)	20 m	−1.8–+0.5 °C	~1500 µm	66.7°S (45.6°W)
Ceratoserolis trilobitoides	present study	23 m (?)	−1 °C	3000 µm	King George and Signy Island 60.7–62.1°S
Serolis marplatensis	Bastida and Torti (1970)	15–30 d	?	?	38.0°S (57.5°W)

ger. This is understood as a consequence of adaptations to the subterranean way of life, where a long life cycle is necessary (and possible due to the presence of few competitors) to reach maturity in spite of the scarce and periodically oscillating supply of food (Graf and Michaut 1975; Henry 1976; Magniez 1978). Why also the *marsupial phase* is prolongued is not clear, it seems that the genetically fixed slow growth also has an effect on the embryonic stages.

This strategy includes a reduction in the number of eggs. It also reminds of the adaptations of infauna amphipods (in comparison to epifauna amphipods) to the reduced risks of their way of life (Van Dolah and Bird 1980; Nelson 1980). Genetically fixed adaptations to different latitudes have been discovered in copepods (*Acartia, Pseudocalanus*: Corkett and McLaren 1978) and, with a greater effect, in mysids (Wittmann 1984).

In polar benthos above all adaptations to the periodical short phytoplankton bloom are discussed to explain seasonality and retardation phenomena of reproductive cycles (i.e. Thorson 1946; Pearse 1966, 1969). It is possible that also in *Ceratoserolis* seasonal spawning is usual, as already discussed, and maturation of the ovary and release of young are adapted to the seasonality of environmental factors, as shown for *S. polita* by Luxmoore (1982 b). But the cause for such an evolutionary adaptation cannot be the phytoplankton itself. It might be that mancas preferably feed on young polychaetes or other small invertebrates, which should be primary consumers and profit from the short summer rain of algae. In those parts, where temperature fluctuates seasonally, it is also possible that a small increase of temperature is advantage enough to ensure a more rapid growth of the mancas. This would reduce the high mortality of these first stages. In this context it is interesting that Bregazzi (1972) found a mortality of up to 90% during the first year of life of the Antarctic amphipods *Cheirimedon femoratus* and *Tryphosella kergueleni*. That such adaptations of the life cycle are fixed genetically could also be shown by Vitagliano and Valentino (1964) for different European populations of *Asellus aquaticus*.

With the present data we cannot estimate, which influence the genetically fixed adaptations have. That they exist in *C. trilobitoides* can be seen in the variations of egg size and clutch size. The third factor influencing the duration of incubation, namely egg size, is best studied by intraspecific comparisons (e.g. Corkett and McLaren 1978), but we have no data to try such an analysis with an isopod species. The interspecific variations allow no unequivocal conclusions. *C. trilobitoides, S. polita* and *Glyptonotus* probably have the same incubation time, in spite of their different egg sizes. That small eggs develop fast can be proved with the epicaridean *Clypeoniscus hanseni* (Table 3, Fig. 7). *Caecosphaeroma burgundum* has large eggs (750 µm) and a long incubation time, but the latter is probably not caused by egg size: *Idotea emarginata* has similar large eggs (700 µm) and needs only 1/11 of this time. In *Caecosphaeroma* the cause for retardation is, as in *Proasellus*, the subterranean way of life.

These few examples suggest that above all temperature and evolutionary adaptations are the main causes for slow development (probably also for the low fecundity and long life cycles) of Antarctic ectotherms. This result

is not in accordance with the opinion of Clarke (1982), who, after discussing Bělehrádeks function, emphasizes the importance of egg size. In mysids, where good data are available, it seems that egg size has only a small effect on incubation periods and that latitudinal adaptations occur independently of egg size. Therefore "only species with the same geoclimatic distribution should ... be compared" (Wittmann 1984).

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