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THE REPRODUCTION AND LARVAL DEVELOPMENT OF *NEREIS FUCATA* (SAVIGNY)

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(Text-figures 1–7)

The wide variety of reproductive patterns and behaviour in the many species of Nereidae already studied clearly justifies further research. But the life history of *Nereis fucata* (Savigny) is not only of interest from the comparative point of view. Its commensal habit (it occurs within shells occupied by hermit crabs) immediately gives it a special importance. This alone warrants a detailed study, particularly as no commensal polychaete has yet been reared through to metamorphosis and settlement on its host (Davenport, 1955; Davenport & Hickok, 1957). The numerous interesting problems which arise, and the experimental methods needed to study them, are, however, beyond the range of a paper on nereid development. It is therefore proposed to confine the present account to the reproduction and development up to the time when the larvae settle on the bottom. The complete life cycle, the mechanism of host-adoption, and related topics, will be reported in later papers.

MATERIAL AND METHODS

Many of the shells occupied by hermit crabs in the Plymouth area are also occupied by *Nereis fucata*. It is a large and easily recognized nereid, but a few specimens have been checked against the description given by Fauvel (1923) for this species. Ripe heteronereids were collected from Plymouth trawling grounds during 1955 and 1956. The area extended as far as the Looe Grounds, the Eddystone Inner Channel Grounds, and Bigbury Bay. All were from otter-trawl hauls except a few from the Rame Mud area where an Agassiz trawl was used.

Artificial fertilizations were made in the usual way. Clean oocytes were obtained by partially stripping a female. They were then thoroughly washed in three changes of water. Sperm was produced when a few oocytes were added to a dish containing a ripe male. The time when the oocytes and sperm were mixed has been taken as the time of fertilization. After fertilization the eggs were washed, either by allowing them to sink through a long column of water, or else by three changes of filtered 'outside' sea water. Each culture was divided amongst as many bowls as possible. A few of these were then

kept at laboratory temperature for close study, while the remainder were placed in cold rooms at 11° and 12–13° C. The after-care of the cultures was substantially that described by Just (1922). In the young stages food consisted of *Phaeodactylum* and *Isochrysis* cultures.

At frequent intervals 35 mm photographs were taken of each culture in order to obtain a continuous record of size and the grosser morphological changes (number of setigers, etc.). At less frequent intervals detailed drawings were made with a camera lucida. The very fine details were usually added by eye afterwards. Nicotine was the most useful narcotic for the young ciliated stages, but magnesium chloride was needed as soon as much muscular movement began. Details of the parapodia were obtained from larvae fixed in Bouin and then cut up under a dissecting microscope. Each parapodium was then mounted directly in polyvinyl pyrrolidine and drawn with a camera lucida.

REPRODUCTION

At maturity *Nereis fucata* undergoes a 'complete metamorphosis' (Herpin, 1926) to form a typical heteronereid with an anterior unmodified region and a posterior natatory region. It has been fully described and figured by Fage (1904), and Charrier (1921) has given a detailed account of the internal modifications which take place.

Mature worms from shells housing *Eupagurus bernhardus* were obtained in gradually increasing numbers from March to June in 1956. The numbers then rapidly declined, and in both 1955 and 1956 no mature worms were collected after the middle of June, while two females with degenerating oocytes were obtained on 30 June 1955. Breeding therefore occurs sometime during the period from April to the beginning of June. More detailed information has been difficult to find. There is some evidence to suggest that the main breeding season is between the middle of May and the middle of June, since the percentage of heteronereids dropped from 4 to 0·1% during this period. However there is no record of nereid eggs or larvae in the plankton at this time, although an examination was made of thirty standard hauls taken between 18 April and 28 June from the Looe, Looe-Eddystone and Rame-Eddystone grounds. This suggests that the eggs and larvae are not in the upper layers. On four occasions from 16 to 30 May the early part of the night was spent over the grounds with a submerged light, but no heteronereids were seen. Since this species occurs in 30 fathoms or more it is possible that the swarming and development of the eggs takes place near the bottom. It is presumed that *N. fucata* normally leaves the hermit crab and swarms, as do other nereids, since no spent worms have been collected and because ripe worms swarm readily in the laboratory. Their behaviour is exactly similar to the swarming nereids described by Herpin (1926).

These mature worms are conspicuously coloured as a result of the usual

morphological changes associated with epitoky. The body wall loses its pigment until the white sperm and coloured oocytes are clearly visible, and the vascularization of the parapodia becomes so increased that a red colour predominates. In *N. fucata* the creamy-white pre-natatory region of the male is divided down the middle by the bright red dorsal blood vessel. In the natatory region this order is reversed since the blood vessel disappears leaving a broad white band in the mid-line, bordered on either side by the rose-red parapodia. The female coloration, on the other hand, is much more variable because it is dependent on the colour of the oocytes. In *N. fucata* the females are either lilac, turquoise, or blue. As in the male the parapodia add a pink border down either side of the natatory region.

The sexes are therefore very easy to distinguish and 47% of the heteronereids collected during this period were males. This probably indicates a 1:1 sex ratio. This seems to be the normal ratio for epitokous species since Reish (1954) got a 1:1 ratio in his cultures of *N. grubei*, and Takahasi (1933) reported a 5:4 ratio in *Perinereis nuntia brevicirris*. In some atokous species (e.g. *Nereis diversicolor*) the ratio may be less (Dales, 1950; Bogucki, 1953).

Ripe males were readily stimulated by the presence of a few oocytes, shedding sperm within 30–40 sec. This could be repeated after rinsing the male in clean water, as described by Herpin for *N. irrorata* and *Perinereis marionii*. When both sexes were present ovulation usually occurred after the sperm was shed, but this was less consistent. *Nereis fucata* seems to resemble *N. succinea* closely in this respect (Lillie & Just, 1913, as *N. limbata*). In an aquarium sperm streams from the posterior end, apparently from the anus, but possibly from anal papillae (Defretin, 1949). The oocytes pour from the undersides of the last few segments. Many species shed their eggs through rents in the body wall (e.g. *Platynereis megalops*, Just, 1914; *Nereis grubei*, Reish, 1954).

EMBRYONIC DEVELOPMENT

The mature oocytes rapidly acquire a smooth regular outline when released from the female, and assume a diameter which varies between 200 and 250 μ, the range for any one female being about 20 μ. The average oocyte diameter for this Plymouth population was 225 μ. This is a little on the large side for most epitokous nereids, but compares favourably with the epitokous form of *Perinereis cultrifera*, a worm of approximately similar size (Herpin, 1926). The lilac, blue, or turquoise colour is obtained from numerous small oil droplets which are visible within the oocyte. The range of colour is presumably due to varying proportions of the turquoise and purple pigments distinguished by Green & Dales (1958).

The first indication of a successful fertilization is a separation and a piling up of the eggs on the bottom of the culture dish. This is due to the rapid formation of a gelatinous envelope round each egg. At 15° C it first appears

about 15–30 min after fertilization. The pile of eggs then begins to resemble diminutive frog-spawn, and this resemblance increases during the next $2\frac{1}{2}$ h until each egg is almost 1·5 mm in diameter. A thick non-adhesive envelope is a characteristic feature of those nereids with pelagic larvae. It is not adhesive in *Nereis fucata*. The elevation of the fertilization membrane is quite normal and first appears 1–2 h after fertilization at 15° C.

The embryology of the nereids has been described and figured by E. B. Wilson (1892). More recent workers have shown that all the species closely follow Wilson's description despite differing amounts of yolk in the different species: (compare, for instance, the pelagic eggs of *N. japonica* (150 μ, Izuka, 1908) and the incubated eggs of *N. caudata* (420–520 μ, Reish, 1957)).

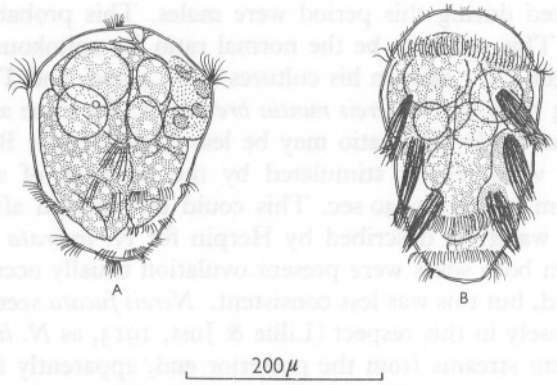

Fig. 1. A: trochophore; lateral view of the right side. Only the margins of the prototroch are shown. B: late trochophore; dorsal view.

In *N. fucata* the first cleavage occurs $4\frac{1}{2}$–5 h after fertilization at room temperature, and is closely followed by the second and third (6–7 h). Epibolic gastrulation proceeds in the normal way, and after about 12 h can be easily seen, since the small micromeres form a colourless cap of cells on top of the large coloured macromeres. By the end of the first day gastrulation is complete and sufficient cells have been formed to give a smooth regular outline to the embryo. With the further multiplication of cells the embryos continue to gain in compactness and regularity, but they remain more or less spherical with the fertilization membrane still standing out from the surface in places. Spasmodic rotation usually begins after about 33 h, although cilia cannot be seen. The prototroch first becomes visible some 3 h later, when the embryos are actively rotating. It is almost complete on the second day, and its cilia are large and conspicuous by the end of 3 days when the embryos have developed into monotrochophores. The typical shape has been achieved by an elongation of the body and some slight local swelling equatorially at the base of the prototroch.

During the next 24 h the larvae develop into complex and highly motile trochophores (Fig. 1A). The increase in motility is most marked and is derived from additional ciliary bands, especially the ventro-lateral paratrochs. In some larvae a band of pigment is formed at the base of the prototroch. Internally, continued differentiation has produced longitudinal muscles, shown by an occasional muscle twitch, and six pairs of setal bundles are clearly visible (Fig. 1B). It seems very probable that in nature hatching normally takes place at this stage, since it did so in all cultures kept between 11° and 13° C. In these cultures, hatching is only prevented by the presence of the gelatinous envelope. This disappears 4–6 days after fertilization irrespective of temperature so that larvae reared at 11° C hatch at an earlier stage (trochophores) than those reared at 15° C (3-setigers). As hatching is therefore not directly dependent on temperature or development, a comparison with other nereids is difficult. In general terms, however, *N. fucata* corresponds with other epitokous forms in having a shorter embryonic period than the atokous forms.

LARVAL DEVELOPMENT

Although swimming persists, the next stage (Fig. 2A) is characterized by the presence of long setae. These are highly mobile and each setiger is composed of noto- and neuropodial bundles. In *N. fucata* (at 15° C) their emergence occurs about 5 days after fertilization. This is rather later than in many species (e.g. 30 h in *N. irrorata*, see Herpin, 1926), but resembles *N. pelagica* ($4\frac{1}{2}$–5 days), which was also reared at Plymouth (D. P. Wilson, 1932). In *N. fucata* all three setigers are formed at about the same time, although the second may appear first, followed closely by the first and third. This order, however, is apparently determined only by the length of the setae in each setiger, which is in contrast to some species where there is a definite time lag before the formation of the third setiger (e.g. 20 h in *N. succinea* and *Platynereis megalops*, see E. B. Wilson, 1892).

At first these larvae are simply setigerous larvae (Fig. 2A), but during the next few days a gradual change takes place to form young 3-setiger worms (7 or 8 days at 15° C). Externally the features (Fig. 2B, C) which are most responsible for this change are: an increase in length, emphasized by the development of a pair of very small anal cirri; and, perhaps most characteristic, the formation of distinct parapodia, beginning as small lobes between the noto- and neuropodial bundles of setae. The rudiments of the cephalic appendages, each bearing sensory hairs (E. B. Wilson, 1892), then become prominent at about daily intervals. The anterior tentacular cirri are the first to appear, followed by the antennae, and, towards the end of this stage, a pair of small pimples on either side of the mouth which represent the future palps (they lie immediately beneath the prototroch in Fig. 2C). Two irregularly shaped patches of pigment are also often formed ventro-laterally on

either side of the head. These, however, are very variable and some larvae may not have them. Internally, blocks of tissue appear representing the proboscis, the large yolk-filled mid-gut, and the hind-gut.

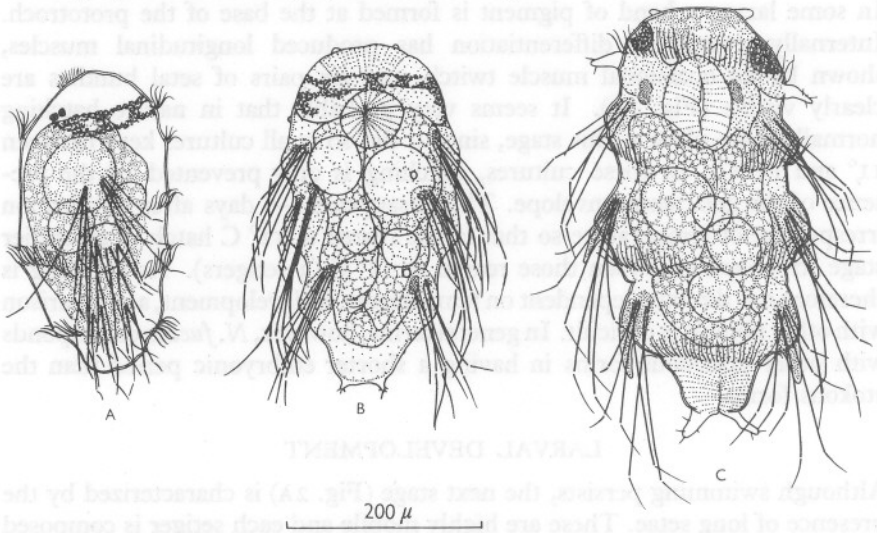

Fig. 2. A: setigerous larva; lateral view of right side. Only the margins of the prototroch are shown. B: early 3-setiger larva; ventral view. No cilia were seen in this specimen. C: 3-setiger larva; ventral view.

The growth rate now becomes a little more variable, and the cultures begin to contain larvae at different stages. At 15° C the fourth setiger is formed some time between 6 and 11 days after fertilization, while at 11° C it appears at 15–23 days. At first only a few setae project, but these rapidly increase in length and number (Fig. 3A). The cephalic appendages, the anal cirri, and all the parapodial lobes continue to grow in size. As in *Nereis pelagica* (see D. P. Wilson, 1932) and *N. costae* (see Durchon, 1956), the minute jaws become visible at this stage, and the gut, especially the proboscis and hind-gut, become more differentiated. In the 5-setiger stage (Fig. 3B), which occurs at about 2 weeks at 15° C and at about 3 weeks at 11° C, this process of elaboration continues. The setae are now very long and all the parapodia bear distinct noto- and neuropodial lobes with ventral cirri on the second to the fifth. In addition, the jaws and the proboscis can be everted and the gut is sufficiently formed for the larvae to swallow food, although yolk reserves are still present in the mid-gut. The cilia remain very active, but their disappearance has begun with the division of the prototroch into two lateral bands.

The appearance of the sixth setiger, which occurs at about 18 days, marks the beginning of the end of the larval period. By the time another setiger has been formed (at 26 days) the larvae have become juveniles and have commenced a crawling life upon the bottom (Fig. 4). Associated with this change

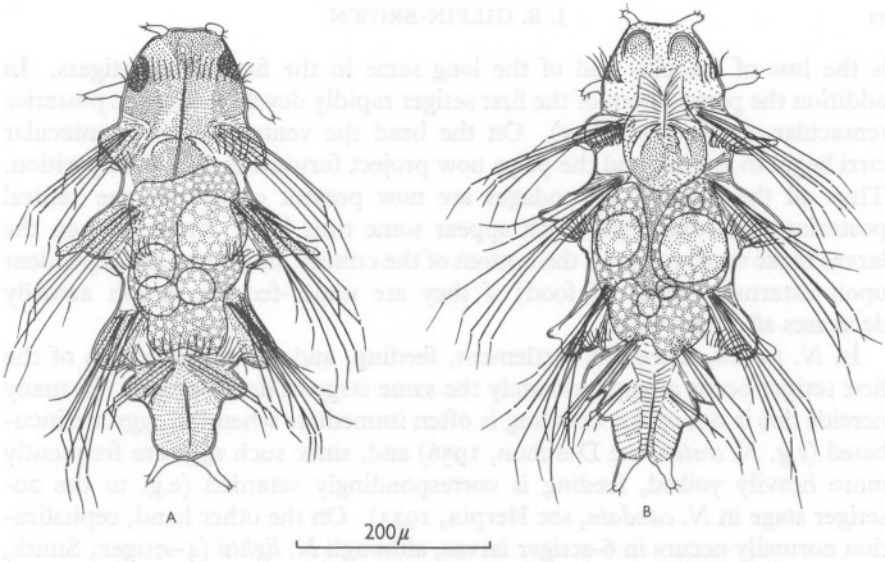

Fig. 3. A: 4-setiger larva; ventral view. B: 5-setiger larva; ventral view.

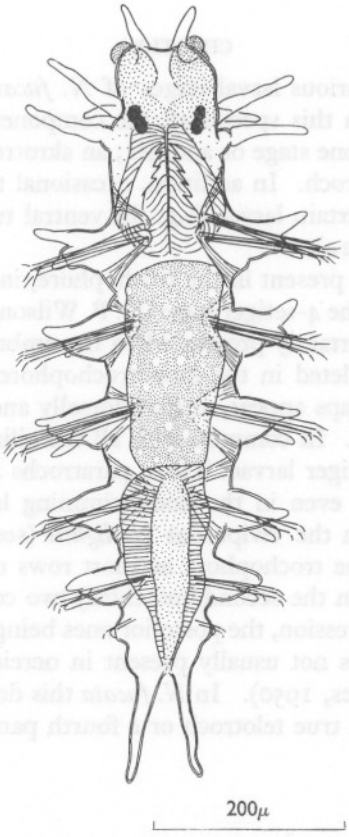

Fig. 4. 6-setiger (7-segmented) larva; dorsal view.

is the loss of the cilia and of the long setae in the first three setigers. In addition the parapodium of the first setiger rapidly develops into the posterior tentacular cirrus (see below). On the head the ventral anterior tentacular cirri begin to appear, and the palps now project forward in the adult position. Thus all the cephalic appendages are now present except for the ventral posterior tentacular cirri which appear some time later. From now on the larvae make small tubes on the bottom of the culture dishes and are dependent upon external sources of food; if they are under-fed the length actually decreases after this stage.

In *N. fucata*, therefore, settlement, feeding, and the cephalization of the first setiger occur at approximately the same stage of development. In many nereids this is not so, for crawling is often immediate when the eggs are incubated (*e.g. N. costae*, see Durchon, 1956) and, since such eggs are frequently more heavily yolked, feeding is correspondingly retarded (e.g. to the 20-setiger stage in *N. caudata*, see Herpin, 1923). On the other hand, cephalization normally occurs in 6-setiger larvae, although *N. lightii* (4-setiger; Smith, 1950) and *N. diversicolor* (9-setiger; Dales, 1950) are exceptions.

CILIATION

The ciliation of the various larval stages of *N. fucata* is set out diagrammatically in Fig. 5. In this species all the components of the basic nereid pattern are present at one stage or another; an akrotroch, a prototroch, three paratrochs, and a telotroch. In addition, occasional tufts of cilia may occur in other positions in certain larvae (e.g. the ventral tuft immediately behind the prototroch in Fig. 2A).

An akrotroch is only present in the trochophore, in contrast to *N. pelagica* where it remains until the 4-setiger stage (D. P. Wilson, 1932). An incomplete prototroch is almost certainly present when the embryos are rotating, but it is probably only completed in the monotrochophore. It then persists as a complete girdle until gaps appear, at first dorsally and then ventrally, in the 5-setiger stage (Fig. 5). In common with all the ciliary bands it disappears completely in the 6-setiger larvae. Three paratrochs are a regular feature in nereids, being present even in the non-swimming larvae of *N. costae* (see Durchon, 1956) and in the viviparous *N. lightii* (see Smith, 1950). In *N. fucata* they begin in the trochophore as short rows of cilia (Fig. 1A) which then join up to form (in the second and third) two complete rings. There is then a fairly steady regression, the posterior ones being a little more persistent (Fig. 5). A telotroch is not usually present in nereids, though it occurs in *N. diversicolor* (see Dales, 1950). In *N. fucata* this does not last long enough to show whether it is a true telotroch or a fourth paratroch.

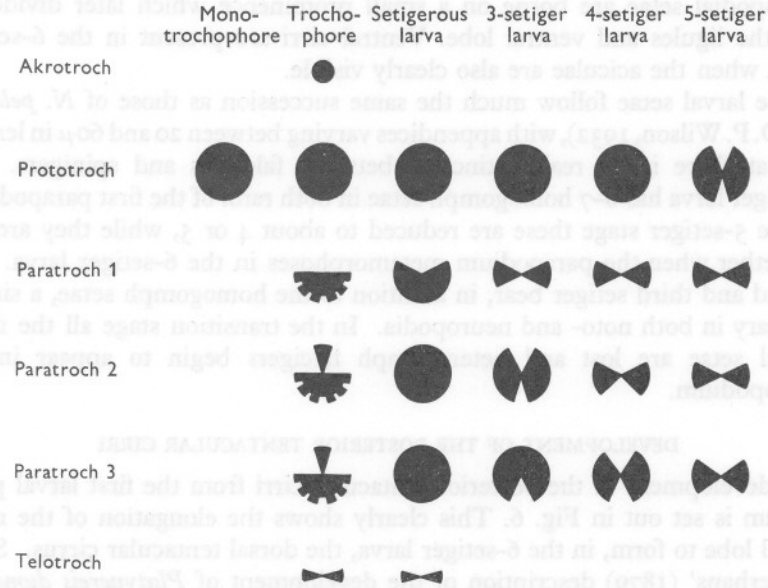

Fig. 5. Diagram of the larval ciliation. The black segments show the extent of each ciliary band at the various larval stages.

COLOUR

Pigment first appears in small patches around the prototroch (Fig. 2A, B). In the 3-setiger stage it has disappeared, but the majority of the larvae have two reddish patches ventro-laterally on either side of the head (Figs. 2C, 3A), which begin to diminish at the 5-setiger stage. The larvae are practically colourless at seven setigers. Irregularly shaped patches of pigment on the head are fairly common in this family. E. B. Wilson (1892) reported them first in the 3-setiger stage of *N. succinea*, where they were derived from the equatorial band of the trochophore. They are also present in the epitokous form of *Perinereis cultrifera* (see Herpin, 1926) and in some 3-setiger larvae of *Nereis pelagica* (see D. P. Wilson, 1932). They are not confined to the epitokous forms since they have also been reported in the 4-setiger larvae of both *N. costae* (see Durchon, 1956) and, occasionally, *N. diversicolor* (see Dales, 1950).

PARAPODIA AND SETAE

The early stages in the formation of the parapodia are very similar to those described and figured by Finke (1936) for *N. diversicolor*. A very small lobe between the noto- and neuropodial setae first appears in the setigerous trochophore. During the succeeding stages this increases in length and forms the notopodial lobe in the first two adult parapodia. In the 3-setiger stage the

neuropodial setae are borne on a small prominence which later divides to give the ligules and ventral lobe. Ventral cirri are present in the 6-setiger larva, when the aciculae are also clearly visible.

The larval setae follow much the same succession as those of *N. pelagica* (see D. P. Wilson, 1932), with appendices varying between 20 and 60 μ in length, so that there is no real distinction between falcigers and spinigers. The 3-setiger larva has 6–7 homogomph setae in both rami of the first parapodium. In the 5-setiger stage these are reduced to about 4 or 5, while they are lost altogether when the parapodium metamorphoses in the 6-setiger larva. The second and third setiger bear, in addition to the homogomph setae, a simple capillary in both noto- and neuropodia. In the transition stage all the notopodial setae are lost and heterogomph falcigers begin to appear in the neuropodium.

DEVELOPMENT OF THE POSTERIOR TENTACULAR CIRRI

The development of the posterior tentacular cirri from the first larval parapodium is set out in Fig. 6. This clearly shows the elongation of the notopodial lobe to form, in the 6-setiger larva, the dorsal tentacular cirrus. Since Langerhans' (1879) description of the development of *Platynereis dumerilii*, it is usually assumed that these cirri are derived from the dorsal and ventral cirri of the first parapodium. In *Nereis fucata*, however, this is not strictly true, for it can be seen that the dorsal tentacular cirrus develops from a lobe which is inferior to the notopodial setae at a time when the parapodium has no dorsal cirrus. *N. fucata* therefore agrees with *N. pelagica* in which the dorsal tentacular cirrus is derived from the middle lobe of the parapodium (D. P. Wilson, 1932). It probably also agrees with *N. diversicolor* (see Finke, 1936), and may further agree with *N. vexillosa* (see Johnson, 1943), *N. grubei* (see Reish, 1954), *N. succinea* (see Banse, 1954), and *N. lightii* (see Smith, 1950), since the derivation of this cirrus is not considered in detail. Many other species, however, resemble *Platynereis dumerilii* (see Hempelmann, 1911), where this cirrus is formed from the dorsal cirrus of the first parapodium (e.g. *Nereis caudata*, see Herpin, 1926; *N. costae*, see Durchon, 1956; *Perinereis marionii*, see Herpin, 1926; and *Micronereis variegata*, see Rullier, 1954). E. B. Wilson (1892), on the other hand, records that in *Platynereis megalops* and *Nereis succinea* the first parapodium never carries parapodial cirri.

GROWTH OF THE LARVAE

Although weight would be the best indication of growth and growth rates, its measurement is difficult and it has not been used for larval nereids. Length is more practical and provides a reasonable indication. It has been widely used, and the figures given by Bogucki (1953) for *N. diversicolor* give the usual sigmoid growth curve. In the same species Dales (1950) has shown that in the

early stages (0–9 weeks) length increases at a constant rate of 0·04277% per day. It will be seen from the graph (Fig. 7) that in the young stages of *N. fucata* the increase in length occurs at two speeds; an initial high rate during the first week, followed by a much slower one (Table 1). The length measured excludes appendages.

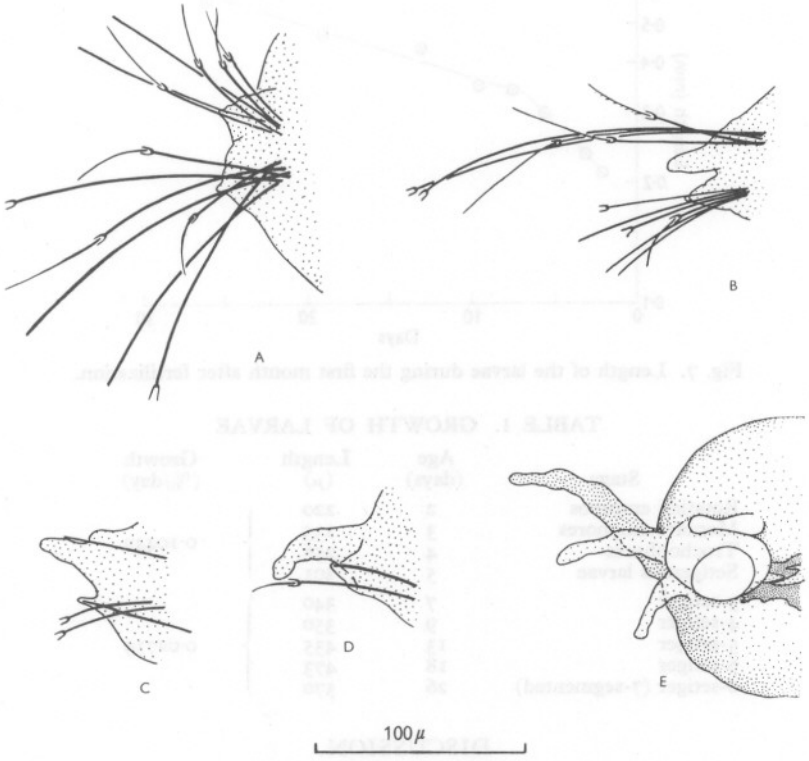

Fig. 6. Stages in the cephalization of the first parapodium. A: 3-setiger larva. B: 4½-setiger larva. C: 6-setiger larva, setae falling out. D: 6-setiger larva; elongation of the notopodial lobe. E: 6-setiger larva; frontal view after cephalization is complete.

The formation of segments is a natural and simple method of following development and has been recorded in most species. The figures for *N. fucata* are also given in the table and are in broad agreement with other species, though a close comparison is difficult. Segment-formation cannot be a strict measure of growth since it is always positive and may cease at a relatively early stage. Thus in *N. grubei* the production of segments stops when 8–85% of the final weight has been reached (Reish, 1954). In agreement with the high positive correlation between length and segments in the young larvae of *N. diversicolor* found by Dales (1950), their curves are a close fit, at least in the early stages. It seems likely that this similarity only holds good while the

embryonic yolk reserves last. The figures provided by Hempelmann (1911) for individual 'nereidogene' larvae of *Platynereis dumerilii* (since referred to *P. massiliensis* by Hauenschild, 1951) confirm this, for they show that after this stage the rate of segment formation varies considerably.

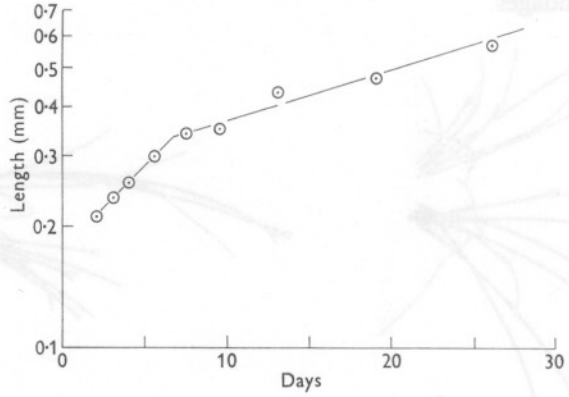

Fig. 7. Length of the larvae during the first month after fertilization.

TABLE 1. GROWTH OF LARVAE

Stage	Age (days)	Length (μ)	Growth (%/day)
Rotating embryos	2	220	
Monotrochophores	3	235	0·10449
Trochophores	4	256	
Setigerous larvae	5	301	
3-setiger	7	340	
4-setiger	9	350	
5-setiger	13	435	0·02719
6-setiger	18	473	
6-setiger (7-segmented)	26	570	

DISCUSSION

The development described in this paper refers to worms kept and reared in the laboratory. There must remain, therefore, some uncertainty about their behaviour and development under natural conditions. The rate of development is probably by far the most variable character and will presumably be mainly determined by temperature. The larvae are probably near the bottom, where the temperature will increase from about 9° C in May to about 12° C in July. It follows that the record of larvae reared at 11° C will give the best indication of their normal rate of development; but this remains a very rough approximation. This inaccuracy is further increased since, after settlement, growth will be closely linked with the availability of their natural food; and this, and its effects, are completely unknown. However, subject to these limitations the reproduction and early life history of *N. fucata* at Plymouth is probably as follows.

As no free-living population of this commensal is known (reports probably refer to the occasional single specimen, e.g. Hornell, 1891), the species may be presumed to come to maturity slowly, because only some 10% of the worms collected were mature. At maturity the development of the definitive heteronereid characters takes place while the worms are still within the shells of the host crabs. Then, probably in the month beginning in the middle of May, these brilliantly coloured worms come out of their shells to swarm in a normal nereid manner, perhaps just off the bottom. It is not known whether this is periodic or not, but some synchronization mechanism would seem necessary. The actual spawning and fertilization mechanism is again the same as in other epitokous species. Blue, lilac, or turquoise eggs are produced which, when fertilized, have the usual thick gelatinous envelope. The embryonic development is normal and highly motile larvae, with abundant cilia, are formed. These may swim around on or near the bottom, finally settling on to it when six setigers have been developed. The behaviour of the young worms in the laboratory strongly suggests that, some 4–6 weeks after fertilization, they will be living and feeding on the bottom within small tubes they have constructed. Their precise habitat, if they have one, is unknown. Young *N. fucata* have been recorded from Rame Mud, after sieving through stramin netting (Mare, 1942), but attempts to repeat this have been unsuccessful. However, McIntosh (1910) records them from *Filograna* and from stones and shells in deep water, so that they appear fairly widely distributed.

The reproduction and larval development is therefore very similar to the other members of the family. In particular, the feeding and tube-building habit is quite normal. Up to this stage, therefore, no special adaptation to commensalism can be seen. The young probably settle on the bottom first and enter hermit crab shells later. Davenport (1955) has discussed this problem of settlement in commensal polychaetes and has suggested that the young stages may first settle on the same substrate as their hosts. This would increase their chances of finding a host, and the development of a specific host reaction would then quickly lead to its adoption. *N. fucata* therefore fits the first part of this hypothesis very well, although it is not known if there is a preference for a particular substrate. This can only be determined by further experiments, but it seems possible that a high degree of selection may not be necessary for such motile and widespread hosts. The next problem is to determine the specific reaction which ensures the adoption of the host. Preliminary experiments suggest that in this respect *N. fucata* also fits Davenport's hypothesis.

It is a pleasure to record my gratitude not only to the Director and all his staff at the Plymouth Laboratory for their generous help during the course of this work, but also to the Council of the British Association for allowing me the use of their table. My thanks are due in particular to Mr P. G. Corbin

for first drawing my attention to the mature heteronereids, to Dr M. W. Parke for supplying the *Isochrysis* and *Phaeodactylum* cultures, to Mr A. C. G. Best for the use of his polyvinyl pyrrolidine mountant, and to Mr G. R. Forster for so willingly taking me over the grounds at night in his yacht 'Sunset'.

SUMMARY

The reproduction and larval development of *Nereis fucata* (Savigny) is described up to the time of settlement (6- to 7-setigers).

Mature heteronereids are found at Plymouth from March to June, in a 1:1 sex ratio. In an aquarium the spawning mechanism is similar to other species.

The embryonic development is typical of an epitokous species with pelagic development. The eggs, whose mean diameter was 225 μ, are lilac, blue, or turquoise in colour. Cleavage and gastrulation are normal. Rotation begins at 36 h and monotrochophores are formed after 3 days. Hatching probably occurs 4–6 days after fertilization when a highly motile trochophore has developed.

The setae of the first three segments appear after about 5 days. The differentiation of the parapodia, and the larval succession of setae, are essentially the same as in other species.

Settlement, the cephalization of the first parapodium, the loss of the cilia and the long larval setae, all take place between 6- and 7-setigers. After this stage the larvae construct small tubes and feed on the bottom.

The development of the dorsal posterior tentacular cirrus from the first larval parapodium is described and figured. This cirrus is formed by the elongation of the lobe lying between the noto- and neuropodial setal bundles. It is not, therefore, strictly derived from the dorsal cirrus of the first parapodium.

The reproduction and development is discussed and shown to be very similar to that of the other members of the family. No special commensal adaptation was observed during the larval period. It is therefore concluded that this occurs after settlement.

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