NOTES ON THE REPRODUCTION AND EARLY DEVELOPMENT OF THE CIRRATULID *THARYX MARIONI* (ST JOSEPH)

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(Text-figs. 1, 2)

The larval development of the Cirratulidae is not well known, although an account of the development of *Raphidrilus nemasoma* Mont. was published by Sokolow in 1911 (under the name of *Ctenodrilus branchiata*), and of *Audouinia tentaculata* (Montagu) by Wilson in 1936. Apart from these two publications, only scattered observations may be found in the literature, and these are listed by Wilson (1936). Unfortunately, attempts to rear the larvae of *Tharyx marioni* (St Joseph) beyond the hatching stage have failed, and as it seems unlikely that further data may be gathered for some time, such results as have been obtained are presented here.

The main points of interest in the development and reproductive habits of *T. marioni* are: (i) the adults are atoquous; (ii) the eggs are comparatively large and yolky, and unlike *Audouinia tentaculata*, the pelagic stage is omitted; and (iii) the larva on hatching is achaetous, as in other cirratulid larvae.

The worms and larval stages were collected from a small population at Chalkwell, Essex, on the north side of the Thames estuary, in fairly clean sand just above half-tide mark. The adults were buried vertically in the top few centimetres, entirely within the oxidized layer, and with the cirri exposed on the surface.

The morphology of the adults agrees well with the description given by Fauvel (1927) except that: (i) the sexually mature adults were never more than 35 mm. in length (Fauvel states the length to vary between 35 and 100 mm.); (ii) the adults were devoid of all pigment other than the red blood pigment (Fauvel describes them as 'reddish brown'); (iii) the ripe oocytes were colourless and appeared chalky white in the mass (Fauvel states that they are 'greenish').

I am indebted to Dr D. P. Wilson for kindly checking my identification.

Reproduction and Spawning

It is impossible to distinguish the sexes with the naked eye. They do not differ in size, and when ripe both appear white due to the presence either of spermatozoa, or oocytes. The females, however, may be detected with a hand lens, as the oocytes may then be distinguished in the coelom. Males and females occurred in equal numbers. From a sample of thirty-seven worms, eighteen were females, nineteen were males.

The gametes are restricted to the mid-body region, being absent from the anterior region, and from the last few segments, in both sexes. Ripe females have about fifty genital segments, with a total number of between 1000 and 1500 oocytes.

Unfortunately spawning was not observed, but the oocytes are probably released singly into the sand. The spawning period was sharply defined, nearly all the worms spawning between 16 and 18 April 1949, about 3–5 days after full moon, when the highest tides occur at Chalkwell. There was a sharp rise in temperature at this time, which may have stimulated spawning (Fig. 1). Unspawned females quickly resorbed their oocytes after this, and a week or two later they had lost the white appearance characteristic of the sexually mature worms.

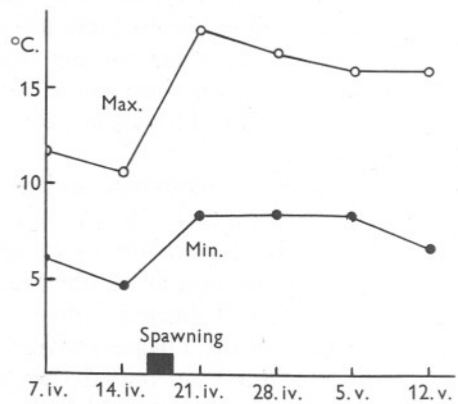

Fig. 1. Temperature of the natural habitat during spawning and early development. (Recorded by a max.–min. thermometer lying at a depth of 5 cm.)

There was little difference in size between the oocytes, either within a single female, or throughout the population. When ripe the oocytes are round, or slightly oval, and are surrounded by a fairly thick transparent layer which is adhesive at first, but which seems to lose this property when ready for spawning. They contain a large germinal vesicle, and a fine, opaque, granular cytoplasm (Fig. 2A).

The sperm plates are rather irregular in size and shape, and vary between 20 and 50 μ across. The sperm head is acorn-shaped, and bears a tail about 40 μ in length (Fig. 2B).

Early Development of the Larvae

Development from artificial fertilizations, which were achieved by slitting open the adults and mixing the ripe gametes in a dish, proceeded only as far as late cleavage, and unfortunately no active larvae were obtained. Naturally spawned and fertilized eggs and cleavage stages were, however, collected from the sand.

A fertilization membrane was thrown off soon after artificial fertilization, and remained so close to the egg, that in many instances its presence was

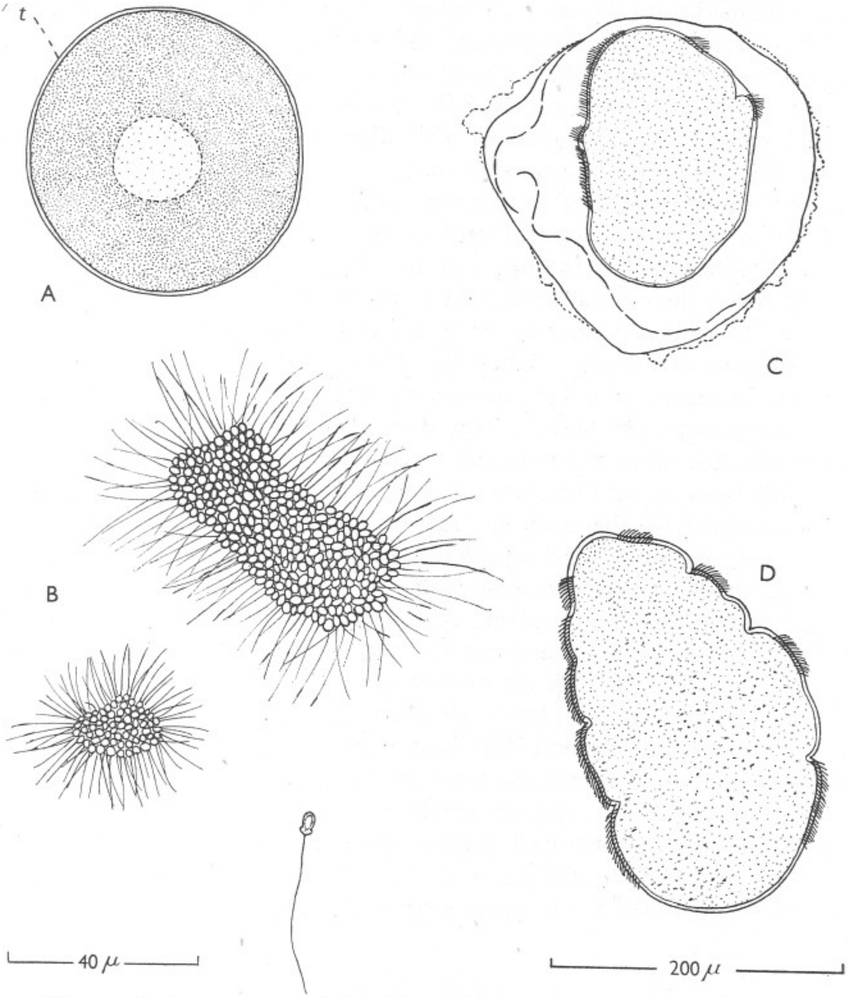

Fig. 2. Ripe coelomic gametes, and developmental stages obtained from the sand. A, unfertilized oocyte (*t*, transparent layer); B, sperm plates, and a motile spermatozoan; C, young unhatched larva; D, hatching stage. The scale on the left applies to B only; that on the right to A, C and D.

difficult to detect until the first cleavage. Polar bodies were conspicuous, and were thrown off about an hour after fertilization. The first cleavage, which takes place at right angles to the longitudinal axis of the egg, occurred after about 2 hr., the 4-cell stage being reached after about $3\frac{1}{2}$ hr., whilst 6 hr. after fertilization 8-cell stages may be seen.

In the natural habitat a jelly layer is very conspicuous, and stands away from the developing larva, and although in artificially produced larvae this layer was obviously present, it did not stand away from the surface of the egg as in those stages obtained from the sand. In nature, this layer forms a capsule in which the larva is free to rotate, and is practically opaque, owing to the rich growth of diatoms and other algae which it supports, so that in practice it is necessary to dissect off this capsule in order to see the larva. It may be added that the capsules can only be distinguished with difficulty from the surrounding sand grains which are much the same in size.

About 2 or 3 days after fertilization, cilia begin to grow out through the fertilization membrane, which then becomes the larval cuticle, and the larva begins to rotate within the egg capsule (Fig. 2C). The ciliation gradually extends down the ventral surface in a posterior direction, and well-marked bands of fine short cilia extend over the dorsal surface, the larva becoming more vigorous in its movements. Later, this ciliary movement is supplemented by muscular movement, the larva becoming highly contractile, but chaetae and other appendages are absent. Ten days after fertilization, the contractile movements are fairly vigorous and stretch the walls of the capsule, which eventually breaks open to release the larva. Late cleavage stages and gastrulae were collected from the sand on 19 April 1949, and on the 21st most of the larvae were rotating in their capsules, but no hatched larvae were found until the 28th, about 10 days after spawning.

On hatching, the larva is about $250\,\mu$ long, and has two to three segments delimited, but owing to the absence of chaetae, and to the extreme contractility of the body wall, it is difficult to determine the exact number of segments present. The larva is completely opaque, white, sausage-shaped, and with a slightly pointed anterior end. The ventral surface is uniformly ciliated, while bands of cilia extend round the dorsal surface in each segment (Fig. 2D), but the cilia are very short, and are insufficient to lift the larva off the bottom. Indeed, in spite of their well-marked muscular movements, the larvae are rather sluggish and are difficult to detect. Owing to the opacity of the body wall, no details of the gut or other internal structures could be seen.

Discussion

The larva of this species is interesting in that it is typically bottom-living, non-pelagic, and lecithotrophic, as are the larvae of many other intertidal polychaetes, and has no pelagic stage, unlike any of the other cirratulid larvae known. Correlated with this habit are the relatively large oocytes and capsule in which the larva develops until two or three segments have been formed. The hatching larvae are similar to the early bottom stages of *Audouinia* *tentaculata*, described by Wilson, in the absence of chaetae, and in the extreme contractility of the body. Also, in the absence of chaetae, they resemble the corresponding stages of *Dodecaceria concharum*, figured by Mésnil and Caullery (1898). The larvae of *Audouinia tentaculata*, however, develop from much smaller eggs than those of *Tharyx marioni*, and the larvae of the former hatch in a relatively short time as ciliated planktonic trochophores. It is the metamorphosed bottom stages which may be compared with the hatching larvae of *T. marioni*, which develop from eggs one and a half times the size of those of *Audouinia tentaculata*. The development of *Tharyx marioni*, therefore, affords an interesting new example of the formation of a yolky egg and loss of an active pelagic stage.

Summary

Males and females of *T. marioni* occur at Chalkwell in equal numbers. The species is atoquous, the large oocytes being spawned into the sand where they are fertilized. Spawning took place over a sharply defined period (16–18 April 1949) following a sharp rise in temperature, and at a time when the highest monthly tides occurred. The larva hatches about 10 days after initiation of development. It is lecithotrophic, and at first achaetous and poorly ciliated, but very contractile. These two latter characters appear to be common to all cirratulid larvae known. There is no pelagic stage.

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