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FAUNISTIC AND BIOLOGICAL NOTES ON MARINE INVERTEBRATES III.

The Reproduction and Larval Development of some Polychaetes from the Isefjord, with some Faunistic Notes.

BY

ERIK RASMUSSEN

(Report from the Isefjord Laboratory No. 3)

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København 1956
i kommission hos Ejnar Munksgaard

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CONTENTS

Synopsis.

The reproduction and larval development of ten polychaete annelids from the Isefjord (Zealand, Denmark) are described.

The species are: *Harmothoë imbricata* (L.), *Harmothoë impar* Johnston, *Eteone longa* (Fabr.), *Magalia perarmata* Marion and Bobretzky, *Microphthalmus sczelkowi* Mecznikow, *Nereis pelagica* L., *Scolecolepis fuliginosa* (Claparède), *Heteromastus filiformis* (Claparède)?, *Capitella capitata* (Fabr.), and *Metatrochophora* I of an unidentifiable species.

The material used was collected during a number of years. The collecting methods employed were simple, consisting of both dredgings and plankton samples; quantitative vertical hauls were only taken in 1950 and 1951. Rearing in the laboratory of the larval stages in question was only occasionally carried out.

The hydrography of the area is mentioned and the importance of the temperature to spawning is shown.

The polychaete fauna of the Isefjord is briefly discussed, and the possible relation of the southern faunal element to climatic changes is touched on.

Printed in Denmark.
Bianco Lunos Bogtrykkeri A-S.

Introduction.

Like the preceding two reports—from 1944 and 1951—the present paper, dealing with the breeding habits of some polychaete annelids, is to be considered a continuation of the series of marine biological investigations started by me in the Isefjord from a laboratory on the small creek of Vellerup Vig (Zealand, Denmark).

The knowledge of the reproduction of the bottom animals with the settling of their larvae and the growth of the young individuals is of fundamental importance to the study of the production of bottom invertebrates and thus to the ecology of the sea area in question.

The results now published were obtained from the early beginning of the research work and were gathered throughout the years often together with other work. However, during the last few years the work has been intensified, especially after the acquisition in 1950 of the present house, which now yields good conditions for marine biological investigations. To a rather great extent this is due to the "Statens almindelige Videnskabsfond", which in 1953 has contributed to the installation of electricity with a grant. In this connection it may seem natural to point out that the laboratory is a private institution, established and run by the author since 1942.

My thanks are due to Prof. MATH. THOMSEN, Ph. D., and Lektor GUNNAR THORSON, Ph. D., for their valuable advice during the preparation of the manuscript.

All the figures of animals in the paper have been drawn from living specimens by the author with the camera lucida of Abbe.

The investigations were carried out with support from the "Japetus Steenstrups Legat".

Methods and Technique.

As already stated in the introduction, the material used in this paper was collected during a number of years. The methods employed have always been very simple, especially during the first years, and the direct observation in nature has played a dominant rôle as far as conditions would allow. However, it has always been tried to follow the whole life cycle of the single species, from egg to the full-finished bottom stage. So not only numerous plankton samples have been taken, but the results obtained by this technique have as far as possible been supplemented with collections of adult individuals by dredgings, digging up followed by sifting, and by the use of other collecting apparatus.

Quantitative vertical plankton samples were collected for the first time in 1950 and I am indebted to Cand. mag. Preben Metz for submitting to me the results of his studies of these samples, which have supplemented my own observations in a very valuable manner. The samples were collected regularly, every fortnight from November 1950 to June 1951 in Vellerup Vig. They were taken with a conical net with a diameter at the mouth of 30 cm, about 60 cm deep and ending in a small plankton pail. The gauze of the net was No. 12, i. e. 12 meshes per mm. Each sample included two hauls from the bottom to the surface with an average depth of about eight metres. After the transferring of the samples to glass vessels in the laboratory the total contents in both hauls of bottom invertebrate larvae were counted and as far as possibly roughly determined as to species or genus. The purpose of this work was to obtain material for a later calculation of the production of the most important bottom invertebrate groups similar to the results published in 1946 by Thorson from the Sound (Øresund). Unfortunately the investigations had to stop in July 1951, and this important work is still unfinished, but forms a prominent part of the future programme of the laboratory.

Up to the renewal of the laboratory building in 1950 most of the study on the larval development of the single species could only be carried through by continuous procuring of fresh material since the aquarium conditions were too poor and incomplete.

However, during the last year it was possible to rear some of the larval forms here described, especially *Nereis pelagica*, cf. p. 58.

Hydrography.

As to hydrographical conditions the Isefjord is exceptional in several respects.

The salinity of the water has been discussed by me in a previous paper (Rasmussen, 1951). The average annual salinity seems to be rather constant about 20 $^0/_{00}$, and in the innermost areas it is a little higher than at the opening of the fjord into the open sea.

To a very high degree these conditions are due to the small supply of freshwater to the Isefjord from rivers in connexion with a rather high evaporation from the surface of the area. For further information see E. Steemann Nielsen (1951).

From an ecological point of view the rather stable salinity can only be of very slight or no importance to the breeding habits of the polychaete species described here.

Conditions of the temperature are quite different. As pointed out in several cases in the following descriptions of the single species, the temperature is the direct stimulus to the start of the spawning by the mature individuals. In order to clarify this correlation, I have tried to compare the measurements of the annual temperature with the spawning periods of practically all the polychaete species dealt with in this paper; cf. fig. 1 (p. 6). I am indebted to Mrs. E. Hagelund, who in 1949 to 1950 rendered valuable assistance by taking daily measurements of the temperature of the surface water in Vellerup Vig. In fig. 1 the temperature (degrees centigrade) is calculated on the basis of one diurnal measurement, but in the graph, the average of only every third of each month is marked. Even if the temperature graph published represents one year's measurements only, while the spawning periods are based on several years' observations, I have nevertheless ventured to compare these results, since in broad outlines this one-year temperature graph represents an average picture of the temperature conditions of the area, apart from the very severe winters, which of course will have a dominating and often very fatal influence on the fauna of lower bottom animals.

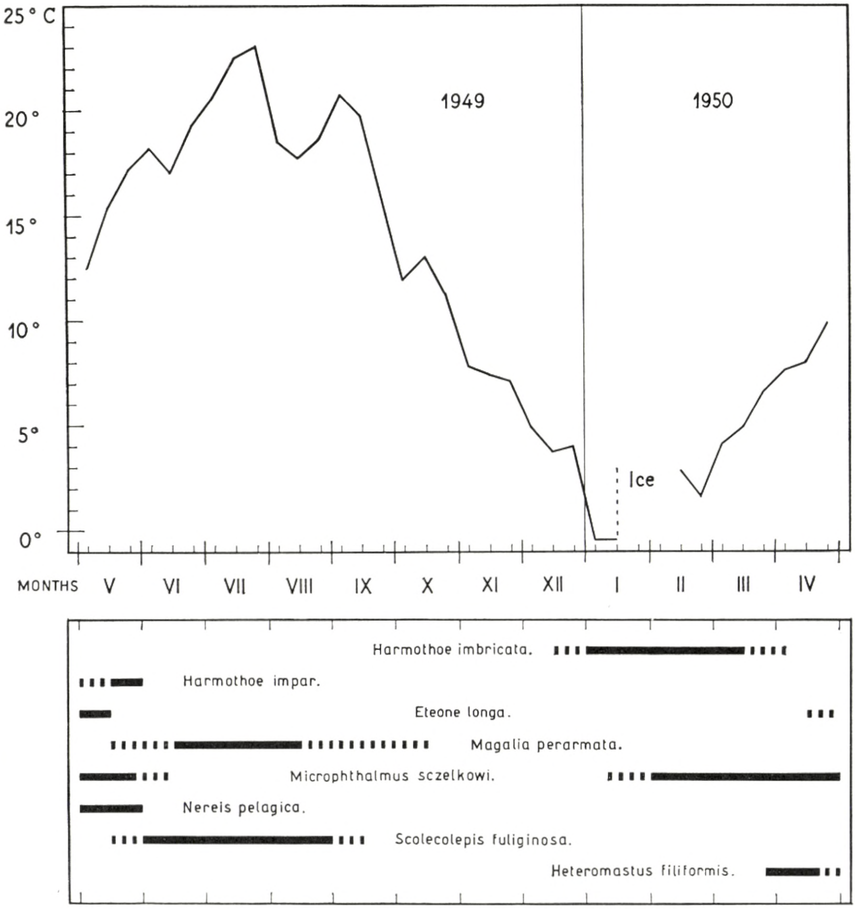


Fig. 1. Spawning periods in the Isefjord of most of the polychaete species dealt with in this paper (continuous lines = main spawning, dotted lines = beginning or decreasing spawning activity) in relation to the water temperature.

The recording of the spawning periods is based on results gained during several years, whereas the temperature curve, calculated from daily samples, represents one year's measurements only, from 1949 to 1950, cf. the text on p. 5.

As to the spawning activity the species can be divided into three groups; those with their main spawning in winter, comprising *H. imbricata* and *Microphthalmus sczelkowi*. Another group comprising the species which breed in the spring, *H. impar*, *Eteone longa*, *Nereis pelagica*, and *Heteromastus filiformis*; as appears from the figure *M. sczelkowi* may also be included in this group as its spawning period extends to June. The third group comprises the summer-spawning species, *Magalia perarmata* and *Scolecolepis fuliginosa*, representing the heat-loving faunal element of the Isefjord polychaete fauna. Both are true southern (Mediterranean) species hitherto unrecorded in the Danish fauna. Cf. the text on p. 48.

In this connection it is well worth remembering the character of the Isefjord area, which is small, not only in extension but also in the depths, which again means that the temperature of the water masses is highly influenced by the air temperature.

The species of the fam. *Aphroditidae* found in Vellerup Vig.

Since the beginning in 1942 of my research work in the Isefjord, regular collecting of plankton samples has played a prominent part in the work of the laboratory. Among the quantitatively important groups, the pelagic larvae of scale worm species have always played a dominating rôle in that part of the zooplankton which consists of bottom invertebrate larvae.

However, not until in the last few years the species of the family have been studied in so much detail by me that the breeding habits of two of the most common species have now been cleared up. The species are the two closely related ones *Harmothoë imbricata* (L.) and *Harmothoë impar* Johnston, both of which are very common in Vellerup Vig.

In all, four scale worm species have so far been reported from the innermost part of the Isefjord; the other two are *Lepidonotus squamatus* (L.) and *Pholoë minuta* Fabricius. All species are extremely common, especially *Pholoë minuta*, which is found, often in great numbers, from the shallow sandy areas along the shore to the deepest parts where the bottom consists of mud (maximum depth about 10 metres). Also hard stony bottom is inhabited by this small delicate sigalionid worm, which, like *L. squamatus*, does not enter into the present investigations.

The three polynoid species of the area are more restricted in their occurrence. They are true epifauna-animals, which live among the huge masses of *Mytilus edulis* often found in the littoral and sublittoral zone of Vellerup Vig. The mild winter climate during the last few years, practically without any ice layer in the low water, has increased the *Mytilus* banks so that even pure sand flats are now covered by a thick layer of mussels. Again, this means that the polynoid species have had optimal conditions of life and have offered the investigator an excellent material for study.

1. *Harmothoë imbricata* (L.).

A survey of the literature reveals the rather surprising fact that the reproduction and larval development of the common scale worm *Harmothoë imbricata* (L.), which is one of the commonest polychaetes in the northern hemisphere (cf. E. Wesenberg-Lund, 1953) are by no means fully known.

In his small and remarkable paper about the development of annelid worms Sars (1845) as the first author describes and figures the spawning and early larval stages of the species. According to this description *H. imbricata* off the Norwegian coast is spawning in February to March. The opaque eggs—50 μ across—are rosy in colour and, when just spawned, they are found under the elytra of the female. There the early development takes place and about a fortnight after the spawning the young larvae will leave the mother animal as very simple, almost spherical trochophores, which now have a light greyish-green colour.

McIntosh (1900) states the egg size to be from 56 to 78 μ and mentions the first week of March as the period of the swarming of the young trochophores, which were observed to be positively phototactic. His observations as well only deal with the early pelagic stages.

From the bay of Kiel Leschke (1903) mentions the larvae of two polynoid species. One of these taken from January to February in the Trochophora stage might be the larva of *H. imbricata*. Unfortunately no descriptions nor figures accompany his statement. The other, referred by Leschke to *Lepidonotus squamatus*, is probably a *Harmothoë* larva. Its occurrence in the Kiel plankton from June to October makes it unlikely that it could be *H. imbricata*, as claimed by Thorson (1946), nor can it be *H. impar* (see below). The number of chaetigerous segments, eight, of Leschke's old Nectochaeta (Pl. VII, fig. 2) and the warty condition of tentacles, tentacular cirri, and the dorsal cirri of the segments also exclude *H. imbricata* as a possibility.

Izuka (1912) and Sæmundsson (1918) confirm the observation by Sars concerning the presence of brood protection, and the latter found the eggs attached to the back of the female in April-May off Iceland.

The extensive survey by NOLTE (1936) discusses the identity of a large number of *Harmothoë* larvae described by earlier authors; efforts which, however, have not been crowned with success, since the confusion about these incomplete old descriptions is even worse after than before NOLTE's activities.

Larvae of a *Harmothoë* species which presumably belong to *H. imbricata,* are briefly described and pictured by E. SMIDT (1944, p. 253), who as to the determinations of his stages from the harbour of Copenhagen only writes that they are "based on observations at Ven." The occurrence of his larvae in the plankton is limited to "the cold part of the year (Nov., Jan., Feb., March)."

The most detailed account of the larvae of *H. imbricata* is found in THORSON's paper (1946). His descriptions, however, are all based on material from plankton samples; results which have not been verified by observations on the breeding habits of the adults. Thus the larvae from the Sound cannot with complete certainty be determined as *H. imbricata,* even if it seems highly probably that they do belong to this species (cf. THORSON, p. 48). His larval descriptions, exclusively based on observations from the Sound, deal with the metatrochophores I—II and the Nectochaeta. The young bottom stage (THORSON, fig. 18, A, p. 47), the smallest one found, seems to be somewhat defective, since the scales and probably also the tentacles and the tentacular cirri are missing. That the appendages of this stage should be undeveloped, as supposed by the author, seems to me to be unlikely owing to the broken appearance of for instance the basal parts of the lateral tentacles. Furthermore, the hindmost segment with the pygidium is lacking. It is hardly to be believed that THORSON's bottom stage represents the newly settled and metamorphosed bottom animal, since its body length, 1.2 mm, is double the length of the largest free-swimming Nectochaeta (fig. 17, C—D) about 600 μ. According to THORSON (*l. c.* p. 47) "the larvae have their maximum occurrence in spring, summer and autumn, while they are rather rare in the winter, but they may occur in any month throughout the year." This is a very interesting fact, because it is in clear contrast with the literature, which with a few exceptions says that *H. imbricata* propagates in the cold parts of the year. Also the present results show a well-defined winter breeding of the same species in the Isefjord (cf. diagram fig. 2). The explanation of this seasonal difference is maybe to be sought in a different biology of *H. imbricata* in relation to the exceptional hydrographical conditions of the Sound, which has a distinct stratification both as to temperature and salinity. Another possibility might be that the material of *Harmothoë* larvae from the Sound comprises not one species, *H. imbricata,* but several, closely related species, only distinguishable with great difficulty, and having their spawning maxima spread over the year so that this obscure picture will appear.

The more detailed discussion of the single stages from the Sound will be given in the later description.

M. Pettibone (1953) has found egg-carrying females in Puget Sound in June, July, and August, but says that "it does not necessarily exclude the other months as very little collecting was done other than in the summer months." In mature females the eggs were found in the body segments 8—30. The egg-size is stated to be 136 μ; Furthermore, a short description with figures of the early larval development is given.

In 1954 Davenport, in his paper about the early stages of the commensal polynoid *Acholoë astericola* (Delle Chiaje), gives a brief summary of what is known in the literature about the development of polynoids. Newell (1954, p. 333) has observed *H. imbricata* carrying the young beneath the elytra in January.

In the Isefjord *Harmothoë imbricata* seems to be a widespread and in the right type of locality (mussel-banks, cf. above) very common polychaete worm. However, owing to the difficulty in the determination of the species in connection with great variation as to pigmentation and shape of the scales I am only able to give reliable information about its occurrence in the neighbourhood of the laboratory, where adult individuals have been collected in great numbers and determined with certainty to *H. imbricata.*

Very often the species is found in specimens of considerable size, up to more than four cm, and most of the individuals used for the following description were large animals with an average length of about three cm.

No distinct difference in the size or in other external morphological characters was found between the males and females.

Spawning season. The first considerable number of spawning

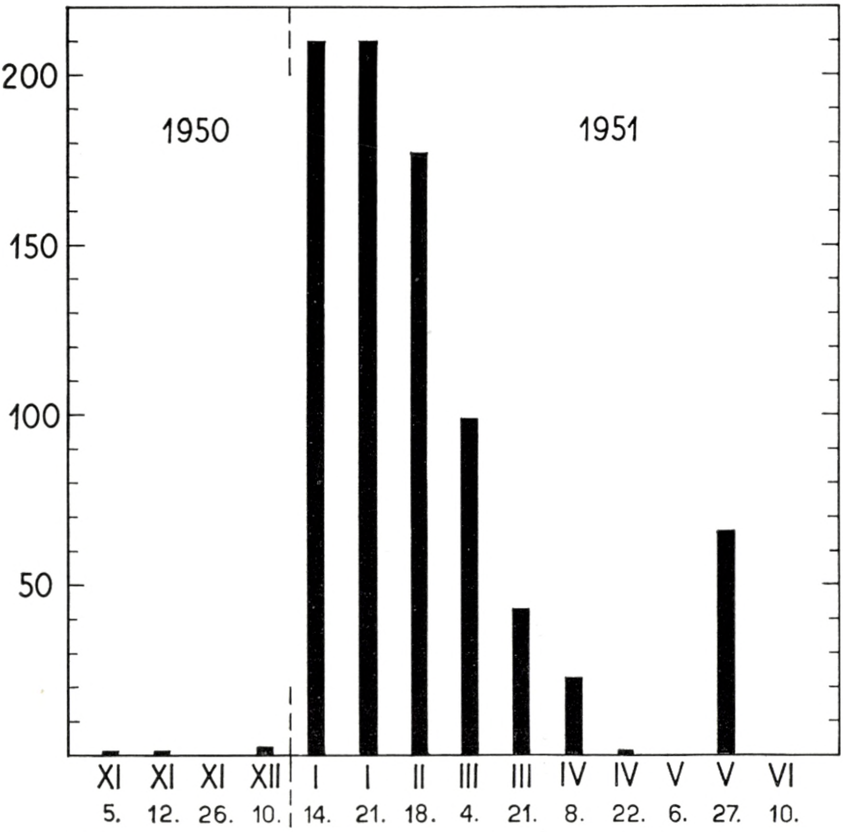


Fig. 2. The occurrence of polynoid larvae in the plankton in the Isefjord, Vellerup Vig, from November 1950 to June 1951.
The results are based on quantitative plankton samples from this period, each column showing the total number of larvae from two vertical hauls from the bottom to the surface, at a depth of about eight metres. The abscissa gives the dates of collection. The large winter maximum is exclusively made up by the larvae of *Harmothoë imbricata* (L.), while the column in May represents the larval maximum of *Harmothoë impar* Johnston. Cf. the text p. 13 and 27.

females were recorded in the second half of December, an observation which I have made in 1950, 1953, and 1954. The main spawning happens to come very soon after the first appearance of females with eggs beneath their scales, and in January, when the water temperature in Vellerup Vig has reached the lowest level of the year, *the spawning culminates* (cf. fig. 2). In February the intensity decreases and early in April the last few pelagic larvae are found in the plankton; cf. fig. 1, which shows the spawning period in relation to the temperature. On January the 5th (1954) about 50 $^0/_0$ of the females collected had eggs or young trochophores under their scales, while the rest contained large eggs — 130 to 150 μ — ready for spawning. Only a very few were spent. On April the 5th (1953) about 50 $^0/_0$ of both males and females were quite empty and only a few per cent. contained ripe sexual products.

All eggs just spawned measured 150 μ across and were whitish in colour. According to M. SARS (1845), the new-laid egg is rosy, and SÆMUNDSSON has found the egg to be pink. A distinct egg membrane can be seen round the spherical yolk. This comparatively large egg-diameter is rather noteworthy as compared with the diameters given for the same species by SARS (50 μ) and McINTOSH (1900) (from 56 to 76 μ). If the determination to species by these two authors is correct, this means that *H. imbricata* has *a most varying egg size.* Unfortunately no descriptions of the larval development accompany the egg-size statements of SARS and McINTOSH so that the possible deviations which may be present, cannot be compared with the present results.

When lying under the elytra of the female the eggs are placed in lumps on the dorsal part of each parapodium. Generally these lumps will fuse so that one coherent mass of white eggs can be found. The eggs are protected and hold together by a clear and sticky, very elastic mucus, especially developed as two broad longitudinal walls on the sides of the egg mass. M. SARS has also observed this mucus (1845, see p. 13). As a rule any segment from the 8th up to the 34th chaetigerous segment is carrying eggs.

A female, 3.3 cm in length, with about 150 eggs on each of the egg-carrying segments had in all about 3750 eggs. Another female, only 3.0 cm long, was estimated to have a total of about 5000 eggs beneath its scales.

When the females carry new-laid eggs and especially when having young trochophores on their backs, they have a tendency to leave the shelter between the mussels and seek the opener places with turbulent water. This phenomenon was observed several times by me in 1953—1954 during the main spawning period.

The larval development. As already noticed by several authors, SARS, McINTOSH and others, *H. imbricata* has a sort of brood protection, which ends when the quite young Trochophora is ready to hatch. The same condition was found in the Isefjord material, but the duration of the protected larval period was not recorded. According to Sars two weeks elapse from the hatching of the eggs to the beginning of the free-swimming stage.

The young Trochophora has—just as the egg—a whitish hue. There are two distinct dark-brown eye-spots with lenses. Round the almost spherical larval body there is a girdle of cilia together with an apical tuft.

The pelagic stages. During the period, from November 1950 to June 1951, when regular quantitative samples were taken in Vellerup Vig (compare p. 4), no distinction in species was made between the scale worm larvae, and in our lists these were only indicated as "polynoid larvae". When taking up the closer examination in 1953 of the breeding biology of the two *Harmothoë* species here described, I took test samples in the same months as in 1950—51 in order to determine the number of species of the two maxima found (fig. 2). As expected, and in good accordance with the results published above, the large maximum of larvae, beginning in January, decreasing during the early spring, and ceasing in April, exclusively belonged to one species only, which through transitional stages to the young, newly settled bottom individuals could rather easily be determined as belonging to *H. imbricata*. The short and rather small maximum in May, however, was only composed of larvae which without doubt belonged to *Harmothoë impar*. The columns (fig. 2, see text below) show the total number of larvae comprising all stages of development in two vertical hauls from bottom to surface; the average height of the water column was eight metres.

It appears from the figure that the number of *H. imbricata* larvae of one single haul in Vellerup Vig is remarkably high. Thus in January 1951, when the largest number was found, more than 210 specimens of all stages were collected. Compared with the records from the Sound (cf. Thorson, p. 47), off Elsinore, the largest number being 45 in one main series, i. e. 10 vertical hauls 18 m high = the number of larvae in a water column over $^1/_2$ sq.m of bottom (Thorson, p. 369), the density is much larger. If the number from the Isefjord is converted to the Sound scale, *thus maximally almost* 1000 *H. imbricata larvae* *against* 45 *from the Sound are present in a water column above* $^1/_2$ *sq. m* of bottom; that is on an average about 250 individuals per one cubic metre water or one larva in about four litres of water!

From January to March (1951) the larvae of *H. imbricata* play a dominating part in the plankton of Vellerup Vig. Thus in January they constitued *about* 80 $^0/_0$ *of the total number of bottom animal larvae.*

The older Trochophora (fig. 3) has a size varying between 250—400 μ. The individual pictured was about 370 μ long and is a transitional stage between the Trochophora and the Metatrochophora, since a beginning segmentation is visible. Its shape is like a double cone as usually present in the annelid trochophores.

The segmentation of the larval body has just begun, and seven segments in all can be distinguished. Almost every segment has both the notopodial (no.) and the neuropodial section (neu.), the latter being the most advanced by far. A small refractive dot in each setigerous sac represents the first developing larval seta (se.). On the ventral side of the body, in the furrows between the fine superficial segmentation a rather clear, bluish green pigmentation is found (b. g. pi.), being most evident posteriorly. Pigmentation is also present round the mouth; thus the upper lip has a conspicuous reddish brown colour (r. b. pi.). Apart from these two groups of pigment cells no other pigment is present. The whole larva has a clear, slightly yellowish colour. On both sides of the prototroch girdle, this yellowish colour is more concentrated, almost lemon-coloured (c. l.), and apparently this thickened cell-layer contains a circular girdle of muscular tissue. At any rate this region of the larval body is very contractile and often during swimming, the Trochophora will be seen changing its shape to a more elongate one.

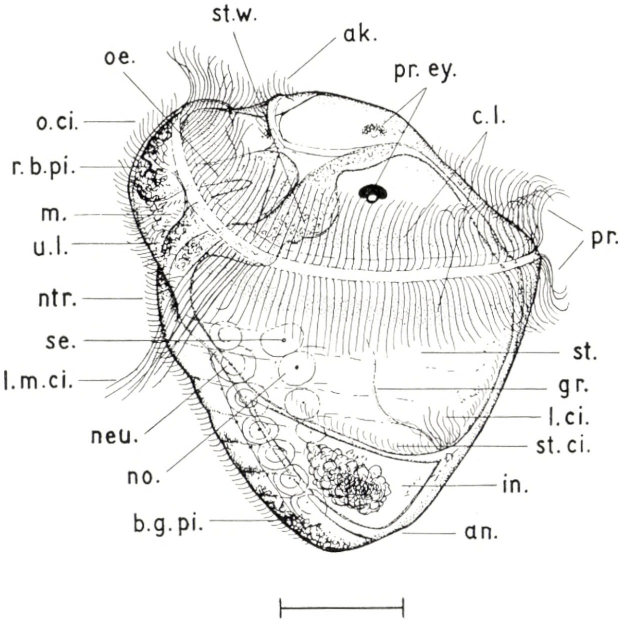
The ciliation on the body surface mainly concentrates on a prototroch (pr.) round the larva, but a small anterior row of cilia, the akrotroch (ak.) is found (see a. o. Gravely, 1909, p. 11, pl. I and Nolte, 1936). There is not yet any apical tuft nor telotroch, the latter being totally absent during the whole larval development. The prototroch consists of two rows of long cilia, the anterior of which is forming one unbroken ring passing above the mouth (m.). The posterior row stops just before the upper lip, ending on each side in one group of exceptionally long cilia, which are motionless and always held straight (l. m. ci.). Round the mouth aperture there is a dense ciliation of fine short cilia (o. ci.). The narrow longitudinal neurotroch is well-developed (ntr.).

In front of the prototroch one pair of black (in transmitted light) eyes with distinct lenses is present. The eyes, being of an oblong shape, are the first developed of the three later pairs. These primary eyes (pr. ey.) are later totally reduced when the metamorphosis occurs and only two pairs are left.

The mouth opens below a very prominent upper-lip (u. l.), and leads to the oesophagus (oe.), a rather thick-walled duct, which at the stage pictured does not yet seem to be in open connection with the stomach cavity. Close behind the oesophagus there is a double thickening, which seems to represent part of the stomach wall (st. w.). However, this tissue may be identical with the region which Gravely on his polynoid Trochophora from Port Erin (see Gravely, 1909, p. 11) characterizes as a "rudiment of the supra-oesophageal ganglion". The same region is correspondingly developed in the polynoid Trochophora pictured by Leschke (1903, p. 129 as *Lepidonotus squamatus*, Pl. VI, fig. 14), but no importance is attached to this detail by the author.

As to volume the larval stomach (st.) is far the most dominating section of the alimentary system. It is clear and quite empty. The colour is faintly greenish against the yellowish body colour. The stomach ciliation consists of fine short cilia (st. ci.), apart from one small part of the hindmost wall, which has a bundle of long cilia (l. ci.). There is a fine groove (gr.) in the stomach wall. The intestine (in.) is very small and leads directly to the dorsally placed anus, which has no opening so far. A rather interesting thing is the contents of the intestine. Owing to the above-mentioned lacking passage through the alimentary system this indefinable mass cannot be food remnants, true excrements. I have examined a number of larvae of this species from the plankton which were at the same stage of development, and they all had the same dark-brown body in the intestine and always of about the same size and appearance.

The Trochophora of *Harmothoë imbricata* is not described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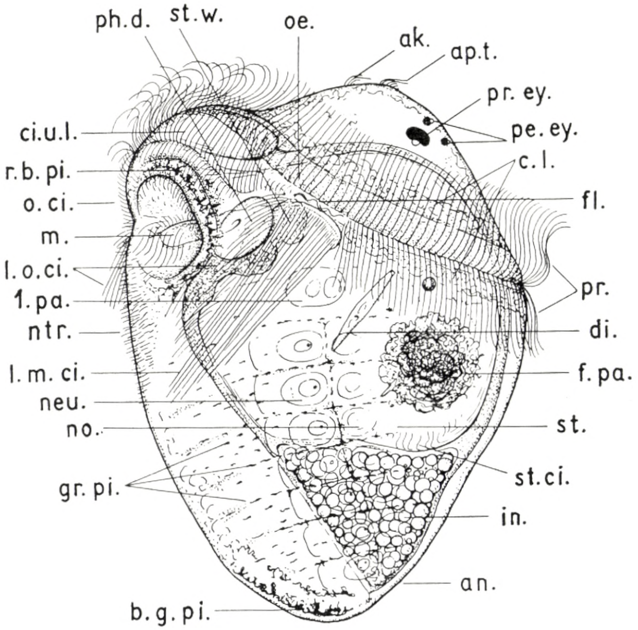
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neu.
no.
st.
st.ci.
gr.pi.
in.
an.
b.g.pi.

Fig. 4.

by THORSON in his larval descriptions from the Sound; his youngest stage being the early Metatrochophora.

Metatrochophora I (fig. 4). The full length of this stage is varying between 430 and 450 μ, or about the same as THORSON (1946) states for the same stage from the Sound.

The shape is now more elongate and roundish, as the region posterior to the prototroch is stretched and the segmentation more advanced. Eight setigerous segments in all can now be distinguished. The first one (1. pa.) is more distinct from the others and represents the first modified setiger of the adult individual wearing among others the tentacular cirri. The noto- and neuropodial parts (no. and neu.), the latter of which is still the best developed, are more clearly separated. The budding parapodia and setigerous sacs are lying closely beneath the surface and their outlines are marked by small green pigment granules (gr. pi.).

Besides, chromatophores are found as a border of reddish-brown pigmentation round the mouth opening (r. b. pi.). On the ventral side of the hind part there is a bluish-green pigmentation (b. g. pi.) just as at the preceding larval stage. The lemon-

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Fig. 3. *Harmothoë imbricata* (L.).

Older Trochophora with developing segmentation as seen from its left side and a little from above, Vellerup Vig, Isefjord, 17.1.54.

ak., akrotroch; an., developing anus; b. g. pi., bluish green pigment; c. l., lemon-coloured, thickened cell-layer on both sides of the prototroch; gr., stomach groove; in., intestine; l. ci., small bundle of longer cilia in the stomach wall; l. m. ci., bundle of long motionless cilia on each side of the mouth; m., mouth; neu., neuropodial section of developing parapodia; no., notopodial section of developing parapodia; ntr., ventral ciliary groove, neurotroch; oe., oesophagus; o. ci., oral ciliation; pr., prototroch; pr. ey., primary eyes with lenses; r. b. pi., reddish brown pigment; se., notopodial setae; st., stomach; st. ci., stomach ciliation; st. w., a bilobed thickening of the stomach wall?; u. l., upper-lip.

Fig. 4. *Harmothoë imbricata* (L.).

Metatrochophora I in left-side view, seen a little from the ventral side; the Isefjord, Vellerup Vig, 31.1.54.

an., anus placed dorsally; ak., akrotroch; ap. t., rudimentary apical tuft?; b. g. pi., bluish green pigmentation; ci. u. l., border of cilia on the upper lip; c. l., lemon-coloured, thickened cell-layer on both sides of the prototroch; di., a diatom in the stomach; fl., larval nephridium with flagella; f. pa., food particles?; gr. pi., small, green pigment granules marking the furrows in the segmentation; in., intestine; l. o. ci., fringe of long oral cilia on each side of the mouth; l. m. ci., bundle of long, motionless cilia; m., mouth; neu., neuropodial section of the parapodia; no., notopodial section of the parapodia; ntr., ventral ciliary groove, neurotroch, shortened and reduced in comparison with the Trochophora stage; o. ci., oral ciliation; oe., the oesophagus; 1. pa., first pair of parapodia; pe. ey., permanent eyes in development (lenses); ph. d., left pharyngeal diverticle; pr., prototroch; pr. ey., left primary eye; r. b. pi., reddish brown pigment round the mouth aperture; st., stomach; st. ci., stomach ciliation; st. w., thickened stomach wall.

coloured cell-layer on each side of the prototroch girdle (c. l.) is even more conspicuous than before and is more granular.

The ciliation is now at its highest and rather complicated. The prototroch is exactly as before: two rows of long vibrating cilia, the anterior of which passes before the mouth, forming one unbroken ring. The other ends on each side before the mouth in the long, motionless cilia (l. m. ci.). Furthermore a border of long cilia is developed on the upper lip just beneath the prototroch (ci. u. l.). The dense layer of fine short oral cilia is still found to be continued in the mouth and oesophageal ciliation. On both sides of the mouth before the long motionless cilia a fringe, a "whisker", of long vibratile cilia has been formed (l. o. ci.). The neurotroch on the ventral body surface is much reduced, being now only a patch or "bib" of fine cilia just beneath the mouth opening (ntr.). Besides the akrotroch (ak.) also a small and short-ciliated apical tuft (ap. t.) is formed.

The eyes are now present in their maximum number, three pairs. However, the two pairs most dorsally placed, are not full-sized even if distinct lenses are visible. These make the permanent eyes of the adult animal (pe. ey.), the larger pair being the primary eyes, which later during metamorphosis will disappear (pr. ey.).

On each side within the mouth opening (m.) there are two thick-walled pharyngeal diverticles (ph. d.), which are rudiments of the later well-developed muscular pharynx. The oesophagus (oe.) is now connected with the stomach cavity, which often may contain different sorts of food particles (st.). Thus the larva pictured has among other things the siliceous skeleton of a diatom in its stomach (di.). The intestine still makes a very small part of the alimentary system (in.), but contains a dense mass of rather large oil globules. The anus (an.) has free connection with the surrounding water.

The previously mentioned thickening of the stomach wall (st. w.) or possibly the supra-oesophageal ganglion is more distinctly bilobed and has a position close to the pharyngeal diverticles.

During the closer examination of the living larval stages under the microscope a very interesting detail was found on Metatrochophora I. Close to the base of the bundle of long, motionless cilia (l. m. ci.) and immediately beneath the anterior row of cilia of the prototroch a fine bundle of undulating flagella was observed (fl. in fig. 4). In spite of a very thorough search for more details only these flagella lying in a fine membranous tube could be seen. The flagella were fixed ventrally and the undulating movements ran against the dorsal part of the body. Without doubt the tissue surrounding this organ is so hyaline in the living larva that only a fixation with a following staining of the region will show the true structure of this larval organ. However, it is a reasonable supposition to regard the flagella as a larval protonephridium. This idea is highly supported by observations on other annelid worms, e. g. the well-known results of WOLTERECK (1902) on the *Polygordius* Trochophora, which has a protonephridium of exactly the same structure.

The Metatrochophora I of THORSON (1946, pp. 46—47, fig. 17 A) differs in several details from the description just given. Thus the ciliation is limited to the prototroch, which only has one row of uniform and rather short cilia. Also the pigmentation is different. The whole larva has "a purplish tint, which seems to be characteristic of eggs as well as of larvae of all stages of this species." Anteriorly to the prototroch above the mouth, spots of black pigment are present. The bluish-green pigment of the segments is totally absent.

The next stage (fig. 5) cannot be considered the true Nectochaeta, since the primary ciliation persists and together with the now well-defined parapodia with setae constitutes the swimming apparatus. Thus it is more like Metatrochophora II. The Nectochaeta, which I never found, seems to be of very short duration and the metamorphosis very soon follows.

The total length of Metatrochophora II is about 520 μ. The head part of the body before the prototroch is still Trochophora-like while the rest of the larva is developed as a young scale worm. There are seven chaetigerous segments with bundles of long setae, the ventral ones. The setae of the first setiger, which can be ascertained by the dorsal tentacular cirri (d. t. c.), are not yet observable, and the dorsal setae of the following segments are only very poorly developed (d. se.). Close ventrally to the dorsal tentacular cirri, which are always the first to appear, the palps (pl.) are developing. If the segment with the tentacular cirri is considered the first chaetigerous segment, dorsal cirri (d. c.) are present on the following segments: nos. 3, 6, and 8, the latter being only small buds. The chaetigerous segments are not yet biramous, but the dorsal and ventral bundles of setae are separated. Two anal cirri (a. c.) end the body. All cirri are of the same type, a simple rounded-oblong appendage. There are four pairs of plain scales, elytra (el.), with almost smooth surfaces. They are attached to the chaetigerous segments nos. 2, 4, 5, and 7, or quite as in the adult individuals (cf. Fauvel, 1923, p. 40).

At this larval stage the pigmentation is found to vary very much. The type pictured here has two groups of chromatophores. First, the bluish-green pigment on the posterior ventral side, which also is present as a ring round the pygidium (b. g. pi.); this group was seen in all larvae of this stage examined. Furthermore, distinct brownish pigment cells are visible in the intestinal wall (b. pi.). However, the variations can be seen round the head. Here there can be two almost parallel rings of brownish pigmentation of about the same appearance as sketched by Thorson (1946, p. 47, fig. 17 B—C). The larva pictured represents a type with quite colourless head.

This variation of the pigmentation is also a common detail of Metratrochophora II of *Harmothoë impar* (see text below, fig. 7 and 8).

The prototroch (pr.) is still developed, even if some reduction has taken place. Thus only one row—apparently the anterior one—of long vibrating cilia is present and nearly all the patches of cilia round the mouth have disappeared. This holds good also of the bundles of long, motionless cilia of the younger stages. On the head (p.) the apical ciliation, which at the previous stage was a tuft of cilia, is now formed as a dense cover of fine, short cilia (ap. ci.). The akrotroch (ak.) is still found.

The prostomium has all six eyes fully developed (pr. ey. and pe. ey.) and of equal size, being black in transmitted light. Of the head appendages, besides the palps, only the developing median tentacle can be seen (m. t.). The two lateral tentacles will not appear until later.

As to the alimentary system the pharynx cannot be seen in dorsal view. The larval stomach seems to be quite reduced and instead the intestine (in.) has gained a more adult appearance,

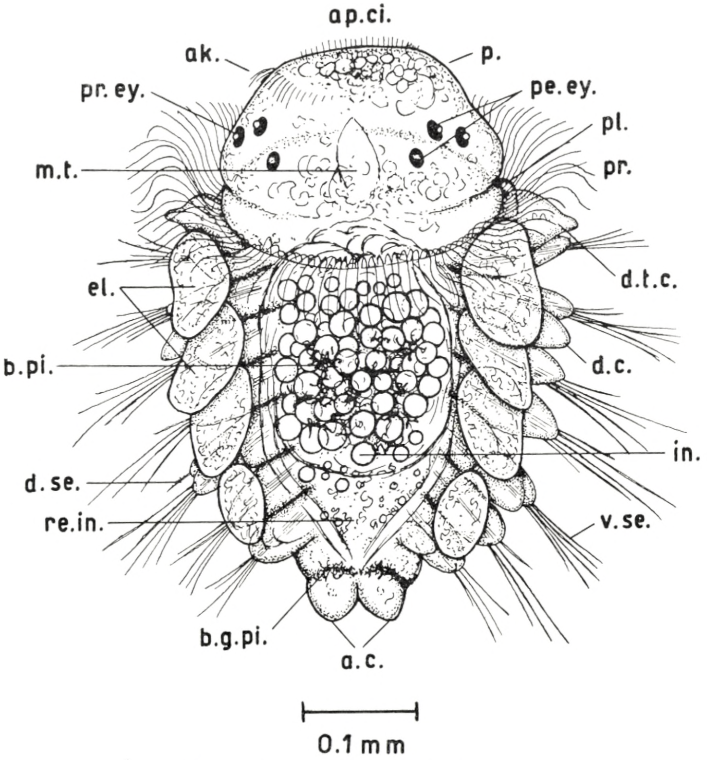

Fig. 5. *Harmothoë imbricata* (L.).
Metatrochophora II, in dorsal view, the Isefjord, Vellerup Vig, 4.4.54.
a. c., anal cirri; ak., rudimentary akrotroch?; ap. ci., apical cilia; b. g. pi., bluish-green pigment; b. pi., brownish pigment in the intestinal wall; d. c., dorsal cirrus of a cirrigerous segment; d. se., dorsal setae; d. t. c., right developing dorsal tentacular cirrus; el., elytra; in., intestine full of oil globules; m. t., developing median tentacle; p., prostomium; pe. ey., permanent eyes; pl., right developing palp; pr., prototroch; pr. ey., left primary eye; re. in., rectal part of the intestine; v. se., bundle of ventral setae.

being divided into a mid-part (in.) in which numerous oil globules are embedded in the wall, and a rectal part (re. in.).

Thorson (1946, p. 47, fig. 17 B) has a drawing and a short description of what he considers the transitional stage between Metatrochophora II, and the Nectochaeta of the same species. Considering that Thorson's transitional type is somewhat more advanced than the Isefjord larva (cf. fig. 5) its size is nearly the same, 480 μ as against 450 μ. Furthermore, the full numbers of chaetigerous segments and of the scales are the same. As to the pigmentation there is some difference, since the bluish-green anal pigment and the intestinal colour is completely absent on the Sound larva. However, on account of the great variation in my material, this detail does not invalidate the probability of both belonging to *H. imbricata*. Also the true Nectochaeta stage from the Sound (fig. 17 C—D) seems to show great resemblance with my larvae.

The newly metamorphosed bottom stage (fig. 6). It seems remarkable that the large pelagic larvae of *Harmothoë imbricata* in the Isefjord are normally found to metamorphose in the water far above the bottom. Thus the samples from the beginning of April 1954 (i. e. near the end of the larval occurrence in the plankton, cf. fig. 2) contained almost exclusively large stages either in metamorphosis or having just metamorphosed.

The quite young bottom stages from the plankton were thoroughly compared with equal-sized individuals of the same species at the same stages, taken in bottom samples also from April 1954, and both were of exactly the same appearance and structure. So the metamorphosed specimens in the plankton represent the young adult bottom individuals.

It also seems beyond doubt that larger individuals (up to about 7—9 mm in length) live not only as true bottom animals, but for some time—before they are full-grown—*may live a semi-pelagic life* swimming briskly in the water at some distance above the bottom.

When all the larval attributes have disappeared and the young animal is ready for adult life, the full body size without

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Fig. 6. *Harmothoë imbricata* (L.).
Young bottom stage, only a few hours after metamorphosis; the Isefjord, Vellerup Vig, 4.4.54.
a. c., anal cirri; b. g. pi., girdle of bluish-green pigment round the pygidium; c. se., strong curved setae of the first setiger (actually the ventral setae of the reduced first parapodia); d. c., dorsal cirrus of a cirrigerous segment (setiger no. 3); d. c. 6, developing dorsal cirrus of the 6. setiger, a cirrigerous segment; d. el. ph., developing elytrophore of the 9. setiger; d. l. v., pulsating dorsal longitudinal vessel with an endothelial wall; d. se., dorsal setae of a parapodium (setiger no. 7); d. t. c. and v. t. c., first pair of cirri, dorsal and ventral tentacular cirrus; el., elytra; el. ph., elytrophore of the 2. setiger; in., intestine with a dense layer of oil globules in the wall; j., jaws; l. t., two lateral tentacles; m. c., muscle cylinder in the palps; m. t., median tentacle; pa., parapodium of the 2. setiger (the parapodia are not yet biramous as in the adult individual); pe. ey., permanent eyes with lenses; ph., muscular pharynx; pl., palps; pp., small blunt papillae with fine sensory hairs on the marginal surfaces of the elytra and on the tentacular cirri; re. in., rectal part of the intestine; v. c., small ventral cirrus of an elytrigerous segment (no. 4); v. se., bundle of ventral setae of a parapodium (setiger no. 7).

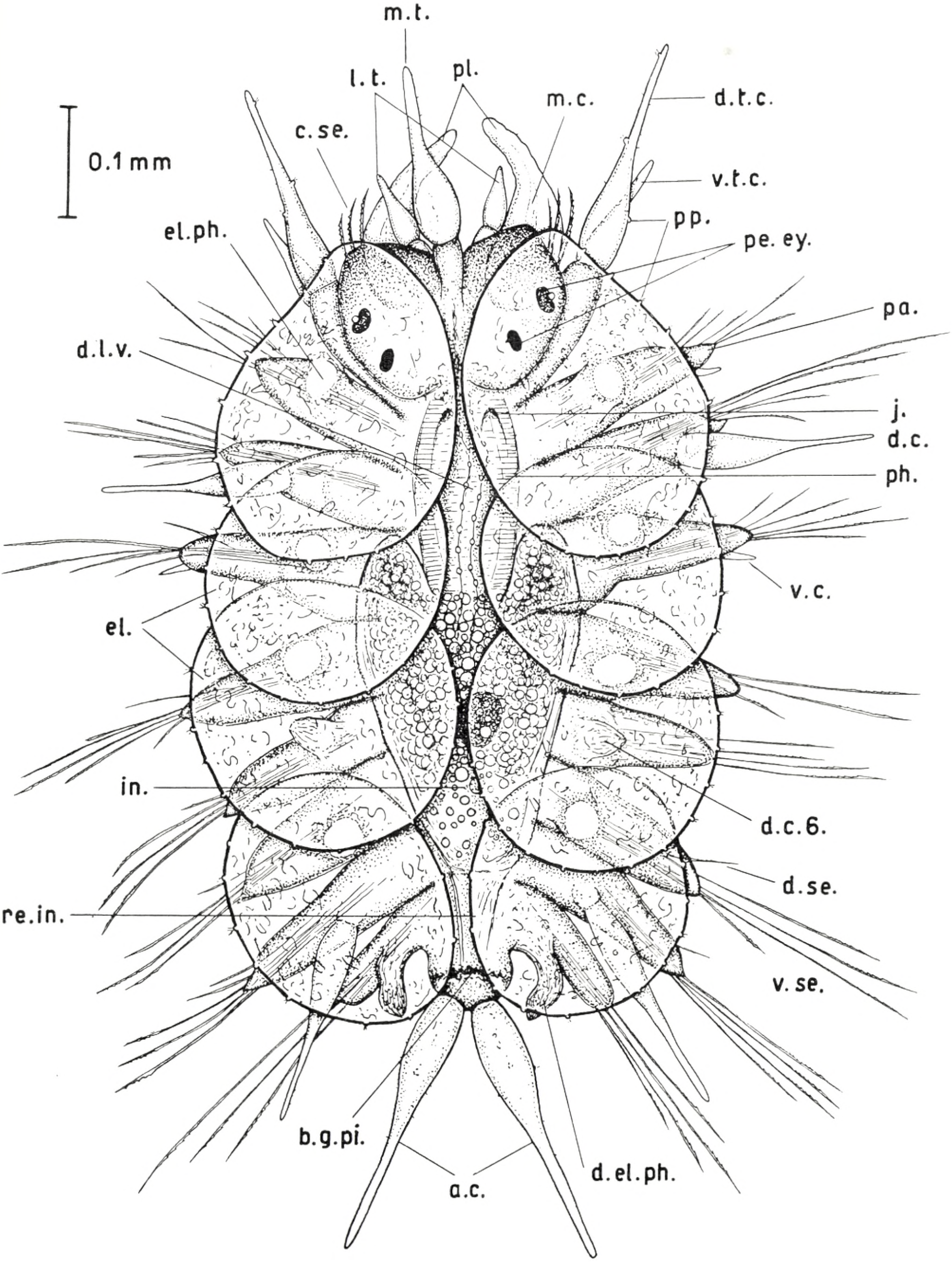
m.t.
l.t.
pl.
m.c.
d.t.c.
0.1 mm
c.se.
v.t.c.
pp.
el.ph.
pe. ey.
pa.
d.l.v.
j.
d.c.
ph.
v.c.
el.
in.
d.c.6.
d.se.
re.in.
v.se.
b.g.pi.
a.c.
d.el.ph.

Fig. 6.

the head and anal appendages is 700 μ. With the tentacles (the median tentacle) and the anal cirri included the length is about 950 μ. A number of metamorphosed specimens were measured, and the above sizes were found almost invariably. It is worth while stressing the importance of this detail, since the size is a decisive distinctive factor between the newly settled bottom stages of *H. imbricata* and *H. impar* (see below).

Including the first modified chaetigerous segment the total number of setigers immediately after the metamorphosis is always nine.

The first segment has two pairs of tentacular cirri, the dorsal ones being the largest (as in the adult animal) and first developed (d. t. c. and v. t. c.). The parapodia of this segment are highly reduced and only the ventral section has a few strong and curved setae (c. se.). Apart from aciculae the other setae are lacking. As to the supply of setae the following eight segments are more typical, having both short dorsal setae (d. se.) (few in number) and long numerous finely dentate ventral setae (v. se.). It is rather remarkable that the two types are not yet divided into two distinct bundles; similarly the parapodia (pa.) are not yet biramous.

All true body segments have small, slender ventral cirri (v. c.). The dorsal cirri (d. c.) are long and slender, about 200 μ in length and only present in two fully developed pairs on the body: on the chaetigerous segments no. 3 and 8. The dorsal cirrus of setiger no. 6 is only visible as a small bud on each side of the segment (d. c. 6). There are two long slender anal cirri (a. c.). All the body appendages are not quite smooth, but have some few scattered, blunt papillae (pp.) with fine sensory hairs.

There are four pairs of elytra (el.) as in the larvae, situated on the segments in the same succession as on the adult, on segment no. 2, 4, 5, and 7. Number 9 is not developed and is only a small bud (d. el. ph.). The single scales, except the first pair, which are tapering in front, have an almost circular shape. Like the body appendages the elytra have a scattered supply of tiny blunt papillae (pp.) with fine hairs. The elytra which are colourless and translucent, have well-defined elytrophores (el. ph.), appearing as clear, round dots about 30 μ across. The first pair has a central position, the following are connected with the anterior part of their elytra (see fig.).

Pigmentation is practically absent on the body. Only the girdle of bluish-green pigment round the pygidium (b. g. pi.) is preserved.

Also the ciliation is highly reduced. All the larval bands of cilia, first of all the prototroch, have disappeared. Instead transverse bands of fine cilia are now seen on the dorsal surfaces of the segments. Since they were only recognizable and their extensions not visible on the living individuals even at rather high magnifications, I have chosen to omit the ciliation completely in my sketch (fig. 6).

The prostomium is now almost quite like the head-lobe of the adult. The larval eyes are lacking and the permanent eyes (pe. ey.) have changed their position towards the adult condition. *This point is very important for the identification of this stage of H. imbricata.* According to several authors the eye position of this species is very characteristic. Thus E. WESENBERG-LUND (1953, p. 20) in her description of *H. impar* writes: "... in *H. imbricata* the anterior pair of eyes is situated partly wholly on the ventral side of the prostomium, whereas in *H. impar* both pairs are visible from the dorsal side." Furthermore the *anterior pair of eyes is situated nearer to the tips of the frontal peaks of the head than is the case with H. impar.* This important adult character is also described in the literature, thus E. BERKELEY and C. BERKELEY (1948, p. 11, fig. 9) give a good figure illustrating this detail.

On the bottom stage from the Isefjord both characters can be seen. The anterior pair of eyes is far more ventrally situated than pair no. 2, and in comparison with the same stage of *H. impar* (fig. 9) the position is closer to the frontal peaks, a condition which on the larger specimens will prove still more pronounced.

The front margin of the head has now attained a very remarkable reddish-brown colour, a feature also present in the adult animal, where the head contrasts against the paler body (N.B. when all the scales have been removed!). All the head appendages are developed; the median tentacle (m. t.) is longer than the two lateral tentacles (l. t.). All three are distinctly separated from their basal part. Ventrally the two large and very mucous palps (pl.), each containing a muscular cylinder (m. c.), are developed.

The alimentary canal also shows its full adult structure. The muscular pharynx (ph.), about 170 μ in length, has two jaws in front (j.). In the following section, the intestine proper (in.), the cells have a dense content of rather large oil-globules. It has a characteristic bilobed shape, as a lobe protrudes on each side of the pharynx. The rectal section (re. in.) is narrow and very transparent.

Also the vascular system is partly visible, especially along the dorsal side of the body, where the pulsating, longitudinal vessel is distinguishable (d. l. v.). The endothelial wall of the vessel can also be seen.

The colour of the young bottom stage is faintly yellowish-green except for the head-lobe (see above).

The early bottom stage will mostly use the parapodia for locomotion, whether it crawls or swims. However, sometimes when observing the young specimens through the binocular microscope, I saw another mode of locomotion. The body with the parapodia was kept completely quiet and instead the dense cover of fine cilia of the body surface produced a slowly advancing movement.

It seems that it takes some time before the younger bottom individuals of *H. imbricata* are morphologically fully developed. On May the 16th, 1954, I collected several bottom specimens which in spite of their sizes, from 7 to 10 mm, were still lacking some of the more important systematic characters. Thus the smallest individuals found had only ten elytra and the largest, up to about one cm, had only 13 scales. Also the number of chaetigerous segments were smaller than normally in the adult; from 21 to 28 as against 37, the full normal number according to FAUVEL (1923, p. 55). However, they all had the typical position of the eyes, as emphasized above.

2. ***Harmothoë impar*** **Johnston.**

The contributions to our knowledge of the reproduction and larval development of *H. impar* are remarkably scanty. MCINTOSH (1900 and 1927) is the only one who renders some details about the breeding time and early development, but nothing is stated about the larval stages. Thus up till now these are undescribed.

As is known from other species of the genus, *H. impar* according to McIntosh has brood protection under the scales. The eggs are held together by a transparent mucus. Females carrying ripe eggs in this manner were recorded in February.

From the Sound, where the species is not very common, Thorson (1946, p. 48) is unable to give further information about the reproduction. However, the larvae of the two species may have been mixed up, in particular because *H. impar* is not so common as *H. imbricata.* From Dutch seas, where the species is common, Korringa (1951, p. 64) states that ". . . *Harmothoë impar* breeds in summer, and that young individuals settle down in June and July, sometimes again in September." In the plankton Korringa has taken "very young individuals" and larvae "in the last ten days of June and July, sometimes again in September." No description and figures of the larval development are given.

In the Isefjord, more especially in Vellerup Vig, *H. impar* is about as common as *H. imbricata,* both inhabiting areas where *Mytilus edulis* is distributed. Since the number of polynoid species has not been cleared up until the last few years, as the taxonomy has not been thoroughly studied, I have no doubt mistaken *H. impar* for young *H. imbricata.* This also means that the biology of the former has not been treated so completely. Thus only the larval stages in the plankton were dealt with, while the spawning and early development of *H. impar* is still unknown.

During the period when quantitative plankton samples were regularly taken, i. e. from November 1950 to June 1951, large larvae, which undoubtedly belong to *H. impar,* were only recorded within a short interval in the spring (see fig. 2).

Regular collecting from January to April 1953 of adult bottom specimens revealed the fact that mature individuals could only be found near the time of the occurrence of the pelagic larvae just mentioned. The size of the mature adults from the Isefjord is smaller than the mature *H. imbricata,* ranging from 1.2 to a maximum of 2.3 cm. Fauvel (1923, p. 60) states almost the same order of magnitude. In January 1953 about 20 % of the examined material of males and females contained sexual products (females with only very small eggs). The rest had no eggs or sperm at all. On April the 6th the same year 50 % of the individuals examined were fully mature, while only about 12 % were quite empty. In the mature females the eggs were always present from the 7th chaetigerous segment on, while the number of egg-containing segments was varying with the total number of segments. Thus a female with 35 setigers and 1.2 cm long had eggs in the segments nos. 7—32; and another comprising only 30 setigers, but of the same length, had eggs from 7. to 28. segment.

Among the animals from April a female, 1.2 cm long, had a 1.5 mm long *Corophium* in its intestine.

The diameter of the largest eggs dissected out of the segments was about 70 μ across. The yolk, which was spherical in shape, was whitish and somewhat transparent.

So it seems beyond doubt that the spawning of *H. impar* in the Isefjord will take place, not in the winter months as in the case of *H. imbricata*, but in the spring. Besides supporting this view, the plankton samples will help to define the spawning time, which is restricted to the month of May.

The youngest pelagic stage collected is Metatrochophora II (fig. 7 and 8).

The full length of this stage, which resembles the corresponding stage of *H. imbricata*, varies between 600 and 650 μ.

The number of chaetigerous segments, i. e. the true body segments (the setae of the first modified setiger are not yet visible), is 6. The bundles of setae consist only of the ventral setae (v. se.), and the parapodia (pa.) are not yet biramous. Most of the body appendages are present. Thus the two dorsal tentacular cirri (d. t. c.) can be seen while the corresponding ventral ones are still lacking. Dorsal cirri (d. c.), only as bluntly conical appendages, are developed on body segments no. 3 and no. 6. The anal cirri (a. c.) are distinctly dorsally placed. Similar to Metatrochophora II of the preceding species there are four circular elytra (el.) situated on conspicuous elytrophores (el. ph.) on segments nos. 2, 4, 5, and 7; this is in good agreement with the adults of this and other species of the genus *Harmothoë*.

Just as the larvae of *H. imbricata* the transverse bands of reddish-brown pigment at the anterior and posterior margins of

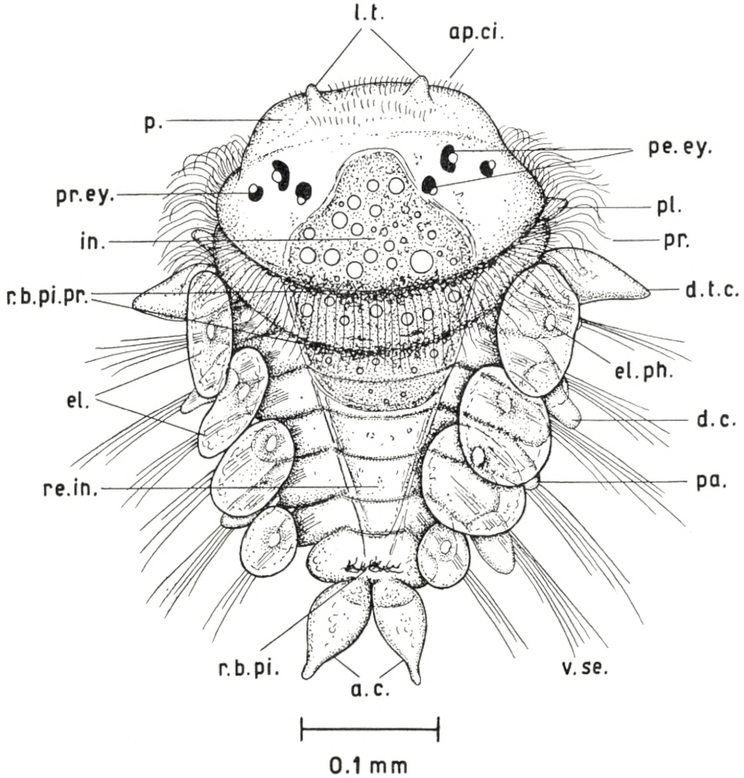

Fig. 7. *Harmothoë impar* Johnston.
Metatrochophora II, in dorsal view; the Isefjord, Vellerup Vig, 10.5.53.
a. c., anal cirri; ap. ci., apical cilia; d. c., dorsal cirrus of a cirrigerous segment (setiger no. 3); d. t. c., right developing dorsal tentacular cirrus, which appears before the ventral one; el., elytra, still without papillae; el. ph., an elytrophore (setiger no. 2); in., intestine with oil globules; l. t., developing lateral tentacles; p., prostomium; pa., parapodium of an elytrigerous segment (setiger no. 5); pe. ey., permanent eyes with lenses; pl., one of the developing palps (the right one); pr., long cilia in the anterior part of the prototroch; pr. ey., left primary eye with distinct lens; r. b. pi., reddish brown pigmentation at the bases of the anal cirri; r. b. pi. pr., two reddish brown pigment bands at the anterior and the posterior margins of the prototroch; re. in., rectal part of the intestine; v. se., bundle of long ventral setae of a parapodium; dorsal setae not yet visible (setiger no. 6).

the prototroch girdle can be fully developed as shown in fig. 7, or they may be totally absent as seen in fig. 8. In one single small plankton sample any type of pigmentation including all transitions may be present on the larvae of *H. impar*. It should be the right place here to emphasize that *the pigmentation as a systematic character in my experience must always be regarded with some* *caution.* Not only the two *Harmothoë* species but several other species described later in this paper show similar variations during their larval stages. Besides the transverse pigment bands chromatophores of the same colour are also present as a small patch on the dorsal side of the pygidium (r. b. pi.). The total colour of the larva is faintly greenish to greenish-yellowish.

The ciliation (see fig. 7) consists of two groups, the apical one and the prototroch. The apical ciliation (ap. ci.) is a dense cover of short fine cilia on the frontal part of the head. While on Metatrochophora I of *H. imbricata* (cf. fig. 4) the apical ciliation is a tuft of cilia, the same stage of *H. impar* has a ring of cilia. The prototroch has two rows of cilia. The most pronounced one, composed of long cilia, is attached to the anterior margin of the prototroch girdle. The smaller and more short-ciliated row posteriorly is disappearing, and at the older stages only one row, the anterior one, is left. These stages correspond to the older Metatrochophora II of *H. imbricata* (fig. 5). On the colourless larva figured (fig. 8), which was drawn on the basis of a previous sketch, only the anterior row is figured.

On the prostomium (p.) all six eyes are visible, the two primary eyes (pr. ey.) and the four permanent eyes (pe. ey.), all with lenses. In front the two lateral tentacles can be seen as two small buds (l. t.). Owing to its transparency the developing median tentacle cannot be seen when the larva is viewed dorsally. Also the palps (pl.) are appearing, in the beginning as lateral buds.

When compared with larvae of *H. imbricata* of the same developmental stage it is interesting to note that the three tentacles of the head are appearing somewhat earlier.

As to the digestive system, only the intestine (in.), finely granulated and opaque and with oil globules in the wall, is observable. The rectal region (re. in.) is clear and transparent.

The newly metamorphosed bottom stage (fig. 9). Like *H. imbricata* the Nectochaeta stage of *H. impar* is of rather short duration. Large metatrochophores of the above type were brought in from the fjord plankton and later in the evening placed in vessels with clean sea-water. Early the next morning most of them were fully metamorphosed bottom stages as figured in fig. 9. There is every reason to believe that the young bottom individuals of *H. impar* behave like the corresponding stages of *H. imbricata*,

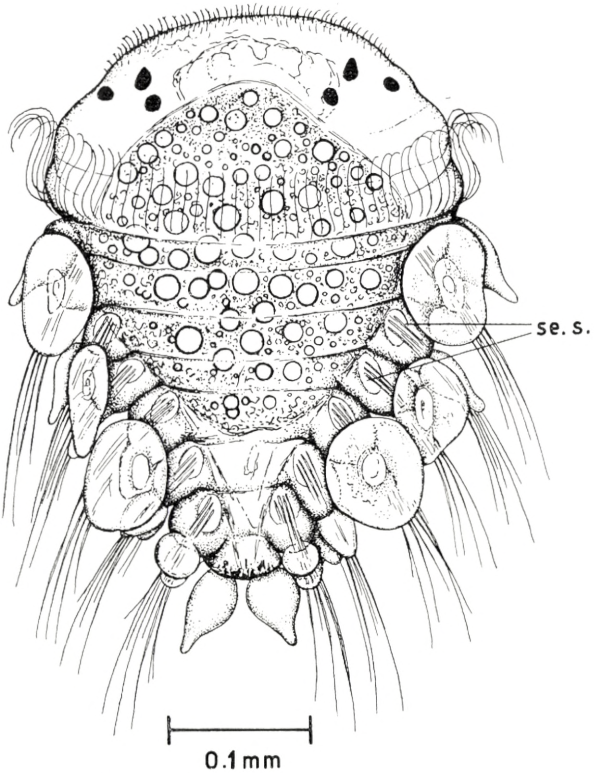

Fig. 8. *Harmothoë impar* Johnston.
Metatrochophora II, in dorsal view, the Isefjord, Vellerup Vig, 23.5.44.
As compared with fig. 7, which is a little more developed, this individual represents an almost non-pigmented larva of the same species.
se. s., seta sacs; these were not visible in the older stages.

being for some time semi-pelagic. Thus most of the specimens contained in the plankton sample of 27-5-1951 (fig. 2) were young metamorphosed worms without larval ciliation.

The few hours old metamorphosed individual measures 435 μ in body size and 670 μ in total length. In comparison with *H. imbricata* this is a considerable difference which is important when the aim is to separate the quite young specimens of the two species.

The complete number of chaetigerous segments immediately after the metamorphosis is *always seven*.

The first modified setiger has the same appearance as in *H. imbricata*. Only the ventral sections of the parapodia are developed with a bundle of few strong and curved setae (c. se.). Both tentacular cirri are present (d. t. c. and v. t. c.), the dorsal ones being the larger. In the parapodia of the other six segments, which are not yet biramous, distinct dorsal setae (d. se.) and large bundles of long ventral setae (v. se.) can be found.

Dorsal cirri (d.c.) are found on the setigers nos. 3 and 6. They are from 80 to 100 μ long, but not so slender as in *H. imbricata* and more claviform in shape. The anal cirri (a. c.) are about 130 μ long. Compared with the previous species the body appendages are more papillated.

There are always four pairs of elytra (el.) fixed by distinct elytrophores on the segments nos. 2, 4, 5, and 7. Except for the first pair, which are somewhat oblong, the other scales are almost circular in shape. In contrast to *H. imbricata* the surfaces of the elytra are characteristic by having numerous conspicuous papillae (pp.) or tubercles with fine hairs. Considering that this structure is among the most characteristic ones of the adults of the species, its value in the larval determination is obvious. The papillae are largest on the last pair of scales.

Pigmentation is found not only at the basis of the two anal cirri, which have two groups of reddish-brown chromatophores (r. b. pi.), but on the posterior margin of the prostomium a patch of dark-green pigment can be seen (d. g. pi.). The colour of the young bottom stage is greenish-yellowish all over.

The shape of the prostomium is different from that seen in *H. imbricata*. There are no tapering frontal peaks and the breadth is greater than the length. Also the position of the eyes is different, since all four eyes (with lenses) are situated on a transverse line and on the same level (p. ey.). This feature is also very important in the determination of the bottom stage of *H. impar*. In transmitted light the eye colour is an intense black. The colour of the prostomium is more brownish than that of the body.

All the head appendages: the median tentacle (m. t.) and the two smaller lateral tentacles (l. t.) are present. The tips of the two ventrally based, large palps (pl.) are only just observable when the animal is viewed dorsally.

The strong muscular pharynx (ph.) is about 125 μ long, but no jaws could be seen; however, the patch of dark green pigment (d. g. pi.) may hide them. The intestine (in.) has the same bilobed

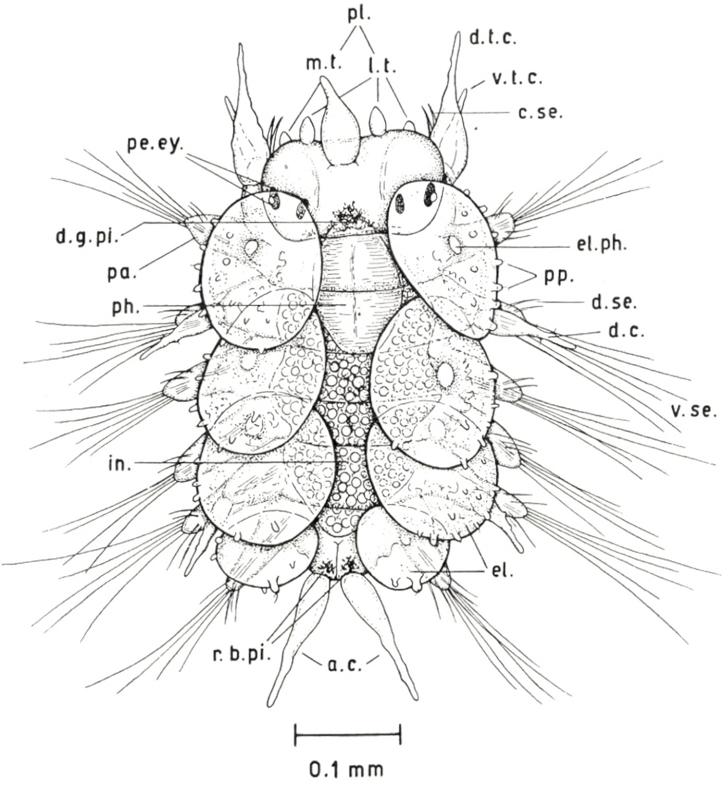

Fig. 9. *Harmothoë impar* Johnston.
Young bottom stage, drawn immediately after metamorphosis, the Isefjord, Vellerup Vig, 10.5.53.

a. c., anal cirri; c. se., strong curved setae of the first setiger (actually the ventral setae of the reduced first parapodia); d. c., dorsal cirrus of a cirrigerous segment (setiger no. 3); d. g. pi., dark-green pigmentation on the posterior margin of the prostomium; d. se., dorsal setae of a parapodium (setiger no. 3); d. t. c. and v. t. c., first pair of cirri, the dorsal and the ventral tentacular cirrus; el., elytra, all covered with rather prominent papillae especially on their posterior margins; el. ph., an elytrophore (setiger no. 2); in., intestine with numerous oil globules; l. t., two lateral tentacles; m. t., median tentacle; pa., parapodium of an elytrigerous segment (setiger no. 2); parapodia not yet biramous; pe. ey., permanent eyes with lenses; ph., muscular pharynx (the jaws are not yet visible); pl., tips of the palps; pp., small tubercular papillae with fine sensory hairs especially on the posterior marginal surfaces of the elytra; r. b. pi., reddish brown pigmentation at the bases of the anal cirri; v. se., bundle of long ventral setae of a parapodium (setiger no. 3).

structure as in *H. imbricata* and its wall has numerous, densely situated oil-globules. The rectal part is very short.

Before finishing the description of the development of *H. impar* it should be well worth *summarizing the main characters separating the young bottom stages of H. imbricata from those of H. impar.*

H. imbricata.—body size: 700 μ.—full length: 950 μ.—number of chaetigerous segments: always 9.—tentacles, tentacular cirri, dorsal cirri and surfaces of the elytra: with few scattered, small papillae.—the 6th dorsal cirri only present as a bud.—prostomium: breadth and length about the same; frontal peaks in development. The first pair of eyes ventral near the frontal peaks.

H. impar.—body size: 400—450 μ.—full length: 600—650 μ.—number of chaetigerous segments: always 7.—tentacles, tentacular cirri, dorsal cirri, and elytra: with numerous conspicuous tubercles.—the 6th dorsal cirri developed;—prostomium: the breadth is larger than the length; no frontal peaks present. The eyes on a transverse line on the same level.

3. ***Eteone longa*** **(Fabr.).**

The spawning habits of *Eteone longa* have never been observed under natural conditions. MEEK and STORROW (1924) have observed spawning in aquaria. The eggs were shed freely in the water without any surrounding mucus.

The pelagic larvae of the species have been described and figured several times. In 1871 R. v. WILLEMOES-SUHM from the bay of Kiel published descriptions and rather rough drawings of the larval development of what he called *Eteone pusilla* Ørsted. From the same area LESCHKE in 1903 gave a new illustrated description of larvae, which he referred to the same species in spite of slight differences. In both cases Trochophora, Metatrochophora and Nectochaeta are described and figured, however, without any statement why they are referred to *E. pusilla*. NOLTE (1938) emphasizes that the larvae described by both authors, owing to the presence of bristles on the second segment, i. e. the segment caudal to the buccal segment with the tentacular cirri, must belong to either *Eteone longa* or *Eteone flava*, which according to FAUVEL (1923) are the only northern species of the genus *Eteone* with this character. Because of the small differences between the descriptions of WILLEMOES-SUHM and LESCHKE, NOLTE concludes that their larvae cannot be referred to the same species, but must belong to two separate species, *Eteone longa*, which name NOLTE gives to the type of larva of WILLEMOES-SUHM, and

Eteone flava, which then according to NOLTE should be the name of the larva described by LESCHKE.

The characters mentioned by NOLTE, according to which the larvae should be considered two distinct species, are: the time for the appearance of the mouth; the predominance of the umbrella; the pigmentation; the eyes with or without lenses; the larval segments; the presence or absence of cilia on the tentacles and tentacular cirri; shape and destiny of the apical tuft and the presence or absence of segmental organs.

The most important objection to the division into species made by NOLTE is to be found in the condition in which the figures of WILLEMOES-SUHM are given. His drawings are so sketchy that most of the characters mentioned by NOLTE are too delicate to be found. This applies e. g. to the pigmentation (which furthermore is able to vary rather much; cf. the larvae from the Isefjord!); the lenses of the eyes; the cilia of the tentacles and the tentacular cirri (cf. NOLTE p. X 240), which however, are not cilia, but sensory hairs! (observed very clearly on the Isefjord larvae, see figs. 11—12). Another objection is to be found in the fact that some of the stages of WILLEMOES-SUHM and LESCHKE cannot be compared owing to their different stage of development. The Metatrochophora of WILLEMOES-SUHM (his fig. 7, pl. XXXVI), e. g., is younger than the Metatrochophora of LESCHKE (fig. 4, pl. VII), a fact which may explain the different shape and development of the apical tuft.

Ignoring these small differences, which in my opinion are of slight value only, the main characters of the larvae are quite identical; a point of view also shared by THORSON (1946), and so it may be inferred that WILLEMOES-SUHM and LESCHKE have described the larvae of one and the same species only.

From the harbour of Copenhagen, SMIDT (1944) has described and figured a Metatrochophora of an *Eteone* species, which may belong to *E. longa*. However, the figure is rather rough and in some respects not correct; thus the first chaetigerous segment bears a distinct dorsal cirrus, a feature which according to FAUVEL (1923) is never found in any species of the genus *Eteone*.

In 1946 THORSON gave further information about the pelagic stages of an *Eteone* species from the Sound. The larvae were found in his so-called plankton main-series taken regularly throughout several years in localities close to the island Ven and off Elsinore. The larvae were only collected in the spring and mostly in the months of March-April and in May. In June only two specimens have been taken. All the stages found belonged —according to THORSON—to one species only and were of the same type as described by WILLEMOES-SUHM and LESCHKE even if slight differences were present. Thus the tentacles of the larvae from the Sound developed at a much later stage than in the larvae of WILLEMOES-SUHM. On the basis of a. o. the discussion of NOLTE and of his own results THORSON concludes that the larvae of WILLEMOES-SUHM and LESCHKE are identical with the larvae from the Sound and that they belong to *Eteone longa,* this species being by far the commonest *Eteone*-species in the Sound.

THORSON gives figures of Metatrochophora II, the Nectochaeta, and the youngest metamorphosed bottom stages. However, the fig. 26 C and D cannot be correctly drawn. At the bottom stage figured in C, the left side of the body has only dorsal cirri (including the first chaetigerous segment, which—as emphasized above—in the *Eteone* species normally has no dorsal cirrus!) while the right side of the body of the same specimen has only the ventral cirri! Also in fig. 26 D both first chaetigerous segments erroneously have dorsal cirri.

In 1951 E. SMIDT again mentioned and pictured *E. longa* among his descriptions of annelid larvae from the wadden sea (p. 48). Only one newly settled bottom stage with seven chaetigerous segments and without any pelagic attributes at all has been found. The individual was taken in a micro bottom sample on 15-5-1942. Also SMIDT's drawing is incorrect owing to the presence of dorsal cirri on the first chaetigerous segments.

Up to now *Eteone longa* is the only species of the genus *Eteone* taken in the Isefjord area. It is among the commonest polychaete annelids and is found in all biotopes, especially characterizing the shallow sandy areas from about mean level to about 1—1.5 m below low water mark.

The adult individuals are generally found crawling in or on the bottom. However, from Vellerup Vig and off Frederikssund on the Roskildefjord several observations are available which show that adult individuals can be found—often in large numbers—swimming very actively near the surface of the water. In

Vellerup Vig, just outside the laboratory such swimming specimens were observed in March 1943, April 1944, and March 1949. At Frederikssund, in the very narrow passage under the bridge connecting the town with the peninsula Hornsherred, strong currents are very frequent. In this place drifting adult specimens were taken swimming near the surface in December 1943 and March 1945. Most of the animals from the spring were mature, while only a single female from December 1943 contained small eggs. Thus the usual time for finding swimming specimens seems to be the early spring, the time just before the beginning of the spawning, that is to say the last half of April, when the temperature of the low water rises to more than about 10° C.

As to the swarming of *E. longa* the following observation from another Danish locality, the low water area round the small island of Vorsø in the Horsensfjord (Eastern Jutland), in a rather instructive way supplements the Isefjord results.

On April the 13th 1949 I examined a small creek at the above-mentioned island. The creek was only about two metres broad and ten long and emerging directly in the large, sandy wadden area on the north side of Vorsø. The water was very shallow and the bottom contained a very thick layer of mud. The bright sunshine had raised the temperature in the small amount of water so that a considerable difference was present between the wadden sea outside (about 8° C.), and the creek. On my arrival just before noon I found a few swarming *Eteone longa*, but soon after, when the temperature passed 12° C., the whole creek was filled with large—up to 10—12 cm—swimming and wriggling *Eteone* individuals. I now made a series of temperature measurements from the warmest part of the creek and out to the wadden sea. Below 10° C. no individuals were seen in the water, but the bottom everywhere in these "cold" areas contained numbers of buried, large mature specimens. Also the swimming animals were mature; most of them being females. No real breeding nor already spawned eggs were observed. These observations together with the results of Meek and Storrow (1924) seem to confirm the swimming habits of *E. longa* as a component of the whole spawning process. Interesting is the swarming temperature mentioned by these authors, from 3.7 to 5.0° C., as against about 10° C. in Danish waters.

On April 1953, when working with the species in Vellerup Vig, I made an observation on a male and a female kept in aquarium which may indicate the existence of a sort of copulation before spawning. A fully mature male—about 20 mm in length—was seen winding itself round the body of a female—length 30 mm—but only with small eggs in the segments thus not being mature. The head and the foremost part of the body of the male moved in a trembling way while the male incessantly was putting its head into the spaces between the parapodia of the female. At small intervals the male projected its proboscis and adhered it to the body of the female although apparently without doing it any harm. During the action of the male the female kept quiet, only the "biting" of the male produced a slight starting in its body. After a while the male left the female and the pre-mating behaviour was not seen again, presumably owing to the immature condition of the female. The temperature during the observation was about 19° C.

The spawning time. It seems beyond doubt that *Eteone longa* everywhere where the species has been examined, spawns within a very short interval and always in the early spring. Both Willemoes-Suhm (1871) and Leschke (1903) mention the month of May as the time when the larvae occur in the plankton. Meek and Storrow (1924) found the swarming individuals in March and especially April. Thorson (1946) indicates also March-April and May as the time for pelagic larvae. The fact that the spawning of *E. longa* in the Sound, as in other areas, is much concentrated is rather interesting, because in a way it confirms the shallow-water distribution of the species. In that respect the Sound is a very good indicator owing to its two distinct fauna elements. Under the influence of the outflow of fresh water from the Baltic, the surface layer of the Sound, that is the shallow-watered areas along the shores, has a typical brackish water fauna with changing temperatures, while the deeper parts of the Sound receive water of permanently high salinity and rather low temperature from the Kattegat and the Skagerrak and for this reason contains a typical marine fauna. Consequently, the spawning time of *E. longa* coincides very closely with the rising of the surface temperature in the spring, 10° C. being the optimal temperature.

The young bottom stage described by Smidt (1951) was also taken in May (15.5.1942).

In the Isefjord I have never observed the spawning under natural conditions. Judging from the appearance of the pelagic larvae in the plankton, it always seems to take place at the end of April or, as just emphasized, at water temperatures of about 10° C. In 1945, 1951, and 1953 I have observed the maximum of larvae very near the 1st of May. In 1951 when monthly plankton samples were regularly collected, the largest number, 104 specimens in one 8 metre vertical haul, was counted on May the 6th. The samples from 22.4 and 27.5 of the same year contained no *Eteone* larvae. In 1953 the last large larvae were collected in the plankton in Vellerup Vig on May the 10th.

In an aquarium I have observed the spawning once. On March 3rd, 1943, a female, which had been kept in a vessel since 2-2-1943, at a temperature of 10° C., spawned its eggs freely on the surface of the muddy bottom layer without forming any sort of surrounding mucus, an observation in full agreement with the results published by Meek and Storrow (1924). Owing to lacking fertilization no development of the eggs took place.

The egg size. The new-laid egg, which had a distinct egg membrane, was quite globular in shape and had a light yellow colour. The diameter of the egg including the membrane was 0.1 mm.

The cleavage and the early development of the eggs could not be followed, since, as mentioned above, the eggs available were not fertilized.

The following description is based exclusively on larvae taken in the Isefjord, Vellerup Vig, with a small conical plankton net with gauze no. 12. The material was collected in the years 1945, 1951, and 1953.

Metatrochophora I (fig. 10) is the youngest stage found. It has a total length of about 270 μ; in comparison with figures 6 and 7 of Willemoes-Suhm the larva pictured here represents a middle stage between these two. The sizes of the stages of Willemoes-Suhm are remarkably small; 73—85 μ.

The larva from the Isefjord is rather transparent and of a yellowish hue. Grass-green chromatophores (g. ch.) are present only in the hindmost part of the body, beginning on the second segment after the prostomium, while in the front part chromatophores are totally lacking. According to Willemoes-Suhm's figures the green pigment is regularly distributed over the whole larval body, while conversely Leschke's youngest larva (his fig. 3, Pl. VII) has only green pigment on the foremost part of the body. Thorson only mentions the presence of the green colour, his drawings of the pelagic stages having no distinct chromatophores.

The prostomium (p.), which is rounded, has in front a distinct group of apical cilia (ap. ci.), in which the tips of the first two tentacles—ventrally based—can be seen (t.). As pointed out by Thorson (p. 59), his pelagic larvae differ from the older descriptions in having the tentacles developed much later.

On each side behind the apical tuft a group of fine twisted tubes can be seen, undoubtedly a pair of mucus glands (m. g.).

There are four red eyes (ey.), the largest of which are the dorsal ones, which have distinct lenses. The smaller ventral eyes are darker red and have no visible lenses.

On the next segment, with the ciliated mouth ventrally, a long-ciliated prototroch is developed round the body (pr.), the cilia being shortest most dorsally.

In the next three segments, which in the older stages represent the chaetigerous segments, the chromatophores are arranged in thin transverse bands, a feature most distinct in the anal segment (b. g. ch.). Setae are not yet visible outside the segments; only a few thin capillary setae (c. se.) are present within the body. When only a little older—when four segments are developed—the parapodia with bristles will appear; this is the stage described by Willemoes-Suhm in his fig. 7, Pl. XXXI; fig. 4 Pl. VII in Leschke seems to be a little older.

The intestine is thick-walled (in.), especially in the hindmost part just before the anal opening (an.), which has a surrounding, glandular epithelium (g. ep.). The intestinal colour is light green and a few small oil globules are found in the wall. At this stage of the development no telotroch was seen.

The older Metatrochophora II (fig. 11) is from 310 to 320 μ long and has four distinct setigers. It corresponds rather closely with Willemoes-Suhm's Metatrochophora (fig. 7). However, the larva from the Isefjord has a more conical prostomium and is

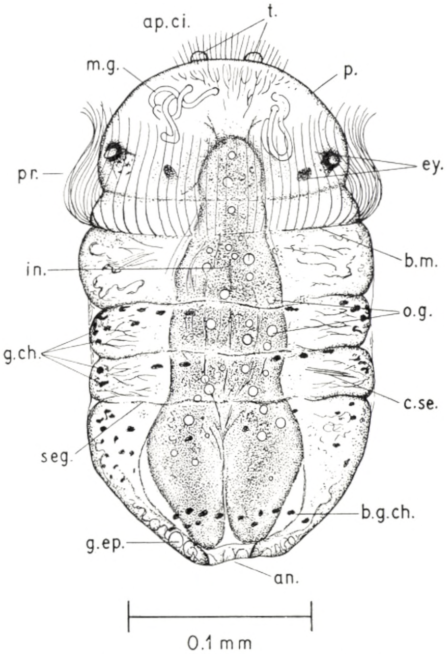

Fig. 10. *Eteone longa* (Fabricius).
Metatrochophora I, dorsal view; the Isefjord, Vellerup Vig, 1.5.45.
an., terminally placed anal opening; ap. ci., apical cilia; b. g. ch., transverse band of green chromatophores round the developing anal segment; b. m., basal margin of the prototroch, cf. the text on p. 40; c. se., capillary setae still inside the body wall; ey., eyes; the largest one (most dorsally) with a distinct lens; g. ch., grass-green chromatophores; g. ep., glandular epithelium (mucus?) round the anus; in., intestine; m. g., mucus glands?; o. g., small oil globules in the intestinal wall; p., prostomium; pr., prototroch; seg., beginning segmentation; t., first two tentacles.

much larger in comparison, 310—320 μ long as against 85 μ in the bay of Kiel larva. LESCHKE's fig. 4, Pl. VII, must be younger, among other things owing to the incomplete formation of the parapodia. LESCHKE gives no indication of the sizes of his pelagic larvae. THORSON's Metatrochophora II (fig. 26 A, p. 60), which is his youngest *E. longa* larva found in the Sound plankton, is remarkable in several respects. As previously mentioned, the tentacles, in spite of its advanced stage of development, are not yet visible and the tentacular cirri and the dorsal cirri of the parapodia have not yet appeared. Another very peculiar feature in his larva of fig. 26 A is the apparent presence of a further segment with a pigment band between the prostomium and the mouth segment, a detail absent in the Nectochaeta in fig. 26 B, which, however, has the pigment band. Perhaps THORSON's drawing is to be explained in the way that the line dividing the mouth segment into two parts is only the basal margin of the prototroch, as also seen in the larva pictured in fig. 10 in this paper (b. m.). The total length of Metatrochophora II from the Sound is rather great, in comparison with stages from the Isefjord and especially with the *Eteone* larvae of WILLEMOES-SUHM, 460 μ. Five chaetigerous segments are seen in THORSON's Metatrochophora II.

On the Isefjord Metatrochophora the green chromatophores (g. ch.) are distributed over the whole body; on the two anal cirri (a. c.) their colour is darker green. Just before these lobes a transverse band of brownish chromatophores is placed round the body (b. pi.). The variations in the concentration of the green pigment of the larger *E. longa* larvae from the Isefjord were remarkable, and very often quite clear and yellowish larvae with few chromatophores were collected together with larvae which were of an intense green. The older Metatrochophora pictured here represents a rather light type.

The prostomium (p.), which has now a shape more like the head of the adult, has four well-developed tentacles (t.) with sensory hairs (s. h.) and placed in their permanent position. The four red eyes (ey.) are still situated in front of the prototroch on the prostomial segment, even if the smaller ones are on the border of the mouth segment. In the latter, with still well-developed prototroch, the mouth is distinctly seen as a transverse, ventrally situated opening (m.), behind which a thick-walled pharynx (ph.) has now been formed. The tentacular cirri (t. c.) are present, one pair on each side. The parapodia with their characteristic compound setae (se.) have all—except in the first setiger—dorsal cirri (d. c.).

The intestine (in.) with distinct and rather thick walls, is dark grass-green and is rather granular. In the above-mentioned brownish-coloured pigment band close to the anal lobes a telotroch is present (te.). As compared with the cilia of the prototroch its ciliary equipment is short and for this reason difficult to see even at high magnifications. In the literature the telotroch has only been observed once in connection with the pelagic larvae

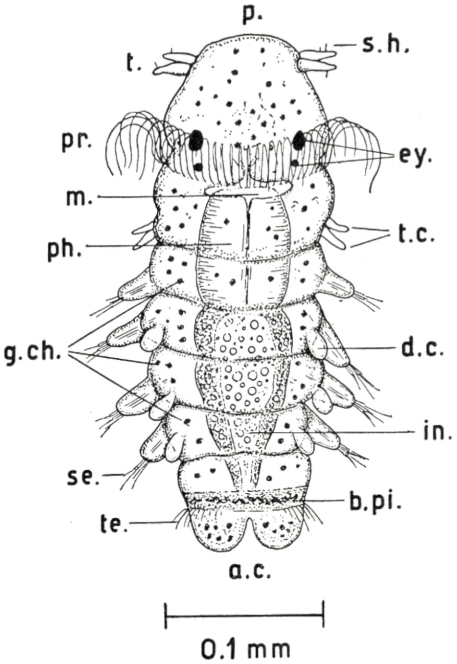

Fig. 11. *Eteone longa* (Fabricius).
Metatrochophora II, dorsal view; as to pigmentation the larva pictured represents a rather light type; the Isefjord, Vellerup Vig, 3.5.53.
a. c., anal cirri; b. pi., brownish pigmentation; d. c., right dorsal cirrus of the 2nd setiger; ey., eyes; g. ch., green chromatophores; in., the rather thick-walled, granular intestine; m., mouth aperture visible through the transparent larval body; p., prostomium; ph., the thick-walled, muscular pharynx; pr., prototroch; se., composed setae of a parapodium; s. h., fine sensory hairs on the tips of the tentacles; t., the tentacles; t. c., developing tentacular cirri; te., telotroch.

of *E. longa*; in the old Nectochaeta figured by Leschke (fig. 5, Pl. VII) a short telotroch can be seen.

The Nectochaeta (fig. 12) has a total length ranging from 480 to 500 μ. The corresponding stage from Willemoes-Suhm (fig. 8, Pl. XXXI) is only 123 μ; Thorson (fig. 26 B, p. 60) states 905 μ for a Nectochaeta consisting of 6 chaetigerous segments. Thus there is still a considerable variation in the size of the larvae described. In my samples from the Isefjord I also always found specimens varying greatly in size even if the same number of segments were present. Also when metamorphosing, the young individuals have different sizes.

Besides the green pigmentation, which on the central part of the head very often forms a triangular figure (g. pi.), dense and dark brownish pigment is found close to the base of the tentacular cirri (t. c.) and on the centre of segment no. two (d. b.pi.).

The eyes (ey.) are now separated by the prototroch (pr.), as also described by LESCHKE, a feature which NOLTE (p. X. 239), however, denies. The colour of the eyes is still red when seen in falling light; when transmitted light is used in the microscope, the eye-colour will appear dense black.

The large, muscular pharynx (ph.) has a typically oblique position in the body; in the Isefjord larvae always turning on the right with the posterior end (cf. figure), as also figured by LESCHKE. It now reaches the posterior margin of setiger no. three. The grass-green intestine (in.) is still very opaque and even more granular than in the younger stages. It ends in a very short and thin-walled rectal part (re. in.).

The two ciliary bands, the prototroch and the telotroch, are still very well developed, especially the prototroch, which has long and very distinct cilia.

The pigmentation of the segments, as usual subject to great variation, form transverse bands, a character also mentioned by THORSON (cf. his fig. 26 E, p. 60, 1946). The ground colour of the larval body is faintly greenish.

During swimming, which in the larger larvae is brought about by the aid of the prototroch, the parapodia are laid along the body with their tips pointing backwards.

The Nectochaeta pictured here—very often with up to six chaetigerous segments—is the largest free-swimming larval stage of *E. longa* found in the plankton in Vellerup Vig.

Only slight differences are to be found in the newly settled bottom stage in comparison with the Nectochaeta. Of course all pelagic attributes, such as the prototroch and the telotroch, disappear. The changes are found e. g. in the development of the intestine. The anterior end of the pharynx is provided with papillae and the intestinal wall is more distinct in its contours and almost devoid of oil-globules so that the lumen of the intestine can be seen.

When summarizing the above, the results here published as compared with the descriptions hitherto given by WILLEMOES-SUHM, LESCHKE, NOLTE, and THORSON, are remarkable, especially in one respect. They show that even if the pelagic larvae of

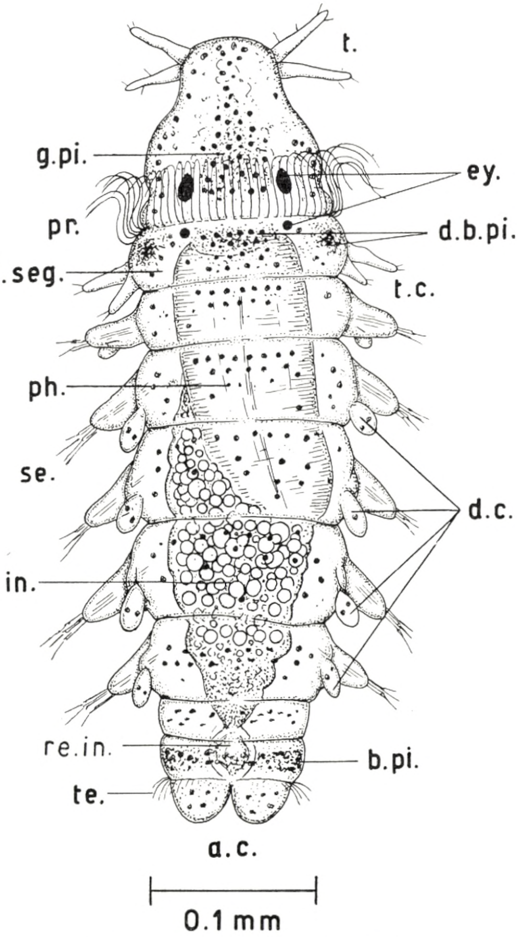

Fig. 12. *Eteone longa* (Fabricius).
Nectochaeta, dorsal view; the Isefjord, Vellerup Vig, 3.5.53.
a. c., anal cirrus; b. pi., transverse band of brownish pigment; d. b. pi., dark brownish pigmentation close to the base of the tentacular cirri and on the centre of the segment; d. c., dorsal cirri of the setigers nos. 2—5; ey., eyes, the posterior (more ventrally than the anterior ones) and smallest pair now behind the prototroch; g. pi., green pigmentation concentrated in a triangularly shaped figure both on the dorsal and the ventral part of the prostomium; in., intestine full of oil globules; ph., the large, muscular pharynx in its characteristic oblique position; pr., the prototroch now separating the eyes; re. in., rectal part of the intestine; se., the composed setae; 1. seg., first segment with the ventrally placed mouth aperture and the two pairs of tentacular cirri. Parapodia and setae not developed; t., tentacles with fine sensory hairs; t. c., tentacular cirri; te., reduced telotroch.

Eteone longa belong to a rather characteristic and rather easily recognizable type, *they differ very much not only from place to place, but even within one small water area.*

The variations mentioned above refer to:

(1) *The size of the larvae.* Thus Metatrochophora II is about 85 μ according to WILLEMOES-SUHM; about 460 μ in the Sound (THORSON) and from 310 to 320 μ in Vellerup Vig in the Isefjord. The Nectochaeta correspondingly, 123 μ (WILLEMOES-SUHM); 905 μ (THORSON), and the larva pictured from the Isefjord, about 500 μ. Even the young newly settled bottom animals vary rather much (e. g. many sizes in one sample from the Isefjord).

(2) *The pigmentation.* As emphasized above, larvae from the Isefjord could be found lacking almost any pigmentation, while others in the same sample were characterized by an intense and dense green pigmentation.

(3) *The time of the appearance of the tentacles.* While in WILLEMOES-SUHM's paper (his fig. 7) the late Trochophora (length about 85 μ) has distinct tentacles, the large Metatrochophora II of THORSON (fig. 26 A, p. 60), length 460 μ, has no traces of tentacles!

(4) *The larvae being monotrochous or exotrochous* (cf. NOLTE, p. X 66, 1938). LESCHKE's Nectochaeta (fig. 5, Pl. VII) according to NOLTE is exotrochous, i. e. it has both the prototroch and the telotroch developed. The corresponding stages of WILLEMOES-SUHM and THORSON have only the prototroch and are consequently of the monotrochous type. On this point the Isefjord larvae correspond closely to the exotrochous type.

In my opinion the correctness of this variation may or may not be right, since in my own experience the telotroch is so poorly developed that at a less careful examination of the larvae at low magnification it can very easily be overlooked.

4. *Magalia perarmata* Marion and Bobretzky.

The larval development of this species is mentioned by few authors.[1] Thus LANGERHANS (1880) states that the eggs are slightly purplish.

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[1] After the finishing of my manuscript I have received two papers by L. CASANOVA describing and figuring the larval development of this species (L. CASANOVA, *Les annelides du plankton dans le Golfe de Marseille*, pp. 29—36, and *Note sur le développement de Magalia perarmata Mar. et Bobretzky* (*Polychaeta, Hesionidae*), pp. 155—162, Pl. I—III, in: *Recueil des Travaux de la Station Marine d'Endoume*, fasc. 8, 1953, and fasc. 13, 1954). The early development is not mentioned and the

On June 24th, 1942, during dredging in Vellerup Vig, some specimens of this small delicate hesionid were taken as new to the Danish fauna. Later collecting has shown that the species is common in practically every biotope in the Isefjord area. Since the first finding in 1942 the species has been taken through the whole year. *M. perarmata* is a very fast moving species and very often it was observed swimming.

The first mature individuals will occur in the middle of May and from now on every single specimen examined will contain mature eggs or sperm. After the culmination of the breeding in July the number of mature individuals will decrease. The last mature specimens were collected in October (cf. fig. 1, p. 6). The percentage of males and females was examined in July 1944. About 70 $^0/_0$ of the animals were females, as against 30 $^0/_0$ males. The mature females seem mostly to be larger than the males; the largest adults found, about 8 mm in length, thus being females. The greatest number of chaetigerous segments noticed was 31.

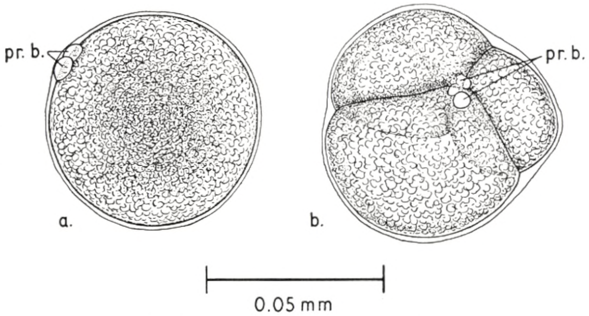

Fig. 13. *Magalia perarmata* Marion & Bobretzky. a. Undeveloped new-laid egg, spawned in aquaria; b. Egg in cleavage; pr. b., polar bodies. The Isefjord, Vellerup Vig, 15.6.44.

In the mature adults the sexual products extend to any part of the body segments. The females can be so distended with eggs that the usually very distinct pharynx is completely hidden.

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first larval stage in the planktonic life, which is of short duration, is the Metatrochophora. This stage is 250 μ long and besides the apical ciliation only the prototroch is found. The number of segments, which consist of two groups, are five. On the ventral side of this stage a median longitudinal pigmentation of brown or dark green colour is found. The next stage, the last pelagic one, is a transitional stage between the Metatrochophora and the Nectochaeta with six or seven segments. Also the young bottom stage is described, length 400 μ. The author emphasizes that the development of *M. perarmata* is of short pelagic duration and that the stages show morphological resemblance with larvae of Phyllodocidae and Aphroditidae. Further the presence of provisional larval bristles as in the Spionidae is mentioned.

The paper from 1953 gives some information concerning the occurrence of the larvae in the plankton of the gulf of Marseille.

The eggs are shed freely in the water. The single new-laid egg is very small, about 58 μ across, and quite transparent (fig. 13). Its colour is slightly yellowish and the yolk is granular. The segmentation of the egg seems to be extraordinarily fast, and within a short time the early, ciliated gastrula is formed. At this stage, which has a girdle of fine purplish pigment cells round the body, the embryo leaves the egg-membrane and begins the pelagic life, which in relation to the small size of the egg and the poor content of deutoplasma in the yolk may be of rather long duration.

In spite of repeated experiments to rear larvae from the eggs, I did not succeed in getting the pelagic stages. Also plankton samples taken in the fjord during the spawning time gave no results, and no larvae, which with any possibility could be referred to this species were taken in the period 1942—1952. There may be some reason for this peculiar phenomenon, since the pelagic life may be so short that no larvae will form part of the plankton proper.

From a faunistic point of view *Magalia perarmata* and also *Scolecolepis fuliginosa* (Claparède), the larva of which is described later in this paper (p. 60), are interesting species, first, because they form part of the group of polychaete species of the Isefjord fauna whose main distribution is south of Danish seas. Out of the 45 species of polychaetes—up to now (September, 1954)—recorded from the Isefjord area, 12 species belong to this southern group, which inhabit places with rather high summer temperatures. Of these twelve species, eight—collected during the last few years—were not hitherto recorded from Danish waters and some of them even not from Scandinavian waters. These eight species are: *Eulalia* sp. (this species was quite recently found in Vellerup Vig and has not yet been determined with certainty as to species, however, it seems beyond doubt that it is new to our fauna); *Magalia perarmata* M. and B.; *Grubea limbata* Claparède; *Autolytus rubropunctatus* (Grube); *Autolytus edwardsi* St. Joseph; *Nereis* (*Neanthes*) *succinea* (Leuckart); *Scolecolepis fuliginosa* (Claparède) and *Polydora antennata* Claparède.

The presence of this southern element in the Isefjord constituting about 27 $^0/_0$ of all polychaetes found here and especially the new records within this group, seems to me to be of great interest.

One is tempted to connect these findings with the rise of the temperature and the higher salinity of our seas, which has been noticed during the last decades. As, however, since the thorough investigations of C. G. JOHS. PETERSEN (1889), no systematic collections of Danish marine invertebrates have been performed, the possibility cannot be excluded that the species mentioned are in reality no newcomers in Danish waters, but only hitherto have been overlooked.

However, it is out of the scope of this paper to give further details and information about these peculiar findings, which I hope will be dealt with in a later paper.

5. *Microphthalmus sczelkowi* Mecznikow.

This small peculiar hesionid worm has only been found a few times since the first description was given by MECZNIKOW (1865) on specimens from the North Sea off Heligoland. From Scandinavian waters the species has only been recorded from the Sound (from two localities) by A. ELIASON (1920). Nothing is known concerning the spawning and larval development of this species and on the whole its biology is totally unknown.

MECZNIKOW states that he found females only. Those with eggs had about 33 body segments and the eggs appeared from the 13th to the 24th chaetigerous segment. Those without sexual products had only 23 segments in all. MECZNIKOW gives no information about the spawning season.

In the Isefjord area *M. sczelkowi* (fig. 14) was found for the first time in June 1942. The species proved to be extremely common at depths from 3 to 10 metres and always in muddy bottom. So far the species has been collected in Vellerup Vig, in the Inner Broad and in the Roskildefjord off Frederikssund, but no doubt it is distributed in the whole fjord area where the bottom consists of mud. The number of individuals in the dredgings has been very varying, from several hundred specimens in even small samples of mud to only a single specimen in one sample. The species was collected in February, March, April,

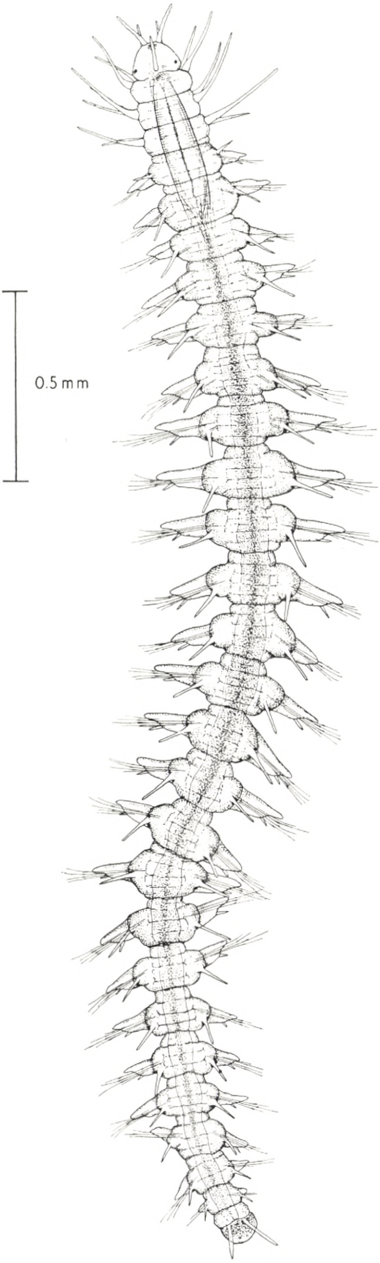

Fig. 14.

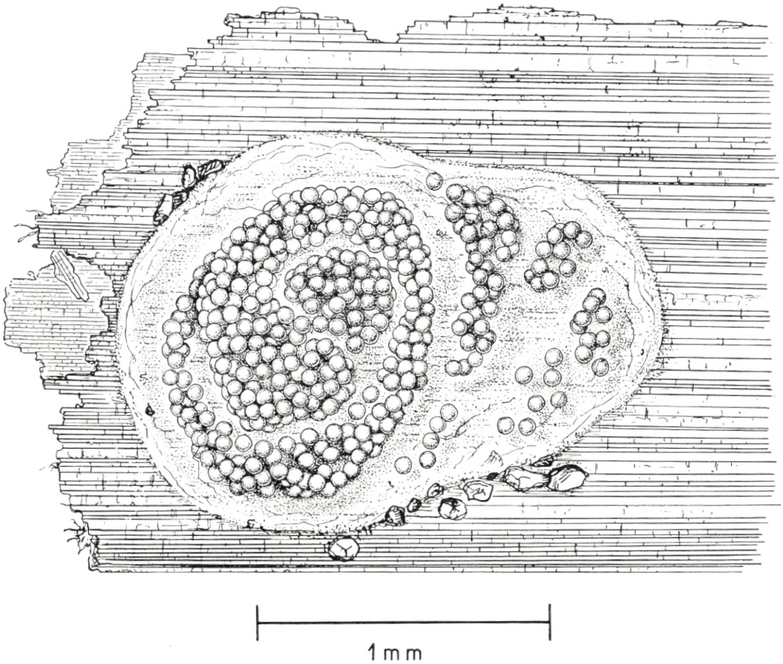

Fig. 15. *Microphthalmus sczelkowi* Mecznikow.
Egg-mass attached to a piece of a *Zostera* leaf.
From the Isefjord, Vellerup Vig, 3,5 m, muddy bottom; 13.3.43.

June, August, and October, thus in almost every season. After 1944 no specimens of this interesting polychaete worm could be found in spite of a thorough search for it. Animals with sexual products in their segments—both males and females—were collected in February, March, and June; all individuals from these collections were large specimens with 23 to 30 chaetigerous segments and from 3.7 to 4.0 mm in length. Most of the animals taken in the autumn were smaller, from 13 to 21 segments and without any traces of eggs or sperm. According to these observations the spawning time seems to occur early in the year. The colour of the mature adults, both males and females, is whitish, also the mature eggs are quite white. In the Danish individuals the eggs occur from the 13th to the 22nd chaetigerous segment.

Fig. 14. *Microphthalmus sczelkowi* Mecznikow.
Adult individual from Vellerup Vig, the Isefjord, 20.8.42.
The drawing was made after a living specimen.

A female with 26 chaetigers taken on February 8th 1942 off Frederikssund in the Roskildefjord was so full of large eggs that the intestine was seen only as a very thin line. When mature, both males and females have their usual shape and their normal supply of bristles.

In order to study the spawning and the larval development several attempts were made to "mate" ripe males and females in aquaria, but without results. In one case only a mature female, collected in Vellerup Vig 13.3.1943, discharged its eggs in the water. The eggs of this "spawning", however, did not seem to have been fertilized, since in a short time they all decayed. Most of the eggs were not laid freely in the water, but were shed surrounded by a clear and very sticky mucus of no definite shape. When just laid, the globular quite white eggs had a diameter of about 75 μ (fig. 16).

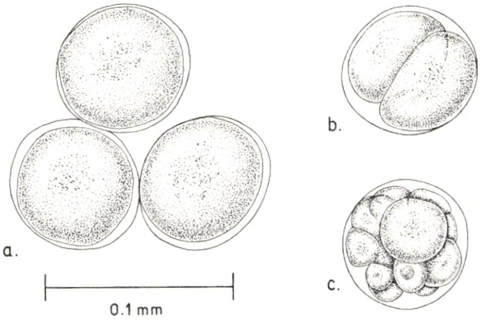

Fig. 16. *Microphthalmus sczelkowi* Mecznikow. a. Undeveloped new-laid eggs. b. Two-cell stage. c. More advanced stage of cleavage. From Vellerup Vig, the Isefjord, 20.3.43.

In a sample from a depth of about 3.5 metres, together with many mature individuals used for the breeding experiments mentioned above, also an egg-mass was found, which no doubt had been spawned by a *M. sczelkowi* female (fig. 15). The shape was irregularly oval and it measured about 1.9 mm in length and about 1.4 mm in breadth. The surface was globularly vaulted. The mucus was quite clear and colourless and was very sticky so that small bottom particles adhered to its surface. The eggs, which in size and colour agreed with the eggs spawned by the above-mentioned female, were placed in an irregularly shaped coil. The number of eggs was about 3—400, but no exact counting was made. The egg-mass was found placed on a piece of a decayed *Zostera* leaf (fig. 15).

Shortly after the collection, the egg-mass began putrifying and no details concerning the development of the eggs were obtained. Thus the larval stages of this species are still unknown. The small egg size, 75 μ, seems to suggest a development connected with a pelagic life.

No larvae, however, which with some reason could be referred to this species, have been found in the plankton of Vellerup Vig.

6. *Nereis pelagica* L.

Spawning has been observed by NORDGAARD (1912), who in August near Bergen in Norway found a pelagic *Heteronereis* specimen spawning its eggs; these were 190 μ across.

The larval development of this species is rather well-known. Thus HERPIN (1925) from the Channel described the spawning in December to January also by epitoquous individuals. The eggs are shed freely in the water, and the new-laid egg, still unsegmented, is 170 μ across. The larvae are hatched seven days after the fertilisation as quite non-pelagic animals only able to crawl on the bottom. The development of the young bottom stage is very slow; after 28 days only four chaetigerous segments are formed. In contrast to this description WILSON (1932) has followed up the whole development at Plymouth (in February) and has reared another type of larva. The egg, which is about 180 μ in diameter, is pelagic and also spawned by *Heteronereis* stages. The hatching takes place $3^1/_2$ days after the spawning. The larva has a typical pelagic stage lasting for about 18 days. This type of larva (WILSON, figs. 4—5) has three chaetigerous segments with ciliation, length about 400 to 450 μ. There are four brown eyes with patches of large brown pigment anterior and lateral to them.

From the plankton of the Sound THORSON (1946, fig. 29, pp. 64—65) during four years' investigations only obtained two larvae, which can be referred to *Nereis pelagica*. They are very similar to those described and figured by WILSON (*loc. cit.* fig. 6), but have no pelagic attributes at all. They were taken in June and November. THORSON concludes that *Nereis pelagica* in the Sound normally will develop in a non-pelagic way.

Mature epitoquous specimens of the same species were found by me in the Isefjord (Vellerup Vig) for the first time in 1953. During dredging on stony bottom on April the 2nd, seven—almost mature—individuals (3 males and 4 females) were collected in their sandy tubes on stones and among the hapters of the seaweed: *Fucus serratus* and *Fucus vesiculosus*. Depth only one metre; temperature about 7° C.

The live males were from 5.0 to 6.0 cm in length and with a total number of chaetigerous segments ranging from 67 to 70. The body was divided into two distinct parts, the anterior and unchanged one consisting in all three males of 16 chaetigerous segments. The rest of the body, containing the sexual products, was shaped in the usual way found in the male epitoquous individuals: the parapodia with crenulated dorsal cirri and large lamella and with numerous fine swimming bristles. The primary colour of the living males was faint orange to yellowish-brown with an iridescent tinge and without distinct pigment cells. This characterization especially applies to the anterior part of the body. The epitoquous section had brighter colours, dorsally the foremost segments of this part had an almost dustlike dark-purplish pigmentation fading in intensity towards the pygidium, which had no special papillae except the usual two anal appendages. In the median line close above the dorsal blood vessel a very distinct dark-purplish pigment line was seen. The primary colour of the epitoquous section was more reddish than of the atoquous one and the whole surface had a light blue silky lustre. The parapodia were bright orange-red with the white sperm masses visible in the most thin-walled parts. The furrows between the parapodia were bright yellow. The ventral side of the epitoquous section had the same colour as the dorsal side, but was a little brighter. The eyes were large and of a bright purplish colour. The space between the hindmost pairs of eyes was formed as a white triangle. All three males were full of sperm.

The live females were 3.0, 6.5, 7.5, and 8.0 cm long and had 70, 68, 75, and 77 chaetigerous segments. The division of the body into two parts was only distinguishable in one individual (7.5 cm, 75 chaet. segments), which had an atoquous part consisting of 19 segments. Only this female had large eggs in the segments, the others having only small oocytes. The diameter of the eggs in this individual was 160 μ, thus smaller than the smallest egg-size described, Herpin (1925): 170 μ. The colour of the egg cell was light bluish-green and the yolk was very dense and opaque.

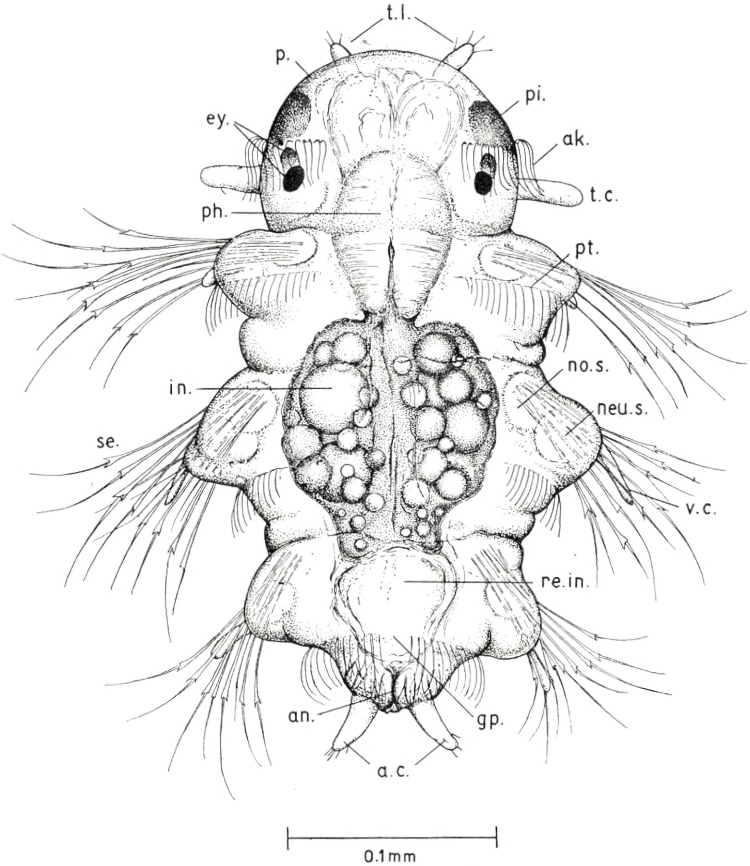

Fig. 17. *Nereis pelagica* L.

Nectochaeta, dorsal view; the Isefjord, Vellerup Vig, 13.5.44.
a. c., anal cirri with sensory hairs; ak., right akrotroch; an., anus; ey., rust-red eyes; gp., a slight gap separating the two hindmost paratrochs, no telotroch developed; in., intestine with a granular mass of different-sized oil globules; neu. s., neuropodial seta-sac; no. s., notopodial seta-sac; p., prostomium; ph., pharynx, still without visible paragnatha and jaws; pi., right rust-red pigment patch just before the eyes; pt., right paratroch of the first chaetigerous segment; re. in., rectal part of the intestine; se., bundle of the characteristic articulated setae; t. l., the developing first pair of tentacles with sensory hairs; t. c., the developing first pair of tentacular cirri; v. c., central cirrus of a chaetigerous segment (no. 2).

The primary colour of the above-mentioned female was much darker and more yellowish-brown than found in the males. The epitoquous section had a bluish-green hue owing to the content of eggs being visible through the skin. The parapodia in the posterior body segments were only a little changed and the cirri were not crenulated as in the male specimens.

The rather immature condition of the females collected, confirm that the *Heteronereis* of *N. pelagica* here described were not yet quite ready for spawning; an observation in agreement with the appearance in May of the pelagic larvae in the plankton (see text below).

The species is common in the area especially in sandy tubes on stony bottom with algae.

The results concerning the larval development of the species are based on plankton samples collected in 1944 and 1950 to 1951 and in 1953 in Vellerup Vig and in 1942 in the harbour of Copenhagen (the Sound). As to the samples 1950—1951 see p. 4.

The larvae from Vellerup Vig, all of the same type (fig. 17), were very similar to those described by Wilson. It was a Nectochaeta with three segments having noto- and neuropodial setasacs (no. s. and neu. s.). All setae were strongly built and of the characteristic articulated type well-known from *Nereis*-species. There was no prototroch, but distinct akrotrochs as mentioned by Wilson, forming "a row of cilia on each side" of the prostomium. The eyes and the pigment patches were rust-red and at the anterior end of the prostomium the first pair of tentacles with sensory hairs were visible. Also the first pair of tentacular cirri were developed. In the pharyngeal region no jaws were seen, the strongly built and muscular pharynx being the only detail marked out. The parapodia of all three body segments were not yet distinguishable, but had distinct ventral cirri and had paratrochs (pt.), the last one with a slight dorsal gap. There was no telotroch. The colour of the intestine was bright green, its contents being a granular mass with oil globules of different size. The anal cirri (a. c.) were well developed and had fine sensory hairs. The total length of the larva was about 350 μ. The larvae could swim as well as crawl. When swimming, the bristles, as also pointed out by Wilson (p. 207), are laid along the body with their tips directed backwards.

The larvae of *Nereis pelagica* were only taken in May. In 1944 larvae of this type were very common from 13.5 to about the beginning of June. In the eight month period 1950—51 with regular investigations only two larvae were collected on May the 6th. In 1953 no larvae were collected at all.

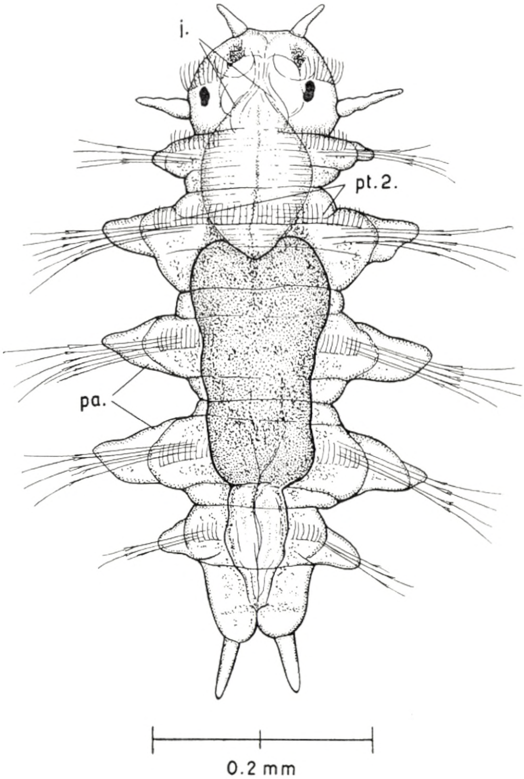

Fig. 18. *Nereis pelagica* L.
Large Nectochaeta in dorsal view, from the plankton of the South harbour of Copenhagen, the Sound, 13.10.42.
j., jaws; pa., well-developed parapodia still without any dorsal or ventral cirri; pt. 2, paratrochs of segment no. 2 united in one row of cilia.

On October 10th, 1942, a pelagic *Nereis*-larva, probably belonging to *N. pelagica*, was found in a horizontal plankton haul in the harbour of Copenhagen (southern part). The larva (fig. 18) was of about the same appearance as the larvae described and pictured by Wilson. However, it was interesting in being larger and still more pelagic than those hitherto known.

The total length was 650 μ and five chaetigerous segments were present. The prototroch was completely absent and only the akrotrochs were visible on the lateral parts of the prostomium. The four eyes and the pigment patches, which were small and pale, had the characteristic dark red colour. In front of the pharynx the first signs of the jaws could be seen (j.). The dorsal parts of the body segments had distinct paratrochs, which, with the exception of the second (pt. 2.), had broad gaps. This larva, in comparison with the type from the Isefjord, is interesting in having well-marked parapodia, but without any dorsal and ventral cirri. No telotroch was visible. The middle portion of the intestine was very finely granular, but without any oilglobules at all, while the rectal part was quite clear and transparent. The intestinal colour was yellowish green.

Only one larva of this type was taken in the plankton sample. The presence of this individual in the south harbour of Copenhagen with its rather brackish water is peculiar, since the species has never been reported from this part of the Sound, neither as adult nor as larva. No doubt the larva has been transported to the place by currents from a more northerly locality in the area. The most interesting thing, however, is the fact that *N. pelagica* besides its probable non-pelagic mode of development in the Sound (see THORSON, 1946, p. 65) has a very distinct pelagic one of rather long duration.

Other observations from the Isefjord (1953) seem to confirm that the same species within the same small area may also have the direct non-pelagic development, as described by HERPIN.

On May the 3rd some samples of the uppermost fine mud-layer of the sandy bottom just outside the laboratory were taken. They were collected at depths of 30 to 100 cm. Normally the adult *N. pelagica* is never found there.

The samples contained large numbers of small *Nereis* individuals, which all apparently belonged to *N. pelagica*. The number of chaetigerous segments were from 5 to 7 and no animal had ciliated bands or other pelagic attributes. Anteriorly to the four eyes many of the small bottom stages had the characteristic brown-red pigment patches, which in other specimens had either totally disappeared or were present only on one side of the head. The intestine of all the individuals examined was bright green and the total colour was yellowish-red. Some of these bottom animals were reared in the laboratory and in May 1954 when having a length of 2 to 3 cm they could easily be determined as typical *N. pelagica*.

Plankton samples taken at the same place in April and May did not contain a single free-swimming *N. pelagica* larva. Thus the only explanation of the occurrence of the bottom stages must be a non-pelagic development. No further observations of this mode of development were made.

Another very peculiar thing is the substratum of the small individuals. As emphasized above, the adults in the Isefjord are never found on open flats of pure sand, such as e. g. *Nereis diversicolor,* but always in sandy tubes attached to stones, shells or the hapters of seaweed and always in larger depths than the small worms.

Since the youngest stages of *N. pelagica* are found outside the natural biotope of the adults, it is a possible conclusion that the small individuals are unable to compete with the other *Nereis* species usually found there, especially a large and to *Nereis kerguelensis* McIntosh closely related species, (*N. southerni* Abdel-Moez and Humphries 1955). This species is now extremely common in the shallow sandy areas in the fjord and owing to its size (maximum length about 30 cm) and voracity it has, in the last few years displaced the normally very common *N. diversicolor* from this area, so that this species can only be found in the most brackish areas, where the low salinities prevent the large *Nereis*-species from being able to survive.

Another noteworthy thing as to the small *N. pelagica* is their free-living existence, an observation which was confirmed in aquaria. The specimens with 5—7 chaetigerous segments were very actively crawling through the fine sandy particles. The size and age of the small *N. pelagica,* when they will begin their tube-building, was not, however, observed.

Besides the above-mentioned species of *Nereis* two others are found in Vellerup Vig near the laboratory, *Platynereis dumerili* (Aud. and M. Edw.) and *Nereis* (*Neanthes*) *succinea* (Leuckart). The former is very common in tubes placed among different species of algae. The latter, which is fairly common among the mussels in shallow water, was found by me for the first time in 1953 and is hitherto unrecorded from Danish seas (see also the text above, p. 48). No results concerning the reproduction and larval development of these species are available from the Isefjord.

7. ***Scolecolepis fuliginosa*** (Claparède).

The reproduction and larval development of *Sc. fuliginosa* have been described by several authors.[1] Lo Bianco (1909) mentions the spawning season at Naples from October to April. Claparède and Mecznikow (1869) and McIntosh (1915) give short accounts of the egg-laying and early cleavage of the egg. The oval egg cells, which are about 120 μ in length, are laid in a common jelly of irregular shape and the yolk of each egg is surrounded by a reticulated and wrinkled egg-membrane. Crowding of males and females during the spawning has been observed by Claparède and Mecznikow. According to these authors the young larva has two red eyes and a long apical tuft of cilia. At eight days old the larva has six eyes and three chaetigerous segments with long provisional setae (cf. fig. 1 M, pl. XII Claparède and Mecznikow).

Day (1934), who describes the whole larval life history, gives the following details of the development: the larvae were reared from the egg (160 μ). When about 24 hours old the trochophores are 200 μ long and of a brown colour. The first bundles of larval setae, which project through the persistent egg-membrane, are developed two days after the fertilisation. At the age of eighteen days to three weeks the larvae, length 776 μ, have seven to nine chaetigerous segments and pairs of dense black pigment spots are present on the dorsal surfaces of the 3. to 6. chaetigerous segments. The larva with 14 segments, length 1000 μ, and from 34 to 36 days old, is the largest free-swimming stage of the species and normally metamorphosis will take place at this size and age. The larval description given by Day is supplemented with excellent drawings. Day and Wilson (1934) have studied the relations of the metamorphosing *Sc. fuliginosa* larvae to the substratum and have shown a distinct importance of the character of the bottom to the process of the metamorphosis. If the right type of bottom is absent, the larvae ready for settling are able to continue their pelagic life a week or more until the suitable

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[1] In a paper received after the finishing of my manuscript L. Casanova (*Les annelides du plankton dans le golfe de Marseille*, pp. 29—36, *Recueil des travaux de la Station Marine d'Endoume*, fasc. 8, 1953) gives some details concerning the occurrence of the pelagic larvae of this species in the plankton of the gulf of Marseilles.

substratum is found. Day (1937) mentions the fact that metamorphosis of the same species may take place at the swimming stage.

On August the 11th, 1941, during dredging in Vellerup Vig this spionid worm was taken by me for the first time in Danish seas. The species was found in mud at depths of about four metres only. Since then, it has proved to be extremely common in the innermost parts of the Isefjord area, especially in the shallow-watered sandy areas along the shores.

Mature specimens have only been collected in July and August; small and quite young larvae were also, however, taken in plankton samples from June, the species thus being a typically summer breeder (cf. fig. 1, p. 6). In spite of the frequency of the adults the pelagic larvae have only been collected in rather few individuals and only a few times. The present description is only based on these larvae; the spawning and the early development not being observed. Thus the material may be too insufficient and the morphological deviations found by me cannot give quite a correct picture of the actual conditions in connection with the spawning and habits of this species in the Isefjord area.

The early stages found, in June, with two to three chaetigerous segments have an appearance very close to the description given by Day (cf. his fig. 5). The most characteristic feature noted by me was the presence round the larval body of the lobulated egg-membrane, easily seen, owing to the transparent space between it and the larval surface.

The larva with nine chaetigerous segments (fig. 19) is the oldest and largest stage hitherto found in my samples. It has a total length of about 500 μ. The body is slender and the prostomium is distinctly broader than the rest of the body and is "square in front" with a shoulder on each side bearing the swimming cilia of the prototroch as also pointed out by Day. However, the front margin of the Danish larva has a greenish hue and on each side just before the shoulders there is a distinct spot of dark pigment. The number of eyes is not six placed on a transverse line across the head, but only five, of which the three, the most dorsal ones, are placed anteriorly to the two others. As in the English larvae the apical tuft of cilia consists of five short fine cilia. The cilia of the prototroch used for swimming are very long, especially in the lateral parts.

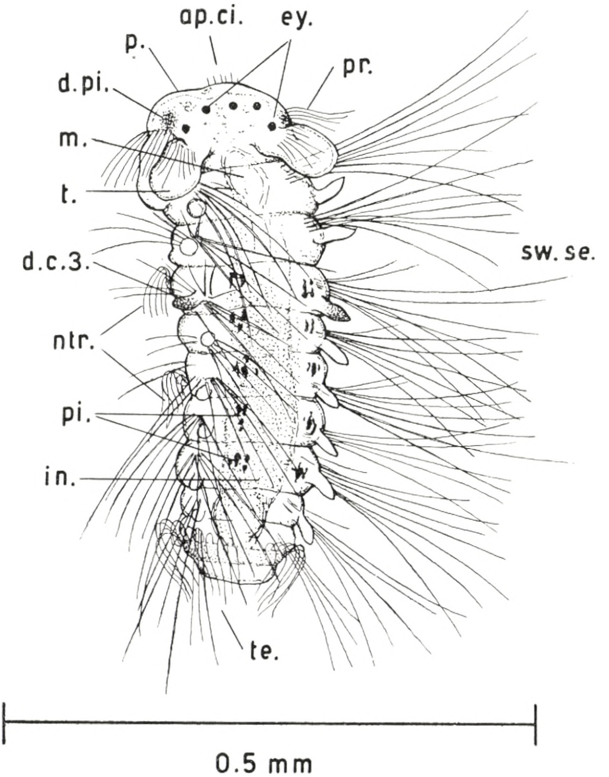

Fig. 19. *Scolecolepis fuliginosa* (Claparède).
Medium-sized larva, 9 chaetigerous segments, seen from its left side and partly from above; the Isefjord, from the plankton, Vellerup Vig, 15.8.41.
ap. ci., apical ciliation; d. c. 3, dorsal cirrus of chaetiger no. 3, with its characteristic purplish pigment; d. pi., dark pigment spots on both sides of the prostomium; ey., eyes; in., intestine; m., mouth visible through the rather transparent anterior part of the body; ntr., the neurotrochs, on chaetiger nos. 3 and 5; p., the broad and angular prostomium bearing "shoulders" on each side; pi., paired, black pigment spots on the dorsal surface of chaetiger nos. 3 to 7; pr., long cilia of the prototroch; t., lateral appendages of the prostomium, the developing tentacles; te., telotroch with a slight dorsal gap in the row of cilia; sw. se., long larval swimming setae.

The lateral appendages of the head, the palpi of Day, are in the Danish specimens peculiar in their placement on the head. They do not rise from the lateral parts of the prototroch ridges but from the dorsal section of the head behind the eyes, and may be considered as the developing tentacles (t.).

The segments of the body are furnished with the characteristic long provisional larval setae (sw. se.) from about 250 to 270 μ

in length, the longest in the first chaetigerous segments. Each segment is well marked off and the parapodia are rather distinct. However, only the dorsal rami of the parapodia are visible, the third one (d. c. 3) being very conspicuous owing to its purplish pigment, a character also emphasized by Day (p. 643). In the English larvae the dorsal surfaces of the segments were furnished with pairs of dense black pigment spots from the third to the sixth chaetigerous segment. This pigmentation is also found on the larvae from the Isefjord, but with some differences. Each single spot consists of about four distinct black pigment dots and pigmentation is also found on the seventh segment. The dorsal bands of ciliation across the single segment were observed by me, but as their extent and placement could not be noticed with accuracy, I have chosen to omit this detail in my drawing. The neurotroch ciliation, however, was rather easily distinguished. Thus rows of cilia were seen on the ventral surfaces of the third and the fifth segment. The telotroch had very large cilia, about 100 μ in length and with a gap in the ciliation dorsally before the anus. The glandular cells with their papillae found by Day on the pygidium were not visible on the Danish material. The mouth and the intestine can be seen dimly when the larva is viewed dorsally (cf. fig. 19).

In spite of several differences between the thoroughly described larvae of Day and the type of larva from the Isefjord, I have nevertheless, although with some hesitation, referred my larva to *Scolecolepis fuliginosa*. The main deviations are: *smaller size, 500 μ as against 800 μ; dark pigment on the lateral parts of the head, number of eyes five, the placement of the palpi, the character of the pigmentation on the dorsal surfaces of the chaetigerous segments and the apparent absence of the glandular cells on the pygidium.*

The justification of my determination is to be searched in the following facts: the larvae from the Isefjord, apart from the deviations mentioned above, are in the main identical with larvae of Day. Thus several structural details are common: *The pigmentation of the third parapodial ramus and the presence of the pigment on the dorsal part of the segments. Furthermore the large stages can be connected by transitional stages with the young Trochophora-stage with its attached egg-membrane very typical of Sc. fuliginosa.*

In the innermost part of the Isefjord proper, *Scolecolepis fuliginosa* seems to be the only species of this spionid genus, and other species of the same genus such as *Sc. ciliata* (Keferstein) are very rare on the whole in Danish seas.

The other spionid species in the Isefjord are: *Spio filicornis* (O. F. Müller), which in 1953 for the first time was found by me in the Vellerup Vig, where it is common now; *Pygospio elegans* Claparède, *Polydora ciliata* (Johnston), *Polydora quadrilobata* Jacobi, and *Polydora antennata* Claparède, this species also being hitherto unrecorded from Danish seas.

The reproduction and the development of *Spio filicornis* and *Pygospio elegans* are rather well-known, and the larvae of both species are of quite another type than the larva described above. They are partly developed on the basis of "nurse-eggs" (cf. THORSON, 1946, pp. 83—88).

The larvae of the *Polydora* species are so characteristic in comparison with the type described here, especially by their modified fifth chaetigerous segment, that they can also be excluded as possible parents of the larvae mentioned above.

8. ***Heteromastus filiformis*** **(Claparède)?**

According to FAUVEL (1927) *H. filiformis* spawns from September to April; LINKE (1939), however, has found spawning only early in the spring in Jadebusen. SMIDT (1951, pp. 65—66) is the only one to describe and picture from the Danish waddensea planktonic larvae at various stages, which can be referred to this species. However, no direct observations of spawning and development of the eggs are available and his determination may still be a little doubtful. All his stages, which show great conformity with the larvae of another capitellid species, *Capitella capitata* (see p. 75), are dark and opaque and have ciliated bands on each segment. According to SMIDT these larvae are lecithothrophic, e. g. they do not take any food from the plankton, but subsist on the yolk mass in their body. The largest one has about 9 segments and a total length of about 0.6 mm. The larvae were found most of the year in the plankton with maxima in the spring and the autumn.

In the innermost part of the Isefjord, where the species has been examined, adult individuals can be found commonly in practically all sorts of bottom material, from soft mud in the largest depths to sandy layers or more stony bottom in shallow water. It can also be collected in the *Mytilus* layer on the piers, but it seems to have its preference in the shallow areas consisting of pure fine sand.

As to the taxonomy of the collected mature specimens several very interesting deviations were found. According to FAUVEL (1927, p. 150) the genus *Heteromastus* among other things is characterized by the presence in the thoracal region of five segments bearing capillary setae. EISIG (1887, p. 839) and later on E. WESENBERG-LUND (1941, p. 38) state that juvenile specimens have four capillary segments only. In the Isefjord not only the new-settled individuals (see p. 72 below, fig. 23), but also any mature male or female—with a maximum length of five to six cm—have only four capillary segments!

A rather large number of adult animals of both sexes has been thoroughly examined and they all showed this character. In this connection it is noteworthy, however, that typical specimens of *H. filiformis*, in full agreement with the description given by FAUVEL, were found by me under the same ecological conditions in other Danish sea areas. Off the small island of Vorsø in the Horsensfjord (Eastern Jutland) I have found such individuals, which in every character were typical *H. filiformis*. Besides the absence of the last capillary segment other anatomical features were different in the Isefjord animals. Eyes should only be present on quite young bottom individuals and gills should be developed on the hindmost segments of the body of the adult. All mature animals from the Isefjord had distinct eyes, but very slight traces of gills, and their colour—owing to the red blood cells—was a brighter red than in the typical specimens from the Horsensfjord, which had a pronounced bluish-red colour.

Now, it is outside the scope of this paper to give a further description of the taxonomy of these two Danish populations of *Heteromastus filiformis*. The deviations described above are only mentioned here in order to give a sort of explanation of the two different types of pelagic larvae now described and pictured from the species in question (cf. SMIDT, 1951). From the facts available it seems to me as if the diverging specimens from the Isefjord population and perhaps also the material from the Ringkøbingfjord (see E. WESENBERG-LUND, 1941), may belong to a special ecological race, or—as may be more probable—a species of its own. However, until a complete and detailed taxonomic description has been made, the results about the reproduction and larval development of the species in question will be published under the name of *H. filiformis.*

The breeding biology has been examined by me in 1944 and 1951 to 1953 in Vellerup Vig. In contrast with the observations of Thamdrup (1935) concerning *H. filiformis*, the Isefjord animals are not living freely in the bottom, but have permanent, vertical sandy tubes and form characteristic masses of excrement on the bottom surface just as *Arenicola marina*, an observation also made by LINKE (1939).

The first mature males and females can be found long before the actual time of spawning, which occurs early in the spring dependent on the water temperature. Thus in January 1944 and 1953 many mature individuals were collected. In 1944 and 1951 the spawning itself, which as a rule seems to be finished within a short interval, took place in the very beginning of April at water temperatures of 6 to 7° C. (cf. fig. 1).

The eggs are laid on the surface of the bottom just above the aperture of the tube of the mother animal in globular jelly egg-masses, which are anchored in the bottom by a hollow thread of mucus (fig. 20). Through this appendage the mother animal will withdraw into its tube when spawning has stopped. The quite clear mucus of the egg-mass is stiff and elastic and very often its surface is covered with small bottom particles. The maximum diameter of the egg-mass is found to be about eight mm. In deeper water with a mud bottom, egg-masses of a more irregular shape are found. They often stick closely to the bottom particles.

In April 1953 I succeeded in following the spawning in detail during most of the breeding time. On April 2nd the first few egg-masses were observed in quite shallow water. The weather was then warm and the sea was calm and had a temperature of about 7° C. As the temperature in deeper water was rising and passing the level mentioned above, the rest of the population began

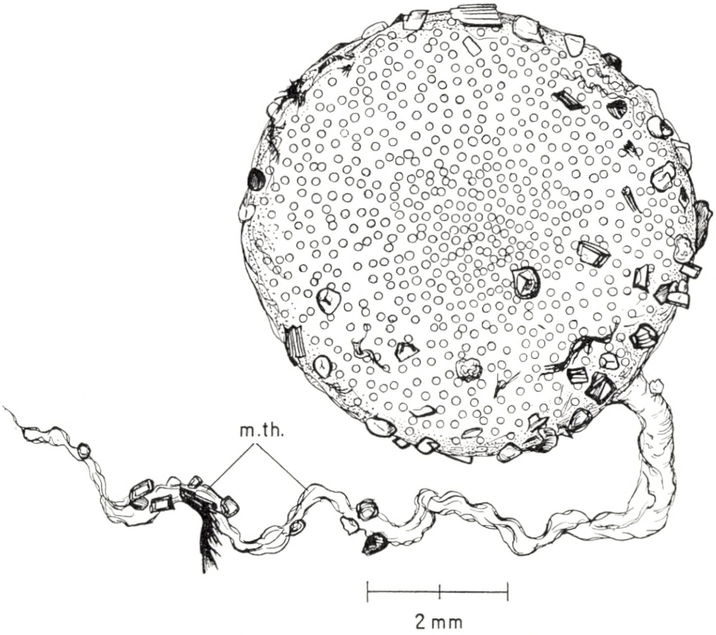

Fig. 20. *Heteromastus filiformis* (Claparède).
Egg-mass from the Isefjord, Vellerup Vig, 15.4.44.
The sticky surface with grains of sand and other bottom particles.
m. th., hollow thread of mucus, by which the egg-mass is anchored in the bottom by the spawning female.

spawning. When on April the 12th the spawning culminated, every type of bottom at any depth was covered with the characteristic yellowish egg-balloons. During the next few days the weather changed and became more windy. On this occasion it was very interesting to note how large a percentage of the egg-masses which was in danger of being destroyed by the sea. In the most exposed parts of the area all egg-masses attached were swept away by the waves and washed ashore. Without doubt the relatively short time from the spawning of the eggs to the hatching of the larvae is among the critical periods in the life of the species since the mature specimens of the area are spawning all at the same time. Thus a heavy gale just in this period may considerably reduce the number of eggs, i. e. the new generation of the year.

On the unsegmented new-laid egg the yolk is 110 μ across and is opaque with a faint yellowish-green colour (cf. LINKE, 1939, p. 316) and the egg membrane is not visible. Soon after the spawning, however, the membrane and the polar bodies can be seen. The exact number of eggs per spawn was not counted, but a single egg-mass may contain several hundred eggs.

The segmentation and early development of this species have not been examined in detail. The young Trochophora seems to be ready for hatching two to three days after spawning (no measurements of the temperature). In aquaria the early pelagic larvae were reared from egg-masses laid here by adult specimens from the fjord and were found to be identical with larvae taken in the plankton from the fjord.

The young Trochophora (fig. 21) is from 140 to 155 μ long. It is very transparent and has a faint greenish colour. In the broad prototroch there are grass-green chromatophores. The cilia are long and placed at the uppermost edge of the band. The two distinct eyes with lenses are dark-red. From the mouth a narrow row of fine cilia runs along the ventral surface, the neurotroch. The apical tuft is well-developed with long and rather thick cilia. Most of the digestive system with the stomach and the oesophagus is visible owing to the transparency of the larva; the characteristic division of the intestine of the Metatrochophora can already be seen.

Metatrochophora II (fig. 22), about 300 μ in full length, has nine chaetigerous segments, most of them with separate notopodial and neuropodial sections (no. and neu.). In the dorsal and ventral part of the first three segments there are distinct capillary setae, while the rest of the setae are typical hooks. The single segments are mutually well demarcated and separated by the dissepiments, which in the figure can be seen especially between the intestine and the body wall (d.). This larval stage, which is very clear and transparent, is more yellowish than in the Trochophora. The grass-green chromatophores, now very conspicuous owing to their more dark-green colour, are present especially above the mouth and as irregular borders behind the prototroch and the telotroch.

The ciliation on the surface of the larval body forms four groups; the first and most anterior one is the apical tuft about 75 μ long, with a surrounding ring of short cilia (r. ci.). The next and most pronounced one is the muscular, thickened prototroch girdle with two rows of cilia. One anterior row consisting

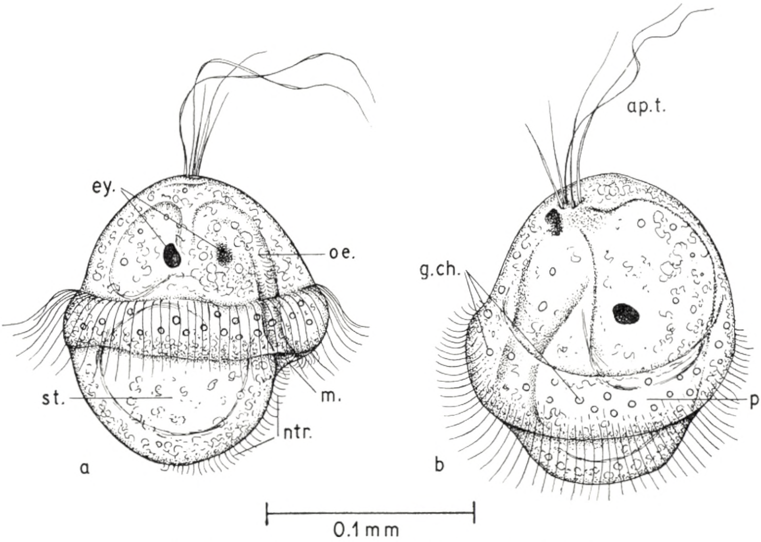

Fig. 21. *Heteromastus filiformis* (Claparède).
Two young trochophores a few hours after the hatching from the egg. Reared in aquaria from egg-masses taken in the Isefjord, Vellerup Vig, 22.4.44.
a. from the right side.
b. from the left side and partly from above.
ap. t., apical tuft of cilia; ey., eyes with lenses; g. ch., grass-green chromatophores in the prototroch girdle; m., mouth; ntr., ventral ciliary groove, the neurotroch; oe., oesophagus; pr., thickened prototroch girdle round the larval body with the long cilia fixed at its uppermost edge; st., larval stomach.

of long and strong cilia and another posterior row of short cilia stopping on each side of the mouth. The telotroch has only one unbroken line of long cilia. The fourth group comprises the cilia in the narrow central groove, the neurotroch, ending before the anus in a small tuft of longer cilia. During swimming the apical tuft is turned backwards along the body. There are no cilia on the segments as described by Smidt (1951).

Close behind each of the two round, dark-red eyes, which have lenses, there is a small group of oblong refracting cells, maybe mucus cells or a sort of glandular cells. Large refracting mucus cells are also observable on the anal protuberance close behind the telotroch.

The digestive system seems rather complicated in organization and is divided into distinct sections. The mouth (m.) is broad, about 40 μ, and densely ciliated and leads to a strongly built, ciliated oesophagus (oe.). On each side of the mouth aperture there is an oblong ciliated sac, both of which might be the pharyngeal diverticles. The main part of the intestine comprises two large ciliated sections containing a few oil globules in their walls. The first one, behind the oesophagus, is the larval stomach, followed by a more opaque section, the intestine proper. There is a short thickwalled rectal part with the anus placed dorsally to a protuberance representing the anal cirrus of the adult (a. c.). The intestinal system has no coloration of its own, only the larger section is darker and more opaque.

Older Metatrochophora. The largest pelagic stage of the species collected in the plankton of Vellerup Vig has about eleven chaetigerous segments and a maximum length of about 400 μ. This stage was still very transparent, but the colour has changed to a more reddish hue. The green chromatophores have completely disappeared. The total shape is now more longish and not so conical as in the previous stage. The ciliation is just the same as before; however, the apical tuft looks shorter. The eyes are darker, almost black. The protuberance of the posterior end is longer and more separated from the anal segment. The movements of the larva are rather slow. A close examination of the plankton samples showed no older stages and the stage described above seems to be the last free-swimming stage before settling (cf. text below).

In the period 1950—51, when the quantitative plankton samples were taken in Vellerup Vig (see p. 4), larvae of all the types mentioned and pictured above were recorded in the fjord plankton on April 22nd, in two hauls, 13 specimens only

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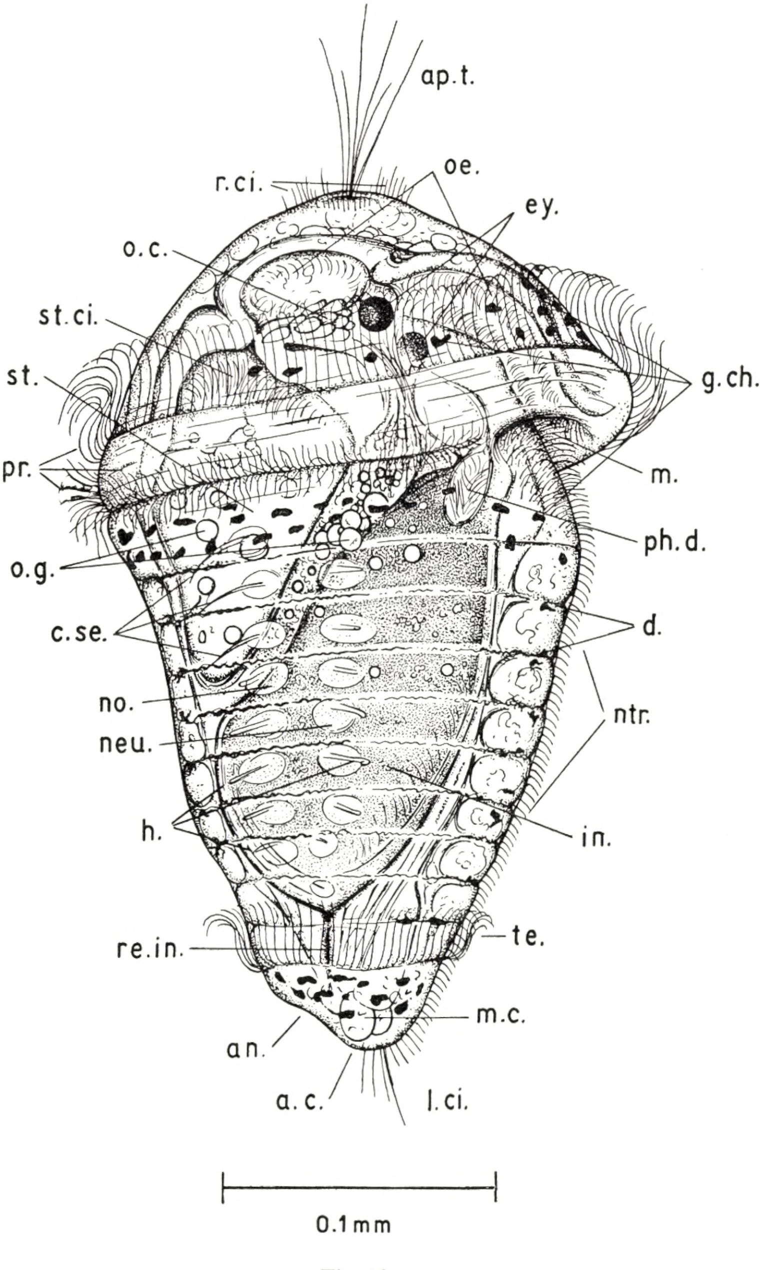
Fig. 22. *Heteromastus filiformis* (Claparède).

Metatrochophora II, right-side view, the Isefjord, Vellerup Vig, 2.5.45.

an., dorsally situated anus; a. c., developing anal cirrus; ap. t., apical tuft of cilia; c. se., notopodial capillary setae of the first three chaetigerous segments; d., dissepiments between the segments; ey., eyes with lenses; g. ch., grass-green chromatophores; h., notopodial and neuropodial hooks of the hindmost chaetigerous segments; in., intestine; l. ci., tuft of long cilia at the posterior end of the neurotroch and just before the anus; m., mouth aperture; m. c., mucus cells; neu., neuropodial section of a chaetigerous segment; no., notopodial section of a chaet. segment; ntr., neurotroch; o. c., group of large, oblong cells close behind the eyes; oe., strong thick-walled and ciliated oesophagus, the posterior part with a narrowing; o. g., oil globules in the wall of the intestine; ph. d., ciliated pharyngeal diverticle (?); pr., muscular prototroch girdle with two types of cilia, the long anterior and the shorter posterior; r. ci., ring of short cilia round the apical tuft; re. in., short rectal part of the intestine; st., larval stomach w. ciliation st. ci. close to the opening between the oesophagus and the stomach; te., telotroch.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0.1 mm

Fig. 22.

trochophores and on May 6th, in one haul 23 old metatrochopores. Samples from May 27th did not contain a single larva, and the plankton occurrence in April—May seems to be the only and normal one of the year (see under the spawning p. 66). As to the duration of the free-swimming stages, about three weeks to one month will be the normal range, but the water temperature may again play an important rôle.

The young, newly metamorphosed bottom stage (fig. 23). In May 1953 a number of the largest pelagic larvae of the type described above were collected in the fjord plankton and were placed in vessels with fjord water and containing a thin layer of fine sand. Within a few days most of the larvae had metamorphosed.

The animal just settled has a total length ranging from 535 μ to 640 μ, of which the anal cirrus makes up the 85—90 μ. The full number of segments comprises thirteen. The opaque and granular prostomium, which at the foremost edge has sensory hairs (s. h.), is rounded conically and has two small palps on the ventral surface. These are post-larval organs and are not present on the larger bottom stages. The eyes, which persist in the adults, are now densely black and have no visible lenses. In the next segment, the achaetous mouth segment, the mouth aperture is situated at the foremost edge. When closed the mouth is about 40 μ broad: that is exactly the same as in Metatrochophora II.

The following ten segments the chaetigerous segments constitute the completely finished thoracal section of the adult individual. In comparison with the young bottom stages of other capitellid worms, cf. *C. capitata* (Eisig 1887 and 1899) and *Notomastus latericeus* (Wilson, 1933), this species is remarkable in having from the beginning the whole number of thoracal

Fig. 23. *Heteromastus filiformis* (Claparède).

Young metamorphosed bottom stage in right-side view and partly from below. Metamorphosed in aquaria, 17.5.53. Taken as Metatrochophora II in the plankton, Vellerup Vig, the Isefjord.

a. c., anal cirrus with blood vessel closed distally; a. v., anastomosing blood vessels; b. c., red blood corpuscles; d., dissepiments; d. c. se., bundles of dorsal capillary setae; d. h., dorsal hooks; d. v. l., dorsal longitudinal blood vessel; ey., eyes; m., mouth; m. s., mouth segment; o. g., oil globules in the foremost part of the intestine; p., prostomium; ph., muscular, protrusible pharynx; pl., palps; s. h., sensory hairs in front of the prostomium; v. se., bundles of ventral setae; v. l. v., ventral longitudinal blood vessel.

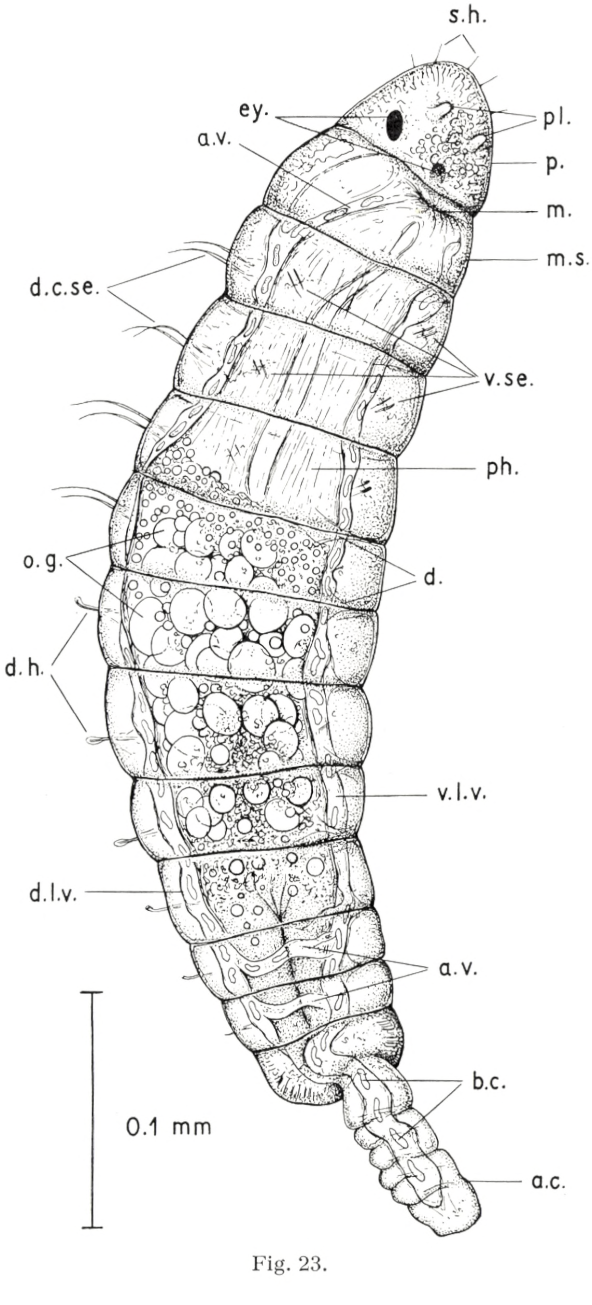

Fig. 23.

segments, eleven in all and not twelve as there should be in the genus *Heteromastus* according to FAUVEL (1927, p. 150). The first four chaetigerous segments have 1—2 long, curved capillary setae in their dorsal parts (d. c. se.); the ventral setae are a little shorter. The following six segments have only hooks and only one in each group (in the figure only the dorsal hooks are visible, d. h.). The last segment is the pygidium with the single, finely wrinkled anal cirrus, with the dorsally placed anus.

The vascular system is remarkably well-developed and longitudinal vessels, dorsal and ventral, are visible even at small magnifications. Round the anterior part of the pharynx and in the last few segments fine anastomoses connecting the dorsal and ventral vessels can be seen. In the anal cirrus there is a well-marked, distally closed vessel. Everywhere in the vascular system blood corpuscles (b. c.), faintly red, can be seen.

The intestinal duct has two main sections. The foremost part is the very thick-walled, protrusible pharynx, which is about 140 μ long and extends to the fifth chaetig. segment. The rest of the intestine is very opaque owing to its contents of often large oil globules. The intestinal colour is reddish brown.

The whole animal is quite transparent and of a faint reddish hue. Dissepiments between the segments are present.

The movements of the very contractile bottom stage are rather quick and very much similar to those of a common earthworm.

9. *Capitella capitata* (Fabr.).

The reproduction and larval development of this species is well known. The following authors: EISIG (1887 and 1899), CLAPARÈDE and MECZNIKOW (1869), LESCHKE (1903), HOFKER (1930), DAY (1937), THORSON (1946), and SMIDT (1951) give almost identical, illustrated accounts of the breeding habits, which, in contrast to what is found for this species in the Isefjord include a full pelagic stage in its development. The details known may be summarized as follows:

The new-laid eggs are found in the tube of the mother animal, which protects the brood until the larvae hatch 10 to 14 days later.

The young larva, which is provided with distinct ciliary bands, both prototroch and telotroch, has from 12 to 13 chaetigerous segments. The first three segments have capillary bristles, while the rest only carry hooks in their bundles of setae. There are two distinct red eyes in older larvae. The mouth and the intestine are well developed. The colour of the intestine, which according to Day contains no food until after the metamorphosis, is most varying, from greyish to olive-green or navy-blue.

After a free-swimming stage of seven days, the pelagic attributes disappear and the larva goes to the bottom metamorphosed as a fully equipped bottom stage, having the same number of chaetigerous segments as the plankton larva. The size of the plankton stage is about 400 to 500 μ.

In the Isefjord area *Capitella capitata* is a wide-spread, but not very common species. Regularly only a few specimens can be found, even if thoroughly searched for, and only very seldom, e. g. in the Roskildefjord near Frederikssund, it occurs in considerable numbers.

The species has been taken in all months of the year. Mature specimens with eggs or larvae in their sandy tubes were only recorded in two periods: from April to May and from October to November, but there seems to be some evidence of a spawning also in the intermediate summer months. Individuals examined from January to March contained no eggs or larvae in the tubes. Since my observations of the extension of the breeding time of *C. capitata* are so fragmentary, I have found it natural to omit the species in fig. 1.

As other marine invertebrates in the Isefjord fauna, this species is remarkable by having two modes of larval development and even at the same time of the year. As described in the literature (see above) it has free-swimming larvae with a short pelagic stage and another and—as far as I can see, not previously known—nonpelagic, direct development.

The pelagic larvae, which were taken in the plankton in Vellerup Vig, correspond very closely to the description given by several authors.

They were collected in May 1944 and 1945, very few in number in horizontal hauls. They had a length of 500 to 600 μ and had always 13 chaetigerous segments in all, the first three of which carried capillary setae. The rest of the segments were only supplied with hooks. There were two dark red eyes on the conical head and a distinct prototroch and telotroch. The colour of the larval body was always faintly yellowish and almost transparent. The intestine was dark with greenish contents and the foregut in the foremost three segments was coiled. The larvae were very fast swimming and could assume any shape owing to the great elasticity of the body. One larva taken in the plankton on May the 14th, 1944, metamorphosed 60 hours after being collected. The temperature in this period was constantly 9° C.

Adult female individuals with eggs or embryos in their tubes were collected by me in October—November 1949 and in April—May 1954. The material from the autumn gave no evidence of a deviation in development from that hitherto known, since the embryos were too young. They were placed in a mucus string built as a transparent tube in the walls of which the embryos were lying close together. Thus the sandy tube of the female was as a case round the egg-string.

The material of *C. capitata* tubes from May 1954 gave the proof of a completely non-pelagic development with individuals going directly from the mother tube as fully equipped animals to the bottom life. One quite intact egg-string from 16.5.1954 contained individuals with a length ranging from 1100 to 1200 μ. Most of the specimens dissected out of this egg-string were of the same stage of development while very few represented an earlier stage. Most of the young animals had 13 chaetigerous segments and only a single one comprised 14 segments with setae.

Any individual removed from the mucus was a typical bottom stage without any pelagic attributes at all and crawled away from the tube. Moreover, they all agreed with the type of the young bottom stage hitherto described; thus the first three segments besides hooks in their dorsal parts also had capillary setae and the following segments contained hooks only. The main colour of the body was more whitish than yellowish as recorded about the pelagic larvae from the same locality (May 1944 and 1945). There was one very conspicuous feature which furthermore characterized the young bottom stage. The intestine in all the specimens was opaque and filled with a dense yolk mass, which began in the fifth chaetigerous segment and stretched through the whole rest of the body to the anus.

The presence of this yolk mass seems to me to explain the non-pelagic development of *Capitella capitata*. Probably the egg-size and with that the yolk volume have been larger than usually found. However, a development connected with nurse-eggs cannot be excluded as a possibility. In this connection it is worth while calling attention to the extraordinarily large size of the bottom stage when leaving the egg-string, maximally more than 1200 μ or exactly twice the size of the bottom stage developed from pelagic larvae.

As mentioned above, a double mode of larval development is also known from other marine invertebrates of the Isefjord area. Within the polychaetes, up to now 14 species out of the 45 species known from the innermost part of the Isefjord have been examined by me as to breeding biology. Three of these species have both a development by pelagic larvae and a direct one without a free-swimming stage at all. The three species are: *Nereis pelagica* L. (described in this paper p. 53–59), *Pygospio elegans* Claparède, the non-pelagic mode of which is based on nurse-eggs; both modes occur simultaneously within the same egg-string (the investigations of this species have not yet been finished), and finally *Capitella capitata* Fabr. just described.

Within the Gastropoda nine species have so far been examined out of the 41 species recorded from the Isefjord (See E. Rasmussen, 1944 and 1951). Of the nine three in all have the pelagic as well as the non-pelagic development, viz: the two prosobranchs, *Rissoa membranacea* Adams (not published) and *Brachystomia rissoides* (Hanl.) and the nudibranch, *Embletonia pallida* A. and H. (cf. Rasmussen, 1944 and 1951). This rather high percentage of invertebrate species, which in the same area have two quite different modes of development is extremely interesting.

10. *Metatrochophora* sp.

On May the 13th, 1944, several young metatrochophores were collected in plankton samples from the Vellerup Vig.

The species represented by these free-swimming and typic-

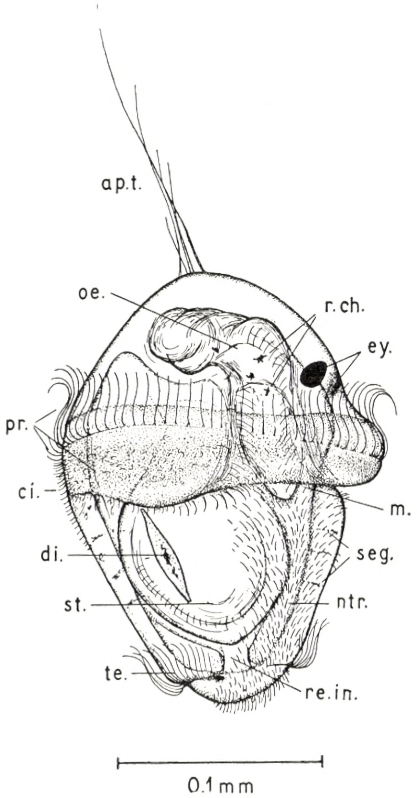

Fig. 24. *Metatrochophora* I sp.
The Isefjord, Vellerup Vig, 13.5.44.
ap. t., apical tuft of long cilia; ci., a dense cover of fine cilia on the prototroch girdle, only visible at the contours; di., diatom in the stomach; ey., dark red eyes, no lenses visible; m., mouth aperture beneath the prototroch girdle; ntr., neurotroch; oe., oesophagus; pr., broad prototroch girdle, rather opaque and with one row of long anterior cilia and short posterior cilia; r. ch., red chromatophores; re. in., rectal part of the intestine; seg., slight traces of a developing segmentation; st., larval stomach; te., telotroch with a ventral gap between the cilia.

ally pelagic larvae, is either rare in the area or the larvae may have been transported by currents from elsewhere, as the larvae in question have only been taken on this single occasion.

The total length of the larva (fig. 24), without the apical tuft of cilia, was about 200 μ. The colour was slightly yellow with a few small red chromatophores behind the large dark-red eyes. The prototroch formed a complete ring of long cilia arranged in a single row anteriorly in the broad, densely ciliated girdle round the body. The ciliation on the larval surface was limited to a longitudinal groove, the neurotroch running from the mouth aperture to the anus on the hindmost tip of the animal. The telotroch was not a complete ring, for a slight ventral gap was present where the longitudinal ciliation was passing through. The segmentation of the body was very incomplete and no setae were visible. The apical tuft of cilia was very long, about 140 μ, consisting of a few stout cilia. The oval mouth had a largest diameter of about 60 μ and was followed by a ciliated oesophagus leading into the larval stomach. The whole intestine was rather thick-walled and had a dense ciliation. The rectal part of it was very short.

The identification to species of this larval type when no other stages are available is of course very difficult, but there might be some reason to refer it to the capitellidae, owing to various typical details in its structure. For instance the ciliation, the apical tuft and the neurotroch, cf. the description given above of the larval stages of *Heteromastus filiformis*; cf. also WILSON (1933), who describes the development and larval stages of another capitellid sp., *Notomastus latericeus* Sars.

Summary.

An account is given of the occurrence, reproduction and larval development of 10 polychaete annelids from the Isefjord (Zealand, Danmark).

The species are: *Harmothoë imbricata* (L.), *Harmothoë impar* Johnston, *Eteone longa* (Fabr.), *Magalia perarmata* Marion and Bobretsky, *Microphthalmus sczelkowi* Mecznikow, *Nereis pelagica* L., *Scolecolepis fuliginosa* (Claparède), *Heteromastus filiformis*? (Claparède), *Capitella capitata* (Fabr.), and Metatrochophora I of an unidentifiable species.

The temperature is shown to be the main factor initiating spawning, (cf. fig. 1).

H. imbricata. The larval stages, which are truly pelagic, including Trochophora, metatrochophores I and II (figs. 3—5) and the young newly metamorphosed bottom stage, are described (fig. 6). It is shown that the pelagic larvae dominate the zooplankton in January. Metamorphosis normally occurs in midwater and younger adults live a semi-pelagic life.

H. impar. The pelagic larvae—Metatrochophora II is described—and the young bottom stage (figs. 7—9) rather much resemble those of *H. imbricata.* It is pointed out that the pigmentation is subject to so much variation within the single species that its value as a systematic character is doubtful.

E. longa. Metatrochophores I and II, the Nectochaeta and the young bottom stage are described and pictured (figs. 10—12). Variations in the types of larvae in comparison with older descriptions are also given.

M. perarmata. A species new to the Danish fauna. The results are very scanty and the larval development is not described (fig. 13). In connection with the description of the breeding habits a brief discussion of the zoogeographic composition of the polychaete fauna of the Isefjord is found. Out of 45 recorded species 12 constitute a faunal element, the main distribution of which is south of the Scandinavian seas. Out of these 12, 8 are hitherto unrecorded in Danish seas.

The possible relation of these findings to climatic changes in our seas is briefly touched on.

M. sczelkowi. The spawning, the egg-mass and the egg-size are described (figs. 14—16). No observations on the larval stages are available.

N. pelagica. Epitoquous males and females were found. A description of these stages is given, based on live specimens. Planktonic larvae (Nectochaeta, fig. 17) were collected in the Isefjord and in the harbour of Copenhagen (the Sound); the latter represents a type indicating a pelagic stage of far longer duration than hitherto known (fig. 18). Evidence is brought forward to show that also a totally non-pelagic mode of development of *N. pelagica* is found within the same small area in the Isefjord. A short notice concerning the *Nereis* species of Vellerup Vig (vicinity of the laboratory) is given (p. 59).

Sc. fuliginosa. Pelagic larvae from the plankton in Vellerup Vig are described and pictured (fig. 19), and some deviations from former descriptions are pointed out. On p. 64 the other spionid species hitherto recorded in the Isefjord are mentioned and their larval development briefly compared with that of *Sc. fuliginosa.*

H. filiformis? The results obtained include the whole development with descriptions of egg-laying, egg-mass, pelagic stages comprising Trochophora and Metatrochophora II, and the newly settled bottom stage (figs. 20—23). However, the determination as to species of the adults is doubtful owing to some important differences, which may indicate a new and undescribed capitellid species.

C. capitata. In the Isefjord the species has two modes of larval development even in the same period of the year. One —as known from the literature—with free-swimming larvae, and another, non-pelagic, direct development. The presence of this double mode of reproduction is discussed (p. 77) and a comparison is made with another invertebrate group, the Gastropoda, where similar conditions have been found in the Isefjord.

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