EMBRYOLOGICAL DEVELOPMENT IN *Tryphosella kergueleni* (Miers) AND *Cheirimedon femoratus* (Pfeffer) (CRUSTACEA : AMPHIPODA)

By P. K. BREGAZZI*

ABSTRACT. A descriptive account, based on examination of live and preserved material, is given of the embryological development of *Tryphosella kergueleni* and *Cheirimedon femoratus*, most features of which are typical of amphipods.

At about the mid-stage of development of both species, an outer egg membrane is shed, and the embryo, invested with a single embryonic membrane, increases in size. There is a prominent dorsal organ, perhaps concerned with the moulting process. Embryos lose weight during development but soon after hatching there is an increase in dry weight, probably due to the uptake of inorganic materials for incorporation into the integument.

THE few species of polar amphipods which have been studied in any detail have been found to undergo a period of embryological development which is long when compared with that of species from lower latitudes, and generally a female produces fewer broods. *Tryphosella kergueleni* (Miers) has two broods each year, one in summer and one in winter, and *Cheirimedon femoratus* (Pfeffer) produces one relatively large brood during the winter (Bregazzi, 1972). Both species are members of the family Lysianassidae which is well represented in Antarctic waters. Up to the present time, there has been no account available of embryological development within the family. The present paper gives an account of such development in *T. kergueleni* and *C. femoratus*, and discusses it in relation to that of other crustaceans.

METHODS

Developing eggs and embryos, flushed from the maternal brood pouch with a pipette, were examined alive and also preserved in 5 per cent neutral formalin.

Material for sectioning was fixed in Smith's formol bichromate and then transferred to 5 per cent formalin after washing. Embryos were dehydrated in alcohols to 95 per cent, then cleared in methyl benzoate followed by benzene to avoid the hardening action of absolute alcohol on yolky material, then embedded in paraffin wax (m. pt. 54·5° C). Sections were cut at 8 μm. and stained with Heidenhain's haematoxylin and eosin.

Microphotographs were taken of living embryos using transmitted light.

Development of individual embryos was followed by keeping various stages in small Perspex tubes, 3 cm. by 1 cm., having a nylon mesh bottom, suspended in racks in sea-water maintained at $0 \pm 1°$ C and continuously aerated. Embryos could be examined by placing a tube from the rack into a small vessel of sea-water beneath a binocular microscope. All investigations upon living material were carried out in a constant temperature room at $0 \pm 1°$ C.

To determine dry weights, groups of living eggs placed on coverslips, were washed three times in distilled water to remove traces of sea-water, and dried to constant weight at 100° C. Samples were weighed to the nearest 0·1 mg.

Living egg dimensions were measured using a binocular microscope with micrometer eyepiece.

The five arbitrary developmental stages adopted for eggs within the brood pouch are as in Bregazzi (1972).

DEVELOPMENT IN *T. kergueleni*

Descriptive account

Pre-copulative pairing has not yet been observed in any Antarctic species of Gammaridea, and this may be related to the relatively large size of the female in most of these cases.

Mating was not observed in *T. kergueleni*, either in laboratory tanks or during dives by night when the animals are active, and may occur beneath the sand surface. It is likely that, in common with other gammaridean species, the male deposits sperm in the brood chamber of the recently moulted female, whereupon ova are liberated and fertilization takes place.

* Present address: Department of Zoology, University College of Swansea, Swansea, Wales.

The eggs are full of oil droplets and vary in colour from pale orange to deep red. A single egg membrane is apparent. Almost without exception, the eggs in any one brood of the several hundred that were examined were all the same colour and at the same stage of development. Occasionally one or two apparently unfertilized eggs were noted in an otherwise normal brood. Six individual examples were found of healthy developing broods including eggs at different developmental stages, some of which were also different colours (Table I).

TABLE I. INDIVIDUAL BROODS OF *T. kergueleni* WITH EGGS AT DIFFERENT DEVELOPMENTAL STAGES

	Total number of eggs in brood	*Number of eggs*	*Stage*	*Colour*	*Number of eggs*	*Stage*	*Colour*
10 October 1968	9	6	II, early	Orange	3	II, late	Red
9 November	10	9	III	Red	1	I, 16 cell	Orange
9 November	16	8	III	Orange	8	I, 16 cell	Orange
9 November	11	10	III	Red	1	IV	—
27 December	6	5	III	Red	1	II	Orange
20 January 1969	10	8	III	Red	2	I, many cells	Orange

The first two cleavage divisions are total, vertical and perpendicular to each other, resulting in a group of four cells, one of which is almost always noticeably smaller than the other three (Fig. 1a). The next division is horizontal and near the ventral (but at this stage, uppermost) surface of the egg, resulting in four small micromeres lying upon four larger macromeres. Again, one of the micromeres is usually much smaller than its neighbours. Material at the micromere side of the egg appears more dense than elsewhere, and is a slightly darker colour. The micromeres are sometimes displaced spirally (but just as often they are not) and it is not possible to describe the arrangement of cells at the 8-cell stage as either clearly spiral or clearly radial.

The smallest macromere and the smallest micromere confer an asymmetry on the egg, and these cells can be on either side of the longitudinal axis, the one case being a mirror image of the other. The ratio of the two sorts of egg in all broods examined is roughly equal, but it may

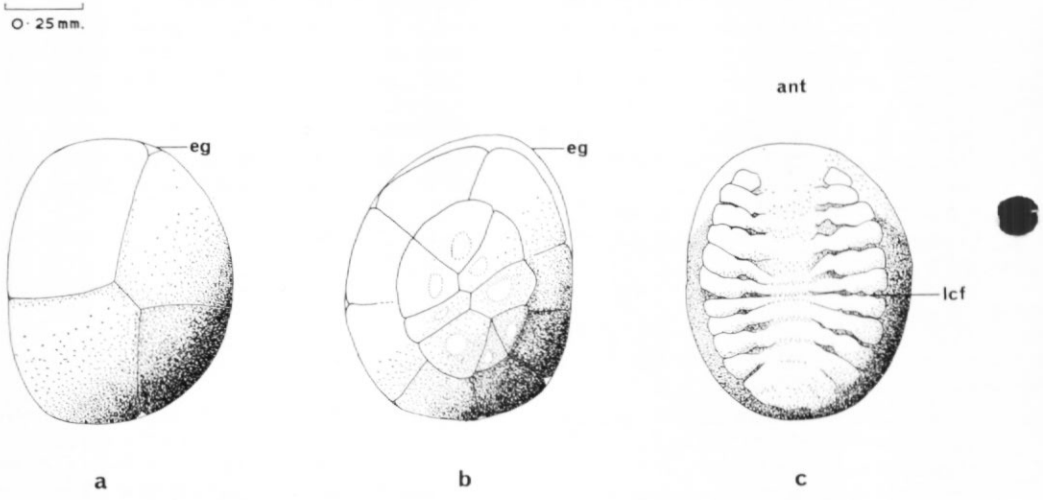

Fig. 1. Development of *T. kergueleni*.
a. Stage I, 4-cell stage egg.
b. Stage I, 16-cell stage egg, ventral aspect.
c. Stage II, ventral aspect of embryo, before formation of caudal furrow, showing paired somites.
ant anterior; lcf level at which caudal furrow will develop; eg egg membrane.

be up to 3 : 1. The significance of the mirror images is not known. It is still apparent at the 16-cell stage (Fig. 1b), which arises by radial division of each cell of the 8-cell stage, but thereafter it is not obviously present.

The micromeres divide more rapidly than the macromeres, resulting in a ventral germinal disc, composed of relatively small and eventually non-pigmented cells (beginning of stage II). The germinal disc begins to extend over the entire surface of the egg, enclosing the yolk cells which are derived from the macromeres, and constituting the blastoderm (Fig. 2a). Ventrally, gastrulation apparently proceeds by the proliferation of cells inwardly to form the embryonic mesoderm and endoderm, and paired somites appear, longitudinally arranged, which give rise to the appendage rudiments (Fig. 1c).

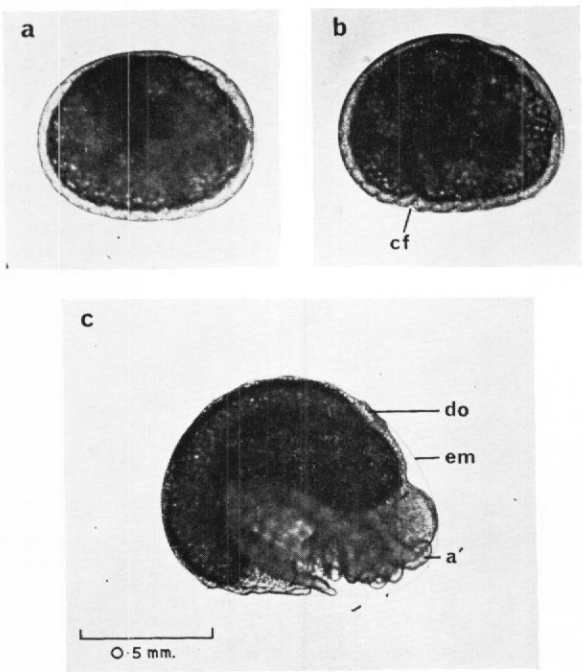

Fig. 2. Development of *T. kergueleni* (photographs of living material).
a. Stage II, blastoderm enclosing yolk cells, lateral aspect.
b. Stage III, ventral somites and early stage of caudal furrow development.
c. Stage III (late), embryo about to develop eyes; darkest pigmented area is digestive caecum.
a′ 1st antenna; cf caudal furrow; do dorsal organ; em embryonic membrane. Anterior margins at right.

The dorsal organ is now visible, situated on the mid line dorsally, just posterior to the head lobes, and composed of a small cluster of cells. Posterior to the ninth pair of appendage rudiments, a transverse caudal furrow appears (beginning of stage III) (Fig. 2b) and this extends as a deep cleft dorsally into the embryo and eventually divides the future peraeon from the pleon. Further appendage rudiments appear around the margin of the caudal furrow (Fig. 3a).

The cells of the dorsal organ are now elongated and clearly glandular. Their apices converge and are invested with a single cap (or micropyle) of dark-staining material which is in intimate contact with, or indeed part of, the inner or embryonic membrane (Fig. 4a). The outer or egg membrane is separate but also closely applied at this point and the location of the dorsal organ cap is seen on the outside surface of a whole specimen as a small raised portion of membrane, surrounded by a slight depression.

The relative position of the inner margin of the caudal furrow is progressively displaced backwards as the peraeon grows, and the embryo assumes a "comma" shape.

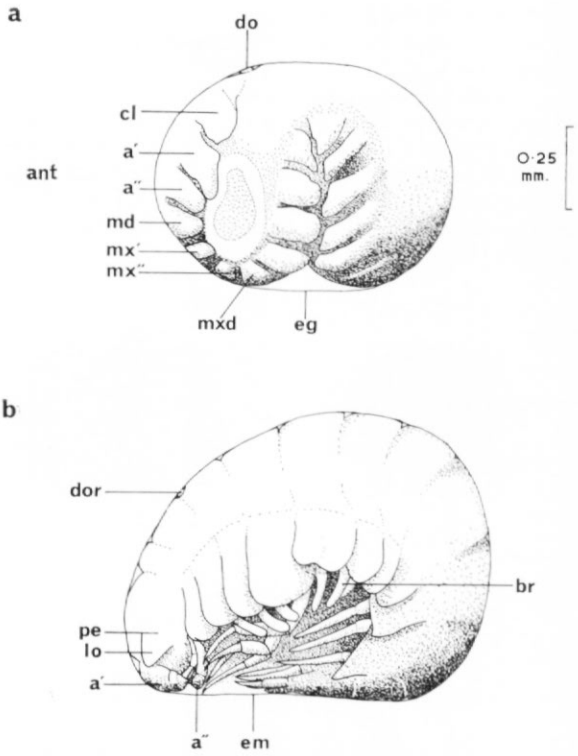

Fig. 3. Development of *T. kergueleni*.
a. Stage III, embryo with well-developed caudal furrow and appendage rudiments, lateral aspect.
b. Mid-stage IV, eye pigment destroyed by fixative.
a′ 1st antenna (or rudiment); a″ 2nd antenna (or rudiment); ant anterior; br branchia; cl cephalic lobe; do dorsal organ; dor dorsal organ remains; eg egg membrane; em embryonic membrane; lo lateral lobe; md mandible (or rudiment); mx′ 1st maxilla (or rudiment); mx″ 2nd maxilla (or rudiment); mxd maxilliped (or rudiment); pe position of eye.

At about this stage, the egg membrane splits ventrally and is lost, the last point of attachment being in the region of the dorsal organ, and the embryo, enclosed within a single embryonic membrane, begins to increase in size. Development of the appendages proceeds and the enlarged first articles of the peduncle of the first antennae, a characteristic of members of the family Lysianassidae, can be made out.

The embryo is free within the embryonic membrane, except where the latter is still closely applied to the dorsal organ (Fig. 2c).

Branchiae appear on the inner surfaces of the coxae of peraeon segments 2–7 and the heart is formed dorsally. A pair of digestive caeca extend posteriorly into the abdomen, one from each side of the mid gut (Fig. 2c). When they have reached three-quarters of their final length, eye rudiments appear just posterior to the head lateral lobes and progressively develop red pigment, beginning with the centremost optic elements (beginning of stage IV).

The dorsal organ meanwhile degenerates and its previous location is marked on the anterior margin of peraeon segment 3 by the dark-staining cap which is still also incorporated into the embryonic membrane (Figs. 3b and 4b).

Later, movement of the limbs and gut can be seen, and later still, the heart-beats, irregular at first, become regular and more rapid in frequency. About 4 days after the onset of regular heart-beats, the membrane splits and the hatchling, with full adult complement of body segments and appendages, is released into the brood pouch (stage V). Red/orange oil droplets from the yolk are still present within the gut and the eyes are densely pigmented and bright red. There is no trace of the dorsal organ or dorsal organ cap in the newly hatched juvenile.

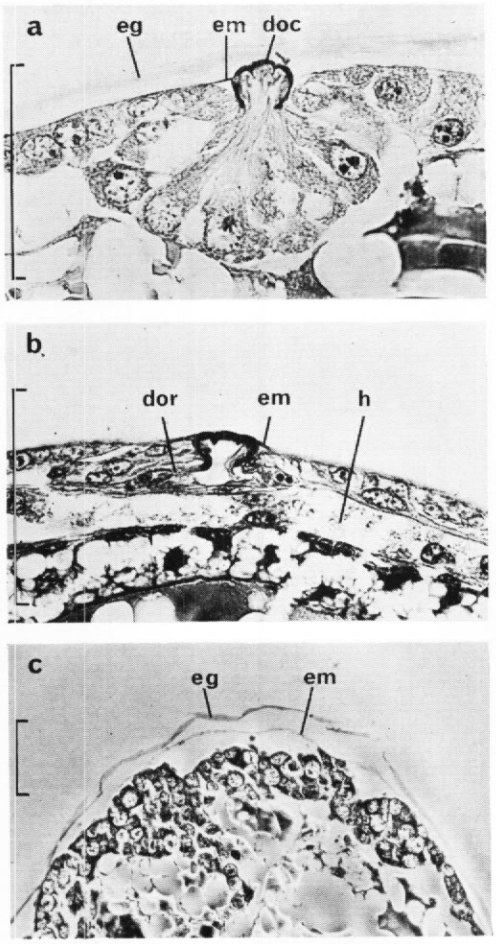

Fig. 4. Development of *T. kergueleni*.
a. Stage III, vertical section through dorsal organ.
b. Stage IV, vertical section in region of degenerating dorsal organ.
c. Stage III (early), vertical section through anterior part of embryo showing egg membrane and embryonic membrane.
doc dorsal organ cap; dor dorsal organ remains; eg egg membrane; em embryonic membrane; h heart.
Scale 0·1 mm.

There is no evidence to suggest that either moulting or feeding occurs before hatchlings are released from the brood pouch (Bregazzi, 1972).

Duration of development

Considerable difficulty was experienced in maintaining the cultured embryos in a healthy state. Fungal strands and populations of ciliates often infected entire broods, especially in the early stages of development, and an ozonizer, incorporated into the aerator pump, gave no obvious benefits. No eggs were successfully reared from the 1-cell stage to hatching and the data presented in Table II are drawn from a total of 110 eggs in 26 broods. The development stages were selected in this instance on account of their clear-cut nature. The mean development time in the experimental tubes from the 1-cell stage to hatching was 97 days, or about 3 months.

TABLE II. DURATION OF EMBRYONIC DEVELOPMENT IN *T. kergueleni* (EXPERIMENTAL CULTURES)

	Stage	*Number of eggs*	*Number of broods*	*Mean duration (nearest day)*	*Range*
1 cell to 16 cells	I	39	6	6	—
To caudal furrow	II	33	11	15	12–18
To digestive caeca	III	13	7	28	19–37
To eye rudiment	III	27	8	17	14–26
To hatch	IV	33	13	31	26–40
				97	71–121

Changes in dry weight during development

It was necessary to use eggs from more than one brood in each sample during determination of dry weights on account of the small size of the brood in *T. kergueleni* (3–18 eggs). Up to 60 eggs were used in each sample.

There is a mean decrease in dry weight of 0·01 mg. (9·09 per cent) per egg from stage I (0·11 mg.) to stage IV (0·10 mg.), followed by an increase in dry weight after hatching at stage V (Fig. 5a). A "*t*" test was applied to these data but the difference was not found to be statistically significant at the 5 per cent level. However, a trend is clearly shown in the mean values for successive developmental stages.

Ovigerous females, less broods, of a given body length, show an increase in dry weight to about stage III, and thereafter a decrease (Fig. 5b).

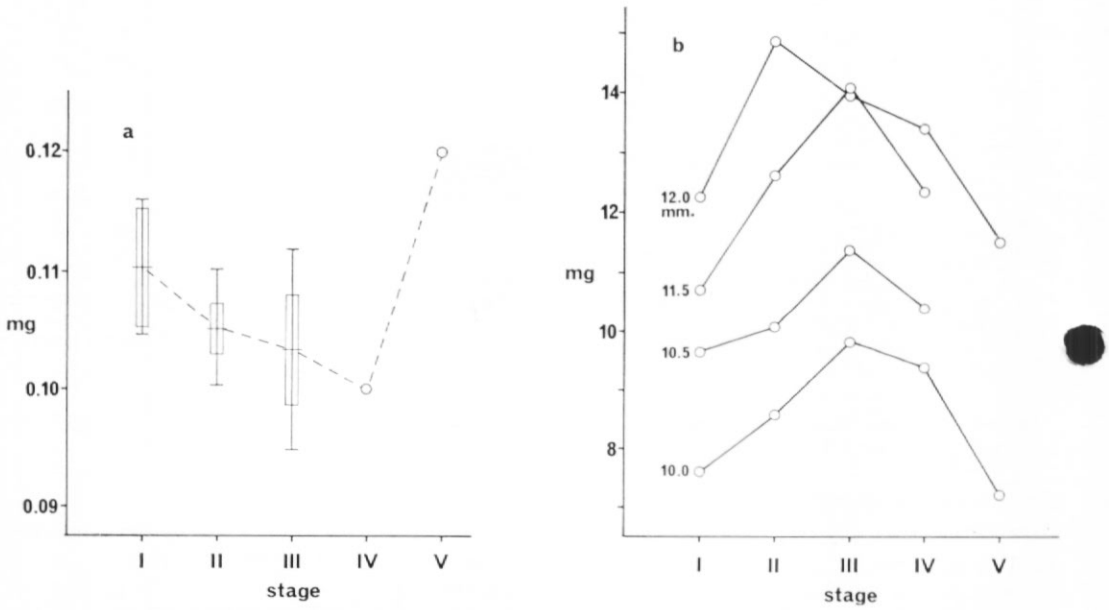

Fig. 5. a. Mean dry weights of different stage eggs/embryos of *T. kergueleni*. One standard deviation (line) and two standard errors (rectangle) are shown on each side of the mean. Number of samples used: stage I 6; stage II 20; stage III 12; stage IV 4; stage V 1.
b. Mean dry weights of ovigerous females (less broods) of *T. kergueleni* bearing different stage broods. Length of female, with number of samples used: 10·0 mm. 22; 10·5 mm. 37; 11·5 mm. 27; 12·0 mm. 21.

Changes in dimensions of eggs during development

The length (l) and width (w) of 51 stage I eggs from seven separate broods were measured, and also the length, width and depth (d) of 31 stage IV eggs from five separate broods. Mean volumes (v) of eggs at both stages were calculated using the following formulae (Thurston, 1968):

$$\text{Stage I: } v = \frac{\pi l w^2}{6}. \qquad \text{Stage IV: } v = \frac{\pi l w d}{6}.$$

The results (Table III) show an increase in volume during development by a factor of about two.

TABLE III. DIMENSIONS OF EGGS OF *T. kergueleni*

Stage I (51 eggs)	Mean length	0·8411 mm. (0·793–0·914)
	Mean width	0·6476 mm. (0·595–0·716)
	Mean volume	0·185 mm.^{3}
Stage IV (31 eggs)	Mean length	1·1135 mm. (1·035–1·207)
	Mean width	0·7227 mm. (0·672–0·750)
	Mean depth	0·8975 mm. (0·828–0·966)
	Mean volume	0·377 mm.^{3}
	$\frac{\text{Mean volume stage IV}}{\text{Mean volume stage I}}$	= 2·04.

DEVELOPMENT IN *C. femoratus*

Descriptive account

The details of development described for *T. kergueleni* are followed closely by *C. femoratus*, except as described in this section. Mating was not observed in *C. femoratus*.

One female was preserved in the act of egg-laying. Several eggs were still visible in both ovaries, whilst the brood pouch contained 19 eggs enclosed in a single membranous package, and a further 19 loose eggs, a few of which still adhered to the remains of a membrane. Mucous sacs have been described in three species of *Gammarus* and in *Crangonyx pseudogracilis* Bousfield (as *C. gracilis* Smith) by Hynes (1955), and Sheader and Chia (1970) recorded sacs in *Marinogammarus obtusatus* (Dahl) containing eggs and, initially, a gelatinous substance which dissolves after about 12 hr. In view of the absence of gelatinous material within the two egg sacs seen in *C. femoratus*, the disintegration of one of the sacs while the ovaries contain many eggs yet to be laid and the finding of only one ovigerous female with egg sacs, it is likely that the egg sacs persist for a short time only in this species also. About four egg sacs would be needed to provide a brood of normal size, assuming each sac contained about 19 eggs. In all the temperate species mentioned, only two sacs are present.

Without exception, all the eggs of each brood examined in *C. femoratus* were at the same developmental stage, although one or two apparently unfertilized eggs were occasionally present.

The eggs are slightly smaller than those of *T. kergueleni* and are pale yellow to pale orange in colour. Eggs are almost always the same colour in any one brood, but occasionally about half are a slightly different shade. This is more obvious in preserved material.

Cleavage divisions and the occurrence of "mirror images" in early stage eggs appear identical with that of *T. kergueleni*, as does subsequent development, including loss of the egg membrane, except that the eye, initially crimson, is dense black soon after hatching.

Moulting does not occur prior to release from the brood pouch but feeding may take place very rarely (Bregazzi, 1972).

Duration of development

Even greater difficulty than with *T. kergueleni* was experienced in maintaining the cultures of eggs of *C. femoratus*. Every early stage egg died after a few days, often invested with a rich fungal growth. However, the development of 77 eggs from nine separate broods was followed from the appearance of the eye rudiment to hatching. The mean development time for these

eggs was 37 days (range 33–43 days). This compares with a mean of 31 days (26–40 days) for development between the same stages in *T. kergueleni*, and so the time for *C. femoratus* represents an increase of about 20 per cent over *T. kergueleni*. Application of this factor indicates a total mean development time in *C. femoratus*, from one cell to hatching, of about 115 days.

Changes in dry weight during development

Entire broods of up to 96 eggs were used for each sample.

There is a mean decrease in dry weight of 0·01 mg. (12·65 per cent) per egg from stage I (0·079 mg.) to stage IV (0·069 mg.), followed by a substantial increase in dry weight after hatching at stage V (Fig. 6a). Again, the difference between stages I and IV was not statistically significant, in spite of the clear overall trend.

Ovigerous females of a given body length, less broods, show a continual decrease in dry weight throughout development of the brood (Fig. 6b).

Changes in dimensions of egg during development

The length and width of 60 stage I eggs from three separate broods were measured, and also the length, width and depth of 80 stage IV eggs from six separate broods. Mean volumes of eggs at both stages were calculated as described for *T. kergueleni*. The results (Table IV) show an increase in volume during development by a factor of about two.

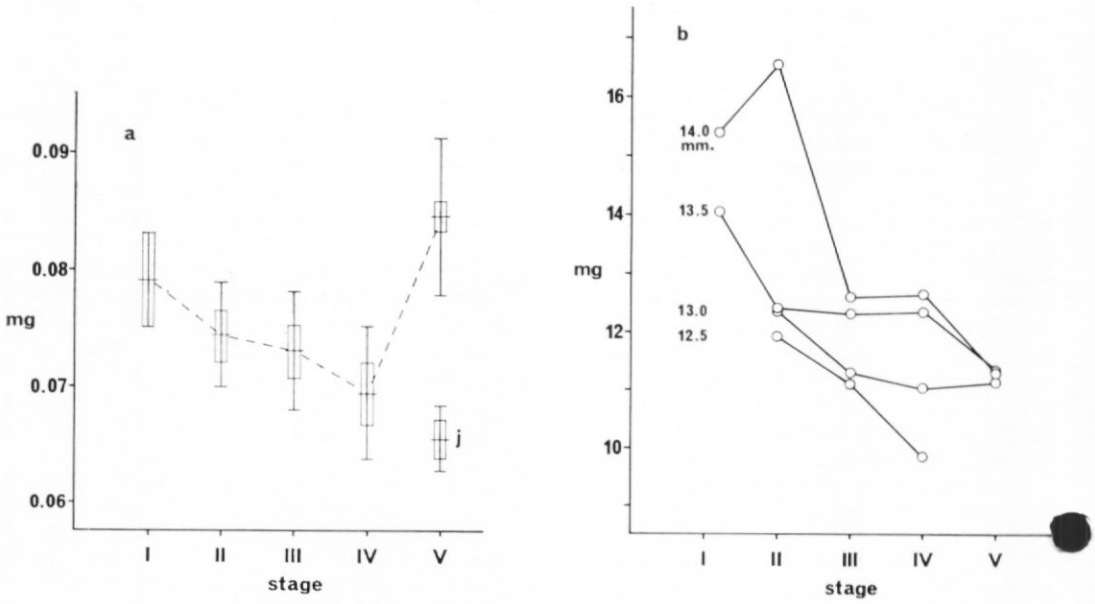

Fig. 6. a. Mean dry weights of different stage eggs/embryos of *C. femoratus*. One standard deviation (line) and two standard errors (rectangle) are shown on each side of the mean. j just hatched. Number of samples used: stage I 4; stage II 20; stage III 23; stage IV 16; stage V (j) 3; stage V 29.
b. Mean dry weights of ovigerous females (less broods) of *C. femoratus* bearing different stage broods. Length of female, with number of samples used: 12·5 mm. 7; 13·0 mm. 13; 13·5 mm. 13; 14·0 mm. 15.

Discussion

The eggs of the great majority of Crustacea are all at the same stage of development in any one brood on account of their being fertilized at the same time (Green, 1965). Exceptions are provided by *Limnoria*, three species of which frequently contain widely different developmental stages in the same brood (Eltringham and Hockley, 1961), and *Dynamene bidentata* (Adams) in which 25 per cent of broods are composed of eggs of more than one stage, but of which one

TABLE IV. DIMENSIONS OF EGGS OF *C. femoratus*

Stage I (60 eggs)	Mean length	0·7573 mm. (0·672–0·871)
	Mean width	0·5805 mm. (0·526–0·629)
	Mean volume	0·134 mm.^{3}
Stage IV (80 eggs)	Mean length	0·9756 mm. (0·914–1·034)
	Mean width	0·6295 mm. (0·560–0·672)
	Mean depth	0·8026 mm. (0·750–0·879)
	Mean volume	0·258 mm.^{3}
	$\frac{\text{Mean volume stage IV}}{\text{Mean volume stage I}} = 1{\cdot}93.$	

stage always predominates (Holdich, 1968). Broods with eggs of more than one developmental stage are clearly of rare occurrence in *T. kergueleni* and can be accounted for either by some developmental abnormality in part of the brood or by an incomplete oviposition in the first instance followed by a second one later, presumably with a second mating. The second alternative seems the most likely on account of the apparent good health of all the eggs and the clear-cut nature of the two stages. Intermediate stages of development would be expected in an unhealthy brood. The possibility of partial parthenogenesis cannot be ruled out, but no report of this is known from within the order.

The manner of cleavage and formation of the germinal disc, blastoderm and caudal furrow in *T. kergueleni* and *C. femoratus* is typical for that of Amphipoda. As far as can be judged from available literature, the occurrence of "mirror images" in early stage eggs has not been previously reported, and at present no suggestion can be made as to its significance. The shedding of the egg membrane during development also appears not to have been reported before within the order. It is worth noting, however, that the bulk of studies on amphipod development have been concerned with the members of one family, the Gammaridae. Loss of such a membrane is not included in the descriptions of *Macrinogammarus obtusatus* (Sheader and Chia, 1970), *M. marinus* (Leach) (Vlasblom, 1969) or *Gammarus duebeni* Lilljeborg (Steele and Steele, 1969), and Weygoldt (1958), in a most detailed account of development in *Gammarus pulex* (L.), stated that such a moult does not occur. The secretion by the blastoderm of an embryonic membrane ("tunique larvaire") within the egg membrane or chorion was reported by Rossiiskaya (1888) for *Orchestia littorea* Spence Bate (Talitridae) but she did not record the fate of the egg membrane.

In the present study, no live embryos were observed in the act of shedding the egg membrane, but discarded membranes were found in the tubes containing cultured broods, and several preserved broods in both species included discarded membranes and also embryos with portions of membrane still attached at the dorsal organ region. Furthermore, at about the time of completion of the caudal furrow during stage III, it is possible to dissect away the egg membrane with needles, leaving the embryonic membrane intact, and stage IV embryos undoubtedly possess only one covering membrane, apart from the embryonic cuticle. Examination of sections of stage III embryos confirms the presence of two membranes during the earlier stage (Fig. 4c).

Embryonic dorsal organs have been recorded in several groups of Crustacea, including Branchiura (Pyatakov, 1926), Nebaliacea (Manton, 1934), Mysidacea (Nussbaum and Schreiber, 1898; Manton, 1928), Isopoda (Bullar, 1879; Nair, 1956), Amphipoda (Rossiiskaya, 1888; Heidecke, 1904; Weygoldt, 1958; Steele and Steele, 1969; Sheader and Chia, 1970) and Decapoda (Sollaud, 1923; Weygoldt, 1961). Sometimes, paired dorso-lateral organs are also present, e.g. *Hemimysis lamornae* (Couch) (Manton, 1928). In *Argulus foliaceus* (L.) two successive dorsal organs occur, one elongated and one smaller and round (Pyatakov, 1926). In the Amphipoda the dorsal organ is particularly well developed (Dawydoff, 1928).

The role of the dorsal organs is by no means established. Suggestions have been made for various Crustacea, including supply of nutrients to developing muscles (Rossiiskaya, 1888), concern with the moulting process (Pyatakov, 1926; Dawydoff, 1928), absorption of excess ectoderm (Nussbaum and Schreiber, 1898), absorption of yolk (Manton, 1928; Nair, 1956)

and uptake of oxygen (Weygoldt, 1958). The present study cannot add to these observations, except that in *T. kergueleni* and *C. femoratus*, a possible connection with the moulting process cannot be ruled out. This is because the maximum development of the cells of the dorsal organ coincides with the loss of the egg membrane and thereafter the organ slowly degenerates, and also, the secretions of the dorsal organ are intimately connected with, or part of, the embryonic membrane, and the organ is also associated, to a lesser degree, with the egg membrane.

The figures given for duration of embryonic development must be treated with some reserve on account of the high mortality of embryos during the culturing experiments. The estimated development time of 115 days in *C. femoratus* does not agree with the period of about 6 months deduced from field observations (Bregazzi, 1972). The discrepancy may be accounted for in part by the vigorous aeration of water in the culture tank, and also by the experimental temperature of $0° \pm 1°$ C being slightly higher than that experienced by animals in the field during the time of embryonic development from April to October (mean sea temperature $-1{\cdot}46°$ C). The influence of temperature, within limits, upon the development time of Crustacea is well documented, with the lower temperatures inducing longer development, e.g. *Gammarus duebeni* (Hynes, 1954), *G. zaddachi* Sexton subsp. *salinus* Spooner (Kinne, 1960; as *G. salinus*), *Balanus balanus* (L.) and *B. crenatus* Brugiere (Patel and Crisp, 1960), *Dynamene bidentata* (Holdich, 1968) and *Limnoria* spp. (Eltringham, 1967). That the developmental period in *T. kergueleni* may be a little shorter than that for *C. femoratus* could be in part due to the former producing two broods per year and the latter one brood.

The continual decrease in dry weights of ovigerous *C. femoratus* during brood development, and the initial increase followed by a decline in the dry weights of ovigerous *T. kergueleni* during the same period, reflect the different feeding and breeding habits (Bregazzi, 1972). *C. femoratus* feeds for a time after egg-laying, until the brood is at about the mid-point of development, and almost entirely upon plant material. One brood is produced, after which the female dies. *T. kergueleni* also feeds well into the period of brood development but includes a necrophagous diet, large numbers of ovigerous females being taken in baited traps, and three or more broods are produced. As one brood develops in the brood pouch, so the oocytes for the following brood enlarge in the ovaries.

The steady loss in dry weight in the embryos during development to hatching in both species can be attributed to the depletion of respiratory materials. Losses in dry weight during pre-hatching development are common in other Crustacea. For example, there is a 16–25 per cent loss in *Daphnia magna* Straus and a 16 per cent loss in *D. curvirostris* Elymann emend. Johnson (Green, 1956), a 7 per cent loss in *Homarus gammarus* (L.) (Saudray, 1954; as *H. vulgaris* Milne-Edwards), a 30 per cent loss in *Crangon crangon* (L.) (Pandian, 1967) and a 48 per cent loss in *Porcellana longicornis* (L.) (personal communication from G. Smaldon). In *Artemia* there is no loss in dry weight during development on account of any respiratory losses being balanced by the uptake of inorganic salts from the surrounding water (Dutrieu, 1960). Salts are also taken up by embryos during development in *Pagurus* (*Eupagurus*) *bernhardus* (L.) (Pandian and Schumann, 1967), *Crangon crangon*, *Ligia oceanica* (L.) and *Homarus gammarus* (Pandian, 1967). The increase in dry weight of developing embryos of *Dynamene bidentata*, especially between the last two stages, is thought to be most likely due to uptake of inorganic salts, but also ingestion of exuvia, absorption of materials from degenerating embryos and transfer of materials from the female parent to the brood are cited as sources of possible increase in dry weight (Holdich, 1971). The dry weight of *Ligia oceanica* embryos increases by 36 per cent during development, most of which increase is probably effected by the maternal secretion of nutritive substances into the brood pouch (Saudray, 1954).

From the present data for *T. kergueleni* and *C. femoratus* it cannot be determined whether or not inorganic salts are absorbed by embryos during development. However, the rapid increase in dry weight after hatching can be most readily attributed to this since feeding by juveniles while still in the brood pouch does not occur, except very rarely in *C. femoratus* (Bregazzi, 1972). The salts likely to be taken up are almost certainly for incorporation into the integument, because the young of both species, being very soft and weak at hatching, increase in size slightly and become very much more firm and robust within 1 or 2 days.

Increase in volume of embryos during development is common in Crustacea, and indicates a percentage increase in water content. The two-fold increase in volume in *T. kergueleni* and

C. femoratus can be compared with a factor of 2·5 times in *Marinogammarus obtusatus* (from data in Sheader and Chia (1970)) and 3 times in *Bovallia gigantea* Pfeffer (Thurston, 1968).

ACKNOWLEDGEMENTS

I am grateful to Professor E. Naylor, Marine Biological Station, Port Erin, for valuable discussion, and to Professor E. W. Knight-Jones, Department of Zoology, University College of Swansea, for the provision of laboratory facilities. D. G. Bone, British Antarctic Survey, and Mr. C. Stockton, Department of Zoology, University College of Swansea, kindly helped with photography.

MS. received 8 April 1972

REFERENCES

BREGAZZI, P. K. 1972. Life cycles and seasonal movements of *Cheirimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) (Crustacea : Amphipoda). *British Antarctic Survey Bulletin*, No. 30, 1–34.

BULLAR, J. F. 1879. On the development of the parasitic Isopoda. *Phil. Trans. R. Soc.*, **169,** No. 2, 505–21.

DAWYDOFF, C. 1928. *Traité d'embryologie comparée des invertébratés*. Paris, Masson et Cie.

[redacted]UTRIEU, J. 1960. Observations biochimiques et physiologiques sur le développement d'*Artemia salina* Leach. *Archs Zool. exp. gén.*, **98,** No. 1, 1–134.

ELTRINGHAM, S. K. 1967. The effects of temperature on the development of *Limnoria* eggs (Isopoda: Crustacea). *J. appl. Ecol.*, **4,** No. 2, 521–29.

————. *and* A. R. HOCKLEY. 1961. Migration and reproduction of the wood-boring isopod, *Limnoria*, in Southampton Water. *Limnol. Oceanogr.*, **6,** No. 4, 467–82.

GREEN, J. 1956. Growth, size and reproduction in *Daphnia* (Crustacea : Cladocera). *Proc. zool. Soc. Lond.*, **126,** Pt. 2, 173–204.

————. 1965. Chemical embryology of the Crustacea. *Biol. Rev.*, **40,** No. 4, 580–600.

HEIDECKE, P. 1904. Untersuchungen über die ersten Embryonalstadien von *Gammarus locusta*. *Jena. Z. Naturw.*, **38,** No. 3, 505–52.

HOLDICH, D. M. 1968. Reproduction, growth and bionomics of *Dynamene bidentata* (Crustacea : Isopoda). *J. Zool.*, **156,** Pt. 2, 137–53.

————. 1971. Changes in physiology, structure and histochemistry occurring during the life-history of the sexually dimorphic isopod *Dynamene bidentata* (Crustacea : Peracarida). *Mar. Biol. Berl.*, **8,** No. 1, 35–47.

HYNES, H. B. N. 1954. Ecology of *Gammarus duebeni* Lilljeborg and its occurrence in fresh water in western Britain. *J. Anim. Ecol.*, **23,** No. 1, 38–84.

————. 1955. The reproductive cycle of some British freshwater Gammaridae. *J. Anim. Ecol.*, **24,** No. 2, 352–87.

KINNE, O. 1960. *Gammarus salinus*, einige Daten über den Umwelteinfluss auf Wachstum, Häutungsfolge, Hertzfrequenz und Eientwicklungsdauer. *Crustaceana*, **1,** No. 3, 208–17.

MANTON, S. M. 1928. On the embryology of a mysid crustacean *Hemimysis lamornae*. *Phil. Trans. R. Soc.*, Ser. B, **216,** No. 438, 363–463.

————. 1934. On the embryology of the crustacean *Nebalia bipes*. *Phil. Trans. R. Soc.*, Ser. B, **223,** No. 498, 163–238.

NAIR, S. G. 1956. On the embryology of the isopod *Irona*. *J. Embryol. exp. Morph.*, **4,** Pt. 1, 1–33.

NUSSBAUM, J. *and* W. SCHREIBER. 1898. Beiträge zur Kenntniss der sog. Rückenorgane der Crustaceenembryonen. *Biol. Zbl.*, **18,** No. 20, 736–45.

[redacted]NDIAN, T. J. 1967. Changes in chemical composition and calorific content of developing eggs of the shrimp *Crangon crangon*. *Helgoländer wiss. Meeresunters.*, **16,** No. 3, 216–24.

————. *and* K. H. SCHUMANN. 1967. Chemical composition and calorific content of egg and zoea of the hermit crab *Eupagurus bernhardus*. *Helgoländer wiss. Meeresunters.*, **16,** No. 3, 225–30.

PATEL, B. *and* D. J. CRISP. 1960. Rates of development of the embryos of several species of barnacles. *Physiol. Zoöl.*, **33,** No. 2, 104–19.

PYATAKOV, M. L. 1926. The dorsal organs of *Argulus* and their relation to the hatching of the larva. *Q. Jl microsc. Sci.*, **70,** No. 277, 159–71.

ROSSIISKAYA, M. 1888. Le développement d'*Orchestia littorea* Spence Bate. *Bull. Soc. Nat. Moscou*, **2,** No. 4, 561–81.

SAUDRAY, Y. 1954. Utilization des réserves lipidiques au cour la ponte et du développement embryonnaire chez deux Crustacés: *Ligia oceanica* Fab. et *Homarus vulgaris* Edw. *C. r. Séanc. Soc. Biol.*, **148,** No. 5, 814–16.

SHEADER, M. *and* F. S. CHIA. 1970. Development, fecundity and brooding behaviour of the amphipod *Marinogammarus obtusatus*. *J. mar. biol. Ass. U.K.*, **50,** No. 4, 1079–99.

SOLLAUD, E. 1923. L'embryonogenie de Crustacés Decapodes de la sous-famille de Palaemoninae. *Bull. biol. Fr. Belg.*, Suppl. 5, 1–234.

STEELE, D. H. *and* V. J. STEELE. 1969. The biology of *Gammarus* (Crustacea, Amphipoda) in the north-western Atlantic. I. *Gammarus duebeni* Lillj. *Can. J. Zool.*, **47,** No. 2, 235–44.

THURSTON, M. H. 1968. Notes on the life history of *Bovallia gigantea* (Pfeffer) (Crustacea, Amphipoda). *British Antarctic Survey Bulletin*, No. 16, 57–64.

VLASBLOM, A. G. 1969. A study of a population of *Marinogammarus marinus* (Leach) in the Oosterschelde. *Neth. Jnl Sea Res.*, **4**, No. 3, 317–38.

WEYGOLDT, P. 1958. Die embryonalentwicklung des amphipoden *Gammarus pulex pulex* (L.). *Zool. Jb.*, Abt. Anat. Ontog. Tiere, **77**, No. 1, 51–110.

————. 1961. Beitrag zur Kenntnis der Ontogenie der Dekapoden: embryologische Untersuchungen an *Palaemonetes varians* (Leach). *Zool. Jb.*, Abt. Anat. Ontog. Tiere, **79**, No. 2, 223–70.