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The Larvæ of the Decapoda Macrura and Anomura of Plymouth.

By

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Assistant in Zoology, University College, London; late Temporary Assistant Naturalist at the Marine Biological Laboratory, Plymouth.

With Plates I-IV.

THE larvæ of the Decapod Macrura occur throughout the year in the townettings taken in Plymouth Sound; while during the summer months they form an important and conspicuous feature of the coastal plankton.

In only a few cases have their life-histories been fully worked out, owing probably to the difficulty of rearing the larvæ under artificial conditions; and the literature on the subject is consequently both scanty and scattered. It has therefore been suggested that a brief review of the larvæ already described, together with a few additional ones which have been identified during two years' examination of the Plymouth plankton, from 1917–1919, might be of some use to future investigators.

The object of the present paper is to enable future workers to see at a glance how far these forms have been investigated, and especially to facilitate the identification of the living larvæ from the tow-nets.

No attempt has been made to describe the appendages in detail, as such particulars can generally be found in the literature cited. A general outline drawing is given of the more important forms in their first larval stage, and a figure of the telson and uropods in the fourth or last larval stage is also shown.

As the coloration of the larva is often of great assistance in identifying the living animal, it is here described rather fully, and, whenever possible, the drawings and the colour notes have been made from the living larva. In cases where no direct observations were available the colour descriptions are quoted from other authorities.

The larvæ of three families of Decapods commonly found at Plymouth —namely, the Hippolytidæ, the Galatheidæ and the Paguridæ—are known as yet very incompletely; and even when the larvæ have been described, it is often very doubtful whether they have been referred to their correct species. In such cases, therefore, a typical larva has been described, without attempt to refer it to a particular species.

The nomenclature adopted throughout this paper is that used in the Plymouth Marine Invertebrate Fauna List (1904).

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I am indebted to Dr. Calman, of the British Museum, and Dr. E. J. Allen, of the Plymouth Laboratory, for valuable advice on various points, and to Miss M. V. Lebour, D.Sc., for her assistance to me throughout, and particularly for her help in the rearing of the larvæ in the Laboratory.

Family PALÆMONIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :--Leander serratus (Pennant). Leander squilla (Linnæus). Palæmonetes varians (Leach).

FEATURES CHARACTERISTIC OF THESE LARVÆ OF PALÆMONIDÆ.

Rostrum. Long, slender, and pointed, reaching almost to end of first antenna.

Eyes. Sessile in early stages, later stalked and movable.

First Antenna. Long and straight (cf. Pandalidæ).

Telson. In early stages spatulate, truncated, bearing three plumose setæ at each corner and eight at regular intervals along the posterior margin. In later stages telson becomes long and narrow.

DISTINGUISHING FEATURES OF THE FOUR LARVAL STAGES.

Stage I (First Zoœa Stage) :---

- (a) Caudal plate simple.
- (b) Uropods absent.
- (c) Three pairs of setose exopodites.

Stage II (Second Zoœa Stage) :---

- (a) Caudal plate unchanged.
- (b) Uropods absent.
- (c) Five pairs of setose exopodites.

Stage III (Intermediate Stage) :--

- (a) Telson narrower, cleft slightly in middle line.
- (b) Outer uropods well developed and armed with spines; inner uropods present, but small and spineless.
- (c) Six pairs of setose exopodites.

Stage IV (Mysis Stage) :---

- (a) Telson long and narrow.
- (b) Both pairs of uropods well developed and armed with spines.
- (c) Six pairs of setose exopodites.

| Species. | Size. | Rostrum. | Colour, |
|---------------------|--------------------|---|--|
| Leander serratus . | 4 mm. Stage I. | Reaches beyond 1st joint of 1st Ant. | General coloration red and yellow, fore-part of abdomen barred with transverse red and yellow stripes. |
| Leander squilla . | 2∙9 mm. Stage I | Reaches beyond 1st joint of 1st Ant. | Scattered red chromatophores on dorsum; three red chromatophores transversely on 3rd abdominal segment, one on 5th abdominal seg- ment and one at base of telson. |
| Palamonetes varians | 3∙7 mm. Stag∂ I | Does not reach to end of 1st joint of 1st Ant. | Pale yellowish, with bright yellow chromatophore dor- sally on 3rd abdominal seg- ment and at base of telson. A faint red streak of diffuse pigment generally runs down |

Literature.

Couch, R. Q. 1844. Mayer, P. 1881. Sollaud, E. 1912. Thompson, J. V. 1836.

centre of telson.

Family PANDALIDÆ.

Other larvæ occurring at Plymouth, adult not recorded from this district :- Pandalus Bonnieri Caullery.

FEATURES CHARACTERISTIC OF THESE LARVÆ OF PANDALIDÆ.

Eyes. Sessile in early stages, later stalked and movable.

First antenna. Slightly concave on outer side in late stages.

Telson. Similar to that of *Crangon vulgaris*; rather deeply indented in middle line in early stages. In later stages telson becomes long and narrow, similar to that of Palæmonidæ.

Coloration. In early stages very transparent, but later there is a great development of red and orange chromatophores, especially on the thorax, and developing endopodites of thoracic limbs.

DISTINGUISHING FEATURES OF THE FOUR LARVAL STAGES.

Stage I. Caudal plate simple, bearing fourteen spines; uropods absent.
 Stage II. Caudal plate simple, bearing sixteen spines; uropods absent.
 Stage III. Telson and outer uropods well developed and armed with spines; inner uropods present, but small and spineless.

Stage IV. Both pairs of uropods well developed and armed with spines.

Literature. Sars, G. O. 1900.

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Species. Pandalus Montagui. Hatched in Laboratory.

Pandalus brevirostris.

Pandalus Bonnieri.

N.B.—In Stage I there is a median dorsal spine behind the rostrum. In Stage II this is replaced by two curved, dorso-lateral horns. (Sars, 1900.)

Size. 4 mm. Stage I.

2.1 mm. Short and pointed.

Stage I.

Long and slender, reaching almost to end of first antenna.

Rostrum.

Short and pointed.

Colour.

- Stage i. Very transparent; yellow chromatophore on eyestalk and one at base of telson. Stage IV. Numerous orange and red chromatophores, giving a general orange shade to the larva.
- Stage I. Transparent, with orange and red chromatophores on eye-stalks, yellow on third and fifth abdominal segments, at base of telson and on caudal plate.

Stage IV. Orange coloration similar to late stages of P. Montagui.

Stage II. Red chromatophores on eye-stalks, deep yellow on thorax and endopodite of pereiopods. Scattered chromatophores on third and fifth abdominal segments and at base of caudal plate.

Family HIPPOLYTIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :---

Hippolyte fascigera Gosse. Hippolyte varians Leach. Hippolyte viridis (Otto). Spirontocaris Cranchi (Leach).

The family Hippolytidæ is represented at Plymouth by the above four species. Of these the larval development of one only, *Hippolyte varians* Leach, has been fully described (Sars, 1911), and although the larvæ of this genus occur fairly frequently in the plankton samples at Plymouth during the summer months, they have not yet been described in detail.

They are distinctly smaller than the larvæ of the other families of Decapods at Plymouth, *Hippolyte varians* in its first zœa stage measuring only 1.5 mm. in length. This larva, which may be considered typical of the genus, bears a strong resemblance to certain members of the Crangonidæ, e.g. *Crangon vulgaris*; the telson of *H. varians* and *C. vulgaris* in the first stage being almost identical, both in shape and armature (cf. Pl. I, Fig. 3, and Pl. II, Fig. 1).

The Hippolyte larva, however, is distinctly shorter and stouter in build than C. *vulgaris*; it has a more pronounced caridean bend, the abdomen is quite unarmed, the eyes are relatively much larger and the rostrum rather longer than in C. *vulgaris*.

The coloration consists of a luminous yellow shade over the thorax and part of the telson, with scattered orange and red chromatophores in certain definite positions, e.g. on the eye-stalks, base of rostrum, the first three and the fifth abdominal segments and the base of the telson.

The larva of Spirontocaris Cranchi is of a more slender character than H. varians, measuring about 2 mm. in length in the first zœa stage; and the rostrum is very short or absent; but in other respects it closely resembles that of H. varians, and the distribution of the chromatophores, which are of a rather brighter red than in H. varians, is almost identical, although the larva is more hyaline in appearance, owing to the absence of the luminous yellow network on the thorax.

Literature.

Sars, G. O. 1911.

Williamson, H. C. 1915.

Family ALPHEIDÆ.

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FEATURES CHARACTERISTIC OF THESE LARVÆ OF ALPHEIDÆ.

Thoracic Legs. Last (fifth) pair elongated and styliform, carried pointing forwards beneath the body (not developed until third larval stage in Alpheus ruber).

For distinguishing features of the first four larval stages, see table given under Pandalidæ on page 387.

Alpheus ruber Milne Edwards.

The accounts of the larval stages of *Alpheus ruber* are very incomplete; a short description of the various larval stages, founded on material collected at Plymouth, is therefore given here.

Stage I. In the first stage the larva measures about 2.6 mm. from the tip of the rostrum to the end of the swimming-plate. The body is somewhat compressed laterally, and the typical caridean bend in the third abdominal segment is quite distinct. There are three pairs of setose exopodites, one on each of the three pairs of maxillipeds, and the endopodite of the third maxilliped is rather long and slender and ends in a sharp point. Behind the third maxilliped are the rudiments of the first two pairs of thoracic legs, of which the first are already biramous. The terminal swimming-plate is of spatulate shape, armed around the posterior margin with fourteen strong setæ, and bearing a close resemblance to the caudal plate of *Crangon vulgaris* in the same stage.

Stage II. The larva in this stage is very similar to that of the preceding stage, from which it differs in the following points :

Its length is now about 2.8 mm. The endopodite of the third maxilliped terminates in a very long, slender spine, about twice the length of the exopodite. The use of this long spine is not clear, but it is apparently functionally replaced in the next larval stage by the fifth thoracic leg, which is there drawn out into a similar process, while that of the third maxilliped simultaneously disappears. The rudiments of the first thoracic legs are longer, and the swimming-plate is armed with sixteen spines, an additional pair having appeared in the middle of the posterior border.

Stage III. The length at this stage is about $3 \cdot 2 \text{ mm}$. The third pair of maxillipeds have lost the long spine on the endopodite, which now terminates in a short point. The exopodite of the first pair of thoracic legs is now setose, making four pairs of setose exopodites in all. Behind the first thoracic legs the rudiments of the second and third pairs are plainly visible. The fourth pair is not yet apparent; but the fifth pair, prematurely developed, each takes the form of a three-jointed process terminating in a long, slender spine which extends beyond the end of the first antenna in front, and is very similar to that found on the third maxilliped in the previous stage. These appendages are carried pointing forwards underneath the body, and appear to be characteristic of the larval stages of the Alpheidæ. The pleopods are still absent, but there are now two pairs of uropods, the outer pair fully developed and setose, but the inner small and unarmed. The telson is narrower, but armed with sixteen setæ, as in the previous stage.

Stage IV. The larva is rather shorter and stouter in this stage, measuring about 2.8 mm. in length from rostrum to telson. The rudiments of all the thoracic legs are now present, the fifth pair still ending in a long spine reaching well beyond the first antenna. The pleopods are not yet distinct, the telson is longer and narrower, and both pairs of uropods are well developed and armed with plumose setæ.

The larval stages of Alpheus differ from those of most Decapods in that the fourth larval stage is not immediately followed by the first postlarval, resembling the adult form, but is succeeded by a series of stages during which the characters of the adult are acquired by degrees. At the fourth larval stage described above, the telson and uropods have reached a stage of development typical of this period of the larval life; but the thoracic legs and the pleopods are still comparatively little formed. During the following larval stages these appendages are further developed.

After the fourth larval stage the subsequent stages are not so sharply defined, but five further stages (V-IX) can be discerned, distinguished by the following points :---

Stage V.

Length about 2.8 mm.

Five pairs of pleopods, small but distinct.

Stage VI.

Length about 3.5 mm.

Five pairs of setose exopodites—from the first maxilliped to the second thoracic leg.

Pleopods biramous, about the length of one abdominal segment.

Stage VII.

Length about 3.6 mm.

Thoracic legs distinctly larger and more developed.

Pleopods extending over about one and a half abdominal segments; divided into distinct base and two distal rami.

Stage VIII.

Length about 3.9 mm.

First and second pairs of thoracic legs chelate ; third and fourth pairs jointed.

Pleopods covering two abdominal segments.

Stage IX.

Length about 4 mm.

Spine on fifth thoracic leg absent (possibly broken in my specimens). Pleopods and thoracic legs fully developed, but still enclosed in the larval sheath.

The following colour notes were taken from a larva of the second stage : Pale yellow on eye-stalks, first antennæ, sides of thorax, third and fifth abdominal segments and the terminal swimming-plate. Bright red chromatophores on eye-stalks, first antennæ, base of rostrum, at junction of thorax and abdomen, on second, third and fifth abdominal segments and on terminal swimming-plate.

Athanas nitescens (Leach) (Pl. I, Figs. 4 and 8).

Full descriptions of the later larval stages of this species have been given by Sars (1906), who believed the first stage figured by him (Pl. I, Figs. 1 and 2) to be the earliest free larval stages. Two younger larval stages have, however, been found in material collected at Plymouth in August and September, 1920, and that figured by Sars as the first therefore corresponds to the third larval stage of Alpheus or other Decapods. The first and second larval stages only are here described.

Stage I. The larva measures about 1.9 mm. from the end of the first antennæ to the end of the swimming-plate, or 1.6 mm. from the tip of the rostrum to the same spot. The thorax is less than half the length of the abdomen; the carapace is evenly rounded behind and ends in front in a short acute, median rostrum; the eyes are large and directed slightly forwards. The abdomen is long and slender, with a distinct caridean bend at the third segment, and ending in a flattened triangular swimming-plate armed with plumose setæ. There are no pleopods, the animal swimming actively through the water by means of the setose exopodites on the three pairs of maxillipeds.

The *First Antenna* is a simple unjointed process bearing at the end a short palp with tactile appendages, and on the inner side of the palp a stout plumose seta and several fine spines.

The Second Antenna consists of a basal joint prolonged on its inner border into a short spine and bearing an antennal scale, about half as long again as the base, bordered by eleven plumose setæ; and a small process on the inner side of the scale, tipped with a short serrate spine.

The Mandible is very small, apparently with a small palp.

The *First Maxilla* is small but bilobed, the masticatory lobe beset with a few weak setæ, and bears a rudimentary palp.

The Second Maxilla is a simple unjointed process tipped with a single

seta, but showing indications of secondary lobes along its inner edge. The scaphognathite is not jointed off from the base, and bears three to five scattered marginal setæ.

The *First Maxilliped* consists of a basal portion bearing a seta-tipped endopodite (not jointed off from the base), and a curved exopodite with two terminal plumose sete.

The Second Maxilliped has a base with a short endopodite (unjointed), tipped with a stout serrate spine and a few weak setæ, and a curved exopodite with three terminal plumose setæ.

The *Third Maxilliped* has a basal part jointed off from the rest and bearing an endopodite about three-quarters the length of the exopodite, tipped with a serrate spine and a few slender setæ, and a curved exopodite with three terminal plumose setæ and one just below the tip.

The first thoracic leg rudiment is already biramous and about as long as the endopodite of the third maxilliped. There is no trace as yet of the second to the fourth thoracic legs, but the fifth is a well-developed uniramous process, fully as long as the first thoracic leg rudiment and carried pointing forward beneath the thorax.

Stage II. The second larval stage closely resembles the first, from which it differs in the following points: The length is 2 mm. from first antenna to caudal plate, or 1.7 mm. from the rostrum to the same point.

The *First Antenna* consists of a long basal and a short terminal joint, bearing two palps, the outer and larger tipped with three tactile appendages, and the smaller with a single stout plumose seta. A slender seta also occurs at the outer margin of the proximal joint.

The *First Maxilla* has both masticatory lobe and palp tipped with setæ. The *Second Maxilla* is tipped with two setæ, and bears three more along its inner edge.

The *First Maxilliped* has an endopodite distinct from the basal joint ; the exopodite bears four terminal plumose setæ.

The Second Maxilliped has an endopodite which is indistinctly threejointed, and bears a second serrate spine on the inner edge; the exopodite ends in four plumose setæ.

The *Third Maxilliped* has a distinctly jointed endopodite with a serrate spine on the inner edge. The first thoracic leg rudiment is distinctly longer than in the previous stage, and very small rudiments of the remaining pairs of thoracic legs are also present. The fifth pair is well developed forming a process reaching forward beyond the first thoracic leg.

The *Swimming-Plate* is unchanged in shape, but bears an extra pair of small setæ in the middle of the posterior border, making sixteen setæ in all.

The following colour notes were taken from a larva of Stage II : The larva is almost perfectly transparent, with a few scattered red and yellow

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chromatophores very similarly distributed to those of Alpheus, namely, pale luminous yellow on the eyes, the first antennæ, at the base of the thoracic appendages, on the third and fourth abdominal segments and the terminal swimming-plate; while bright red chromatophores occur on the first antennæ, on the eye-stalks, between the eyes, on the third, fourth and fifth abdominal segments and at the base of the swimming-plate.

Literature.

| Brooks, W. K., and Herrick, F. H., | Lo Bianco, S. 1902. |
|------------------------------------|---------------------|
| 1891. | Lo Bianco, S. 1904. |
| Coutière, H. 1899. | Sars, G. O. 1906. |
| Coutière, H. 1907. | |

Family CRANGONIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :--Crangon Allmanni Kinahan. Crangon vulgaris (Linnæus). Ægeon fasciatus Risso. Ægeon sculptus (Bell). Pontophilus spinosus Leach. Cheraphilus nanus (Kröyer). Cheraphilus trispinosus (Hailstone).

FEATURES CHARACTERISTIC OF THESE LARVÆ OF CRANGONIDÆ.

Rostrum generally fused with carapace at base.

Eyes round, set rather close together, apparently continuous with carapace behind and on inner side; often somewhat swollen at base, resembling an acorn and cup.

Thorax short, sometimes very short in proportion to abdomen, e.g. *P. spinosus.*

Colour. Rather dense coloration, especially on inner antennæ; varies from pinkish brown to lemon-yellow.

For distinguishing features of the four larval stages, see table given under Pandalidæ on page 387.

Literature.

| Gurney, R. | 1903 (i). | Sars, G. O. 1890. |
|------------|------------|-------------------------|
| Gurney, R. | 1903 (ii). | Williamson, H. C. 1901. |

| Species. | Size. | Telson. | Abdominal Spines. | Antennæ and Setose Exopodites. | Colour. | |
|--|---|---|--|--|---|--|
| Crangon vulgaris. | Stage I, 2·3 mm. Stage IV, 4·7 mm. | Roughly triangular. Slightly indented in middle line. | 1 short median dorsal on 3rd abd. seg. | Short. 4 prs. setose exopodites in <i>Stage I V</i> . | Scattered yellow and brown chromato- phores. | |
| Crangon Allmanni. | Longer and thin- ner than C. vul- garis. Stage IV, 6 mm. | Similar to C. vul- garis. | 2 short lateral on 5th abd. seg. | Short. 4 prs. setose exopodites in Stage IV. | | |
| Ægcon fas c iatus. | Stage I, 2 2 mm. | Similar to <i>C. vul-</i> garis but more indented. | 2 dorso-lateral on 3rd seg. 2 small lateral on 4th seg. 2 long lateral on 5th seg. | Moderate. 5 prs. setose exopodites in <i>Stage IV</i> . | Dense brown and yellow chromato- phores, giving a deep golden brown colour. | |
| Ægeon sculptus. Pontophilus spinosus. | Larva unknown. <i>Stage I</i> , 6 mm. | Very deeply in- dented—Y-shaped. | 1 long median dorsal on 3rd abd. seg. 2 long lateral on 5th seg. | Very long. 5 prs. setose exopodites in <i>Stage IV</i> . | Yellow, pink and brown chromato- phores, giving yellow colour by reflected light. | |
| Cheraphilus nanus. | Stage I, 1.8 mm. Stage IV, 3.3 mm. | Similar to C. vul- garis. | 2 short dorso-lateral on 3rd abd. seg. 2 short lat. on 4th seg. 2 short lat. on 5th seg. | Short. 5 prs. setose exopodites in Stage IV. | "Golden-green back- ground, greater part of ventral sur- face covered with more or less intense red-brown coat." | |
| Cheraphilus trispinosus | Stage I, 3 mm. | Similar to C. vul- garis. | Absent. | Short. 5 prs. setose exopodites in | Very dense yellow and brown chroma- | |
| | | | | Stage IV. | tophores especially thick on thorax and 1st 3 abd. segs., giving dark yellow- ish-brown colour. | |

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Family NIKIDÆ.

Species recorded in the Plymouth Marine Invertebrate Fauna :--

Nika edulis Risso.

I have not succeeded in identifying the larva of this species in the Plymouth plankton, and although the occurrence of the larval stages is recorded by Gurney in the Plymouth Marine Invertebrate Fauna, I do not think any description of this larva has been published. Unfortunately Mr. Gurney was unable to supply me with any specimens.

Family NEPHROPSIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :--

Homarus vulgaris Milne Edwards.

The larva of the Lobster is hatched at a rather more advanced stage of development than is usual among Decapod larvæ. It is about 10 mm. in length at the first stage, and already possesses all five pairs of pereiopods and six pairs of setose exopodites, although no pleopods are yet present. The telson is large and spatulate, with a strongly concave posterior border, which is beset with a row of small spines and one larger median spine. The exact number of larval moults has not been ascertained, but at least three well-defined larval stages may be distinguished.

DISTINGUISHING FEATURES OF THREE LARVAL STAGES.

Stage I.

Length 10 mm. Rostrum large, triangular, pointed. Pleopods absent. Uropods absent. Telson spatulate, concave posterior border.

Stage II.

Length 14 mm.

Rostrum beset with a few marginal spines.

Pleopods present, but small.

Uropods absent.

Telson not quite so concave behind.

Stage III.

Length 17-18 mm.

Rostrum larger and more spinous.

Pleopods larger.

Uropods. Two pairs present, fully armed. Telson only slightly concave behind.

The following description of the coloration of the larva of *Homarus* vulgaris is translated from Sars (1874, p. 14) :--

"The colour is light yellowish, shading over more or less, on some parts of the body, to a luminous blue-green. But the body generally appears more intensely coloured by reason of the numerous star-shaped branching red-brown pigment spots, which are thickly crowded together on the carapace, as well as on the sides of the abdomen, and especially on the caudal plate. Also one notices similar but smaller pigment spots on the inner antennæ and the chelæ of the first pair of legs. The eye pigment is dark brown with glints of bluish green."

Literature.

Sars, G. O. 1874.

Williamson, H. C. 1904.

Family SCYLLARIDÆ.

Family PALINURIDÆ.

The larval form of both *Arctus ursus* and *Palinurus vulgaris* is a transparent flattened organism known as a Phyllosoma larva.

The thorax of the Phyllosoma is strongly compressed dorso-ventrally and forms a thin leaf-like plate, from beneath the margins of which spring the thoracic limbs.

The abdomen is extremely small and narrow, and devoid of pleopods or uropods in the early stages. The larval stages of these two species are very similar and have been somewhat confused, but apparently the chief points of difference are as follows :—

Arctus ursus.

Palinurus vulgaris. 1. Length 3.1 mm, when hatched.

- 1. Length 2 mm. when hatched.
- 2. First pair of maxillipeds absent in Stage I.
- 2. First pair of maxillipeds present in Stage I in rudimentary condition.

- 3. In young stages the first antenna longer than second antenna, but in later stages they are of almost equal length.
- 4. Reaches at least 24 mm. length before losing the flattened form.
- 3. In young stages the first antenna longer than second antenna, but in later stages the reverse is the case.
- 4. Reaches 21 mm. length before losing the flattened form.

Literature.

Claus, 1863. Cunningham, J. J. 1891. Dohrn, A. 1870. Bouvier, E. L. 1914.

Family GALATHEIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :--

Galathea dispersa Spence Bate. Galathea intermedia Lilljeborg. Galathea squamifera Leach. Galathea strigosa (Linnæus).

FEATURES CHARACTERISTIC OF THESE LARVÆ OF GALATHEIDÆ.

Rostrum. Long, slender and pointed; reaches beyond first antennæ. Eyes. Large and oval.

Carapace. Terminated postero-laterally by a strong spine, fringed on either side by a row of smaller spines.

Telson. Large and spatulate; in early stages deeply cleft in middle line.

Coloration. Varies considerably, but there are generally bright red chromatophores on thorax, and some smaller ones on abdomen and telson. Thorax often shows a yellow or luminous green shade. Eyes tinged with green. Sometimes there is a red chromatophore on the first antenna.

DISTINGUISHING FEATURES OF THE FOUR LARVAL STAGES.

Stage I. Caudal plate simple, bearing twelve spines; uropods absent. Stage II. Caudal plate simple, bearing fourteen spines; uropods absent.

Stage III. Telson and outer uropods well developed and armed with spines; inner uropods present, but small and spineless.

Stage IV. Both pairs of uropods well developed and armed with spines.

I have been unable to identify the larva of *Galathea strigosa* with certainty, but the larvæ of the three remaining Plymouth species may be distinguished by the relative length of the terminal spine on the antennal plate and of the outermost spine on the telson.

These spines are longest in G. squamifera and shortest in G. intermedia.

In G. squamifera the spine on the antennal plate is more than half the length of the plate itself; while in G. intermedia it is about one-third the length of the plate.

The outermost spine on the telson is very short in G. *intermedia*, of medium length in G. *dispersa* (about half as long as the next spine), and in G. squamifera it is longer still, being about two-thirds the length of the next spine.

All the above measurements refer to larvæ of the first zœa stage. The relative differences are stated to be constant for all the larval stages, but certainly they are most plainly marked in the young stages; and some little difficulty is experienced in distinguishing the late larval species by this test. For this reason I have labelled the figure of the Stage IV telson (Pl. IV, Fig. 4) as belonging to Galathea sp.

Literature.

Bell, T. 1853.
Boas, J. E. V. 1830.
Claus, C. 1876.
Claus, C. 1886.

Couch, R. Q. 1843. Sars, G. O. 1889. Williamson, H. C. 1910.

Tribe THALASSINIDEA.

Species recorded in Plymouth Marine Invertebrate Fauna :---

Family AXIIDÆ.

Calocaris Macandreæ Bell.

Family CALLIANASSIDÆ.

Upogebia stellata (Mont.).

Other species recorded from south-west coast, but not mentioned in Plymouth Fauna List :--

Family AXIIDÆ.

Axius styrhinchus Leach.

Family CALLIANASSIDÆ.

Upogebia deltura Leach. Callianassa subterranea Leach.

The above five species have been recorded from the south coasts of Devon and Cornwall, and full accounts of all the adults have been published. The larvæ of this group, however, have not all been identified, or have, in some cases, been identified wrongly. This confusion is doubtless due partly to the difficulty of obtaining the mature females in a living condition owing to their fossorial habits, and partly to the difficulty of reproducing in the Laboratory sufficiently life-like conditions in which to hatch the larvæ from the berried females or to rear the living larvæ obtained from the tow-nets.

From larvæ taken in this way from the tow-nettings at the Plymouth Marine Laboratory I have succeeded in rearing specimens of four Thalassinideans as far as the first post-larval stage. Of these, two are *Upogebia stellata* Mont. and *U. deltura* Leach, which have been described in an earlier paper (Webb, 1919); while of the other two, one (Larva A) should be identified as the young stage of *Callianassa subterranea* Leach, and the other (Larva B) as that of *Axius styrhinchus* Leach. Of these four species, three (all but Larva A) have been successfully reared to a later stage.

Before describing the above forms it is necessary to call attention to some points in the related literature on which much confusion prevails.

Apparently the same larva has been described by Claus (1876, p. 44, Figs. 14–18) as Hippolyte, by Cano (1891) as *Axius styrhinchus* and by Sars (1884) as *Calocaris Macandrea*.

The situation is still further complicated by Sars' description, which seems to be drawn from two different larvæ, one of which (Tab. 6 and 7) is very similar to, if not identical with, that described by Cano as *Axius* styrhinchus, while the other (Tab. 2) is a larva differing in many respects from the first, but stated by Sars to be an intermediate form between the larval and post-larval stages of the same species, although he did not actually obtain one stage from the other by moulting.

The first stages of this larva, described under different names by Claus, Cano, and Sars, occur quite frequently in the tow-nettings at Plymouth during the late summer, while the post-larval stage is also found there (Larva A in this paper), though not so frequently; but I have never found the "intermediate stage" stated by Sars to belong to the same species.

Moreover, both the last larval stage, which, according to Sars, immediately precedes this "intermediate stage," and the first post-larval, which succeeds it, have two pairs of large and well-developed uropods fully armed with plumose setæ (Tab. 7, Fig. 17); yet the so-called "intermediate stage" has uropods which are very small, entirely spineless and obviously in an undeveloped or a vestigial condition (Tab. 2, Fig. 17).

It would be an extremely unlikely occurrence for an animal to acquire fully armed uropods during its larval existence, lose them for a single stage, and then re-acquire them in the following stage.

This "intermediate" larva of Sars also differs from the early stages described in other important points, such as the rostrum, the abdominal spines, and the shape of the telson.

I have now succeeded in obtaining the first post-larval stage (Larva A) direct from the earlier larval stages described by Sars, so that this moulting of the larva into a post-larval form provides definite proof that the "intermediate stage" does not really belong to this species at all, and that Sars has described two different larvæ as belonging to the same species.

This post-larval stage (Larva A) is described below, and clearly shows the characters of Callianassa; the larval stages, therefore, described as Calocaris by Sars and as Axius by Cano, must now be recognised as the young stages of Callianassa.

Williamson's attitude (1915) with regard to the identification of this larva is not easily understood, for he states that "the larva described by Claus as belonging to Hippolyte is an Axius larva, as is also the form described by Sars as *Calocaris Macandrea*," and then he proceeds to use Sars' figures as an illustration of the larva of Calocaris, having just stated them to be wrongly identified as such.

Claus (1876, Taf. VIII, Fig. 1) and Cano (1891, Tav. III, except the post-larval stage) have both published figures of yet another Thalassinid larva, which they have identified as Callianassa, but which should now be regarded as the unidentified larval form of some other Thalassinidean; while the post-larval stage on Tav. III of Cano's paper is apparently the same as Larva A of this paper, and rightly regarded as Callianassa.

Bjorck (1913) has published a description of the young stage of *Calocaris Macandreæ*, at a length of 8 mm., and mentions that he has obtained a larval stage similar to the "intermediate stage" of Sars, but younger (apparently with the uropods still undeveloped, Taf. 1, Fig. 1). It seems probable, therefore, that the "intermediate stage" of Sars is truly a larval stage of *Calocaris Macandreæ*, of which a younger and a post-larval stage are figured by Bjorck.

The fact that this larva has not been obtained in the Plymouth townettings is possibly accounted for by the fact that *Calocaris Macandreæ* is an animal with a much deeper water habitat than most Thalassinideans. It has never been recorded from less than 25 fathoms, and has been

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obtained from as great a depth as 700 fathoms (Selbie, 1914), so that one would not expect its larvæ to be often washed so far inshore as Plymouth Sound.

The following table gives a list of references to the figures of various Thalassinid larvæ published in previous papers, together with their new identifications (if altered) :—

| Author, | Date. | Figure, | Old Name, | New Identifica- tion. |
|-------------|-------|---|--|--------------------------------|
| Bjorck, W. | 1913. | Taf. I. | Calocaris Macandreæ. | No alteration. |
| Cano, G. | 1891. | Tav. II — except post-larval stage. | Axius styrhinchus. | Callianassa. |
| | | Tav. III — except post-larval stage. | Callianassa subterranea. | Thalassinid larva indet. |
| | | Tav. III — post- larval stage. | Callianassa subterranea. | No alteration. |
| Claus, C. | 1876. | p. 44, Figs. 14–18. | Hippolyte. | Callianassa. |
| | | Taf. VIII, Fig. 1. | Callianassa subterranea. | Thalassinid larva indet. |
| Sars, G. O. | 1884. | Tab. 2. Tab. 6 and 7. | Calocaris Macandreæ. Calocaris Macandreæ. | No alteration. Callianassa. |
| | | | | |

Family CALLIANASSIDÆ.

Others species occurring at Plymouth :---

Upogebia deltura Leach.

Although only one species of this genus, U. stellata (Mont.), is recorded in the Plymouth Marine Invertebrate Fauna, the other species, U. deltura Leach, is also found, though more sparingly, in that district (De Morgan, 1910), and the larvæ of the two species occur in about equal abundance in the plankton of Plymouth Sound.

The larvæ of the two species are almost identical in appearance, and in some stages can only be distinguished with certainty by dissection. Their colouring is transparent, with scattered red chromatophores and dark eyes tinged with green.

The more minute differences of structure characterising the two species have been described in a previous paper (Webb, 1919), but one point of difference is afforded by the armature of the maxillipeds in the two species, as follows :—

| Stage. I and II. | First Maxilliped. Seta or second joint of endopodite | U. stellata. Present. | |
|---------------------|--|--------------------------|--|
| III and IV. | Second Maxilliped. Seta or second joint of endopodite | Present. | |

DISTINGUISHING FEATURES OF THE FOUR LARVAL STAGES.

Stage I. Caudal plate simple, bearing twelve spines; uropods absent.
 Stage II. Caudal plate simple, bearing fifteen spines; uropods absent.
 Stage III. Telson and outer uropods well developed and armed with spines; inner uropods present, but small and spineless.

Stage IV. Both pairs of uropods well developed and armed with spines.

Literature. Webb, G. E. 1919.

Larva A. Callianassa subterranea Leach.

The larval stages of this form have already been fully described by Sars (1884) under the name of *Calocaris Macandrea*. Figures of the first larval stage (Pl. III, Fig. 2) and of the telson and uropods of the last larval stage (Pl. III, Fig. 5) are given here. The larva is perfectly transparent, and colourless save for a large branched red-and-yellow chromatophore on the dorsal region of the carapace, and a tinge of green over the eyes.

The *First Post-larval Stage* which moulted from the last larval stage is similar in general appearance to Upogebia at the same stage. The animal measures about 3.7 mm. from the front of the eyes to the end of the telson; the body is very slightly compressed laterally, the carapace rounded and slightly concave behind, with the linea thalassinica and cervical groove well marked. The rostrum is a triangular projection which bends downwards in front of the eyes, which are short and thick and flattened on the inner side, so that they are pressed closely together in the middle line; the cornea is slightly pigmented.

The *First Antenna* has a three-jointed peduncle and two short flagella about as long as the distal joint of the peduncle. Both flagella are armed with scattered setæ, and the outer one is tipped with a group of æsthotascs.

The Second Antenna consists of a two-jointed base with a short process on the outside representing the antennal scale, and a flagellum of about twenty-three joints which reaches well beyond the end of the carapace.

The Mandible is fairly well developed with a distinct palp.

The *First Maxilla* has its inner edge produced into a basal and a masticatory lobe, both bordered with short setæ; a weakly developed maxillary palp is present on the outer side of the masticatory lobe.

The Second Maxilla has four lobes on the inner margin, of which the anterior three are armed with setæ along the inner border; the maxillary

palp is armed with three setæ, and the long oval scaphognathite on the outer side is bordered with about thirty plumose setæ.

The *First Maxilliped* has the base produced on the inner side into two lobes, both bordered with setæ; the maxillary palp is large, with a row of ten plumose setæ on the outer edge. There is a large flattened epipodite on the outer side of the base.

The Second Maxilliped is slender and pediform, curved inwards and armed with setæ, especially on the inner edge; there is a small epipodite on the outer side and a process representing the remains of the exopodite.

The *Third Maxilliped* is pediform (not operculiform, as in *C. Stebbingi*). The ischium and merus are broader than the carpus and propodite, and the whole limb is thickly armed with setæ, especially on the inner edge. The exopodite is represented by a spineless process on the outer surface.

The *First Pereiopods* or *Chelipeds* are only very slightly unequal in size at this stage. The carpus and propodite are large and massive, the ischium and merus more slender; the inner edge of the carpus and propodite is armed with long setæ, and there is a cluster of similar setæ at the base of the dactyl. The fixed finger is fully as long as the rest of the propodite, and the dactyl rather longer; both dactyl and fixed finger are thickly set with long setæ.

The Second Pereiopods are also chelate; they are similar to the first pair, but smaller, and the propodite is proportionately shorter and broader. The dactyl is slightly longer than the fixed finger, and the whole limb is set with long setæ, particularly on its inner edge.

The *Third Pereiopods* have a rather slender ischium and merus, and a carpus which is narrow at the base but wider at the distal end where it joins the propodite, which is expanded into a flattened rectangular plate, thickly set with plumose setæ; the dactyl is triangular and also set with setæ. (The expansion of the propodite of the third pereiopod is a feature particularly characteristic of Callianassa.)

The *Fourth and Fifth Pereiopods* are slender and set with scattered setæ, particularly towards their distal ends; the fifth pereiopod has a tendency to be subchelate. The first four thoracic legs or pereiopods each bear a spineless process on the outer side of the base, representing the setose exopodite of the larva.

The *Abdomen* is long, slightly narrower at either end than in the middle and with moderate-sized abdominal pleura. There are only three pairs of *pleopods*, on abdominal segments three to five. This is a point of some importance, since even in the fully grown Callianassa the first two pairs of pleopods are stated to be much more slender than the last three (Selbie, 1914), and in a specimen of about three inches in length in the museum of University College there is as yet no trace of the first two pairs.

Each pleopod has a short basal joint and two lobes bordered with plumose setæ; the inner lobe is shorter than the outer and bears an appendix interna on its inner margin.

Both pairs of *uropods* are well developed and set with plumose setæ; the inner pair is slightly shorter than the outer.

The *Telson* is almost rectangular, bearing setx on its posterior margin and a few spines at the posterior corners. It is slightly longer than the inner uropods (a point which, together with the pediform third maxillipeds, distinguishes this species from *C. Stebbingi*).

The striking resemblance which the above form bears to the adult *Callianassa subterranea* cannot fail to be noticed. Not only are the general features of the body, such as the presence of the linea thalassinica, the absence of a suture on the uropods, the weak development of the rostrum and the flattening of the eyes against each other, all extremely characteristic of that genus, but the resemblance even extends to the detailed structure of the appendages. The following points are of especial importance :—

- (1) The antennular flagella are shorter than the peduncle.
- (2) The ischium and merus of the third maxillipeds are broader than the carpus and propodite.
- (3) There is no epipodite on the third maxillipeds or on the pereiopods, but a large one on the first maxillipeds and a small one on the second maxillipeds.
- (4) The propodite of the third pereiopods is much flattened and expanded.
- (5) The fifth pereiopods tend to be sub-chelate.
- (6) There are no podobranchs on the pereiopods.
- (7) Only the last three pairs of pleopods are present, on segments 3–5.

The only points in which this form differs from the descriptions of the adult C. subterranea are that the eyes are not well pigmented, and the chelipeds have not yet attained their adult structure : they are only slightly unequal, and the process on the merus, which is present on the cheliped of the adult, is not yet developed.

There is, however, no doubt that this form is the young stage of *Callianassa subterranea* Leach.

Literature.

Bjorck, W. 1913. Borradaile, L. A. 1903. Cano, G. 1891. Claus, C. 1876. Sars, G. O. 1884.
Selbie, C. M. 1914.
Williamson, H. C. 1915.

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Larva B. Axius styrhinchus Leach.

FIRST LARVAL STAGE (Pl. III, Fig. 3).

The larva in this stage measures about 8.7 mm. from the tip of the rostrum to the end of the swimming-plate.

The *Carapace*, which is less than half as long as the abdomen, is somewhat compressed laterally, and produced in front into a long, slender, pointed rostrum, equal in length to the rest of the thorax; there is a well-developed sub-ocular spine on each side of the anterior border of the carapace.

The Antennæ are long and narrow, very similar to those of Upogebia, and the antennal plate reaches about three-quarters of the length of the rostrum.

The *First Antenna* consists of a long, slender process with a terminal palp (the outer flagellum) bearing a group of æsthotascs, and a stout plumose seta representing the inner flagellum.

The Second Antenna has a basal joint, bearing on the outer side a long, slender antennal scale, tipped with a stout spine and bordered along its inner edge with a row of fourteen long, plumose setæ, and on the inner side a flagellum fully as long as the antennal scale.

The *Mandible* is well developed, with a double row of teeth along its inner edge and a well-marked mandibular palp.

The *First Maxilla* has an oval basal lobe, edged with a row of strong plumose setæ, and a stout masticatory lobe, bordered with strong teeth along its inner margin. The maxillary palp is well developed and bears four pairs of setæ on its inner edge.

The *Second Maxilla* is produced on its inner edge into four masticatory lobes, all thickly set with setæ, and a maxillary palp in front bearing five pairs of plumose setæ. On the outer edge is the exognath, a long, oval lobe edged with about thirty plumose setæ.

The *First Maxilliped* has its basal part produced on the inner side into two masticatory lobes, of which the distal is thickly set with long spines and the proximal bears about five long, plumose setæ. The palp is long and bears five pairs of setæ; the exopodite, which is about half as long again as the palp, ends in a cluster of six plumose setæ. On the outer side of the base is a long, oval, membranous expansion, the epipodite.

The Second Maxilliped has a two-jointed base and a five-jointed palp bearing setæ along both edges, and a cluster of strong spines at the end. The exopodite is twice as long as the endopodite or palp, and terminates in seven plumose setæ.

The *Third Maxilliped* is similar to the second, but the palp is longer;

the exopodite is about two-thirds the length of the palp, tipped with seven long and one short plumose setæ.

Thoracic Legs or Pereiopods. All five pairs of these are present, the first three pairs being already biramous and the first two chelate. The last two pairs are uniramous and carried pointing forwards beneath the body. All five pairs show indications of jointing beneath the larval cuticle.

The *Abdomen* is long and powerful; the second, third and fourth segments bear a backwardly directed median dorsal spine on the posterior border, and the fifth has two pairs of dorso-lateral spines on its hind border. The presence of these lateral spines on the fifth abdominal segment is interesting as indicating a possible affinity between the Thalassinidea and the Crangonidæ, in which family similar spines occur.

The four pairs of *Pleopods* are fairly large and already biramous, a remarkable fact for a larva in the first zoœa stage.

Uropods are absent; and the caudal Swimming-Plate is large, deeply cleft in the middle line and produced at the postero-lateral corners into a strong spine on each side. A similar but smaller spine occurs in the middle of the posterior border, the concave margin of which is armed with about thirteen setæ on each side.

This remarkable telson, reminiscent of that of the Norway Lobster, is very similar to one described by Thompson (1903) in another Thalassinid larva, i.e. *Naushonia crangonoides*, which occurs on the coasts of New England. The larva is almostly perfectly hyaline, with scattered red chromatophores on the rostrum, along the lateral borders of the carapace, on the ventro-lateral surface of the first five abdominal segments and on the telson. There is also an orange chromatophore at the base of the telson, a transverse band of luminous yellow on the thorax, and a tinge of pale blue over the eyes.

SECOND LARVAL STAGE.

This stage moulted in the Laboratory from the preceding stage, which it closely resembles, the chief structural advance being the presence of six pairs of setose exopodites (from the first maxilliped to the third pereiopod) in place of the previous three pairs.

The larva now measures about 9.2 mm. in length.

The *First Antenna* has two transverse joints on the peduncle indicated by two groups of four short setæ on the outer margin; the outer flagellum bears a terminal bundle of æsthotascs; an inner flagellum is represented by a process tipped with a single seta, having two plumose setæ at its base and one more just below on the inner border of the peduncle.

The Second Antenna now has a two-jointed base, with a stout spine at

the base of the antennal plate and a smaller one, with a seta, at the base of the flagellum. The antennal scale is unchanged, save for the addition of a single seta about half-way up its outer margin; and the flagellum is now half as long again as the scale.

The *Mandible* is similar to that of the previous stage, but the row of teeth is thicker on the inner edge.

The *First Maxilla* has the epipodite fringed with hairs, otherwise it is unchanged.

The Second Maxilla has five or six lobes on the inner side besides the maxillary palp; the most posterior lobe has an especially thick border of stout setæ.

The three pairs of maxillipeds are unchanged, save that the first pair now has a two-jointed base, and the exopodites of the second and third pairs each bear eight terminal setæ.

The first two pairs of *Pereiopods* are chelate, with setose exopodites about half as long as the endopodite, and tipped with seven and six plumose setæ respectively. The third pair has an exopodite tipped with five setæ; the fourth and fifth pairs are well developed and uniramous.

The armature of the abdominal segments has increased; there are now three pairs of spines on the posterior border of the fifth segment and a small ventral spine on segments two to five.

The *Pleopods* are larger, but there is still no trace of uropods.

The *Telson* (Pl. III, Fig. 6) is similar to that of the previous stage, but somewhat more flattened along the posterior border.

FIRST POST-LARVAL STAGE.

This stage immediately follows the preceding larval stage, from which it moulted in the Laboratory.

The animal now no longer swims near the surface of the water, but sinks to the bottom, and if a suitable substance, such as fine sand or mud, is provided it commences to burrow. It measures 6-6.75 mm. in length, and the carapace is somewhat compressed laterally.

The eyes are short and thick, but fairly well pigmented. The rostrum is triangular in shape, bluntly pointed and curved downwards. It bears about five serrate teeth and a few scattered hairs on its lateral margins, and extends about to the end of the second joint of the antennal flagellum.

The *First Antenna* has a three-jointed peduncle, tufted with setæ, of which the basal joint shows a swelling containing an otolith. The outer flagellum is six-jointed, bearing scattered setæ and ending in a short conical joint tipped with a strong seta. The fourth and fifth joints each bear a pair of æsthotascs on their inner margins. The inner flagellum has five joints, of which the last is very short, and is sparsely set with setæ.

The Second Antenna has a two-jointed base, produced into a short spine on the inner edge of the second joint. The flagellum is long and slender and comprises about twenty-two joints, set with scattered setæ; the antennal scale is reduced to a small process on the outer side of the base.

The *Mandible* is large, with a well-developed masticatory edge and a three-jointed palp.

The *First Maxilla* has both masticatory and basal lobes well developed and fringed with setæ, which are particularly short and dense on the masticatory lobe. There is a distinct two-jointed palp with five setæ.

The Second Maxilla has four masticatory lobes, of which the basal one is the largest, and all of which are densely fringed with setæ. The maxillary palp bears four setæ, and on the outer side there is a long scaphognathite fringed with about thirty-five plumose setæ.

The *First Maxilliped* has the masticatory lobes on its inner edge armed with a dense row of plumose setæ. The exopodite is curved, with ten setæ along its outer border; the endopodite, or palp, is two-thirds the length of the exopodite and almost spineless. There is a large bilobed epipodite, and the basal joint bears gill processes.

The Second Maxilliped has a two-jointed base—the proximal joint with gills on its outer border. The exopodite is rather long and curved, with a few terminal setæ. The endopodite is five-jointed, rather shorter than the exopodite and fairly thickly set with setæ, especially on the inner border.

The *Third Maxilliped* is similar in general form to the second maxilliped, but the exopodite is tipped with six terminal setæ, and the endopodite is long and pediform, all the five joints being set with setæ, and the inner edge of the ischium or proximal joint bearing a row of seven flattened teeth.

The *First Thoracic Leg* or *Pereiopod* is chelate, very similar to that of *Upogebia deltura*, but with the dactyl longer than the fixed finger. A small process on the outer side of the base represents the exopodite. Each thoracic leg bears a pair of gills on the outer side of the basal joint.

The Second Pereiopod is chelate and similar to the first, but more slender. Both the second and third pereiopods bear a rudiment of the exopodite.

The *Third*, *Fourth* and *Fifth Pereiopods* are rather long and slender, and terminate in a slender point.

There are four pairs of *Pleopods*, each of which consists of a basal joint and two rami fringed with long plumose setæ. The inner ramus is rather longer than the outer, and bears an appendix interna on its inner edge.

There are two pairs of *Uropods*, the inner slightly the longer, and both fringed with long plumose setæ. There is no suture on either uropod.

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The *Telson* is roughly oblong, with the posterior edge rounded and slightly indented in the middle line. The whole of the posterior margin is thickly set with setæ, and a short spine occurs on the lateral edge.

On August 30th, 1920, I obtained a specimen of the above species in the first larval stage, taken alive from a tow-netting at Plymouth. It was isolated in a jar of fresh sea-water, and on September 2nd it moulted into the second larval form described above. On September 7th it moulted again into the first post-larval stage. It was now placed in a shallow dish with the bottom covered with a layer of fine sand and organic debris from one of the aquarium tanks, and almost immediately started to burrow. The following day a drawing of the burrow was made, and showed a round aperture, about 1 mm. across, surrounded by a raised margin of sand and mud. The animal remained completely hidden in the burrow, and was not disturbed again until November 20th, when it died and was then taken out and preserved.

On examination it proved to exhibit almost all the characters of an adult female *Axius styrhinchus*. I have carefully compared it with the excellent descriptions of this species given by Borradaile (1903) and Selbie (1914), and find that, with the exception of certain very minor points enumerated below, which would probably not be developed in a very young specimen such as this, it agrees in every way both with the text description and the accompanying figures. The absence of the linea thalassinica and the size of the abdominal pleura place it in the family Axiidæ, while the lateral compression of the body and the absence of a median dorsal ridge on the carapace, and of a suture on the uropods, indicate that it belongs to the genus Axius.

In the general body-form, the shape and armature of the rostrum, the carapace, the abdominal pleura, and the telson, as well as the size and pigmentation of the eyes, which are half covered by the rostrum, it agrees exactly with *Axius styrhinchus*.

The structure of the antennæ, of the mouth parts and the thoracic and abdominal appendages is (with the exception of the few points mentioned below) identical with that of the adult Axius ; while the presence of the peculiar structure situated between the coxæ of the fourth pereiopods and carefully described by Selbie (1914) indicates that the present specimen is a female and is of some interest in showing at what an early stage the secondary sexual characters are developed.

The following are the minor points on which the present specimen differs from that of Selbie's description :

The fringe described as present on the last three peduncular joints of the second antenna is absent. The anterior chelipeds have not yet attained their full development—the left and right chelipeds are still

about the same size; the carpus is only fairly short; the palm is nearly twice as long as the fingers (not one and a half times, as in the adult), and the crushing tubercles and fringe of setæ are not fully developed. The distribution of setæ on all the thoracic limbs is not so thick as in the adult, and the uropods are barely as long as the telson.

The rearing of this young form from the larva proves conclusively that the species described above is the true larval form of *Axius styrhinchus* Leach.

Literature.

Thompson, M. T. 1903.

Borradaile. 1903. Selbie. 1914.

Family PAGURIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :---

Eupagurus Bernhardus (Linnæus). Eupagurus cuanensis (Thompson). Eupagurus Prideauxi (Leach). Eupagurus sculptimanus (Lucas). Diogenes varians Costa. Anapagurus lævis (Thompson).

FEATURES CHARACTERISTIC OF THESE LARVÆ OF PAGURIDÆ.

- (1) Rostrum. Long and pointed, reaches beyond first antenna.
- (2) Eyes. Large and oval.
- (3) Carapace. Relatively broad and short; concave behind, and terminating postero-laterally in a sharp point; no fringe of spines on either side (cf. Galatheidæ).
- (4) Telson. Roughly spatulate, with truncated posterior margin.
- (5) Setose Exopodites. Three pairs (first to third maxilliped) in Stage IV larva.

DISTINGUISHING FEATURES OF THE FOUR LARVAL STAGES.

Stage I. Caudal plate simple, bearing twelve spines; uropods absent. Stage II. Caudal plate simple, bearing fourteen spines; uropods absent.

Stage III. Telson and outer uropods well developed and armed with spines; inner uropods represented by a small spineless process at root of outer pair. Thoracic legs moderately developed.

Stage IV. Telson and uropods as in Stage III. Developing thoracic legs much larger, extending back to cover all but last two pairs of pleopods.

G. E. WEBB.

Of the six Plymouth species of Paguridæ, the larvæ of only two have been identified with certainty, namely, *Eupagurus Bernhardus* and *Eupagurus Prideauxi*.

These may be distinguished from one another by the following features :--

(1) Length.—Eupagurus Bernhardus measures $3\frac{1}{2}$ mm. in its first larval stage; Eupagurus Prideauxi is considerably shorter. The additional length of *E. Bernhardus* is chiefly due to the excessive length of the last abdominal semite (not yet separated from the telson).

(2) Telson.—This is shorter and more triangular in E. Prideauxi, especially in Stage I. The third spine from the outside is equal in length to the other spines and jointed to the telson; while in E. Bernhardus there is no suture between the third spine and the telson, and the spine itself is half as long again as the inner spines.

The larva of *Eupagurus Bernhardus* is almost transparent, with a redand-yellow chromatophore on the dorsum, the mouth parts flecked with deep crimson, and a conspicuous orange chromatophore (most noticeable in late larval stages) on the developing chela of the first leg. The eye is dark, with glints of luminous yellow.

The fourth larval stage in the Paguridæ is followed by a transitional stage known as the "Glaucothöe." At this stage the animal alternately walks on the bottom, and swims actively by means of its four pairs of pleopods. The asymmetry so characteristic of the adult makes its first appearance at this stage, in that the right uropod is now smaller than the left. During this stage the liver, excretory bladder and gonads shift to the abdomen, the right pleopods disappear and the left degenerate. At the next moult the animal assumes more or less completely the adult form and seeks a shell in which to make its home.

Literature.

Bouvier, E. L. 1891. Issel, R. 1910. Jackson, H. G. 1913. Mayer, P. 1877. Sars, G. O. 1889.

Family PORCELLANIDÆ.

Species recorded in Plymouth Marine Invertebrate Fauna :--

Porcellana longicornis (Linnæus). Porcellana platycheles (Pennant).

The larvæ of the two species are very similar, but P. platycheles is slightly the larger, measuring 6 mm. in the first stage ; while P. longicornis measures 5 mm. in the same stage.

The exact number of larval stages has not been ascertained, but the larvæ present several interesting developmental features. The rostrum is produced into a very long spine, fully twice as long as the rest of the body; and the carapace is produced backwards into two spines, about half the length of the rostral spine. This feature renders the larvæ easily distinguishable in the tow-nets, but it also adds to the difficulty of rearing the larvæ under artificial conditions, as the long spines are easily caught in the surface film, so that the animal cannot free itself.

The last larval stage, preceding the first post-larval, has pleopods but no uropods, nor has the number of setose exopodites increased from the original two (first and second maxillipeds) of the first stage; although the terminal setæ on the exopodites have increased in number from four to eleven. The larva is transparent, with bright red and yellow pigment in the region of the mouth parts, and red chromatophores on the sides of the abdominal segments. The rostral spine is tipped with red, as are also the posterior carapace spines; and two bands of reddish or yellowish colour are also present on the more proximal part of the rostrum.

The eyes are dark brown in colour, and the telson sometimes bears a yellowish tinge.

Literalure.

Faxon, W. 1879.

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PLATE I.

..... DECOMPANY TO BUTHEL

| Fre | . 1. Leander squïlla. | First La | rval | Stage | ×38. | | |
|-----|--------------------------------------|----------|------|-------|--------------|--------|-----------------|
| | 2. Pandalus Montagui. | ,, | ,, | ,, | ×31. | | |
| | 3. Hippolyte varians. | >> | " | ,, | \times 71. | | |
| | 4. Athanas nitescens. | Third | 29 | ,, | ×41, | | |
| | 5. Palæmonetes varians. | Fourth | 28 | 22 | Telson and | Uropod | s. \times 71. |
| ., | 6. Pandalus brevirostris. | " | " | ,, | ,, | >> | " |
| | 7. Hippolyte sp. (probably H. varian | ns). ,, | ,, | ,, | " | | >> |
| | 8. Athanas nitescens. | Late | ,, | ,, | " | ** | ** |


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PLATE II.

| FIG. | 1. | Crangon vulgaris. | First Larval Stage. | | imes 46. | | | | |
|------|----|-----------------------|---------------------|----|----------|--------------|-----|---------|--------------|
| ,, | 2. | Ægeon fasciatus. | ,, | ,, | ,, | $\times 62.$ | | | |
| ,, | 3. | Pontophilus spinosus. | ,, | ,, | ,, | imes 27. | | | |
| ,, | 4. | Crangon vulgaris. | Fourth | ,, | ,, | Telson | and | Uropods | $\times 44.$ |
| ,, | 5. | Ægeon fasciatus. | "" | ,, | ,,, | ,, | ,, | ,, | imes 55. |
| | 6. | Pontophilus spinosus. | | | ,, | ,, | ,, | 27 | $\times 16.$ |



Larvæ of Decapoda. [421]

PLATE III.

| FIG. | 1. | Upogebia s'ellata. First Larval St | | Stage. | $\times 43$ | |
|------|----|---------------------------------------|--------|--------|-------------|-----------------------------------|
| " | 2. | Callianassa subterranea (Larva A). | " | " | " | ×48. |
| ;, | 3. | Axuis styrhinchus (Larva B). | ** | " | ,, | imes21. |
| | 4. | Upogebia stellata. | Fourth | ,, | ,, | Telson and Uropods. $\times 71$. |
| ,, | 5. | Callianassa subterranea (Larva A). | " | " | " | " " " ×71. |
| " | 6. | Axius styrhinchus (Larva B). | Last | " | " | Telson. ×44. |

II STADI

PLATE III.



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PLATE IV.

| FIG. | 1. | Galathea squamifera. | First La | rval | Stage. | imes 45. | |
|------|----|-------------------------|----------|------|--------|-----------------------|--------------|
| ,, | 2. | Eupagurus Bernhardus. | " | ,, | ,, | ×44. | |
| ,, | 3. | Porcellana platycheles. | ,, | ,, | ,, | imes 38. | |
| ,, | 4. | Galathea sp. | Fourth | ,, | ,, | Telson and Uropods. | $\times 44.$ |
| ,, | 5. | Eupagurus Bernhardus. | ,, | | ,, | ,, ,, ,, | $\times 44.$ |
| | 6 | Porcellana sp. | Last | | | Telson. $\times 71$. | |



G. E. WEBB. Larva of Decapoda.

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The Larval and Post-Larval Stages of the Pilchard, Sprat and Herring from Plymouth District.

By

Marie V. Lebour, D.Sc. Naturalist at the Plymouth Laboratory.

With Figures 1-12 in the Text.

THE young clupeoid material which had been collected from 1913 onwards and sorted out with a view to future biological study, especially of the Pilchard, was handed over to me by Mr. R. S. Clark with the main object of differentiating the three species Pilchard, Herring and Sprat. A research was therefore undertaken to find out the best way of distinguishing them through all their life history until metamorphosis. This was practically finished when the thesis by Fage (1920) on young clupeoids of the "Thor" expedition was published, rendering a large part of my work unnecessary, as, thanks to him, it is now almost impossible to mistake them at any period of their development, and they are clearly differentiated at any time in their life history.

My own observations have, however, brought out some interesting facts, and as they are entirely based on our local material it is interesting to compare them with those of Fage, which are based on material from the Mediterranean, the Channel, and the Atlantic, from the Bay of Biscay to the north of Scotland, including the Irish Sea.

The material here investigated and separated into species consists of all hauls with the Young Fish Trawl and tow-nets available up to the end of 1920, thus including Young Fish Trawl material captured by the *Oithona* 1913, 1914 and 1919 (Clark 1914, 1920, Allen 1917) and also 1920. Besides these there are a few scattered earlier hauls and separate specimens, notably one Young Fish Trawl haul (30.5.06) containing some thousands of young Sprats and a few Herring in late post-larval and metamorphosing stages. Finally, there are a few specimens from the tow-nets of various dates. A table showing all this material sorted into their species will be found at the end of the paper.

M. V. LEBOUR.

INTRODUCTION.

The best distinguishing character is, as Fage points out, the number of myotomes which is characteristic for the species. Indeed, this is the only absolutely reliable character until the time of the appearance of the pelvic fins, that is to say, up to a length of 18 mm. or more. Thus the usual number for the Pilchard is 51 to 52, for the Sprat 46 to 48, and for the Herring 56 to 58, i.e. the number of myotomes equals the number of vertebræ, the small undeveloped myotomes running to the head in front of the vertebræ being disregarded.

In practice, however, it is difficult to count the myotomes at the tailend of the body, especially in the youngest forms, therefore I took the number from the back of the operculum to the anus, the "trunk" region of Fage, and this method was found to be perfectly satisfactory. In making these accounts it was found that the number of myotomes diminished between the operculum and anus as the fish grew. That is to say the anus was migrating forward over several myotomes. The position of the anus in all three species most certainly alters during the growth of the fish, the alteration being chiefly due to the larger growth of the region from the anus to the end of the caudal fin than of the region from the tip of the snout to the anus, as is shown very clearly by Fage (p. 14) in the Anchovy. Although, however, the actual migration of the anus over five to six myotomes is not nearly so large a factor in the alteration of its position on the body, this migration undoubtedly takes place and the alteration in the number of myotomes in the trunk region must be considered when using these for identification of the species.

The number of myotomes in the trunk does not exactly correspond with those from the first vertebra to the vertebra nearest the anus for two reasons.

Firstly, the operculum tends to cover the first myotome in fish from about 10 mm. to about 25 mm. in length, or more, after that it tends to cover two. The first myotome counted is thus one or two short in front.

Secondly, in the larger fish, from about 25 mm. or more, the posterior myotomes slope more obliquely than those in front and overlap the vertebræ, so that there are one or two more myotomes in front of the anus than there are vertebræ (see Fig. 1).

The counts of the myotomes have been carefully checked by alizarin stained specimens to show up the vertebræ. The first vertebra counted is the first behind the head, the last the urostyle.

Bearing these facts in mind we may with safety take the number of whole myotomes in the trunk region as a reliable character, freely acknowledging that this number does not correspond to the vetebræ in the same region.

Thus in the Plymouth specimens the most frequent number in the Sprat is 37 dwindling to 31, in the Pilchard 42 dwindling to 35, and in the Herring 47 dwindling to 39; 31, 35, and 39 being the usual adult numbers. These numbers may vary slightly, but never overlap in the different species in fish of equal lengths. By means of stained specimens we find that the anus moves over 5-7 vertebræ. The fact of the migration of the anus is emphasized here, because it is apparently disregarded altogether by previous writers, or deemed negligible compared with the undoubtedly larger growth of the tail region.

Besides the moving forward of the anus, and with it the anal fin, there is in all three species a forward migration of the dorsal fin, although



FIG. 1.—Diagram of Clupeoid. A B, length of body; A D, snout to anus; A E, snout to last ray of dorsal fin; O, operculum; P, pelvic fin; d.j., dorsal fin; a.j., anal fin; I, first vertebra; X, last vertebra (urostyle); m, first myotome counted; $t.t^{1}$, first and last trunk myotomes counted from outside. (The myotomes are counted from The centre of the body.) P Y, pylorus. In the diagram the fish has 52 vertebræ, and there are 35 whole myotomes in the trunk,

i.e. between operculum and anus.

this is regarded by Fage as negligible in the Sprat. In the Pilchard this movement is large, the fin advancing over many myotomes (10-11) before it reaches its final resting-place, and in the Herring it is also large, although less than in the Pilchard. In the Sprat, however, the movement is much less apparent. There is, nevertheless, an undoubted movement in the front over 4-5 myotomes, the back of the fin only moving over 2 or 3. As there is little change in the position of the fin up to well over 25 mm., the forward movement chiefly occurs close upon the time of metamorphosis. It is, however, quite insignificant compared with the increase of growth in the tail region, the region of the dorsal fin increasing little, whilst the front end of the body grows to a certain extent and the tail end grows a large amount. The explanation given by Fage as to the change of position in the dorsal fin agrees with my specimens in so far as he lays greater stress on the growth of the front and tail ends of the body, but he allows a movement of the front of the fin over only one myotome from 20 to 31.5 mm., saying that it has not, so to speak,

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changed its place, whereas in my specimens at 32 mm. the fin has moved forward in front over $3\frac{1}{2}$ to $4\frac{1}{2}$ myotomes, and he does not mention the movement of the anus over the myotomes in any of the species.

In order to show the change of position of the anus and dorsal fin I have prepared four curves and a diagram for each species. The curves are based first on the number of myotomes in the trunk region (i.e. from the end of the operculum to the anus), and secondly on the number of myotomes between the operculum and the last ray of the dorsal fin. The third and fourth curves are based on the relative lengths of the distance from the tip of the snout to the anus AD (see text, Fig. 1) and the distance from the tip of the snout to the last ray of the dorsal fin AE, respectively, with the total length AB (from the tip of the snout to the snout to the tip of the snout to the s

The ratios $\frac{AD}{AB}$ and $\frac{AE}{AB}$ are thus plotted on the curve, the mean of the length AB in ten specimens and the mean of the ratios $\frac{AD}{AB}$ and $\frac{AE}{AB}$.

When possible ten specimens were taken between each two millimetres starting at 11 mm. in the Sprat and 13 mm. in the Pilchard and Herring, up to the time of metamorphosis. After this only a few specimens were examined for comparison. The Sprat series is nearly complete, but gaps appear in the Pilchard series between 35 mm. and in the Herring between 46 mm. and the fully metamorphosed forms, also in some of the smaller Herring stages.

The last ray of the dorsal fin was used preferably to the first because the first ray is much later in appearing, but in the Sprat the front of the fin moves over more myotomes than the back, so that finally the whole fin occupies an area extending over two or three more vertebræ than it does at first. In the Pilchard and Herring the fin extends over an equal number throughout its migration.

The diagrams showing the migrations of fin and anus and their relations with the pelvic fins were taken from specimens stained with alizarin to show up the vertebræ. The smaller fish were mounted whole, the larger were bisected so as to leave the backbone and fins, and were then stained and mounted.

The number of vertebræ in the Plymouth specimens, chiefly counted in post-larval and adolescent specimens, is 47 to 48 in the Sprat, rarely 46 or 49, 51–52 in the Pilchard, rarely 50, 53, or 54; and 56–57 in the Herring, rarely 58 or 59 (see also for Herring, Orton, 1916).

The pelvic fins occupy a position relative to definite myotomes and vertebræ, and move slightly towards the dorsal fin as the fish grows, the front of the dorsal fin passing the pelvics in the Pilchard and Herring, but remaining behind them in the Sprat. This movement is regarded by Fage as entirely due to alteration in the abdominal cavity, as in the Pilchard and Sprat the position of the fins is always in the vicinity of a particular rib, the 15th. This is undoubtedly the case in all the Plymouth specimens also, the movement taking place over a space equal to two or three myotomes.

The first ray of the dorsal fin is in all three species very small, and



FIG. 2.—Diagram of dorsal fin, *d.f.*, of a post-larval clupeoid; *p.r.*, proximal radials; *d.r.*, distal radials; *f.r.*, fin rays.

only comes up at about 25 mm. in the Sprat, and still later in the Pilchard and Herring. In any case, it is so small that it makes little difference in front of the fin with regard to the myotomes.

In both dorsal and anal fins there are three series of elements which may be termed the proximal radials, distal radials, and fin rays (Figs. 2–3). The first to appear are the proximal radials, which are simple rods

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FIG. 3.—Diagram of anal fin, a.f., of a postlarval clupeoid; p.r., proximal radials; d.r., distal radials; f.r., fin rays.

projecting slightly from the body. Those in the centre are the first formed, next those behind from the centre backwards, and lastly those in front from the centre forwards. In this way the first radial is the last to be formed. The distal radials form next and consist of small knobs above the proximal radials. These form in the centre, whilst the hind and front proximal radials are forming, so that some are present before the full number of proximal radials is complete. The distal radials also arise from the centre backwards and forwards, the last to be formed being those in front. Finally the fin rays appear, which consist of rods fitting on to the distal radials. The central fin rays form first, and may be present before either the proximal or distal radials are complete, those at the hind end forming next from the centre backwards, and, lastly, those in front. In the older post-larvæ the rays are jointed, except the first two which are shorter than the others and in the anal fin spring from the same radial. The number of proximal and distal radials is equal and corresponds to the number of fin rays in the dorsal fin, but in the anal fin there is one more fin ray than radial, owing, as is stated above, to the first radial bearing two rays. The last ray in both fins is double and is here counted as one.

The usual number of rays in the Plymouth specimens in the Pilchard is 18 in the dorsal (rarely 17–20), 18–19 in the anal (rarely 17–21); in the Sprat 17 in the dorsal (rarely 15–18), 19–20 in the anal (rarely 18–21); and in the Herring 19 in the dorsal (rarely 17–21), and 18 in the anal (rarely 15–19).

During larval and post-larval growth the various parts of the body are all growing in definite proportions, but during the time of metamorphosis, as Fage shows clearly (and the fact is borne out in the Plymouth specimens), there is an almost complete cessation of growth in the trunk region, the head and tail only growing in any marked degree. During this period the scales are indicated, pyloric cœca formed, and adult colouring begun, until at last the completely scaled fish appears. This cessation of growth in the trunk region accounts for the fact that some of the metamorphosed forms are of the same length as some of the postlarvæ, but of different proportions, the head especially being much larger in the former. There seems, however, to be an indication, at any rate in the Sprat, that a real reduction in length takes place also at metamorphosis, as we have fully metamorphosed specimens as small as 30.5 mm., and post-larvæ of that length also which are a very long way from metamorphosis, those about 34-35 mm. being much nearer to the small metamorphosed forms, except in length.

In comparing our specimens with those of Fage there is a distinct indication that our post-larval Pilchards are slightly more backward for the same length than those of the Mediterranean, the Herring slower* in development than those from the north of Scotland (this latter agreeing with Fage's observations), and the Sprat, although in some respects slightly more forward in its younger stages than those from the north of Scotland yet staying longer in its later post-larval stages; specimens of 41 mm. occurring which have not completed their metamorphosis.

* The term slower is here and elsewhere in the paper used not in the sense of time, but as being more backward in development at the same length.

THE PILCHARD.

SARDINA (CLUPEA) PILCHARDUS (Walb.)

The main spawning of the Pilchard occurring in the Plymouth area is further out to sea than that of the Sprat and Herring, particularly in the region of the Eddystone. The earliest record is April 2-3, 1920, 8 miles S.E. of the Eddystone, when a large quantity of Pilchard eggs were caught at night and young hatched from them.* The latest record is November 26th, 1913, of a young Pilchard 11 mm. long. The breeding season certainly (Clark, 1920) extends from April to October, maximum June to August. The very young Pilchards may be brought close to the shore ; one from the tow-nets, West Channel, 27.4.20, measured 5 mm., still with a yolk sac. Post-larval stages (18 to 32 mm.) were collected by Dr. Orton (October, 1919) in Millbay Docks, and three specimens (30-35 mm.) were obtained from Salcombe Harbour. Postlarval stages between 10 and 30 mm. occur abundantly in the Young Fish Trawl hauls and occasionally in the tow-nets all through the summer. In following up the biology of the Pilchard Mr. Clark has been successful in capturing large numbers of adolescent Pilchards mixed with Sprat and Herring in September and October, 1920, in the Plymouth estuaries and also close inshore in the bays. These were fully scaled and ranged from 39 to 90 mm.

Unfortunately there is a large gap in the material from the postlarval stage at 35 mm., and the smallest scaly forms of 38 mm., the length at metamorphosis probably being 40–50 mm. or more.

The eggs measure 1.5-1.9 mm., and both these and the early larval stages from Plymouth have been described and figured by Cunningham (1889–1894), who draws attention to the larval sense papillæ along the sides of the body, which are similar to those in the Sprat here figured (Fig. 7). The embryo, just before hatching, and the newly hatched young in all specimens examined by me were pigmented freely with small black chromatophores on the head and dorsal surface. This pigment is not figured by Cunningham, who says his newly hatched young were without pigment except for a few black chromatophores in the dorsal region of the body. The figures given here (Fig. 4) were taken from specimens brought in as eggs and hatched in glass jars in the Laboratory. The larval pigment very soon disappears and small chromatophores, similar to those described by Fage, below the noto-chord occur instead.

* Since sending this to press Pilchard eggs nearly ready to hatch were taken in the West Channel, March 17th, 1921.

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The newly hatched larva is 3.3 to 3.5 mm. long and loses its yolk sac at about 5.5 mm. A specimen 7.5 mm. showed 4 proximal radials in its dorsal fin, which is interesting as Fage's Mediterranean specimens of 7.2 mm. showed no trace of fin at all. In other respects, however, the young from Plymouth seem further backward. Fage found no difference in the post-larvæ from the Atlantic, the Channel, and the Mediterranean, but I find that our specimens develop more slowly than the Sprat with regard to the unpaired and pelvic fins and the tail, whilst Fage found the reverse to be the case, and the pelvic fins are certainly longer in appearing than in the Mediterranean forms. Thus generally speaking



FIG. 4.—Egg and newly hatched young of Pilchard; [a., cgg of Filchard]nearly ready to hatch, 1.8 mm.; b., newly hatched Pilchard, 3.3 mm. (hatched in Aquarium); c., Pilchard 7 days old, 5 mm. (hatched in Aquarium). [All frcm eggs, tow-net, April 2–3, 1920, 8 miles S. of Eddystone.

the notochord remains straight at a greater length than the Sprat, and, although it usually begins to turn up after 11 mm., may remain straight up to 12.5 mm., whilst in the Sprat it is always turned up to a certain extent at 11 mm. The dorsal and anal fins are also usually further advanced in the Sprat than in the Pilchard of the same length, and, more important still, the pelvics do not appear at 18 mm., as they do in Fage's specimens, but at 20-22 mm., whereas they appear in the Sprat from 17.25 to 20 mm. As soon as they appear the difference in position is at once noticeable, as, although they are in both species at their origin on a level with the 18th myotome, yet in the Sprat the pelvics are separated from the pylorus by a space equal to at least $2\frac{1}{2}$ to 3 myotomes, whereas in the Pilchard the pelvics originate on a level with the pylorus, a character rightly regarded by Fage as an unfailing distinction between

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the two species. The position of the pelvic fins is further forward on the body than in the Sprat and the Herring.

The Plymouth specimens are thus rather slower in development than, at any rate, those of the Mediterranean. The dorsal fin is complete



FIG. 5.—Diagram showing the relations of the fins and anus to the vertebrae in the Pilchard at various lengths; p., pelvic fins; 1—x., first and last ray of dorsal fin; a., anus; v., vertebrae; M., metamorphosed specimens.

except for the first ray at 21 to 25 mm., the last ray coming up at about 26 mm., the anal fin being completed a little later.

In other respects the Plymouth specimens agree with Fage's very closely. At the time of appearance of the pelvic fins the dorsal fin has not begun to move forward; its first apparent ray (in reality the second) is usually in the neighbourhood of the 27th-28th myotomes and stands

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FIG. 6.—Curves showing the change of position of dorsal fin and anus in the Pilchard; A, showing number of myotomes in the trunk in Pilchards 13 to 50 mm. long; B, showing number of myotomes between operculum and last ray of dorsal fin in the same specimens; A^1 , showing ratio of distance from snout to anus $(A \ D)$ and body length $(A \ B)$ in the same specimens; B^1 , showing ratio of distance from snout to last ray of dorsal fin $(A \ E)$ and body length in the same specimens; o=metamorphosed specimens. Correction for curve A (approximate) to show true number of myotomes from head to anus. +=myotomes covered by operculum, -=myotomes overlapping anus: -13 to 23 (+1), 23 to 27 (+1-1 or 2), 27 to 35 and metamorphosed forms (+2-2). Cf. page 437.

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above the division between the 28th and 29th vertebræ, its last ray being above the division between the 37th and 38th. There are usually 36–37 myotomes in front of the last ray (35 or 36 from the operculum to the ray) and 42 in front of the anus (41 from the operculum to the anus). The pelvics originate as small thickenings 10 or 11 myotomes in front of the dorsal fin, under the 18th–19th vertebræ, the rays of the pelvics originating under the 21st vertebra (Fig. 5). These positions are very regular and vary little in specimens of the same size and until the fins begin to move. The proportions of the body agree very well with those given by Fage, and, except for the slowness in development of the fins differ hardly at all.

The anus is moving forward slowly relative to the myotomes, but the dorsal fin has not yet begun its migration. However, the position of both fin and anus is gradually coming further forward on the body because the tail region from the anus to the tip of the caudal fin is growing faster than the rest of the body. The curve (Fig. 6) shows that the

ratio $\frac{AD}{AB}$ has changed from $\cdot 80$ to $\cdot 76$ in a fish 16 mm. to 20 mm., and

the ratio continues to decrease up to 35 mm., when it is at $\cdot 66$. Here our post-larval specimens stop, but most certainly it continues after that, for in the smallest metamorphosed specimen of 38 mm. it is at $\cdot 63$, and it remains between $\cdot 62$ and $\cdot 63$ in the larger metamorphosed forms. The anus thus attains its permanent position shortly before metamorphosis. Unfortunately, we have none of these intermediate specimens. Judging from Fage's observations where he finds metamorphosis takes place from 35 to 45 mm., and since at 40 mm. his specimens are still at the stage when the pelvic fin is in front of the dorsal, it is highly probable that our specimens would metamorphose as late as 40–50 mm., and that the smallest metamorphosed specimens have undergone a reduction in length.

The anus migrates usually from the region of the 43rd to the 37th vertebra, but may stop at the 39th in specimens with 54 vertebræ. Indeed, in all there may be a variation of a vertebra or two owing to the corresponding variation of total vertebræ in the body. The usual extent of the migration is thus over 5–6 vertebræ. Finally there are 35–36 myotomes to be counted between the operculum and anus, two of which have overlapped from behind, but as the operculum covers two the resulting number is the same as the true number of myotomes from head to anus. This I have represented at the foot of the Table as 35 or 36+2-2.

It is easy to see at a glance that the movement over at the most 5-6 vertebræ is but a very small factor in the alteration in position of the anus. As an illustration we may take the following measurements of

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young Pilchards 13.5–38 mm. long. AB=length, D=position of anus, δ =the imaginary position of the anus when corrected for shift in position :

| AB | AD | DB | Dδ | $\frac{A - \delta}{\delta - B}$ |
|-----------|-------|------|------|----------------------------------|
| 13.5 | 10.75 | 2.75 | 0 | $\frac{10.75}{2.75} = 3.9$ |
| 24.5 | 18.25 | 6.25 | 0.75 | $\frac{19}{5\cdot 5} = 3\cdot 5$ |
| 35 | 23 | 12 | 1.75 | $\frac{24.75}{10.25} = 2.4$ |
| 38 (met.) | 24 | 14 | 2 | $\frac{26}{12} = 2 \cdot 2$ |

The ratio $\frac{A\delta}{\delta B}$ decreasing showing that the distance δB increases pro-

portionally more than the distance $A\delta$.

The migration of the anus begins at about 16 mm., but the dorsal fin does not begin to move over the myotomes until about 22 to 25 mm. beginning with its front ray over the 29th vertebra, and its hind ray over the 38th. In a specimen of 25 mm., with 53 vertebræ the first and last rays are between the 28th and 29th, and the 37th and 38th. respectively, the rays of the pelvic fins under the 21st, their origin under the 18th. In a specimen 26-27 mm., with 52 vertebræ they are between 25-26 and 34-35, the pelvics in the same position as before. The fin is thus moving gradually forward. At 31 mm., the front and back rays are between 24-25 and 33-34, the pelvics as before, and at 35 mm. the same. Here, unfortunately, our specimens stop until we get small metamorphosed forms. The smallest metamorphosed specimen measures 38 mm., has 52 vertebræ, the front ray of the dorsal well in front of the pelvic fins, between the 18th and 19th vertebræ, the last ray over the 28th, the pelvic rays between 21 and 22, their origin still under the 18th. The dorsal fin has thus performed a migration forward over at least 10 vertebræ, the pelvics having moved backward over one. In still older specimens the pelvics have moved over three more, the origin having also moved, the dorsal fin in a specimen of 82 mm, being in the same position as at 38, but some metamorphosed specimens have it one vertebra further forward, and Fage has shown that it only stops at 106 mm. when it lies in the region of the 16th myotome. The movement of the dorsal fin and pelvic fins thus continues after metamorphosis, but only to a very small extent with regard to the dorsal fin compared with its movement between 35 mm. and metamorphosis.

The position of the dorsal fin is thus largely influenced by its migration

over many vertebræ and myotomes, the larger growth of the tail portion of the body compared with the fore part also taking its part.

Although my own specimens show a large and important gap between post-larval forms of 35 mm. and fully metamorphosed forms beginning at 38 mm., yet the observations of Fage fill in these gaps to a great extent, although being from a different locality the comparison cannot be strictly accurate.

He finds that at 40 mm, the specimens are still in the process of metamorphosis, having the pelvic fins still in front of the dorsal, and he regards the metamorphosis as taking place between 35 and 45 mm. As our specimens are slower in development it is probable that metamorphosis would take place in these at about 40-50 mm. My specimen of 35 mm. is so far backward in development that a glance at the curve will show how far from metamorphosis it is if only the dorsal fin be taken into account, but besides this the anus has not finished its migration, the pelvics are 4 vertebræ in front of the dorsal fin, and the body is thin and narrow, with a small head without any sign of a near metamorphosis. When we compare this with our metamorphosed form of 38 mm. with fully scaled, silvery, plump body, large head, anus in the adult position, and dorsal fin and pelvics having very nearly finished their migrations, we cannot help believing that this latter specimen has come from a post-larval fish of greater length, and that a reduction of a few millimetres has taken place at the time of metamorphosis, besides the cessation of growth in the trunk region described by Fage.

The method of growth in the Plymouth Pilchards agrees with Fage's observations. Thus in the post-larval forms the increase in length in the trunk is equal to that of the head and tail together, that of the metamorphosed forms the same. The much greater length of the head and tail in proportion to the body in the smallest metamorphosed forms makes it almost certain also that there is that cessation of growth in the trunk region during the period of metamorphosis, which is proved by Fage, but the absence of specimens during these stages makes these observations impossible with ours.

THE SPRAT.

CLUPEA SPRATTUS L.

The eggs of the Sprat may begin to appear in January and are usually very abundant in February and March in Plymouth Sound, often close to the shore, but also beyond the Breakwater in the region of the Knap and Panther buoys and the Mewstone. They dwindle after that, so that very few are found in May and after, although they occur as late as July (Hefford, 1910), and a young specimen of 6 mm. has been obtained in November.

The eggs measure 0.96 to 1.08 mm. across.

Just before hatching the young Sprat is speckled with black on its head and dorsal surface, and it is hatched whilst still possessing this larval pigment at about 3 mm. A noticeable feature in these newly hatched young are the lateral sense papillæ along the sides of the body, about six on each side, placed alternately and not opposite to one another



FIG. 7.—Newly hatched young of Sprat ; a., just hatched in bowl in Aquarium, 3 mm., from egg from tow-net, Breakwater 3.5.20 ; b., another specimen hatched in bowl, probably 2 days old, 3.5 mm., from egg from tow-net, Breakwater, 27.1.20 ; c., the same specimen, ventral view, showing sensory papilla.

(Fig. 7). These are similar to those described and illustrated by Cunningham in the Pilchard. At 3.5 mm, the dorsal speckles have almost disappeared and the yolk sac dwindles until at 5 mm, both yolk sac and first larval pigment has gone, the eye becomes pigmented and the usual chromatophores along the alimentary canal appear.

From February to May young Sprats are found abundantly in the tow-nets and rather larger specimens later on through the summer, the largest haul being one from Whitsand Bay in June, 1906, consisting of thousands of Sprats from 25 to 41 mm., the largest not having finished their metamorphosis and still in the transparent stage. Very few were taken in the autumn, except those that were fully metamorphosed and scaly, which occur in enormous numbers all round the coast close inshore.

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The researches of Fage have been made on a large number of young Sprats, from 4 to 35 mm., taken from the west of the British Islands, the Channel, and the northern part of the Bay of Biscay. Those from the Channel being from much the same waters as ours, but most of them small, the largest being 30 mm.

The chief fact that strikes one when examining the Plymouth specimens is the variability as to development, so that it is very difficult to fix a certain length for certain features to be present. Generally speaking up to about 20 mm, they agree with Fage's description and figures. He points out that the very young stages after the loss of the volk sac resemble those of the Pilchard very closely, and that the only safe guide is the number of myotomes, that the pelvic fins begin to appear at 18 mm., and that they are separated from the pylorus by a space (unlike the condition in the Pilchard, where the pelvics originate close up to the pylorus). The position of the pelvics, with regard to the pylorus, shows well in all the Plymouth specimens, and forms a good distinguishing character from the time of the appearance of the pelvic fins. In our specimens the fins appear at the earliest at a length of 17.25 mm., at the latest at 20.25 mm., the 18 mm, given by Fage being a good average size, but compared with the Pilchard they arise earlier and as a general rule the Sprats are further forward for the same length than the Pilchards of this district. In the Pilchards here they seldom show as early as 20 mm., and may be absent at 22 mm. Thus, agreeing with Fage, in the Plymouth Sprats at 20 mm., the "tail" as defined by him (i.e. the portion of the body from the anus to the base of the caudal fin), has grown longer and measures rather more than $\frac{1}{6}$ of the total length, the pelvics have no rays and are inserted almost exactly in the centre of the trunk in the region of the 18th myotome with the pylorus well in front of them. The dorsal fin has its first apparent ray (in reality the second) in the region of the 26th myotome, and its distance from the head is contained $1\frac{2}{5}$ in the length of the trunk. At this stage Fage states that all the rays in the dorsal and anal fin have appeared. In my specimens all the dorsal radials are present, but not the first ray, and the anal fin has all its elements except the first two rays. Seventeen is the usual number of dorsal rays (rarely 16 or 18), all but the first being formed by about 16 mm., the last being formed as early as 11 mm. The anal fin has usually 19-20 rays, one more ray than radials, all of which, except the first two, are present at 16 mm.

It is at this time, from about 20 mm., that the Sprat is so variable in its development. The head now tends to become longer, and the tail longer, but from 20 to 25 mm. or more it may either become much stouter with a longer head and tail compared with the body length, or it may stay in the slender larval form with its head still about $\frac{1}{7}$ of the

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total length. On the whole the long slender form predominates, which is still so like the Pilchard, the head thus beginning to grow longer from 22 to 26 mm.

It was found that at 25 mm. in a specimen with 48 vertebræ the



FIG. 8.—Diagram showing the relations of the fins and anus to the vertebræ in the Sprat of various lengths; *p.*, pelvic fins; 1—*x.*, first and last ray of dorsal fin; *a.*, anus; *v.*, vertebræ; *m.*, metamorphosed specimens.

pelvics had their origin under the 18th vertebra in connection with the 18th myotome, but the actual rays began under the 21st vertebra in connection with the 20th myotome (Fig. 8). The first ray of the dorsal fin was between the 26th and 27th vertebræ or over the 27th in connection with the 26th or 27th myotome, the last ray over the 34th

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vertebra in connection with the 33rd myotome and the anus between the 37th and 38th vertebræ. Slight variations might occur in the numbers owing to the difference in vertebræ, but as a rule they are very constant.

At 32 mm. the position of the pelvics is practically the same, but the first dorsal ray has advanced to between the 22nd and 23rd vertebræ, which is the usual position in the metamorphosed forms, the last ray standing over the 31st vertebra (in this case the fin is rather far forward owing to there being one vertebra less). In a specimen of 40 mm., not yet metamorphosed and having 48 vertebræ, the first ray was between the 22nd and 23rd and the last between the 31st and 32nd, the anus being under the 33rd. The pelvics have slightly changed their place, so that although the origin is as before, the rays begin under the 22nd vertebra and are only half a vertebra from the first ray of the dorsal.

We thus see that from 25 to 40 mm. the dorsal fin has advanced in the front over 4–5 vertebræ, the back only having advanced 2–3, the fin having grown in length so as to overlap two more vertebræ than when the full number of rays first appeared. The rays of the pelvic fins have slightly altered their position and are nearer the dorsal fin, and the anus has moved forward over 4–5 vertebræ. In the metamorphosed specimens of 33 and 39 mm. the positions are much the same, the fin and anus having accomplished the amount of migration necessary to bring them to the adult position relative to each other and to the pelvics at from 32 to 41 mm.

The accompanying curve (Fig. 9) shows the number of myotomes in the trunk region and in the distance between the operculum to the last ray of the dorsal fin in Sprats, from 11 to 41 mm. Starting at 11–12 mm. there are 37 myotomes in the trunk region which are reduced to 30–31 slightly before the time of metamorphosis, and between the operculum and the last ray of the dorsal fin there are 32 myotomes which are reduced to 28–29, the last ray of the fin thus usually passing over 2–3 myotomes only. The anus begins to change its position with regard to the myotomes almost at once, but the dorsal fin does not change at its hind end until it reaches about 30 mm., although the front end begins between 25 and 30 mm. and passes over 4–5 myotomes.

The position of both fin and anus is, however, influenced to a much greater extent by the growth of the abdominal region and tail, especially the latter, while the hind end of the trunk grows very little, and in this way the fin and anus come to lie nearer the head. This change of position is shown in curves II A^1 and B^1 . The ratio $\frac{AD}{AB}$ gradually lessens from $\cdot 80$ to $\cdot 61$, and the ratio $\frac{AE}{AB}$ lessens from $\cdot 71$ to $\cdot 59$. The change is



FIG. 9.—Curves showing the change of position of the dorsal fin and anus in the Sprat. A, showing number of myotomes in the trunk in Sprat, 11.5–50 mm. long; B, showing number of myotomes between operculum and last ray of dorsal fin in the same specimens; A^1 , showing ratio of distance from snout to anus $(A \ D)$ and body length $(A \ B)$ in same specimens; B^1 , showing ratio of distance from snout to last ray of dorsal fin $(A \ E)$ and body length in same specimens; o=metamorphosed specimens. Correction for curve A (approximate) to show true number of myotomes from head to anus. +=myotomes covered by operculum, -=myotomes overlapping anus: -11 to 25 (+1), 25 to 33 (+1-1 or-2), 33 to 41 and metamorphosed forms (+2-2).

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greater in $\frac{AD}{AB}$, but the reduction starts in both at 11–12 mm., whereas the movement of the fin over the myotomes takes place later.

There is thus undoubtedly a change of position in the dorsal fin so that it lies further forward in the metamorphosed Sprat than it does in the larval and post-larval forms. This is to a very small extent due to a movement over a few myotomes which takes place chiefly near the time of metamorphosis, but is also due, and more largely, to the fact that there is little growth in the region of the dorsal fin, whilst the tail region increases to a much greater degree. Fage has shown that, like the Pilchard, the position of the pelvic fins depends on the 15th rib, and changes in the abdominal cavity affect slightly their position in the body. This movement causes them to be brought nearer to the dorsal fin by 1–2 myotomes. The growth of the tail region also affects the position of the anus, its change being due partly to this and to a slight extent to a migration over 4–5 myotomes.

It is here that my results differ slightly from those of Fage, for, as is shown above, the change of relative positions of the pelvics, dorsal fin, and anus can be accounted for by the actual change of position with regard to the myotomes, and not merely to the greater growth of the tail and abdominal regions, but the larger change of position of dorsal fin and anus which brings them nearer the head is, as Fage states, dependent much more on the increase of the tail region and the small growth of the region of the trunk.

The following measurements show the larger growth of the tail region :---

| AB | AD | DB | $D\delta$ | $\frac{A\delta}{\delta B}$ |
|-------|------|-----|-----------|---|
| 11.75 | 9.25 | 2.5 | 0 | $\frac{9\cdot 25}{2\cdot 5} = 3\cdot 7$ |
| 24.5 | 17 | 7.5 | 0.75 | $\frac{17.75}{6.75} = 2.6$ |
| 41 | 25 | 16 | 2.5 | $\frac{27.5}{13.5} = 2.0$ |

 δ being the imaginary position of the anus when corrected for shift in position.

The ratio $\frac{A\delta}{\delta B}$ decreases, showing that the distance δB increases proportionately more than the distance $A\delta$. In the same way the growth of the tail region influences the position of the dorsal fin, the migration over the vertebræ and myotomes being only a very small factor in the change.

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At the time when the changes begin to take place prior to metamorphosis the dorsal fin and anus are almost in a straight line one above the other, and the pelvics are about two myotomes in front of the dorsal fin. The anus is now in its permanent position with regard to the myotomes, that is to say, it is in the region of the 32nd or 33rd vertebra. The dorsal fin, however, goes further after this, so that just before or during metamorphosis it is separated from the anus by two or more myotomes, and its final position is usually in connection with the 31st vertebra. It is thus at the time of general changes that the chief migration takes place in the dorsal fin, but as we have specimens undergoing metamorphosis still in the transparent post-larval condition at 41 mm., we find that the changes begin about 32 mm. and may continue until 41 mm. On the other hand, the metamorphosis (if it be correct to call this gradual change a metamorphosis) may begin about 32 mm. We have metamorphosed specimens as small as 30 mm., and these have larger heads in proportion to those not metamorphosed, and have other points of difference. Thus in the Plymouth specimens, from 32 to 41 mm., changes are taking place which lead to the scaled silvery stage, and at this time there is a much slower growth of the trunk compared with the head and tail, leading up to an almost complete cessation of growth at the actual time of metamorphosis, as is shown by Fage. I think it highly probable that in the Plymouth specimens there is an actual reduction in length, for the smallest metamorphosed forms are much further forward than any of the later post-larvæ of the same length, i.e. they are much pigmented, have scales, or the scales clearly marked out if not actually through the skin, a longer head and a longer tail, and the pelvic fins nearer to the dorsal, the dorsal fin and anus being practically in the adult position, although in some larger metamorphosed specimens it may be one myotome further forward. Moreover, if we take a post-larval and metamorphosed specimen of the same length, besides the difference in shape, longer head, presence of scales in the latter, we find that there are more myotomes in the same space in this than in the post-larval form. For instance, if the trunk measures 13 mm. in a metamorphosed form, 16 in a post-larval form of 30.5 mm., there are 31 myotomes in the trunk of the former, 34 in the latter, but if we measure 13 mm. from the operculum in the post-larval form we find there are only 27 myotomes, showing that the myotomes are more crowded together in the metamorphosed form, and it is not until at least 33 or 34 mm. that there are only 31 myotomes in the trunk of the post-larval forms.

In the metamorphosing Sprat from 32 to 41 mm. we find the 7 pyloric cœca fully formed. Even at 26 mm. there are 7, but only present as very minute buds. The ventral spinous scales are formed before the

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side scales, and begin as early as 35 mm. in quite transparent postlarval specimens. From that time the body scales are outlined more or less, although they are not through the skin, and pigment begins externally along the sides and dorsal surface, although it is still quite unlike the final adult silvery state.

It is interesting to find in a large haul of thousands of these young Sprats, with a few Herring, that they are all in the post-larval stages, most of them metamorphosing, but none of them having actually metamorphosed, although ranging from under 30 mm. to 41 mm. in the Sprat, and from 35 to 48 mm. in the Herring. This is probably due to the fact that after metamorphosis the silvery fish instantly congregate together, leaving those which are still transparent, and come closer inshore. Probably they would be too conspicuous to remain with the still more or less transparent forms. This is borne out by the fact of a large haul of Sprats from the Cattewater (1913), 30 to 50 mm., consisting entirely of Sprats evidently only just metamorphosed, for although they have the adult proportions and pigment they are not yet properly silvery, the scales being still underneath the skin. Other hauls consist entirely of perfectly silvery specimens.

The measurements of the growth of the Sprat at different periods of its development agree with the observations of Fage who shows that the growth is different from that of the Pilchard in that in the postlarvæ the increase in growth is due about equally to head, trunk, and tail, whereas in the Pilchard the increase is due about as much to the trunk as to the head and tail together, but in both there is a cessation, or at any rate a great slackening of growth during metamorphosis, and after metamorphosis they are alike in the increase of the trunk, being about equal to that of the head and tail together. The only difference in the Plymouth specimens is that the larger post-larvæ, although slackening in trunk growth, do not so nearly stop, thus as the fish grows its trunk grows gradually less. From 31 to 39 mm. in the post-larvæ the trunk has increased 2 mm., but from a post-larval form of 31 mm. to a metamorphosed form of 39 mm. it has only grown 1.5 mm., the head having increased 4.

If we now compare the Sprat and the Pilchard in the young stages we find them easy to differentiate up to the time of the loss of the yolk sac owing to the oil globule in the Pilchard. After that the only reliable distinguishing character up to the time of the appearance of the pelvic fins is the myotomes. It is easier to count the myotomes in the trunk than in the whole body, usually 37 in the Sprat, 42 in the Pilchard, reduced to 35 and 41 respectively up to 25 mm. In the Plymouth specimens one can usually distinguish them by the more advanced state of development in the Sprat than in the Pilchard throughout its life, especially in the younger stages with regard to the fins, but as Fage finds this is the reverse in those which he describes it is evidently an unreliable character depending on the locality. The myotomes then are the safest guide up to the appearance of the pelvic fins, 17.25-20 mm. in the Sprat, 20-22 mm. in the Pilchard, when their position a few myotomes from the pylorus in the Sprat and on a level with it in the Pilchard clearly distinguish the species, as Fage discovered. The forward position of the pelvics in the Pilchard is also a distinguishing mark, the ratio of snout to pelvics and snout to total body length being about $\cdot 43$ in these early stages of the Pilchard and about $\cdot 45$ in the Sprat. In the later stages the relative position of the dorsal and pelvic fins and the position of the dorsal fin and anus relative to the body length clearly differentiate the species. The anus also in the Sprat is much closer to the dorsal fin than it is in the Pilchard, and near the time of the metamorphosis stands exactly, or almost exactly, underneath it.

THE HERRING.

CLUPEA HARENGUS L.

The eggs of the Herring occur on the sea bottom in bays close to the shore at Plymouth, Bigbury Bay and off Rame being favourite spawning grounds (Cunningham, 1896, and present records). The eggs measure 0.9 to 1.4 mm. across, the newly hatched forms measuring 6–8 mm. These latter begin to appear in the Sound in December (one newly hatched is recorded on October 10th), continue plentifully during January, dwindle in February, and usually disappear in March. The latest record for very young stages is one of 13 mm., April 8th, 1914. The post-larval forms occur occasionally through the spring, but are rare in summer, the haul from Whitsand Bay, 30.6.06, containing several older post-larvæ from 30 to 48 mm. No specimens were obtained between these and fully scaled metamorphosed forms from 55 mm. which occurred with the Sprats and sometimes with the Pilchards near the shore and up the rivers.

The yolk sac may be absorbed as early as 8 mm., but in the Plymouth specimens it is often present at 10 mm., and remnants may even persist as late as 12 mm. During the absorption of the yolk, however, the young Herring may be taking solid food, such as larval molluscs, copepod eggs, and nauplii, and small cladocera. When the yolk sac has gone the dorsal fin begins to appear, but if the yolk sac be still present, even at a greater length, there is no trace of dorsal fin (Fig. 10).

The notochord is straight until at least 17 mm., the smallest seen

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with the notochord turning up being 17.25 mm., but it is usually straight at 18 mm., and only completely turned up at 21 mm., or more.

The dorsal fin is complete as to its full number of rays at about 28–29 mm. The hindmost fin ray is formed at about 18–19 mm., when there are usually 7–8 myotomes between the anal fin and the last dorsal ray. The anal fin is complete soon after the dorsal, so that both are complete at 30 mm. The number of rays in the Plymouth specimens (Orton, 1918) is usually 19 in the dorsal, but may vary from 17 to 21, and 17 in the anal, rarely 15 to 19. The pelvic fins do not begin to appear until 22 to 23 mm. Fage shows that they occur a long distance



FIG. 10.—Newly hatched and very young Herring; a., newly hatched Herring, 7 mm., Rame Head, N.N.W 3½ miles, midwater, 22.1.14; b., young Herring having lost its yolk sac, dorsal fin beginning, 9-5 mm., Breakwater, 2.1.20; c., young Herring with yolk sac still present, 10-5 mm., T.N., Penlee-Knap, 6.1.20.

from the pylorus, a character which is striking and easily differentiates the Herring from the Pilchard and Sprat. They are usually situated under the 24th vertebra, about 7 mm. from the first ray of the dorsal fin and near the beginning of the 24th myotome. The pylorus is far forward, but not so far forward in my specimens as it is in Fage's. This indeed is a rather striking difference between his and my specimens, and one which, as he regards it of sufficient importance to base part of his key upon, should have special stress laid on it.

Fage shows that the length from α sophagus to pylorus at 20.5 mm. is contained at least 3 times and $\frac{1}{3}$ in the length of the trunk. I find that it is always longer than this in my specimens until a very much

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greater body length. The following measurements of nine specimens show that up to 23 mm. or more it is contained under three times in the trunk, only at 35 mm. does it approach $3\frac{1}{3}$:—

Herring.

| | 11.011 | eneg. | |
|-----------------|---|--------|---------------------------------|
| Body length. | Beginning of Œsophagus to Pylorus. | Trunk. | Trunk. Œsoph. to Pylorus. |
| 18.75 | 5 | 13 | $2 \cdot 6$ |
| 21 | 5.5 | 14.25 | 2.7 |
| 22.5 | 5.25 | 15 | 2.8 |
| 22.23 | ea 5 | 14 | 2.8 |
| 26.5 | 6 | 17 | 2.9 |
| 26.5 | 5 | 15.5 | 3.1 |
| 28 | 6 | 17.75 | 3 |
| 33 ca | 6 - | 18 | 3 |
| 35 | 5.5 | 18 | 3.3 |
| | | | |

Comparing these with the Sprat we find that the Sprat may very nearly approach the Herring, although the length from except ages 2 of the trunk as the usual length. The following measurements show that although this is usual, yet the length may in certain cases approach very near the Herring :—

| | Spi | ·at. | |
|-----------------|---|--------|---------------------------------|
| Body length. | Beginning of Œsophagus to Pylorus. | Trunk. | Trunk. Œsoph. to Pylorus. |
| 18.5 | 4.5 | 10.5 | $2 \cdot 3$ |
| 19.75 | 4.5 | 11 | 2.4 |
| 22.5 | 4 | 11 | 2.7 |
| 23 | 4.75 | 12 | 2.5 |
| 25 | 5.5 | 14.5 | 2.6 |

The Pilchard is much the same as the Sprat, but keeps more regularly to the $2\frac{2}{5}$ given by Fage :— *Pilchard*

| | 1 ach | ana. | |
|-----------------|---|--------|---------------------------------|
| Body length. | Beginning of Œsophagus to Pylorus. | Trunk. | Trunk. Œsoph. to Pylorus. |
| 19.5 | 5 | 13.5 | 2.5 |
| 22.75 | 5.5 | 13.5 | 2.4 |
| 25.5 | 6 | 14.5 | 2.4 |
| | | | |

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The greater length of the fore part of the alimentary canal in the Plymouth Herrings is easily explained by the fact that the head is shorter and the trunk longer in these than in the northern forms, which is shown by Fage, and also that they develop more slowly also,



FIG. 11.—Showing the relations of the fins and anus to the vertebræ in the Herring of various lengths; p., pelvic fins; 1-x., first and last rays of dorsal fin; a., anus; v., vertebræ; m., metamorphosed specimen.

as the front part of the alimentary canal increases much less than the hind part, the ratio of the trunk to the front part increases as the fish grows. In this way the desired ratio is reached much later in the Plymouth specimens than in those from the north. Comparing this with the Sprat we have a similar decrease in the ratio as the fish grows. If,

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therefore, we have a very forward Sprat, as for instance the specimen of 22.5 mm. measured above, the distance from œsophagus to pylorus is short compared with the intestine, and the ratio is similar to that of the Herring at 21 mm. Thus the forward Sprat and the backward Herring of equal length are much alike in this respect, and I should suggest omitting this character as a specific difference in the key. The position of the pelvics is, however, quite distinct from this, and occurs much further away from the pylorus in the Herring than it does in the Sprat in all specimens.

Comparing Fage's notes on the differences in the northern and Channel forms (p. 114) we find that he shows the Channel forms from winter eggs to develop more slowly, have a shorter head and longer trunk than the northern Scottish Herrings from summer eggs, and we find the same differences—the shorter head, longer trunk, and slowness of development—are characteristic of the Plymouth post-larval Herrings.

The anus in the Herring migrates over 6-7 vertebra, beginning at about 22 mm., when there are 47 whole myotomes in the trunk, and its position is usually under the 49th vertebra, and moving forward, so that its position is under the 42nd vertebra at 40 mm. and onwards. It thus takes up its permanent position relative to the myotomes and vertebræ at about 40 mm. (Fig. 11).

The position of the anus depends more largely also, as in the Sprat and Pilchard, on the greater growth of the region from the anus to the end of the caudal fin than on that from the snout to the anus. Thus we have the following measurements, δ as before denoting the imaginary position of the anus when corrected for shift in position :—

| | | | | 10 |
|------|------|------|-----------|---|
| AB | AD | DB | $D\delta$ | $\frac{A\delta}{\delta B}$ |
| 26.5 | 20.5 | 6 | 0 | $\frac{20\cdot 5}{6} = 3\cdot 4$ |
| 33 | 23.5 | 9.5 | 1 | $\frac{24\cdot 5}{8\cdot 5} = 2\cdot 9$ |
| 45.5 | 29 | 16.5 | 3.5 | $\frac{32.5}{13} = 2.5$ |

the ratio $\frac{A\delta}{\delta B}$ decreasing, showing that the distance δB increases pro-

portionally more than the distance $A\delta$.

A comparison with the curves (Fig. 12) will show that the alteration of position is mainly due to the increase in the tail region.

Similarly with the dorsal fin, the forward movement over the myotomes only begins about 27 mm. and stops probably just before metamorphosis, which in the Plymouth specimen probably only begins shortly



FIG. 12.—Curves showing the change of position of the dorsal fin and anus in the Herring; A, showing number of myotomes in the trunk in Herring, 13 to 55 mm. long; B, showing number of myotomes between operculum and last ray of dorsal fin in same specimens; A^1 , showing ratio of distance from snout to anus $(A \ D)$ and body length $(A \ B)$ in same specimen; B^1 , showing ratio of distance from snout to last ray of dorsal fin $(A \ E)$ and body length in same specimens; o=metamorphosed specimen. Correction for curve A (approximate) to show true number of myotomes from head to anus. +=myotomes covered by operculum. -=myotomes overlapping anus: -13 to 27 (+1), 27 to 36 (+1-1 or -2), 36 to 46 (+2-2).

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before 48 mm. At this length the dorsal fin has not quite finished its migration and scales are indicated, but the proportions of the body are still those of the post-larva.

The hind end of the dorsal fin usually begins between the 42nd and 43rd vertebræ and the front ray over the 33rd. The fin migrates over nearly eight vertebræ. It does not grow at a greater rate than the vertebræ as it does in the Sprat, so that with rare exceptions (when, as in the specimen of 45.5 mm, in the diagram, over 10 vertebræ are involved) it extends over 9-10 vertebræ. The final position of the fin, as shown in the small metamorphosed forms, is with its front ray over the 26th vertebra, just behind the 25th myotome,* and the last ray between the 34th and 35th vertebræ. The pelvic fins originate under the 26th vertebra, the rays finally taking up their position under the 28th vertebra, about two myotomes behind the front of the dorsal fin. Transition stages after 48 mm. are wanting, but in the specimens from 41 to 48 mm. the scales are indicated as a slight pattern on the body, and the ventral keeled spines are developing. The pigment is also beginning along the lateral line and dorsally, but in shape the fish is still in a post-larval condition with a small head, and the dorsal and pelvic fins not yet in the final position. The smallest metamorphosed forms available measured 55 mm. It is thus probable that at 48 mm. the Plymouth specimens are not quite ready for metamorphosis, but nearly so. The pyloric cœca begin to develop as early as 33 mm., and are very numerous at 43 mm. Heincke (1898, p. 30) has shown that the autumn Herrings begin to metamorphose at 45-50 mm., the metamorphosis being complete at 60 mm., and ours seem to agree fairly well with this.

The method of growth of the post-larvæ up to about 41 mm. is much the same as it is in the northern forms, but differing in that the trunk is longer in proportion to the head and tail. Thus we have the following measurements :—

Post-larvæ from 10.5 to 41 mm., Plymouth.

| | Length | 10.5 mm. | 41 r | nm. | | |
|------|-------------|-----------------|------|------|----------|------|
| | Head | 1.5 | 7 | | increase | 5.5 |
| | Trunk | 7.5 | 20 | | ,, | 13.5 |
| | Tail | 1.5 | 7 | | ,, | 5.5 |
| anus | to base of | f caudal fin) | | | | • |
| Wh | ilst from 4 | 41 to 48 mm. we | have | e :— | | |
| | Length | 41 | 48 | | | |
| - | Head | 7 | 10 | | increase | 3 |
| | Trunk | 20 | 21 | | " | 1 |
| | Tail | 7 | 10 | | ,, | 3 |

* Used in the true sense as elsewhere, except in the curves showing myotomes in trunk.

Northern specimens (Fage, p. 115):

| Length | 10.8 | 41 | | | |
|--------|------|----|----------|-------|--|
| Head | 1.35 | 8 | increase | 6.65 | |
| Trunk | 7.81 | 19 | ,, | 11.19 | |
| Tail | 1.72 | 8 | ,, | 6.28 | |

Thus up to 41 mm. the same kind of growth is apparent, but the trunk is longer and the head shorter in the older Plymouth specimens. Fage has no specimens later than 41 mm. from the "Thor," but ours show in those from 41 to 46 mm. that growth in the trunk region is arrested as in the Sprat and Pilchard, so that there is only a growth of 1 mm., whilst the head and tail have each increased 3.

SUMMARY.

In summing up the differences between the three species in their postlarval stages I am in complete agreement with Fage that the myotomes are the essential characters for the differentiation of the younger forms, but it is here proposed to use those from the operculum to the anus (the "trunk" region of Fage) as being more easily counted and more readily seen. Differences in rate of development are not good characters to distinguish between the Sprat and the Pilchard, as this differs with the locality, but the Herring is always much more backward in development for the same size than either the Sprat or the Pilchard. The length of the fore part of the alimentary canal also varies with locality, although it is shorter in the Herring than in the Pilchard and Sprat. When the pelvic fins appear (the length at which they appear varying slightly with the locality) the difference in position with regard to the pylorus is distinct, being on a level with the pylorus in the Pilchard, a slight distance from it in the Sprat and still further away in the Herring. Their position on the body is nearest the head in the Pilchard and usually furthest away in the Herring.

From the time that the pelvic fins appear the alteration in the position of the dorsal fin and anus makes the differentiation of the species still more easy, the anus coming to lie close up to the hind end of the dorsal fin in the Sprat and the migration of the dorsal fin being only very slight, whilst in the Herring it is considerable and in the Pilchard even greater, so that in these the anus lies far from the dorsal fin. The tail in the Sprat is the longest, in the Herring the shortest.

The Sprat metamorphoses at the smallest size, the Pilchard the next, and the Herring the greatest. The method of growth as Fage shows in the post-larval Sprat is different from that in the Pilchard and Herring, the increase in the trunk being about the same as in the head and tail,
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whilst in the Pilchard and Herring it is greater, the increase of the trunk being about equal to that of the head and tail together, there being a cessation of growth in the trunk in all three during metamorphosis, after which they all grow in the same way.

In order to utilize the key given by Fage and adapt it so that it embraces our own specimens it might be altered slightly, and applying it only to our three species herein treated, the Herring, Pilchard, and Sprat, use it as follows :—

Young 8–10 mm, long.

Distinguished by myotomes only.

| Fotal number in body. | | umbe trunk | | | |
|--------------------------|---------|---------------|--|--|----------|
| 46-48 | usually | 37 | | | Sprat |
| 51 - 52 | ,, | 42 | | | Pilchard |
| 56-58 | ,, | 47 | | | Herring |

10-20 mm.

| Pelvic fins appear at 17.5–20 mm., some distance (4–5 myo- tomes) from the pylorus, 37–35 myotomes in trunk . | Sprat |
|--|----------|
| Pelvic fins appear at 18-22 mm., on a level with the pylorus, | - |
| 42–41 myotomes in trunk | Pilchard |
| Pelvic fins not appeared, 47–46 myotomes in trunk . | Herring |

20-40 mm.

| a. Pelvics on a level with the pylorus, 41–36 myotomes in trunk | Pilchard |
|---|----------|
| b. Pelvics situated behind the pylorus : | |
| (1) Length of tail * comprised well under 6 times in the | |
| total length, 35–31 myotomes in trunk | Sprat |
| (2) Length of tail comprised more than 6 times in the total | |
| length, 46–41 myotomes in trunk. Pelvic fins situated | |
| 7–8 myotomes from pylorus | Herring |

 $\ast\,$ The tail is here used in the same sense as given by Fage, i.e. from the anus to the base of the tail fin.

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TABLE SHOWING RECORDS OF YOUNG HERRING, PILCHARD AND SPRAT, ARRANGED IN MONTHS.*

(For chart of stations see Clark, 1914.)

| Month. | Year. | Depth | h. Herring. | Pilchard. | Sprat. |
|----------|-------|--------|------------------|--------------------------------------|-------------------------------------|
| January | 1908 | A | 15 (8·5–13 mm.) | | |
| ,, | 1914 | Ā | Several (6.5-10 | | A few eggs. |
| " | | | mm.) | | 00 |
| | | C, | Very many (6.5-9 | d had it. | |
| | | | mm.), many eggs | 3 | |
| | 1920 | A | 816 (8-14 mm.) | | Several eggs. |
| February | 1914 | A | Many (7-10 mm.) | | Several eggs and newly |
| | | | | | hatched young (2.5- |
| | | | | | 6 mm.). |
| | | С | 10 (7–10 mm.) | | Many (3-6 mm.) and |
| | | | | | eggs. |
| | | D | 32 (8–11 mm.) | | Several (4–5 mm.). |
| " | 1920 | A | 541 (9–22 mm.) | | Many eggs. |
| March | 1901 | A | 3 (14–18 mm.) | | |
| ,, | 1907 | D | 1 (14.5 mm.) | | 6 (11–14·5 mm.). |
| " | 1914 | ? | | | Many (4-6 mm.) and |
| | 1000 | | 0.00.10 | | eggs. |
| ** - | 1920 | Α | 6 (9–12 mm.) | | Several eggs. |
| A | 1014 | | 14 /12 94 mm) | | 5 (3.5-7 mm.). |
| April | 1914 | A B | 14 (13–24 mm.) | | $105 (3 \cdot 5 - 20 \text{ mm.}).$ |
| | | C | 9 (18–22 mm.) | 15 (5·6-6 mm.) | 18 (5·5–23 mm.). 99 (7–22 mm.). |
| | | D | | 10 (0.0-0 mm.) | $74 \ (7-16.5 \text{ mm.}).$ |
| | 1920 | A | | 2 (5-17 mm.) | 5 (5–16 mm.), 1 egg. |
| ,, | 1520 | Ď | | Over 2000 eggs | 5 (5-10 mm.), 1 egg. |
| May | 1906 | A | 30 (35-46 mm.) | Over 2000 eggs | Over 2000 (12-41 mm.). |
| | 1914 | A | 00 (00 10 mm.) | 64 (7-16 mm.) | Very many (7–24 mm.). |
| •• | TOTT | B | | 29 (6 - 17.5 mm.) | 51 (13–24 mm.). |
| | | D | | Very many (6.5- | Very many (7-25 mm.). |
| | | * | | 18.5 mm.) | |
| | | ? | 1 (22 ca mm.) | | |
| June | 1913 | A | | 130 (8·5-22 mm.) | 99 (10-25 mm.). |
| | | В | | 37 (12-23 mm.) | 250 (11.5-32.5 mm.). |
| | | С | | 51 (11-20 mm.) | 388 (9–25 mm.). |
| | | D | | 48 (9–19 mm.) | 218 (14–20 mm.). |
| ,, | 1914 | В | | 5 (14–24 mm.) | 7 (14·5–19·5 mm.). |
| | | C | | 1258 (6–25 mm.) | Many (12–28 mm.). |
| | | D | | 21 (7·5–19 mm.) | |
| July | 1913 | A | | 5 (17–22 mm.) | Ca 200 (30.5–50 mm.). |
| | | B | | 1 (26 mm.) | - 110 00 1 |
| | | C | | 21 (11-26 mm.) | 5 (10–22 mm.). |
| | 1014 | D | | 1 (23 mm.) | 1 (10 |
| " | 1914 | A | | 9 (13·5–24 mm.) | 1 (18 mm.). |
| | | B C | | 157 (0.5.96 | 1 (20 mm.). |
| | | D | | 157 (9.5-26 mm.) | 29 (18.5-27 ca mm.). |
| Anoust | 1012 | A | | 79 (5.7-21 mm.) | 39 (11.5 - 35.5 mm.). |
| August | 1913 | C | | 2 (24.5-25 mm.) 2 (23-24.5 mm.) | 1 (36 mm.). |
| | | D | | 2(23-24.5 mm.) 87 (9.5-23 mm.) | 1 (11 mm.). |
| | | D | | or (5.5-25 mm.) | r (11 mm.). |

 $\ast\,$ For records in 1917–18–19, see Lebour (1918, 1919, 1920) and Clark (1920). Further records for 1920 will be shortly published by Clark.

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| Month. | Year. | Depth. | Herring. | Pilchard. |
|-----------|-------|--------|---------------|--|
| September | 1913 | Ā | in the second | 70 (4·75–24 mm.). |
| | | В | | 30 (4.5-13 mm.). |
| | | С | | 148 (3.5–23 mm.). and many eggs. |
| | | D | | 10 (6·5–8 mm.). |
| September | 1914 | • A | | 1 (24.5 mm.). |
| - | | В | | 2 (20.5–22.3 mm.). |
| October | 1913 | Α | | 7 (7–10 mm.). |
| | | В | .oB.80 | $52 (3 \cdot 5 - 13 \text{ mm.}).$ several eggs. |
| | | С | | 343 (5.5-25 mm.). |
| November | 1913 | A | | 27 (5.5–18 mm.). |
| | | В | | 4 (11–16 mm.). |
| | | С | | 61 (7–21 mm.). |
| | | D | | 1 (13 mm.). |

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Sprat.

The Food of Young Clupeoids.

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With One Figure in the Text.

WHILST investigating the food of young fishes in general (Lebour, 1918– 1919–1920) some thousands of young Clupeoids were examined, with the result that by far the larger proportion of post-larvæ were found to be empty. Here and there, however, food was present, and by bringing these records of 1917 to 1919 together, with some from 1920 and 1921, we have a good idea of the food of our three common Clupeoids—Herring, Sprat and Pilchard—in their young stages.

A probable reason for this apparent absence of food in the transparent stages is that the food must be very quickly digested on account of its being so conspicuous; thus it is probably taken only at long intervals and rapidly got rid of. It would follow that under these circumstances we should only occasionally catch the fish when food was inside it.

The observations on the food of the young Herring are perhaps the most interesting of the three on account of the fact that it eats solid food some time before the yolk sac is absorbed, the mouth being open when the fish is hatched, whereas the Sprat and Pilchard, being much less advanced, are only able to feed on outside food much nearer the time when the yolk sac disappears. Unfortunately we have no records of Pilchard food in the very young stages (under 12 mm.), green food remains being found in those of the Sprat before the yolk sac has completely disappeared.

Later transparent stages show that the food of all three species is mainly composed of copepods or copepod eggs, the latter apparently being a favourite food of the Pilchard. In the small, fully metamorphosed forms the food seems to be different in each species, even if they are caught together. Examination of these shows that the small Pilchards from the estuaries seem to be feeding nearer the bottom than the Sprat and the Herring caught with them. The Herring, which are larger than the Sprat and the Pilchard, eating larger food which sometimes consists of fish, presumably other Clupeoids.

The few records of the post-larval Pilchard food are interesting on

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account of the small amount of information hitherto recorded on this subject and the very large proportion of empty fishes.

CLUPEA HARENGUS L. HERRING.

Newly hatched Herring are commonly caught in the tow-nets in all parts of the Sound in January and February, usually disappearing in March. Young stages up to about 18 mm. occur also, but only rarely in later spring, summer and autumn, the usual time for them being from February to March.

Of these young Herring, those from 7 to 8 mm. long, nearly always possessed a yolk sac, from 8 to 9 mm. the yolk sac was usually still present, and up to 10 mm. it often persisted. Even at 12 mm. remnants of the yolk sac could sometimes still be recognised.

In the following table the food of 140 specimens, from 7 to 12 mm. long and still retaining at least part of the yolk sac, is given. Over a thousand caught at the same times were empty, but the food present gives a good idea of what is eaten :—

| No. of | | | | |
|------------------------------|------------------|---------------|-------------------|---|
| Speci- mens. | Length in mm. | Date. 1917 | Locality. | Food. |
| | | | | |
| 2 | 8.5 | Feb. | West Channel * | Larval gastropod. |
| $2 \\ 2 \\ 1 \\ 2 \\ 1 \\ 1$ | 8.5 | 1 | | Green food remains. |
| 2 | 9 | | | . ,, ,, ,, |
| 1 | 9 | | | 3 larval gastropods. |
| 2 | 9.5 | | | Larval gastropod. |
| | 9.5 | | | Green food remains. |
| 10 | 9 | | Off White Patch | ,, ,, ,, |
| 7 1 1 1 | 9 | | | Larval gastropod. |
| 1 | 9 | | | 2 larval gastropods. • |
| 1 | 9 | | | Larval bivalve. |
| 1 | 9 | | | Larval bivalve, Paralia sul- cata. |
| 1 | 9 | | | Copepod nauplius. |
| .1 | 9 | | | Green food remains, larval gastropod, Prorocentrum micans, Goniaulax spinifera. |
| 1 | - 9 | | | Harpacticid. |
| | 9.5 | | | and publicities |
| 1 | 10 | | | " |
| ĩ | 10 | | | Larval gastropod. |
| î | 10 | | | 2 larval gastropods, 1 larval bivalve. |
| 1 | 10.5 | 6 | Jennycliff Bay | Copepod egg (?). |
| 1 | 11.5 | 6 | Jennycliff Bay | 3 larval gastropods. |
| 1 | 12 | | 5 | Temora nauplius. |
| 1 | 10.5 | | Batten Bay | Larval bivalve, 2 larval gas- |
| | | | Datton Day | tropods. |
| 1 | 11 | | North Anna Daniel | Copepod egg (?). |
| | 11.5 | | Off Breakwater | Green food remains. |
| 1 | 11.5 | | | Larval gastropod. |
| 1 | 12 | | | |
| 2 | 12 | | | Temora nauplius. |

* For plan of Sound see Lebour, 1918, p. 459.

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| No. of Speci- | Length | Date. | in the second second | and the second second |
|------------------|------------|--------------|-------------------------------|--|
| mens. | in mm. | 1917 | Locality. | Food. |
| 1 1 | 8 9 | 9 | New Grounds | 2 larval gastropods. 3 larval gastropods, green |
| 2 | 9 | | Off White Patch | food remains. Copepod egg (?). |
| ĩ | 9 | | On white Fatch | Larval gastropod. |
| 1 | 9 | | | Larval gastropod, copepod re |
| 1 | 0 | | | mains, green food remains |
| 1 | 8 | | Jennycliff Bay | Copepod egg (?). |
| 3 | 9 | | | |
| 1 | 10 | | | " " |
| 1 | 9 | | | Larval gastropod. |
| 1 | 10 | | | |
| 1 | 9 | | West Channel | Copepod remains. |
| 1 | 9 | | Of White Detail | Copepod egg (?). |
| - | 8 | 13 | Off White Patch | Green food remains. |
| 1 | 8·5 10 | 27 | Panther Buoy |)))) 9 Palanaio noumlii |
| 1 | 10 | 1010 | | 2 Balanus nauplii. |
| 2 | 9 | 1919 Jan. | Knon Donthon | Lanval gastronod |
| 4 | 9 | 13 | Knap-Panther | Larval gastropod. |
| 1 | 9 | 10 | | Corycœus anglicus (juv.). |
| î | 8 | | West Channel to | 2 larval gastropods. |
| - | | | Breakwater | 2 mi fui guotropous. |
| 1 | 9 | | | Green food remains, |
| î | 9 | | , - | Copepod (juv.). |
| 1 | 9 | | | 2 larval gastropods. |
| 1 | 9 | | | Larval gastropod. |
| 1 | 8 - | | Knap to Penlee | ., ., |
| 2 | 9 | | | ,, ,, |
| 1 | 9 | | | 2 larval gastropods. |
| 1 | 8.5 8.5 | 15 | West Channel to Breakwater | 3 " " 5 larval gastropods, larval bi |
| 4 | 9 | | | valve. |
| * 3 | 9 | | | Larval gastropod. 2 larval gastropods. |
| 2 * | 9 | | | 3 |
| ĩ | .9 | | | 3 larval gastropods, larval bi |
| - | · | | | valve. |
| 1 | 9 | | | 5 larval gastropods. |
| 1 | . 9 | | | Larval gastropod. |
| 1 | 9 | | | 3 larval gastropods. |
| 1 | 7 | | | 3 larval gastropods, larval bi |
| | | | | valve. |
| 1 | 8 | | | 6 larval gastropods. |
| 1 | 9 | | Brookmeter | Larval gastropod. |
| 8 6 | $9 \\ 9$. | | Breakwater to New Grounds | 2 larval gastropods. |
| 6 | - 9 | | to new Grounds | 3 |
| 5 | 9 | | | 1 |
| 1 | 9 | | | 5 |
| i | 9 | | | 6 ,, ,, |
| 1 | 7 | 17 | Panther Buoy | Green food remains. |
| 3 | 8.5 | | | Larval gastropod. |
| 1 | 8.5 | | | 4 larval gastropods. |
| 1 | 9 | | West Channel to | Larval gastropod. |
| | 10 0 | | Middle Sound | |
| 1 | | | Breakwater | Larval gastropod. |
| 1 | 9 | | THE DATE | |
| 1 | 8.5 | Feb. | White Patch to | Balanus nauplius. |

FOOD OF YOUNG CLUPEOIDS.

| No. of | | | | |
|-----------------|------------------|---------------|-------------------|--|
| Speci- mens. | Length in mm. | Date. 1917 | Locality. | Food. |
| | | 1921 Jan. | | |
| 1 | 9 | 19 | New Grounds | 3 larval bivalves. |
| 1 | 9•5 | 20 | Penlee-Breakwater | 3 larval bivalves, Tintinnopsis beroidea. |
| 1 | 9.5 | | | 3 larval bivalves. |
| 1 | 11 | | | 2 |
| 1 | 10 | 24 | Breakwater | 3 larval gastropods. |
| 1 . | 10 | | | 4 copepod eggs. |
| 1 | 9.5 | 26 | East Channel | Larval gastropod. |
| 1 | 9 | 27 | New Grounds | Larval bivalve. |
| · 1 | 9.5 | | | >> >> |
| | | | | |

The food of these 140 was as follows: Larval gastropods in 91; green food remains in 22; larval bivalves in 13; copepod eggs in 11; copepod nauplii in 4; harpacticids (juv.) in 3; copepod remains indet. in



FIG. 1.

(a) Young Herring, 0.9 mm., with remains of yolk sac. Tail end showing food, consisting of 3 larval gastropods. Tow-nets, Penlee-Breakwater (January 20th, 1921).
(b) Young Herring, 10.5 mm., after the disappearance of yolk sac. Tail end showing food, consisting of *Pseudocalanus*. Tow-nets, Breakwater (January 24th, 1921).

2; Balanus nauplii in 2; Peridinians, diatoms and a tintinnid each in 1. Larval gastropods thus head the list of food taken by these larval Herrings. The green remains are probably the remains of unicellular plants; these make up the rest of the food with larval bivalves, small crustacea, chiefly young copepodid stages and nauplii, and eggs which

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are probably those of *Calanus finmarchicus*. Full-grown copepods, such as *Pseudocalanus elongatus*, were taken as soon as the yolk sac had gone, but were not seen before.

Green food remains in 74, Balanus nauplii in 69, larval gastropods in 39, copepod eggs in 33, larval bivalves in 24, *Pseudocalanus* in 20, *Euterpina acutifrons* in 9, copepod remains in 9, harpacticids indet. in 4, *Oithona similis* in 4, *Corycœus anglicus* in one, *Oncœa* sp. in one, *Evadne Nordmanni* in one, *Campylodiscus* sp. in one, *Coscinodiscus radiatus* in one. Sand grains occurred in a few specimens.

In 1918 out of 87 (17–29 mm.) the only food was *Pseudocalanus* in 17 specimens.

In 1919 out of 536 (8.5–15 mm.), the smallest without the yolk sac, the following food was found : Larval gastropods in 128, *Pseudocalanus* in 29, larval bivalves in 8, copepod nauplii in 6, copepod juv. indet. in 6, copepod egg (?) in one, *Corycœus anglicus* in 3, harpacticid indet. in one, *Oithona similis* in one, *Paracalanus parvus* in one, *Oncœa* sp. in one, *Acartia clausi* in one, *Tintinnopsis* sp. in 3, *Coscinodiscus* sp. in one.

In 1920 the numbers were not recorded for food, but several Herring, 9.5-11.5 mm., without the yolk sac, contained larval gastropods and *Pseudocalanus*.

In 1921 out of 22 Herring (9–13 mm.), without the yolk sac, 14 contained *Pseudocalanus*, 5 contained larval gastropods and 3 contained larval bivalves. Three mounted specimens from Plymouth Sound, date unknown (18.75-23.5 mm.), contained *Pseudocalanus* and *Centropages*; one of 12.5 mm. from the Cattewater contained *Pseudocalanus*.

A careful investigation into these records shows that the green food remains do not occur in those over 12 mm., and as the yolk sac in these may have only just disappeared, it is in the very young stages close to the disappearance of the yolk sac in which green food is taken. At the same time most of the other food recorded may be taken; but larval gastropods occur more frequently in the smaller specimens, disappearing altogether after about 12 mm., and crustacea becoming the chief food. In the older specimens *Pseudocalanus* occurs most frequently, *Centropages* and other copepods also being found. The largest post-larval specimen containing food measured 28.5 mm., the food being copepods, genus indistinguishable.

Owing to lack of specimens no further records of the food of the postlarvæ were taken.

Food of metamorphosed forms caught with Sprat and Pilchard in various localities inshore showed that they were feeding on crustacea, chiefly mysids and amphipods. In certain cases remains of fish and clupeoid scales in the stomach showed that they were probably eating the Sprat and Pilchard which lived side by side with them.

Herring (98–105 mm.) from the Lynher River (Sept. 17th, 1920) contained many *Praunus flexuosus* and several mysids. Out of 54 larger specimens (115–145 mm.) from Saltash (Sept. 24th, 1920) 31 contained clupeoid scales, sometimes with remains of fish; a few were empty, and the remainder contained mysids and amphipods.

From the oyster beds at the River Yealm (Oct. 13th, 1920) 4 Herring (74–130 mm.) contained mysids, *Crangon, Caprella* and other amphipods, and many copepods. Three Herring (110–125 mm.) from Anthony Passage, Lynher River, Saltash, contained *Pranus inermis*. From copepods the Herrings thus go on to feed on larger crustacea and fish.

The food of the young Herring may be tabulated thus :--

STAGE.

Before disappearance of yolk sac.

FOOD.

Larval gastropods, green food (probably diatoms and flagellates), larval bivalves, nauplii and other young stages of small crustacea, including their eggs.

After disappearance of yolk sac up to about 12 mm.

After 12 mm. and probably until Copepods. metamorphosis.

After metamorphosis.

The same, but with small adult copepods.

Copepods, decapod, crustacea, amphipods, fish.

CLUPEA SPRATTUS L. SPRAT.

The records of food of the early stages of the Sprat show that it eatsgreen food before and for some time after the yolk sac is absorbed.

Only a few records show food taken before the absorption of the yolk :---

| No. of Speci- mens. | Length in mm. | Dàte. 1917 | Locality. | Fo | ood. |
|---------------------------|------------------|--------------------|-------------|---------|---------|
| 2 | 4.2 | Jan. 30 Feb. | White Patch | Green r | emains. |
| 1 | $4.5 \\ 4.5$ | 27 | Panther | л. " | " |
| 2 | 4 | March 30 | New Grounds | ,, | ,, |

In 1917–18–19, out of 106 which had lost the yolk sac (4.5–8.5 mm.)-60 contained green remains, amongst which could occasionally be recognised a diatom (*Thalassiothrix nitzschioides*, *Pleurosigma* sp., *Navicula* sp.,

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Coscinodiscus sp.), or, in the larger specimens, copepod eggs and copepod nauplii. *Tintinnopsis ventricosa* occurred in one of 5 mm. The only adult copepods seen were in 3 (15-27 mm.) containing *Pseudocalanus*, and an harpacticid and a copepod egg in one of 20 mm. A very large number of the post-larval Sprat were empty.

Records from Whitsand Bay (May 30th, 1906) of older post-larvæ (32-40 mm.) show the food to be copepods, chiefly *Pseudocalanus* and harpacticids.

We then come to the small metamorphosed forms :---

| No. of Speci- | Length | Date. | | |
|------------------|--------|-------|-----------------------------|--|
| mens. | in mm. | 1918 | Locality. | Food. |
| | | Sept. | | |
| 1 | 32 | 16 | Middle Sound | Cypris cirripede larvæ and |
| | | 1919 | | larval gastropods. |
| | | July | | |
| 1 | 55 | 2 | (?) | Porcellana larva, copepod re- |
| | | 1920 | | mains. |
| | | Sept. | | |
| 15 | 43-45 | 17 | Lynher River | Harpacticids. |
| 50 | 51-80 | 23 | River Yealm oyster bed | Bivalve larvæ (probably oyster spat), one with also an harpacticid, one with an ostracod. |
| 1 | 70 | 28 | Whitsand Bay | Copepods and larval gastro- |
| | 10 | Oct. | Wintsand Day | pods. |
| 8 | 42-90 | 4 | Anthony Passage, Saltash | Copepod remains, chiefly har- pacticids. |
| 7 | 48-52 | 13 | River Yealm oyster bed | Copepods and young amphi- pods. |

The young Sprat from its metamorphosis to 90 mm. or more thus feeds on small crustacea and molluscs. Up the rivers harpacticids seem to be the chief food unless larval molluscs are in great abundance, and then apparently every Sprat in the locality feeds upon these, which are presumably the spat of the Oyster. Thus they take different food from the slightly larger Herring which are with them, the Herring taking the larger crustacea or fish.

The food of the Sprat can be tabulated thus :----

STAGE.

FOOD.

- Before disappearance of yolk sac.
- Green food (probably diatoms and flagellates).
- After disappearance of yolk sac up The same, with small copepod to about 8.5 mm. nauplii and eggs.
- From about 8.5 mm. to metamorphosis.
- After metamorphosis up to at least 90 mm.
- Cirripedes, copepods and larval molluscs.

Chiefly copepods.

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SARDINA (CLUPEA) PILCHARDUS (WALB.). PILCHARD.

No food was found in any of the Pilchards with a yolk sac and for some time afterwards, the smallest seen with food being 12 mm. long.

In 1918, September 27th, one of 26 mm. contained a copepod.

The following records in 1919-21 are given in detail, as so little is known of the food of the post-larvæ. This shows the whole amount of the food from 400 specimens examined—39 with food, 361 empty. These all came from the Young Fish Trawl material taken by Mr. Clark :—

| No. of | | | | |
|-----------------|------------------|---------------|--|--------------------------------------|
| Speci- mens. | Length in mm. | Date. 1919 | Locality. | Food. |
| | | July | Rame N. 37° W. | |
| 1 . | 15 | 7 | 11 miles | Copepod egg. |
| 1 | 16 | | - | |
| 1 | 18 | | | ., ., |
| 1 | 24 | | | Copepod remains. |
| 1 | 13 | 9 | Eddystone E.N.E. 6 miles | Copepod nauplius remains. |
| 1 | 15 | | | Pseudocalanus. |
| 1 | 19 | | | |
| 1 | 20 | | | Copepod remains. |
| 1 | 20 | 10 | Rame N. 14° E. 4 ¹ / ₂ miles | Calanus nauplii. |
| 1 | 14 | 21 | Rame E. 1 N. 51 miles | Acartia (juv.). |
| 1 | 14 | August | | Oithona similis. |
| 1 | 12 | 1 | Rame N. 60° E. 3 ¹ / ₂ miles | Copepod nauplius remains. |
| 1 | 19 | | | Copepod nauplius. |
| 1 | 22 | 8 | Eddystone W.S.W. 21 miles | Copepod nauplius, 3 copepod eggs. |
| 1 | 22 | 1920 July | | 2 copepod eggs. |
| 1 | 22 | 6 | Rame N. 45° W. 11 miles | Many Calanus eggs. |
| 23 | 21-27 | 15 | Eddystone S. 60° W. 4 ³ / ₄ miles | » » » |
| | | | | |

It is thus shown that all food seen in the post-larval Pilchards from 12–27 mm. is copepod food, either eggs, nauplii or adults. No green food of any kind was seen and no remains of diatoms nor peridinians, an interesting fact when one refers to observations on the food of the smaller metamorphosed forms (Cépède, 1907, Mangin, 1912, and many others, including the present records).

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The following table shows the food of young metamorphosed Pilchards, taken by Mr. Clark, chiefly from up the estuaries in the autumn of 1920 :---

| No. of Speci- mens. | Length in mm. | Date. 1920 | Locality. | Food. |
|---------------------------|------------------|---------------|-----------------------------|--|
| i | 65 | Sept. 17 | Lynher River | Fine mud containing small organisms, many Prorocen- |
| | | | | trum micans, Halosphæra viridis and Navicula sp. |
| 1 | 68 | | | Fine mud containing many Prorocentrum micans, Para- lia sulcata, Lithodesmium undulatum. |
| Many | 65-82 | | | Mud with diatoms and Proro- centrum micans. |
| 1 ; . | 66 | | | Mud and diatoms, many Prorocentrum micans, one harpacticid. |
| 5 | 61-65 | 23 | Oyster bed, River Yealm | Mud with diatoms and Proro- centrum micans, a few larval bivalves (probably oyster spat). |
| 4 | 58-68 | 28 Oct. | Whitsand Bay | Copepod remains, including Temora. |
| 12 | 60-75 | 4 | Anthony Passage, Saltash | Fine mud, with diatoms and Prorocentrum micans. |
| | | | | |

The food of the young Pilchards may be tabulated thus :----

STAGE.

FOOD. Post-larvæ from 12-27 mm. and Copepods, adults, larvæ and eggs.

probably up to the time of metamorphosis.

Metamorphosed forms up to at least 82 mm.

Usually mud with unicellular organism's, chiefly Prorocentrum micans and diatoms. Occasionally copepods or larval molluscs.

There seems here to be a distinct change in diet at metamorphosis. The pelagic post-larvæ in the open sea feeding on copepods and their eggs, the metamorphosed forms coming inshore and probably usually feeding near the bottom on mud with unicellular organisms. The only metamorphosed specimens in our records which did not contain mud were from Whitsand Bay, and these contained sand and copepods, including Temora, one of the commonest of the planktonic copepods. All those from up the estuaries had evidently been feeding near the bottom on microscopic unicellular food taken in with the mud. This agrees with the observations of Cépède and Mangin, who found that the small metamorphosed Pilchards feed on a minute vegetable diet, peridinians being specially taken, with occasional zooplankton.

Fage (1920) gives a summary of the food of the Pilchard from the small metamorphosed forms to the adults from the Channel and the Bay of Biscay, showing first a predominantly vegetable diet, afterwards the animal portion increasing. According to Swithinbank and Bullen (1914), the adult Cornish Pilchards feed on a varied plankton predominantly zooplanktonic.

Peridinians are evidently a favourite food of the young metamorphosed Pilchards. *Prorocentrum micans* is usually at its maximum in September in this district and perhaps the commonest Peridinian species up the estuaries. It is not surprising, therefore, that this should form a large part of the Pilchard's food.

In comparing the food of the young Herring, Sprat and Pilchard we thus find that for the post-larvæ it is much the same for all three species, except that the very young Herring is specially fond of larval gastropods. They all eat much the same sort of pelagic food, copepods being the commonest in all after about 12 mm. The metamorphosed forms, however, occurring together up the rivers usually feed on different organisms, the Pilchards feeding near the bottom chiefly on mud and unicellular organisms, the Sprats above them feeding chiefly on copepods or larval molluscs, and the Herring, which are larger, on decapod larvæ, amphipods and fish. The diet is seldom very much mixed, and each fish generally keeps to one kind of food at one time. Thus the Herring will eat mysids and amphipods in one place, fish in another ; the Sprat will eat copepods in one place and all of them will be full of larval bivalves (probably Oyster spat) in another. Whatever is most abundant and also suitable is taken, but usually one kind of food at one time.

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A Contribution to Our Knowledge of the Life-Histories of the Dogfishes Landed at Plymouth.

By

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With Figures 1-19 in the Text.

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INTRODUCTION.

In view of the fact that dogfishes are now of undoubted importance as marketable food fishes, it is necessary that the life-history of each of the species concerned should receive closer attention than hitherto. The present publication is the result of an endeavour to gain a personal working knowledge of the general life-history of the species which are landed at Plymouth. In carrying out a scheme of work of this kind it is certain that many of the observations made will have already been carried out previously by other workers, but, nevertheless, the results obtained are of value, not only in regard to the degree of confirmation which they afford, but also in the building up of an account of the lifehistory under the local conditions. In some instances, too, it will be seen that the actual numeric results in themselves are of little statistical value. but they yield very interesting suggestions which may be confirmed or disproved by a repetition of the experiments on a larger scale. I express my thanks to the fish-buyers at Plymouth fish-market, particularly Mr. J. Vanstone, for their kindness in allowing me to handle their fish before dispatch, and for their assistance in obtaining a regular supply of material for many months.

SPECIES WHICH OCCUR.

Five species of dogfish are landed at Plymouth :---

| to the classification by | | | | |
|--------------------------|---|---|---|-----------------|
| Regan (10) and (11)). | | | | Local Name. |
| Squalus acanthias . | | | | Spur-dog. |
| Scyliorhinus canicula | | | | Rough-dog. |
| Scyliorhinus stellaris | | | 7 | Nursehound. |
| Mustelus vulgaris | | | | Sweet William.* |
| Galeus canis 🖇 🖇 | • | • | • | Sweet William. |

* No distinction is made locally between these two species.

Of these the Spur-dog is by far the most important, and during the winter months in particular, catches are landed by all classes of fishing craft. They are sold by public auction in lots, usually of one or two hundred, according to the size of the fish and the numbers available, and after being gutted, skinned and beheaded are dispatched by rail under the commercial name of Flake. A varying number of skins, according to demand, are forwarded with the fish for disposal to commercial dealers. The Rough-dog is landed fairly regularly throughout the year, chiefly by the sailing trawlers, but the catches can hardly be considered of economic importance. They are sold for local consumption.

The Nursehound also occurs fairly regularly, but only in very small numbers, and, like the rough-dog, is sold for local food purposes. The skins are of some commercial value, provided they are of a certain size and undamaged.

Sweet Williams are irregular in occurrence. Of the two species thus designated *Mustelus vulgaris* is the more common, and on several occasions upwards of one hundred have been observed in one day's landings, but generally the species is represented by a solitary specimen here and there among the heaps of the other species. The second species, *Galeus canis*, is rarely seen, and during the winter of 1919–1920 only five specimens were obtainable for examination. The professional gutters are careful to pick out Sweet Williams from the other dogfish, explaining that the offensive smell affects the flesh of the spur-dog. They are, however, purchased locally for food.

SQUALUS ACANTHIAS (Spur-dog).

MAXIMUM SIZE OF ADULT.

The fact that the female of this species normally grows to a longer length than the male receives confirmation in the size of the largest female and male fish as yet observed at Plymouth, viz. 110 cm. and 83 cm. respectively.

SEXUAL MATURITY.

The sexes differ also in regard to the length at which they become sexually mature. In the male, the attainment of maturity is indicated externally by a distinct increase in the length and size of the claspers. The smallest male so far observed, in which the claspers were thus enlarged, measured 59 cm. in length. There is no corresponding external expression of sexual maturity in the female, so that it is necessary to direct attention to the internal reproductive organs. The presence of embryos in the uterus is, of course, a clear indication of maturity, and the smallest female in this condition had a length of 72.8 cm., but this information is not sufficient. In the next section of the present publication it will be demonstrated that in the ovaries of a female carrying a brood of embryos in the uteri, a set of eggs is developing whose rate of growth is proportional to that of the embryos, so that when the latter are born, the ovarian eggs will be in a condition ready to enter the oviducts. In other words, an ovarian egg, in order to reach its full size, requires a period of time equal to that which is necessary for the complete develop-

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ment of a uterine embryo. There seems no reason to assume that the initial set of ovarian eggs in a young female will develop at a different rate, so that it may be concluded that a female before becoming mature undergoes an extended adolescent period during which her first set of eggs are developing in the ovaries. During the month of February, 1921, a number of female fishes from 68 cm. to 98 cm. in length were measured and the condition of the ovaries and uteri in each examined. The specimens under 70 cm. in length were quite immature, and no conspicuous eggs were present in the ovaries. Adolescent fishes, in which a set of eggs were developing in the ovaries, but the uteri were empty and undeveloped, varied in length from 71 cm. to 81 cm. Mature fishes with embryos in the uteri were of lengths from 74 cm. to 98 cm. :—

| | Num | ber of speci | mens in the | e following | size-groups | (cm.) |
|---------------|-------|--------------|-------------|---------------------------------------|-------------|-------|
| Type of fish. | 71-74 | 75-79 | 80-84 | 85-89 | 90-94 | 95-99 |
| Adolescent | 7 | 12 | 1 | · · · · · · · · · · · · · · · · · · · | | |
| Mature . | 1 | 3 | 13 | 14 | 6 | 2 |

THE MATURE FEMALE.

On December 12th, 1913, sixty-three female fishes were measured, and the number of the uterine embryos and the obviously developing eggs in each was determined together with their size. In the first place it was found that in any one parent the embryos were of the same general size, and, similarly, the developing ovarian eggs. (*Vide* Smitt, 13, page 1162, and Borcea, 1, page 205.) Secondly, it was observed that the size of the ovarian eggs was related to the size of the corresponding embryos, in that the larger eggs were associated with the larger embryos:—

| Diam. of Ovarian | Ν | umber of E | mbryos in | the followin | ng 2 cm. gr | oups. |
|-------------------------|--------------------------|-------------|-------------|--------------|---------------|-------------|
| Egg in cm. | $9 \cdot 0 - 10 \cdot 9$ | 11.0 - 12.9 | 13.0 - 14.9 | 16.0 - 17.9 | 23.0-24.9 | 27.0 - 28.9 |
| 1.0-1.9 | 2 | 49 | 13 | _ | — | _ |
| $2 \cdot 0 - 2 \cdot 9$ | - 1 - | 9 | 19 | 5 | - | |
| 3.0 - 3.9 | _ | _ | | | 4 | |
| $4 \cdot 0 - 4 \cdot 9$ | — | — | | | 1303 <u>-</u> | 6 |

During the month of February, 1921, a similar set of observations was made in order to ascertain the size of the ovarian eggs which would be associated with newly formed embryos, and, as was expected, the ovarian eggs were always quite small. These results justify the conclusion that in a pregnant female, during the time that a brood of embryos are developing in the uteri, a fresh batch of ovarian eggs are increasing proportionately in size, so that, eventually, when the embryos are born, there is a set of fully developed eggs in the ovaries ready to pass into the oviducts. at which the capsule breaks and the embryos become free in the uterus, nor is the ultimate fate of the remains of the ruptured capsule clearly understood. Kerr (6, page 478) states that as development goes on (embryo of 7–8 cm.) the thin horny shell of the capsule becomes still thinner, breaks up, and disappears. Unruptured egg-capsules have been taken during the present series of observations enclosing embryos up to a length of 7 cm., but it seems possible that under natural conditions the capsule may remain unbroken for a longer period. On November 23rd, 1920, a female embryo of 13.5 cm., when extracted from the uterus, was found to be encased almost completely by the slightly torn shell of the capsule, and it is quite feasible that the rupturing of the latter was a post-mortem injury. On December 2nd, 1920, the remains of the capsule were present in a uterus containing three fully grown embryos of 28–29 cm., so that the capsular remains may rest in the uterus until the embryos are ready for birth.

There is a large amount of variation in the size of egg-capsules. During the months of January and February, 1921, the volume, as a convenient expression of size, of each of 148 newly formed capsules taken from fishes of varying lengths, was determined by the method of displacement. The results obtained, which are summarized below, will convey a fair idea of the general range in volume of egg-capsules derived from fishes irrespective of length :—

| Number of Embryos per capsule (n). | Number of Capsules. | Range in Volume in ccm. (R). | Average Volume in ccm. (Vn). | $\left(\frac{Vn}{n}\right)$ |
|---------------------------------------|------------------------|---------------------------------|---------------------------------|-----------------------------|
| 1 | 27 | 29-68 | 45.7 | 45.7 |
| 2 | 86 | 40-125 | 91.4 | 45.7 |
| 3 | 32 | 65-196 | 136.9 | 45.6 |
| 4; | 2 | 165-210 | 187.5 | 46.9 |
| 5 | 1 | 200 | 200.0 | 40.0 |

The successive values of the ratio $\left(\frac{Vn}{n}\right)$ show that, on average, the

volume of an egg-capsule is approximately proportional to the number of embryos it contains, but the corresponding values of the range in volume (R) indicate equally clearly that this relation is merely an average probability which by no means applies to individual capsules. Thus, it will be seen that a capsule containing a single embryo may exceed in volume one containing two or even three embryos. These individual differences in volume are of considerable significance, for they are undoubtedly due to differences in the quantity of yolk associated with the enclosed embryos. It would be expected, therefore, that the embryos in the larger capsules, having a larger available supply of yolk, would be able to grow to a correspondingly larger size before birth, and, assuming

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that the rate of embryonic growth is independent of the quantity of yolk, they would remain for the longer time in the uterus (see page 477).

While watching the gutters at work on the quay, the impression was gained that the egg-capsules extracted from the smaller fishes were of a smaller size, and in consequence of this a number of ungutted females were purchased in February, 1921, and measured, and the volume of the egg-capsules, when present, was determined. Unfortunately, the percentage of specimens containing egg-capsules in the total of sixty fish opened was not large, but the results do not conflict with the above impression :—

| Number | Length | 1 | Egg-Capsules | • |
|----------------------------------|----------------------------|-------------------------|-------------------------------------|--|
| of Fishes. 4 | of Fish (cm.). 70–79 | No. of Embryos. 2 | Range in Volume (ccm.). 45–75 | Average Volume (ccm.). 62.2 |
| 5 1 | 80–89 90–99 | " | 81–115 90 | 94.8 90.0 |
| ineranti by here <u></u> rede | 70–79 | 3 | | . No la serie de la serie d Transmission de la serie de |
| $\frac{4}{3}$ | 80–89 90–99 | ,, | $116-130 \\ 124-170$ | $126.5 \\ 156.5$ |
| | | | | |

In the first place it is seen that the four specimens from 70 cm. to 79 cm. in length contained capsules which were all considerably under average size. The resultant embryos would, therefore, according to expectation, be below average size at birth. It has already been shown on previous pages, also, that the number of embryos may be dependent on the size of the parent fish, so that there is a combined indication that fishes from 70 cm. to 79 cm. in length give birth to embryos which are below average size and fewer in number. The adolescent period of a female fish is usually undergone, however, when the length is between 70 cm. and 80 cm., so that it is probable that any fish which is carrying embryos and whose length lies between these two limits, is pregnant for the first time. The above results may thus provide some degree of confirmation to the assertion that the embryos of the initial brood of the pregnant female are smaller and lesser in number than those of the subsequent broods.

In the second place, it will be noticed that the egg-capsules containing three embryos are greater in volume in fishes from 90 cm. to 99 cm. in length than in those from 80 cm. to 89 cm. in length. This may indicate that the largest fishes contain the largest egg-capsules, and will therefore produce the largest embryos.

A repetition of the above observations on a much larger scale would thus yield some exceedingly interesting information.

E. FORD.

THE EMBRYO.

The external gill filaments, which are so conspicuous a feature of young Elasmobranch embryos, cease to be visible to the naked eye in this species at a varying length between 10.0 cm. and 14.0 cm. :—

| | Number of | Embryos. |
|-------------------------------|--|--|
| Length of Embryo in cm. | Gill filaments visible to naked eye. | Ğill filaments invisible to naked eye. |
| 10 | 29 | 1 |
| 11 | 33 | 2 |
| 12 | 42 | 12 |
| 13 | 14 | 25 |
| 14 | 3 | 29 |

The size at which embryos may be regarded as ready for birth needs careful attention. The sex of embryos may here be ignored, for no difference has yet been observed between the male and female in respect to size at any corresponding stage of embryonic development. It is first necessary to determine the condition by which an embryo may be assumed to be ready for birth. It does not appear feasible that the young of this species will be born with any more than a mere external remnant of the yolk-sac. The newly hatched embryos of both the rough-dog and the nursehound usually have a tiny pin-head remnant still unabsorbed, as is also the case in the young of Raia sp., so that this condition has been accepted as the determining factor as to whether or no an embryo of the spur-dog is ready for birth. It has been shown on previous pages that the amount of yolk associated with embryos varies considerably, and that, in consequence, it would be expected that there would be a corresponding variation in the size at birth. From May 8th, 1920, onwards, notes were kept in regard to the degree of absorption of the yolk-sac in embryos from 23 cm. in length upwards, and the results obtained may be summarised thus :---

| | | | | | | | | N | U | MB | El | R (|) F | E | MI | BR | YC | S. | | | | | | | | |
|-------|------|----|----|----|----------------------|-----|----|----|----|----|----|-----|---------------------|-----|----|----|----|----|----|------|-----|------|------|------|----------------------|----|
| Mor | nth. | | | 1 | euou pres f Ei | ent | | | | | | 1 | nan pres f Ei | ent | | | | | in | 1 pr | oce | ss o | f he | alin | d, or ng. 1 cm | |
| | | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
| May, | 1920 | 3 | | - | - | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | - | - | - | - | - | - |
| June | | 12 | 6 | 1 | - | - | - | - | - | - | - | - | - | - | | - | - | - | - | - | | - | - | - | - | |
| July | | 33 | 20 | 4 | - | - | - | - | - | | - | | - | - | - | - | - | - | - | - 1 | - | 4 | - | - | - | - |
| Aug. | | 15 | 40 | 25 | 18 | 7 | - | - | - | - | - | 3 | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - |
| Sept. | ,, | 8 | 21 | 16 | 7 | 2 | 1 | 1 | - | 3 | 4 | 14 | 5 | 4 | 1 | 2 | - | - | 2 | 2 | - | 2 | 4 | - | - | - |
| Oct. | | - | 1 | 2 | 3 | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| Nov. | ,, | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - | - | 2 | 4 | 3 | 6 | 5 | 11 | 1 | - |
| Dec. | | - | - | | - | - | - | - | - | - | - | - | - | - | - | - | | - | - | - | 3 | 3 | 10 | 19 | 16 | 2 |

From May until the end of August the great majority of the embryos had a conspicuous bag-like yolk-sac (Fig. 1 is a drawing of a specimen of 25 cm. in length taken during this period). It was quite inconceivable to me that any of these could possibly be able to carry on a separate existence. There were, however, three specimens of 25 cm. in length during August in which the yolk-sac was reduced to the pin-head size, and thus complied with the arbitrary condition of readiness for birth. Towards the end of September there was a noticeable change, and many of the embryos from 23 cm. upwards had the reduced yolk-sac, while in others from 24 cm. the yolk-sac was not only completely absorbed, but the umbilical scar was actually healed or in process of healing. It was rather surprising to learn that so many embryos may remain in the uterus after the complete absorption of the yolk-sac.

Thus, then, these results indicate that it is not until the end of August that any embryo is in a condition ready for birth, but from September onwards specimens from 23 cm. to 31 cm. inclusive (the largest measuring 31·1 cm. in length and weighing 83 grammes) satisfy the conditions for birth. It may be remembered that when dealing with the variation in the volume of egg-capsules from different fishes (page 475), it was suggested that the embryos from the largest capsules would remain for the longest time in the uterus. It is interesting, therefore, to notice that the largest embryos in the above observations occurred most frequently in December, thus providing some measure of confirmation to this suggestion.

For purposes of comparison, the records of investigators in other districts may be given :---

| Recorded by. | Locality. | Size at birth in cm. |
|---------------|-----------------------|----------------------|
| Borcea (1) | Roscoff | 23-25 |
| Le Danois (2) | La Manche occidentale | 25 |
| Lo Bianco (7) | Naples | 20-24 |
| Smitt (13) | Scandinavia | 22-25 |

The late embryos possess a fairly constantly occurring scheme of round spots of light colour arranged symmetrically in regard to the long axis of the body (see Figs. 1 and 2) :—

- (1) A pair of spots, one on either side of the commencement of the first dorsal fin (Fig. 1 and 2, 1).
- (2) A pair of spots, one on either side of the middle line at the level of the hinder end of the first dorsal fin (Figs. 1 and 2, 2).
- (3) A pair of spots, one on either side of the commencement of the second dorsal fin (Figs. 1 and 2, 3).
- (4) One spot on either side of the body immediately above and just behind the insertion of the pectoral fin (Figs. 1 and 2, 4).



FIG. 2.—Squalus acanthias. Same specimen as in Fig. (1) viewed from above.

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- (5) One or more spots on the gill region on either side (Figs. 1 and 2, 5).
- (6) A more or less continuous row of irregularly circular or ovalshaped spots roughly united to form a light line along either side of the body from the pectorals backwards along the lateral line (Figs. 1 and 2, 6).

Pairs 1, 2 and 3 are interesting in their origin. In an embryo of 8 cm. in length, instead of the two distinct spots there is a single transverse light-coloured bar. As development proceeds, this bar gradually becomes constructed in the middle, thus producing the pair of spots. The rows (6) along the lateral line arise as a continuous line of light colour, and subsequently break up into the spotted condition.

The fins are typically pigmented. The pectorals and dorsals are brownish black in colour except for the white posterior edge, but the pelvics are uniformly white. The caudal fin is edged with white except for the very deep black tip of the dorsal lobe. This black tip of the dorsal lobe of the caudal and an equally prominent blackened area on the uppermost edge of the first dorsal are the most densely pigmented areas in the embryo. The spines of the dorsal fin conform to the coloration of the fins, except that their protective caps are white.

Examined microscopically, the black pigment appears to be arranged in three layers, one above the other. The most deeply seated layer is composed of fairly large stellate chromatophores. Immediately above this there is a layer of coarse black blotches or dots. The uppermost layer is the least noticeable, and consists of stellate chromatophores which are fewer in number and more widely scattered than those of either of the layers beneath. The light spotted effect is produced partly by a scarceness of black pigment in certain areas, and partly by the presence of greyish white pigment.

The scales of the embryo do not present any unusual feature. They are uniform in character, and although in the largest embryos they are contained each in a finger-like pouch of the skin which projects from the general surface, they do not actually penetrate the latter. The tips of the spines of the dorsal fins are covered by fleshy caps. The scales may be pigmented on their posterior face in a finely granular to stellate manner.

THE BREEDING SEASON AND THE TIME OCCUPIED BY Embryonic Development.

The information which is at present available in the literature upon these two important subjects is rather indefinite. Some investigators have contended that this species breeds throughout the year (*vide* Lo



FIG. 3.—Squalus acanthias. Graphic representation of the results summarised in Table (A). The range in size of the embryos on any particular day is shown by a thin vertical line. The thickened curves indicate the average length of the embryos on successive days. Average values of less than 1 cm. are represented by the broken lines

Bianco, 7, p. 538, in regard to the Mediterranean, and Day, quoting Mr. Dunn, 3, p. 317, for the English Channel). Le Danois (2, p. 134) states that the fishes of "La Manche occidentale" give birth to their young towards the end of winter. Borcea (1, p. 205) believes that at Roscoff the month of April is the chief time at which embryos in a condition ready for birth are found in the uteri of the females. He gives the range in size of the uterine embryos for different periods during the year, and concludes that embryonic development requires nearly one year to complete. Day (3, p. 317) was of the opinion that the British fishes breed throughout the summer and autumn, but he also quoted the view of Mr. Dunn already referred to above. Yarrell (15, p. 402) expressed the view that the young are born at various periods from June to November, while Garstang (4, p. 229) has recorded the breeding season at Plymouth as from January to March. Smitt (13, p. 1161) has given some interesting information :—

"Aristotle stated that on the coast of Greece this fish copulates in August, and brings forth its young from May till August. The case is apparently as a rule the same in Scandinavian waters. Ekström concluded from his observations in Bohüslan that the breeding is performed in shoals during August or September in rather deep water. According to many corroborative statements the young are born most plentifully at the end of April and the beginning of May, and afterwards, in less number, throughout the summer."

Since the beginning of March, 1920, embryos and egg-capsules have been collected continuously from the Plymouth fish-market in an endeavour to obtain the range of variation in size of the embryos during the successive months of the year. In the case of unruptured egg-capsules, the number of enclosed embryos was ignored, so that in the summarised results one unbroken capsule simply represents one embryo of a particular size. The results obtained are summarised in the accompanying Table A, and shown in graphic form in Fig. 3.

It will be observed that, on any one day, the embryos are separable into two or three distinct size-groups, according to the time of the year. In addition, the mean values for the corresponding size-groups of successive samples conform to fairly regular curves. It may therefore be concluded that the breeding season of this species has definable limits.

If we accept the twelve months from March, 1920, until February, 1921, both inclusive, as an average year, then the average growth of an embryo may be expressed by a composite curve constructed by linking together the separate elements AB, CD, and EF, of Fig. 3. This curve would be at its lowest point in November, and require a period of about twenty-

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five months to reach its maximum in the month of December. Embryos measuring less than 1 cm. in length would occur from November until the beginning of July, but in view of the relatively large average length from late May until July, it seems probable that newly formed embryos would only be met with from November until the middle of May. Again, on page 477 it was shown that embryos in a condition ready for birth occur only from the end of August until the end of December. These two results when applied to our composite curve enable us to conclude quite reasonably that an embryo commencing its growth in November may be ready for birth in the month of August after a lapse of twenty-one months, having attained a length of 25 cm. On the other hand, it may be that at this length the embryo has not yet absorbed sufficient yolk to make a separate existence possible, and in consequence it may continue in the uterus, not only until all the yolk is absorbed, but until the umbilical scar is completely healed, with a resultant increase of length to an observed maximum of 31 cm.

It may be useful to give a summary of the range in size of embryos for each month from March, 1920, until February, 1921 :---

| | | Range | in size of Embryos | s in cm. |
|----------|-------|---------------|--------------------|-----------------|
| Month | 1. | Size-group I. | Size-group II. | Size-group III. |
| March, | 1920 | >1-1 | 12-20 | |
| April | ,, | No ol | oservations | |
| May | ,, | >1-3 | 16-23 | - |
| June | ,, | , >1-3 | , 18–25 | |
| July | . ,, | >1-5 | 15 - 25 | — |
| August | " | 4-10 | 21-28 | |
| Septembe | er ,, | 5-13 | 22-29 | |
| October | ,, | 10-11 | 24-26 | |
| Novembe | r ,, | 10 - 17 | 23-30 | >1 |
| December | r ,, | 8–19 | 26-31 | >1 |
| January, | 1921 | 11-21 | 1000 0 <u></u> | >1-1 |
| February | ,, , | 13-21 | | >1-2 |

THE CONSTITUTION OF THE SHOALS.

Some general observations on this interesting question were commenced in October, 1919, when the daily landings, irrespective of the method of capture, showed a very great predominance of females, the majority of which were of large size, and in a gravid condition. From November 4th to November 19th, of a total of 885 fish picked up at random from the quay 810 were females and only 75 were males. Towards the end of November, however, it became noticeable that fish of a smaller size were being landed in increasing numbers, while the proportion of

| TABLE A. | 1 | l'A | B | LE | Α. |
|----------|---|-----|---|----|----|
|----------|---|-----|---|----|----|

| | в | Sinbry | s from | u Unru | pture | d Egg | e-Cap | sules. | | 1 | | | | | | | | | | Embr | yos fr | om Ri | upture | d Egg | capsu;-Capsu | les, or | Free i | n the l | Jterus. | | | | | | | | | | | | Embryo | os froi | in all S | ources. | | | |
|---|--|--|--------|-------------------------------------|-------------------------|-------------------------|-------|--------|---|---|--|---|---|-----------------------|---|--------|---|---|----|------|--------------------|-----------------------------|---|--|---|--|---------|--|---|------------------------------|------|------|--------------------------------------|---|------|----------------|------|----|--|--|--|---|-------------------------|---|--|--|---|
| | | 1 | | | | | | | | | tal No. | | - 14 - 19 - 19 - 19 - 19 - 19 - 19 - 19 | | | 11200 | | • | | | | | Siz | e of E | Smbryo | s in en | n. grot | ups, | | | | | | | | | | | Total No. | - | | 2 | Mean V | 'alues. | | | Date. |
| Date. | Total No. of Egg- Capsules. | | | e of E | | | | | 7 | | of nbryos, | 4 | 5 | 6 | 7 | s | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 ; | :4 : | 25 5 | 26 | 27 2 | 8 2 | 9 30 | 31 | of Embryos | No, of Embryo | Average 8, S-ze in cu | No Emb | b. of bryos, S | Average size in cm. | No. of Embryos, | Average Size in cm | |
| 1920 Mar. 4 May 5 , 8 , 10 , 18 , 27 Jule 2 , 9 , 23 July 5 , 6 Aug. 13 , 18 , 18 , 19 , 25 | $\begin{array}{c} 14\\ 7\\ -\\ 2\\ 13\\ 21\\ 19\\ -\\ 19\\ 24\\ 26\\ -\\ 1\\ 17\\ 26\end{array}$ | $\frac{13}{6}$ | 1 | 1 was 5 4 11 8 12 | 1 cr 4 8 5 8 8 | n.) 4 2 1 5 | | | | | 87 15 3 70 77 15 56 54 123 4 37 66 69 | | | 211 10 | | | | 2 | | | 2 | 6 | | | | | | $\frac{16}{11}$ | 5 27 4 | 1 5 21 5 15 9 | | | 1 - 1 - 1 - 1 - 5 - 8 | | 4 1 | | | | $\begin{array}{c} 101\\ 22\\ 3\\ 2\\ 83\\ 21\\ 96\\ 15\\ 75\\ 78\\ 149\\ 4\\ 38\\ 83\\ 95\\ \end{array}$ | $\begin{array}{c} 14\\ 7\\ -\\ 2\\ 13\\ 21\\ 19\\ -\\ 19\\ 24\\ 26\\ -\\ 3\\ 50\\ 48\\ \end{array}$ | $\begin{array}{c c} <1 \\ <1 \\ <1 \\ <1 \\ <1 \\ cal \cdot 5 \\ 2 \cdot 0 \\ \hline cal 2 \cdot 3 \\ 2 \cdot 7 \\ 2 \cdot 4 \\ \hline cb 5 - 6 \\ 5 \cdot 6 \\ 5 \cdot 6 \\ 5 \cdot 8 \end{array}$ | | 37 15 3 | $\begin{array}{c} 16\cdot 3\\ 20\cdot 0\\ 22\cdot 7\\\\ 19\cdot 4\\ 21\cdot 4\\ 21\cdot 1\\ 21\cdot 1\\ 21\cdot 0\\ 22\cdot 1\\ 24\cdot 5\\ 24\cdot 1\\ 24\cdot 0\\ 24\cdot 9\end{array}$ | | | 1920 Mar. May , 1 , 2 June , 2 June , 2 June , 1 , 1 , 1 , 1 , 2 , 2 , 2 , 2 , 2 , 2 , 2 , 2 , 2 , 2 |
| ", 25 Sept. 9 ", 10 ", 29 Oct. 14 Nov. 13 ", 18 ", 23 Dec. 2 ", 7 ", 15 ", 20 ", 31 | | | | | | | | - 1 | | | 35 23 137 11 54 134 143 90 100 119 105 93 | | | 2 | | 29 | | $ \begin{array}{c} 3 \\ 10 \\ 2 \\ 1 \\ 1 \\ 3 \\ 2 \\ $ | | | $\begin{array}{c}$ | 15 18 16 25 | $ \begin{array}{c} 1 \\ 12 \\ $ | *6 9 16 23 26 | $ \begin{array}{c} 1 \\ 7 \\ 4 \\ 7 \\ 13 \\ 17 \end{array} $ | 3 5 4 | | | | | | 2 | 3 - | 3 - 3 - 3 - 3 - 3 - 3 - 3 - 3 - 3 - 3 - | | 5 1 - 1 | } | | $\begin{array}{c} 35\\ 24\\ 137\\ 11\\ 56\\ 134\\ 143\\ 103\\ 102\\ 125\\ 110\\ 100\end{array}$ | $\begin{array}{c} 13\\ 2\\ 82\\ 4\\ 54\\ 110\\ 134\\ 77\\ 74\\ 109\\ 101\\ 93\\ \end{array}$ | $\begin{array}{c} 8 \cdot 9 \\ 6 \cdot 5 \\ 8 \cdot 7 \\ 10 \cdot 5 \\ 12 \cdot 1 \\ 13 \cdot 2 \\ 13 \cdot 2 \\ 14 \cdot 5 \\ 14 \cdot 9 \\ 14 \cdot 9 \\ 14 \cdot 9 \\ 15 \cdot 1 \\ 15 \cdot 0 \end{array}$ | 2 5 2 9 1 2 1 2 1 | 22 22 55 7 | $23 \cdot 9$ $24 \cdot 6$ $25 \cdot 7$ $25 \cdot 1$ $28 \cdot 3$ $25 \cdot 8$ $29 \cdot 2$ $28 \cdot 8$ $29 \cdot 9$ $26 \cdot 3$ | 2 13 2 6 5 7 | $\begin{array}{c} - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - $ | Sept. " 1 " 2 Oct. 1 Nov. 1 " 1 " 2 Dec. " 1 " 1 " 2 " 1 " 1 " 1 " 2 " 1 " 1 " 1 |
| ,, 01 1921 Jan. 6 ,, 14 ,, 27 ,, 29 Feb. 5 ,, 11 ,, 12 ,, 28 | $7 \\ 4 \\ 24 \\ 15 \\ 18 \\ 13 \\ 21 \\ 40$ | $7 \\ 4 \\ 23 \\ 14 \\ 17 \\ 12 \\ 17 \\ 35$ | 4 | 1 | | | | | - | | 107 100 59 65 32 32 44 37 | | | | | | | | | 52 | | 5 14 2 3 5 — | $ \begin{array}{c} 14 \\ 13 \\ 1 \\ 9 \\ 6 \\ 4 \\ \end{array} $ | $36 \\ 30 \\ 3 \\ 9 \\ 2 \\ 4 \\ 4 \\ 1$ | | $ \begin{array}{r} 15 \\ 9 \\ 16 \\ 14 \\ \overline{} \\ 15 \\ 16 \\ 11 \\ \end{array} $ | | $\begin{array}{c}3\\2\\5\\6\\1\\5\\4\end{array}$ | $\frac{2}{2}$ $\frac{2}{2}$ $\frac{2}{1}$ | | | | | | | | | | $ \begin{array}{r} 114 \\ 104 \\ 83 \\ 80 \\ 50 \\ 44 \\ 65 \\ 77 \\ 77 \\ \end{array} $ | $ \begin{array}{c} 107 \\ 100 \\ 59 \\ 65 \\ 32 \\ 32 \\ 32 \\ 44 \\ 37 \\ \end{array} $ | $\begin{array}{c} 16 \cdot 2 \\ 16 \cdot 1 \\ 17 \cdot 6 \\ 16 \cdot 9 \\ 16 \cdot 4 \\ 17 \cdot 8 \\ 18 \cdot 0 \\ 18 \cdot 7 \end{array}$ | | | | $7 \\ 4 \\ 24 \\ 15 \\ 18 \\ 13 \\ 21 \\ 40$ | $\begin{array}{c} <1 \\ <1 \\ <1 \\ <1 \\ <1 \\ <1 \\ <1 \\ <1 $ | 1921 Jan. ,, 1 ,, 2 ,, 2 Feb. ,, 1 ,, 1 ,, 2 |

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the conspicuously large fish was diminishing. In consequence of this, attention was directed to the landings of individual boats in order to ascertain the degree of variation in size of the fish in each case. The impression gained was that the fish caught by an individual boat on any one day were of a fairly uniform size, but that the average daily size varied considerably on different occasions. This suggests, first, that the shoals are constituted of fish of a similar size, and second, that during the period of observation shoals of large fish and shoals of small fish were present on the fishing grounds.

As often as possible the proportion of sexes in the fish of individual boat-landings was ascertained, and it soon became evident that the former was closely related to the average size of the fish. For instance, in the largest fish, as shown above, the females were overwhelmingly predominant, but in the smallest fish examined the sexes were approximately equal in numbers.

Observations of this kind have been continued, and a number of the results obtained are tabulated below, from which it is possible to derive a good deal of interesting information in regard to the shoaling habits of this species.

| Refer- ence No. | Date. | Details of Sample of Fish Examined. | Total No. of Fishes | No. of Fe- males. | No. of Males, |
|-----------------------|------------------------|--|---------------------------|-------------------------|------------------|
| 1 | Nov. 4th-19th, 1919 | Random samples from landings, irrespective of the method of capture. Majority of the fish over 80 cm, in length. | 885 | 810 | 75 |
| 2 | Nov. 25th, 1919 | From the catch of s.s. Condor. Average size of fish 50-70 cm. | 258 | 51 | 207 |
| 3 | Nov. 26th, 1919 | A small heap of discarded fish of sizes from 36–50 cm. | 56 | 30 | 26 |
| 4 | Jan. 8th, 1920 | From s.s. <i>Condor</i> which landed about 9000 uniformly medium-sized fish. | 284 | 200 | 84 |
| | | N.B.—On the same day the local sailing boats had catches of fish of large size showing the predominance of the female element. | | | |
| 5 | Jan. 17th, 1920 | A small heap of discarded fish of sizes from 40-50 cm. | 75 | 41 | 34 |
| 6 | Jan. 21st, 1920 | A sample of "drift" fish of average size from 45-50 cm. with which were a very small number of males from 70-73 cm. | 290 | 180 | 110 |
| 7 | Feb. 7th, 1920 | A sample of fishes of sizes from 50-60 cm. | 104 | 52 | 52 |
| 8 | Mar. 10th, 1920 | From the catch of s.s. $Trojan$ consisting of small fish with an occasional larger \vec{a} and $\hat{\varphi}$. | 272 | 142 | 130 |
| 9 | July 5th, 1920 | From s.s. Oithona off Looe, of average size from 50-60 cm. | 97 | 48 | 49 |
| 10 | July 29th, 1920 | From local smacks off Falmouth, sizes 45–60 cm. | 300 | 150 | 150 |
| 11 | Aug. 19th, 1920 | From French boat <i>Resurrection</i> , about 15 miles E.S.E. of the Start. Average size 80–90 cm. | 100 | 98 | 2 |
| 12 | Aug. 25th, 1920 | Hook and line fish from a Fowey boat. Average size 80-90 cm. | 101 | 100 | 1 |
| 13 | Sept. 23rd, 1920 | From local trawler. Average size 45-60 cm. | 100 | 45 | 55 |

Before proceeding to the discussion of these results it is necessary to recall to mind several biological facts which have already been dealt with in preceding pages, viz. :—

- (1) The adult female normally grows to a longer length than the male.
- (2) Sexual maturity in the male is acquired at a length of about 59-60 cm., but in the female at between 70 and 80 cm.
- (3) Males and females are born in equal numbers and at the same length.

With these facts in mind one is led to suggest that size and sexual condition are important factors in the constitution of the shoals in this species, the former probably being the more influential one. It seems reasonable to expect that in general it is more advantageous for fishes of the same average size to run together, both from the point of view of ensuring a fair chance of obtaining food, and of adapting the speed and extent of the swimming to the limit of endurance of the majority of the shoal. In shoals of fish of greatly varying sizes it is probable that the small fish would suffer in their chances of obtaining food, and would also have difficulty in maintaining the speed and endurance of the larger and stronger members. On the other hand, when it is remembered that the females in the pregnant condition may carry as many as ten embryos all of the same general size which may be as much as 30 cm. before birth, it is equally logical to expect that they require to move at a more leisurely rate and under conditions favourable to their temporary disability. In this case the factor of size may be of lesser importance. There would therefore appear to be a balance between these two factors of size and sexual condition whereby the shoals of fish are formed to ensure maximum comfort and equal chances of survival for the members of the shoal. The catch of s.s. Condor on November 25th, 1919 (Ref. No. 2), however, in which males were greatly predominant, is not explained by the above factors. The occurrence of shoals of males has been recorded by other investigators, e.g. Borcea (1, p. 205), Meyer (9) and Smitt (13, p. 1161), so that there is evidence of the segregation of males, for some part of the year at any rate. At present it is difficult to suggest a reason for this, unless, on reaching maturity, the male, unlike the female, prefers to remain in deeper waters and does not approach the coast (vide Borcea, 1, p. 205).

If it be assumed that during the period of investigation the two factors of size and sexual condition were in operation, it would be expected theoretically that shoals of the following constitution would be met with :—

A. Shoals of large fish consisting exclusively of females, the majority in the pregnant condition.

- B. Shoals of medium-sized fish exclusively males in the mature condition.
- C. Shoals of medium-sized fish of which the majority were immature females.
- D Shoals of immature fish in which the males and females were equal in number.

These theoretical expectations are not inconsistent with the practical observations which have been tabulated above :---

| Reference No. of sample of Fish. | Theoretical category of shoal from which derived. |
|-------------------------------------|---|
| 1 | Α |
| 2 | В |
| 3 | ' D |
| 4 | С |
| 5 | D |
| 6 | D |
| 7 | D |
| 8 | D |
| 9 | D |
| 10 | D |
| 11 | A |
| 12 | А |
| 13 | D |
| | |

THE FOOD OF THE SPUR-DOG.

From the beginning of November, 1919, until the end of January, 1920, samples of stomachs were obtained from the fish-market, and their contents examined in the Laboratory. Of the 143 stomachs which contained recognisable food, 137 contained remains of fish, 6 contained crustacean remains, and 3 molluscan remains. Of the 137 containing fish remains, the percentages of various species of fish are given in the following table :—

| Species. | | Percentage of stomachs in which present. |
|-------------------|------------------------------|---|
| Clupea sp. | C. pilchardus C. harengus | . 67.2 |
| Scomber scomber . | | . 19.0 |
| Gadus sp. | G. merlangus | |
| • | G. luscus . | . 4.0 |
| | . G. minutus | |

E. FORD,

| | Species. | | | | | ge of stomachs ch present. |
|----------------|----------|-----------------|---|---|-----|-------------------------------|
| Pleuronectes s | р | | | | | 1.4 |
| Trigla sp. | | urnar uculus | | • | • | 1.4 |
| Callionymus ly | ira . | | • | | • | 1.4 |
| Raia sp. | | | | | | 1.4 |
| Species uniden | tified | | | | • . | 10.1 |

It must be remembered that the time during which these estimations were made coincides with that of the local pelagic fisheries for herring, pilchard and mackerel, so that there was a large available supply of these fishes as food for the dogfishes. The high proportion of the former fishes in the stomachs of the latter may therefore be due to this fact, quite apart from any selective action by the dogfishes. On November 26th, 1919, eighteen stomachs of fish from 36 cm. to 50 cm. in length were obtained, but owing to the stale condition it was not possible to determine the nature of the whole of the stomach contents. Remains of herring, mackerel and callionymus sp. were recognised, however, so that at this small size fish may form part of the diet.

SCYLIORHINUS CANICULA (ROUGH-DOG).

MAXIMUM SIZE AND SEXUAL MATURITY.

Unlike the spur-dog this species exhibits no marked difference between the male and female in regard to the maximum length to which they may grow, and the largest specimens of both sexes measured at Plymouth do not exceed 70 cm. in length. Mr. A. J. Smith of the Plymouth Laboratory, who has had the handling of several thousands of roughdogs yearly over a long period, has informed me that during the autumn of 1919 he observed some unusually large specimens which he estimated were at least 30 inches in length. Although no actual measurements of these specimens are available, the observation is noteworthy in view of the fact that the fish were sufficiently unusual in size to command attention.

A second difference from the spur-dog is that sexual maturity is in this species acquired at approximately the same length in both male and female, usually from 57 to 60 cm., although one female of 54 cm. was found to be carrying fully developed egg-purses in the oviducts. The claspers of the male do not appreciably lengthen on the attainment of sexual maturity.

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THE EGG-PURSES.

According to Philip White (14, p. 6) the egg-purses of the rough-dog are obtainable by shore-collecting at the lowest spring tides at Careg Dion on the Anglesea side of the Menai Straits, but no such convenient ground has yet been discovered at Plymouth. (Cf. the nursehound on p. 492.) They may be obtained quite easily, however, either from the local trawlers or by actual removal from adult females landed on the quay. The embryos from specimens obtained in the latter way will hatch out quite satisfactorily in aquaria. The egg-purses exhibit a good deal of variation in size, as will be seen from the results tabulated below, of the measurements of fifty-five egg-purses extracted from adult females on August 17th, 1920 :—

| | Minimum Length (in cm.). | | | | | | | | | Maximum Width (in cm.) | | | | | | | | | | | | | | | |
|-------------------|--------------------------|-----|-------|-----|-------|------|-------|-----|--------|------------------------|----------------------|-----------|------|-----------|-----|----|----|-----|----|-----|-----|----|----|-----|----|
| | $5 \cdot 3$ | 5.4 | 5.5 | 5.6 | 5.7 | 5.8 | 3 5 . | 96. | 0 6 .1 | 6 .2 | 6.3 | 6. | 4 2 | 2.1 | 2 . | 22 | .3 | 2.4 | 2. | 5 2 | 2.6 | 2. | 75 | 2.8 | 2. |
| No. of Egg-purses | 3 | 3 | 6 | 2 | 4 | 10 | 8 | 10 | 2 | 3 | 1 | 3 | | 3 | 22 | 1 | 3 | 12 | 3 | | 1 | - | | - | 1 |
| | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | Va | nge riati n cm | on | | era cm | | | | | | | | | | | |
| | | Л | Cinir | nun | ı leı | ngth | | | | Va (in | riati | on .). | (in | | | | | | | | | | | | |

THE EMBRYO.

Egg-purses extracted from adult females from time to time have been kept in aquaria, and notes made on the embryos at various stages of development. The external gill-filaments cease to be visible to the naked eye in specimens at between 6 and 7 cm. in length, and the young fish are hatched at between 9 and 10 cm. with a tiny globular remnant of the yolk-sac. When hatched they seem particularly helpless and weakly. Their eyes are closed and they remain practically motionless. If they are induced to swim, they show little powers of equilibrium and easily turn over, continuing to swim with the ventral surface uppermost. These signs of weakness may, of course, be entirely due to the artificial incubation, and may not be the normal feature under natural conditions in the sea.

The consideration of the development of scales, and the scheme of pigmentation of the embryo is deferred to a separate section on page 493 in conjunction with the closely allied species, *S. stellaris*.

THE BREEDING SEASON.

There is evidence that the breeding season of this species is a protracted one. In May, 1920, the plan was adopted of keeping a continuous record of the number of females in which fully developed egg-purses were

| Mont | h. | Total number of females examined. | Total number carrying egg-purses. | Percentage. |
|-----------|------|---|---|-------------|
| May, | 1920 | 80 | 18 | 22.5 |
| June | ,, | 313 | 74 | 23.6 |
| July | ,, | 109 | 27 | 24.8 |
| August | ,, | 5 | 2 | 40 |
| September | ,, | 71 | 7 | 9.9 |
| October | ,, | 198 | 19 | 9.5 |
| November | ,, | 143 | 24 | 16.8 |
| December | ,, | 138 | 24 | 17.4 |
| January, | 1921 | 147 | 18 | 12.3 |
| February | ,, | 113 | | 19.5 |

Although results for the months of April and March have not yet been obtained, it is definitely known from past experience that egg-purses are deposited in considerable numbers during this time of the year, so that there is the strongest evidence that in the waters off Plymouth the rough-dog may deposit egg-purses in any month. (Cf. Lo Bianco, 7, p. 544, in regard to the fishes at Naples.) The numerical results suggest that egg-deposition takes place principally during the spring and summer, and is least during the autumn.

THE PROPORTION OF THE SEXES IN THE ADULTS.

A fairly regular supply of adult fishes is received at the Plymouth Laboratory throughout the year for disposal chiefly to universities and schools, and while, admittedly, only reasonably large specimens are accepted, yet there is no attempt at sexual selection in the daily consignments from the fish-market. It has already been pointed out that there is no appreciable difference in maximum size between the males and females of this species, so that these daily consignments may be accepted as a rough estimate of the relative frequency of the sexes for the particular day. The numbers of males and females in each sample of fish received have been noted, and the results summarised as in Table B.

These results, when plotted as in Fig. 4, show a curious alternating predominance in the sexes—during the winter the males are the predominant element, whereas in the summer the females are the more numerous. The curves suggest that in late spring and late autumn the sexes will be approximately equal in number. It is difficult to under-

| Date. | Total No. of Samples Examined. | No. of Samples in which & predominant. | No. of Samples in which Q predominant. | No. of Samples in which Sexes were equal. | Total No. of Fishes Examined. | Total No. of 3 | Total No. of 9 | Percentage of ර් | Percentage of ♀ |
|-----------------------|--------------------------------------|--|--|---|-------------------------------------|--------------------------|--------------------------|-----------------------|-----------------------|
| Nov., 1919 Dec. ,, | 13 6 19 | 8 6 14 | 5 5 | | 654 1028 374 | 353 254 607 | 301 120 421 | 54 68 59 | 46 41 32 |
| Jan., 1920 Feb. ,, | 8 9 1 | 7 8 1 | 1 1 | | 524 579 55 | 337 38 375 | 187 204 17 | 64 69 65 | 36 35 31 |
| May ,, June ,, | 5 16 21 | 1 5 4 | 4 10 14 | 2 | 186 735 549 | 90 236 326 | 96 409 313 | 48 43 43 | 52 57 56 |
| July ,, Aug. ,, | 5 6 1 | 1 | 5 5 | | 181 12 193 | 72 7 79 | 109 5 114 | 40 58 41 | 60 59 42 |
| Sept. ,, Oct. ,, | 7 10 17 | 3 2 5 | 3 8 11 | 1 | 140 474 334 | 69 205 136 | 71 198 269 | 49 41 43 | 51 59 59 |
| Nov. ,, Dec. ,, | 8 10 10 | 4 9 | 4 4 | 1 | 260 369 629 | 117 231 348 | 143 281 138 | 45 63 55 | 55 37 45 |
| Jan. ,, Feb. ,, | 11 ¹ 6 17 | 9 14 5 | 2 3 | | 352 730 378 | 205 461 256 | 147 269 122 | 58 68 68 | 42 32 37 |

TABLE B.

17. 5

stand the significance of these results unless there be a distinct difference in habits in the two sexes.



FIG. 4.—Scyliorhinus canicula. Graphic representation of the percentage of males and females in the adult fishes received at the Plymouth Laboratory (see Table B).

THE FOOD OF THE ROUGH-DOG.

From November, 1919, until February, 1920, the stomach contents of a total of 146 fish were examined and recorded :---

Number of

| Stomach | Contents. | | | | stomachs in which present. | Percentage. |
|----------------------|---------------------|----------|-----|------|----------------------------------|-------------|
| PISCES | | | | | 73 | 50 |
| Clupea sp. | C. haren chardus | | * | us | 20 | |
| Elasmobranch remains | Dogfish | and ray | S | | 8 | |
| Scomber scomber . | | | | | 6 | |
| Pleuronectes sp. | | | | | 5 | |
| Gadus sp. | G. merla | ngus, G. | min | utus | 4 | |
| Syngnathus sp | | | | | 1 | |
| Gobius sp | | | | | 1 | |
| Callionymus sp | | | | | 1 | , |
| Remains unidentified | | | | | 32 | |

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| | | | | | | Number stomach | |
|-------------------------|-------|--------|----------|---------|----|-------------------|----|
| Stomach Cont | ents. | | | | | in which present. | |
| CRUSTACEA | | | | | | 131 | 90 |
| Eupagurus sp. | E F | Pernh | ardus | · |) | 101 | 00 |
| Europagaras sp. | | ridea | | | 1 | 6 | 7 |
| Alpheus sp | , ' | 1. | | 0.19 | | 3 | 6 |
| Upogebia sp. | U.d | elturo | ı, U. si | tellata | | 2 | 4 |
| Portunus sp. | P.p | uber, | P. de | purato | rl | 1 | 0 |
| | P.p | usillu | s, P.h | olsatu | sj | 1 | 9 |
| Galathea sp | | | | | | 1 | 1 |
| Nika edulis . | | | | | | | 9 |
| Amphipoda | | | | | | | 8 |
| Atelocyclus septemdenta | tus | | | | | | 7 |
| Crangon sp | | | | | | | 5 |
| Gonoplax rhomboides | | | | . ' | | | 4 |
| Palaemon sp | | | | | | | 2 |
| Ebalia sp | | a. | | | | | 2 |
| Inachus sp | | | | | | | 1 |
| Remains unidentified | | | | | | | 6 |
| MOLLUSCA | | | | | | 35 | 24 |
| Buccinum undatum | | | | | | 1 | 0 |
| Pecten sp | | | | | | - | 7 |
| Loligo sp | | | | | | | 6 |
| Cardium sp | | | | | | | 3 |
| Tritonia sp | | | | | | | 3 |
| Scaphander lignarius | | | | | | | 2 |
| Mya truncata . | | | | | | | 2 |
| Remains unidentified | | | | | | | 8 |
| DOLYGITADEL () . | - | | | | | | |
| POLYCHAETA (unclassifie | d) | • | · | · | • | 73 | 50 |
| ECHINODERMA (Thione | sp.) | | | | | 22 | 15 |
| GEPHYRAEA (unclassified | l) | • | | • | | 25 | 17 |

The presence of the remains of such typically pelagic fish as herring and mackerel in the stomach of an essentially bottom feeder may appear strange. The suggestion is offered that the remains represent fish which have either been dropped from the commercial drift nets, or have been actually picked out from the nets by the dogfish themselves. It is improbable that any free-swimming pelagic fish is likely to be attacked by the rough-dog. The remains of dogfishes and rays were easily
recognisable as the sliced-off spurs and fins of the spur-dog and the offal from rays, which had been removed from the fish-market and dumped into the sea.

SCYLIORHINUS STELLARIS (NURSEHOUND).

It has not been possible to obtain sufficiently large numbers of specimens of this species to derive reliable indications in regard to the adult form, but, on the other hand, whereas the egg-purses of S. canicula cannot be obtained by shore-collecting, those of S. stellaris have been found during exceptionally favourable spring-tides in rock pools at Wembury Bay. In the months of March and September, specimens have been discovered attached to the base of bunches of Cystisira sp. On March 20th, 1920, twenty egg-cases were collected, varying in minimum length from 11.0 to 12.5 cm., and in maximum width from 4.0 to 4.5 cm. (cf. S. canicula, p. 487). The developing embryos were separable into two distinct sizegroups, twelve being of a length not exceeding 1.2 cm., and the remaining eight of sizes from 9.8 to 16.0 cm. The absence of individuals of lengths between 1.2 cm. and 9.8 cm. recalls the experience in the case of the embryos of the spur-dog, and suggests that the breeding season has definable limits. On September 13th, 1920, only one egg-capsule could be found owing to unfavourable conditions, but it contained an embryo measuring 4.4 cm. in length. It will be noticed that embryos of this size were not found in the previous March, and it may be assumed that this September specimen belonged to the same size-group as the March specimens which did not exceed 1.2 cm. in length.

From an examination of the Laboratory collection of embryos it has been concluded that the external gill-filaments cease to be visible in embryos of about 10 cm. in length, and that hatching occurs when the embryo is about 16 cm. in length, a tiny globular remnant of the yolksac being present, as in the rough-dog.

There is a noticeable difference in regard to the sizes at birth of dogfish between the records of investigators in other districts, and those observed at Plymouth, particularly in the case of the nursehound. For instance, Borcea (1, p. 206) states that *Scyllium catulus* (=*Scyliorhinus stellaris*) at Roscoff at the moment of leaving the egg-case has a length of from 10 to 12 cm., as compared with the length of 16 cm. in the case of Plymouth specimens. The sizes recorded by Borcea for the newly born or newly hatched young of *Squalus acanthias*, *S. canicula* and *S. stellaris* are all smaller than those given in the present publication for the Plymouth fish. These differences are very interesting, and may be of significance.

As in the case of *S. canicula* the characters of the embryonic scales and pigmentation are dealt with in a separate section on page 493.

LIFE-HISTORIES OF DOGFISHES.

FOOD OF THE NURSEHOUND.

It has only been possible to examine the stomach contents of eighteen fish, but the records confirm the belief that this species like the rough-dog is a bottom-feeder :—

| Stomach Conter | nts. | | | No. of st | | |
|-----------------|-------|----|--|-----------|---|--|
| PISCES | | | | 13 | | |
| Scyliorhinus co | anicu | la | | | 3 | |
| Clupeoid rema | ins | | | | 3 | |
| Callionymus ly | yra | | | | 3 | |
| Trigla sp. | | | | | 2 | |
| Gadus sp. | | | | | 2 | |
| Pleuronectes s | | | | | 1 | |
| CRUSTACEA | | | | 7 | | |
| Cancer paguru | 1.8 | | | | 5 | |
| Eupagurus sp. | | | | | 2 | |
| MOLLUSCA . | | | | 2 | | |
| Loligo sp. | | | | | 1 | |
| Moschites cirre | osa | | | | 1 | |
| | | | | | | |

In three stomachs the more or less complete bodies of small specimens of *S. canicula* were present, suggesting that the nursehounds from which the stomachs were extracted had attacked and eaten the rough-dogs.

The suggestion receives confirmation by the observation in the Aquarium at Plymouth of a nursehound actually devouring a small living roughdog.

The presence of large specimens of the edible crab in five stomachs may prove to be of commercial importance if it signifies that the nursehound shows a preference for this species of crustacea.

DEVELOPMENT OF SCALES AND PIGMENTATION IN THE YOUNG OF SCYLIORHINUS.

These two subjects may be more conveniently treated in a separate section than as part of the specific descriptions on the preceding pages.

Development of Scales.

The first scales to appear in the embryos of both S. canicula and S. stellaris are symmetrically arranged in a sequence of transverse pairs forming two longitudinal rows, one on either side of the middle line in a dorso-lateral position. The rows commence anteriorally just in front of and above the level of the insertion of the pectorals, and extend

posteriorally as far as about the middle of the pelvics (see Figs. 5, 6, 8 and 9). The number of scales per row is of specific value (see below, and cf. Mayer, 8, p. 227). The scales themselves develop each in a roughly



oval-shaped "cup" in the dermis (Fig. 7), and they possess a single medium dorso-ventrally flattened cusp with a bluntly rounded apex. The markedly characteristic appearance of these primary scales is retained not only throughout embryonic life, but for some time after the young are hatched. They are always conspicuously larger than the

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normal body scales of the embryo, and, unlike the latter, penetrate the skin some considerable time before hatching (Fig. 19). In the young adolescent fish it would seem that they develop into typical body scales of enlarged size (Fig. 14), but they lose their individuality eventually



FIG. 7.—S. stellaris. Semi-diagrammatic representation of a piece of skin taken from the right side of the body of an embryo of 14.8 cm. in length in the region of the modified primary scales.

A. Modified scale projecting from its dermal "cup."

B. Portion of the epidermis which actually covers the whole, except the cusp of the dorsal modified scale.

C. Black chromatophores which cover the floor of the dermal "cups."

D. A normal body scale developing in its dermal "cup." Note the granular pigmentation.

E. One of the more deeply seated, less developed and heavily pigmented scales.

owing to the presence of equally large and similar scales which have grown up around them.

The occurrence of these modified primary scales is not confined to the two species of the Scyliorhinidæ under consideration. I examined recently a number of embryos of different species in the collection at the Natural History Museum, South Kensington, and found that with slight specific modifications similar scales were present in the embryos of *S. ventriosus*, *S. buergeri*, *S. Edwardsii* and *S.* (species ?), and also



FIG. 9.-S. canicula. Same specimen as in Fig. 7 viewed from above

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in the young of *Pristiurus melanostomus*. It was of interest to notice that in *S. chilensis* they persist in the adult fish, an exception which is utilised by Regan (11, p. 456) in his classification of the family Scyliorhinidæ. In a young Orectolobid, *Chiloscyllium plagiosum* of about 15 cm. in length, irregular rows of prominent scales were present one on either side of the body, which extended posteriorally to the tail. The young of Chimæra (cf. Günther, 5, p. 403) and embryos of *Callorhynchus antarcticus* also possessed modified scales arranged in a roughly similar system to that seen in Scyliorhinus (cf. Günther, 5, p. 351).

Rynberk (12) has dealt at some length with the general differences between scales from the various parts of the body of the embryos of *S. canicula* and *S. stellaris*, and it will be sufficient to add, in this connection, that the scales constituting the "caudal rasp" are of a larger size and more elongate, almost from the time of their appearance (Figs. 11, 13, 15 and 17).

The degree of development of scales in embryos and young adolescent fish of different lengths has been observed, and may be summarised thus :—

SCYLIORHINUS CANICULA.

Length 4.4 cm.

The dorso-lateral rows of primary scales are visible in their dermal cups, and they are covered by the epidermis. The scales on the body generally have not yet become distinct.

Length 6.5 cm.

The primary scales are well marked, but their median cusps, although just at the surface, have not as yet penetrated it. They possess quadriradiate bases, and the cusps are directed upwards, backwards and outwards. The normal body scales have now made their appearance, and are seen to be developing in smaller dermal cups. The scales which will eventually form the "caudal rasp" are distinctly larger than the others (Figs. 10 and 11).

Length 9.5 cm.

All the scales have broken through the skin, and they are mounted on prominent quadriradiate pedestals. The appearance suggests that the floors of the cups in which the scales had developed had been pulled up to form these pedestals, so that in the final stage the scales are elevated above the general surface, leaving a series of hollows between them. The primary scales still retain their characteristic appearance (Figs. 12 and 13).

The number of the modified primary scales in each of the two rows in 23 embryos of lengths from 6 cm. to 11.3 cm. was determined. In 15 NEW SERIES, ----VOL, XII, NO. 3. SEPTEMBER, 1921. 2 I



FIG. 10.—S. canicula. Embryo of length 6.5 cm. Portion of skin from the region of the modified primary scales on the left side of the body.
FIG. 11.—S. canicula. Embryo of length 6.5 cm. Portion of skin from the region of the "caudal rasp."
FIG. 12.—S. canicula. Embryo of length 9.7 cm. Piece of skin from the region of the modified primary scales on the left side of the body.
FIG. 13.—S. canicula. Embryo of length 9.7 cm. Piece of skin from the region of the "caudal rasp."
FIG. 14.—S. canicula. Young adult fish 30.3 cm. in length. Piece of skin from the region of the modified primary scales on the left side of the body. The modified primary scales have assumed the characters of normal scales of large size.
FIG. 15.—S. canicula. Young adult fish 30.3 cm, in length. Piece of skin from the "caudal rasp."

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specimens both rows had the same number of scales, and in the remaining 8 there was a difference of 1 only. The range in variation in the number of scales per row was from 27 to 32, with a maximum frequency of 31 (cf. Mayer, 8, p. 228, who gave the range as 27–31).

SCYLIORHINUS STELLARIS.

Length 14.8 cm.

The modified primary scales are more conspicuous than in *S. canicula*, and the cups in which they are developing have thickened rims which are more or less coalesced in front and behind to form a pronounced ridge on either side of the body (Figs. 5, 6 and 7). The normal body scales are tricuspid, and their elongate medium cusps are contained in projecting pockets of the skin, so that the surface of the body assumes a warty appearance (Fig. 18).

A number of more deeply seated and less developed scales are disposed rather irregularly on either side of the cups in which the modified scales are developing. They are densely pigmented, so that when the embryo is examined by the naked eye they appear as a series of black dots along the longitudinal ridges referred to above (E, Fig. 7).

Length 16.0 cm.

The normal body scales are just at the point of breaking through the skin.

Length 17.3 cm.

All scales have penetrated the skin.

Length 35 cm.

The modified primary scales are still distinct in their rows. Most of them, however, have apparently developed into normal tricuspid scales of enlarged size, although one or two still retain their original character.

Length 36 cm.

The rows of modified primary scales are barely distinguishable, as they are masked by the presence of equally large and similar tricuspid scales in this part of the body.

The number of modified primary scales per row in 15 embryos from 9.8 cm. to 22 cm. showed a variation of from 33 to 40, with a maximum frequency of 36 (cf. Mayer, 8, p. 228, who gave the range as 34–38).

Pigmentation.

S. canicula and S. stellaris agree very closely in regard to the general scheme of pigmentation in the embryos. In both there are a very distinct series of transverse bands of dark colour. Figure 5, representing an embryo of S. stellaris 14.8 cm. in length, may be used conveniently to

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indicate the main outlines of the pigment scheme common to both series. The transverse bands are separable into several distinct series according to their position on the body. There is, first, the dorsal series of seven bands which are numbered consecutively from 1 to 7 in Fig. 5; and second, a more lateral series along either side of the body of which the bands have their dorsal boundaries resting on the lateral line (Fig. 5, a to h). Of the latter, the bands a, b, c and d are very regularly and



FIG. 16.—S. stellaris. Embryo of length 14.8 cm. Piece of skin from the region of the dorsal modified primary scales on the right side of the body. FIG. 17.—S. stellaris. Embryo of length 14.8 cm. Piece of skin from "caudal rasp."

FIG. 18.—S. stellaris. Embryo of length 14.8 cm. Section of piece of skin showing the normal body scales covered by the epidermis.

FIG. 19.—S. stellaris. Embryo of length 14.8 cm. Section of piece of skin showing the cusp of a modified primary scale projecting through the epidermis.

clearly represented, whereas the others occur sometimes very prominently, but at others less obviously. In addition to the above there are two bands X and Y situated between dorsal bands 4 and 5, and 5 and 6 respectively, which are only feebly represented in *S. stellaris*, but which may be very conspicuous in *S. canicula*.

The pectoral fins are transversely barred, more especially in *S. stellaris*. In the latter species also the pelvic and anal fins are similarly barred, but in *S. canicula*, instead of the bars, there are one or more dots of pigment on the anterior portion of the pelvics, and a single dot at both

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the anterior and posterior ends of the anal. The ventral lobe of the caudal fin is marked by three bands in *S. stellaris*, of which the anterior two lie one on either side of the sixth dorsal band. In *S. canicula* the middle one of these three bands does not appear to be represented, although the others are quite distinct.

The microscopic study of cleared and mounted pieces of skin shows the body to be covered with chromatophores of two types. Those of the first type are lemon-vellow in colour and stellate in form, and they are anastomosed to form a lacy network which is spread all over the body beneath the epidermis. In the earlier embryos, when the scales are situated in distinct dermal cups, this yellow pigment is more pronounced between the cups than within the cups themselves, so that a chequered effect is produced. The chromatophores of the second type are brownish black to black in colour, and vary in shape from roughly stellate to irregular masses and dots. They are present practically all over the body immediately beneath the epidermis, and the banded appearance of the embryos is produced by the segregation of chromatophores of this type in certain areas. The detailed structure of the dorsal transverse bands in particular presents some interesting specific features. In S. stellaris up to 15 cm. in length they are very distinct and uniform, and their boundaries are sharply differentiated. The abrupt change from banded to non-banded areas of the body is accentuated by the slightly darker edges of the bands in which black spots are beginning to differentiate. In S. canicula, at quite a small size, the transverse bands are definitely marked out by two or more of a normal series of four dots which are disposed in a very regular manner, two being at the dorsal end of the band, one anterior and the other posterior, and two at the ventral end of the band arranged anteriorally and posteriorally in a similar way (Figs. 8 and 9). At hatching size in both species a secondary irregular sprinkling of small dark dots is present over the whole of the dorsal and lateral surface, which appears independent of the banded scheme originally laid down. Subsequent to hatching the banded areas are important centres for the development of dark spots which for a considerable time are larger and more pronounced than those arising between the bands.

MUSTELUS VULGARIS (SWEET WILLIAM).

On the few occasions when the number of specimens landed was reasonably large, the proportion of sexes was determined :---

| Date. | Total No. of Fishes. | No. of Males. | No. of Females. |
|-----------------|-------------------------|------------------|--------------------|
| Nov. 13th, 1919 | 55 | 42 | 13 |
| ,, 14th, 1919 | 49 | 41 | 8 |
| March 4th, 1920 | 34 | 22 | 12 |

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Although the samples were small it may be of significance to note that the male element was conspicuously predominant in each case.

THE EMBRYO.

In the collection of embryos at the Plymouth Laboratory there is a sample of thirty-four embryos of this species which were taken from the uterus in April, 1900. They vary in size from about 19 cm. to 33 cm. inclusive. The smallest specimen in which the yolk-sac is at absorption point measures 29 cm., but one individual of 32.5 cm. still retains a tiny globular remnant. In some of the specimens a similar condition to that observed in the case of *Squalus acanthias* is apparent, namely that the yolk-sac has been completely absorbed, and the umbilical scar is either partially or completely healed.

FOOD OF THE SPECIES.

During the period from November, 1919, to February, 1920, the stomach contents of forty-eight fish which had eaten recognisable food were examined and recorded as follows :—

| | | | | | No. of stomachs in which | | | | |
|---------------------------|----|---------------------|---|------|-----------------------------|----------|-------------|--|--|
| Stomach Contents. | | | | | | present. | Percentage. | | |
| PISCES | | | | | | 2 | 4.2 | | |
| CRUSTACEA | | | | | | 48 | 100.0 | | |
| Eupagurus sp. | | E. Bern E. pride | | 3 } | | 31 | | | |
| Portunus sp. | | | | | | 29 | | | |
| Atelocyclus septemdentati | ıs | | | | | 19 | | | |
| Galathea sp | | | | | | 19 | | | |
| Inachidae | | nachus Iacrop | * | b. } | | 7 | | | |
| Upogebia sp | | | | | | 6 | | | |
| Hyas coarcticus . | | | | | | 2 | | | |
| Crangon sp | | | | | | 1 | | | |
| Remains unidentified | | | | | | 4 | | | |
| POLYCHAETA (unclassified | l) | | | | | 6 | 12.5 | | |

GALEUS CANIS (SWEET WILLIAM).

Only five specimens of this species have been obtainable, namely, one adult male and four immature fish from 42 to 52 cm. in length. The stomach contents of each consisted exclusively of fish, including remains of Callionymus sp., Gadus sp., and mackerel.

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A SUMMARY OF THE MORE IMPORTANT OBSERVATIONS ON THE GENERAL LIFE-HISTORY.

SQUALUS ACANTHIAS (SPUR-DOG).

- 1. Both the maximum attainable length and that at which sexual maturity is acquired are greater in the female than in the male (cf. Scyliorhinus canicula).
- 2. The female, before becoming sexually mature, undergoes an extended adolescent period during which the initial set of ovarianeggs are maturing.
- 3. In a pregnant female the embryos are of the same general size, and similarly the ovarian-eggs.
- 4. Males and females are equally represented in the embryos and may occur together in the same uterus; they do not differ in size at any corresponding stage of embryonic development.
- 5. The number of embryos carried by one fish, if the length of the parent is ignored, is most frequently from 3 to 4 in an observed range from 1 to 11. It may be possible, however, that the number of embryos is dependent on the length of the parent, for the largest number of embryos was found in the largest fish (vide 7 below).
- 6. The remains of the egg-capsule in which the earlier developmental stages are undergone may continue in the uterus until the embryos are ready for birth.
- 7. In samples of egg-capsules collected at random, the average volume of a capsule is approximately proportional to the number of embryos enclosed, but there is a considerable overlapping in the range of variation in volume for successive number-classes of capsule. The results suggest two possibilities :—
 - (a) The largest fish contain the largest capsules, and will therefore produce the largest embryos (cf. 5 above).
 - (b) The embryos in the *initial* brood of a pregnant female are smaller and fewer in number than those of subsequent broods.
- 8. Newly formed embryos were obtained from November until the middle of May.
 - Embryos considered ready for birth occurred from the end of August until the end of December. It was surprising to learn that so many embryos may remain in the uterus after the absorption of the yolk-sac, the umbilical scar either in progress of healing or actually healed.

- 10. The determination of the average sizes of embryos at frequent intervals during the twelve months from March, 1920, until February, 1921, indicated that a curve of the average growth of an embryo would be at its lowest point in the month of November, and require a period of about twenty-five months to reach its maximum (31 cm.) in the month of December.
- 11. The combined results of observations 8, 9 and 10 above showed that an embryo commencing its growth in November may be ready for birth in the month of August after a lapse of twenty-one months, having attained a length of about 25 cm., or it may continue in the uterus for a longer period with a resultant increase in length to an observed maximum of 31 cm.
- 12. The constitution of the shoals of the adult fishes is governed by the factors of size and sexual condition.

SCYLIORHINUS CANICULA (ROUGH-DOG).

- 1. The maximum attainable size and the length at which sexual maturity is acquired do not differ in the two sexes (cf. Squalus acanthias).
- 2. Egg-purses have not been obtained at Plymouth by shore-collecting (cf. S. stellaris).
- 3. Egg-purses may be deposited in any month of the year, but chiefly during the spring and summer, and in least number during the autumn.
- 4. There is a curious alternating predominance of sexes in the adults. During the winter the males are the predominant element, whereas in the summer the females are the more numerous.

SCYLIORHINUS STELLARIS (NURSEHOUND).

- 1. Egg-purses have been found at Plymouth by shore-collecting.
- 2. There is an indication that the breeding season has definable limits, as in the case of the spur-dog.
- 3. There is a marked difference in regard to the sizes at birth of dogfishes between the records of investigators in other districts and those observed at Plymouth, particularly in regard to this species.

MUSTELUS VULGARIS (SWEET WILLIAM).

- 1. During the period of observation the males were conspicuously predominant in the adult samples. This may indicate a similar condition in this species to that found in the rough-dog.
- 2. A number of the fully grown embryos extracted from the uterus had the umbilical scar either partially or wholly healed (cf. Squalus acanthias).

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Intersexes in Gammarus chevreuxi and Related Forms.

Bv

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With Figures 1-6 in the Text and Plates I-IX at the end.

SINCE 1912 extensive investigations have been carried on in the Laboratory of the Marine Biological Association at Plymouth on the genetics of *Gammarus chevreuxi* Sexton, a brackish-water amphipod (Allen and Sexton '17 and '20, see also Sexton '13 and Sexton and Matthews '13).

During the course of the work, numerous individuals have appeared showing abnormalities in sexual behaviour or structure. In view of the interest attaching to such forms, especially after the work of Goldschmidt ('20), Banta ('16), Sturtevant ('20) and others, it was deemed advisable to collate and publish the available data in spite of their somewhat fragmentary character.

In normal circumstances, the males of *Gammarus chevreuxi* mate with the females some days (3 to 9 days) before fertilisation is due to take place. Unless the female is mated for the first time she will normally be carrying in her brood-pouch a brood of developing embryos. After hatching, the young are carried about 24 hours before extrusion, and during that time they come to the anterior end of the brood-pouch and feed on what the mother is eating. Finally they are extruded by a voluntary opening of the brood-pouch. Immediately afterwards the female moults, whereupon fertilisation occurs and a new batch of eggs is extruded into the pouch.

The pair have by now separated, and remain separated usually until the embryos have gone through about half their development in the pouch.

Cannibalism is of fairly frequent occurrence, the male eating the female immediately after she has moulted. It is extremely rare for the normal female to eat a male.

The following description of the normal male and female will show their distinctive characters, and the points in which the abnormal forms differ from them.

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INTERSEXES IN GAMMARUS.

In *Gammarus chevreuxi*, the sexes are indistinguishable on hatching. The young animals moult every few days until sexual maturity is reached, at which period the secondary sexual characters are well developed, and it is then easy to distinguish male from female at a glance. The characteristic sensory hairs of the male, and the broodplates of the female are represented one or two moults before maturity, and will be described later, but it requires microscopic examination to perceive them at this stage.

The size of male and female is similar until sexual maturity is reached; after this the male increases in size more rapidly than the female, but moults at less frequent intervals, taking generally from 4 to 6 days longer between moults. For adult females the period between moults (and normally between fertilisations) varies from about 10 days in summer to about 30 in winter in laboratory conditions.

The adult male is always larger than the female of the same age, and has the body more laterally compressed, and the colour much lighter. The locomotion also shows characteristic differences, the male swimming freely and swiftly with extended body, the female usually moving along the surface of the substratum with the body more curved.

In the female the ovaries are visible as dark green masses above and on either side of the intestine in the peræon, extending through more or fewer segments according to the state of maturity. In the male, nothing can be seen of the gonad in life.

The points by which the sexes can be definitely distinguished are as follows (see Plates I, II, and the description of these plates for the young male last immature moult and first mature moult; Plates III and IV, for the young female, moult before eggs were laid, and moult after young were hatched) :—

1. The setose armature of the second antennæ. These antennæ, in the male, are larger and much more setose than in the female, the setæ being longer as well as more numerous. In addition to the straight setæ common to both sexes, the adult male carries dense tufts of coiled sensory hairs on the inner surface of the 4th and 5th joints of the peduncle, and of most of the joints of the flagellum (Plate II, Fig. 13).

These sensory hairs are peculiar to the male. They are also developed on the inner surfaces of the two gnathopods, the first pair of peræopods, and the third pair of uropods, and are very striking in appearance. They are long, very fine and delicate, with the tips coiled round. It must be noted that the sensory hairs are not coiled until the male is fully mature. In the young male a few *curved* hairs are produced one or two moults before maturity, at first on the second antennæ only (Fig. 1); in the succeeding moults on the other appendages modified at maturity, the second gnathopod appearing to be the last to develop them. The normal female never has any of them.

2. The gnathopods. In the male, the gnathopods are not only considerably larger, but differ greatly from those of the female in the shape, proportions, and sensory armature of the subterminal joint, or "hand," the differences increasing with age. The gnathopod hand is always much larger in the male, with the palm oblique (Figs. 14–19); in the female, the palm is transverse (Figs. 37–42). The palmar margin, in both sexes is crenulate, microscopically spinose, with a row on either side of tiny sensory setæ along its whole length, ending at the palmar angle.

The palmar angle is furnished with a graduated row of spines or setæ on the upper or outer side of the hand; and on the under side with a pair of sensory spines, inset close together. Between these two groups, the tip of the claw closes down.

This angle-row, in gnathopod 2, is one of the best characters for distinguishing the sexes. In the normal female, it always consists of rigid, serrated sensory setæ, the number in the row increasing with age from 3 in the immature female, to 6 in the oldest adult, 679 days old. In the normal male the row is composed of large stout sensory spines, the type and number of spines varying according to the degree of maturity ; in the immature male the spines are pointed, in the adult there are some pointed, and some small broad and truncate. In addition to the row at the angle the male is provided with a large spine inset about the middle of the palmar margin, of the long pointed type in the immature animal (Figs. 3 and 7), and of the truncate type, very large and broad, in the adult (Figs. 15 and 18). This type of truncate spine is peculiar to the mature male. The normal female never has any spines in the angle-row, nor the one in mid-margin.

The sensory setæ, and the pointed sensory spines carry a long curving flagellum near the tip; this flagellum can be seen in the small truncate spines, but is only rudimentary in the very large ones.

In gnathopod 1 the male develops the full number of spines at the second moult after maturity, i.e. 1 very large truncate spine in midmargin, 1 long, pointed spine and 3 short truncate ones on each side of the palmar angle. The palm bends so far round to the under surface of the hand, that part of the upper group of spines at the palmar angle is turned completely over, and only 3 of the spines show when looked at from the upper side (see Fig. 15).

The coiled sensory, male hairs are, in both gnathopods, on the inner surface of the hands and the preceding joint (i.e. joint 5) of the appendages.

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3. The first pair of percopods. The coiled hairs are found on the inner surface of joints 4, 5, and 6 in the male, and are absent in the female.

4. The third pair of uropods. These are very massive in the male, with the outer ramus much longer in proportion to the inner than in the female. In addition to the masses of coiled sensory hairs on both rami, the male has, on the terminal point of the outer ramus, 1 to 2 clusters of setæ besides the large group of setæ at the tip. The female never has these lateral clusters.

5. The brood-plates. There are 4 pairs of these in the normal female, attached to gnathopod 2, and peræopods 1, 2, and 3. They are large and fringed with long fine hairs which are longer and set more closely together on the anterior margins. A short time before reaching sexual maturity, the immature female develops small brood-plates, with the rudiments of hairs indicated on the margins; in the last moult before the eggs are laid, a few short hairs are present (see Fig. 29); but the fully developed hairs never appear in the normal animal until it is quite mature. There is never any trace of these brood-plates in the male.

The distinction between the normal male and female, as has been said before, can be made perfectly easily with the naked eye, the general appearance and the mode of swimming being sufficient criteria without resort being necessary to microscopic examination. All matings for the nine years of breeding experiments have been made in this way, and mistakes in sexing have never occurred except with the abnormal individuals to be described.

Up to the time of writing (July 13th, 1921) 35 of these abnormal individuals have been found, three of which are reserved for future discussion. The remaining 31 individuals—or "female intersexes" as we have called them in this paper—have some of the characters of the male, and some of the female. They resemble the male in general appearance, size, colour, and habit of swimming, while all are provided with the brood-plates of the female, developed to a greater or less extent. The curved sensory hairs and the palmar spines of the young male are present also in many of them.

The most remarkable thing about the appearance of these female intersexes is that, with the exception of four, they have all occurred in one strain, and that an abnormal one. This strain, which we call the Irregular Stock, is a derivative of the original stock brought into the Laboratory in 1912 (Sexton '13). It is characterised by an irregularity in the shape of the eye which affects coloured eyes and appears to be of a different nature from the irregularity seen always in Albino eyes.



It originated from a mating (CN.I.b) of Black No-white male (BbCCww) with an Albino female carrying Black (BBccWW). This female had large dorsal patches and spots, and came of spotted ancestry for 4 generations. The pair gave four broods (see Chart, p. 510); the members of each brood were mated inter se. One brood died out without giving any descendants. A second brood has produced 572 descendants in 5 generations with practically no eye-irregularity (nine showing it in a slight degree) and with only three intersexes.

The 3684 descendants of the two remaining broods have given numerous irregular-eyed individuals, and many intersexes. Whether there is any correlation between the irregularity of eye and of sexual constitution cannot at present be stated.

In addition to the appearance of these intersexes, other variations from the normal have been noted :—e.g. the infertility discussed on page 544; and the cannibalism of the males, which is much worse than in any of the other strains. It is almost impossible to mate the males with the females of the Irregular Stock, and outside mates have to be provided. In consequence of this cannibal tendency, the descendants are comparatively few in number.

As a rule, the intersexes take much longer in reaching maturity than the normal animals, but attain a greater size. Text figure 1 gives a comparison of size of an intersex with the normal male and female—as nearly as possible of the same age.

Normal full-grown males generally run to 10 or 11 mm. in length, normal females 7 to 8.5 mm. The largest female CN.22.a measured barely 9 mm. at the age of 679 days; the largest male CN.22.a, age 579 days, was 14.5 mm. long; the largest intersex, CN.284.a, age 310 days, was 17 mm.

The large size of the gills in all the intersexes is noteworthy. It is possible that this may be explained as a nutritional effect. The gills develop in the near neighbourhood of the brood-plates, and when these are inhibited by the male internal secretions, the growth-energy of this region, deprived of its normal outlet, expresses itself for a time in increased growth of gills.

There have been so far 35 of these intersexes in the *Gammarus* stock. One specimen from another Amphipod genus, *Tmetonyx*, is treated separately on page 544.

The *Gammarus* intersexes, while all resembling the male in general appearance, size, colour, and habit of swimming, fall into three groups according to the degree of development of the brood-plates. These groups each again divide into sub-groups according to the "more" or "less male" character of the second gnathopod hand. In some the palmar row is distinctively female, all the setæ being of the rigid serrated

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type; in others one hand, usually the right, is more male than the other, and carries one or more sensory spines with the serrated setæ in the row; in others again both hands have these spines, and in one or two specimens, the most male of all the intersexes, there is a sensory spine in the middle



TEXT FIGURE 1.—A. Gammarus chevreuxi. Normal male. HN.50.a. Age 332 days. × 8. B. Normal female. CN.136. Age 355 days. × 8. C. Intersex. HN.50.a. Age 331 days. × 8.

of the palmar margin, as in the young immature male (cf. Fig. 3 with Fig. 103).

That it is possible for an animal to pass from one sub-group ("less male") to another ("more male") as its age increases, has been proved e.g. in the case of specimen 6, CN.229h., in Group II, p. 523.

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Not much is known as to the possibility of the intersexes mating; as a rule they are so male in appearance at maturity that they are recorded as males with a query, and females have been put into their bowls to test them. The moults are usually too fragmentary for any evidence as to sex to be deduced from them, and by the time the animals are recognised as female intersexes they are too old to breed.

One specimen in Group I, HN.50.a., laid eggs three times, but none hatched. Another in Group II, CN.216.b., mated with a male, with no results, being probably too old ; whilst a third one, CN.259.b., Group II, page 521, mated and hatched 2 very remarkable young, but there is some doubt as to whether this animal was an intersex at the time the eggs were laid, or whether it developed intersexuality later. It did not show any sign of an ovary after the young were extruded from the pouch, although it moulted and mated twice afterwards. At its death, three months later, its brood-plates were found to be of the partially developed type, and one hand was more male than the other.

Animals with fully developed brood-plates, with the Group I. fringing hairs of normal length, but with some male characters, notably the third uropods.

There are 2 specimens in this group, both of the "more male" type, one more so than the other.

- 1. HN.50.a. (text fig. 1). Gnath. 2, right hand more male than left, 1 sensory spine developed; gnath. 1, both hands with one spine extra below; third uropods of the male type, and with curved sensory hairs, 2 lateral clusters; mated and laid eggs.
- 2. CN.224.a3. Gnath. 2, both hands with 1 sensory spine developed; gnath. 1, both hands with an extra spine below; third uropods of the male type, no lateral clusters; sectioned.

Group II. Animals with partially developed brood-plates, i.e. the brood-plates nearly normal in size, but with a greater or lesser number of the fringing hairs rudimentary, those that are developed being usually on the posterior margins. There are 14 specimens in this group, 2 in Sub-group A (the "less male" class) with serrated setæ on the second gnathopod; 1 which hatched young; 1 which passed from the "less male" class to the "more male," developing sensory spines; 10 in Sub-group B, the "more male" class, 1 of which mated ; and 1 the most male of all the intersexes, CN.183.m., which had the spines of the immature male, and only 1 or 2 hairs on brood-plate 4.

In Sub-group A the 2 specimens are :--

3. CN.293.a, and 4 CN.157.a. Both were sectioned (text fig. 4). Both had, on the left hand of gnath. 2, a rigid seta inset, apart 2 K

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from the angle-row; third uropods of large size, with latera clusters.

- 5. CN.259.b. (Plate V) which hatched two young.
- 6. CN.229.h. (Plates VI and VII) is figured in detail to show the development from the female type of hand to the more male type; sectioned.

In Sub-group B are :---

- CN.189.a₁. Gnath. 2, both hands with 1 sensory spine developed; gnath. 1, no extra spines; brood-plates with a few small hairs on first two pairs; 1 lateral cluster on uropods.
- 8. CN.224.a₂. Gnath. 2, right hand more male than left, with 1 sensory spine developed; gnath. 1, right hand with 1 extra spine below; brood-plates with a few very small hairs on first two pairs; 1 lateral cluster on uropods; sectioned.
- **9.** CN.265.b. Gnath. 2, both hands with 2 spines developed; gnath. 1, both hands with 1 extra spine below; a few very small hairs on fourth brood-plates only; 1 lateral cluster on uropods; 2 lateral clusters developed three months later.
- 10. CN.189.a₂. Gnath. 2, both hands with 2 sensory spines developed; gnath. 1, both with 1 extra spine below; brood-plates with a few small hairs, most on first two pairs; 2 lateral clusters on uropods.
- 11. CN.216.b. Gnath. 2, right hand with 3 sensory spines developed, left hand with 2 sensory spines, 1 of which is in mid-margin as in immature male; gnath. 1, both hands with 1 extra spine below; a few small hairs on the brood-plates; third uropods of the adult male type, 1 lateral cluster. Mated with a male; sectioned.
- 12. CN.289.a. Gnath. 2, right hand missing, left hand with 2 sensory spines developed, and 1 below the angle-row (the only instance of this, fig. 98); gnath. 1, both hands with 1 extra spine below; brood-plates with hairs all present but unequally developed; uropods very massive, of male type, 3 lateral clusters on one, 2 on the other.
- 13. CN.247.d. Gnath. 2, right hand with 2 sensory spines, left hand with 1 developed; gnath. 1, both hands with 1 sensory serrated seta extra on upper and under sides of palmar angle; brood-plates with numerous hairs; differs from the others in having the hairs of the last two pairs better developed than in the first and second pairs; uropods with 2 lateral clusters; sectioned.
- 14. CN.265.a. Right hand with 2 sensory spines developed, left hand

with 1, left hand also carries a stout seta inset in mid-margin; gnath. 1, both hands with 1 spine extra below; a very few small hairs on the brood-plates, most on the first two pairs; uropods with 3 lateral clusters on one, 2 on the other.

- 15. CN.284.a. Right hand with 3 spines, and 1 spine inset in midmargin, claw impinging against the under surface of palm; left hand with 3 spines; gnath. 1, both hands with 1 extra spine above and 2 below; hairs on first two pairs of brood-plates; uropods nearly as large as in oldest adult male, 4 lateral clusters, 1 plumose hair in 2 of the clusters, the only instance of this. The largest specimen of G. chevreuxi vet seen.
- 16. CN.183.m. The most male of all the intersexes; curved hairs on second antenna; gnath. 2, right hand 2 spines in angle-row, and 1 inset in mid-margin as in immature male; left hand 2 in angle-row and 1 stout sensory seta in mid-margin; right hand with 1 extra spine below; gnath. 1, right hand with 1 sensory spine in mid-margin, 3 in angle-row, with 2 extra spines below; left hand with 4 spines in angle-row, and 1 extra below. Only 2 or 3 very tiny hairs developed on fourth brood-plates; third uropods of male type, more spinose than usual, with 2 lateral clusters on each.

Group III. Animals with the small brood-plates of the young immature female, the hairs quite rudimentary.

There are 15 specimens in this group, 7 in Sub-group A, 1 of which passed to Sub-group B, and 8 in Sub-group B.

Sub-group A, the "less male" type :---

- R.F.1. Gnath 2, both hands with 4 servated sensory setæ; gnath. 1, not known, uropods comparatively small, 1 lateral cluster on each uropod.
- 18. CN.289.f₃. Gnath. 2, both hands with 5 serrated setæ; gnath.1, both hands with 1 serrated seta extra below; 1 lateral cluster on the right uropod.
- CN.157.a₂. Gnath. 2, right hand with 5, left hand with 4 serrated setæ; gnath. 1, no extra spines; 1 lateral cluster on right uropod, left missing.
- 20. CN.257.d. Gnath. 2, both hands with 6 serrated setæ, 1 a little apart on left hand; gnath. 1, both with 1 spine extra below; no lateral clusters on uropods.
- 21. CN.309. Gnath. 2, both hands with 6 serrated setæ; gnath. 1, no extra spine; no lateral clusters on uropods.

- 22. CN.323.a₁. Gnath. 2, left hand with 6 serrated setæ; gnath. 1, both hands with 1 spine extra below, right hand with 1 extra spine above also; no lateral clusters on uropod.
- 23. CN.323.a₂. Gnath. 2, right hand with 6 serrated setæ, left hand with 8 setæ, 7 in the angle-row and 1 apart ; gnath. 1, with 1 extra below (sensory seta on right hand, spine on left), left hand with 1 extra spine on upper surface also ; 1 lateral cluster on left uropod, 2 on right. Two months later this specimen had passed from Sub-group A to Sub-group B.

Sub-group B, the "more male" type :---

- 24. Abn.Exp.3. Gnath. 2, right hand not known, left hand with 1 sensory spine developed; gnath. 1, right hand not known, left hand, no extra spine; uropods very large, 2 lateral clusters on each.
- 25. Abn.Exp.4.
- 26. CN.183.c. Gnath. 2, right hand with 1 sensory spine developed; gnath. 1, right hand with 1 extra spine below, left hands missing; antennæ of the immature male type, with curved sensory hairs; one uropod missing, no lateral clusters on other; sectioned (text fig. 5).
- 27. CN.224.b. Gnath. 2, both hands with 1 large sensory spine, a little apart from the angle-row; gnath. 1, both hands with 4 spines above, and 1 extra spine below; uropods regenerating, left one with 2 lateral clusters.
- 28. CN.52. Gnath. 2, right hand with 2 sensory spines, 1 in angle-row and 1 inset in mid-margin, left hand with 2 in angle-row, and 1 serrated seta in mid-margin; gnath. 1, not known; uropods, 1 lateral cluster on left, more spines than usual on right; sectioned (text fig. 6).
- 29. CN.293.a₁. Gnath. 2, right hand with 2 sensory spines developed, left hand with 3, i.e. 2 in angle-row and 1 inset apart in mid-margin; gnath. 1, left hand with 4 spines in angle-row and 1 extra below; uropods with 2 lateral clusters; sectioned.
- 30. CN.285.a. Gnath. 2, both hands with 3 sensory spines developed, left hand with 2 extra spine-like sensory setæ below; gnath. 1, both hands with 1 extra spine below, left hand with 1 extra spine above also; uropods with 2 lateral clusters.
- St. CN.218.b. Gnath. 2, 3 sensory spines developed on each hand, 1 on right hand inset apart in mid-margin; right claw impinging against under surface of hand (the second instance of this, cf. spec. 15); gnath. 1, both hands with 1 spine extra below; uropods very spinose, with 2 large lateral clusters.

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The life-history of the different specimens is given below :---

Group I, Sub-group B.

Specimen 1. HN.50.a. (see text fig. 1, p. 512).

The male parent of this specimen was a Black No-white (BBCCww) from the original stock (brought into the Laboratory June, 1912). Its female parent was derived from a pure wild stock (BBCCWW), brought into the Laboratory in 1915, in which the "Gradual No-white" strain developed. When hatched, her eyes were Black, with the normal white reticulation, and she had large white dorsal patches. Later she became almost completely No-white, the dorsal patches fading out also.

On 18 August, 1919, a brood of 20 was produced. Only 5 came to maturity, 1 male, 3 females, and 1 "intersex." The 3 females mated normally and produced normal young. The intersex was first entered as "female," but grew more male in appearance as time went on. It mated repeatedly with two mates, but only produced eggs three times ; these eggs were all infertile. The eggs were laid on 20 March ; 6 April ; and 12 June, 1920. On the first two occasions a normal number was produced ; but on the last occasion it was noted that only 2 or 3 eggs were extruded into the pouch. The specimen was then very large, and on examining it microscopically on 3 July, 1920, the entry was made " looks like a male, no ovary seen." It died on 14 July, age 331 days, length 11 mm., as compared with about 8 mm. for a normal female of such an age.

This intersex was as large as the male in the same brood (see text fig. 1) and indistinguishable from it except by microscopic examination. Although younger than the normal female, it was much larger and its brood-plates were even better developed. The first brood-plate, e.g. had 38 hairs fringing it, compared with the 33 of the normal animal (fig. 1. B). The brood-plate was as large, in fact, and had as many hairs as that of female CN.22.a. This, the oldest female we have had, died at the age of 679 days, after having hatched 227 young in 15 broods.

First antennæ broken. Second antennæ large and setose ; flagellum 17-jointed.

The gnathopods are as large as those of the young mature male (Plate II), and much more setose, but have no curved sensory hairs.

Gnath. 1. The hand as long as in the young male, but wider; palm slightly oblique, with the usual row of 3 sensory spines, 1 long and 2 short, inset on the upper side of the palmar angle; on the under side, an extra spine is developed on each hand, as in the immature male (cf. Fig. 51). The normal female never has more than the usual pair of spines on the under surface of the hand.

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Gnath. 2. The hands are very large and wide; palm slightly oblique; the right hand more male than the left (cf. Figs. 54 and 56). The row at the palmar angle consists of 1 large pointed sensory spine, and 3 rigid serrated sensory setæ on the right hand; on the left is a graduated row of the rigid sensory setæ, as in the female, 5 in number, the fifth very small; both hands have the usual pair of sensory spines on the under side.

The gills are very large, longer, and wider than in the normal male of the same brood, extending to below the fourth joint in percopod 2.

The third uropod on the left side is broken; that on the right side is very remarkable. It is nearly a third as long again as in the young mature male (Fig. 20), whilst, compared with the uropods of fully adult males, it is very nearly as long as and more massively built than that of its normal brother HN.50. at the same age, 331 days, though with fewer clusters of setæ; compared with that of the oldest male, CN.22.a., 579 days (Fig. 12), it is three-quarters its length, almost as wide, with the same number and position of spines, but with only half the number of setæ-clusters on the margins; on the other hand it has 2 lateral clusters of setæ on the terminal joint of both outer rami. It is densely setose, and carries a large number of very long, delicate, curved sensory hairs, as does the immature male.

Specimen 2. CN.ex.224.a₃. F₃ from CN.I.b. Irregular Stock.

Four survivors were found in the brood-bowl February 8, 1921—two normal females, one with a rudimentary ovary and very large gnathopods of the female type, and one with no ovary visible but with female characters (Spec. 8). These two were put in a separate bowl. By February 28 they were seen to be intersexes, and could not then be distinguished from each other, as the ovary before noted had completely disappeared. They increased rapidly in size. On May 14 they were preserved and examined.

This specimen measured 9 mm. Its brood-plates were large, of perfect form, with all the hairs present and of normal length; on the left side, 25 on the first brood-plate, 17 on the second, 12 on the third, and 9 on the fourth.

First antenna with 29-jointed primary, and 5-jointed accessory flagella. Second antenna, large, densely setose ; flagellum 17-jointed.

Gnathopods very large, densely setose.

Gnath. 1. Both hands, as in the preceding specimen, carry an extra spine on the under side of the palmar angle.

Gnath. 2. The hands in this animal are more male than in Spec. 1, both having developed 1 large sensory spine in the angle-row in addition to the 3 serrated setæ. The right hand has the 2 sensory spines on the

under side, but in the left hand the second spine is not fully developed (cf. Fig. 39).

Third uropods very large and massive, as large as in Spec. 1, but with no curved hairs nor lateral clusters developed.

This animal was sectioned; the gonads showed asymmetrical differences in size, the smaller ovary about the same as in text fig. 6, the other one more developed.

It is not known if this animal could have mated, as did HN.50.a. It looked so male, after February 28, that it was kept under observation to see if the male hairs would develop, in order to try it with a female. The moults were eaten at once, and so the brood-plates were not seen until the animal was dissected.

Group II, Sub-group A, the "less male" type.

Specimen 3. ex CN.293.a₂. F_4 from the Cross CN.I.b. Irregular Stock.

On February 9, 1921, three survivors were found in the brood-bowl, 1 Black irregular-eyed male, and two others, this specimen and Spec. 29.

This one was entered as "normal eyes. Intersex ? No ovary visible, but microscopic examination (1 inch) showed a transparent mass full of tiny dark specks lying on top of the intestine." By March 11 this had gone. On May 14, 1920, it was preserved ; it then measured 10.5 mm.

The antennæ and gnathopods are large and very setose; second antenna with 19-jointed flagellum.

Gnath. 1. The left hand has the usual cluster of 3 spines at the angle, but in the right there are only 2 of the spines, and 1 rigid seta; both with the usual pair below.

Gnath. 2. The right one was broken at the 3rd joint. The left hand has the graduated angle-row of 4 rigid setæ, and, in addition, 1 by itself inset nearly in the middle of the palmar margin (Fig. 95). It is interesting to note that this same feature occurs in the other specimen of this class, $CN.157.a_1$.

The first two pairs of brood-plates show all variations in the size of the hairs, from the quite rudimentary to the quite normal; on the third and fourth pairs the hairs are all rudimentary; 31 hairs on the first pair, 22 on the second, 12 and 13 on the third, and 8 on the fourth.

The third uropods are very large with 2 lateral clusters on the terminal joint, right side, 3 lateral clusters on the left.

Sections show gonads resembling those of the next specimen $(CN.157.a_1)$ in structure, not as large, with an occasional oocyte; larger than in its sister intersex, Specimen 29.

Specimen 4. CN.157.a₁. F_3 from the Cross CN.I.b. Irregular Stock.

One of a brood of 28, extruded December 15, 1919, of which two only came to maturity, this the larger one and Spec. 19, both intersexes and both irregular-eyed. On March 30, 1920, it was entered as "female." Placed with three different males it did not mate. It was examined on July 7 and again marked as "female," but it gradually grew more masculine in appearance and on August 24 the entry was made "no sign of ovary.



TEXT FIGURE 2.—Transverse section of normal male, where the gonal is of maximum size. The testes are very small and dense. Int. = intestine, gon. = gonad, hep. = hepatic cæcum. Reichert, $\frac{1}{3}$ objective, No. 4 ocular, drawing at table level. J.S.H. del.

looks like a male." It was preserved and sectioned on August 30, age 260 days.

First antenna with 31-jointed primary, and 5-jointed accessory flagella. Second antenna, large, massive and very setose; 15-jointed flagellum.

Gnathopods half as long again, as in its sister intersex, Spec. 19.

Gnath. 1. The right hand has, in the angle-row, 2 sensory spines and 1 small serrated seta, as in the preceding specimen; with 1 very stout serrated seta below. The left hand has the usual number, 3 sensory spines on the upper surface of the angle, and 2 below.

Gnath. 2 has on each hand 4 of the rigid serrated setæ of the female type; those in the graduated row of the right hand larger and stouter than in the normal female; on the left hand they are of the usual slender form, but the longest of the four is separate from the others, inset nearly in the middle of the palm, as in the preceding specimen (cf. Fig. 95); the usual pair of large sensory spines below.

The brood-plates show all variations in the length of the hairs, from the quite rudimentary to some of almost normal length; first brood-plate with 31 hairs, most of them rudimentary, 5 of the posterior ones partly developed.

Third uropods large and massive, with 2 lateral clusters on the terminal joint, right side, 1 lateral cluster on the left.

The gonads are shown in text fig. 4. They are nearly as large as in a normal female. Ova with yolk grains are present, and an occasional oocyte is seen. The two ovaries differ from each other in size more than in a normal female. (Compare with text figures 2 and 3.)

Specimen 5. CN.259.b. F₃ from CN.I.b. Irregular Stock.

One of a brood of 16 Black-eyed young, extruded June 4 and 5, 1920, of which only 6 had normal eyes. This specimen had the left eye irregular. on September 6 it became mature, a female ; and a male from the same brood was added ; the male had both eyes irregular. The female moulted on September 21, mated, and laid eggs ; on October 6, 2 young were extruded from the pouch. Both of these were very remarkable, having very irregular eyes, and one with its head malformed also ; the right eye in each was black, the left eye white.

On October 7 the female moulted and mated ; no eggs were laid ; the male moulted on October 8. The animal was examined microscopically on October 14, as no ovary had been seen since the extrusion of the young. None developed after this date, although it mated, and moulted again on October 26. As it looked ill on Nov. 9, it was removed to a separate pot ; moulted again on November 15; it was later marked as "intersex ?" and kept under daily observation till its death on March 10, 1921. Its last moult was on March 3, from which it did not recover. Length 11 mm., age 280 days.

The moult of November 15 measured 8 mm., that of March 3, 10 mm. It is impossible to say if the animal was an intersex at the time of mating, or if it developed intersexuality later. Unfortunately no broodplates nor gnathopods were found in the fragments of the early moults; and only one first gnathopod and one brood-plate in the November 15 moult. The third uropods are left in all the moults, but evidence based on these is not enough (Figs. 68 and 69).

First antennæ, both diseased in all the moults. Second antennæ very

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TEXT FIGURE 3.—Transverse section of normal female, where the gonad is of maximum size. Large ovaries containing eggs loaded with yolk. Magnification, etc., as in text fig. 2; h.=heart. J.S.H. del.



TEXT FIGURE 4.—Transverse section of intersex. CN.157.a₁., where the gonad is of maximum size. Magnification, etc., as in text fig. 2. J.S.H. del. large, about as large as Fig. 81, and densely setose, with a great number of long sensory hairs, one or two lightly curved; tips of both flagella regenerating, 15 joints on left one.

Gnath. 1. Only the right hand was found in the moult of November 15, 1920; 2 spines on the upper surface of the palmar angle, 1 spine and 1 sensory serrated seta below. On March 3, 1921, 3 spines were found on the upper side, and, on both sides, 1 extra spine was developed below on the under surface, besides the usual pair.

Gnath. 2. March 3, 1921, right hand with the angle-row composed of 1 sensory spine, and 5 serrated setæ, the spine coming second in the row (Fig. 54); left hand with 5 stout serrated setæ in the row; both hands with the usual pair below; many long sensory hairs, but none curved.

Brood-plates. The fourth brood-plate, left side, from the moult of November 15, 1920, was the only one found in the early moults (Fig. 57); it may be compared with the same brood-plate in Figs. 62 and 67. The brood-plates of the March 3 moult, and of the dead animal March 10, are figured to show the curious changes in the length of the hairs at different moults.

Third uropods, Figs. 68 and 69; proportions are the same in all the moults; the number and arrangement of the spines also (2 on the inner ramus margin, right side, and 3 on the left); the setæ-clusters have increased in number; no lateral clusters.

Specimen 6. CN.229.h. F_4 from CN.I.b. Irregular Stock (Plates VI and VII).

This animal is very interesting, in that we have been able to trace its change from the typical "less male" Sub-group A to the typical "more male" Sub-group B.

One of a brood of 25, extruded May 12, 1920, many of them irregulareyed; 2 normal males and I female came to maturity besides this intersex. The males ate several females each; the female mated and was eaten by her mate. The intersex developed slowly at first, but on August 26 it was very large, as large as its normal brother from the same pot and was marked "male." A female was added but no mating took place so, on October 13, it was examined microscopically, "no ovary; looks exactly like a male, and swims in the characteristic manner, but the setæ and gnathopods are of the intersex type, no male hairs; very large, 9.5 mm." It was then larger than its normal brother, which did not reach that size till November 12, 1920.

It moulted September 9; October 11; October 26; November 13, 1920; and small fragments of moults were found on March 16, 1921; April 8; and April 30. On May 14, 1921, it was preserved and sectioned, age 367 days, length 10.5 mm.

The moult of October 26, 1920, is perfect, 9.5 mm. long. It has been figured for comparison with the dead animal, about 6 months older (Plates VI and VII).

The first and second antennæ were attacked by disease, and although continually regenerating during the animal's life, they never reached the normal length.

First antennæ; on October 26, primary flagella 25-jointed, accessory 4-jointed. On May 14 primary flagella with 34-joints, and accessory flagella with 5.

Second antennæ, large, densely setose. On May 14, many sensory hairs were seen, but none curved ; flagella broken or diseased in all the moults.

Gnath. 1. October 26, right hand with 3 sensory spines and 1 small serrated seta on the upper side, left hand with 4 spines; both with the usual pair below, right side having 1 small serrated seta extra. Cn May 14, both hands had 4 spines in the angle-row; the usual pair below, right hand with 1 seta extra, left hand with 1 spine extra. There is an extra hair on the back of the claw of the left hand.

Gnath. 2. The greatest change will be seen in this appendage. On October 26 both hands had 6 of the rigid sensory serrated setæ in the angle-row (the sixth very small); and the usual pair below. On May 14, the angle-row on the right hand consisted of 4 sensory spines (the first not fully metamorphosed), and 2 very stout spine-like serrated setæ, with 2 small ones a little behind the line. The left hand (Fig. 87, cf. also Fig. 54) had the same number in the row, but the first is a stout spinelike seta (not so far advanced as in the right hand), 2 large sensory spines, and 3 serrated setæ, with 1 small seta behind the line ; the usual pair of spines below in both hands.

- The delicate sensory hairs are well developed (October 26 and May 14), but none are curved. It will be seen, especially in Fig. 88, that the palmar row of hairs on May 14 is approaching the male type, the hairs massing together in a cluster, and not spreading out in a line as in the normal female.

Gills very large, extending, in percopod 3, on October 26, to below the margin of the third joint.

Brood-plates (Figs. 78 and 79). The hairs are quite rudimentary on the first three pairs; a very few small hairs are developed on the fourth pair (cf. also CN.265.b., and CN.183.m.). The number of hairs was, on October 26, 30 and 28 on the first pair; 18 and 17 on the second; 10 and 9 on the third; 6 and 8 on the fourth. On May 14, there were 35 on the first pair; 20 on the second; 11 on the third; and 9 on the fourth.

Third uropods. On September 9, 1920, both of these were alike, with

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1 spine on each side of the two inner rami; on October 11, the right side had 2 spines on the outer margin of the inner ramus, the left had 1; on October 26, there was no increase in spines, nor in setæ-clusters, only in size, but 1 lateral cluster had developed on each terminal joint, outer rami; November 13, no change except in size; on March 16, 1921, the right side had 2 spines, the left, 3; 2 lateral clusters on each terminal joint; great increase in size and in number of setæ; on May 14, larger, but no other change.

Sections show very small gonads, with some rudimentary oocytes present.

Sub-group B, the "more male" type.

Specimen 7. ex CN.189.a1. F4 from CN.I.b. Irregular Stock.

On January 22, 1921, six animals were found in the brood-bowl, 3 normal females and 3 others larger, which were then marked as "male ? no sign of ovary." They were left together to mate. On January 28, on examining them again, the three were seen to be intersexes, but so male in appearance that two normal females from another family were put in to test them. No mating occurred, and the females were removed on March 4. By this date, one intersex was eaten, one was dead (this specimen), and one was left, described below as Specimen 10.

The animal was 9 mm. in length.

First antennæ, 29 joints in primary, 6 in accessory flagella. Second antennæ, setose ; 14-jointed flagellum.

Gnath. 1. Both hands with 3 sensory spines on the upper side of the palmar angle and 2 on the under side.

Gnath. 2. In both hands the angle-row consists of 1 sensory spine and 3 stout serrated sensory setæ; with 1 sensory spine and 1 very stout spine-like seta below.

The brood-plates are barely two-thirds the normal length, the hairs on the first two pairs irregularly developed and short, those on the other pairs quite rudimentary; 27 on the first brood-plate, 22 on the second, 11 on the third, and 7 on the fourth.

Third uropods of the young male type, but with no curved sensory hairs; 1 lateral cluster on each terminal joint.

The gills, as is usual in the intersexes, are of great size, reaching, in the second perceoped, well below the third joint of the appendage.

Specimen 8. ex CN.224.a₂. F_3 from CN.I.b. Irregular Stock. Sister intersex of Specimen 2.

On February 8, 1921, it was noted as having "no ovary, but the female type of gnathopod." February 28, "Intersex." On May 14 it was preserved and sectioned; length 10 mm.

First antennæ, 29 joints in primary, 5 in accessory flagella. Second antennæ large and very setose, with some fine, delicate sensory hairs, but none curved; 6 clusters of setæ on joints 4 and 5 of the peduncle; flagellum 16-jointed.

Gnath. 1. Right hand with a small extra spine developed on the under surface of the palmar angle (cf. Fig. 84).

Gnath. 2. Right hand, as in Specimen 1, has 1 sensory spine and 3 rigid serrated setæ in the angle-row; left hand has a graduated row of 5 rigid serrated setæ; the usual pair of sensory spines on the right hand below, 1 sensory spine and 1 very stout spine-like seta on the left hand (cf. Figs. 39 and 42).

The brood-plates are about three-quarters the normal length with only a few short hairs, mostly on the posterior margins of the first two pairs, those on the other pairs rudimentary; 22 hairs on the first broodplate, 14 and 15 on the second pair, 9 on the third, and 6 and 8 on the fourth.

Third uropods large and setose, 1 lateral cluster on each terminal joint, larger on the right side.

Sections show the gonads very small, much resembling those of CN.183.c., text fig. 5.

Specimen 9. CN.265.b. F₃ from CN.I.b. Irregular Stock.

From the same brood as Specimen 14, hatched June 15, 1920. It was noted as "exceedingly small" on September 10, when the others in the bowl were mature. On October 4 it was recorded as "male," but on January 28, 1921, it was recognised as an intersex. Died July 12, 1921, age 393 days; length 12.5 mm.

First antennæ with 32 joints in the primary and 8 in the accessory flagella.

Second antennæ very large, with great masses of sensory hairs on the under surface, several of them curved; flagellum 21jointed.

Gnath. 1. Both hands with 3 sensory spines on the upper side of the angle; 1 extra spine below, in addition to the usual pair.

Gnath. 2. Both hands have 2 large sensory spines and 3 serrated setæ in the angle-row: usual pair below.

The brood-plates are a little more than two-thirds the normal length; the hairs quite rudimentary on the first three pairs; 2 or 3 developed on the fourth pair (Figs. 96 and 97); 31 on the first brood-plate, 20 on the second, 11 on the third, and 6 and 7 on the fourth on March 11; increase in hairs but not in size, July 12th.

Third uropods very large and massive; 1 lateral cluster on each terminal joint March 11; 2 lateral clusters on July 12.

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Specimen 10. ex CN.189.a₂. F₄ from CN.I.b. Irregular Stock.

This is a sister intersex of Specimen 7. It moulted on April 6, 1921, the same day as a normal female in the same brood; the moults were microscopically examined and compared. The intersex measured 9.5 mm.; the normal female, 8 mm. It died on May 11, 1921; length 11.5 mm.

First antennæ, both broken in the moult of April 6; on May 11, one had 39 joints, the other 37 joints in the primary, and 5 joints in the accessory flagella. Second antennæ large and very setose, with 3 or 4 rather short curved hairs on the peduncle; flagellum, 15 joints, April 6; 17 joints, May 11.

Gnath. 1. Both hands, with 3 spines in the angle-row; and the usual pair below, with 1 extra spine developed on each hand.

Gnath. 2. In both hands the angle-row consists of 2 large sensory spines, and 3 rigid serrated setæ; both have the usual pair of sensory spines below, but the right hand carries, in addition, a serrated sensory seta facing the second seta of the angle-row (cf. CN.183.m.).

The brood-plates are about three-quarters the normal length; the hairs very small and unequally developed, mostly on the posterior margins of the first two pairs. On April 6 there were 29 hairs on the first brood-plate; 19 on the second (the normal female had 21 very long hairs on this brood-plate); 11 on the third, most of them rudimentary, while the normal animal had 13 very long ones. On May 11, although the intersex had grown larger, the brood-plates were practically unchanged in size; the hairs, however, had increased in number and length, e.g. there were 35 hairs on the first brood-plate, the posterior 7 being all developed (cf. CN.259.b. Figs. 58 and 59).

Third uropods with 3 spines on the margin of the inner ramus right side, 2 on the left; 2 lateral clusters on the terminal joints.

Specimen 11. CN.216.b. F₃ from CN.I.b. Irregular Stock.

One of a brood of 14 Black-eyed, extruded April 24, 1920. Three came to maturity, normal male, normal female, and this intersex which was very slow in development. On October 2 it was marked "female," but two days later, when examined microscopically, it was noted as "male ? or intersex ? no male hairs on antennæ, but gnathopods look like young male." On October 20, "the gnathopods look more male, and the antennæ have 2 or 3 curved hairs ; no ovary." It moulted on November 2 and a fertile female was added to test it. It did not mate ; February 7, 1921, "female gone." The moult of April 25, 1921, was examined, and, as partially developed brood-plates were found, a male was put in, on May 2, to see if it would mate. There were no results till May 21, when
mating took place. By the next morning they were separate; no eggs were laid. The male died on May 26, the intersex on May 27, 1921.

On April 25 it measured 11 mm, age 366 days.

First antennæ, May 27, with 40 joints in the primary, 7 in the accessory flagella. Second antennæ as large as those of the adult male, densely setose, with many long fine sensory hairs, and 2 or 3 curved ones; flagellum 18-jointed.

Gnathopods very large and setose, the setæ exceedingly numerous and long with many of the fine sensory hairs on the under surface.

Gnath. 1. Both hands with 3 spines at the palmar angle, one unusually long, and two smaller, divergent; an extra spine below on each hand; this spine was also found in the moult of April 25.

Gnath. 2. The right hand, April 25, had in the angle-row 3 large sensory spines and 4 serrated setæ; with the usual pair of spines below. It was missing on May 27, the appendage having been broken at the third joint. In the left hand of this date, the angle-row consists of 1 large sensory spine, and 3 stout serrated setæ; in addition it has another large sensory spine, separate from the row, in the middle of the palmar margin as in the immature male (cf. also Fig. 106); the usual pair of sensory spines below.

Peræopod 1, very massive and setose with some long fine sensory hairs as in the gnathopods, but none curved.

The brood-plates are about two-thirds the normal length, all with a few short hairs developed, mostly on the posterior margins, the other hairs quite rudimentary. On April 25 the first brood-plate had 29 hairs, the second 17, the third 11, and the fourth 6; the number slightly increased May 27.

Third uropods exceptionally large and setose, of the adult male type and proportions, with a great number of long fine sensory hairs, a few lightly curved; 1 lateral cluster on each terminal joint.

Sections show the gonads, very small, loose and irregular in structure, very like text fig. 6.

Specimen 12. CN.289.a. F₄ from CN.I.b. Irregular Stock.

It was extruded on July 17, 1920; one of a brood of 13 Black-eyed young, of which only four were normal-eyed. Five reached maturity; 2 males, one reserved for future discussion grew very slowly, the other developed disease; 1 female, also with disease, and 2 intersexes, Spec. 18 and this specimen, very large and healthy.

On October 19 it was marked as "male," but on November 24 microscopic examination showed that it had none of the typical male hairs. It was therefore recorded as an intersex, and a female was added to see

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if it would mate. In the pot it looked so exactly like a male that it was taken out at frequent intervals and examined for the male characters. It devoured its moults so quickly that it was not till April 7 and April 25 that enough fragments were found to prove that it was not a male.

The fragments consist of the second antennæ, the terminal joints of the two gnathopods, and first peræopod, some of the brood-plates and gills, and the third uropods.

Second antennæ large and very setose, long sensory hairs but none curved ; flagellum 19-jointed.

Gnathopods very large and setose.

Gnath. 1. With the usual 3 spines on the upper side of the palmar angle; 1 extra spine developed below.

Gnath. 2. Right hand missing. Left hand with 8 clusters of setæ on the posterior margin (7 on the fifth joint); angle-row composed of 2 large sensory spines and 4 serrated setæ. It carries another spine on the upper surface, below the angle-row (Fig. 98), the only instance of a spine being found in such a position; 1 extra spine developed below.

Peræopod 1 also resembles that of the immature male, with 3 or 4 long curving sensory hairs.

The gills are very large. The brood-plates are almost perfect, the fringing hairs all present, but unequally developed, those at the tips being very small.

Third uropods are about as large as in Specimen 1, much more setose, with more spines and with some long fine sensory hairs. They are very massive; 3 lateral clusters on the terminal joint, right side, 2 on the left side.

This specimen is still alive (July 13, 1921) and has been placed with a male to see if it is capable of mating.

Specimen 13. CN.247.d. F4 from CN.I.b. Irregular Stock.

One of a brood of 14 Black-eyed, extruded 26 May, 1920. It had both eyes irregular; developed very slowly; on September 11 marked "small male." It moulted on September 14 and a female was added. No mating occurred, and on the 15th it was examined microscopically and seen to be an intersex. By October 23 it had increased greatly in size, and looked exactly like a male; no sign of ovary. A female, put in to test it, was eaten. On May 14, 1921, it was preserved, age 354 days, length 10 mm.

First antennæ, both broken; longer primary flagellum 30-jointed, longer accessory, 6-jointed. Second antennæ very setose; 8 clusters of setæ on joint 4, 9 on joint 5 of the peduncle, left side; flagellum 17-jointed.

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Gnathopods large and very setose, setæ of a great length.

Gnath. 1. Both hands have a stout serrated seta at the palmar angle in addition to the 3 spines, that on the right hand being more spinelike than the one on the left; 1 slender serrated seta extra on the under side.

Gnath. 2. Angle-row on the right hand consists of 2 large sensory spines and 4 rigid serrated setæ; on the left hand, of 1 sensory spine and 5 of the rigid setæ; usual pair of spines below.

Gills of great size.

The brood-plates are interesting, varying from those previously described in having most of the hairs on the hinder pairs developed, many of normal length, while those on the first pair of brood-plates are nearly all rudimentary; 34 on the first, 25 on the second, 14 on the third, and 10 on the fourth.

Third uropods with 2 lateral clusters on each terminal joint.

Sections show the gonads very little developed, about the same development as in text fig. 5.

Specimen 14. CN.265.a. F₃ from CN.I.b. Irregular Stock.

One of a brood of 26 Black-eyed, extruded on June 15, 1920; sister intersex of Specimen 9. It developed very slowly at first. On January 31, 1921, it was marked "Intersex? No ovary seen." It is still alive, (July 13), and now very large; the moult of May 11 measured 12 mm. A male has been added to see if it will mate.

Second antennæ large and setose ; flagellum 18-jointed.

The gnathopods are very interesting, showing the development of extra spines on all the hands.

Gnath. 1. Both hands with 4 spines in the row on the upper surface of the angle; the usual pair below and 1 extra spine developed.

Gnath. 2. Right hand has the angle-row composed of 2 large spines and 3 stout serrated setæ, with an extra spine developed on the under side; the left hand has in the angle-row 1 large spine and 4 stout setæ, but in addition it carries 1 long stout spine-like seta inset in mid-margin (cf. Fig. 108). In the moult of July 6 the left hand has 2 spines and 3 setæ in the angle-row.

The sensory hairs on the under surfaces of the joints are short but lightly curved.

The brood-plates have only a very few short hairs developed; the rest quite rudimentary; 35 and 36 on the first, 22 and 23 on the second, 11 and 12 on the third, and 9 on the fourth pair.

Third uropods large and massive, very setose with 3 lateral clusters on the terminal joint, right side, 2 on the left. Specimen 15. CN.284.a. F₄ from CN.I.b. Irregular Stock. Figs. 99, 100 and 101.

One of a brood of 37 Black-eyed, extruded on July 9 and 10, 1920. On January 24, 1921, three animals were found in the brood-bowl, 2 normal females and this specimen marked "very large male?" Two males were put into the bowl with the intersex, and at first it looked as if there would be a mating, the intersex and one of the males following each other about for several days, continually meeting and touching each other with their antennæ. However, no mating occurred. On February 7, it moulted and was then larger than the males. Another male was added on May 11, with no results. The intersex moulted on May 12, the moult measuring 14.5 mm. It died on May 25, 1921, length 17 mm., the largest specimen of *Gammarus chevreuxi* that we have seen.

All the appendages are very massive and densely setose, with numerous long fine sensory hairs, a few lightly curved.

The first antennæ are the longest yet recorded for this species, consisting of 47 joints in the primary, and 8 in the accessory flagella. Second antennæ each with a 21-jointed flagellum.

Gnath. 1. Both hands with 1 extra spine on the upper side of the angle, the usual pair and 2 extra sensory spines developed below.

Gnath. 2 is interesting as showing the development of spines in succeeding moults. On May 12, the angle-row of the right hand consisted of 2 large sensory spines and 3 rigid serrated setæ, with a long spine inset by itself in mid-margin; claw impinging against the under surface of the hand (cf. CN.218.b. for the only other instance of this); palmar margin a little bent in under; 1 extra spine was developed on the under side of the angle. On May 25, the angle-row had 3 large spines and 3 serrated setæ. The row on the left hand angle on May 12 contained 2 spines and 4 setæ, with the usual pair of spines below; on May 25, it had 3 spines and 3 setæ. Both hands are furnished with a number of long, lightly curved sensory hairs; 9 clusters of setæ on the posterior margin (8 on the 5th joint).

Brood-plates. The hairs on the brood-plates are most of them quite rudimentary, a few very small ones appearing on the first two pairs; none on the 3rd and 4th pairs; 38 and 40 on the first pair; 28 on the second, 14 on the third, and 11 on the fourth.

The third uropods are of great size, almost the length of those of the oldest male, CN.22.a., and much more massively built; densely setose, but with no curved sensory hairs; no less than 4 large lateral clusters on each terminal joint, the largest number yet seen. These clusters are still more noteworthy for the presence of a plumose hair in the first two clusters never seen in the normal animals.

Specimen 16. CN.183.m. F₃ from CN.I.b. Irregular Stock (Figs. 102 to 110).

This is the most male of all the intersexes. Sister intersex of Specimen 26.

On April 10, 1920, it was entered as "male; left eye irregular." As it had not mated with a normal female in the same bowl it was taken out on July 3, and microscopically examined, "sex doubtful." Another female and a male were placed with it, but no mating occurred. The "curved hairs on the second antennae" were seen on July 20. It died on September 9, 1920, in the effort of moulting; age 204 days; length 10.5 mm.

First antennæ, all the flagella broken, 37 joints left in the primary, and 7 in the accessory flagella. Second antennæ, large, very setose, with many of the curved sensory hairs, such as are found in the immature male (cf. Fig. 1); in the intersexes, however, the curved hairs are shorter than in the normal animals; flagellum 18-jointed.

Gnath. 1. The right hand is very remarkable. It has the long sensory spine in mid-margin, as in the immature male (Figs. 103 and 104; cf. Fig. 3); 3 sensory spines on the upper side of the palmar angle, and 4 spines below, all large. The left hand has the row at the angle, of 4 spines; 1 extra spine developed below.

Gnath. 2. The right hand in this gnathopod also has the spine in midmargin, as in the immature male (Figs. 106 and 107; cf. Fig. 7), 3 sensory spines and 4 stout serrated setæ in the angle-row, and 2 extra spines developed below. The left hand has 1 large serrated spine-like seta in mid-margin, 2 sensory spines, and 4 serrated setæ in the angle-row; with the usual pair below.

Brood-plates. All the hairs are quite rudimentary except on the fourth pair, where 2 or 3 almost microscopic ones are found (Figs. 109 and 110). These tiny ones are evidently always developed, the new ones being plainly seen through the old cuticle. The hairs have been counted, but the number given for the first three pairs may not be exact. The animal had commenced moulting, and as the new brood-plates were partly withdrawn from the old cuticle which was crumpled, 1 or 2 may have been overlooked.

First brood-plate with 30, second with 20, third with 13, and fourth with 9 and 10.

Gills very large.

Third uropods very large, of the male type, densely setose, no curved hairs; inner rami more spinose than is usual; 2 lateral clusters on each terminal joint, outer rami.

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Group III, Sub-group A, the "less male" type.

Specimen 17. R.F.1.

The male parent of this specimen was an F_2 from the Cross CN.I.b., Irregular Stock; the female parent was derived from the original stock (June, 1912).

One of a brood of 10, extruded on September 4, 1920. It was exceptionally slow in development, even for an intersex. On November 3, 1920, three males in the same bowl had reached maturity, but it was not till November 27 that this animal was marked as "male?" It was examined several times, and on February 3, 1921, was recorded as an "intersex." On March 11 the gnathopods were noted as "female type." It did not recover from the moult of April 25, 1921.

It measured only 6.5 mm., although its age was 234 days, but the characters modified at sexual maturity, are very large for the size of the animal, as large as in Specimen 21, CN.309, which was 8.5 mm. in length, but they are not as well developed, nor furnished with as many setæ as specimens in Group I and Group II.

First antennæ, both diseased. Second antennæ, flagellum 13-jointed. Gnath. 1. Hands missing.

Gnath. 2. Right hand has 4 rigid serrated setæ in the angle-row, and the pair below consisting of 1 large sensory spine, and 1 very stout spinelike serrated seta; the left hand also has 4 serrated setæ in the angle-row, but the under surface is too crumpled to see what is there.

The brood-plates are small, all the hairs quite rudimentary; 22 and 23 on the first, 15 on the second, 8 on the third, and 6 on the fourth.

The third uropods are much smaller than in the specimens previously described, and less male in appearance; 1 lateral cluster on each terminal joint.

Specimen 18. CN.289.f.3. F₄ from CN.I.b. Irregular Stock.

This is a sister intersex of Spec. 12. It was irregular-eyed, slow in development, but healthy; entered as "male?" on October 19, 1920, and as "female? or Intersex?" on November 24. It died on November 27, aged 134 days.

The antennæ, gnathopods, and uropods are not as large as in the preceding group. They are all furnished with numerous very long setæ; the sensory hairs on the under surfaces are very short, none curved except on the left second antennæ, where 2 curving ones were found.

First antennæ, with 24 joints in the primary, and 3 in the accessory flagella. Second antennæ, one with 12 joints, the other with 14 in the flagellum.

Gnath. 1. Right hand has 2 spines on the upper side of the palmar

angle; and the usual pair below, with 1 small but stout, serrated seta extra; the left hand has 3 spines in the angle-row; the pair below consisting of 1 large spine, and 1 spine-like seta, with 1 very small stout sensory seta extra.

Gnath. 2. Right hand has 5 serrated setæ in the angle-row, the setæ stouter than on the left side, one almost a spine; usual pair of sensory spines below. The left hand has 5 serrated setæ in the angle-row; the pair below consisting of 1 large sensory spine, and 1 stout spine-like serrated seta, with an extra similar seta behind the pair.

The brood-plates are very small, comparatively speaking, only about half the size of the normal animal's; the hairs quite rudimentary, 23 on the first brood-plate, 16 on the second, 7 and 8 on the third brood-plates, and 7 and 6 on the fourth.

The third uropods have the proportions of the normal female's, but are larger; 1 lateral cluster on the right side.

Specimen 19. CN.157.a₂. F₃ from CN.I.b. Irregular Stock.

Sister of Spec. 4; irregular-eyed; entered as "male" on March 30, 1920. It was looked at daily, but as no mating occurred, on July 7 it was taken out and examined microscopically. It was then marked "Female? doubtful. No male hairs, but the setæ are as long and as numerous as in a male; gnathopods are of the female type, but in swimming and appearance it is male." July 24, "male?"; July 26, "Just moulted. Female, judging by the absence of male hairs; no ovary visible." A male was added, but on August 27, 1920, the intersex moulted, and was eaten; age 257 days; the moult measured 8.5 mm.

First antennæ, August 27, flagella regenerating, longer primary with 32 joints, accessory with 6 joints. Second antennæ, very setose; flagellum 15-jointed, regenerating.

Gnath. 1. Both hands with 2 sensory spines, and 1 stout serrated seta in the row on the upper side of the angle; the usual pair below.

Gnath. 2. Right hand has 5 rigid serrated setæ in the angle-row, the left hand has 4; both with the usual pair of spines below.

The brood-plates are rather longer in proportion than in most intersexes; the first pair with 28 hairs on the right one, 29 on the left.

The third uropods rather small; 1 lateral cluster on right terminal joint; left uropod missing.

Specimen 20. CN.257.d. F₃ from CN.I.b. Irregular Stock.

One of a brood of 19, extruded June 3 and 4, 1920, an albino, very irregular-eyed. Besides this intersex, 2 normal males and 2 normal females reached maturity. On August 5 a pair were mated, whilst this

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one was marked "very small, male?" Examined again on August 6 this entry was altered to "not mature;" on August 14, "intersex.?" It moulted August 31, September 9, September 20, and October 6, and died on October 8, 1920, age 128 days; length 8.5 mm.

First antennæ, 29 joints in the primary, 6 in the accessory flagella. Second antennæ, great increase in the number of setæ noted, in the succeeding moults from August 31 ; the flagellum increased by 1 joint in each moult ; 17-jointed on October 8.

Gnath. 1. Right hand has 3 spines in the angle-row, the usual pair of large sensory spines below, and 1 smaller spine extra. The left hand has the same number, but the third spine below is larger than in the right, and the palm margin bends under the hand, as in the young male.

Gnath. 2. Right hand has 6 rigid serrated setæ in the angle-row, the second one stouter than the others; the left hand also has 6 in the row, the second stouter than the others, the first one a little apart from the other five; both have the usual pair below.

Gills are of very large size.

Brood-plates. The hairs are so rudimentary that it is difficult to count them; first brood-plate on September 9, 1920, had 24 hairs, on October 8 it had 28; the third had 9 on September 9, 11 on October 8.

It is interesting to note that, while the other characters have increased regularly in setose armature and in size (the second antennæ, e.g. increased to a quarter as long again in 29 days), the brood-plates remained practically unchanged.

Third uropods with no lateral clusters.

Specimen 21. CN.309. F₅ from CN.I.b. Irregular Stock.

One of a brood of 7, extruded August 26, 1920. Two came to maturity, a normal female and this specimen. It was very slow in development, on October 15 being marked as "male?" As no mating had taken place by February 9, 1921, it was examined microscopically and then recorded as "intersex? Female characters (gnathopod hands, no male hairs) but no ovary." It died on February 22, 1921, in the effort of moulting; age 181 days; length 8.5 mm.

First antennæ broken. Second antennæ with some sensory hairs, but none curved; 13-jointed flagellum.

Gnath. 1. Right hand has 3 spines in the angle-row; the left hand has 2 spines and 1 sensory serrated seta; usual pair below.

Gnath. 2. Both hands with 6 of the rigid serrated setæ in the anglerow; on the under surface the right hand has 1 large spine and 1 very stout spine-like seta, the left hand appears to have 2 spines; the second spine is larger than the stout seta on the right side, but it is difficult to see owing to the new spines below showing so plainly through the cuticle. The gills are exceptionally large, extending, in gnathopod 2, beyond the fifth joint.

Brood-plates, with 22 and 24 rudimentary hairs on the first pair, 16 on the second.

Third uropods with no lateral clusters.

Specimen 22. CN.323.a1. F4 from CN.I.b. Irregular Stock.

One of two survivors of a brood of 21, extruded September 11, 1920, both intersexes, and both very slow in development, this one being the smaller. On January 17, 1921, it was marked as "male.?" On February 22 the other was noted as looking like an intersex; March 11, "Smaller one also an intersex?"; March 16, "Dead in the act of moulting; partly eaten. Intersex?"; length 6.5 mm., age 187 days.

It very much resembles specimen 17 in its small size and large appendages. The proportion of the antennæ, gnathopods, first peræopods, and uropods are the same, but the appendages themselves are slightly larger, and the brood-plates are distinctly larger, the second one having the rudiments of 31 hairs as against the 23 of Specimen 17.

First antennæ broken. Second antennæ, 15-jointed flagellum.

Gnath. 1. Right hand with 4 spines on the upper surface, 1 of them very large, and nearly in mid-margin; usual pair of large spines, and 1 extra good-sized spine below. The left hand has 3 very large spines above, and 3 below, i.e. the usual pair and 1 imperfectly developed small spine extra; the palmar margin is slightly bent under the hand.

Gnath. 2. Left hand has 6 rigid serrated setæ in the angle-row, and the usual pair below; the cuticle of the right hand has been broken at the palmar angle, and it is not possible to distinguish the old setæ from the new ones, nor to count them.

Both gnathopods have fine sensory hairs, but none curved.

Third uropods; one left, no lateral cluster on the terminal joint.

Specimen 23. CN.323.a₂. F₄ from CN.I.b. Irregular Stock.

Extruded September 11, 1920, sister intersex of Specimen 22; very slow in development at first. On January 17, 1921, it was marked "male?" on February 22 "Just moulted, looks intersex." On March 11 the entry was made "large intersex"; it then had gill-disease (a disease in which the gills turn black), but from this it recovered later. It moulted April 12, April 26, and May 11. The moult of May 11 measured 11 mm. It died July 9, 1921, age 302 days, length 12 mm.

The second antennæ and both gnathopods are very setose, with many long sensory hairs, some of them lightly curved (as in the immature male).

First antennæ, primary flagellum with 33 joints; accessory with 6. Second antennæ, flagella 15-jointed.

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Gnath. 1. Right hand with 3 sensory spines in the angle-row; pair of large spines below, with 1 serrated seta extra. The left hand is more developed than the right, having 4 spines on the upper surface, the pair of large spines below, and 1 good-sized spine extra.

Gnath. 2. Right hand with 6 serrated setæ in the angle-row; left hand with 8 setæ, 7 in the angle-row and 1 apart; usual pair below.

The first brood-plate had 38 rudimentary hairs on May 11, 2 more than in the moult of April 26, but was no larger.

Gills very large.

Third uropods, with 1 lateral cluster on the left side, 2 on the right. By July 12, 1921, the change to the more male type had taken place.

Second antennæ had several curved hairs well developed.

Gnath. 1. Both hands with 4 spines in the angle-row, right hand with 1 stout seta extra below, left hand with 1 spine extra.

Gnath. 2. Densely setose, the 3 terminal joints bent at an angle to the rest of the appendage; right hand with 1 sensory spine and 6 very large stout serrated setæ in the angle-row; left hand with 2 spines and 6 setæ; usual pair below.

Gills of extraordinary length.

First brood-plate with 40 rudimentary hairs.

Third uropods with 3 lateral clusters on the right side, 2 on the left.

Sub-group B, the "more male" type.

Specimen 24. Abn.Exp.3.

In 1915, two abnormal individuals were found in making the crosses to determine the Mendelian inheritance of eye colour, both in the F_2 from one brood of F_1 , from the original cross Black-eye \times Red-eye.

This specimen was one of a brood of 22 Black-eyed, hatched on June 9, 1915. Twenty-one came to maturity, 7 males, *13 females, and 1 marked "sex not known" on August 23. A male and a female were added to see if it would mate with either. The female was taken out again, but the male and another added later, were both eaten. It was examined microscopically on September 14 and marked "no ovary, but a mass of granular material can be seen lying on top of the intestine, in the position of the normal ovary." On examining it again a month later, October 14, this mass had apparently completely disappeared, and the gnathopods were noted as "intermediate in type, neither male nor female." Again examined, December 6, 1915, it is recorded "no coiled hairs on the antennæ, but the setæ are much more numerous than in a female ; gnathopods more male in appearance ; no sign of ovary ; no mating."

* One of these females was mated with four different males and laid five batches of eggs, but none hatched.

It was found macerating on December 29, 1915. Age 204 days ; length 9 mm.

The flagella of all the antennæ broken. Second antennæ very large and setose.

Only the gnathopods of the left side were found.

Gnath. 1 had 2 spines at the palmar angle, and 2 on the under surface.

Gnath. 2 had the row at the angle composed of 1 large sensory spine and 3 rigid serrated setæ, the usual pair of spines under, the second one not quite as well developed as the other.

The brood-plates were small, about two-thirds the normal size ; hairs quite rudimentary ; 26 on the first pair, 17 and 18 on the second, 13 on the third, fourth not found.

Gills large.

Third uropods very large, massive, setose, with 2 lateral clusters on each terminal joint.

Specimen 25. Abn.Exp.4.

Of the same origin as intersex Specimen 24. One of a brood of 12, hatched on February 3, 1915, of which 4 survived to maturity, 2 males, 1 female, and this specimen. On July 20 it was marked "not sure if male or female." It was examined microscopically on September 8, "many more setæ on antennæ than in normal female, and gnathopod hands a different shape, but not developed as in a typical male and with none of the male hairs." On September 14 it was again examined and the gonad was described as much resembling that of Abn.Exp.3, looking "almost like soft eggs much broken up." This had disappeared three weeks later, when it was noted as "looks more like a male." Several females were added at different times to test it; two were eaten. No mating occurred, and on November 4, 1915, it died, probably in moulting ; the females in the pot were found eating it.

Its male parent was a brother of the female parent of the previous specimen Abn.Exp.3. The relationship of the two specimens is noted, in view of the fact that intersexuality appears to have some genetic basis. Three other examples in the same strain were found "resembling Abn.Exp.3," all of which were an exceptionally long time in developing. Their male parents were also brothers of the female parent of Abn.Exp.3. They were not kept under observation.

Specimen 26. CN.183, c. F₃ from CN.I.b. Irregular Stock.

One of a brood of 23, hatched on February 19, 1920. Only 4 survived to maturity, 2 females normal in appearance, and 2 intersexes, both irregular-eyed, this animal, and Specimen 16. One of the females mated, and was eaten by its mate; the other died, after developing and recovering from "antennal disease" (a disease in which the antennæ gradually rot off joint by joint).

This specimen developed very slowly. Another of the brood, a normaleyed in the same bowl, became sexually mature on April 15, but this one was not recorded as "male?" till May 3; on May 19, it was marked "male." Three females were added at different times to test it, but as no mating occurred it was taken out on July 7 and microscopically examined; "no ovary; a few young-male curved hairs on the second antennæ; other hairs of the female type, but longer and nearly as



TEXT FIGURE 5.-Transverse section of intersex CN.183.c, where the gonad is of maximum size. Magnification, etc., as in text fig. 2. J.S.H. del.

numerous as in the normal male; male in appearance." It moulted on July 14, "the character of the hairs unchanged; no ovary seen, but great masses of colourless globules in the third to the seventh peræon-segments, above the intestine, the seventh segment containing also a number of bright red globules." On July 26, 1920, it was preserved and sectioned, age 157 days.

The gonad (text fig. 5) was seen on sectioning to be extremely small. While in size and form it approached a testis, it was not so crowded with nuclei and showed occasional larger cells, perhaps representing aborted oocytes. It had 5 instead of 4 hepatic cæca.

Second antennæ (cf. Fig. 102), both very setose, and furnished with a number of long fine sensory hairs, many of them curved, as in the immature male; flagellum 16-jointed.

Only the gnathopods of the right side are present.

Gnath. 1. Right hand with 3 sensory spines on the upper side of the palmar angle; the usual pair below with 1 good-sized spine extra.

Gnath. 2. Right hand has 5 in the graduated row at the angle, 1 long rigid serrated seta, then 1 large sensory spine, and 3 more of the serrated setæ (cf. Fig. 54), the usual pair of spines below.

The brood-plates are small, only half the normal length, hairs quite rudimentary; first brood-plate with 30.

Third uropods; only one left, no lateral cluster on the terminal joint.

Specimen 27. ex CN.224.b. F3 from CN.I.b. Irregular Stock.

On January 22, 1921, 12 survivors were found in the brood-bowl, 4 adult F_1 probably hatched at the end of September, 1920, and 8 F_2 . The adults were 1 male, 2 normal females, one ovigerous, and this specimen which was marked as "male ?" Examined microscopically on February 7, 1921, it was noted, "left eye irregular; no ovary." By February 28 it had developed gill-disease, and died on March 2, 1921; length 8.5 mm.. age about 151 days.

First antennæ, the longer primary has 35 joints, and the accessory flagellum 6. Second antennæ with clusters of long fine sensory hairs, but none curved ; flagellum 17-jointed.

Gnath. 1. Both hands with 4 sensory spines in the angle-row, and 1 extra spine below in addition to the usual pair.

Gnath. 2. Both hands have the angle-row with 5 serrated setæ, and 1 large spine inset apart from the row almost in mid-margin; the usual pair below.

Gills of exceptional size.

Brood-plates small, little more than half the normal length, hairs quite rudimentary; in the moult of February 28 there were 29 hairs on the first brood-plate, 16 on the second, 10 on the third, and 6 on the fourth.

Third uropods regenerating ; left one the larger, with 2 lateral clusters on the terminal joint ; other one very small.

Specimen 28. CN.52. F₂ from CN.I.b. Irregular Stock.

The only survivor of a brood of 4, extruded March 14, 1919. It was exceedingly slow in development. July 30, 1919, marked "not yet mature." On March 26, 1920, it was recorded as "male—added a female"; May 18, "male and female in pot, but no mating." July 1, "there are no coiled hairs, is it possibly a female ?" It was examined microscopically on July 27, and marked "intersex ? No ovary; looks like a male but has no male hairs." Again on August 24, "hairs of the female type, but longer and more numerous; no ovary; added a male

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to test it." As no mating had taken place by August 20 the animal was preserved and sectioned; age 536 days.

The gonad, see text figure 6, is interesting microscopically as showing the structure to be expected of an aborted ovary. It is larger than a testis, and irregularly lobulated. Nuclei do not occur in the smooth outer layer; occasional dark masses, apparently of degenerating nuclei, are to be found.

First antennæ, both broken; 33 joints remaining in the primary,



TEXT FIGURE 6.—Transverse section of intersex CN.52., where the gonad is of maximum size. Magnification, etc., as in text fig. 2.

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6 in the accessory flagella. Second antennæ, densely setose, with many long sensory hairs, but none curved ; 23-jointed flagellum.

Gnath. 1. The hands missing.

Gnath. 2. (cf. CN.183.m., Specimen 16). The right hand has, in the angle-row, 1 large sensory spine, and 4 stout serrated setæ, and, in addition, 1 large spine inset in mid-margin as in the immature male; 1 extra spine developed below. The left hand has 2 large spines and 4 serrated setæ in the angle-row, and 1 stout serrated seta apart, in mid-margin; the usual pair below.

Brood-plates small, 27 rudimentary hairs on the first.

Third uropods of the male type with many long sensory hairs; 1

lateral cluster on the terminal joint of the left side; 4 spines developed on the inner ramus, right side.

Specimen 29. CN.293.a₁. F₄ from CN.I.b. Irregular Stock.

Sister to Specimen 3. When found on February 9, 1921, it was entered as "Intersex ?; no gonad visible to the naked eye, but under the microscope (1 inch) it looks as if there is a disintegrated ovary lying on the intestine; eyes very irregular, the left eye twice the size of the right." On March 11 " no sign of the structure (disintegrated ovary) seen a month ago." It was preserved on May 14, 1921, length 10.5 mm.

First antennæ with 38 joints in the primary, 7 in the accessory flagella. The second antennæ are large, and densely setose ; flagellum 18-jointed.

Gnath. 1. The right hand is quite normal, i.e., 3 spines on the upper surface at the angle, and 2 on the under surface; but the left hand differs in having an extra spine developed on each side.

Gnath. 2. The right hand has, in the angle-row, 2 large spines and 4 serrated setæ; the left hand has 3 spines, 2 in the graduated row with 4 serrated setæ at the angle, and 1 large spine inset a little apart from the others about the middle of the palmar margin (cf. CN.224.b.); both have the usual pair below, the right hand provided with 1 serrated seta extra, also.

The brood-plates small, 32 rudimentary hairs on the first, 18 and 21 on the second pair, 11 and 12 on the third, and 8 on the fourth.

Third uropods of the male type massive, with unusually long spines; 2 lateral clusters on each terminal joint.

Sections show an almost rudimentary ovary; an occasional large mass is seen, which may probably be a degenerate oocyte.

Specimen 30. CN.285.a. F₄ from CN.I.b. Irregular Stock. Fig. 111.

One of a brood of 24, hatched July 10, 1920. It was noted as "intersex, large, with curved hairs on the second antennæ" on January 24, 1921.

It was preserved and sectioned on May 14; length 10 mm.; age 309 days.

The appendages are large, and massive.

The first antennæ are unusually long; 41 joints in the primary, and 7 in the accessory flagella of each. The second antennæ very setose, with several curved hairs on the 4th and 5th joints of the peduncle (cf. Fig. 102); flagellum 17-jointed.

Gnathopods densely setose, with many fine sensory hairs but none curved.

Gnath. 1. Left hand with an extra spine developed on each side of the

palmar angle; right hand with 3 spines in the angle-row and 1 extra below.

Gnath. 2 has 3 large sensory spines and 3 serrated setæ in the row at the angle, on both hands; right hand with the usual pair below; left hand with 2 very stout spine-like serrated setæ, in addition to the usual pair of spines below (Fig. 111).

The brood-plates have the hairs quite rudimentary, 36 on the first, 22 on the second, 13 on the third and 7 on the fourth.

The gills are very large.

Third uropods very massive, densely setose, with many long hairs but none curved; 2 lateral clusters on each terminal joint.

Specimen 31. CN.218.b. F₃ from CN.I.b. Irregular Stock. Figs. 112 and 113.

The only survivor of a brood of 36, extruded April 29, 1920.

On January 22, 1921, it was marked as "very large intersex." It was examined on February 8, and the note made, "three or four curved hairs on the second antennæ; intersex gnathopods; very large animal; eyes nearly normal, but with the reticulation irregular and the colour dilute." It died on February 28, 1921; length 11.5 mm.; age 306 days.

First antennæ, broken. Second antennæ very setose, with many sensory hairs, 9 or 10 of them curved as in the immature male ; flagellum 19-jointed.

The gnathopods are exceedingly interesting in this specimen. They are densely setose, with many sensory hairs, several lightly curved.

Gnath. 1. Both hands with 3 spines in the angle-row; and 1 spine extra below.

Gnath. 2. Right hand with 3 spines, 2 in the angle-row with 3 serrated setæ, and 1 apart in mid-margin as in the immature male; the claw impinging against the under surface (Fig. 112). This and Fig. 100, CN.284.a, are the only instances of the claw in this position that we have found in the intersexes. The left hand is quite different; it has 3 large spines, and 4 serrated setæ on the upper side of the angle, the 3 spines and the 2 largest of the setæ, very stout and spine-like, in a row, the 2 smaller setæ behind, not in the same line; the claw is in the normal position (Fig. 113).

The brood-plates are very small for the animal's size, not half the normal length, 33 rudimentary hairs on the first.

Some of the gills are damaged, whether by injury or disease is not evident; the one attached to the second gnathopod on the right side is very small and bi-lobed, the anterior lobe differentiated, but not the larger posterior one. The gills that have developed are exceptionally large, even for an intersex. Third uropods massive, of the adult male type, with more spines on the inner ramus than usual; 2 large lateral clusters on each terminal joint.

Specimen 32. CN.328 was of the Group III type. It was eaten by a male.

It may be of interest also to note the occurrence of a similar intersex in another Amphipod genus.

This, a *Tmetonyx similis* (G. O. Sars) has already been described by one of us (Sexton '11, p. 200; and see Sars '95), as "a very large, fullgrown female, which has apparently developed the secondary sexual characters of the male." It was ovigerous, with a large brood-pouch, but with both antennæ of the length characteristic of the adult male, and provided with calceoli (which are not found in the normal female). Professor Sars most kindly sent us his type specimens from Sogne Fjord for comparison, and the interesting fact was established that the antennæ of the ovigerous specimen described above are exactly the same in every particular, even to the number of joints in the flagella, as those of his type male. The intersex was much larger than the normal animals ; the length of the normal male was 14.25 mm. ; of the two normal ovigerous females, 15 mm. ; and of this ovigerous intersex, 18 mm.

Reference was also made (loc. cit.) to a similar case among Schizopoda, recorded by Tattersall ('11); where a full-grown ovigerous female of *Nematoscelis megalops*, Sars, had developed the rostrum characteristic of the adult male. Dr. Tattersall has informed us that his experience is, that it is not uncommon in *Nematoscelis* to find a female with a male rostrum. In this species the secondary sexual characters are well marked and these "intersexual" specimens are easily picked out.

Attention may be drawn to an account of an abnormal female appendage in *Asellus* which approached the male appendage in character (Journ. Linn. Soc. 34, 1920, p. 342). Mr. Unwin informs us that the eggs from this female hatched.

Another sexual abnormality in Gammarus also deserves mention. Seven pairs from the Irregular Stock which have been under observation since March, 1920, have shown remarkable behaviour. Mating occurs, lasts for much longer than normal (in one case, CN.110.a., up to 44 days), and then ceases. The female moults, but without laying eggs. Mating again follows after a few days. One pair has done this 8 times in less than three months; the periods of mating were as follows :—5 days; 7; 1; 10, ended by the male moulting; 8; 12; 10; 10, ended by the male moulting again. The length of time during which these pairs have been mated much exceeds that during which they have been separate, e.g., in CN.68.a. the periods of being paired between June 15 and August 27 were as follows :—10 days; 12, female moulted, no eggs, mated again for another day; 3; 3; 7 days, female moulted, no eggs, mated again for another day; 13; and 4 days, the female died 3 days later.

The gonads appear normal in life. In two cases, a male was tested with another female and normal fertilisation resulted. The presumption here is, therefore, that the cause lies in the females. In one case, however, M.III, it was proved that the male was infertile. It mated with no less than 32 different ovigerous females in the usual way, carried them the usual time until the broods were extruded, and they moulted; and it twice mated again for a day after the moult; all, however, with no results. No eggs were ever laid, although all the females hatched broods with other males.

DISCUSSION.

Careful examination is necessary to reveal the sexual abnormalities considered in this paper, but once attention has been drawn to them, they are seen to be not uncommon.

In normal broods of Gammarus there is usually a considerable mortality before maturity is reached, and no means exist until then for telling the sex. It is therefore not possible to decide, as in Lymantria (Goldschmidt '20), from a study of the sex-ratio whether the abnormal individuals are to be regarded as modified males or modified females.

The evidence points strongly towards the specimens described in the present paper being modified females. Thus we have first the fact that in all these "intersexes" there has been a progressive increase of male characters with time. There are also all gradations between specimens which have ovaries capable of forming eggs, and possess normal broodplates, and specimens in which the gonad is minute, the brood-plates extremely reduced, and marked male characters are shown in the hairs and gnathopods. In sections of the intersexes the gonad has usually been definitely recognizable as an ovary, reduced to a greater or lesser extent.

The suggestion may, of course, be made that all these abnormal individuals are simply unhealthy females in which the ovary is diseased or atrophied, and no longer produces the internal secretion necessary to maintain the female characters. For instance, one specimen showed an apparently normal ovary at maturity, and hatched two young. After the next two moults it became very unhealthy for some time. The ovary ceased to be visible after the two young were hatched. It then moulted several times, growing less female in appearance at each moult, until it finally looked a typical intersex—i.e. with general male appearance, and increase of hairs on antennæ, gnathopods and uropods, but no curvature of the hairs (CN.259.b. Plate V).

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It would appear, however, that in most of the intersexes here described a typical full-sized ovary is never formed; and, although the animals take a longer time than usual to reach maturity, they are not unhealthy, eventually attain to a great size and are of normal vigour. The progressive increase in the degree of "maleness" fits well with Goldschmidt's theory of intersexuality (the moults allowing a progressive change which is impossible with Lepidoptera), and we may provisionally call these specimens *female intersexes* until more light is thrown upon their genesis.

An important fact in which our intersexes differ from those described by other observers is that whilst the new male characters increase in the direction of maleness, the female characters may continue to develop. For example, the number of hairs on the brood-plates may become even greater than in the normal mature female (e.g. Specimen 23, $CN.323.a_2$). The length of the hairs may also continue to increase. (Specimen 5, CN.259.b. Plate V.)

It is interesting to note the association of intersexes with the "irregulareyed" condition. Further, the tendency for intersexes to appear repeatedly in the same strain is what we should expect after the work of Banta ('16), Goldschmidt ('20), and Sturtevant ('20).

It should be noted that perfectly normal males and females appear in the same broods with intersexes, so that the phenomenon is certainly not *identical* with that observed by Goldschmidt in Lymantria, whereas it *might* possibly be due to a single Mendelian factor, as in Drosophila (Sturtevant '20).

Another important point is that the female intersexes all took longer to reach maturity than their normal brothers and sisters. The extra time taken to mature is often very considerable.

This, in conjunction with the fact that the intersexes are not unhealthy, seems to point to a genetic basis for the condition.

It is impossible without further analysis to advance definite theories as to the nature and cause of the abnormalities here described. In view, however, of recent work on the subject, and of the success of Goldschmidt's explanation of his intersexes as individuals which have started their development as organisms of one sex but have been switched over at a given point of time to continue their development as organisms of the other sex, we may adopt the following provisional hypothesis. By means of this, the facts are accounted for, while they do not seem to be capable of explanation on any other hypothesis now current.

The difference between the various types described is due partly to the different moment of time at which the transformation from one type of metabolism to the other has been effected, partly to the length of time which has elapsed since this turning-point, and possibly also to the strength of the agency operating to produce maleness. If, for instance, a female has arrived at sexual maturity before the turning-point to maleness has been passed, she will possess all the female secondary sexual characters-e.g. fully developed brood-plates. After the turning-point. male characters will begin to appear, but since development seems to be very slow in all these intersexes, they will not reach any very full degree of development. If, on the other hand, the turning-point to maleness comes earlier, at a stage when only the first rudiments of brood-plates have formed, these, the female characters, will not develop much further, while the male characters, having started their development earlier, will attain a correspondingly higher degree of perfection. Any structure once chitinized appears to persist, as in Insects (cf. also the male copulatory appendages in Sacculinized crabs); this is shown, e.g. in the persistence of the brood-plates of the same size, in spite of progressive masculinization of male characters, e.g. in specimen CN.257.d. (p. 534). The soft parts, however, such as the gonads, cannot maintain themselves as either male or female when the metabolism is intermediate, are much degenerated during the change, and do not have time to become completely reconstituted as male after the turning-point. From this point of view, we must regard as female structural characters only the brood-plates, as male structural characters only the coiled sensory hairs, the special shape and spines of the gnathopods, and the size and shape of the uropods. The converse of all these characters, such as the absence of brood-plates in the male, or the shape and spines of the gnathopods in the female, is, physiologically at least, non-sexual or neutral, a basis common to both sexes, which is acted upon by the internal secretion of one sex only. Similar distinctions are to be found among the secondary sexual characters of Vertebrates (see Lipschütz, '19).

In support of this hypothesis, it is especially to be noted that of the two sub-groups into which our Group III falls, that with few and poor male characters has a smaller average size than that with numerous and better developed male characters. This of course indicates that although the turning-point came at the same period in the life-history in all individuals of Group III, those of the second sub-group had lived longer since the turning-point, and therefore show better male characters. This explanation presumably holds also for the sub-groups of the other two groups, although in all cases it is of course possible that different intensity of the tendency to maleness may enter as a third variable. This is strongly supported by specimen CN.229.h. (p. 523) and specimen

CN.323. a_2 (p. 536), which changed at successive moults from Sub-group A to Sub-group B.

We must emphasize that we only propose this as a hypothesis capable of explaining the facts in terms of our knowledge of the physiology of sex in other forms, not as proved by the facts here presented ; a demonstration of its truth for Gammarus is impossible until we get further information on the sex-ratio, and until we succeed in raising young from the end-terms of the intersexual series.

If this hypothesis is correct, it should be noted that our intersexes are unlike those recorded in other species in the slowness of their development of sexual characters.

The sterile females and males which indulged in abnormally long periods of pairing are of interest. It is *possible*, of course, that there are two tissues present in the gonad of Gammarus, as in that of Mammals, one concerned with gamete-production, the other with the control of sexual characters and instincts, and that in these specimens only the former was impaired. Whether this is so or not, only further research can decide.

In any case, the modification of female Crustacea towards the male type is of interest in view of the well-known fact that parasitic castration in the group modifies the males in the direction of femaleness, and not vice versa. This strongly supports the contention of Geoffrey Smith ('06) who insisted that, in the case of Sacculina, the parasite produced its effects, not by castrating its hosts, but by having a metabolism resembling that of the host's ovary. This interpretation is further strengthened by the fact that the presence of Sacculina caused immature Inachus to develop the full female characters prematurely (a fact which has not been sufficiently emphasized in subsequent discussion).

SUMMARY.

In stocks of *Gammarus chevreuxi* kept for genetic experiments 35 individuals have appeared with abnormalities of secondary sexual characters; three of these have been reserved for future discussion. The remaining 32 we have described in the paper as female intersexes. These female intersexes on reaching maturity usually resemble normal females more or less closely, but gradually come to resemble males more and more nearly. Finally, in size, general appearance, and mode of swimming they resemble males, while the structural characters (broodplates, gnathopods, and sensory hairs) are intermediate between male and female, but to a varying extent. Characters which are never present in normal males, such as brood-plates, are present, together with others

never present in normal females, such as gnathopod-size and shape, sensory spines, excessive hairiness of antennæ, etc., and, in extreme cases, curvature of the sensory hairs. On analysis, the individuals are found to fall into three groups :

- I. With the hairs of the brood-plates fully developed, brood-plates of normal size;
- II. With the hairs of the brood-plates partially developed, broodplates of moderate size;
- III. With the hairs of the brood-plates rudimentary, brood-plates smaller than normal.

All show some development of male characters (particularly in size, mode of swimming, and sensory hairs). Each of the 3 groups falls into 2 sub-groups :—(A) with the gnathopod setæ of female type; (B) with the gnathopod spines of the type found in males immediately before maturity: but individuals may pass at successive moults from sub-group (A) to sub-group (B), though apparently not vice versa.

One specimen (CN.259.b.) has produced fertile eggs. One (HN.50.a.) has mated and produced infertile eggs, one (CN.216.b.) mated with no results, the rest have never mated, either with males or females. The ovary in those which have not mated never assumes the normal appearance or size. It appears often to decrease in size after maturity. Microscopically it presents the appearance of a reduced ovary; the degree of reduction varies very considerably.

There can be but little doubt that these individuals are modified females, and can be called female intersexes.

They have occurred in three separate strains, but the majority have appeared in one particular strain, and mostly in the two families of that stock which have given irregular-eyed forms. Cannibalism is marked in all the strains which have given intersexes.

A very slow attainment of maturity characterizes these forms, and usually a final size which is abnormally large, even for a male.

The continuance of the development of the female characters after the male characters have appeared is to be remarked.

As a provisional hypothesis, all the above types may be regarded as genetically females which have been converted to a male type of metabolism during their life history. The degree of development of broodplates will depend chiefly upon the stage at which conversion from female to male metabolism occurred, while the degree of development of male characters will depend upon the length of time which has elapsed since this stage. Individuals which are normal in structure and appearance but are infertile and show abnormality in their mating habits have also appeared.

Reference is made to an intersexual condition in a wild individual of the Amphipod *Tmetonyx similis* (Sars).

Our thanks are due to Professor G. O. Sars for kindly sending us his type specimens of Tmetonyx for comparison, and to Dr. E. J. Allen for constant advice and help.

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EXPLANATION OF PLATES I TO IX.

ALL the drawings were made with the camera lucida, and pains have been taken to make the details exact, all the hairs having been counted and figured, except in Fig. 12.

The abbreviations used are as follows :----

| m. |
|----|
| |
| |
| |

PLATE I.

IMMATURE NORMAL MALE.

The last moult before sexual maturity, showing the mature characters through the cuticle.

The specimen figured was from the first generation hatched in the Laboratory. It died on August 31, 1912, in the effort of delayed moulting; age 59 days. (Others of the brood were breeding at 52 days.)

| Fig. | 1. | Part of second antenna, R.S., showing the curved hairs characteristic of the immature male; the left antenna has 1 more joint in the | |
|------------|----|--|-------------|
| | | flagellum, and 2 more clusters of setæ on joints 4 and 5 of the peduncle. | |
| | | (First antennæ with 22 joints in the primary flagella; in the accessory flagella, there are 4 joints R.S., 3 joints L.S.) | $\times 39$ |
| ,, | 2. | First gnathopod, R.S. | $\times 39$ |
| 9 5 | 3. | First gnathopod, R.S.; palm and claw enlarged, showing the sensory pointed spine characteristic of the immature male in mid-margin, with the truncate spines (<i>ad.sp.</i>) of the adult animal visible through the cuticle. | $\times 97$ |
| " | 4. | First gnathopod, R.S.; under surface of the palmar angle, showing through the cuticle the mature characters which will be established at the next moult. | $\times 97$ |
| ,, | 5. | First gnathopod, L.S.; under surface of the palmar angle. | $\times 97$ |
| ,, | 6. | Second gnathopod, R.S., showing gill (g.). | $\times 39$ |
| " | 7. | Second gnathopod, R.S.; palm and claw enlarged, showing the sensory pointed spine in mid-margin. The mature characters are visible through the cuticle. | $\times 97$ |
| ** | 8. | Second gnathopod, R.S.; under surface of the palmar angle, with 1 sensory spine of the pair below well developed, the other still a | ×97 |

9. First peraeopod, R.S., showing the curved hairs and gill. ×39

...

Fig. 10. Third uropod, R.S., showing the curved hairs, and a lateral cluster commencing on the terminal joint of the outer ramus, represented by 1 seta.

" 11. Third uropod, L.S.

", 12. Third uropod, R.S., of the oldest male, C.N.22a., age 579 days, in which the development of the coiled hairs reached a maximum. The coiled hairs were so numerous that only a few of them could be represented in the figure. There were 2 lateral clusters of setæ on the terminal joint of the outer ramus of the right side. On the left side there was only one lateral cluster.

PLATE II.

MATURE NORMAL MALE.

The specimen figured was the first male to mature of the second generation hatched in the Laboratory; hatched August 8, 1912; moult September 30, 1912; length 8 mm.

| Fig. | 13. | Part of second antenna, L.S., showing the coiled sensory hairs of the mature animal. (First antennæ with 25 joints in the primary | |
|------|-----|---|-------------|
| | | flagella; 5 joints in the accessory flagella.) | imes 39 |
| ,, | 14. | First gnathopod, R.S.; the 3 terminal joints. | imes 39 |
| ,, | 15. | First gnathopod, R.S.; palm and claw enlarged, showing the truncate spine peculiar to the adult male, in mid-margin (<i>t.sp.</i>). The palmar marginal setæ and those of the palmar row are omitted for the sake | |
| | | of clearness. | imes 97 |
| " | 16. | First gnathopod, L.S.; palm enlarged, showing the torsion of the palmar margin (<i>p.m.</i>). Setæ omitted as in Fig. 15. | $\times 97$ |
| ,, | 17. | Second gnathopod, R.S., with gill (g.). | $\times 39$ |
| >> | 18. | Second gnathopod, R.S.; palm and claw enlarged, showing the charac- teristic truncate spine in mid-margin. Setæ omitted as in Fig. 15. | $\times 97$ |
| " | 19. | Second gnathopod, R.S.; under surface of the palm. Setæ omitted as in Fig. 15. | imes 97 |
| " | 20. | Third uropod, L.S., with 1 lateral cluster developed on the terminal joint of the outer ramus | ~ 20 |

PLATE III.

IMMATURE NORMAL FEMALE.

The last moult before eggs were laid.

The specimen figured was from the first generation hatched in the Laboratory. Moult 25 July, 1912; age 36 days; length 6.5 mm.

| rıg. | 21. | 4 joints in the accessory flagella.) | imes 39 |
|------|-----|---|-------------|
| ,, | 22. | First gnathopod, R.S.; the 3 terminal joints. | imes 39 |
| " | 23. | First gnathopod, R.S.; palm and claw enlarged, showing 2 modified serrated setæ in the angle-row, developing into spines. | ×97 |
| ,, | 24. | First gnathopod, R.S.; under surface of the palmar angle. | imes 97 |
| " | 25. | First gnathopod, L.S.; upper surface of the palmar angle, 1 spine of the angle-row well developed, the other imperfectly so. | imes 97 |
| " | 26. | Second gnathopod, R.S., showing the partially developed broodplate and gill. | $\times 39$ |

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 $\times 39$

 $\times 39$

 $\times 39$

E. W. SEXTON AND J. S. HUXLEY.

| Fig. | 27. | Second gnathopod, R.S.; palm and claw enlarged, showing 3 of the sensory serrated setæ in the angle-row. The left gnathopod has | |
|------|-----|--|-------------|
| | | I seta less in the palmar row (the small one, crossing the others). | imes 97 |
| | 28. | Second gnathopod, R.S.; under surface of the palmar angle. | $\times 97$ |
| ,, | 29. | First broodplate, L.S., showing difference from the one on the right side | |
| | | | $\times 39$ |
| ,, | 30. | First peracopod, R.S., with broodplate and gill. | $\times 39$ |
| ,, | 31. | Second broodplate, L.S. | $\times 39$ |
| ,, | 32. | Third broodplate, R.S.; under surface. | imes 39 |
| ,, | 33. | Fourth broodplate; R.S., showing the aperture of the oviduct (ap.) under | |
| | | | $\times 39$ |
| ,, | 34. | Third uropod, R.S. | imes 39 |
| ,, | 35. | Third uropod, L.S. | imes 39 |

PLATE IV.

MATURE NORMAL FEMALE.

The first moult after sexual maturity.

The specimen figured is the same female as in Plate III, after the first brood of eggs was hatched; moult 7 August, 1912; age 49 days; length 7.5 mm.

| Fig. | 36. | joints in the accessory flagella.) | $\times 39$ |
|------|-----|--|-------------|
| ,, | 37. | First gnathopod, R.S.; the 3 terminal joints. | $\times 39$ |
| " | 38. | First gnathopod, R.S.; palm and claw enlarged, showing 1 spine of the angle-row well developed (small palmar marginal set& omitted). In the left gnathopod both spines are well developed. | imes 97 |
| " | 39. | First gnathopod, R.S.; under surface of the palm, showing the usual pair of spines, only one of which is fully developed. On the left gnathopod, both spines are well developed. | imes 97 |
| " | 40. | Second gnathopod, R.S., broken at the fourth joint in moulting ; showing the first broodplate. Left gnathopod exactly the same. | imes 39 |
| " | 41. | sensory serrated setæ in the angle-row. The left gnathopod has one seta less in the palmar row (the small one crossing the others). | × 07 |
| | | Small palmar marginal setæ omitted. | ×97 |
| ,, | 42. | Second gnathopod, R.S.; under surface of the palm. | $\times 97$ |
| " | 43. | First peracopod, R.S.; under surface, showing broodplate. The brood- plate on the left side has 21 fringing hairs. | imes 39 |
| " | 44. | Second peraeopod, R.S.; under surface, showing portion of sideplate, joint 2, broodplate, and gill, for comparison of the relative propor- tions. Left peraeopod has 2 notches in the sideplate posterior margin | |
| | | and 13 hairs on the broodplate. | imes 39 |
| ,, | 45. | Fourth broodplate, L.S., showing the aperture of the oviduct (ap.). | imes 39 |
| ,, | 46. | Third uropod, R.S. | imes 39 |
| ." | 47. | Third uropod, L.S. PLATE V. | ×39 |
| | | | |

C.N.259.b. INTERSEX. (See p. 521.)

| Fig. 48. | First gnathopod, R.S.; palm and claw enlarged (the palmar marginal | |
|----------|---|-------------|
| | setæ and those of the palmar row are omitted for the sake of clear- | |
| | ness). November 15, 1920. | $\times 97$ |

| Fig. | 49. | First gnathopod, R.S.; under surface of the palmar angle. November 15, 1920. | ×97 |
|------|-----|--|-------------|
| ** | 50. | First gnathopod, R.S.; palm and claw enlarged. Setæ omitted as in Fig. 48. March 3, 1921. | imes 97 |
| " | 51. | First gnathopod, R.S.; under surface of the palmar angle, showing extra spine developed in addition to the usual pair. March 3, 1921. | $\times 97$ |
| ,, | 52. | First gnathopod, R.S.; the 3 terminal joints. March 3, 1921. | $\times 39$ |
| 17 | 53. | Second gnathopod, R.S.; the 3 terminal joints. March 3, 1921. | $\times 39$ |
| ·,, | 54. | Second gnathopod, R.S.; palm and claw enlarged; more male than the left gnathopod. Setæ omitted as in Fig. 48. March 3, 1921. | ×97 |
| " | 55. | Second gnathopod, R.S.; under surface of the palmar angle. March 3, 1921. | imes 97 |
| " | 56. | Second gnathopod, L.S.; upper surface of the palmar angle, no spines developed. March 3, 1921. | ×97 |
| ,, | 57. | Fourth broodplate, L.S.; under surface. November 15, 1920. | $\times 39$ |
| ,, | 58. | First broodplate, R.S.; upper surface. March 3, 1921. | $\times 39$ |
| ,, | 59. | First broodplate, L.S.; upper surface. March 3, 1921. | $\times 39$ |
| | 60. | Second broodplate, L.S.; upper surface. March 3, 1921. | $\times 39$ |
| " | 61. | Third broodplate, R.S.; upper surface; with part of the sideplate of peraeopod 2. March 3, 1921. | $\times 39$ |
| " | 62. | Fourth broodplate, L.S.; under surface, showing the aperture of the oviduct (ap.). March 3, 1921. | $\times 39$ |
| " | 63. | First broodplate, R.S.; upper surface, showing the greater development of the fringing hairs than in the last moult. March 10, 1921. | imes 39 |
| ,, | 64. | First broodplate, L.S.; under surface. March 10, 1921. | imes 39 |
| ,, | 65. | Second broodplate, L.S.; upper surface. March 10, 1921. | imes 39 |
| ,, | 66. | Third broodplate, R.S.; upper surface. March 10, 1921. | imes 39 |
| ,, | 67. | Fourth broodplate, L.S.; upper surface. March 10, 1921. | imes 39 |
| ,, | 68. | Third uropod, L.S.; moult before eggs were laid. September 21, 1920. | imes 39 |
| | 69 | Third wround L.S last moult large intersey March 2 1021 | V 90 |

PLATE VI.

C.N.229.h. (SUB-GROUP A.)

Showing the development of the intersex from Sub-group A, the "less male" type, to Sub-group B, the "more male" type. Moult of October 26, 1920.

| Fig. | 70. | Second antenna, L.S.; tip of flagellum diseased. | imes 39 |
|------|-----|---|-------------|
| " | 71. | First gnathopod, R.S.; palm and claw enlarged (small palmar-margin setæ omitted, and setæ of the palmar row indicated). | imes 97 |
| " | 72. | First gnathopod, R.S.; under surface of the palmar angle, showing the usual pair of spines, and 1 extra serrated sensory seta developed. | $\times 97$ |
| ,, | 73. | Second gnathopod, L.S.; broken at the fourth joint in moulting, showing broodplate, and gill, slightly crumpled. | imes 39 |
| " | 74. | Second gnathopod, L.S.; palm and claw enlarged, showing 5 of the sensory serrated setæ (characteristic of the normal female) in the | |
| | | angle-row. Setæ omitted as in Fig. 71. | $\times 97$ |
| ,, | 75. | Second gnathopod, L.S.; under surface of the palmar angle. | $\times 97$ |
| • ,, | 76. | Second broodplate, R.S.; upper surface. | $\times 39$ |
| | | | |

| Fig. | 77. | Third broodplate, R.S. ; under surface. | imes 39 |
|------|-----|--|-------------|
| ., | 78. | Fourth broodplate, R.S.; upper surface, showing a few minutely | |
| | | developed fringing hairs. | $\times 39$ |
| ,, | 79. | Fourth broodplate, L.S.; upper surface. | imes 39 |
| ,, | 80. | Third uropod, L.S., showing 1 lateral cluster commencing on the terminal | |
| | | joint, represented by one seta. | imes 39 |

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PLATE VII.

C.N.229h. (SUB-GROUP B.)

Preserved May 14, 1921.

| Fig. | 81. | Second antenna, L.S. | imes 39 |
|------|-----|---|-------------|
| ,, | 82. | First gnathopod, L.S.; the 3 terminal joints. | imes 39 |
| ,, | 83. | First gnathopod, L.S.; palm and claw enlarged (palmar row indicated, small palmar-margin setæ omitted), showing extra spine in angle- row; 2 setæ developed on the claw, the only case in which more than one has been seen. The right gnathopod claw has one only, as is normal. | ×97 |
| " | 84. | First gnathopod, L.S.; under surface of the palmar angle, showing extra spine developed, besides the usual pair. | $\times 97$ |
| " | 85. | First gnathopod, R.S.; under surface of the palmar angle, showing a slender seta developed, besides the usual pair of spines. | $\times 97$ |
| " | 86. | Second gnathopod, L.S., showing broodplate. The right gnathopod is exactly similar. | ×39 |
| " | 87. | Second gnathopod, L.S.; palm and claw enlarged, showing the develop- ment of sensory spines in the angle-row in addition to the sensory serrated setæ. Sctæ omitted as in Fig. 83. | $\times 97$ |
| " | 88. | Second gnathopod, R.S.; upper surface of the palmar angle, showing greater "male" development of the angle-row than in the left gnathopod. | $\times 97$ |
| " | 89. | Second gnathopod, R.S.; under surface of the palmar angle, with the usual pair of spines. | $\times 97$ |
| ,, | 90. | First peraeopod, R.S.; the 4 terminal joints. | $\times 39$ |
| ,, | 91. | Second broodplate, R.S.; upper surface. | $\times 39$ |
| " | 92. | Second peraeopod, R.S., with third broodplate and portion of sideplate (s.). (The left peraeopod 2, sideplate and broodplate exactly similar.) | $\times 39$ |
| " | 93. | Fourth broodplate, L.S.; upper surface, showing the few partially developed hairs. | × 39 |
| ,, | 94. | Third uropod, L.S.; 2 lateral clusters present. | imes 39 |

PLATE VIII.

INTERSEXES.

| Fig. | 95. | Spec. 3. C.N.293a2. Second gnathopod, L.S.; palmar angle, | |
|------|-----|---|-------------|
| | | showing one sensory seta inset apart from the angle-row. | imes 97 |
| ,, | 96. | Spec. 9. C.N.265b. Fourth broodplate, R.S.; under surface. | imes 39 |
| - 7, | 97. | " " Fourth broodplate, L.S.; under surface. | imes 39 |
| " | 98. | Spec. 12. C.N.289a. Second gnathopod, L.S., showing extra spine developed below the angle-row, the only in- stance of this. | $\times 97$ |

| Fig | . 99. | Spec. | 15. | C.N.284a. | First gnathopod, L.S.; under surface of palm Palmar-marginal setæ omitted. | ×97 |
|-----|-------|-------|-----|-----------|---|-------------|
| ,, | 100. | | " | " | Second gnathopod, R.S., showing claw impinging against the under surface of the palm (cf. Fig. 112, the only other instance of this). Palmar margin a little bent. Setæ omitted as in Fig. 99. | $\times 97$ |
| 3: | 101. | | " | " | Third uropod, R.S., showing its great development, and the 4 lateral clusters on the terminal joint of the outer ramus. In two of these clusters a plumose hair is present, the only instance of this. Plumose hairs are never seen on the terminal joint in normal animals. | × 39 |
| " | 102. | Spec. | 16. | C.N.183m. | Second antenna, R.S., showing the curved hairs (as in the immature male). | × 39 |
| ,, | 103. | | " | " | First gnathopod, R.S.; palm and claw enlarged, showing sensory spine inset in mid-margin. | ×97 |
| " | 104. | | " | " | First gnathopod, R.S.; under surface of the palmar angle, showing the 2 extra spines. | $\times 97$ |
| " | 105. | | " | " | First gnathopod, L.S.; under surface of the palmar angle, showing the 1 extra spine. | $\times 97$ |
| " | 106. | | " | ;; | Second gnathopod, R.S.; palm and claw enlarged, showing sensory spine inset in mid-margin. | $\times 97$ |
| " | 107. | | " | " | Second gnathopod, R.S.; under surface of the palmar angle. | imes 97 |
| " | 108. | | " | " | Second gnathopod, L.S.; upper surface of the palmar angle. | $\times 97$ |
| ,, | 109. | | ,, | ,, | Fourth broodplate, R.S.; under surface. | $\times 39$ |
| | 110. | | | ., | Fourth broodplate, L.S.; under surface. | $\times 39$ |
| " | 111. | Spec. | 30. | C.N.285a. | Second gnathopod, L.S.; under surface of the palm with 2 extra spines developed. | $\times 97$ |
| 33 | 112 | Spec. | 31. | C.N.218b. | Second gnathopod, R.S.; palm, showing claw im- pinging against the under surface (cf. Fig. 100). (The hand has been flattened a little, under a cover-glass. In life the whole palm was bent of an angle to the next of the head.) | $\times 97$ |
| " | 113. | | " | " | at an angle to the rest of the hand.) Second gnathopod, L.S.; under surface; position | |
| | | | | | of the claw normal. | $\times 97$ |

PLATE IX.

TMETONYX SIMILIS (G. O. SARS).

| Fig. | 114. | First antenna, R.S.; under surface; normal ovigerous female. | $\times 42$ |
|------|------|--|-------------|
| ,, | 115. | Second antenna, R.S.; under surface; normal ovigerous female. | imes 42 |
| " | 116. | First peraeopod, R.S.; under surface, showing broodplate and gill; normal ovigerous female. | $\times 42$ |
| :, | 117. | First antenna, R.S.; under surface; ovigerous intersex. | imes 42 |
| ,, | 118. | Second antenna, R.S.; under surface; ovigerous intersex. | imes 42 |
| :, | 119. | One of the calceoli enlarged. | imes 265 |
| " | 120. | First peraeopod, R.S.; under surface, showing broodplate and gill; | |
| | | ovigerous intersex. | $\times 42$ |







PLATE II.

PLATE III.



Journ. Mar. Biol. Assoc. XII.-3.

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Note on the Occurrence of Arthopyrenia foveolata at Plymouth.

By

Lily Batten, M.Sc., Ph.D.

WHEN shore-collecting for marine algae at Plymouth in early April, an organism which has now been identified as a calcareous lichen was brought to my notice by Dr. Orton. It occurred in large patches on the rocks both above and below high-water mark in the neighbourhood of the Marine Biological Station, and was also very frequent on the limpets and barnacles in the vicinity. When examined with a lens, the thallus of the lichen was observed to be thickly dotted either with perithecia or with well-marked pits which had apparently been previously occupied with fruits. The lichen was found to be identical with the species collected in Robin Hood Bay, Yorkshire, by E. M. Holmes, in 1901, and described by A. Lorrain Smith as Arthopyrenia foveolata.* Arthopyrenia differs from Verrucaria in the fact that the associated alga is Trentepohlia, and the above species is easily distinguished by the pits which occur on the thallus.

The same species has been recorded by M. C. Knowles † ‡ from various places round the coast of Ireland, including the western shore of Blacksod Bay. It occurred on limestone rocks at about high neap-tide level, and also on live and dead barnacles where it was almost always associated with colonies of *Rivularia atra*. At Plymouth, the frequent occurrence of the lichen on limpet shells is a conspicuous feature in the distribution.

Arthopyrenia is a genus of the Pyrenulaceae, in which the algal cells are a species of Trentepohlia. It has therefore yellowish filamentous gonidia. A. foveolata is distinguished from the closely allied A. litoralis by the fact that the perithecia are foveolate, i.e. almost completely immersed and leaving small pits in the sub-stratum. The perithecia are minute black bodies with the perithecial wall sub-entire, black above, brown below. Paraphyses are very scanty or wanting and not mucilaginous. The asci are cylindrical, clavate, 0.070-80 mm. long, 0.017 mm. thick, and contain 8 spores. Spores uni-septate, colourless, oblong-ovate, thinner at the end, 0.015-18 mm. long, 0.006-7 mm. thick.

Spermogones small, globose or ovid with simple sterigmata and rodlike spermatia.

I should like to express my thanks to Miss Lorrain Smith for her help in identifying the species and in locating references.

- * A. L. Smith, "British Lichens," Part II, p. 325. London, 1911
 † "Fisheries, Ireland, Sci. Invest., 1914," III (1915), p. 26.
 ‡ Knowles, "Notes on West Galway Lichens," Irish Naturalist, XXI, 1912, p. 31.

Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Gonospora minchinii, n.sp., a Gregarine inhabiting the egg of Arenicola. By Edwin S. Goodrich, F.R.S., and H. L. M. Pixell Goodrich, D.Sc.

Quart. Journ. Micr. Sci., Vol. 65, Part 1, New Series, 1920.

THE new species of gregarine to which we have given the name Gonospora minchinii, occurs in the coelomic fluid of the female Arenicola ecaudata. The adult trophozoite is pear-shaped, and the ripe spore has a thin cyst without distinct funnel. The young trophozoite lives in the egg floating in the coelomic fluid of the Arenicola, where it grows at the expense of the food-material stored in the ovum. To reach the ovum it pierces the vitelline membrane and perivitelline layer. The growing trophozoite occupies a deep depression it causes in the egg, to which it adheres by its epimerite. The margin of this depression becomes drawn out into delicate protoplasmic processes. The cytoplasm and nucleus of the hostcell, and also the development of the perivitelline layer, are affected by the presence of the parasite. When full-grown the trophozoite escapes from the egg by a hole pierced in its envelopes, and leucocytes then enter the space so left to complete the destruction of the ovum.

E. S. G. AND H. L. M. P. G.

The Pseudopodia of the Leucocytes of Invertebrates. By Edwin S Goodrich, F.R.S.

Quart. Journ. Micr. Sci., Vol. 64, Part 1, New Series, 1919.

The leucocytes of the blood or coelomic fluid of the invertebrate Coelomata are provided with more or less extensive membranous processes of cytoplasm. The freely projecting pseudopodia usually described are either figured from optical sections of the folded membranes or from cells which have produced them under abnormal conditions. These fine pseudopodia may be present on cells in fluid withdrawn from the body and which has been allowed to stand, and are probably derived from pre-existing membranes. The delicate motile membranous folds are usually expanded in the normal fluids of the living animal. E. S. G.

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ABSTRACTS OF MEMOIRS.

The effects of Ions upon Ciliary Movement. By J. Gray.

Quart. Journ. Micr. Sci., 64, 1920.

- 1. With the exception of the wave action of the lateral cilia, isolated fragments of the gills of *Mytilus* continue to function normally in sea-water for many days.
- 2. Ciliary activity is dependent upon a certain minimal concentration of hydroxyl ions.
- 3. Stoppage of the cilia by acid is reversible by the addition of alkali.
- 4. If the hydroxyl ion concentration of the medium is above PH 9.0 the ciliated epithelium rapidly breaks up into its constituent cells, but ciliary movement does not stop either in the isolated cells or in those which remain in situ.
- 5. Little evidence was obtained of qualitative effects of the metallic ions in sea-water. Attention is drawn to the necessity of controlling the hydrogen ion concentration in all solutions used in the investigation of antagonistic ion action.

J. G.

The Relation of Spermatozoa to certain Electrolytes. II. By J. Gray.

Proc. Roy. Soc., 91B, 1920.

A suspension of the spermatozoa of *Echinus miliaris* in sea-water behaves towards trivalent positive ions in exactly the same way as a suspension of negatively charged particles of such colloids as albumen or globulin. It is only in solutions capable of maintaining a negative charge on such particles that movement of spermatozoa can take place. In the presence of acid spermatozoa behave as though they were positively charged particles.

J. G.

The Fragrance of Calcinean Sponges and Spermatozoa of Guancha and Sycon. By G. P. Bidder, Sc.D.

Journ. Linn. Soc., 34, 1920.

The scent from Clathrinidæ is very noticeably stronger and more pleasant than from Calcaronea. It is probably due to the porocytes' granules, which give to the Calcinea their characteristic colours; the author suggests that the scent may indicate a chemiotaxic function of the granules, attracting spermatozoa to the pores.

In *Guancha coriacea* a cloud of Minchin's "minute wandering cells" were observed to break out from the sponge wall. It is suggested that these were spermatozoa. The spermatozoa of *Sycon raphanus* is a "dolly-cell," with an external button-nucleus, and fertilises the ovum directly under the wall of the cloaca.

G. P. B.

ABSTRACTS OF MEMOIRS.

Syncrypta Spongiarum, nova. By G. P. Bidder, Sc.D.

Journ. Linn. Soc., 34, 1920.

The name is given to an organism described by the author in 1895 as an alga found in the flagellate chambers of *Grantia compressa* at Plymouth; described by Dendy in 1914 as sperm-morulæ of the sponge. It is suggested that this is a dangerous parasite to sponges, and that while *Grantia compressa* overcomes it by phagocytosis, its victorious entry into other sponges has resulted in red, yellow, and brown cells observed in the merogleæ by Urban, Dendy, Schulze, and Poléjaeff. Poléjaeff described its spheres as sperm-morulæ and enveloping phagocytes as "coveringcells."

G. P. B.

Notes on the Physiology of Sponges. By G. P. Bidder, Sc.D.

Journ. Linn. Soc., 34, 1920.

- A. The "minute wandering cells" of Minchin are named "Cercids."
- B. Cessation of the current in sponges can be caused by the clogging of afferent canals with the particles suspended in turbid water.
- C. The author has been unable to obtain evidence of the deposit of indigo carmine in the ectocytal or porocytal granules of Calcaronea; it seems possible that in this, as in odour, the Calcaronean granules differ from those of Clathrinidæ.
- D. The fæces of the collar-cells of G. compressa are further described; Dendy's explanation of them as clusters of spermatozoan-heads is refuted, and it is pointed out that Poléjaeff's spermatozoan-heads were also probably cellular fæces.
- E. It is suggested that intracellular pores in sponges may have originated through the passing on of an ingested spermatozoan to the subjacent ovum.
- F. A living ovum, which had fed on a green alga, was observed in the cavity of the flagellate chamber of *Grantia compressa*.
- G. The ingestion by the collar-cell of a large body such as Syncrypta causes the nucleus to move temporarily from its apical position.

G. P. B.

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Spontaneous Fission in Hydroids. By P. L. Kramp.

Videnskabelige Meddelelser fra Dansk naturhistorisk Forening, Bd. 67, Copenhagen, 1916.

Spontaneous fission in hydroids was first observed by G. J. ALLMAN (Quart. Journ. Microsc. Sci. N.S. Vol. XI, 1871, p. 18) in an unknown species of Laomedea ("Schizocladium ramosum" Allman). The phenomenon has been more thoroughly studied by BILLARD (Annales des Sciences naturelles. Zool. Sér. 8. Tome XX. Paris, 1904), who found it in 6 species of thecaphore hydroids. The present writer has observed spontaneous fission on two occasions. During my stay at the Plymouth Laboratory in May and June, 1914, I had placed some fertile colonies of Laomedea longissima in a bell jar provided with a plunger. A few days later I observed a large number of small polyps on the plunger-plate and on the sides of the jar. I preserved some specimens and brought them back to Denmark. In May, 1915, I collected some colonies of Laomedea geniculata in the harbour of Frederikshavn on the east coast of Jutland. In some sterile colonies I found a large number of frustules in various stages of development. I then undertook an examination of the whole subject. The two species behave very much alike, only the frustules are much larger in L. geniculata than in L. longissima. A bud formed in the usual way at the base of a hydranth, grows out like a thread, covered with a perisarc ; the coenosarc becomes thinner in its middle part, withdrawing itself from the perisarc : at last the coenosarc is cut in two, leaving an isolated, sausage-shaped mass in the distal end of the perisarc tube. By the power of the movements of the water the thin chitinous tube is broken beneath the frustule, which swarms out into the surrounding water, still covered with a layer of perisarc. The frustule sticks to any solid object and creeps forwards over the support, secreting new chitin and leaving behind itself a delicate, empty tube, open behind. During a short resting period a transverse chitinous wall is formed, separating a closed chamber, containing the coenosarc, from the empty tube. From this primary stolon a small hydranth is developed, from which other hydranths are budded later on. BILLARD considers spontaneous fission to be the result of strong movements of the water. In quiet water frustules are, however, likewise developed, though not liberated, because the chitinous tube is not broken. I am more inclined to think that the phenomenon is due to starvation. In any case, the ability of reproduction by spontaneous fission is a factor of importance to the species in which it occurs, as under unfavourable conditions (lack of food ?) they are able to develop, within a short space of time, a considerable number of frustules which may be carried away to more favourable localities. Thus the phenomenon is an interesting example of adjustment in nature. P. L. K.

NEW SERIES.-VOL. XII. NO. 3. SEPTEMBER, 1921.

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Marine Biological Association of the United Kingdom.

Report of the Council, 1920.

The Council and Officers.

Four quarterly meetings of the Council and one special meeting were held during the year, at which the average attendance was fourteen. A committee of six members of the Council visited and inspected the Plymouth Laboratory. The thanks of the Association are due to the Council of the Royal Society, in whose rooms the meetings have been held.

The Council has to record with regret the death of Mr. T. T. Greg, one of the representative Governors appointed by the Worshipful Company of Fishmongers, who took a great interest in the work of the Plymouth Laboratory.

Grant from the Development Fund.

In 1919 the Development Commissioners appointed a special Committee on Fishery Research to advise them as to grants to be made from the Development Fund. Evidence was given on behalf of the Marine Biological Association before this committee, and proposals for the development of the work of the Plymouth Laboratory were laid before it. After discussion of the proposals with the committee, a formal application was made by the Association to H.M. Treasury for grants sufficient to carry them into effect. The committee recommended that these grants should be made, and with certain modifications the Development Commissioners adopted the recommendations of their committee, which, with these modifications, were sanctioned by the Treasury.

The scheme adopted includes the provision of more adequate salaries for the present scientific staff of the Laboratory, a sufficient sum for the upkeep of the Laboratory to meet increased prices, additional money to enable the Association to run a steam-drifter all the year round in place of the present steamer *Oithona* which has been used in the summer months only, and the necessary funds to establish and maintain a new Department of General Physiology, with an adequate scientific staff. It is recommended that annual grants for the above purposes amounting to £11,000 a year be provided for a period of five years. In addition to this annual grant a capital sum of at least

REPORT OF THE COUNCIL.

£16,000 will be required for the purchase of a steam-drifter and for the erection of new buildings to allow provision to be made for increased laboratory accommodation. Following their usual policy as regards capital expenditure, the Development Commissioners are prepared to recommend a grant on a pound for pound basis equivalent to the amount which the Association can raise by voluntary contributions. The Council has therefore issued an appeal for subscriptions for the steamer and the new buildings, and has received up to 31st December, including the amounts subscribed in 1919 for the Electrical Installation Fund, a total of £3670. To this will be added the amount which may be realised by the sale of the *Oithona*, estimated at £1000. From £3000 to £4000 therefore remains to be found before the full scheme can be carried out.

The Plymouth Laboratory.

The portion of the new building referred to in the Report of the Council for last year has been erected. This has provided two good workrooms, accommodation for the museum collection of type specimens, a new dark-room for photography, a storeroom for glass and apparatus, and new lavatories. This will allow of the whole top floor of the west wing of the main building being used for a much needed extension of the Library.

The engines and machinery have been maintained in good working order, and the efficiency of the ejector, used for pumping water from the sea, has been greatly increased by the provision of a new aircompressor, which is worked by the small gas engine.

The demand for specimens for teaching purposes and for museums has continued to expand, the gross receipts for the year being £928. Large numbers of drift-bottles, for the purpose of determining the surface and bottom currents in the North Sea, have been made at the Laboratory for the Ministry of Agriculture and Fisheries, and several expeditions have been provided with dredges, trawls and other collecting apparatus required for oceanographical work.

The Boats.

The steamer *Oithona* was used during July, August and September, but owing to the high cost of coal and wages it was not possible to keep her in commission for a longer period. The vessel is now being offered for sale, with a view to her being replaced by an Admiralty steam-drifter.

The sailing boat *Anton Dohrn* has been used for general collecting work throughout the year and is still in good condition.

REPORT OF THE COUNCIL.

hydrographical conditions. The most abundant post-larval fishes during the period of the investigation this year were the wrasses, which show for four species a good series of development stages, which were far from being well known. The appearance of two larval Anglers (*Lophius piscatorius*) is interesting. This species is probably an Atlantic spawner, and the drifting of the fry may be correlated with the influx of Atlantic water. The few records of pelagic Anglers in Plymouth waters show periodic occurrences, which so far are triennial. No early young mackerel were secured, though many Caranx.

The Trawling Grounds were again examined with the Otter Trawl for further data to compare the present conditions with those which existed before the war. Investigation shows that the area has been subjected to unusual upheavals, which have made the story rather difficult to interpret. There are, however, many interesting biological facts.

An Otter Trawl of cotton with $\frac{1}{2}$ -inch mesh proved very successful in capturing small fishes, and a large collection has been made which will be useful for determinations of age and rate of growth. A fine meshed seine was also worked from the shore in the bays and rivers, the most interesting captures being sardines, 2 inches to 4 inches in length, thus proving that the young of the pilchard is also estuarine in its distribution. One haul of this net in the Lynher River (Oct. 4th, 1920) yielded 30,000 fish, of which about 90 per cent were sardines from 40 to 70 mm. ($1\frac{1}{2}$ to $2\frac{3}{4}$ inches) in length. The tinned sardine of commerce ranges from 5 to 7 inches in length, so that the young fish recorded above are well on the way towards a useful size. It remains, however, to follow up the migration of these young sardines and to find out their relative abundance, as only with a steady supply of fish could a sardine fishery be exploited on our coast.

Mr. Clark is also continuing a systematic study of the skates and rays, for which a good deal of material has been collected. The young of *Raia clavata* and *Raia nævus* have been hatched out in the Aquarium. For *R. clavata* the period of incubation, after deposition of the eggs which were secured from the adult, was 177 days, from June to November.

Mr. Clark has also nearly completed a study of the young stages of the different species of gurnards, and a list of the rarer fishes captured in the neighbourhood of Plymouth, with biological notes, is being prepared.

Dr. Lebour has been working chiefly on the larval and young stages of Clupeoids, a paper distinguishing the young of the herring,

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Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association :---

- ALLEN, E. J., and SEXTON, E. W. Eye-Colour in Gammarus. Journ. of Genetics, Vol. IX, 1920, pp. 347-366.
- BIDDER, G. P., The Fragrance of Calcinean Sponges and the Spermatozoa of GUANCHA CORIACEA and SYCON RAPHANUS. Journ. Linn. Soc. Vol. XXXIV, 1920, pp. 299-304.
- BIDDER, G. P., Syncrypta spongiarum, nova. Journ. Linn. Soc., Vol. XXXIV, 1920, pp. 305-313.
- BIDDER, G. P., Notes on the Physiology of Sponges. Journ. Linn. Soc., Vol. XXXIV, 1920, pp. 315-326.
- FORD, E. The Economic Value of the Dogfish. Fish Trades Gazette, Mar. 20, 1920.
- GRAY, J. The Relation of Spermatozoa to Certain Electrolytes, II. Proc. Roy. Soc., B. Vol. XCI, 1920, pp. 147-157.
- GRAY, J. The Effect of Ions upon Ciliary Movement. Quart. Journ. Micr. Sci., Vol. LXIV, 1920, pp. 345-371.
- NELSON, E. W. Appendix to "On the Occurrence of Diatoms on the Skin of Whales," by A. G. Bennett. Proc. Roy. Soc., B. Vol. XCI, 1920, pp. 354-357.
- ORTON, J. H., Mode of Feeding and Sex-Phenomena in the Pea-Crab (PINNO-THERES PISUM). "NATURE," Dec. 23, 1920, p. 533.

The Library.

The thanks of the Association are again due to numerous Government Departments, Universities, and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library. Thanks are due also to those authors who have sent reprints of their papers to the Library.

Donations and Receipts.

The receipts for the year include a grant from H.M. Treasury of $\pounds 1000$, a grant from the Development Fund, through the Ministry of Agriculture and Fisheries, of $\pounds 2000$, one from the Fishmongers' Company, $\pounds 600$, and one from the Royal Society, $\pounds 60$. In addition to these grants there have been received Special Donations to the Steamer, Building and Electrical Funds ($\pounds 2348$), Annual Subscriptions ($\pounds 132$), Composition Fees ($\pounds 15$ 15s.), Rent of Tables in the Laboratory, including $\pounds 25$ from the University of London and $\pounds 20$ from the Trustees of the Ray Lankester Fund ($\pounds 118$), Sale of Specimens ($\pounds 928$), and Admission to Tank Room ($\pounds 243$).

List of Annual Subscriptions e. E. S. Por . Man J. W. J. Manhle,

Paid during the Year 1920.

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the Year ending 31st December, 1920.

FUND.

| | | | | | 0 | | |
|----|---|-------|----|-----|--------|----|----|
| By | Salaries and Wages- | £ | s. | d. | £ | 8. | d. |
| | Director | 500 | 0 | 0 | | | |
| | Naturalists | 1,136 | 13 | 7 | | | |
| | Assistant Naturalists | 437 | 13 | 10 | | | |
| | Salaries and Wages | 1,588 | 5 | 10 | 3,662 | 13 | 3 |
| ,, | Travelling Expenses | | | | 66 | 16 | 8 |
| ,, | Library | 85 | 12 | 8 | | | |
| | Less Sales | 0 | 7 | 6 | 85 | 5 | 2 |
| ,, | Journal | 283 | 1 | - 7 | | | |
| | Less Sales | 17 | 9 | 7 | 265 | 12 | 0 |
| | Buildings and Public Tank Room- | | | | | | |
| | Gas, Water, and Coal | 278 | 19 | 9 | | | |
| | Stocking Tanks and Feeding | 19 | 18 | 2 | | | |
| | Maintenance and Renewals | 388 | 11 | 11 | | | |
| | Rent, Rates, Taxes, and Insurance | 121 | 15 | 6 | | | |
| | | 809 | 6 | 4 | | | |
| | Less Admission to Tank Room | 243 | 6 | 1 | 566 | 0 | 3 |
| ,, | Laboratory, Boats, and Sundry Expenses- | | | | | | |
| | Glass, Apparatus, and Chemicals | 1,168 | 17 | 8 | | | |
| | Purchase of Specimens | 72 | 7 | 6 | | | |
| | Maintenance and Renewal of Boats, Nets, etc | 914 | 0 | 11 | | | |
| | Coal and Water for Steamer | 126 | 9 | 2 | | | |
| | Boat Hire and Collecting Expenses | 30 | 3 | 6 | | | |
| | Stationery, Office Expenses, Carriage, Printing, etc. | 290 | 19 | 5 | 2,602 | 18 | 2 |
| ,, | Balance : | | | | | | |
| | Cash at Bankers | 502 | 12 | 1 | | | |
| | Cash in hand | 75 | 5 | 11 | 577 | 18 | 0 |
| | | | | | £7,827 | 3 | 6 |
| | | | | | | | - |

AND BUILDING FUND.

| | | | | and the second se | | And in case of the local division of the loc | |
|---------------------------------|-----|---|---|---|----|--|--|
| | | | | £3,220 | 4 | 0 | |
| On Current Account | 50 | 0 | 0 | 676 | 6 | 0 | |
| On Deposit at Bank | 626 | 6 | 0 | | | | |
| ,, Balance : | | | | | | | |
| By Expenditure on Building, etc | | | | 2,543 | 18 | 0 | |
| | | | | A | 0. | | |

| Examined and foun | d correct, |
|-------------------|-------------------|
| (Signed) | N. E. WATERHOUSE. |
| | W. T. CALMAN. |
| | W. T. BRAND. |
| | J. O. BORLEY. |

Cr.

3 Frederick's Place, Old Jewry, London, E.C. 2 25th January, 1921.

OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

The late Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the late Duke of ARGYLL, the late Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr. CARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY, the late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000. Since that time investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the seawater circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the hire and maintenance of fishing-boats, and the salary of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council, by an Honorary Secretary and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances. The reader is referred to page 4 of the Cover for information as to membership of the Association.

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NOTICE.

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this Journal excepting when those statements are contained in an official report of the Council.

TERMS OF MEMBERSHIP.

| | | | | | £ | 5. | a. | |
|----------------|--|----------|-------|-----|-----|----|----|--|
| Annual Members | | . per | annu | ım | 1 | 1 | 0 | |
| Life Members | | Composit | ion F | Tee | 15 | 15 | 0 | |
| Founders | | | | | 100 | 0 | 0 | |
| Governors | | | | | 500 | 0 | 0 | |

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, &c.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Plymouth.