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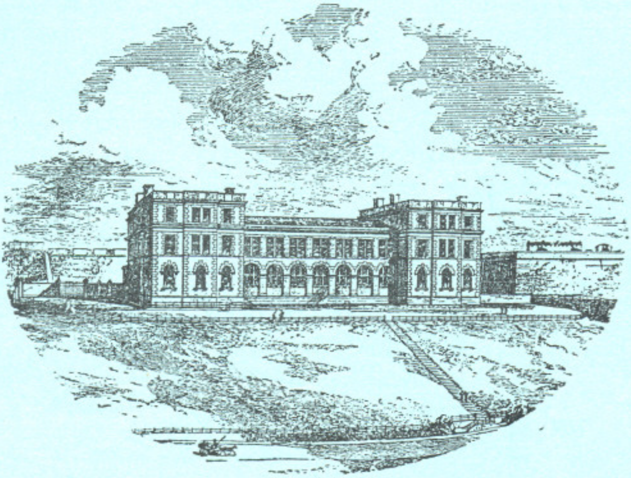
# Journal

OF THE

# MARINE BIOLOGICAL ASSOCIATION

OF

# THE UNITED KINGDOM.



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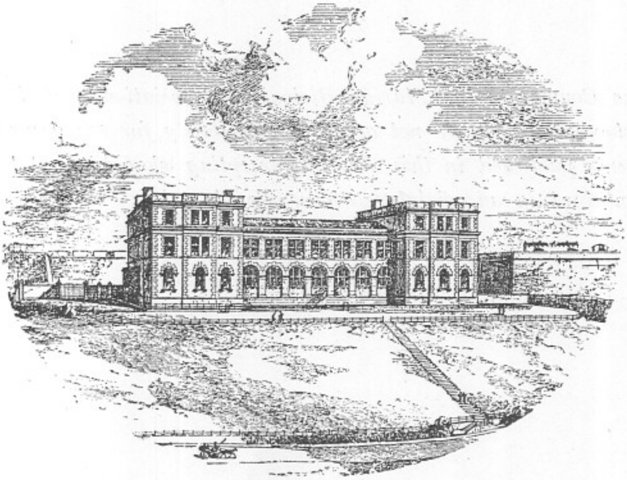

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PLYMOUTH:
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# The British Edwardsidae.

By
**Oskar Carlgren**
*Professor, Zoological Institute, University, Lund, Sweden,*
and
**T. A. Stephenson, D.Sc.,**
*Senior Assistant, Zoology Department, University College, London.*

With 18 Figures in the Text.

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## PART 1.

By
T. A. STEPHENSON.

### 1. INTRODUCTION.

THE genus *Edwardsia* is one known to most zoologists as an example of a primitive eight-rayed Zoantharian from which (or from a form resembling which) the higher forms are derived. It is only comparatively recently, however, that our knowledge of Edwardsias has become at all extensive, and even now it is incomplete; but it is desirable to produce a revision of the British forms since no adequate account of these exists.

In some of the textbooks best known in this country (Lankester's *Treatise*, Sedgwick, Parker and Haswell) Edwardsia is quoted as a form with eight mesenteries only, and the impression produced thereby has been perpetuated, although it has long been known that Edwardsia has more mesenteries than eight, and although this fact is recorded in the *Cambridge Natural History* and by Delage and Hérouard. There is, in fact, no Actinian which in its adult condition possesses eight and only eight of these organs, the simplest forms possessing at least six pairs of mesenteries, eight only of which are perfect. If an example of an anemone of simple structure be required, this may be found in Gonactinia, which represents the nearest approach to the probable primitive condition which is now extant. Edwardsia is in many ways an advanced and specialised form, and its limited number of mesenteries is on the whole more likely to be a reduction or an arrest of development than anything else, connected with its vermiform shape.

Gonactinia has eight perfect mesenteries and eight imperfect, four of the latter pairing with four of the former to make up the typical six-rayed Actinian condition. It has a very generalised structure, the ectoderm being as little differentiated in the different parts of the body as can be the case in an anemone; it retains the ectodermal muscle-sheet and nerve-net on the column and in the throat. The musculature is weak and generalised, and even on the mesenteries is very little concentrated. There is no sphincter, and the tentacles are non-retractile. The aboral end is little specialised. The filaments are simple and not trifid in their upper parts. The animal reproduces habitually by a kind of strobilisation, and it is the only known anemone, so far as I am aware, in which a tentacle alone is able to regenerate the whole of the rest of the organism.*

In Edwardsia, by contrast, though the mesenteries may be as few as in Gonactinia, they are strongly specialised for rapid retraction, having very highly differentiated muscles. The ectoderm is by no means generalised, but is differentiated into regions even on the body (where it has lost its ectodermal muscle-sheet), on part of which it is often invaginated into the mesoglœa as a series of deep pits with narrow mouths, the pits containing large nematocysts and acting as stinging batteries. The filaments are trifid in their upper parts, as in the majority of forms.

Even Gonactinia is possibly considerably removed from the primitive ancestral condition and may itself be a retrograde form; but it offers at least a better picture of the probable early condition than does Edwardsia.

The Edwardsids have had a varied career in the classifications; the most recent view regarding them as a distinct group being that expressed

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* This may not apply to the European form; it was worked out on a Japanese *Gonactinia* (see Okada, 1926, p. 482), which has autotomous tentacles. This form may be a *Boloceroides*, but even so is a species with many primitive characteristics.

by Bourne in 1916, when he held that they should form a group apart from the Dodecactiniaria (Actiniaria+Madreporaria) in general, of equal rank with the latter and with the Zoanthinaria (Epizoanthus, etc.). This view was based mainly upon the mode of development of the micromesenteries and tentacles, as deduced from the comparative study of a series of different species. In my 1921 paper on classification I accepted this view (having studied the Edwardsias personally hardly at all), but since that time I have made a fairly detailed study of some of them, and I now agree with the view expressed by Carlgren (1921, pp. 25–6) that they are simply a family of ordinary Actiniaria with few mesenteries.

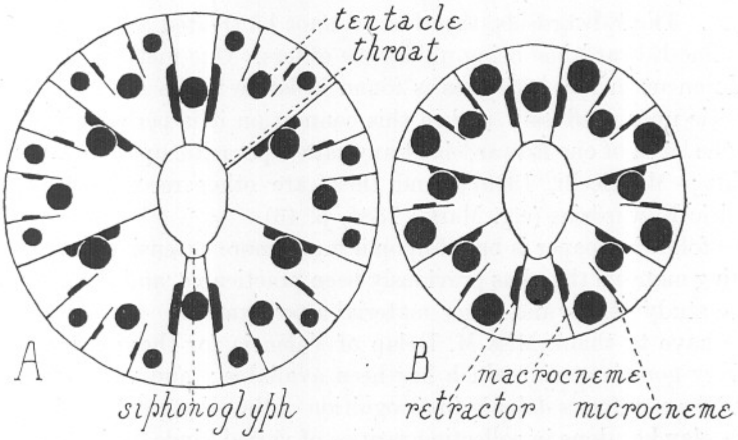

FIG. 1.—Diagrams to illustrate the arrangement of tentacles and mesenteries in *Milne-Edwardsia carnea* and *M. loveni* (A), and in *Edwardsia callimorpha* (B). The relative lengths of the tentacles are indicated by differences of size in the black spots representing them. In *M. carnea* and *M. loveni* there may be more than the 24 tentacles shown. The microcnemes have in reality no retractors, the oblong marks being inserted to show the way in which they pair.

The *actual* succession of tentacles and mesenteries within a single Edwardsian species has never been worked out, the notes given later on in this paper being the nearest approach to it.

The notes mentioned would appear to show at least that in *E. callimorpha* the three tentacles in the dorsolateral macrocœl do not in reality arise in the order supposed by Bourne (his *E. beautempsii* being equivalent to *E. callimorpha* from this point of view), and if this is the case for one form it may well be so for another. Carlgren has shown (and my own study of living material supports him) that in *Milne-Edwardsia carnea* (Fig. 1) the tentacles are arranged according to a plan quite different from that of Edwardsia, and not agreeing with Bourne's interpretation for this species. Carlgren discusses the question in the work referred to (1921, pp. 25–6, etc.), and I need not repeat him here; but I conclude from my work that in the Edwardsids the four microcnemes adjacent on the ventral side to the lateral macrocnemes do in reality correspond to the couples 5 and 6 of the ordinary Actiniaria, that the rest of the microcnemes are to be regarded as genuine pairs and not simply as couples bilateral about the directive axis, and that in whatever way the tentacles appear there is not likely to be a difference marked enough to distinguish the Edwardsias from all other Actinians. There are, in fact, two perfectly distinct plans of tentacle-arrangement among the Edwardsids and at least two also among the Actiniaria; in the latter case it is known that the two different plans are produced by different modes of development, and in the former the same probably holds good although it is not proved. The Edwardsids, therefore, cannot be treated as a single series, the Milne-Edwardsinæ being unlike the others. One method of tentacle-development in the Actiniaria is found in larvæ which are known to be parasitic upon medusæ; and in this connection it is perhaps significant that the larva of one Edwardsia at any rate is parasitic upon a Ctenophore (Bolina; Monticelli, 1899); and there are other records of possibly parasitic Edwardsias (e.g. Mark., 1884, p. 43).

The following paper is based upon a much more extensive examination of living material than has previously been practicable, and upon morphological study of this and other material after fixation.

We have to thank Miss M. Delap of Valencia for the greater part of the very good material which has been available; and we have named one of the new forms *delapiæ* in recognition of the very great service which Miss Delap has done in collecting rarities of varied kinds during a number of years.

## 2. STRUCTURE OF THE FAMILY.

The family Edwardsidæ, part of Gosse's family Ilyanthidæ, was instituted by Andres (1881, p. 333). It contains two sub-families, the Edwardsinæ (Carlgren, 1900, p. 25) and the Milne-Edwardsinæ (Carlgren, 1900, p. 25), which have sometimes been ranked as full families (Carlgren, 1893, pp. 11 and 17).

(1) *Edwardsinæ.* This sub-family contains two genera: *Edwardsia* Quatrefages, and *Isoedwardsia* Carlgren. The latter genus is non-British.

(2) *Milne-Edwardsinæ.* This sub-family also contains two genera: *Milne-Edwardsia* Carlgren and *Paraedwardsia* Carlgren, the latter being non-British.

The details are as follows:—

### Family **EDWARDSIDÆ** Andres, 1881, p. 333, pro parte.

Ilyanthidæ as used by Gosse, 1860, p. 227, pro parte.
Edwardsidæ+Milne-Edwardsidæ of Carlgren, 1893, pp. 11 and 17.
Edwardsinæ+Milne-Edwardsinæ, Carlgren, 1900, p. 25.

Reference should also be made, for a history of the family, to Carlgren, 1892, p. 451, 1893, p. 8, 1900, p. 24, 1921, p. 22; Gosse, 1853, p. 157, 1860, p. 254; Faurot, 1895, p. 43; Bourne, 1916, p. 513; etc.

Athenaria with elongated body, divisible into two, three, or even four regions. Tentacles present. No sphincter or acontia. Mesenteries divided into macrocnemes and microcnemes; of the former there are eight, including two pairs of directives and four lateral mesenteries whose retractors face the ventral directives; of the latter, which are confined to the uppermost part of the body, there are four or more. Filaments trifid, the ciliated tracts sometimes discontinuous.

### Sub-fam. EDWARDSINÆ Carlgren, 1900, p. 25.

Scapus with sunken batteries of nematocysts (nemathybomes) embedded in the mesoglœa. Inner (endocœlic) tentacles shorter than the outer. Nematocysts of upper part of body (scapulus)* small by comparison with those of the nemathybomes.

### Genus **Edwardsia** Quatrefages, 1842, p. 68.

Edwardsiella Andres, 1883, p. 305.
Edwardsioides Danielssen, 1890, p. 100.

Edwardsinæ with the column divisible, at its highest development, into three regions—physa, scapus, and capitulum; the scapus sub-divided into scapus proper and scapulus. Physa without nemathybomes, but often (if not always) pierced by small apertures; scapus extensive, provided with a cuticular sheath and with nemathybomes containing long narrow nematocysts. Uppermost part of column cuticle-free and with small nematocysts not arranged in nemathybomes. Tentacles 12–16 or more. Throat, usually at any rate, with a single weak ventral siphonoglyphe.

The British species of Edwardsia are as follows:—

(1) *E. callimorpha* Gosse, 1853, p. 157.

(2) *E. delapiæ* n.sp.

(3) *E. tecta* Haddon, 1889, p. 329, Pl. 33, Fig. 16, Pl. 36, Figs. 1 and 2. An immature form, possibly the young of *E. delapiæ*.

(4) Apart from the above, three forms have been described, but the data available are insufficient for a determination of their status.
*E. goodsiri* McIntosh, 1866, p. 395.
*E. allmani* McIntosh, 1866, p. 394.
*E. sp.* Haddon, 1886, p. 527.

Foreign species are numerous.

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* For explanation of this term, see p. 19.

### Sub-fam. MILNE-EDWARDSINÆ Carlgren, 1900, p. 25.

Edwardsidæ without nemathybomes. Inner (endocœlic) tentacles longer than outer, usually hexamerously arranged. Nematocysts of upper part of body not markedly different in size from those of scapus.

### Genus **Milne-Edwardsia** Carlgren, 1893, p. 17.

Milne-Edwardsinæ with column divisible into an extensive proximal region with a cuticular sheath, and an upper naked region. A physa is absent in some forms, present in others. Scapus without *Halcampa*-papillæ. Nematocysts of scapus either scattered or arranged in groups; those of upper region (scapulus) occurring mainly on its longitudinal ridges, when such exist. Tentacles 12 or in several cycles. One ventral siphonoglyphe, at any rate usually.

The British species of Milne-Edwardsia are:—

(1) *M. carnea* Gosse, 1856, p. 219, Pl. IX, Figs. 1–4.

(2) *M. dixonii* Carlgren, 1921, p. 59.

There are other foreign species.

## 3. DETAILS OF THE BRITISH SPECIES.

I do not propose to give long descriptions of the species here, as I hope to publish a more detailed account with coloured illustrations, shortly. I therefore give the main points, enough for identification.

### *Edwardsia callimorpha* (Gosse).

(For references, see p. 20.)

This is the commonest British species and is easily recognised. It occurs buried in sand or mud in Zostera beds and similar places. It cannot be called frequent, but is fairly widespread and where it does occur is sometimes common, very probably commoner than we know, being hard to find. The species has been found at Salcombe and other places in the Plymouth area, in the Clyde, Bantry Bay, Valencia (Co. Kerry), Brixham, Channel Islands; it doubtless occurs on the French coast (though in the French records it is confused with other species), and is well known at Naples as *E. claparedii*. There are other records, but those quoted are the most reliable. I have myself seen living specimens from Salcombe, Millport, Naples and Valencia, and from the latter locality many of them. The Plymouth specimens described by Walton and Rees (1913, p. 60) belonged to this species at least in part—i.e. those described as *E. claparedii* are certainly *E. callimorpha*; the one described as *E. timida* being probably the same and certainly not *E. timida*, which is a composite species mainly belonging to Milne-Edwardsia. In the literature in general there is an unfortunate confusion between *Edwardsia callimorpha* and *E. beautempsii;* the two species were considered identical by Andres and Haddon, and others have followed this lead. As a matter of fact, so little is known of *E. beautempsii* that it is impossible to identify anything with it; and now that we know what the constant characters of an *Edwardsia*-species really are, it is evident that *E. callimorpha*, at any rate, is not the same as *E. beautempsii*. To take a single point only, the fact that the tentacles in *E. callimorpha* are transparent, with opaque spots and powderings in cream and maroon (one or the other, usually both), is evidently a stable characteristic of the species; in *E. beautempsii*, as described by Quatrefages, the tentacles were perfectly unmarked except for a spot at the tip, as in *E. delapiæ;* and this is one of the few definite characters of *E. beautempsii* that we have to go upon, Quatrefages' description being very incomplete. Colour alone is no reliable guide for the distinguishing of anemone species; but in a good many cases a pattern, or the structure of a pattern, is fairly trustworthy, at least as much so as most of the characters with which we have to deal in anemones. That these markings on the tentacles (not to mention others on disc and body, and quite apart from structural features) are genuinely characteristic of *E. callimorpha* I feel sure, after examination of some fifty living specimens from various localities.

*Description :—*

Body vermiform in extension. Physa well marked off from scapus, non-retractile, with microscopic adhesive rugæ. Scapus extensive, with a well-marked cuticular investment and with eight single rows of small tubercles running up it longitudinally, midway between the mesenterial insertions; each of these tubercles contains one (rarely two) nemathybome (Fig. 2). The rows usually die out gradually above, and the upper part of the body is free from both these and from cuticle. Tentacles (Fig. 1) sixteen, in two cycles (or 12–15 in young ones). Colours very variable in detail, but general plan of markings remarkably constant; allowing for individual variation, the following scheme is typical. Investment buff, rich chestnut, blackish, etc., varying from thin, smooth, and transparent to thick, rough, and opaque; often deciduous after capture. Nemathybomes and tubercles sometimes very prominent, sometimes inconspicuous and not visible till investment is removed; the rows more or less regular. Colour of upper part of body (scapulus) very variable; there is usually a coronal ring of cream spots just below the tentacles, and above this a very short transparent region, the true capitulum; there may be a second ring of cream marks a little lower down, or the latter alone may be present; there are often longitudinal cream stripes, one to each macrocœle, below the coronal spots, or these may be broken up into irregular dots and splashes. There may also be brown or purple colour variously related to the cream. The tentacles are long and fine, transparent, with dots or powderings of opaque cream, and in adults generally with dots of blackish purple also. Sometimes the outer tentacles or all the tentacles appear sub-opaque because of a cream stripe up the oral and aboral face of each. The disc in adults (Fig. 3) is characterised by a mealy appearance, the colour being dusted on in dots; actually the colour varies indefinitely, but on the average there is a rosette of dark arches close to the mouth and a dark mark shaped like an hour-glass set transversely across the radius, near the foot of each endocœlic tentacle; sometimes the ring made by these marks is completed by similar dark spots on the exocœlic radii. Generally each outer tentacle has a cream spot on the aboral side at the base. These details will cover most specimens, but any given individual may lack some one or other of the features mentioned or may present a modification of its own upon the general theme. Young specimens usually have opaque cream discs, the other colours apparently coming later. The directive radii and tentacles may differ in colour from the others. The animal reaches a length of 10 or 12 cm., at its best.

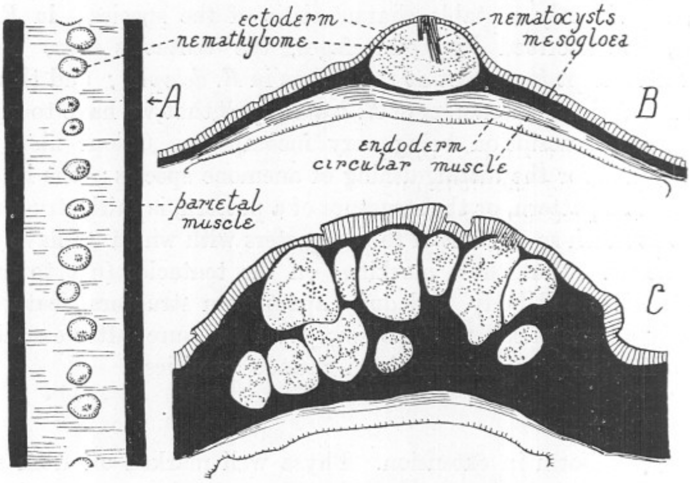

FIG. 2.—A. Part of a whole mount of a portion of column-wall from *E. callimorpha*, showing the arrangement of the nemathybomes between the insertions of two mesenteries.

B. Transverse section of the column-wall between two mesenteries, in *E. callimorpha*, passing through a nemathybome.

C. Similar section from *E. delapiæ*.

### *Edwardsia delapiæ* n.sp.

(For references, see p. 23.)

This species is so far known only from Valencia, where it was discovered by Miss Delap, and from Malahide, Co. Dublin; it is easily distinguished from *E. callimorpha*. The two species may live together.

As is noted later on (p. 23) by Carlgren, part of the specimens included by Haddon (1889, p. 329) under "*Edwardsia timida*" actually belong to *E. delapiæ*, the rest being *Milne-Edwardsia dixonii* (see p. 27).

*Description*:—

Body vermiform in extension, able to become even more attenuated than that of *E. callimorpha*. Physa well marked off from scapus, non-retractile, with microscopic adhesive rugæ, and with eight longitudinal rows of small apertures. Scapus extensive, with a cuticular investment and with a wide band of nemathybomes along each macrocœle, the band nearly filling the space between each two mesenterial insertions; the nemathybomes are irregularly scattered, not mounted on tubercles, and not limited to a linear series as in *E. callimorpha*; in fact, some of them occur even over the mesenterial insertions, only the majority being confined to the main band; they project little, if at all, above the surface (Fig. 2). Tentacles sixteen in adults (fourteen in one case). There is a coronal ring of cream spots just below the tentacles, those corresponding to the endocœls being transparent in their centres and each sending a cream line to join a similar mark on the aboral side of the base of an endocœlic tentacle. Disc with a delicate pattern in cream and maroon

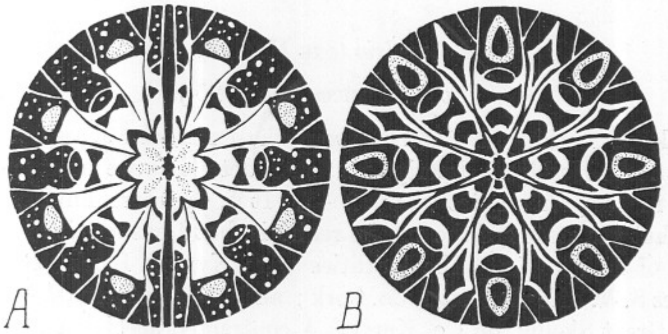

FIG. 3.—Diagrammatic representations of the pattern on the disc and tentacle-bases in *E. callimorpha* (A) and *E. delapiæ* (B). Only the lowest parts of the tentacles are shown. The shaded markings on the tentacle-bases are aboral, and are visible because of the transparency of the oral sides of the tentacles. The vertical dark stripe in A is a band of colour affecting the directive tentacles and radii. In B the aboral markings are omitted from the exocœlic tentacle-bases. × ca. 6–7.

on a transparent ground, but without the mealy aspect of that of *E. callimorpha;* with very wide endocœlic radii. Centre of disc with a star of eight cream rays; radii each with a cream mark of curious form on it (see Fig. 3), the marks on the exocœls much farther out than those on the endocœls. Tentacles long and slender, transparent, unmarked but for the basal markings and a faint brown or cream transverse bar across the tip. A cream mark with a transparent centre, shaped like the eye of a peacock's tail-feather, occurs on the aboral side of each tentacle-base. I have seen only half a dozen specimens of this species, but these exhibited very little variation, showing slight differences in the form of the cream markings on the disc, and so forth; in one a thin powdering of white on the disc obliterated some of the neat cream markings.

The animal reaches a length of about 12 cm. in extension; the diameter of the expanded flower up to about 4·5 cm.

### *Edwardsia tecta* Haddon.

(For references, see p. 25.)

We know nothing distinctive about the external appearance of this species from Haddon's description; such details as we possess are contained in Carlgren's notes on pp. 25–7. It is, therefore, impossible to be sure what the status of the species really is, but I suspect it of being the young of *E. delapiæ.* The localities were Nymph Bank, 52 fathoms, 28 miles S.W. of Ballycotton, Co. Cork; and 70–80 fathoms, 5–8 miles W. of the Great Skellig, off Co. Kerry. A contracted specimen was 12 mm. long and 2 mm. in diameter.

### *Milne-Edwardsia carnea* (Gosse).

(See Gosse, 1856, p. 219, 1860, p. 259; Carlgren, 1921, p. 62; etc.)

This small vermiform anemone (which reaches a length of 2–3 cm. only) inhabits crevices and small holes in rocks and, unlike most Edwardsids, which burrow, it has no true physa (this being essentially a burrowing organ), but an adhesive aboral end which may, it is true, assume rather the appearance of a physa if the animal be detached and left loose, but which is not histologically differentiated as such and does not function as one.

*M. carnea* is known in Britain from a number of localities—Torquay, Tenby, Plymouth, Port Erin, the Clyde, etc., and I have myself seen living specimens from three of the localities mentioned. Abroad it occurs in Sweden, but how far beyond this we cannot tell, since the various species have only been clearly recognised by Carlgren.

*Description :—*

The scapus occupies more than two-thirds of the length of the body and is sub-cylindrical, being often slightly polygonal above ; its investment may be thin, or thick and rugged, pale orange-brown, dark brown, blackish, etc. ; the skin beneath is orange-buff or pinkish, without nemathybomes or papillæ. The scapulus is fairly long and is very sharply marked off from the scapus in partial contraction, though in full extension the division is obliterated ; it bears eight sharply-marked longitudinal ridges which almost vanish in expansion, and these end sharply at its junction with the scapus ; it is translucent, pinkish, generally marked by some other colour as well—the ridges may be white, or there may be a ring of opaque cream or yellow markings round the lower part. The disc may be dusted with pale yellow, which may concentrate round the mesenterial insertions ; or it may be opaque cream ; sometimes red round the mouth ; with variants of this colouration. Throat orange or red, visible by transparency through scapulus ; shorter than scapulus. Tentacles fairly long, slender, translucent pink, unmarked or with alternate bands of less and more positive colour ; in 3–4 cycles—6 . 6 . 12, etc., or a close variant of this, total number up to 34 (Fig. 1). Variation not great, nor departing far from the plan indicated.

Since Carlgren describes the anatomy of all the British Edwardsidæ other than *M. carnea* in the second part of this paper, I will give here the main points in the anatomy of this species from Carlgren's 1921 paper, for comparison with that of *M. dixonii.* The retractors are similar to those of *M. dixonii* (Fig. 17), as also are the parietal muscles ; the former have often twelve folds in the reproductive region and never have more than twenty. The nematocysts of the column are arranged in the ridges on the scapulus, and on the scapus itself are mainly in groups. The nematocysts in general are characterised by being short and wide as compared with those of allied species. Those of the scapus are 29–34 (37) $\times$ 7–8$\mu$ ; those of the scapulus 26–46 $\times$ 7$\mu$ ; of the tentacles partly 18–24 $\times$ 5$\mu$, partly 27 $\times$ 7$\mu$, the first kind numerous, the latter sparse ; spirocysts up to about 24$\mu$ ; in the throat they are partly typical, 17–20 $\times$ 3$\mu$, partly with a distinct basal part to the spiral thread, 22–29 $\times$ 5$\mu$.

I have studied the nematocysts of a Clyde specimen myself, for comparison with the measurements given above ; they are not quite identical in the two forms, but at the same time they are surprisingly near. Scapus, 26–32 $\times$ 6–7·6$\mu$ ; scapulus, 24–42·6 $\times$ 5·4–6·6$\mu$ ; tentacles partly 17–22 $\times$ 4–4·6$\mu$, partly 22–26 $\times$ 5·6–6·4$\mu$ ; throat, partly 17–22 $\times$ 3–3·4$\mu$, partly 20–24 $\times$ 5–5·6$\mu$. This was a small specimen, only half the full size ; the nematocysts measured preserved and unexploded.

### *Milne-Edwardsia dixonii* Carlgren.

(For references, see p. 27.)

The account given here of the externals of this species is entirely taken from Dixon (1886, p. 100) and we cannot therefore personally vouch for it.

I cannot feel certain about the distinctness of this species from *M. carnea* (though I am inclined to think it is different), having never seen it alive. A good deal depends also on whether or no the tentacles are arranged as Dixon describes, and whether there is really a physa ; if Dixon's account is correct in these particulars, it is probably a distinct form ; especially as Carlgren shows (p. 27) that the nematocysts are considerably different from those of *M. carnea ;* and in *M. carnea* their size seems to be rather constant.

*Description :—*

Physa present, provided with minute suckers, retractile into scapus. Scapus polygonal above, scapulus apparently without definite ridges. Tentacles 18–24, curiously arranged. In one specimen they ran 8+14 (or 8.12.2), and in another 10+10, and seemingly had a different relation to the mesenteries than in *M. carnea ;* to judge from Dixon's figure, the inner eight in the first specimen correspond to the two directive endocœls and six symmetrical lateral chambers which do not include the four lateral primary endocœls.

Bourne (1916) gives details of two of Dixon's specimens examined by him, in each of which there were twenty-four tentacles ; this account appears to confirm Dixon. It is possible that we have here a third type of Edwardsian tentacle-plan ; but only a renewed examination of healthy living material can settle it. In a Milne-Edwardsia which is not in the best of health and at the same time very fully expanded, the real comparative lengths of the tentacles may be indistinguishable.

Physa pellucid white. Tentacles varying shades of pink or brownish red, tipped with white or not. Throat brownish red, brick-red, yellow ochre, sometimes with white longitudinal marks. Investment variable, usually tawny orange, black above. Disc usually pellucid pink, with white crescents (developed into H-marks in one case) at the tentacle bases, and a white ring round the mouth (also white specks on disc in one case) ; in one it was cream-white, with brownish red lines indicating the macro-insertions, white blotches at bases of directive tentacles, the other inner tentacles with a basal white bar inside which is a brownish red V, the point mouthwards. Scapulus translucent brownish red or pellucid pink, with a ring of opaque pale marks on it, arranged rather differently from those of *M. carnea.* The animal is larger than *M. carnea,* reaching a length of 6·5–7 cm. in extension. Moreover, it is different in habit, and was found in mud among stones at extreme low water at Malahide, Co. Dublin.

## 4. Note on the Succession of Tentacles in Edwardsia callimorpha.

I have been able to make out the arrangement of tentacles and mesenteries in nineteen young specimens of this species: although some of these were very small, none had fewer than 12 tentacles. The following results were obtained, and I have added to them the case of an adult with only 15 tentacles.

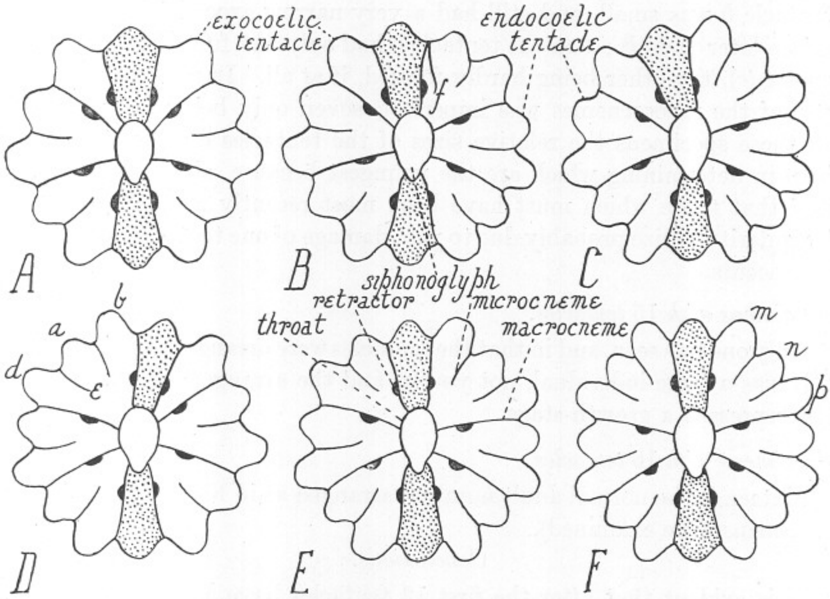

Fig. 4.—Diagrams to illustrate the mode of development of the tentacles 13–16 in *E. callimorpha*. For explanation of lettering, see text.

*Specimens with* 12 *tentacles.*

Of these there were eleven, and in all of them the tentacles were arranged as in Fig. 4, A.

*Specimens with* 13 *tentacles.*

Only two individuals had 13 tentacles, and one of these was abnormal in one of the older sectors; if it had been normal it would have had 14 tentacles, so was of no value as an example of the 13-tentacled stage. The other specimen had the arrangement shown in Fig. 4, B. Note that the newly added tentacle has pushed the directive axis a little out of the straight. The new microcneme (*f*) appeared to be larger than its partner.

*Specimens with* 14 *tentacles.*

There were six of these, three of them with the tentacles arranged as shown in Fig. 4, C, the others as in Fig. 4, D. In these, again, the directive axis is a little out of the straight, pushed to one side or the other according to the sector in which new growth has taken place. One of the specimens, arranged as in Fig. 4, D, seemed to present a stage intermediate between those exemplified by Figs. 4, B and D; in it the tentacle *b* was small, and still had a very narrow exocœl (clearly it had arisen later than *d*); and the tentacle *a* had only one fully formed microcneme (*e*), the other being hardly formed, if at all. In another specimen one of the macrocnemes was imperfect, seven only being fully formed. In these specimens the relative sizes of the tentacles do not give much help in determining which are the youngest because, although one may find that those which must have been most recently formed are small, irregularity of size probably due to past damage of one tentacle or another, also occurs.

*Specimens with* 15 *tentacles.*

Only one was seen, and in that the tentacles were arranged as in Fig. 4, E; this was a large individual, not young, and the arrangement shown may not represent a growth-stage.

*Specimens with* 16 *tentacles.*

Sixteen is the normal adult number, arranged as in Fig. 4, F (numerous specimens were examined).

### *Conclusions.*

It is evident that after the first 12 tentacles have been formed, nos. 13–16 are formed asymmetrically, an endocœlic and an exocœlic appearing first, on one side or other (indifferently) of the directive axis, followed later by another endocœlic and exocœlic on the opposite side. Beyond this the paucity of observed stages with 13 or 15 tentacles prevents certainty, but it would appear that on whichever side of the directive axis growth may be taking place, the tentacle *p* (in Fig. 4, F) is the one which was in existence at the 12-tentacled stage, and that of *m* and *n* the first to be formed is *n*.

## 5. Note on the Regions of the Column in Edwardsias and other Actinians.

The body of an Edwardsia is usually said to be divided into three regions—physa, scapus, and capitulum. These terms are also applied to regions of the body in certain other anemones, and the usage is not uniform. In some cases there are distinctly-marked regions present which are not accounted for in the ordinary terminology, and sometimes a region receives a name which is not its due. It is desirable that precision should be given to the terms in question and that they should be used more carefully. The following notes are an attempt towards this end, and are illustrated by Fig. 5.

(1) *Physa.* This term is accurately applicable only to the vesicular aboral extremity of a burrowing form. A physa is a digging organ; it is generally perforated by small apertures; often provided with irregular microscopic suctorial rugæ which enable it to adhere to foreign bodies; is usually marked off fairly or very distinctly from the next region of the column (scapus), this being most evident when it is contracted. If a living contracted Peachia or Halcampa be viewed from the aboral end, the physa will be seen as a rosette of tissue distinctly different from that of the scapus, and often with a deep pit in its centre. Finally, a well-marked physa has different ectoderm from the scapus above it; and in an Edwardsia it is further marked off by the fact that the nemathybomes cease abruptly where the physa begins.

It is often stated that a physa is " retractile within the scapus." This is sometimes actually the case (e.g. *Edwardsia vegæ*, see Carlgren, 1921, Text-fig. 62); but the statement is also due sometimes to defective observation. There is no British species which I have been able to examine alive which can retract the physa. In *Edwardsia callimorpha* and *E. delapiæ*, *Halcampa chrysanthellum* (=*H. arenaria*) and *Peachia triphylla*, there is a well-developed physa. It is non-retractile, but can contract into a flattened rosette and unless examined very carefully may look as if it had been invaginated because of the pit in its centre. Sometimes an anemone may be found with the end of the scapus tucked in; but this can be due to damage to the physa, which is being regenerated; and is not necessarily true retraction.

There remain the cases where an animal possesses a rounded aboral end which is sometimes inflated after the manner of a physa, and which looks like one at first sight. Such cases are *Milne-Edwardsia carnea* and *Mesacmæa* (*Ilyanthus*) *mitchelli*. In both these the aboral end may look physa-like, and in the latter can apparently be used for digging; but it is not morphologically differentiated from the scapus and it is able to adhere like the pedal disc of an ordinary anemone. *M. carnea* adheres in its normal condition, and Mesacmæa, when comfortable in an aquarium, sometimes adheres with very great force by a broad flat basal area. A true physa can adhere lightly by its suckers, but it is only anchored, not truly attached, and as far as I know can never become a firmly adherent base as in Mesacmæa

There are doubtless intermediates between these two states, though I cannot speak of them from personal observation. These would be very difficult to determine accurately except from living material.

(2) *Scapus.* This region includes the greater part of the body in any anemone which has a differentiated column, the other terms applying to the extremities. The only difficulty connected with the scapus is its limitation—just where does it pass into one of the other regions ? Where there is a well-marked physa the boundary-line is clear enough in a contracted living specimen ; where there is a rounded aboral end which is not a physa there is no definite boundary. The difficulty is greater when it becomes a question of defining the boundary at which the scapus passes into the capitulum.

(3) *Capitulum.* There is no strict homology between the regions of different anemones to which this term has been applied.

(*a*) In Sagartia there is no division of the column into regions, and nothing that can be called a capitulum ; the same is true of Bolocera, etc.

(*b*) In Calliactis and Stomphia there is no actual capitulum, but there is a tendency for the submarginal region to be slightly differentiated from the rest.

(*c*) In Hormathia, Actinauge, Paraphellia (and in some of their relatives, as yet not fully described, e.g. " *Phellia* " *brodricii* and *P. gausapata*), the submarginal zone is distinctly marked off from the main part of the column (scapus) as a separate region with different ectoderm and without the tubercles and cuticle often developed by the latter (though it may have ridges instead of tubercles). It is not, however, a thin-walled region, and in fact is apt to be even more solid as to its mesoglœa than the scapus, since it contains the marginal sphincter or, at any rate, the upper part of this. The region in question is marked *sl* in Fig. 5, D and F.

(*d*) In Metridium (Fig. 5, B) there is an extensive submarginal region (*c*), limited below by the collar which terminates the upper edge of the scapus ; here, however, the sphincter is in the collar, and the more delicate region above the collar is not comparable to the submarginal zone of Hormathia, etc. Sometimes it is even marked off from the scapus by a sharp change of colour ; it is thinner-walled, with modified ectoderm, and modified endodermal circular-muscle layer. The same principle is found in Diadumene, where there is a delicate submarginal region above a scapal collar ; but here there is no sphincter at all. The term capitulum is often applied to the submarginal regions both here and in Hormathia, although they are not homologous.

(*e*) In Tealia (Fig. 5, A) there is a strong marginal fold (*p*) bearing the sphincter, and above this a definite and clearly marked region (*c*) of delicate structure between sphincter and tentacle bases ; this region is not generally called a capitulum, but it is comparable to the similar but

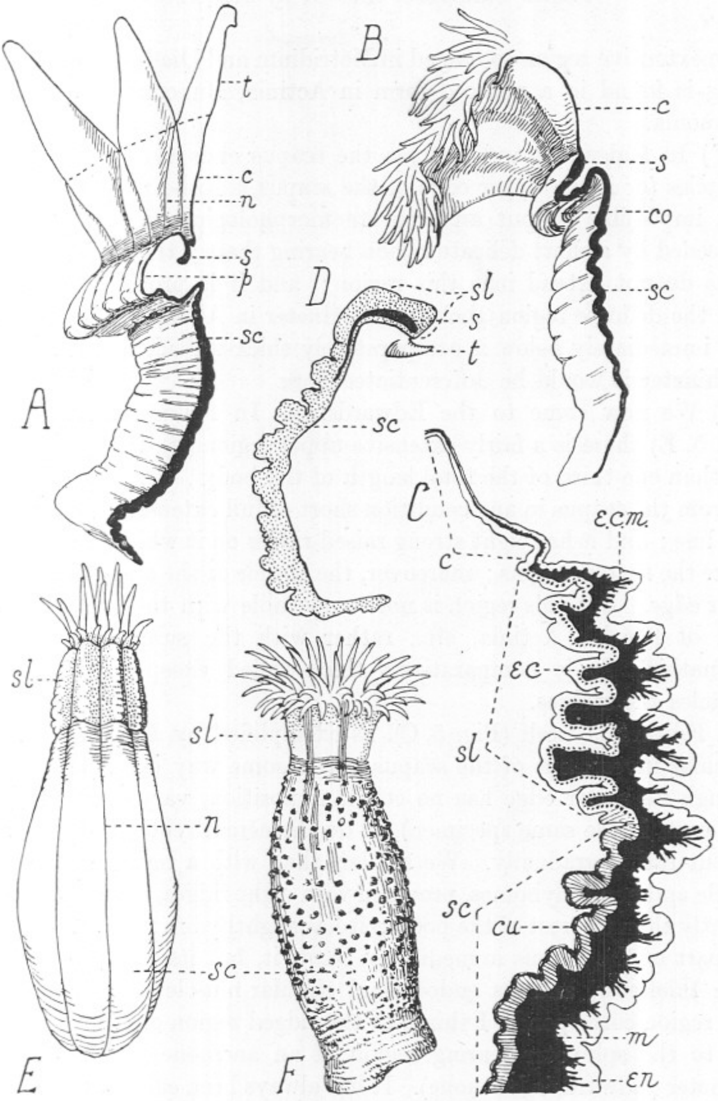

FIG. 5.—The regions of the column wall in Actinians.

A. Sector of column, with tentacles, from Tealia. In this and in B, the cut edge is black. The dotted line indicates upper edge of capitulum. ×1.

B. Sector of column, with tentacles, from Metridium. ×1.

C. Longitudinal section of upper part of column of *Edwardsia callimorpha*. The mesoglœa and the processes of the endodermal muscle-sheet are black. This section did not pass through any nemathybomes. ×15.

D. Vertical section through the body-wall of *Actinauge richardi*. Sphincter black. The thickness of the wall is here largely composed of mesoglœa. ×1.

E. Entire specimen of *Milne-Edwardsia carnea*, in a contracted condition. ×6½.

F. Living specimen of *Phellia gausapata*. ×1.

c, capitulum; co, collar; cu, cuticle; ec, ectoderm; e.c.m., endodermal circular-muscle; en, endoderm; n, mesenterial insertion; m, mesoglœa; p, parapet; s, sphincter; sc, scapus; sl, scapulus; t, tentacle.

more extensive region so named in Metridium and Diadumene. The same thing is found in a reduced form in Actinia, Bunodactis, and even in Anemonia.

(*f*) In Halcampa and Peachia the scapus ends very little below the tentacles (or if the upper edge of the scapus is to be placed lower down it is impossible to put an accurate morphological limit to it) and is succeeded by a short delicate region bearing these; the imperfect mesenteries do not extend into this region; and it is probably homologous with the delicate region above the sphincter in Actinia and Tealia. The part immediately below is comparatively thick-walled, and if there were a sphincter it would be differentiated here.

(*g*) We now come to the Edwardsidæ. In *Milne-Edwardsia carnea* (Fig. 5, E) there is a fairly extensive upper region (*sl*), though it occupies less than one-third of the total length of the body; it is sharply marked off from the scapus in any condition short of full extension, by a recognisable line; and it has eight strong raised ridges on it which cease abruptly where the scapus begins; moreover, the cuticle of the scapus ceases at its lower edge. But this region is not comparable with the tentacle-bearing neck of Peachia, Actinia, etc., rather with the submarginal zone of Hormathia. It is comparatively thick-walled except just below the tentacles themselves.

In Edwardsia itself (Fig. 5, C), as exemplified by *E. callimorpha*, the cuticular investment of the scapus ceases some way below the tentacles (though its upper edge has no constant position, varying from time to time even in the same specimen), so do the nemathybomes, though these die out rather gradually. We are left then with a region (*sl*) devoid of cuticle and nemathybomes, provided with eight ridges, and coloured more brightly than the rest of the body; it has slightly different ectoderm than the part of the scapus immediately below it, but its mesoglœa is of the same thickness, and its endodermal circular-muscle is well developed. This region corresponds, I think, to the ridged region of Milne-Edwardsia and to the sphincter-bearing region of an anemone which has a true sphincter (Edwardsia has none). It has always been called the capitulum. At the same time, Edwardsia possesses, in fact, above this "capitulum" another region (*c*)—a narrow, delicate, thin-walled, colourless part bearing the tentacles; in it the mesoglœa and endodermal circular-muscle are reduced as compared with the part below, and the ectoderm thins out somewhat also; moreover, the microcnemes are practically confined to this region and do not penetrate far into that below. This region is no doubt comparable to the tentacle-bearing region of Peachia and Halcampa, but we have in Edwardsia two kinds of "capitulum" one above the other. Moreover, there is the difficulty that in Edwardsia the lower capitulum is not always marked off at all clearly from the scapus—there may be a distinctive ring of colour at about the point where they join, and at this point the ridges may rise into crests; but sometimes the colour fades off gradually from above downwards and it is very difficult to separate one region from the other—i.e. the coloured region is morphologically part of the scapus.

(*h*) We have then at least two types of capitulum. The first is a comparatively thick-walled region, containing the sphincter (or, in the absence of a sphincter, well-developed mesoglœa and endodermal muscle-sheet); the second is a region above the sphincter and more delicate in structure than the scapus. These two types of region are clearly not homologous, especially as in Edwardsia both are developed. It is necessary to introduce a new term for one of them, or else to continue to use "capitulum" for two different things. The latter course would seem to be undesirable. I therefore propose that the matter be regarded as follows:—

The body-wall in Actinians tends to differentiate into regions; in some cases a delicate submarginal region above the sphincter (or above the place where the sphincter would lie if it existed) can be recognised; this is a true capitulum. In other cases the scapus itself differentiates into regions; an upper part, containing the sphincter or the head of it, but at the same time differentiated from the part below; and a distinct lower region; or, in sphincterless forms the upper part is differentiated but is morphologically part of the scapus. The upper portion of a differentiated scapus such as this I propose to call a *scapulus*. In Hormathia, therefore, the column is divided into scapus and scapulus, and there is no capitulum. In Edwardsia we have both scapulus and capitulum present; in Milne-Edwardsia the upper part is a scapulus, but perhaps has a feebly marked capitular region above it also.

The proposed restriction of the term capitulum does not carry out the original intention of the term to the letter, but to my mind it fulfils the spirit of that intention. It should not be thought from the above discussion that the regions of an Actinian body-wall have the degree of distinctness attained by the segments of an Annelid—far from it; but they are none the less recognisable entities.

# PART 2. ANATOMY.

By

OSKAR CARLGREN.

## EDWARDSIA CALLIMORPHA (Gosse).

*Scolanthus callimorphus* n.sp., Gosse, Ann. Mag. Nat. Hist. (2) 12, p. 157, Pl. 10.

*Edwardsia callimorpha* Gos., Gosse, 1860, Actin. Britan., p. 255, Pl. 7, Fig. 7.

*Edwardsia claparedii* Panc., Andres, Mitt. zool. Stat. Neapel. 2, 1880, p. 123, Pl. 8; Le Attinie, 1883, p. 303, Pl. 11, Figs. 1–5 (pro parte).

*Edwardsia claparedii*, Carlgren, Zool. Anzeig., 27, p. 543; The Danish Ingolf Exp., 5, 9, Actiniaria, pp. 23–25, Figs. 6, 7, 8, 10.

*Edwardsia beautempsii* Quatr., Haddon, 1889, Sci. Trans. R. Dublin Soc. 4 (2), p. 327, Pl. 33, Fig. 17, Pl. 36, Fig. 4.

*Diagnosis.* Physa well developed. Scapus-periderm of ordinary thickness. Nemathybomes rather large, arranged in eight longitudinal rows. Tentacles (12)–16. Pennons of the macrocnemes in the upper part of the reproductive region with numerous folds, often profusely branched, especially in the outer and innermost parts. Outer lamella of the mesenteries attached to the pennons rather far from their outer edge. Parietal muscles in the same region more or less triangular, with numerous folds which are mostly not ramified. Extension of the parietal muscles on to the column-wall only slight. Microcnemes comparatively well developed, but weak as in other *Edwardsia*-species. Nematocysts of the nemathybomes partly (72) 84–113 $\times$4·5–6$\mu$, partly (53) 60–82 $\times$2·5–almost 3$\mu$; those of the scapulus 10–12 $\times$1·5$\mu$; those of the tentacles 18–26 $\times$about 2–2·5$\mu$; those of the actinopharynx partly 24–31 $\times$2·5–3$\mu$, partly 29–41 $\times$ 5–6·5$\mu$ (the latter broader at the basal end and with a visible basal part to the spiral thread). Spirocysts of the tentacles 10 $\times$1 to about 22 $\times$3$\mu$.

Stephenson has identified one of the species from Valencia with Gosse's *Edwardsia callimorpha*, and suggests that this species is identical with *Edwardsia claparedii*, figured by Andres in his work of 1883. A close examination of the anatomy of both these species shows clearly that at least the common form of *claparedii* belongs to *callimorpha*; but probably this does not apply to all the varieties figured by Andres in his Pl. XI, Figs. 1–5. Whether *callimorpha* and Quatrefage's *beautempsii* are identical, as Haddon supposed, it is hardly possible to decide. On the other hand, Haddon's *beautempsii* is certainly the same form as the *callimorpha* from Valencia. From the Dublin Museum I have received a specimen labelled *Edwardsia beautempsii*, Berehaven (one of Haddon's localities). The upper part of the body has been cut off, and only the lower part remains. It is certainly the specimen examined by Haddon. The nematocysts of the nemathybomes agree well with those of *callimorpha*. Also, the parietal muscles examined by me on Haddon's slides show rather good agreement with those in Gosse's species. Haddon's slides of the pennons are very bad, and the figure of such a one in Haddon's paper is quite useless for identification of the species.

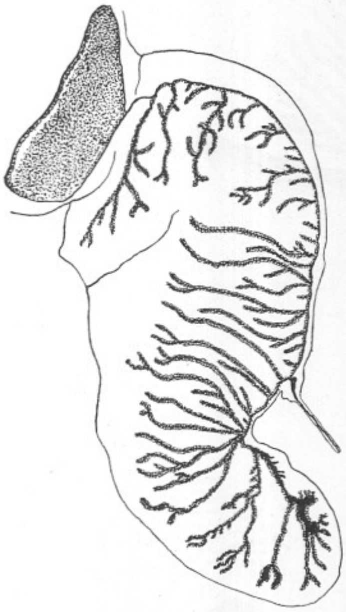

FIG. 6.—*E. callimorpha.* Transverse section of retractor in upper part of fertile region. The dotted area is part of a gonad. Valencia specimen.

FIG. 7.—*E. callimorpha.* Transverse section of retractor in upper part of fertile region. Naples specimen.

*Anatomical Description.* The anatomy of this species recalls that of other *Edwardsia*-species, so that it is not necessary to go into details. The physa is perforated by pores—" cinclides " (observed on slides of *claparedii*). I have already (1904, 1921) given figures of the arrangement of the mesenteries and of the actinopharynx with the weak ventral siphonoglyph. The pennons of the macrocnemes are not concentrated, but more diffuse, in the upper part of the reproductive region, the folds numerous and especially richly branched in the outer and innermost parts. The outer lamellar portions of the mesenteries issue rather far from the outside edges of the pennons. In Figs. 6 and 7 I have reproduced pennons from one Naples specimen and from one Valencia specimen. The parietal muscles are strong and triangular in the upper part of the fertile region, and are provided with numerous but little-branched folds. Figs. 8–10 show parietal muscles from the Valencia specimen, from *claparedii*, and from Haddon's "*beautempsii*."

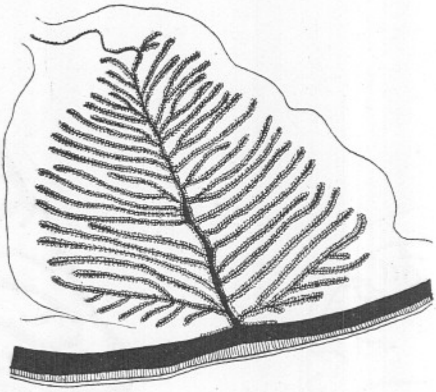

FIG. 8.—*E. callimorpha.* Transverse section of parietal muscle in upper part of fertile region. Valencia specimen.

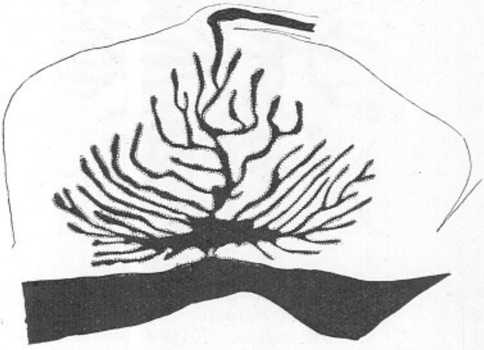

FIG. 9.—*E. callimorpha.* Transverse section of parietal muscle in middle part of fertile region. Naples specimen.

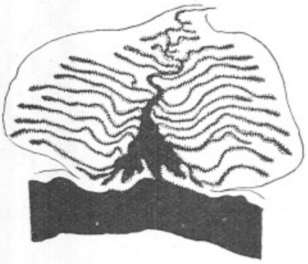

FIG. 10.—*E. callimorpha.* Transverse section of parietal muscle in upper part of fertile region. Haddon's "*beautempsii*" specimen.

The size of the nematocysts from the different regions agrees very well in the three "species," as is evident from the following table (A, B, *claparedii*; C, *callimorpha*; D, Haddon's *beautempsii*):—

*Nemathybomes.*

A. 84–106 × 4·5–6μ; 62–82 × 2·5–3μ.
B. 84–94μ; 65–74μ.
C. (75) 84–113 × about 5μ; 63–82 × about 2·5μ.
D. 72–105 × about 5μ; (53) 60–74 × about 2·5μ.

*Tentacles.*

A. 18–26 × almost 2μ.
B. 17–26 × almost 2μ.
C. 22–25 × almost 2(2·5)μ.
D. . . . . . .

*Actinopharynx.*

A. 26–31 × about 2·5–3μ; 29–34 × about 5–6μ.
B. . . . . . .
C. 24–30 × about 3μ; 31–41 × 5–6·5μ.
D. . . . . . .

### EDWARDSIA DELAPIÆ n.sp.

*Edwardsia timida* Quatref., Haddon, 1889, Sci. Trans. Dublin Soc., 4 (2), p. 329, pro parte; Pl. 36, Fig. 3; p. 331.

*Diagnosis.* Physa well developed. Scapus-periderm of ordinary thickness. Nemathybomes scattered, rather numerous, varying in size but not large. Tentacles (14)–16. Pennons of the macrocnemes in the upper part of the fertile region with numerous (between 20 and 30) folds, which are rather well branched, especially in the outer and innermost parts of the pennons. Outer lamellar portions of the macrocnemes attached to the pennons rather far from their outer edges. Parietal muscles in the same region more or less elongated, considerably weaker than in *callimorpha*, with fewer folds which are only slightly branched. Extension of the parietal muscles on to the column wall about as usual. Nematocysts of the nemathybomes partly 59–77 × 5–5·5μ, partly 46–58 × 3–3·5μ; those of the scapulus 10–12 × 1–1·5μ; those of the tentacles 19–22 × 1·5–2μ; those of the actinopharynx partly 26–34 × 2·5(3)μ, partly 19–22 × 1·5–almost 2μ (sparse); spirocysts of the tentacles about 11 × almost 2μ–22 × 3μ.

Of the Valencia specimens I have seen only one. I have also examined slides of the species described by Haddon in 1889 as *Edwardsia timida*. The appearance of the pennons and parietal muscles in "*timida*" agrees rather well with that of the same organs in our present species; the nemathybomes are scattered and their nematocysts (measured only from slides) are partly 60–67 ×5$\mu$, partly 43 ×2$\mu$. The last-mentioned nematocysts are a little smaller in "*timida*" than in *delapiæ;* but as the nematocysts mostly shrivel a little during the treatment of the slides this small difference is unimportant.

The anatomy of this species agrees with that of other *Edwardsia*-species. I have figured for comparison two pennons, one from the Valencia specimen, and one from Haddon's "*timida*" (Figs. 11 and 12). The slide of "*timida*" is taken from the fertile region, but I cannot decide whether or not it is from the uppermost part of this tract because the upper part of this animal was not sectionised by Haddon. Fig. 13 shows the appearance of the parietal muscle in the upper part of the fertile region in the Valencia specimen.

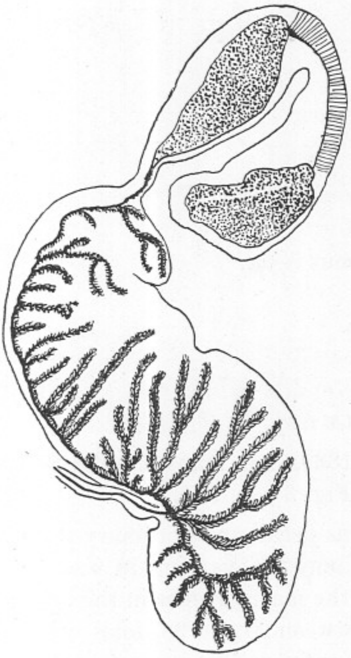

FIG. 11.—*E. delapiæ.* Transverse section of retractor in upper part of fertile region. The dotted areas represent gonad. Valencia specimen.

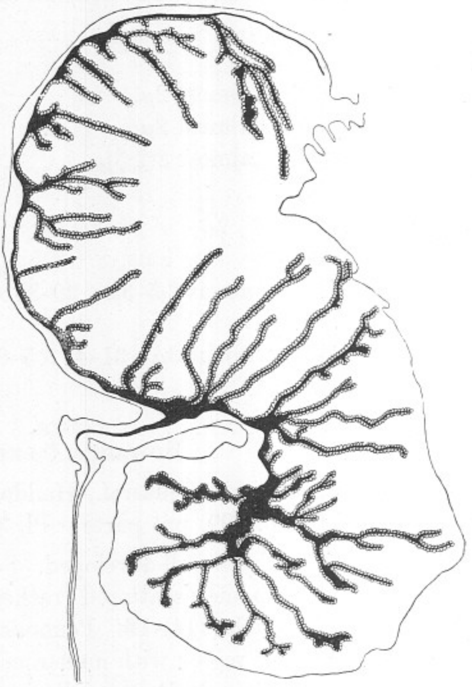

FIG. 12.—*E. delapiæ.* Transverse section of retractor in the fertile region. Haddon's "*timida*" specimen.

The species is closely related to *Edwardsia danica*, but in this latter form the nematocysts of the nemathybomes are smaller.

## EDWARDSIA TECTA Haddon.

*Edwardsia tecta* n.sp., Haddon, 1889, p. 329, Pl. 33, Fig. 16; Pl. 36, Figs. 1–2.

*Diagnosis.* Physa small, delicate, completely retractile within the scapus. Scapus with eight shallow longitudinal grooves, with few scattered nemathybomes not forming tubercles on the surface. Periderm of the scapus thin, translucent, easily deciduous. Scapulus delicate. Tentacles at least 14 in number. A distinct ventral siphonoglyph present. Pennons of the eight macrocnemes (in the upper part of the cnido-glandular tract) with few (about 10–12) high folds, which are unbranched or but slightly forked, except for the outermost fold, which is large and more branched. Outer lamellar part of the macrocnemes attached not far from the outer edges of the pennons. Parietal muscles in the same region triangular, with few but rather high folds; their extension on to the column wall about as usual. Nematocysts of the nemathybomes partly 34–43 × about 3·5$\mu$, partly 55–72 × 4–5$\mu$; those of the scapulus about 10 × 1·5$\mu$; those of the tentacles about 17$\mu$; those of the actinopharynx 24–31 × 2–2·5$\mu$ (size of the nematocysts measured only on slides). Specimens not sexually ripe.

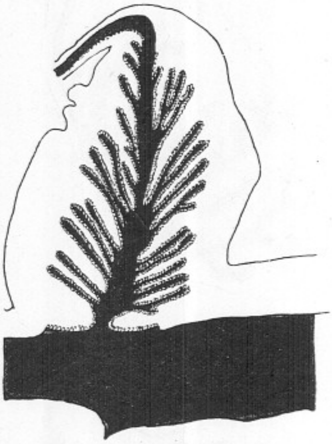

FIG. 13.—*E. delapiæ.* Transverse section of parietal muscle in upper part of fertile region. Valencia specimen.

*Colour, dimensions, and occurrence;* see Haddon, 1889, and this paper, p. 10.

I have examined Haddon's slides of this species. The slides of the specimen from Nymph Bank were well preserved. It is certainly this specimen which Haddon described and figured. A slide including sections of the undermost part of the actinopharynx and of the ciliated tract and also sections of the physa I have, however, not examined. Several other slides labelled *E. tecta* were also present in Haddon's collections. These were, however, very badly preserved; and some longitudinal sections showing numerous very close nemathybomes certainly do not belong to this species.

*External characters.* According to Haddon, the physa is small, delicate, and completely retractile; he has not observed any terminal pore in it. Probably the pores were overlooked by him, as I have found pores in all the physæ which I have examined in the genus Edwardsia. The periderm of the scapus is thin and easily deciduous; in the preserved specimens it is quite loose from the ectoderm. Haddon states that the species lacks tubercles on the scapus. It is true that there are no visible tubercles, but in the mesoglœa nemathybomes are present. They are of ordinary size, scattered and few in number. Some of them are situated exactly in the middles of the intervals between the insertions of the mesenteries, others lie nearer to the insertions themselves. On the whole, the arrangement of the nemathybomes recalls that of *E. danica* (Carlgren, " The Actiniaria of the Ingolf Expedition," 1921, p. 32, Fig. 17), although the nemathybomes here are more sparse than in that species. The uppermost part of the introverted anterior end is polygonal. The boundary between the scapus and scapulus is not distinct, but the scapulus is certainly considerably longer than the microcnemes. Haddon states that there are only 8 tentacles in the single specimen examined by him. As far as I can discover, 14 tentacles are present in the specimen sectionised, arranged as in the *Edwardsia*-species with 16 tentacles, except for the fact that only one tentacle issues from one of the dorso-lateral compartments. The single ventral siphonoglyph is distinct (see also Haddon's Fig. 1, Pl. 36).

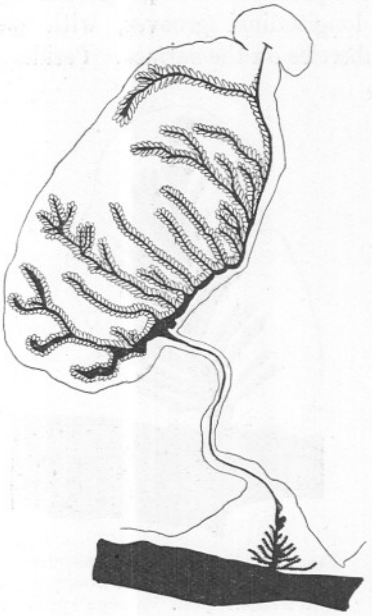

FIG. 14.—*E. tecta.* Transverse section of macrocneme in the region of the cnido-glandular tract.

*Anatomical description.* The ectoderm of the scapus is of average height, its periderm only a little incrusted; the mesoglœa not much wrinkled. The nematocysts in the nemathybomes are numerous. In the introverted part of the scapus the mesoglœa forms ridges between the insertions of the mesenteries. The ectoderm of the actinopharynx is very thick; the siphonoglyph is provided with longer cilia than the other parts of the actinopharynx, but its ectoderm is thinner.

The pennons of the macrocnemes are provided with 10–12 high folds in the upper part of the cnido-glandular tract. The innermost fold is higher than those in the middle of the pennon. The outermost fold is coarse and branched, the other folds are unbranched, or more or less branched (Fig. 14). The parietal muscles are triangular, with about half a dozen folds on each side, which are some of them unbranched, some a little branched (Fig. 14); see also Haddon's Fig. 2, Pl. 36. The microcnemes are six in number in the sectionised specimen, two microcnemes being absent from one of the dorso-lateral compartments. The four microcnemes forming pairs with the lateral macrocnemes are comparatively well developed, the two other microcnemes very weak. The specimens show no traces of reproductive organs.

*Remarks.* As the form is a young one it is difficult to say to which species it belongs, or whether it is a distinct species. In many respects it recalls *E. danica* Carlgr., although the nemathybomes of that species are more numerous than they are in "*tecta*." It is possible that the species is the young of *E. delapiæ*.

### MILNE-EDWARDSIA DIXONII Carlgren.

*Edwardsia timida* Quatref., G. Y. Dixon, Sci. Proc. R. Dublin Soc., 5 (N.S.), 1886, p. 100, Pl. 6; not *Edwardsia timida* of Haddon.

*Milne-Edwardsia dixonii* n.nom., Carlgren, The Ingolf Exp., 5, 9, Actiniaria, p. 59.

*Diagnosis.* Physa well developed, retractile. Scapus long, cylindrical in the lower part, higher up polygonal, at least in contracted state; provided with a rough and opaque but thin periderm, which easily falls away. Nematocysts in the lower part of the scapus arranged in groups, in the upper parts on the ridges between the insertions of the mesenteries. Scapulus cylindrical. Tentacles 18–24 in two (?) cycles. Actinopharynx probably with a ventral siphonoglyph. Pennons of the macrocnemes of average development, forming in the upper part of the cnido-glandular tract about 12–18 high folds, which are branched little or not at all. Outer lamellar portions of the mesenteries attached not far from the outer edges of the pennons. Parietal muscles triangular with few but branched folds. Extension of the parietal muscles on to the column wall about as usual. Nematocysts of the scapus $25–31 \times 5–6\ (7)\mu$, broader at one end and often curved; those of the scapulus $15–25 \times 2{\cdot}5–3{\cdot}5\mu$. of the same appearance as those of the scapus; nematocysts of the tentacles partly about $24 \times 3–3{\cdot}5\mu$, partly $14 \times 1{\cdot}5–2\mu$ (probably also intermediate forms); those of the actinopharynx $17–24 \times 5–3{\cdot}5\mu$.

Many years ago I received three specimens of this species from Mr.

Dixon. Unfortunately they were not well preserved, so that the description here given is somewhat incomplete. I think, however, that it will prove sufficient for the identification of the species. As I have pointed out before (p. 23), the form which Haddon has called *Edwardsia timida* is not identical with Dixon's species. It is very doubtful whether Dixon was right in his opinion that his form was Quatrefages' "*timida*"; as a matter of fact, it is impossible to identify that species on the basis of Quatrefages' description. Therefore in 1921 I proposed a new name, *Milne-Edwardsia dixonii*, for Dixon's form.

*Colour, dimensions, and occurrence.* See Dixon, 1886, and this paper, p. 12.

*External characters.* I have made slides of two specimens; one is sectionised in the lower part, the other in the upper. I cannot determine whether the physa was perforated by pores, as it is badly preserved. The lower part of the scapus is cylindrical, the upper polygonal by virtue of the fact that the ectoderm is considerably higher in the middles of the compartments than at the insertions of the mesenteries. The periderm of the scapus is thin and easily falls away. In the specimen of which I have cut the upper part, the periderm has mostly disappeared from the ectoderm. This species can probably, as in *M. carnea*, form a free tube into which the distal part of the animal can be withdrawn; and because of this fact the boundary between the scapus and the scapulus is not distinct. Since, however, the uppermost cylindrical part of the column, introverted in the sectionised specimen, certainly lacks a periderm, and moreover is provided with smaller nematocysts than the scapus, this part may be the real scapulus. Probably Dixon (see 1886, p. 102) has mistaken part of the scapus for the scapulus. The tentacles are of ordinary length, according to Dixon 18–24 in number and arranged in two cycles, the inner of which should have 8 or 10 tentacles. I cannot confirm this statement, but I think that Dixon's statement as to the arrangement may be incorrect. The outer tentacles are probably

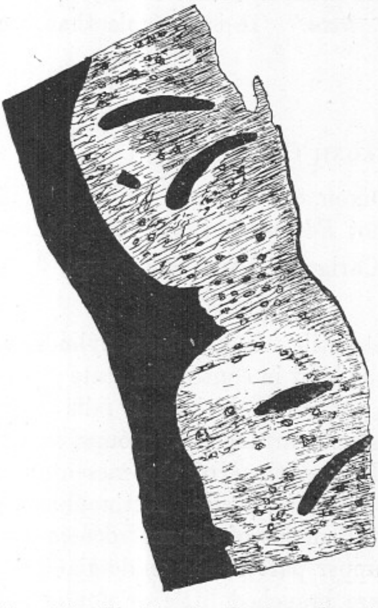

FIG. 15.—*M. dixonii.* Section of part of the scapus-wall. Mesoglœa and nematocysts black, ectoderm shaded.

shorter than the inner (see Dixon's Figs. 2 and 3). The specimen examined by myself had 24 tentacles. The actinopharynx is probably provided with a single and ventral siphonoglyph.

*Anatomical description.* The ectoderm of the scapus is high and contains large nematocysts which are often curved, and in the lower part of the scapus are concentrated into groups (Fig. 15). In the upper polygonal part of the column the ectoderm forms rather high ridges between the insertions of the mesenteries, and the nematocysts are here collected on the ridges, but are absent or very sparse in the furrows (Fig. 16). The ectoderm of the scapulus, which is introverted in the sectionised specimen, is thin, and not thickened in the middles of the compartments. The nematocysts here are smaller than in the scapus. The structure of the tentacles agrees with that of other Edwardsias. The ectoderm of the actinopharynx is very thick, but the cilia are not well preserved.

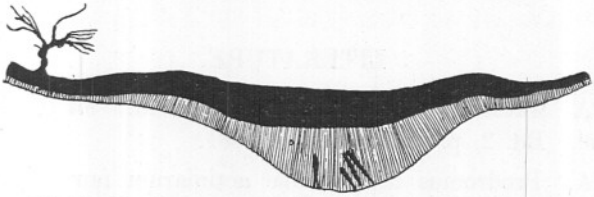

FIG. 16.—*M. dixonii.* Transverse section of a sector of the uppermost part of the wall of the scapus, between the insertions of two macrocnemes. Mesoglœa, nematocysts, and part of a parietal muscle, black; ectoderm shaded.

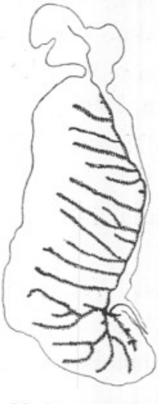

FIG. 17.—*M. dixonii.* Transverse section of retractor near the level of the ciliated tracts of the filaments.

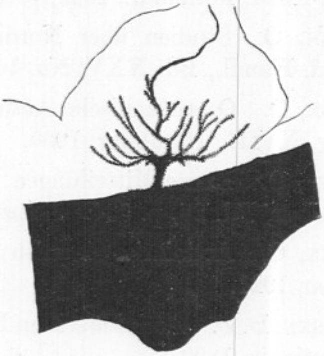

FIG. 18.—*M. dixonii.* Transverse section of parietal muscle in the region of the actinopharynx.

The pennons of the eight macrocnemes (Fig. 17) recall those of *M. carnea*, and form rather few (12–18) folds, issuing from the main lamella. The parietal muscles are also of the same type as those of *M. carnea* (Fig. 18). The microcnemes are present, but not well preserved. The sectionised specimens were not sexually ripe.

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# On the Rearing and Breeding of Gammarus in Laboratory Conditions.

By
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With 1 Figure in the Text.

THE following paper has been prepared in the hope that it will be of assistance to anyone desirous of carrying out experiments on Heredity with *Gammarus chevreuxi*. This Amphipod has been the subject of study at the Plymouth Laboratory since 1912, and the following notes are chiefly concerned with rearing and breeding it under Laboratory conditions.

Details of the work will be found in the papers mentioned in the bibliography on page 54.

## THE GENUS GAMMARUS.

Gammarus,* the earliest established genus of the Amphipoda, has a very extended range and comprises an unusually large number of species. Its representatives are found widely distributed ; in the sea, living either on the shore under stones or seaweed, like *G. marinus*, or leading a more pelagic life, like *G. locusta ;* in the brackish waters of salt marshes and tidal inlets as e.g. *G. duebenii ;* in fresh-water streams and in lakes up to a height of 4000 ft. above sea-level, like *G. pulex ;* in the cold of the Arctic regions ; and even in hot springs.

The species named above are common in British waters, and all have proved very hardy and easy to keep in captivity. In addition to these, numerous other species occur all round our coasts, some of them already known to science, others as yet undescribed, all or any of which would well repay collecting and investigation. The species more particularly dealt with here is a brackish-water form, and was chosen partly because animals of the brackish fauna are able to endure greater variation of conditions than either those from the sea or from fresh water, and partly because this species developed a power of mutation in advance of the other species then under observation. I have little doubt, however,

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* For generic characters, see Stebbing, 1906, *Das Tierreich*, Vol. 21 : Amphipoda, p. 460.

that this power is latent in other Amphipod species and that a closer study will discover its presence. Two or three instances in proof of this statement may be mentioned: the Nowhite-eye mutation which developed in *G. chevreuxi* was also seen in *G. pulex* and *G. duebenii* in the Laboratory; a Red-eye mutation was once seen in *G. pulex;* and another variation, the Irregular Coloured-eye, was found in another Amphipod genus, *Apherusa*. A specimen of *A. ovalipes* Norm. and Scott, captured in the open sea, had the normal round eye on the left side, but the right eye was wedge-shaped and only half the width of the other.

The species of Gammarus vary to a great degree *inter se*, in size, in the number and length of the growth stages to sexual maturity, in the age at which maturity is reached, in the length of the reproductive periods, and in the number and size of the young in a brood.

In all, seven species have been bred for several generations in the Laboratory under practically the same cultural methods. Before proceeding to describe these methods it will be well for the better understanding of a Gammarus and its needs to give a brief account of the structure of the animal. The description is taken from a *Gammarus chevreuxi,* that being the species on which most work has been done.

## DESCRIPTION OF GAMMARUS CHEVREUXI.

The subjoined diagram (Fig. 1) of a male of this species shows the essential points of the external structure of a Gammarus, with the exception of the mouth-parts and the eye, which are omitted in order to avoid confusing the outlines of the proximal joints of the antennæ.

The *body* is elongate and laterally compressed, and consists of head, peræon, and pleon. The *head*, with which the first thoracic segment is fused, carries the two pairs of antennæ, the two eyes, one on each side above the bases of the antennæ, and the mouth-parts. The *peræon* consists of seven segments, each segment provided with a pair of legs, the 2nd to the 7th bearing the gills in addition to these appendages. In the female the incubatory lamellæ of the brood-pouch are attached to segments 2–5. The *pleon* is composed of six segments and the telson, each segment with a pair of appendages, the 6th carrying the telson on its posterior margin.

Taking in order the different parts of the body and their functions they are as follows:—

*First or Upper Antennæ*, each consisting of a 3-jointed peduncle with a long many-jointed *primary* flagellum and a much shorter *accessory* flagellum. The length, i.e. the number of joints, in the latter is frequently used as a specific character, e.g. an adult of *G. locusta* has about 8 joints in the accessory flagellum, *G. pulex* 4, *G. chevreuxi* 5, *G. duebenii* 6, and so on, but this character, though useful, is unsafe unless it is certain that one is dealing with adult animals which have attained their full growth. In the antennal flagella new joints are developed at each growth-stage; in *G. chevreuxi*, for instance, the primary flagellum is 4-jointed

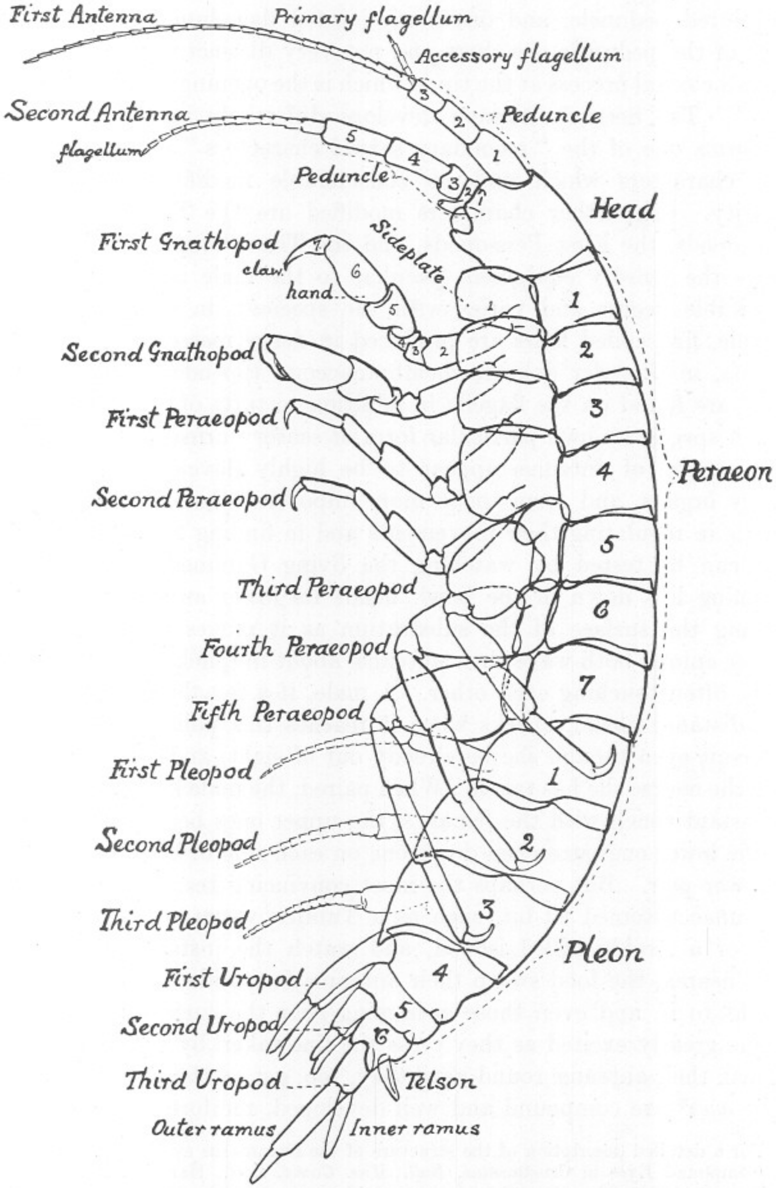

FIG. 1.—Diagrammatic drawing of the male of *Gammarus chevreuxi*. × 10.

on hatching, the accessory 2-jointed. By the time sexual maturity is reached, the number has increased in the female to 20 in the one, and 4 in the other; in the male to 28 and 5; and the number continues to increase until the maximum growth of the species is attained.

*Second or Lower Antennæ*, shorter than the First Antennæ, each with a 5-jointed peduncle, and one many-jointed flagellum. The first two joints of the peduncle are short and not very distinct; the second one carries a conical process at the tip of which is the opening of the " antennal gland." The Second Antenna develops differently in the two sexes, and forms one of the " secondary sexual characters " of the male, i.e. those characters which undergo considerable modification at sexual maturity. (The other characters modified are the First and Second Gnathopods, the First Peræopods, and the Third Uropods.) In all the species the sensory equipment peculiar to the male is developed to a remarkable degree and varies with the species; in *G. chevreuxi*, for example, fine coiled hairs are produced in dense masses on the second antenna, in *G. pulex* delicate membranaceous appendages called " calceoli " are found on the flagella in addition to tufts of setæ, and so on, to each species its own particular form of sensory armature.

Both pairs of antennæ appear to be highly developed tactile and sensory organs, and seem to be more important than the eyes to the animals in regulating their movements and in finding food. This statement can be tested by watching the living Gammarus. An animal swimming low down in the bowl, bends its lower antennæ and keeps touching the surface of the substratum as it moves along; meeting another animal both wave their antennæ about in quick fluttering movements, often touching each other. A male, if a female crosses its path some distance ahead, checks when it reaches this point, turns at once in pursuit even though she be already out of sight, and follows directly along the course she has taken. When paired, the male keeps its antennæ in constant touch with the female's, the upper ones bent to touch hers, and the lower ones stretched down one on each side of her head to reach her lower pair. But perhaps the most convincing test of all is to give some unaccustomed tit-bit, such as a Tubifex worm, a soaked wheat-grain or a freshly killed isopod, and watch the instantaneous effect. Those nearest the food sweep their antennæ from side to side, and dart straight to it, and even those swimming near the surface of the water become greatly excited as they cross the line taken by the falling food, and lash their antennæ round until they, too, get on the right track.

The *eyes** are compound and well developed, reniform in shape, with

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* For a detailed description of the structure of the Gammarus eye, see Parker, 1891, The Compound Eyes in Crustaceans, *Bull. Mus. Comp. Zool.*, Harvard, XXI, No. 2; and Bennitt, 1924, The migration of the retinal pigment in Crustaceans, *Journ. Exp. Zool.*, Vol. 40, Philadelphia.

the corneal cuticle smooth and not facetted (see also p. 45). The superficial aspect of the eye, or ommateum, of the wild *G. chevreuxi* presents the appearance of a chalky-white reticulation with the ommatidia showing as round black spots in the meshes of the network. The ommateum is composed of a number of ommatidia arranged in regular rows, the number increasing at the growth-stages and rising from 10 to 12 in the newly hatched to 70 or 80 in the adult. Each ommatidium possesses, under the thin, transparent, corneal cuticle, a layer of hypodermic cells. Below the hypodermic layer come the crystalline cones, one pair to each ommatidium, the two forming an oval lens. Immediately below the cones, is the rhabdome, a transparent slender rod composed of four elongated segments. The rhabdome is surrounded by five cells, four large and one small, known as the retinular cells, the distal ends of which extend also around the sides of the cone. According to Bennitt (1924) the proximal ends of these retinular cells pass as nerve fibres into the optic ganglion. The retinular cells are deeply pigmented, the pigment in the wild Gammarus being black, and in some of the mutations red. Between the ommatidia lie the superficial accessory-pigment cells, which contain the white pigment of the eye.

*Mouth-parts.*—These consist of an *Upper Lip* attached to the epistome, and a *Lower Lip* at the entrance to the œsophagus : the *Mandibles*, each composed of a basal joint and a 3-jointed palp, the basal joint produced to a dentate cutting-edge with an accessory plate on the inner side, a spine row, and a denticulate tubercle or molar : the 5-jointed *First Maxillæ*, each with the 1st and 3rd joints expanded to form an inner plate carrying setæ and an outer plate with serrate spines, and a 2-jointed palp made up of the 4th and 5th joints ; the 3-jointed *Second Maxillæ* with the 1st and 3rd joints expanded into inner and outer plates fringed with setæ ; and one pair of 7-jointed *Maxillipeds*, with the 1st or basal joints fused, the 2nd and 3rd expanded into inner and outer plates, and the 4th to the 7th joints forming the palps.

*Peræon.*—The peræon contains the heart in a pericardiac sinus, the hepato-pancreatic tubes, and the reproductive organs with the oviducts in the female opening on each side of the 5th segment, and the testes in the male opening on the 7th segment.

*Incubatory lamellæ.*—The brood-pouch of the female is formed of four pairs of broodplates, or lamellæ, attached to the 2nd, 3rd, 4th, and 5th peræon-segments. Several growth-stages (moults) before sexual maturity is reached the broodplates appear, showing first as minute rounded bud-like processes which increase in size at each successive moult and develop hairs along the margins. In the mature female the broodplates are large, the fringing hairs are long and flexible, and can be interlaced in such a way as to make a continuous pouch open only at the two ends where the body-width prevents the plates meeting.

The *branchial vesicles** or gills are attached by slender stalks to peræon-segments 2–7, one pair to each segment; they are of simple structure, and leaf-like in shape.

The seven pairs of *peræopods* are divided into two distinct groups, the first group containing four pairs, the *First* and *Second Gnathopods*, and the *First* and *Second Peræopods*, all bent forward at the third joint, making an open angle in front; and the hinder group with three pairs, the *Third*, *Fourth*, and *Fifth Peræopods* bent backwards at the third joint, making an open angle behind.

The legs are 7-jointed with the first joint greatly expanded in the form of a thin flat plate, known as the *sideplate*. In the first group the sideplates are large and deep, overlapping and protecting the broodplates and gills. The fourth and largest differs in shape from the three preceding by having the distal portion produced to nearly twice the width of the upper part; the shape of this sideplate is a useful character for separating the species of a genus. In the hinder group the sideplates are much smaller, and the second joints are articulated to them in such a way as to allow of an extraordinary flexion of the limb. In Peræopods 3 and 4 the lower margin of the sideplate is deeply cleft, forming two lobes and the widely expanded second joint connected only by a very narrow attachment in the cleft, lies with its anterior expansion below the front lobe and its posterior expansion above the hind lobe, an arrangement which enables the leg to be bent almost to a right angle upwards and backwards against the body. When at rest under a leaf or stone the animal turns its hinder peræopods back in this way and thus brings the terminal claws into a position to hook firmly into the leaf or inequalities of the stone.

The *First* and *Second Gnathopods* are stronger in the male than in the female. They are used for seizing food, and in mating. Both are subchelate, the expanded 6th joint, known as the " hand " forming with the clawlike terminal joint or " finger," a powerful grasping organ.

Of all the parts of the body, the gnathopods, especially those of the male, are the most subject to modification by growth, and as they are the principal external characters employed in specific distinction, it is important to study all the growth stages, and to note in particular the changes in the shape of the hands and the development of their sensory armature. While it is impossible to mistake the fully adult males of the different species of Gammarus, it is easy enough to confuse the young males and females, and the immature. The structure and position of the

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* Sexton, 1913, p. 545, a printer's error in line 20 should be deleted from " and densely " to the end of the sentence.

various sensory spines and setæ will often help in identifying the young stages of any one species.

The *Peræopods* are long and slender, with the terminal joint in the form of a strong curved claw. The sideplates of peræopods 1 and 2 are large and deep; in the hinder pairs the sideplates are short, and the 2nd joints laminarly expanded.

The *Pleon* consists of two groups of three segments each, and the telson. The segments of the first group are wide and deep, increasing in size from the 1st to the 3rd, with the terga produced laterally into large epimeral plates. Each segment bears a pair of *Pleopods,* which function as swimmerets and differ in structure from the other appendages. A pleopod is composed of a stout basal joint or peduncle, and two flexible many-jointed rami. The basal joints are provided with coupling-spines by means of which each pair can be hooked together; the rami carry two long plumose swimming-hairs on each joint, the inner ramus in addition being furnished with cleft spines on its first joint. The pleopods beat with a steady rhythmic movement, keeping up a constant current of water over the gills and through the brood-pouch.

The three remaining pleon-segments, sometimes called the urosome, rapidly decrease in size, the 6th being very small. They are capable of great flexion, and, moving together as one joint, they form a powerful springing or jumping organ. The posterior margins are armed with three groups of spines and setæ, one median and two lateral. The second pair of legs, or uropods, is the shortest, the third the longest. Each uropod consists of a basal joint and two slender rami, beset with spines. The rami of the third pair are broad and fringed in the adult with spines and plumose hairs; the outer ramus is 2-jointed, the terminal joint very small.

The *telson* is small and cleft.

*Size.—Gammarus chevreuxi* is a small species, full-grown males measuring about 11 mm. and full-grown females about 7 mm., the largest recorded being 14·5 and a bare 9 mm. respectively. The measurements are taken from the tip of the rostrum along the dorsal line to the tip of the telson.

The species is easily distinguished (see **1**) from the others of the genus by the antennæ, the shape of the fourth sideplate, gnathopods, and third uropod, and particularly by the fine coiled hairs peculiar to the male secondary sexual characters.

*Colour.*—The body is semi-transparent with the internal organs showing through the thin chitinous cuticle. The normal wild animals are a pale greenish colour, the males yellower than the females, with the antennæ banded with brown, and the mouth organs tinged with crimson. The intestine shows as a line down the body, coloured according to the food last eaten; in the female the dark green masses of the gonads can be seen lying above it in the peræon. The pleon segments have a bright red spot on each side, composed of numbers of red oil globules.

A new mutation has lately arisen in which the body is a translucent pearly-white, with no trace of colour even in the gonads and eggs of the female.

*Growth.*—The development of Gammarus and of Amphipods generally may be described as a series of growth-stages definitely marked off the one from the other by moults, i.e. the complete casting of the hard chitinous cuticle (see **11**).

The period between moults is short in the immature, and the increase in size considerable at each stage up to the time of sexual maturity. This point is reached when the animal is about half-grown, and from then onwards until it attains the maximum length of the species the moults take place at longer intervals and the increase in size though constant is much more gradual and therefore less noticeable at each stage. After full growth is established the difference between the stages is practically imperceptible and is usually concerned with the cuticle and its outgrowths, the chitin becomes thicker, a few more setæ are developed or slightly modified, and the colour darkens.

The rate of development is affected to a large degree by temperature and to a lesser degree by the seasonal rhythm. Young hatched in the winter months take longer to reach maturity, even though the temperature be raised to summer conditions, than those hatched in the spring and summer.

*Sex and Reproduction.*—The sexes cannot be distinguished on hatching nor for several stages afterwards, not, indeed, until the animals are approaching maturity.

The newly-hatched *Gammarus chevreuxi* measures about 1 mm. in length, and resembles the adult in that the full number of the appendages is present. The full number of joints also is present in most of the appendages, as e.g. in the gnathopods, peræopods, and uropods; but certain structures such as the flagella of the antennæ and the rami of the pleopods, develop new joints at each succeeding stage of growth.

The number of stages from birth to sexual maturity varies with the species. In *G. chevreuxi* maturity is reached at the eighth stage, and up to the fifth stage it is impossible to distinguish the male from the female by any external character; they are identical in size and form, even to the number of the setæ and spines. In the fifth stage, broodplates are present in the female, but being microscopic in size, they are exceedingly difficult to trace. In the sixth stage, however, the difference between the sexes becomes plainly evident, one or two of the coiled hairs peculiar to the male appear on the lower antennæ, and the broodplates of the female can be seen as small oval plates, with rudimentary hairs on the margins.

The age at which sexual maturity is reached depends largely on temperature. In summer the time taken may be only 36 to 40 days; in winter conditions 2, 3, or 4 months may pass before breeding begins.

The male pairs with the female several days before mating takes place, sometimes for as many as 8 or 9 days. During this period the male carries the female, and holds her usually with its second gnathopods, the right-hand claw being inserted under the anterior edge of the tergum of her first peræon-segment, and the left-hand claw turned backwards and inserted under the posterior margin of the fifth segment. Sometimes the male's first gnathopods and first and second peræopods are also brought into action to help steady the female when swimming rapidly, or to assist her in moulting. As soon as the female moults pairing takes place, and mating follows usually at once. The sperm is ejected into the open pouch, and the eggs are then laid directly afterwards, two at a time, one from each oviduct, until the ovaries are emptied. The eggs are held together at first by the secretion which accompanies oviposition. They can only be deposited while the skin is soft and elastic after a moult, and the apertures of the oviducts are open.

Oviposition is still possible up to the third day after moulting, but, should no eggs be laid by that time, the pair usually separate and no further mating can take place until the next reproductive period, and then only after another moult. The number of eggs laid at the first mating is usually small, rarely reaching 10; sometimes these hatch normally, sometimes they are thrown off in a day or two. The number of young in a brood increases as the female grows. The largest brood recorded for *G. chevreuxi* numbered 63, but this is an exceptional figure, 30 to 40 being a fair average. The female mates at regular periods; the male, however, has no defined mating period, but can fertilise several females in succession. In this species eggs are never deposited unless a male is present. The females breed continuously all the year round, only now and again missing a period until they reach the age of 12 to 18 months, and become too old to lay. Pairing again and again with no results they usually end either by dying in moulting, or by being eaten by the male.

Twenty-six is the highest number of broods recorded so far for one pair, the number of young hatched being as follows: 8, 21, 39, 31, 29, missed a period, 27, two broods* numbering 17 together, 32, 39, 37, 20,* 39, 33, 34, 29, 41, 48, 42, 32, 52, 43, 29, 26, 29, 3. The female had one brood of 6 with another male, and two batches of eggs which did not develop with a third male, and was then eaten.

The number of young in a brood varies with the species, but the size of the species is no gauge of either the size or the number of young. *G. chevreuxi* is a small species compared with *G. pulex*, yet it produces up to 63 young in a brood, whilst the highest record for *G. pulex* is only 28. The *pulex* young are much larger, but the difference in the size of the young is not correlated with the species size as might be thought from this example. In *G. locusta* the female is practically identical in measurements with the female *G. pulex*, but her young are minute, much smaller even than those of *G. chevreuxi*, and her average brood numbers from 140 to 150.

*Gammarus chevreuxi* was first found in the ditches draining Chelson Meadow, a salt marsh near the mouth of the Plym. The land, reclaimed a little over a century ago, is protected from the tidal waters by an embankment, with the drainage emptying into the Plym at low water by means of sluice-gates. A fresh-water trickle runs in at the upper end of the Meadow, and sea-water occasionally enters over the sluice-gates. Several species of Gammarus are found, *G. pulex* inhabiting the stream, *G. duebenii* and *G. chevreuxi* the brackish ditches near the embankment.

## CULTURAL METHODS.

The animals are kept in finger-bowls covered with square glass plates to exclude dust and prevent evaporation. We find the most useful size is 13 cm. measured across the top. Glass meat-jars can be used and are cheaper, but finger-bowls are better for the purpose. The rounded sides and bottom prevent the settlement of injurious bacteria or infusorians, and the glass being clear enables one to observe the animals without disturbing them unnecessarily.

The bowls are only half filled, in order to expose as large a surface of water as possible to the air and so provide sufficient oxygen for the animals' needs. This applies more especially to *G. chevreuxi* and *G. pulex*, but even the pelagic species such as *G. locusta* which naturally require a far greater amount of oxygen, can also be brought to live in stagnant water, though it may be found necessary at first to give the newly-captured some sort of air circulation and then gradually to reduce the supply for their young.

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* These broods were not examined for some days after extrusion and the number of young found is therefore less than the number hatched.

*Water.*—*G. chevreuxi* in its wild state inhabits brackish water ditches, the salinity of which, affected by the state of the tides and the rainfall, varies from day to day. For Laboratory work we find it better to keep to a constant salinity, and the water used in the experiments has therefore been standardised, one part sea-water to four parts fresh water. The sea-water is brought in from the open sea, beyond the reach of contamination by shore bacteria. Brackish water, however, is not absolutely essential to the culture of this species. It will live equally well in fresh water provided only that the change in conditions be made very gradually and extended over a period of several weeks. All the British Gammarus are hardy creatures, capable of adapting themselves to alterations of environment if, as has just been said, sufficient care is exercised in making the alteration. Three species, the marine *G. locusta*, brackish *G. chevreuxi*, and fresh-water *G. pulex*, which were kept in this Laboratory in different salinities ranging from supersaturated salt water to fresh water, lived and bred equally well in all.

The water in the bowls does not really need changing, although as a matter of practice while the breeding-bowls are under observation it is partly renewed when the broods are hatched. Each brood is given a separate bowl and a little of the water in the parents' bowl is poured off into the brood-bowl, standardised water being then added to both to bring the level right again. Experience has shown that the young do better in a mixture of this kind, and the breeding animals also profit by the change of water. No regular air circulation is needed, but an occasional pipetting of the water with a sterilised pipette is beneficial to them.

*Food.*—Most Amphipods will devour almost anything in the nature of organic matter from rotting seaweed to dead animals, and Gammarus is no exception to this rule. They do not usually attack living creatures unless they have them at a disadvantage, as for example in the exhausted condition following a moult. In such circumstances a female often falls a victim to the male's voracity. Unfortunately, once a cannibal always a cannibal, and any animal caught in the act must be removed at once from the bowl.

Animal food is much preferred to vegetable, but as it seems almost certain that a flesh diet, apart from the danger of fouling the water, encourages the cannibal instincts, we have given it up in favour of a purely vegetable regime. The food found by experience to be the most suitable is rotted leaves, and preferably elm leaves. The harder leaves of oak and beech are sometimes eaten, but only if it is a choice between them and starvation.

The dead leaves are collected in the autumn after a frost, well dried in a sunny window, and stored for use. When wanted, they are washed and soaked in fresh water for a day or two. It is advisable to soak only a small quantity at a time and to change the water at frequent intervals to prevent the formation of slime due to bacterial growth. One medium-size elm leaf is quite sufficient for a breeding pair. By the time the brood is hatched the leaf will be eaten nearly to a skeleton, only the ribs and some of the soft parts being left. The skeletonised leaf is the best food the young can have, and after a thorough washing it should be given to them and a fresh leaf put in the parent-bowl.

A change of food is sometimes beneficial. Wheat grains soaked for two or three days are eagerly taken ; a half-grain is enough to give at a time in addition to the leaf. The hard-boiled yolk of an egg is also acceptable, but proves a costly item when hundreds of Gammarus have to be fed. Green seaweeds such as Ulva and Enteromorpha were given at one time, but their use has been discontinued, owing to the difficulty of getting them free of other Amphipod young.

*Light.*—The bowls should be kept in ordinary diffused daylight and never exposed to direct sunlight. The Gammarus usually shelter under the leaves, out of the light.

*Temperature.*—Experimental work has been done on *G. chevreuxi* in temperatures ranging from 70° to 36° or 38° Fahr. Batches of eggs laid on the same day hatched in 8 days at 70°, but took 80 days in the cold. The species breeds all the year round in the ditches, but the rate of development, as would be expected, is greatly retarded by low temperature in the winter months.

*Sterilisation.*—The greatest care must be exercised when examining the broods to keep the instruments sterilised. The pipette and rubber top should be thoroughly heated after each brood to prevent the risk of a young one creeping into the top and emerging later when another brood is being examined. It is very easy to lose sight of one in this way, as it is semi-transparent and measures only 1 mm. in length, and moves with great rapidity. The glass slip must be sterilised each time as well as the watch glasses into which the young are counted. A very effective steriliser can be made of a large round enamel basin, filled with water deep enough to take a finger-bowl, kept boiling on a tripod over a bunsen burner.

*Examination Methods* for eye-colour, mutations, etc. As soon as a brood is extruded, the young are picked out with a fine pipette, counted, and if possible examined immediately for eye-colour. It is important in all cases that this should be done at once, because of the heavy mortality usual at the first moult ; but in certain instances, such as the Changeling White mutation for example, where the colour alters soon after hatching, the record is of no value unless the examination is done immediately, for animals about which there is any doubt cannot be used in the experiments.

For examination, each young one is taken out separately on a glass slide, the water is drained off and the slide held tipped under the microscope 1 in. obj., and the eye uppermost looked at; then the slide is turned quickly, and the other eye examined, colour, irregularity, and spots being noted. The tipping of the slide is for the purpose of keeping the animal as dry as possible, and so preventing its wriggling. Speed is necessary to avoid a prolonged exposure to the air, and a little practice renders it easy to do the work at the rate of ten seconds to each normal young. Anything abnormal, such as malformation, or irregularity of eye, takes a longer time, and as these abnormal ones need even more care than the others, it is well to add a drop of water at intervals to refresh them.

*System of Records.*—Each experiment has its own distinctive letter or number, and its own series of Record Books. Each breeding pair in an Experiment has a bowl to itself and is given a number, and this number, with the Experiment letter or number preceding it, is marked on a label on the cover, together with the dates on which the bowl is looked at. The details of the daily observations are kept on loose sheets of paper; and include particulars of the derivation of the animals, the dates of matings, moults, oviposition, the date on which the ripening eggs change colour, from dark green to yellow and from yellow to orange, and the date on which the young are extruded. All these details are afterwards entered up for permanent reference in the Record Books.

## MUTATIONS IN GAMMARUS CHEVREUXI.

The first mutations which arose in this species were connected with the eye, its structure, shape, and colour (see **4** and **6**).

The normal eye or ommateum is reniform in shape and convex, with the margin entire (cf. p. 37). It is composed of numerous ommatidia arranged in regular rows, and showing as round coloured spots in a network of white The coloured pigment is contained in deep-seated retinal cells around the bases of the ommatidia; the white pigment on the other hand is quite superficial. The retinal colour in the wild animal is black, and up to the present time none but black-eyed have ever been found in the ditches, although many thousands have been dredged from time to time and examined for eye-colour. That the black, however, was not a pure black was found by observing the developing embryos of females freshly brought in.

Two sets of females were kept under daily observation, 15 which had laid eggs on January 28th, and 13 with eggs on the 29th. The incubatory period of the first set was 12 days; that of the second, owing to a drop in the temperature on the 11th day, was 13 days.

One female was taken daily from each set, and the eggs were removed from the pouch and examined under the microscope. The first sign of the eyes appeared on the 9th day. Three to four ommatidia with minute lenses were seen, and the margin of the ommateum could be traced. The pigment was bright red. By the next day the colour had altered a little and deepened to a darker shade of red, the shape of the ommateum was much clearer and the number of the ommatidia had increased to 8, or to 7 with a rudimentary 8th showing. On the 11th day the eye was well formed, and the colour had changed to dark red, or rather to a mixture of red and blackish brown pigment, darkest in the centres of the ommatidia. The accessory white pigment was also present, particularly around the margin of the ommateum. The eggs hatched on the 12th day, and all the young had black eyes, with the reticulation of the white accessory pigment well developed.

In the second set, as in the first, the same change took place from bright red on the 9th day to the deeper intermediate red on the 10th, and from that to the dark red on the 11th day, but this stage, owing to the colder weather, lasted for two days and the eggs did not hatch till the 13th day.

*Mutant Stock I.*—The original stock, all normal Black-eyed animals, was brought in on June 4th, 1912, and in it the first mutations occurred.

The first to arise was the *Red-eye*, in which the usual black pigment was replaced by red, the white reticulation and the shape of the eye remaining unaltered.

The Red-eye appeared in the $F_2$ generation from the wild Black, from one female only. This female was first mated with a male from the same brood and had 2 broods, with 7 and 6 survivors respectively. The 7 survivors were 1 Black male, 5 Black females, and 1 Red female; the 6 were 1 Black male, 4 Black females, and again 1 Red female. The female parent was then mated with a Black male just brought in from the ditches, and had a brood of 44 young, 4 of which were Red-eyed. She was put with the first male again and had a brood of 39, 3 of which were Red-eyes. With both males, Red-eyed offspring were produced, but these males mated with other females gave only Black-eyed young, and no other instance of a Red-eye appearing has occurred in this stock from then till now. All the Reds of this kind that we have had were derived from 2 heterozygous Black-eyed survivors of this female's third brood.

The Red was mated with Black and proved to be a simple Mendelian recessive. The first 70 $F_2$ broods numbered 1004, 753 Black-eyed and 251 Red-eyed.

In this mutation the red pigment on hatching is almost invariably a vivid bright red; very occasionally a young one is found with the centres of the eyes of a much darker tint, and still more occasionally one with the whole of the eye of the darker colour. In very old animals the colour tends to darken with age, particularly towards the end of a reproductive period, and brightens after a moult has taken place.

This difference in the intensity of the colour is mentioned here for comparison with Mutant Stock IV, in which similar colour variation has occurred. In Stock IV, however, the different colour variations are heritable.

Two instances of a perfect form without colour, i.e. *White-eye*, occurred in a brood of the Pure Reds. One, a female, died without mating; the other, a male, mated with an Albino female and gave 1 brood of coloured offspring, 2 Black, 3 Red. Breeding from this brood was carried on for several generations, Black, Red, and Albino reappeared, but no White-eye, and the conclusion was reached that the male functioned as a Red-eye, and the white condition in this case was pathological and not heritable.

Three years after the appearance of the Red and after the Stock had been kept for several generations in Laboratory conditions another mutation, the *Albino eye*, arose. One of the $F_2$ broods from a mating of Pure Black with Pure Red consisted of 7 Black, 1 Red, and 4 Albinos. The total number of offspring from this mating was 745, 559 Black, 182 Red, and 4 Albino. Two Albinos, females, survived to maturity, and from these all our Albino stock has been derived. No second case of Albino-eye has arisen independently up to the present time.

In this mutation the eye is degenerate, considerably reduced in size, and very irregular and variable in shape, the eyes in the same animal often differing to a great degree in size and shape, and in the number, size, and arrangement of the lenses of the ommatidia. This imperfection of form is always linked with the absence of retinal colour. The white superficial pigment alone is present, not in a regular reticulation as in the normal eye, but in irregular patches or lumps, with the lenses lying usually around the margin or even beyond it.

The Albino Imperfect eye behaves as a simple recessive to the Coloured Perfect eye. The Albinos carry the colour factor for Pure Black, Black and Red, or Pure Red, but they cannot show colour unless mated with colour. Bred together they give all Albino offspring.

In another mutation, the *Nowhite* eye, the white superficial pigment is entirely lacking, and the absence of the white behaves as a recessive to its presence.

This mutation arose suddenly in the Coloured Stock after it had been kept in Laboratory conditions for two and a half years, both Black Nowhites and Red Nowhites appearing in the $F_2$ from a mating of Pure Black with Pure Red.

The Albino Nowhite or Colourless (see **4**) was produced by breeding Coloured Nowhite with Albino. The resultant $F_1$ offspring were normal in appearance, the perfect form and the presence of coloured and of white pigment being dominants. In the $F_2$ the triple recessive appeared, Albino Nowhite, in which the form is imperfect, and both retinal colour and white pigment are lacking. The proportion was 27 Black normal, 9 Black Nowhite, 9 Red normal, 3 Red Nowhite, 12 Albino normal, and 4 Albino Nowhite.

The Nowhite, unlike the other mutations, Red and Albino, has arisen independently many times in our Experimental Stocks and evidently occurs, though very rarely, in different Gammarus species in the wild state. One Nowhite *G. pulex* and one *G. duebenii* have been taken.

The white accessory pigment is subject to a good deal of variation and tends to grow thinner with age, breaking up and even partially disappearing in the very old animals.

In one family of this stock a gradual reduction of the white pigment took place from birth to maturity. The eyes were normal at birth, but in four generations not one single survivor reached maturity with the white reticulation normal. From one pair, e.g. 311 young were hatched, 309 with perfectly normal eyes, and 2 with one eye Nowhite ; 170 were "spotted," i.e. having spots of white pigment apart from the eye. By the time they became mature, some had only a fleck or two of white left, some had one eye Nowhite and hardly any reticulation in the other eye, while others were completely Nowhite and indistinguishable from typical Pure Nowhites. One of these Gradual Nowhites, an Albino Nowhite female, mated with a Pure Nowhite Black male and hatched a brood of 14 young, all normal Black in appearance with perfect white reticulation.

It is a curious fact that large white "spots" apart from the eye are found on many of the Pure Nowhites which arise suddenly from normal parents (see **6**). This is particularly the case when there is any admixture of Albino in the parents' constitution. In the One-sided Nowhites, i.e. those animals with one eye normal and one eye Nowhite, the spots usually occur on the same side as the Nowhite eye, and are very large, much larger than in normal-eyed animals. These spots are usually in definite positions, midway on the head behind the eye, dorsally on the head, or midway on the first peræon-segment over the intestine.

Other mutations to be noted from this stock are the *Imperfect Coloured* eye, the *Blind*, and the *One-eyed*.

The *Imperfect Coloured* eye differs greatly from the Imperfect Albino eye, in that the eye though irregular in shape is not degenerate. The ommatidia present are of normal structure with the retinular cells developed, but the shape of the lenses varies sometimes and the number and arrangement also. In some the number greatly exceeds that of the normal eye, in others it is much below it.

The irregularity of eye appears to be connected with irregularities of development and breeding. The family which produced these abnormal eyes gave rise also to the Blind, the One-eyed, and the *Intersexes*.

Most of the Intersexes (7) appeared in the Irregular-eye family, but once four were found in a dredging brought in from the wild after a prolonged drought. The female intersexes show varying degrees of intersexuality, and may be divided into three groups according to the development of their brood-plates and the character of the gnathopod hands.

In all cases in Mutant Stock I the matings have given results in accordance with the simple Mendelian law, and to illustrate the closeness with which the figures obtained by experiment agree with the theoretical expectation the following instances will serve :—

Matings of Blacks carrying Albino—624 young.

| | Normal Black. | Normal Albino. |
|---|---|---|
| Theoretical Expectation . | 468 | 156 |
| Experiment . . | 468 | 156 |

Matings of Reds carrying Albino—1879 young.

| | Normal Red. | Normal Albino. |
|---|---|---|
| Theoretical Expectation . | 1408 | 470 |
| Experiment . . | 1408 | 471 |

Matings of Blacks carrying Red, Albino, and Nowhite—663 young.

| | Normal Black. | Black Nowhite. | Normal Red. | Red Nowhite. | Normal Albino. | Albino Nowhite. |
|---|---|---|---|---|---|---|
| Theoretical Expectation | 278 | 92 | 92 | 30 | 123 | 41 |
| Experiment . | 278 | 93 | 89 | 50 | 118 | 35 |

Matings of Reds carrying Albino and Nowhite—220 young.

| | Normal Red. | Red Nowhite | Normal Albino. | Albino Nowhite. |
|---|---|---|---|---|
| Theoretical Expectation | 124 | 41 | 41 | 14 |
| Experiment . | 127 | 38 | 42 | 13 |

The Mutant Stocks II, III, and IV originated from three independent Black-eyed pairs from one dredging brought in from the wild in 1922. In all three stocks Red-eyes appeared recessive to Black-eyes. The proof that these were different mutations, distinct from each other and from the old Mutant Stock I, was obtained by cross-mating the Red-eyed recessives of all four forms. Whichever way the mating was made the offspring were all Black-eyed, thus settling the matter beyond question.

*Mutant Stock II.*—Hitherto all the changes had been connected with the eye, and its colour and shape, but in this stock there was a new departure, the *White-body mutation*, a change in the colour of the body as well (**15**).

The body-colour of the normal animal is pale green, the female having dark green, almost black gonads and eggs. The eggs as they develop turn yellow and then orange. In the new mutation the whole animal is pearly-white, even to the gonads and eggs. The eggs are so translucent that it is impossible to see them during the whole period of incubation except by transmitted light.

The mutation appeared in the $F_2$ from the wild. An $F_1$ pair of Black-eyed gave in their offspring, normal body Black-eyed; white body Black-eyed, with white gonads and eggs; normal body Reds; and two white body White-eyed, a male and female, the female with white gonads and eggs. This White-eyed female mated with a Red male of the same brood, and gave all White-eyed young, but these young though indistinguishable from each other at birth proved to be of different constitution, viz. Permanent Whites and Changeling Whites. The Permanent or homozygous Whites remain white through life, eyes, body, gonads, and eggs; but the Changelings develop colour, and by the time they are mature they have all the appearance of normal Reds, that is, green body, dark green gonads and eggs, and bright red eyes (for explanation see **17**).

The different kinds of animals in this Stock are as follows :—

(1) Black-eyes, normal body-colour, which, mated together, give either (*a*) all Black, (*b*) Black and Red, or (*c*) Black, Red, and White young, according to their constitution ;

(2) Black-eyes, white body, giving Black and White ;

(3) Red-eyes, normal body-colour, giving either (*a*) all Red, or (*b*) Red and White in the proportion of 3 : 1 ;

(4) Changelings, which give (*a*) Red and White in the proportion of 3 : 1 when mated together, (*b*) Black, Black and Red, or Black, Red and White when mated with the different Blacks, and (*c*) all Black when mated with recessives from any of the other stocks ;

(5) Permanent or homozygous Whites, which give (*a*) all White when mated together, (*b*) Black and White when mated with Blacks carrying Red, or with Blacks carrying Red and White, and (*c*) all Black when mated with Recessives from any of the other stocks.

When, however, these Permanent Whites are mated with Reds or Changelings of their own stock we get the remarkable result that the reciprocal crosses are quite different; thus, any Red male of the stock mated with a homozygous White female (white gonads) gives all White-eyed young, consisting of Whites and Changelings; but the reciprocal cross homozygous White male by Red female (dark gonads) gives either all Red-eyed young if the female is Pure Red, or Reds and Whites if the Red female carries White. Similarly White male by Changeling female (dark gonads) gives half Reds and half Whites (the actual figures are 131 Reds, 130 Whites), whereas the reciprocal cross, Changeling male by White female, gives all White-eyed young consisting of Whites and Changelings.

*Mutant Stock III.*—This is the only stock so far in which we have found "mosaic" eyes, i.e. eyes with some of the ommatidia black and some bright red. This stock differs from the three others described in that the Red-eye mutation did not arise suddenly, but developed gradually in the $F_2$ generation. In two of the $F_1$ families some of the Black-eyed became reddish black as they matured and produced some Red-eyed offspring.

To take an instance from each family: in one brood of the first family, of the 5 survivors, 4 had become Reddish-black and 1 was still jet-black. This Black, a male, mated with a Reddish-black, gave 30 Black and 13 Reddish-black; only 3 of the 30 survived and all 3 developed the reddish tinge. Two of the Reddish-blacks were mated, and gave 17 Black, 11 Reddish-black, and 2 Dark Red. The female of this pair, mated in the brood-bowl, had 6 young, 5 Black and 1 with the left eye of the curious "mosaic" type mentioned above.

In the second family one Reddish-black became redder as it matured, and its left eye developed into a typical mosaic eye with almost as many bright red ommatidia as black. One pair of this family had 255 young, of which 224 appeared to be Black, 13 Reddish-black, 13 Dark Red, 3 Intermediate, and 2 Bright Red.

The eye-colours in this stock are not only very difficult to define at birth, but are so subject to change with growth that it is almost impossible to give the actual figures of the different kinds with any certainty.

Black is closely allied to Reddish-black (Black with a distinct reddish tinge) and Reddish-black to Dark Red (dark brownish-black in the centres of the ommatidia and red around the margins); but some Blacks remain black and others develop the reddish tinge; some Reddish-black are unchanged, others become Dark Red; some Dark Reds never alter, others lighten a little in colour and lose the brownish tint, and others again become completely red.

*Mutant Stock IV.*—The stock is particularly interesting as having in addition to the Black three distinct kinds of Red-eyes, a Bright Red-eye, with the usual brilliant scarlet pigment; an Intermediate Red like the second stage in the eye-colour of the embryo (p. 46); and a very dark Red almost black, like the last stage of the embryo before hatching. The exceptional feature of the last is that the dark red colour *lightens* as the animal grows older. Sometimes the eye becomes a brilliant red, indistinguishable from the Bright Red-eye, at other times the periphery of the eye lightens, and the centre remains dark. But however great the change may be in the colour of the eye, the constitution of the animals remains unaffected, for those which have lost all the dark pigment, and those which have retained the most of it, give the same results in the offspring.

## Crossing Gammarus Species.

Attempts have been made from time to time in the Laboratory to cross the various species under observation, but although a certain measure of success has been reached in so far that some of the animals mated and laid eggs, yet up to the present the net result is failure; no young have been hatched from a cross. The bars to cross-breeding distinct species appear to be, and probably are, insuperable, though that perhaps is a point on which one ought not to speak definitely without further experiment.

The greatest difficulty to be encountered is the different development of the various species, the size, growth stages, breeding habits, length of the breeding periods, and the incubatory periods, and so on. Other differences, of habitat and salinity for example, can be overcome, provided only that sufficient time is taken in changing the conditions, while bringing salt-water species to fresh water and vice versa. The marine species need a much larger amount of oxygen than either fresh water or brackish, so that it is necessary at first to use with them an air-circulation system, though this may be dispensed with gradually.

Each of the species used in the experiments was divided into three stocks, one stock brought to live in fresh water, one in brackish, and one in sea-water. As a general rule the females were kept to their own waters, and the males subjected to the change of condition, for instance in the crosses *G. Chevreuxi* brackish, with *G. pulex* fresh water, the males were taken from the *Chevreuxi* stock which had been kept for several generations in fresh water.

The species used in the experiments were *G. locusta*, marine; *G. marinus*, marine, littoral; *G. Chevreuxi* and *G. duebenii*, brackish, from a salt marsh; another brackish water species, not yet named, from brackish pools at Cawsand within the tidal zone; and *G. pulex*, fresh water, rivers and streams.

The results are briefly as follows :—

No matings were obtained from the undermentioned crosses.

| | | | |
|---|---|---|---|
| ♂ *locusta* | and | ♀ *marinus* | |
| ♂ *marinus* | ,, | ♀ *locusta* | |
| ♂ *marinus* | ,, | ♀ *duebenii* | ♀s eaten. |
| ♂ *duebenii* | ,, | ♀ *marinus* | ♀s eaten. |
| ♂ *pulex* | ,, | ♀ *duebenii* | |
| ♂ *duebenii* | ,, | ♀ *pulex* | ♀s eaten. |
| ♂ *duebenii* | ,, | ♀ *Chevreuxi* | ♀s eaten. |
| ♂ *Chevreuxi* | ,, | ♀ *duebenii* | ♀s eaten. |
| ♂ *Chevreuxi* | ,, | ♀ *locusta* | |
| ♂ *duebenii* | ,, | ♀ *locusta* | |
| ♂ sp. | ,, | ♀ *duebenii* | |
| ♂ sp. | ,, | ♀ *marinus* | |
| ♂ *marinus* | ,, | ♀ sp. | |
| ♂ *pulex* | ,, | ♀ sp. | ♀s eaten. |

In the cross ♂ *sp.* and ♀ *pulex* in fresh water, 7 males and 14 females were used ; 4 females paired, 1 twice, no eggs were laid ; all the females eaten.

In the cross ♂ *sp.* and ♀ *Chevreuxi*, 144 males and 229 females were tried in the brackish-water experiments, 2 pairings took place, 1 lasting 10 days, no eggs were laid. In the fresh-water experiments 6 males and 12 females were used, no mating ; all the females eaten.

The reciprocal cross—259 ♂ *Chevreuxi* and 201 ♀ *sp.* in brackish water—was successful in that 27 matings occurred, and eggs were laid in six cases, 4 females carried them 9, 6, 13, and 18 days respectively before throwing them off. Two males and 6 females were used in the fresh-water experiment ; 2 matings ; and eggs laid.

The cross, ♂ *pulex* and ♀ *Chevreuxi*, fresh water, 22 males and 35 females, resulted in 5 pairs mating ; no eggs laid.

The reciprocal crosses were made with 104 ♂ *Chevreuxi* and 44 ♀ *pulex* in fresh water ; 15 females mated, 5 batches of eggs were laid, one female mated 4 times ; one 3 times, laid eggs and was eaten ; one mated for 7 days, laid eggs, carried them for 13 days, mated again for 3 days, no eggs, mated again for 13 days, no eggs, mated again and was eaten. Another female mated for 10 days, no eggs ; again for 11 days, eggs laid and carried for 18 days ; mated again and eggs, carried for 13 days ; mated again and eggs once more.

In the experiments referred to above the method of mating was as follows : several ovigerous females of the one species were taken, and kept in a bowl without a male until the eggs were within a day or two of hatching, and the females therefore in the right physiological condition for mating. A paired male of the other species was then separated from its mate, and placed in the bowl with all the females. If it did not pair within a few hours it was taken out, and another male tried. If this one paired, the other females were removed and the pair left to themselves. The bowl was kept under constant observation, the female's own brood being removed immediately on extrusion and a note made of the time at which she moulted and when the new eggs were laid. There could be no question of mistake with the matings done in this way. New eggs show as a small round almost black ball in the middle of the pouch, ripening eggs as a yellow or orange mass filling the whole pouch. Separating a male from its mate can be easily done before the brood is extruded by putting the pair on a glass slide and draining all the water off. If this method fails to part them in two or three seconds, the warmth of the hand under the slide will usually effect it; but if the male refuses to let go, it is better not to continue too long as the struggles of the female may end by injuring her. If possible, a male which has moulted some days previously should be used. A male which has only just accomplished its moult is a great danger even to its own species, as at such a time it is more voracious than usual, and if the female moults while it is still hungry there is little chance of her escaping.

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# The Life History of *Thysanoessa raschii.*

By

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With Seven Plates.

## INTRODUCTION.

### *Thysanoessa raschii* (M. Sars).

Synonyms—*Thysanopoda raschii* M. Sars, *Euphausia raschii* G. O. Sars, *Boreophausia raschii* Norman, *Rhoda jardineana* Sim, Scott, *Rhoda raschii* H. J. Hansen, *Thysanoessa raschii* H. J. Hansen.

*Thysanoessa raschii* is a regular inhabitant of the Firth of Clyde. Adults are found throughout this area, generally in waters not less than 40 fms. deep. Those of large size, 23–25 mm., are apparently consistently found from year to year in Loch Striven in large numbers from October to January within 10 fms. from the bottom in waters of 40 fms. depth. Throughout the rest of the year they occur in small numbers in the tow-nets, and are seldom found at all during the summer months. On one occasion, however, February, 1926, several hundreds were fished in addition to large numbers of *Meganyctiphanes norvegica* at 40–60 fms. in the Cumbrae Deep. *T. raschii* has two spawning periods in the year ; the first from the end of February to the middle of May, the second from the middle of August to the middle of September. These spawning periods may vary by a few weeks in time of commencement and duration from year to year. Eggs are found near the surface, and are specially abundant and most consistently found over depths not less than 40 fms. As is the case with *M. norvegica*, I find that in daylight at all depths during spawning adult specimens are rarely found in the tow-nets, even in those areas where eggs or larvæ are abundant. The appearance of large numbers of adult *T. raschii* in the tow-nettings from Loch Striven shortly after autumn-spawning has ceased is very striking. This congregation of individuals continues till early spring, as mentioned above, when the numbers caught are considerably reduced. From March till the end of the autumn-spawning period, when large numbers again appear in Loch Striven, adults are rarely obtained in the tow-nets. From material in the Museum at Millport Marine Station I have found a characteristic large haul of *T. raschii* made in Loch Striven by the late Sir John Murray in October, 1887. It is strange that during spring, when eggs are found in greatest abundance, adult specimens are rarely fished in the tow-nets. With regard to the occurrence of *T. raschii* and *T. inermis* in the Barents Sea, Mielck (1913) says " Large numbers of nauplii and other larval stages of Euphausids appeared on the surface north and north-west of Kanin and in a remarkable manner at those stations where adult forms were absent." Sars also states, " It is here worthy of note, that in those places at Drobak (Oslofjord, Norway), where the ova occurred in great abundance, not a single adult Euphausid was ever found." Bigelow (1924, p. 155) remarks, when dealing with the distribution of Euphausids in the Gulf of Maine, U.S.A., " However, larval Euphausids of any sort have always been very rare in our offshore catches in the north-eastern part of the Gulf notwithstanding the constant presence of the adults there." With regard to *T. raschii*, Bigelow (1924, p. 143) states that they are found in great abundance in the Gulf of Maine during March and April, but are rare in summer. It appears from my observations that *T. raschii* congregate in large numbers under various impulses, but that on mating during such a " congregation " in spring or autumn they distribute themselves in small groups over a particular area where the females shed their eggs. When spawning ceases, they may congregate once more in large numbers. It may be that sexually mature adults spawn on or immediately above the bottom, and that the pressure found at those depths, 40–70 fms., is specially favourable to mating or spawning. It may also be suggested that they spawn nearer the surface at night during their vertical migrations, and then descend to the bottom, close to which they remain during the day throughout the spawning period. By keeping close to the bottom they would not be caught readily by present methods of tow-netting, and accordingly their scarcity during summer may be less real than is supposed. Russell (1927, p. 605) has drawn attention to the danger of drawing conclusions about seasonal abundance of macroplankton from daylight hauls.

There are two sizes of breeding individuals. Mature males are found measuring *ca.* 13 mm., whereas immature males also occur measuring *ca.* 19 mm. (Plate III, Figs. 10 and 16). A few immature males measuring 25 mm. have been found. The total catches indicate that the two sizes of sexually mature individuals are 13 mm. and 21 mm. respectively. Those immature males measuring 25 mm. may be abnormal, or again may be examples of normal senescence. Lebour (1926, p. 9) also finds two sizes of breeding individuals in *T. inermis*, the larger breeding individuals being found in the Atlantic, whereas the smaller are found in the Channel, parts of Norway, and near Aberdeen.

## THE LIFE HISTORY OF *T. raschii*.

The life history of *T. raschii* agrees very closely with that of *T. inermis* described by Lebour (1926). The material was obtained chiefly from Keppel Pier and Loch Striven. The majority of the stages were examined while yet alive. One-celled eggs were found in the tow-nets, and these developed in captivity to the second nauplius. The nauplius and metanauplius were recognised in the plankton, and developed in captivity to the first and second calyptopis. By this method of intercalation of stages the complete life cycle was worked out. The furcilia forms tended to be caught on the surface film of water in the glass vessels in which they were kept. The cyrtopia forms, on the other hand, no doubt because of the presence of well-grown pleopods, which enabled them to be more powerful swimmers, were not found lying helpless in the surface film, and seldom left the bottom of the glass globe. The young adults, as with the fully grown specimens, were almost invariably found at the bottom of the glass tank where the light was least intense, although at varying intervals they made short excursions towards the surface.

The " eggs " vary in size, the diameter of the outer shell measuring ·40 to ·60 mm., while the egg proper measures ·35 mm. in the unsegmented stage to ·38 mm. in the segmented and young embryo stages (Plate I, Figs. 1–4). The wall of the outer shell has a double contour, the distance between the contour lines measuring $3\mu$. Brook and Hoyle (1888) have observed this double contour. This double contoured appearance may be due to the relatively great thickness of the outer shell wall. The egg is spherical and perfectly transparent during the early stages of segmentation. Presently a very localised carmine pigmentation is seen where division is most active. When the blastopore is formed and the egg is suitably placed under the microscope the pigment material is seen to fill up the blastopore, demarcating it very distinctly, and spreading out in a somewhat scattered fashion over the surface of the egg in the immediate neighbourhood of the blastopore. When viewed from above the egg appears to have an intensely red pigment spot on its surface. This spot is characteristic. As development proceeds the pigmentation almost disappears, leaving a faint tinge on the posterior end of the unhatched nauplius. These last traces of pigmentation usually disappear in the newly hatched nauplius. So far I have not found an egg in the one-celled stage whose outer shell measures more than ·48 mm. in diameter. All sizes of eggs have been found from the mouth to the head of Loch Striven. The smaller eggs, *ca.* ·40–·48 mm., are much more abundant than the larger eggs. It will be noted that the variation in the apparent size of the egg of *T. raschii* is due to an enlargement of the outer capsule, the egg itself varying very slightly, viz. ·03 mm. The larger eggs had frequently the appearance figured by Lebour, 1924, (Plate V, Figs. 3, 5, and 6,) and as suggested by that author are probably abnormal. When describing the eggs of the forms *T. inermis* and *T. neglecta*, Lebour (1924, p. 415) states, " It is, however, the size of these eggs which is quite different in the two forms that primarily warrants one regarding them as distinct species." In both forms, however, it is merely in the size of the outer shell that Lebour finds such a great difference, the egg proper measuring in each form ·32 mm. in diameter. From my observations on eggs of *M. norvegica* and *T. raschii* it would appear that the size of the egg itself is a more reliable specific character. Lebour (1926, p. 2) finds that the eggs of *M. norvegica* found in the Atlantic are rather smaller than those from the Channel. Many more observations in widely separate geographical areas where Euphausid eggs are found must be made before it can be determined what causes this variation in diameter of egg capsule. In this connection it is interesting to note Sollaud's (1922, p. 3) observations on Palæmon eggs. He says that the number of eggs contained in the same laying necessarily bears a relation to their volume, and suggests that this volume is perhaps very different in one species from that of another and may similarly vary according to the geographical race of the same species. He also says that a large number of Palæmon, especially those with a very wide distribution and which frequent supralittoral brackish waters, have the size of the eggs reduced, whereas many fresh-water inhabiting Palæmon spawn very large-sized eggs.

The nauplius gradually develops within the egg capsule, which may increase in size before the nauplius ultimately becomes free swimming. Shortly before hatching the nauplius sets itself free from the vitelline membrane, and can be seen making intermittent jerking movements with its appendages which are now capable of free movement. Ultimately the spines on the appendages tear open the capsule and the nauplius is set free.

## NAUPLIAR FORMS.

The naupliar forms are of a more slender build than those of *M. norvegica*, and conform more closely to those of *T. inermis* figured by Lebour (1926, Plate I, Figs. 1 and 2). The newly hatched nauplius (Plate I, Fig. 5) measures ·45 to ·47 mm. in length, and has three pairs of typical biramous swimming appendages. This form gives rise to the second nauplius (Plate I, Fig. 7), which measures ·47 to ·49 mm. in length. The naupliar eye has now appeared, and there is a foreshadowing of the paired eye of the adult form. Two pairs of short and one pair of long setæ are present at the posterior extremity of the body. In this last point it resembles the second nauplius of Meganyctiphanes (Macdonald, 1927, Plate I, Fig. 6), but differs from the second of the latter as figured by Lebour (1924, Plate IV, Fig. 4), and from the second nauplius of *T. inermis* as figured by Lebour (1926, Plate I, Fig. 2). The second nauplius gives rise to the metanauplius.

## METANAUPLIUS.

This is characteristically slender in form and quite different from the metanauplius of Meganyctiphanes, which is stouter and whose dorsal face has in the middle what Sars (1898, p. 20) described as " an almost gibbous prominence." The metanauplius measures ·56 mm. (Plate I, Figs. 6 and 8). The carapace which is bordered by spines, for the most part regular, covers the body expanding in front to cover the eyes and lying close to the body posteriorly. The telson has six terminal spines and four pairs of lateral spines (Plate IV, Fig. 1). In other respects the metanauplius agrees with that of *T. inermis,* as described by Lebour (1926, p. 3).

## CALYPTOPIS STAGES.

The first calyptopsis arises from the metanauplius. There are three calyptopis stages, all of which are characteristically slender in form and perfectly transparent apart from two pairs of red chromatophores which appear on the telson.

*First calyptopis* (Plate II, Figs. 2 and 8) measures ·96–1·02 mm. in length. The telson has six terminal spines (Plate IV, Fig. 2). A distinct protuberance is seen dorsally near the centre on the carapace. The abdomen is unsegmented.

*Second calyptopis* (Plate II, Figs. 1 and 9) measures 1·8–2·00 mm. in length. The telson has now seven terminal spines. It is noted that there is a tendency for the long outer lateral spines to approximate more closely in length to that of the inner spines (Plate IV, Figs. 1–4). In the cyrtopia stages the outer lateral spines are distinctly longer than the inner lateral spines. From my observations this stronger development of outer lateral spines is characteristic of *T. raschii* and *T. inermis*, and distinguishes the larvæ of these species from the larvæ of Meganyctiphanes and *Nyctiphanes couchii.* There is no trace of a lateral denticle on the carapace. The dorsal protuberance on the carapace is still distinguishable. The first thoracic limb is present. The abdomen has now five segments, and the segments of the thoracic region are indicated by small divisions.

*Third calyptopis* (Plate II, Fig. 10, and Plate VII, Fig. 1) measures 2·4 to 2·5 mm. in length. The abdominal segments are now six in number. The uropods are seen distinctly. There is still no lateral denticle on the carapace. The first thoracic limb is well developed. No more thoracic limbs are present. The compound eye has increased in development. It is noted that in different specimens there is a varying amount of black pigment present in the eyes.

### THE FURCILIA STAGES.

I have found fourteen different "stages," but whether one individual goes through every stage or not has not been proved. All the stages are typically slender in form and transparent, but for two pairs of red chromatophores on the telson, slight red pigmentation on mouth parts and diffuse orange-red spots which are seen while the pleopods are still buds, close to where the luminescent organs ultimately appear. The development of the pleopods corresponds to that of *T. inermis* (Lebour, 1926, p. 6). The lateral denticle on the carapace may not appear till the fifth furcilia, although I have found it present several times as early as the first furcilia. This late appearance of the lateral denticle in a species in which the lateral denticle is present in the adult form is singular. With regard to *T. inermis*, Lebour (1926, p. 6) says, "No lateral denticle is present in any stage, which is interesting, as it occurs in other species of different genera when lacking in the adult, but here it agrees with Stylocheiron, which has no lateral denticle in any stage." The development of the furcilia stages agrees very closely with that of *T. inermis*

*First furcilia* (Plate II, Fig. 11, and Plate VII, Fig. 2); measures 3·1–3·2 mm. in length. The eyes are free and no pleopods are present. There are seven terminal spines on the telson of all the furcilia stages (Plate IV, Figs. 5–7).

*Second furcilia;* 3·4 mm. in length and has one pair of simple non-setose pleopods.

*Third furcilia;* 3·4 mm. long with two pairs of simple non-setose pleopods.

*Fourth furcilia;* 3·5 mm. long with three pairs of simple non-setose pleopods.

*Fifth furcilia;* 3·6 mm. long with four pairs of simple non-setose pleopods.

*Sixth furcilia* (Plate VII, Fig. 3); 3·6–3·9 mm. long with five pairs of simple setose pleopods.

*Seventh furcilia;* 3·8–4·0 mm. long with one pair setose pleopods and four pairs of simple pleopods.

*Eighth furcilia;* 4·0 mm. long with two pairs of setose pleopods and three pairs of simple pleopods.

*Ninth furcilia;* 4·05 mm. long with three pairs of setose pleopods and two pairs of simple pleopods.

*Tenth furcilia;* 4·5 mm. long with four pairs of setose pleopods and one pair of simple pleopods.

*Eleventh furcilia;* 4·6 mm. long with five pairs of setose pleopods.

*Twelfth furcilia;* 4·6 mm. long. The fourth thoracic limb jointed while fifth still a bud. Second thoracic and first abdominal luminescent organs present.

*Thirteenth furcilia;* 4·8–5·0 mm. long. Fifth thoracic limb jointed and sixth just indicated by a simple bud. Second abdominal luminescent organ appears.

*Fourteenth furcilia;* 5·1–5·2 mm. long. Thoracic limbs slightly more developed than in the thirteenth furcilia. The sixth thoracic limb is still unsegmented. Mandibular palp indicated by a small bud (Plate VI, Fig. 5). Third abdominal luminescent organ present.

## CYRTOPIA STAGES.

The cyrtopia stages are easily recognised by the increased development of the antennules and antennæ, the formation of the scale in the latter being characteristic. The mandibular palp, though still a bud in the first cyrtopia, develops rapidly in the succeeding stages, and ultimately assumes the adult form in the twelfth cyrtopia. The lateral denticle on the carapace, which was somewhat posteriorly placed in the furcilia stages, now takes the median position. In the adult form the lateral denticle is anterior to the median position. The rostrum becomes narrower, approximating to that of the adult form (Plate II, Figs. 3, 4, 5). The telson becomes narrower, and shows reduction in the number of terminal spines. The first cyrtopia has seven terminal spines. The second cyrtopia has five terminal spines, the azygous spine being jointed. In the third cyrtopia there are five terminal spines, but here the median spine may be considerably reduced in size and is unjointed (Plate IV, Figs. 8, 9, 14, and 15). The reduction in numbers of the terminal spines may not be symmetrical (Plate IV, Figs. 18 and 19). The long outer lateral spines are absent in the sixth cyrtopia. I have found an indication of "jumping" of stages. The third cyrtopia may be omitted, the second cyrtopia giving rise directly to the fourth cyrtopia (Plate IV, Fig. 10).

The development of the thoracic region is closely similar to that found in *T. inermis* by Lebour (1926). In the first cyrtopia, the second thoracic leg is slightly longer than the first thoracic leg. As development proceeds this difference in length becomes less until, in the adult form, the difference in length is negligible (Plate VI, Figs. 7 and 8; Plate III, Figs. 1 and 2). Thus there is no indication of a greatly lengthened second thoracic limb as is found in *T. inermis* form *neglecta*.

As in *T. inermis* (Lebour, 1926, p. 7) it is interesting to note that the endopodite on the seventh thoracic leg is formed after the exopodite.

The form of the endopodite is different in both sexes at a very early stage in development. The endopodite may appear in the twelfth cyrtopia stage. The endopodite on the seventh thoracic leg of the adolescent male 13 mm. long is a rounded bud bearing six or seven spines. The corresponding endopodite of a similar sized female is also a bud, but this bud is narrowed towards the end where there is a conspicuous spine (Plate VI, Fig. 6 ; Plate III, Fig. 3). In the adult, the endopodite of the seventh thoracic leg of the female develops more rapidly than that of the male (Plate III, Figs. 5 and 6).

As has been stated earlier there are two sizes of breeding individuals. Fully modified males have been found 13 mm. long. The secondary sexual modification on the first pair of pleopods in a male 13 mm. long may not only be as fully developed, but as large as that found on a male considerably larger, e.g. 20 mm. long.

The following is a list of the cyrtopia stages which I have found :—

*First cyrtopia ;* 5·3–6·00 mm. long. Seven terminal spines on telson. Fourth abdominal luminescent organ present.

*Second cyrtopia ;* 6·2–6·4 mm. long. Five terminal spines on telson. Median spine jointed. Luminescent organ present at base of seventh thoracic leg.

*Third cyrtopia ;* 6·4–6·5 mm. long. Five terminal spines on telson. The median spine is unjointed.

*Fourth cyrtopia ;* 6·6–6·95 mm. long. Three terminal spines on telson.

*Fifth cyrtopia ;* 7·0–7·4 mm. long. One terminal spine on telson.

*Sixth cyrtopia ;* 7·5–7·8 mm. long. Outer pair of long lateral spines have disappeared.

*Seventh cyrtopia ;* 8·0–8·45 mm. long.

*Eighth cyrtopia ;* 8·9–9·20 mm. long.

*Ninth cyrtopia ;* 9·5–9·85 mm. long.

*Tenth cyrtopia ;* 10–10·20 mm. long.

*Eleventh cyrtopia ;* 10·5–10·95 mm. long.

*Twelfth cyrtopia ;* 11–11·5 mm. long.

I have great pleasure in recording my thanks to Professor J. Graham Kerr, F.R.S., for helpful advice, and to His Grace the Duke of Argyll for the much appreciated facilities afforded in the Castle for carrying out my work during numerous visits to Inveraray, Loch Fyne. I am indebted to the Carnegie Trustees for financial assistance which made my work possible.

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## EXPLANATION OF PLATES.

Figures in Plate I and Figs. 1 and 2 in Plate II all drawn to same scale. Figures in Plates III, V, and VI all drawn to same scale.

### PLATE I.

*Thysanoessa raschii.*

Fig. 1.—One-celled egg—outer shell 40 mm. in diameter. Ovum ·35 mm. in diameter.

Fig. 2.—Segmented egg—outer shell ·48 mm. in diameter. Ovum ·38 mm. in diameter.

Fig. 3.—Egg with developing nauplius. Egg ·44 mm. in diameter.

Fig. 4.—The same egg as above showing nauplius further developed. Egg ·50 mm. in diameter.

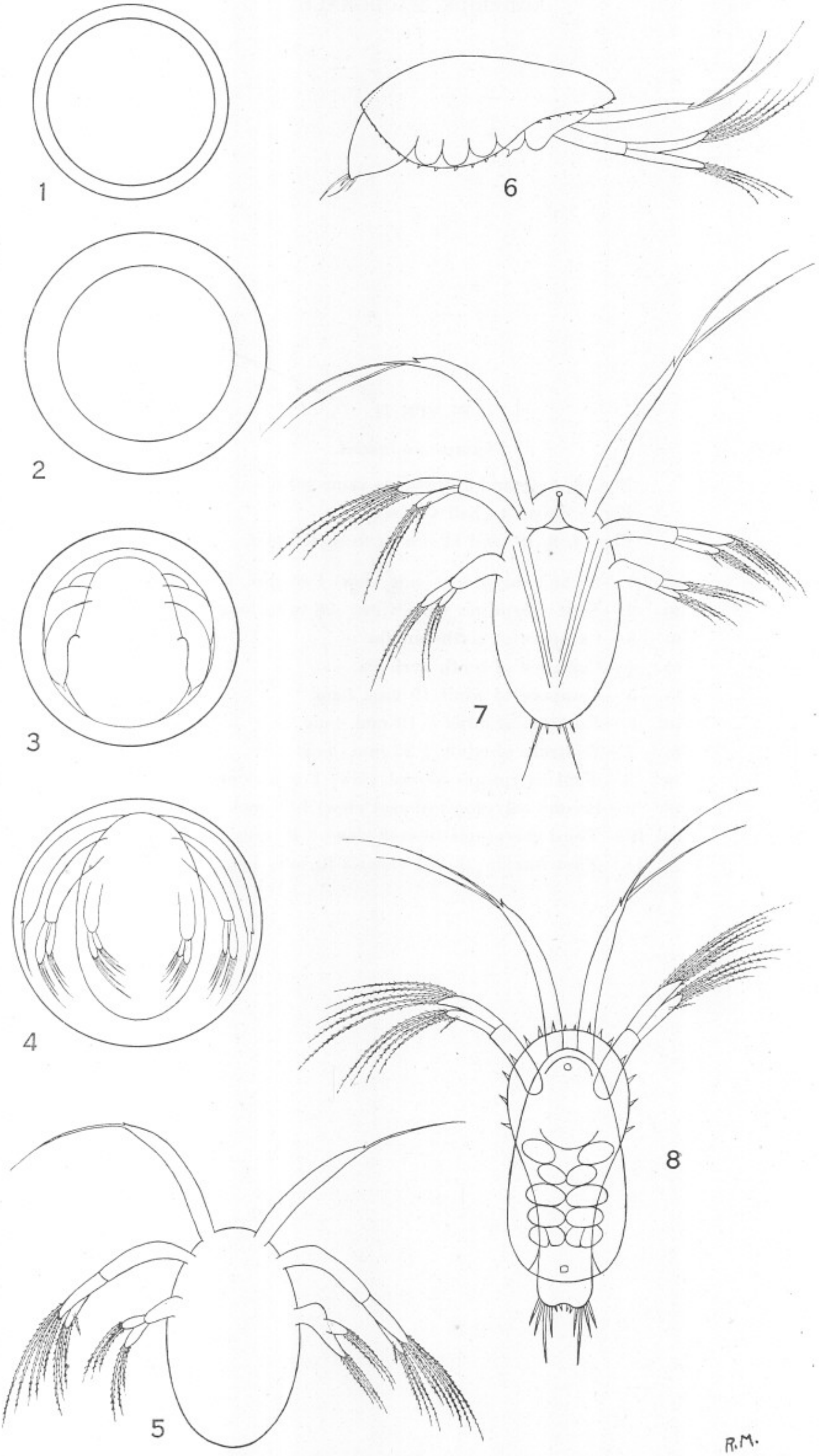
Fig. 5.—First nauplius ·45 mm. long.

Fig. 6.—Metanauplius (side view) ·56 mm. long.

Fig. 7.—Second nauplius ·47 mm. long.

Fig. 8.—Metanauplius (ventral view) ·56 mm. long.

PLATE I.



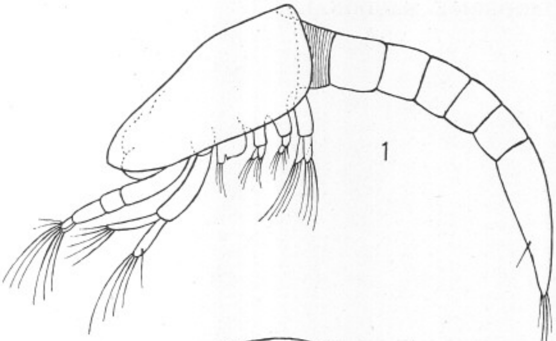
## PLATE II.

*Thysanoessa raschii.*

Figs. 3, 4, 6, and 7 drawn to same scale.
Fig. 5 drawn to half this scale.
Figs. 8, 9, 10, and 11 drawn to same scale.

Fig. 1.—Second calyptopis (side view) 1·85 mm. long.
Fig. 2.—First calyptopis (side view) ·98 mm. long.
Fig. 3.—Carapace of sixth furcilia.
Fig. 4.—Carapace of tenth cyrtopia.
Fig. 5.—Carapace of adult 19 mm. long.
Fig. 6.—Rostrum of adult ♀ 19 mm. long.
Fig. 7.—Rostrum of adult ♂ 22 mm. long.
Fig. 8.—First calyptopis (dorsal view) 1 mm. long.
Fig. 9.—Second calyptopis (dorsal view) 1·95 mm. long.
Fig. 10.—Third calyptopis (dorsal view) 2·40 mm. long.
Fig. 11.—First furcilia (dorsal view) 3·10 mm. long.

PLATE II.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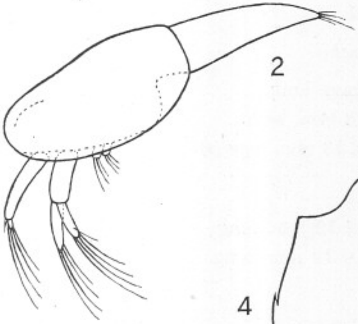
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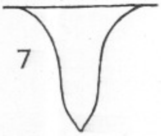
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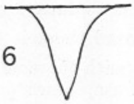
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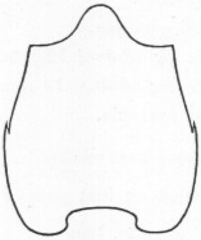
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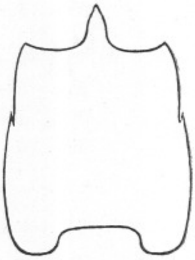
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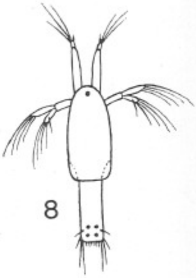
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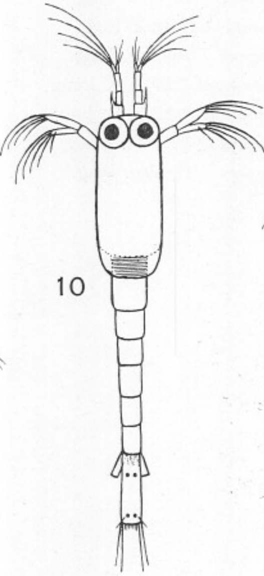
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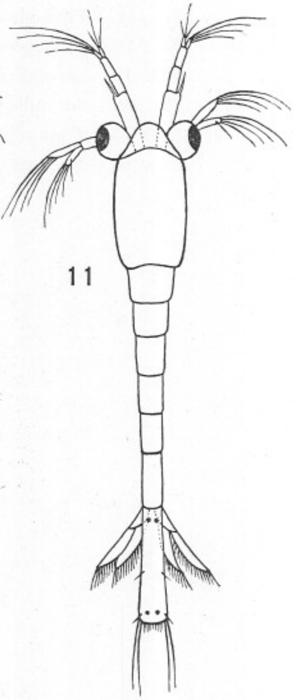
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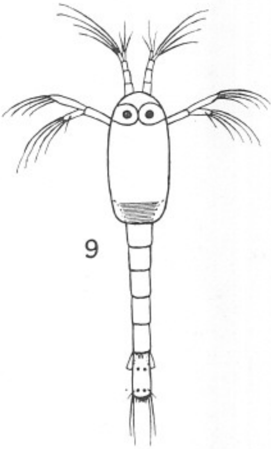
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## PLATE III.

*Thysanoessa raschii.*

FIG. 1.—First thoracic leg adult 18 mm. long.

FIG. 2.—Second thoracic leg adult 18 mm. long.

FIG. 3.—Seventh thoracic leg adult ♀ 13 mm. long (showing characteristic form of endopodite).

FIG. 4.—Mandible of third cyrtopia.

FIG. 5.—Seventh thoracic leg adult ♂ 19 mm. long.

FIG. 6.—Seventh thoracic leg adult ♀ 19 mm. long.

FIG. 7.—Mandible of first cyrtopia.

*Thysanoessa raschii.*

(Development of modification on first pair of pleopods in male.)

FIG. 8.—First pleopod ♂ 22 mm. long.

FIG. 9.—First pleopod ♂ 12 mm. long.

FIG. 10.—First pleopod ♂ 13 mm. long.

FIG. 11.—First pleopod ♂ 15 mm. long.

FIG. 12.—First pleopod ♂ 16 mm. long.

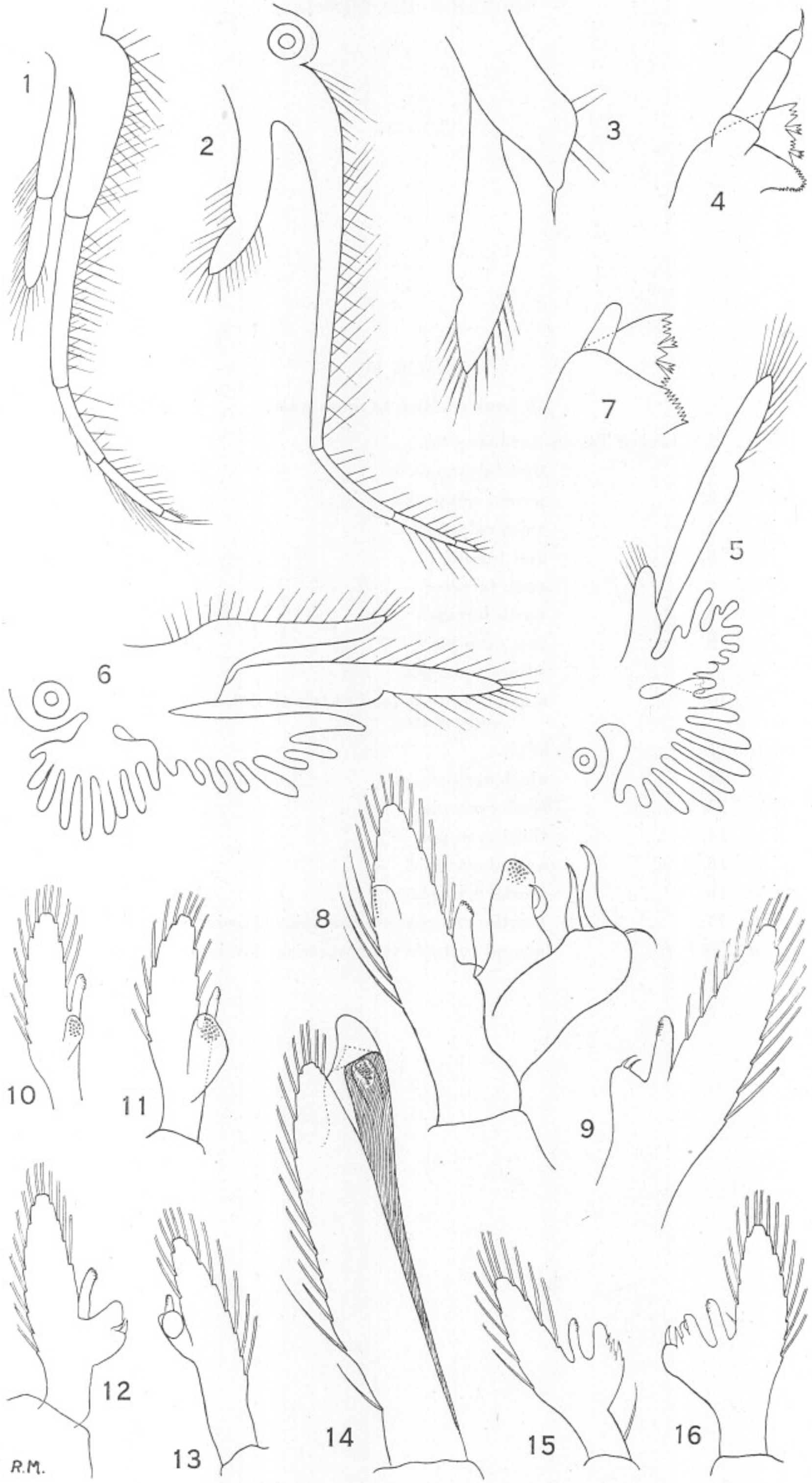
FIG. 13.—Second pleopod ♂ 17 mm. long.

FIG. 14.—Second pleopod ♂ 22 mm. long.

FIG. 15.—First pleopod ♂ 17 mm. long.

FIG. 16.—First pleopod ♂ 13 mm. long.

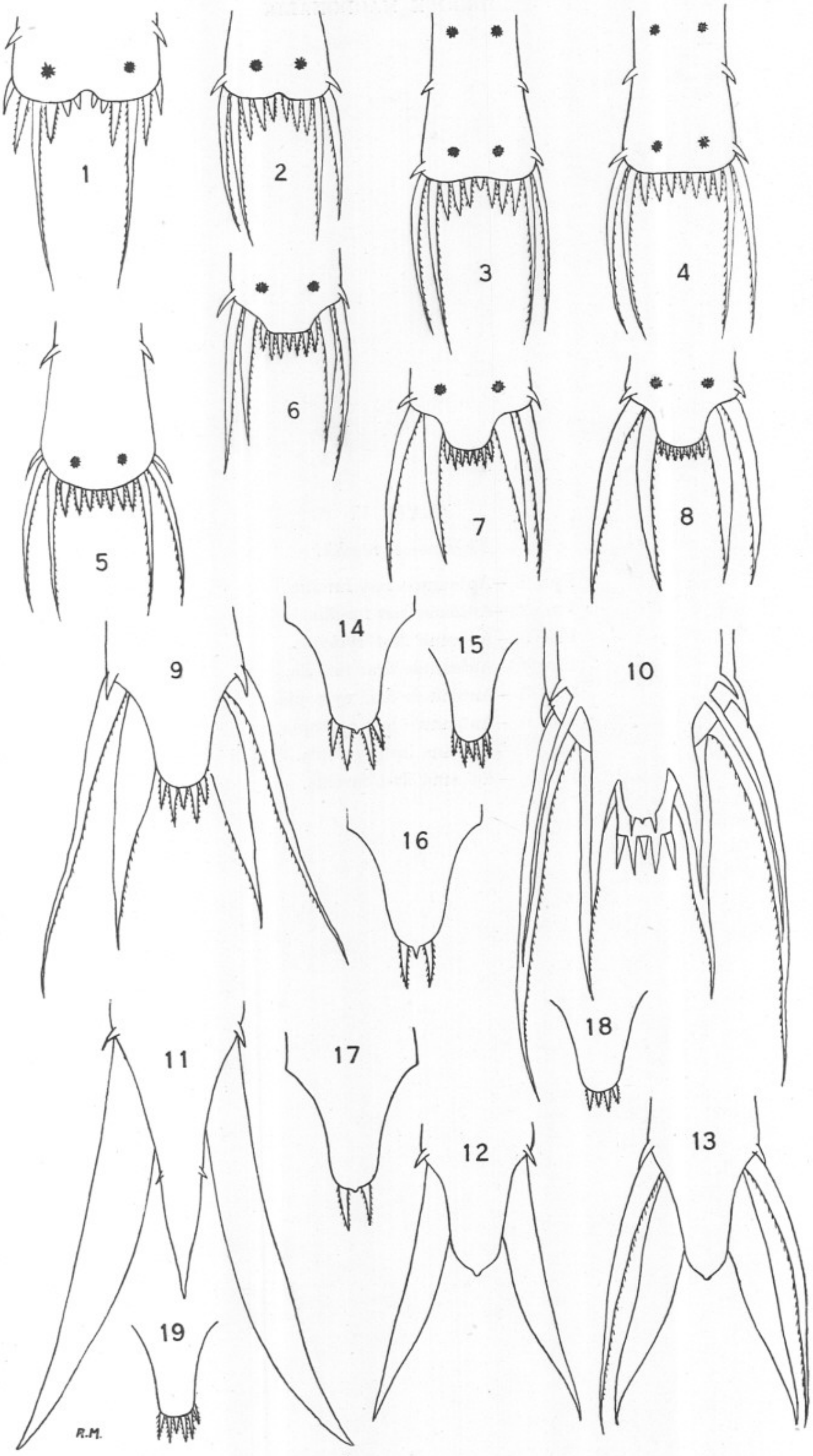
PLATE III.



## PLATE IV.

All figures drawn to same scale.

Fig. 1.—End of Telson metanauplius.
Fig. 2. ,, ,, first calyptopis.
Fig. 3. ,, ,, second calyptopis.
Fig. 4. ,, ,, third calyptopis.
Fig. 5. ,, ,, first furcilia.
Fig. 6. ,, ,, sixth furcilia.
Fig. 7. ,, ,, tenth furcilia.
Fig. 8. ,, ,, first cyrtopia.
Fig. 9. ,, ,, second cyrtopia.
Fig. 10. ,, ,, second cyrtopia (end of telson of fourth cyrtopia showing underneath).
Fig. 11. ,, ,, adult.
Fig. 12. ,, ,, ninth cyrtopia.
Fig. 13. ,, ,, sixth cyrtopia.
Fig. 14. ,, ,, third cyrtopia.
Fig. 15. ,, ,, second cyrtopia.
Fig. 16. ,, ,, fourth cyrtopia.
Fig. 17. ,, ,, fourth cyrtopia (median spine showing less development).
Figs. 18 & 19. ,, second cyrtopia (asymmetrical development).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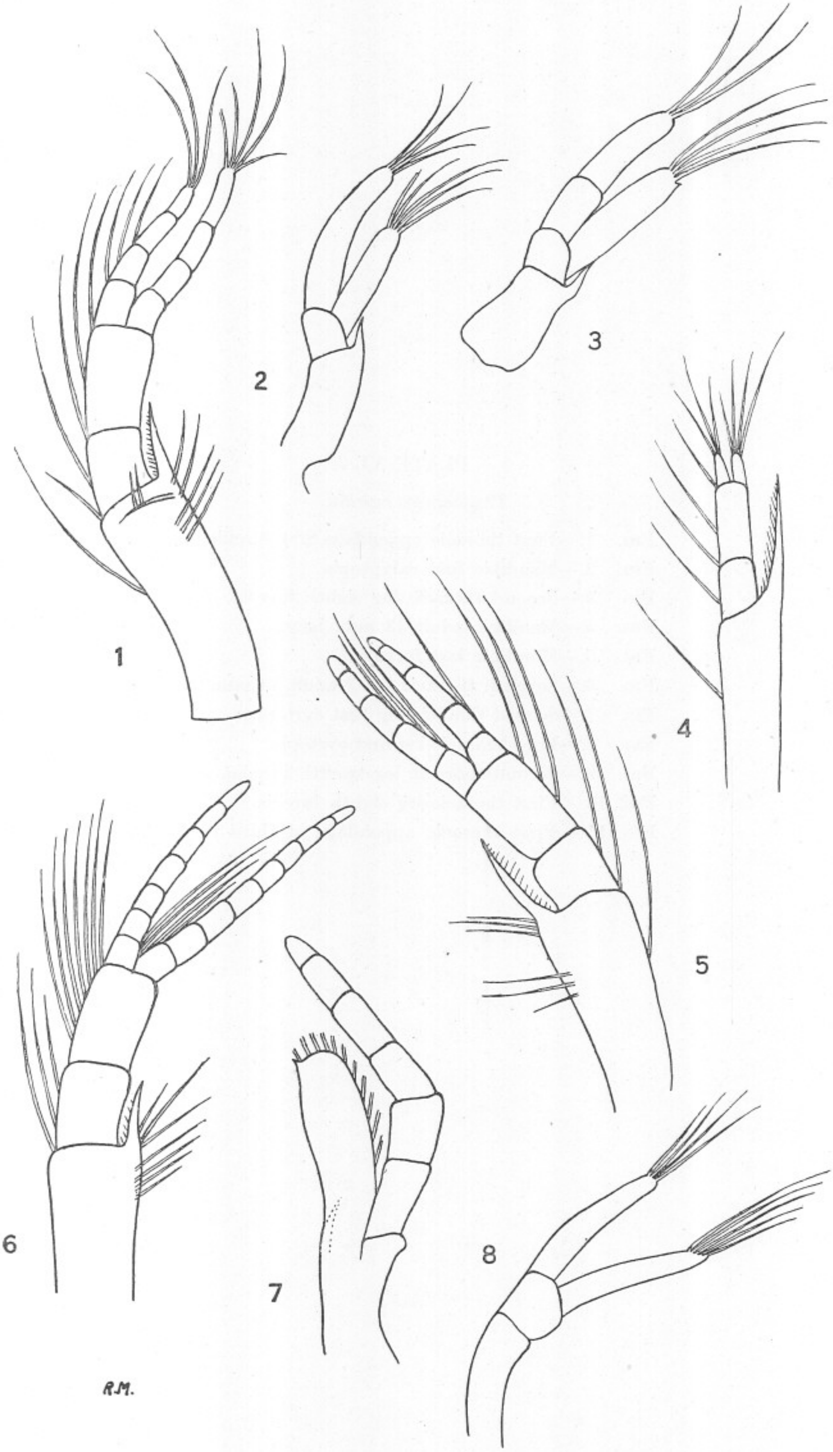
## PLATE V.

*Thysanoessa raschii.*

Fig. 1.—Antennule last furcilia.
Fig. 2.—Antenna last furcilia.
Fig. 3.—Antenna first cyrtopia.
Fig. 4.—Antennule first furcilia.
Fig. 5.—Antennule first cyrtopia.
Fig. 6.—Antennule last cyrtopia.
Fig. 7.—Antenna last cyrtopia.
Fig. 8.—Antenna first furcilia.

PLATE V.

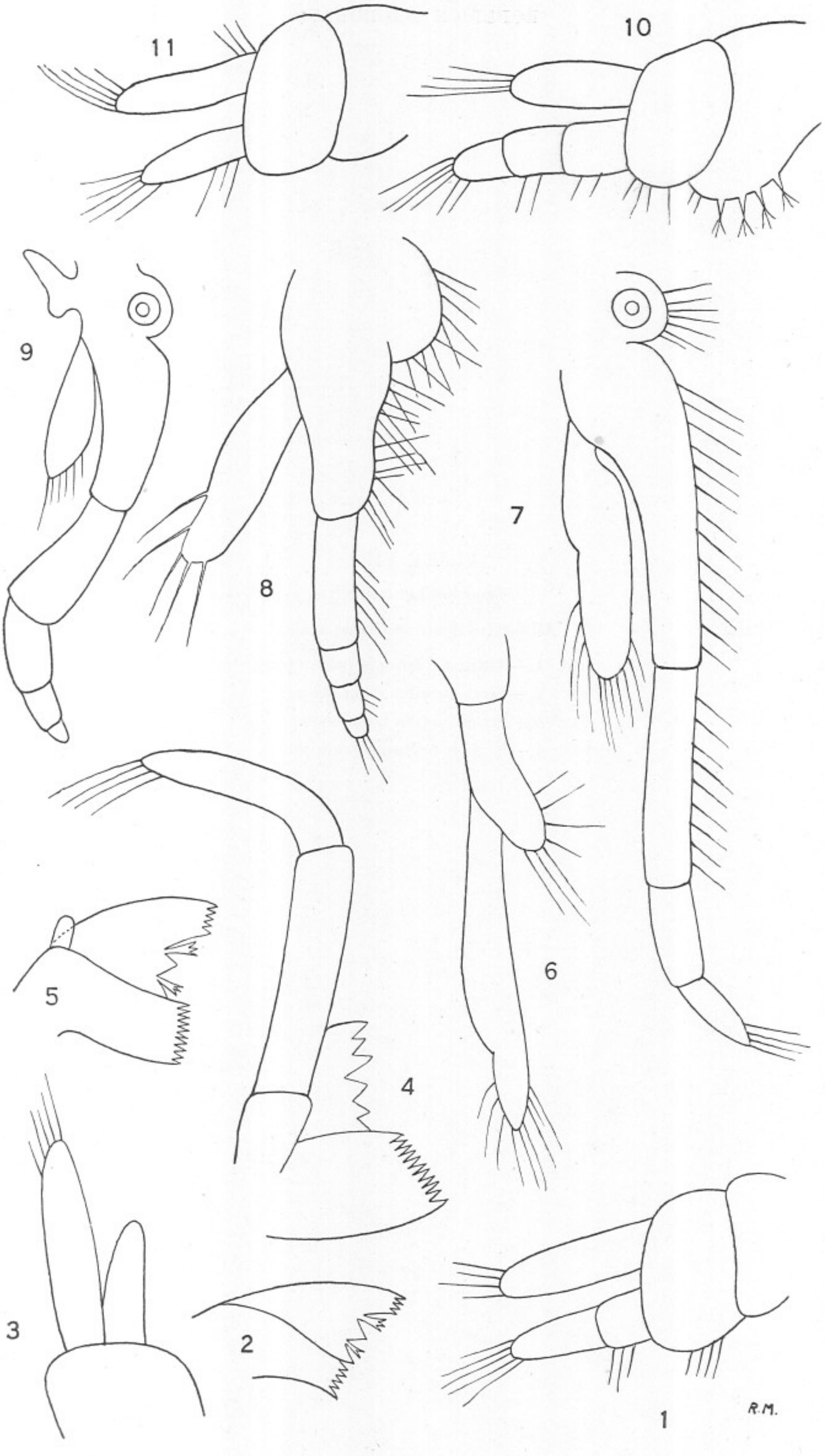


## PLATE VI.

*Thysanoessa raschii.*

FIG. 1.—First thoracic appendage first furcilia.
FIG. 2.—Mandible first calyptopis.
FIG. 3.—Second thoracic leg eighth furcilia.
FIG. 4.—Mandible adult 13 mm. long.
FIG. 5.—Mandible last furcilia.
FIG. 6.—Seventh thoracic leg ♂ adult 13 mm. long.
FIG. 7.—Second thoracic leg first cyrtopia.
FIG. 8.—First thoracic leg first cyrtopia.
FIG. 9.—Second thoracic leg twelfth furcilia.
FIG. 10.—First thoracic leg eighth furcilia.
FIG. 11.—First thoracic appendage of third calyptopis.

PLATE VI.



## PLATE VII.

*Thysanoessa raschii.*

All figures drawn to same scale.

FIG. 1.—Third calyptopis (side view).
FIG. 2.—First furcilia (side view).
FIG. 3.—Sixth furcilia (side view).
FIG. 4.—Eighth cyrtopia (side view).

PLATE VII.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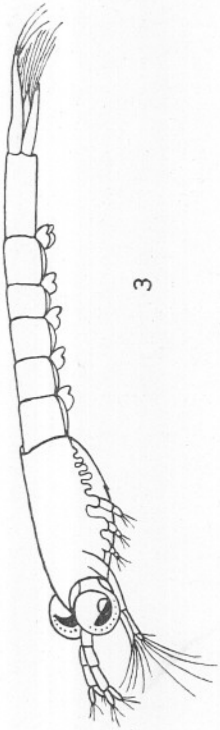
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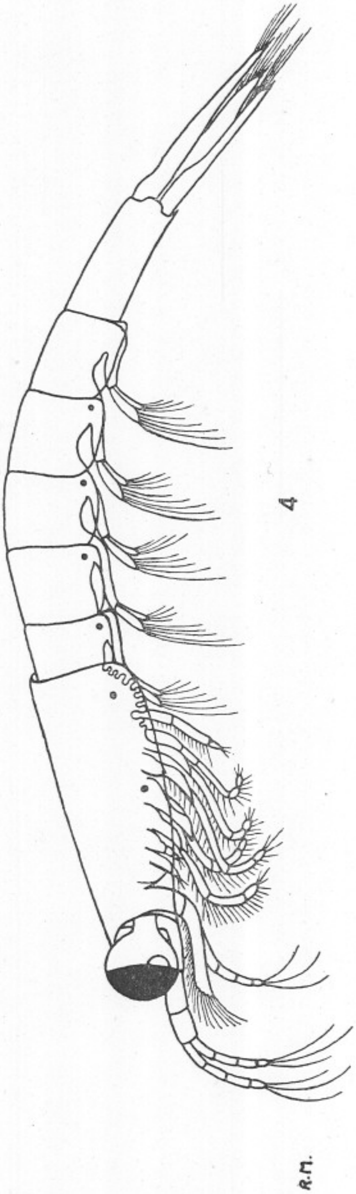
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# The Vertical Distribution of Marine Macroplankton. VI. Further Observations on Diurnal Changes.

By
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*Assistant Naturalist at the Plymouth Laboratory.*

With 7 Figures in the Text.

In 1925 observations were carried out on two consecutive nights, June 17–18th and 18–19th, to study the diurnal changes occurring in the vertical distribution of certain marine plankton animals. Serial hauls were made with the stramin ring-trawl in the manner described in a previous publication (**1**). The series were so timed that they were made approximately in daylight, dusk, darkness, dawn and daylight on the two days in question. The actual details of the collecting, together with the fishing depths shown by the Admiralty depth recorder, are to be found in a previous paper on the behaviour of young fishes on the same occasion (**2**).

## GENERAL RESULTS.

In considering the general results as shown by the collections it is necessary to bear in mind that each haul in a series is consecutive, i.e. that the six depths were not fished simultaneously. Thus, for instance, in the first series the observations extended over a period of nearly two hours, so that, while the deepest haul was taken at 2.35 p.m., the surface haul was not taken until 4.19 p.m. During so long a period there is sufficient time for the vertical distribution of the plankton to become considerably altered. However, during full daylight and in darkness, when the light conditions which appear to control the behaviour of the animals to a large extent are more or less constant, or at any rate only changing slowly, it seems most probable that little alteration will occur in the vertical distribution and that the results shown in the diagrams will illustrate the actual distribution of the animal during that period within small limits. But it may be quite otherwise at dusk and at dawn, when the light is decreasing or increasing in strength very rapidly.

This possibility should be remembered when the results of the collections are examined. To emphasize this point an illustration is here given. In Fig. 3 (p. 88) the distribution of *Tomopteris helgolandica* at dusk

(7.27–9.23 p.m.) on the first night would appear to have been fairly uniform from the surface downwards, but the numbers of individuals at each depth were small. But it must be realised that when the surface haul was being taken at 9.13 p.m. the distribution that existed at 7.27 p.m., when the bottom haul was taken, had probably considerably changed. It is very possible that, by the time this surface haul was taken, the deeper levels had already received a marked addition to their Tomopteris population by the rising of individuals from near the bottom. In the drawing of the diagrams in this paper this time factor has been ignored and Fig. 1 shows how the distribution should have been represented in the case of Tomopteris at dusk. In this figure the diagram B represents the distribution as it has been given in Fig. 3 (p. 88), whereas A shows the same diagram with the time factor introduced. At the same time, by means of unblackened outline diagrams, is shown hypothetically what the actual distribution of Tomopteris may quite well have been at the times that the hauls at the various depths were taken. Thus, while being very close to the bottom at 7.27 p.m., they may have been well on their way towards the surface by 9.13 p.m. when the surface haul was begun. Arguing on the theory that has already been outlined for the behaviour of plankton animals (**4**, p. 237), it is unlikely that at dusk only a few Tomopteris were present at all layers as indicated in Fig. 3, and it may well be that the suggested distribution shown in Fig. 1 comes nearer the truth. In the case of the dusk diagram on the first night for *Turris pileata* (Fig. 2, p. 84), however, if the net has fished each time *below* the mass of upwardly migrating medusæ until the surface layers were reached, a true idea of the actual distribution at about 9 p.m. is possibly given. (It should be quite possible to test the above suggestion by taking the series of hauls on a future occasion in the reversed

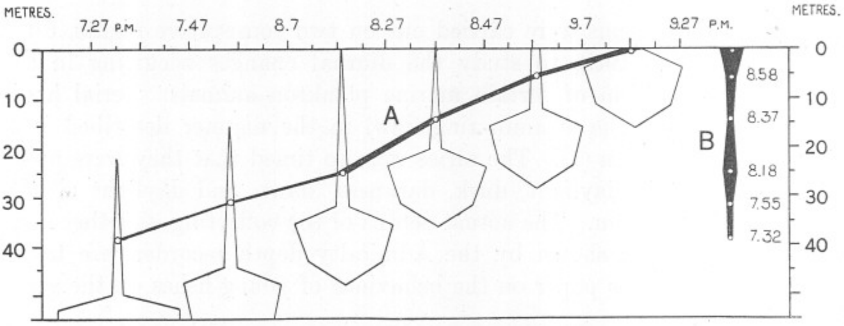

FIG. 1.—Illustrating how the diagram B for the dusk distribution of *Tomopteris helgolandica* may be misleading. Diagram A shows the same distribution with the time factor introduced. Hypothetical distributions for Tomopteris at the various times at which hauls were made are drawn in outline.

order, viz. from the surface downwards. Under such conditions it is easy to see that the dusk distribution for Tomopteris would work out as that suggested for 8.37 p.m. in Fig. 1, if the hypothetical behaviour there outlined is anywhere near correct.) This suggestion is also borne out by an examination of the behaviour of Tomopteris on the night of July 15–16th, 1924 (**1**, p. 785), when the hauls were taken from below upwards as on the present occasion. In Fig. 3 of that publication it can be seen that in the daylight the Tomopteris were already well up in the water, and the resulting diagram for the dusk distribution can be explained in the manner shown here in Fig. 1.

Turning now to the results obtained in this series of collections, it is not the intention in these pages to enter into discussion on the various types of behaviour shown, nor to undertake comparisons between these results and those obtained on July 15–16th, 1924. There are certain very obvious differences between the two, some of which, e.g. Sagitta and Tomopteris, can be explained by the different behaviour of these animals in the daylight at the different seasons that the two collections were made (**3**). The actual details of the behaviour of the various species are given in the following pages, and since another series has already been collected in 1926, and worked up, opportunity will be afforded in a forthcoming publication to compare the results of all four nights.

Full details of the numbers of the different species caught at the different depths are given in Table I on page 100.

Throughout the paper the expressions " daylight," " dusk," " dark," and " dawn " have been used to cover the various periods during which the series were taken. It must be realised that these are purely arbitrary expressions and the actual times are given in the many diagrams and in Table I (p. 100).

The fact that on so many occasions the behaviour of a species on the first night is almost exactly repeated on the second night gives reason for supposing that the method of collecting is efficient and that the numbers of animals caught in the different hauls are strictly comparable.

The catches were sampled in the same way as previously, the larger animals (**3**, p. 563) being picked out completely : in the smaller catches one-fifth of the whole was counted.

## CŒLENTERATA.

### ANTHOMEDUSÆ.

#### Steenstrupia rubra Forbes.

In the daytime there were no specimens of this medusa taken from above 20 metres. On the first night, June 17–18th, the numbers were

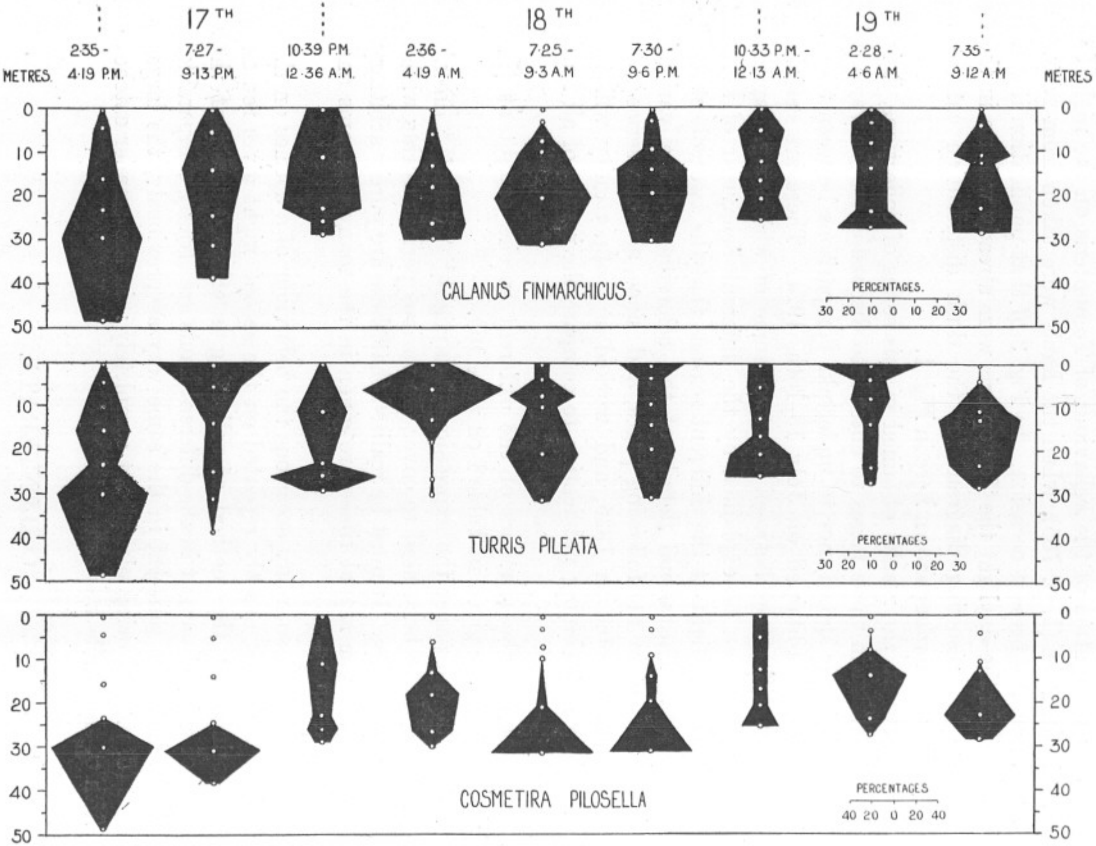

FIG. 2.—The percentage vertical distribution of *Calanus finmarchicus*, *Turris pileata*, and *Cosmetira pilosella*, at the times shown, on June 17–18–19th, 1925. The white spots and black circles indicate the average depths at which hauls were taken.

rather low, only 2 being caught on the surface and 10 and 12 at 26 and 29 m. respectively. However, on the second night the numbers were sufficient to show that in the dark there had been a decided movement into the layers above 20 m., 52 being taken at 12·2 m. and 33 at 16·6 m. Only one was caught at the surface. At dawn on both days the layers above 20 metres had once more been vacated, but on June 18th there were still 54 at 26·8 m.

### TURRIS PILEATA (Forskal).

In the daytime on June 17th and 18th the numbers of Turris in the collections were too low to give a true picture of the vertical distribution. On June 19th, however, they were more numerous, and it is probable that this (Fig. 2) can be regarded as their normal daylight distribution. On both nights—but more markedly on the first—there seems to have been an active migration to the surface itself at dusk, followed by a downward movement at night in the dark and a further upward migration at dawn.

### BOUGAINVILLEA sp.

Although the numbers of Bougainvillea, as shown in Table I, are very small there seems undoubted evidence that they moved into the upper layers at night. None were taken at any depth in the three daylight series, but by dusk on both days they were beginning to appear in the deeper hauls.

In the dark on the first night they were present at the surface itself, and by dawn they were still everywhere between 6 m. and 30 m. On the second night only few were taken, although they were numerous again at dawn.

*Slabberia halterata* Forbes and *Stomatoca dinema* L. Agassiz only occurred in one or two collections and then generally singly.

## LEPTOMEDUSÆ.

### OBELIA SP.

The catches of Obelia were very small, and appear to indicate little coordinated movement. On the two occasions when they were numerous, dusk on June 18th and daylight on June 19th, their distribution was much the same, except that at dusk they were abundant on the surface itself and in the daylight there were few in the upper five metres.

### PHIALIDIUM sp.

There appear to be definite indications of an upward movement on the part of these medusæ at night (Fig. 4). They were almost completely absent in the daylight on June 17th, at dusk they were most abundant below 25 m., and in the dark they were evenly distributed from the surface downwards. At dawn on June 18th the majority were taken below 15 m. In the daylight, however, they appear to have become evenly distributed again from 3 m. downwards, but their numbers are somewhat reduced. A rather similar behaviour was shown on the second night, only, in the dark, the majority were caught between 10 and 20 m.

### COSMETIRA PILOSELLA Hartlaub.

None of these medusæ were captured from above 20 m. in the daylight on June 17th, and the majority occurred at 30 m., or perhaps deeper, there being rather a deep layer between the two bottom hauls. At dusk the distribution was still much the same, most being at 30 m. In the dark Cosmetira was evenly distributed from the surface down to 30 m. At dawn there had been a downward movement and the majority lay between 15 and 30 m. This movement was continued in the daylight so that most were taken at 30 m., and possibly they may have lain even deeper. On the following night the behaviour exhibited by Cosmetira was almost exactly the same (Fig. 2).

### SAPHENIA GRACILIS (Forbes and Goodsir.).

No Saphenia were taken in the daytime on June 17th at any depth. At dusk they were beginning to appear in the deeper hauls, 37 being caught at 31·3 m. In the dark they were distributed from the surface downwards. They had almost completely disappeared by dawn and in the daylight on the following day. On the next night they once more appeared from the surface downwards, although most of them were caught below 15 m. The numbers on all occasions were rather low, and the impression gained is that in its diurnal behaviour Saphenia resembled Cosmetira, except that in the daytime it went possibly deeper.

Of the Scyphomedusæ, *Cyanea capillata* Eschscholtz and *Aurelia aurita* Lamarck, too few were taken to indicate what the changes in their vertical distribution may have been, as was also the case with the Ctenophore, *Pleurobrachia pileus* Fab., and the Zoantharians, Peachia sp. larvæ and *Arachnactis Bournei* Fowl.

# ANNELIDA.

## POLYCHÆTA.

### TOMOPTERIS HELGOLANDICA Greef.

In the daytime on June 17th Tomopteris was extremely rare above 50 m., and the majority were probably very close to the bottom. The dusk diagram (Fig. 3) exhibits a slight upward movement, but, as explained previously (p. 81), this may be misleading, only the forerunners of the main upward moving mass being sampled at each depth. In the dark there was a filling up of the layers from the surface downwards, the majority being at about 10 m. At dawn on June 18th the distribution was somewhat similar to that in the dark, except that most were taken at 20 m. and the surface itself was vacated. By daylight they had presumably once more returned to very near the bottom.

The following night, June 18th to 19th, this behaviour was almost exactly repeated, except that in the dark there were fewer at the actual surface itself.

### LARVÆ OF PŒCILOCHÆTUS SERPENS Allen.

Although these polychæte larvæ were very rare in the catches throughout the first twenty-four hours, on the second night there were definite indications that they had moved into the upper layers, although the numbers taken were still very low.

## CHÆTOGNATHA.

### SAGITTA BIPUNCTATA Quoi and Gaimard.

As was the case with Tomopteris, there are indications that the Sagitta were living very close to the bottom in the daytime. By dark their numbers were enormously increased in the layers above 30 m., and the Sagitta were very abundant at the surface itself (Fig. 3). They had almost completely disappeared again by dawn. This behaviour was repeated in exactly the same manner on the two nights, except that there were fewer at the surface on the second night than on the first. That the Sagitta may have been lying very close to the bottom in the daylight on these occasions is borne out by experiments carried out this year (1927). In a net specially constructed to sample the layers a few inches above the bottom there have on occasion been extremely large catches of Sagitta made (see **5**, p. 108 of this Journal).

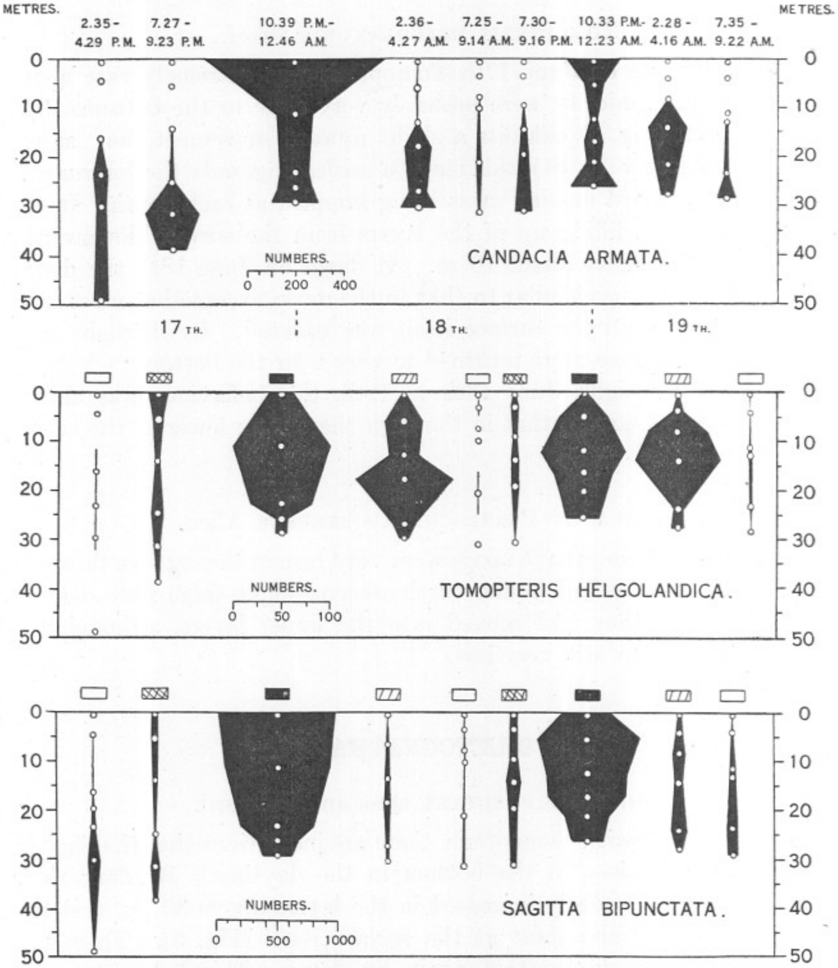

FIG. 3.—The vertical distribution of *Candacia armata*, *Tomopteris helgolandica*, and *Sagitta bipunctata*, at the times shown, on June 17–18–19th, 1925. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

## CRUSTACEA.

### COPEPODA.

#### CALANUS FINMARCHICUS (Gunner).

In the daylight on June 17th the majority of this copepod were taken at 30 m. (Fig. 2). By dusk there had been a marked upward movement in the water, the greatest catch being at 15 m. In the dark they were mostly distributed between the surface and 25 m. At dawn on June 18th they had left the surface and the majority lay between 15 and 30 m. and perhaps deeper ; a somewhat similar distribution was shown in daylight, but the actual surface layers down to 5 m. were almost completely emptied. At dusk on June 18th there seems to have been little change, except that there were more in the layers between the surface and 5 m. In the dark they were evenly distributed from 5 m. downwards with fair numbers at the surface itself. At dawn the distribution was still very similar, but in the daylight the surface layers were vacated. It is evident that the movements as indicated by these collections were not as marked on the second night as on the first.

#### CANDACIA ARMATA (Boeck.).

It is probable that in the daytime these copepods were living very close to the bottom, none being taken above 20 m. and only a few in the hauls below this depth (Fig. 3). At dusk on June 17th the majority were caught between 30 and 35 m. In the dark there was a great massing in the surface layers, while considerable numbers were present down to 30 m. By dawn on June 18th the layers between the surface and 10 m. had been vacated and only a few Candacia were taken between 15 and 30 m. ; by daylight it would appear that they had all moved down below 30 m., the lowest depth sampled. The behaviour on the following night, June 18–19th, was almost exactly similar, the numbers at the surface in the dark being, however, not so great.

Of the remaining copepods, *Anomalocera Patersoni* Templt. were too few and unevenly distributed to give any indication of their behaviour ; *Metridia lucens* Boeck appeared at any rate in small numbers in the dark on the first night, and in still smaller numbers on the second night, while it was almost completely absent in the daylight ; *Caligus rapax* Milne Edwardes was only taken in small numbers and showed a very irregular distribution.

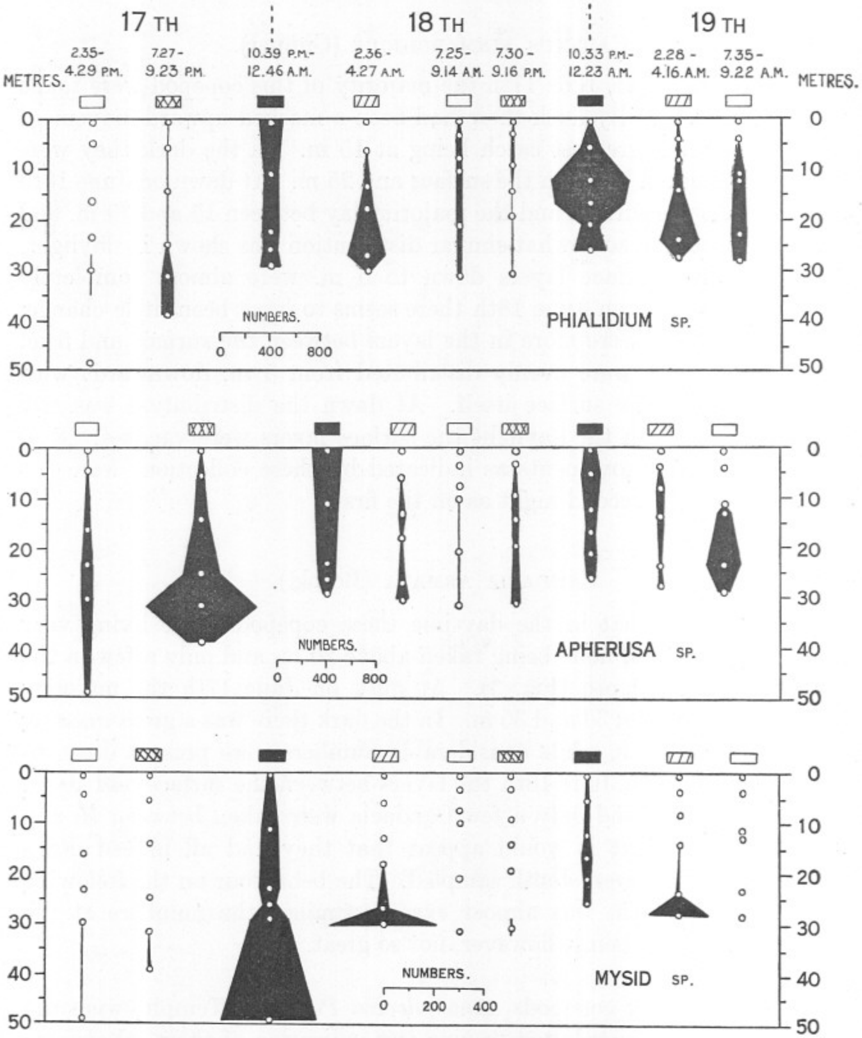

FIG. 4.—The vertical distribution of Phialidium sp., Apherusa sp., and Mysid spp., at the times shown, on June 17–18–19th, 1925. The plain, cross-hatched, black, and shaded rectangles represent " daylight," " dusk," " dark," and " dawn " respectively. The white spots and black circles indicate the average depths at which hauls were taken.

## MYSIDACEA.

### Mysid spp.

The mysids, consisting mostly of the species *Leptomysis gracilis* (G. O. Sars), with a few Schistomysis sp., Dasymysis sp., and *Haplostylus Normanni* G. O. Sars, were evidently living in the layers adjacent to the bottom in the daytime, and at dusk they were still absent in the upper layers down to 30 m. (Fig. 4). At night on June 17–18th the layers between the bottom and 30 m. had been greatly filled up. (The mysids, such as could be found, were washed out from the sand that filled the bucket when the net struck bottom during the dark haul.) At the same time there were a few mysids present in the layers between 30 m. and the surface itself. By dawn on June 18th the surface layers down to 25 m. had been completely vacated, but there were still many present at 30 m. In the daylight on June 18th none were caught. This behaviour was repeated on the following night. In the dark series, however, the net was not fished deep enough to sample the layers below 30 m., where the mysids were probably most abundant.

### Anchialus agilis G. O. Sars.

This mysid was entirely absent at all depths sampled in the daytime and at dusk on both days. In the dark on both nights they were taken in small numbers at all depths from 5 m. downwards, and on the first night three were taken at the surface itself. At dawn on both days a few were still taken below 20 m.

## EUPHAUSIACEA.

### Nyctiphanes Couchii (Bell).

These euphausiids, while being taken only singly in the deeper layers in the daytime, appeared in small numbers at all depths in the dark on the two nights.

## CUMACEA.

Cumaceans, Diastylis sp. and others, appeared in the collections only in the dark (except at dawn on June 19th, when two were caught at 27·5 m.), when they were present at almost all depths sampled.

## AMPHIPODA.

### Apherusa spp.

While these amphipods were present in the daytime on June 17th in small numbers from 5 m. downwards, there was a very great increase in

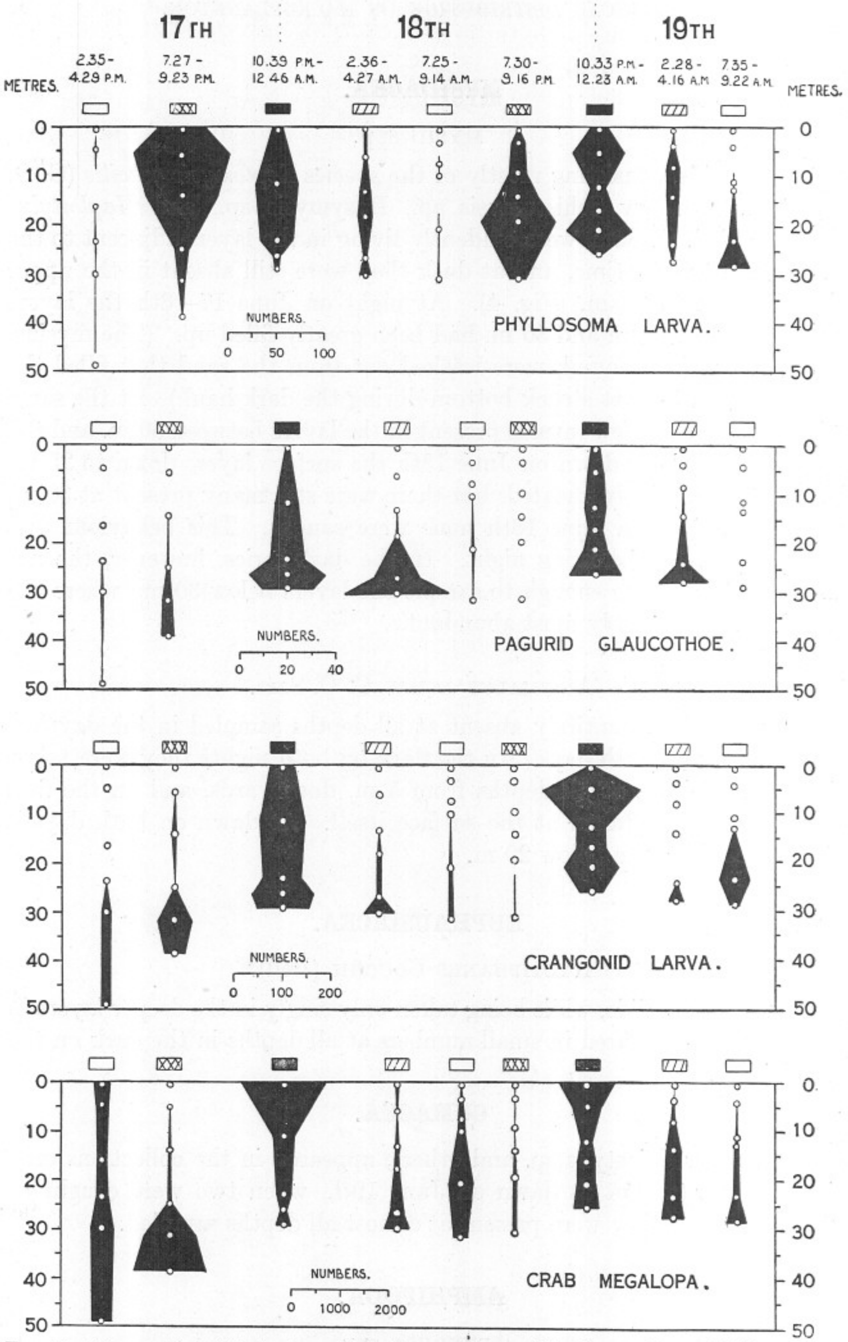

Fig. 5.—The vertical distribution of Phyllosoma larvæ of Palinurus, Pagurid Glaucothoë larvæ, Crangonid larvæ, and Crab megalopæ, at the times shown, on June 17–18–19th, 1925. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

numbers between 30 and 40 m. at dusk (Fig. 4). In the dark they were almost evenly distributed from the surface downwards. At dawn they were still taken at all depths, but in very small numbers, and the majority were below 20 m. In the daylight on June 18th the layers from the surface down to 10 m. at any rate were practically vacated. On the following night the behaviour seems to have been much the same, except that the numbers caught were much smaller on all occasions.

Of other amphipods, Hyperiid sp. appeared almost only singly and in the deeper layers in the daytime, while in the dark on June 18–19th four were taken on the surface. Such truly bottom-living amphipods as Ampeliscus appeared also in the night hauls and at 27·5 m. at dawn on June 19th.

## DECAPODA.

### PANDALID LARVÆ.

In daylight on June 17th most of these larvæ were taken at 30 m. (Fig. 6). At dusk they were still most abundant about this depth, although a slight diminution is apparent in the layers above. By dark there has been a marked filling up of the layers above 25 m., but the numbers actually at the surface are low. By dawn on June 18th the surface layers have been emptied and the majority of Pandalid larvæ were once more at 30 m. A similar condition was apparent in the daylight on June 18th, but unfortunately owing to lack of observations from the deeper levels it is not possible to say whether, in reality, the majority were then below the depths sampled. By dusk on June 18th there is an apparent filling up of the layers up to between 10 and 15 m., and in the dark there was a further extension upwards to the surface itself, though the majority were caught at about 15 m. A downward movement exactly similar to that of the previous day was exhibited at dawn on June 19th, but there is a slight increase again in the daylight, possibly due to a swarm.

### CRANGONID LARVÆ.

Only very few Crangonid larvæ were taken in the daylight, and those only in the deeper layers (Fig. 5). There were, however, in the dark on both nights considerable numbers caught at all depths from the surface downwards, indicating a definite upward movement. At night the catches included many post-larvæ and a few early adult stages.

### PHYLLOSOMA LARVÆ OF PALINURUS VULGARIS Latreille.

These larvæ appear to have been very near the bottom during the daylight on June 17th (Fig. 5). By dusk the majority had already

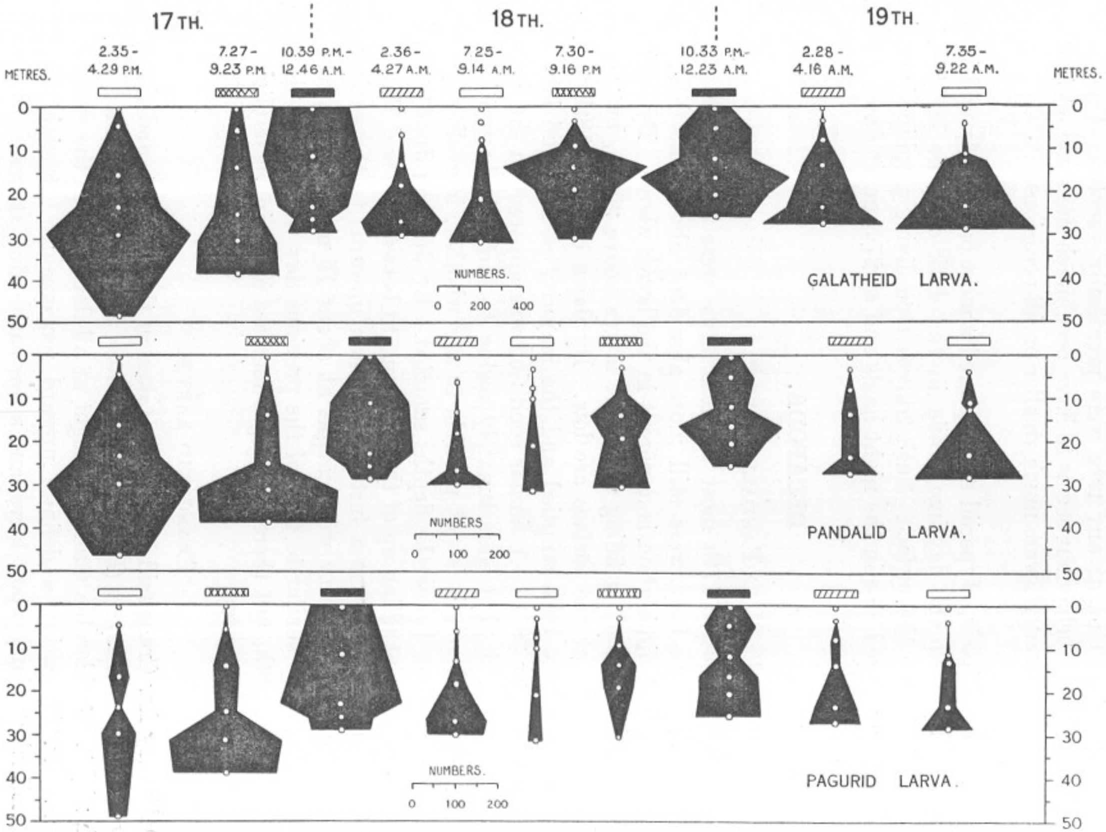

FIG. 6.—The vertical distribution of Galatheid larvæ, Pandalid larvæ, and Pagurid larvæ, at the times shown, on June 17–18–19th, 1925. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

reached the layers between 15 m. and the surface. In the dark the distribution was fairly even from the surface down to about 25 m., but the numbers were somewhat less than at dusk, possibly owing to unevenness in horizontal distribution. By dawn there had been a very considerable reduction in numbers, and by daylight on June 18th they had almost completely vacated the layers down to 30 m. A very similar behaviour was exhibited on the following night.

### GALATHEID LARVÆ.

In daylight on June 17th the majority of these larvæ were taken at about 30 m. (Fig. 6). At dusk they were still in this region, but by dark the upper layers were filled up to the surface itself. At dawn on June 18th the surface layers down to about 15 m. had been vacated and the majority were taken at 25 to 30 m. In the daylight there is an indication that a further downward movement had taken place, the majority being at 30 m. and perhaps below this, though the deeper layers were not sampled. By dusk on June 18th there had evidently been a marked upward movement, most of the larvæ being captured at about 15 m., but the surface layers down to between 5 and 10 m. were still empty. In the dark the surface layers were filled up, but not so completely as on the night before, the majority being taken between 15 and 20 m. A downward movement was again shown at dawn on June 19th, but there was little alteration in the daylight beyond a more complete emptying of the surface layers down to 10 m.

### GALATHEID POST-LARVÆ.

Although in the daylight on June 17th some of these post-larvæ were present high up in the water layers it seems most probable that the majority were really close to the bottom. There was on both nights a considerable increase in the numbers in all layers sampled up to the surface itself, followed by an emptying of the surface layers and a massing at depths between 20 and 30 m. at dawn. (Amongst these may also have been included Porcellana spp. post-larvæ.)

### UPOGEBIA LARVÆ.

On June 17th in daylight the majority of these larvæ were below a depth of 25 m. (Fig. 7). By dusk they were extending their distribution up to between 10 and 15 m., and in the dark they were most abundant actually at the surface. By dawn on June 18th they had left the upper layers and were mostly below 15 m. In the daylight on June 18th they were apparently slightly higher in the water than at dawn, up to 10 m.;

albeit the numbers were rather low, and it is perhaps possible that the majority lay below the depths sampled. By dusk on June 18th there was an evident increase in numbers up to a depth of between 10 and 15 m., an increase which extended up to a depth of 5 m. in the dark; but the surface itself was not fully populated as on the previous night. At dawn on June 19th the surface layers were emptied down to a depth of 5 to 10 m., most of the larvæ being captured from about 15 m. In the daylight there was an indication that the majority had moved down to 25 m. and may be deeper.

The post-larvæ of this species were not taken in the daytime. They only occurred in very small numbers at night and at dawn, while one was caught deep down at dusk.

### LARVÆ OF CALLIANASSA sp.

The numbers of these larvæ in the collections were rather low, it being early in the season for them. In consequence the results are somewhat irregular, but there is a definite indication of upward movement at night.

### PAGURID LARVÆ.

In the daylight on June 17th very few Pagurid larvæ were taken above a depth of 25 m., and the numbers below this were also somewhat low, possibly indicating that the majority were very near the bottom (Fig. 6). By dusk there had been a large increase in numbers at 30 and 40 m. In the dark the water layers from 30 m. up to the actual surface were completely filled. By dawn on June 18th the larvæ had left the surface layers and most were caught at 25 to 30 m., and in the daylight there is an indication that they may have been below 30 m. At dusk on June 18th there was an increase at 15 to 20 m., though the numbers are rather low, and in the dark an upward movement had filled the layers between the surface and 30 m. A downward movement similar to that of the previous day was exhibited at dawn and in daylight on June 19th.

### GLAUCOTHOË LARVÆ OF PAGURIDS.

The behaviour of these bottom-living stages was very similar to that exhibited by the mysids. In the dark they moved up into the upper water layers as far as the surface itself, though the largest catches were still below 25 m. (Fig. 5).

### PORCELLANA spp. ZOEÆ.

The behaviour of Porcellana zoeae appears to have been extremely irregular. Lying mostly at 30 m. in the daylight on June 17th, they were by dusk almost evenly distributed from the surface downwards

(Fig. 7). At midnight there were enormous numbers at the surface. By dawn the layers down to 15 m. had been vacated, but in the daylight on June 18th there appears to have been a slight upward movement. At dusk the distribution of Porcellana was much the same as in the daytime, but in the dark there was a large massing at 15 m., the surface layers being almost empty. Dawn and daylight results on June 19th exhibit a progressive downward movement. The midnight behaviour on these two nights was apparently very uncoordinated, but may possibly have been upset by the presence of swarms.

### CRAB ZOEÆ.

An examination of Fig. 7 shows that in the case of the crab zoeae (probably mostly Portunus spp.) there was a considerable increase in numbers in the layers above 15 to 20 m. on both nights, an increase which was pronounced also at the surface itself. It is not quite obvious at what depth the majority were in the daytime. A study of the last five series (daylight, June 18th, to daylight, June 19th) seems to indicate definitely that in the daylight on June 18th the majority must have been below the depths sampled, because by dusk there was a considerable filling up of the layers up to a depth of between 10 and 15 m., and this increase extends right to the surface in the dark. There was clearly a diminution in numbers at dawn on June 19th, with an almost complete emptying of the actual surface layers. In daylight on the 19th, while the upper layers have been depleted almost completely down to a depth of 10 m., there is a great increase in numbers below this depth, possibly caused by a swarm. In the first five series the upward movement at dusk is not so marked; this is because in the daylight on June 17th the crab zoeae appear to have been almost equally abundant at all depths except at the actual surface. Whether this is a false impression due to the fact that the zoeae were extremely abundant at that time, and the majority lay even deeper than was sampled cannot be said.

### CRAB MEGALOPÆ.

In the daylight on June 17th the crab megalopæ appear to have been more or less evenly distributed from the surface downwards, but at dusk, while hardly any were taken above 20 m., there seems to have been a very marked increase in numbers below 30 m. (Fig. 5). In the dark they had migrated to the surface itself where they were caught in greatest numbers. At dawn on June 18th they seem to have retired once more to below 30 m. In the daylight there was a slight upward movement, though there were fewer in the surface layers than on the previous day. At dusk very few were caught at all down to 30 m., but there is again a

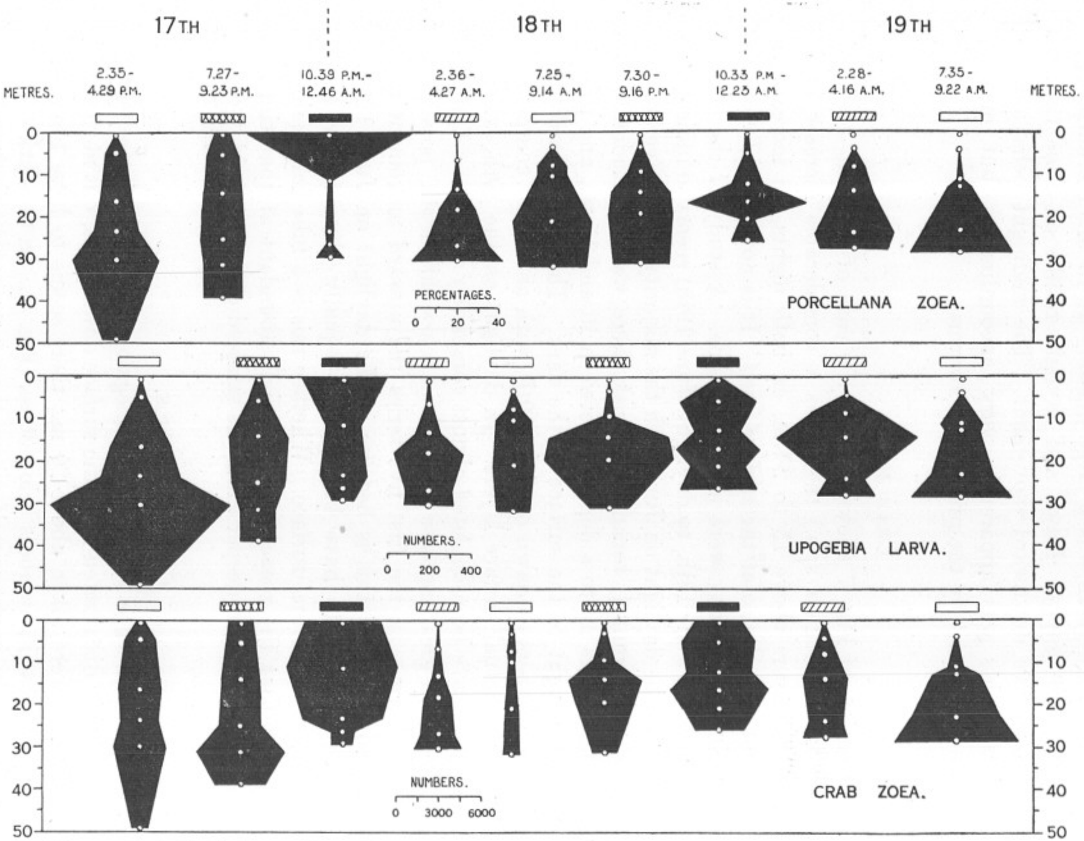

FIG. 7—The vertical distribution of Porcellana spp. zoeae, Upogebia sp. larvæ, and Crab zoeae, at the times shown, on June 17–18–19th, 1925. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

N.B.—Owing to the very large numbers, the diagram for Upogebia larvæ at daylight on June 17th is half the scale of the others.

marked movement to the surface in the dark. At dawn on June 19th they had moved downwards to below 10 m., and in daylight this downward movement has apparently continued.

Leander sp. larvæ, Alpheus larvæ, *Pontophilus spinosus* larvæ, *Homarus vulgaris* larvæ, and Axius larvæ were present only in very small numbers in the collections.

The presence of a few young Portunid crabs up to about ¼ inch in width was noticed at night at all depths.

Echinospira larvæ, *Limacina retroversa*, and Tornaria larvæ were only taken in small numbers. In the case of Echinospira and Tornaria larvæ there is, however, a slight indication of upward movement at night.

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## TABLE I.

### June 17th, 18th, 19th, 1925.

| | Time. | *Depth in metres.* | Steenstrupia rubra. | Slabberia halterata. | Stomatoca dinema. | Turris pileata. | Bougainvillea sp. | Obelia sp. | Phialidium sp. | Cosmetira pilosella. | Saphenia gracilis. | Cyanea capillata. | Aurelia aurita. | Pleurobrachia. | Peachia sp. larvæ. | Arachnactis larvæ. | Tomopteris helgolandica. | Pœcilochætus larvæ. | Sagitta bipunctata. | Calanus finmarchicus. | Anomalocera Patersoni. | Candacia armata. | Metridia lucens. | Caligus rapax. | Mysid spp. | Anchialus agilis. | Nyctiphanes Couchii. | Cumacea. | Hyperiid sp. | Apherusa sp. | Bottom amphipods. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DAYLIGHT, | 4.19 p.m. | *S.* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 40 | – | 1 | – | – | – | – | – | – | – | – | – |
| June 17th. | 4.0 ,, | *4·5* | – | – | – | 6 | – | – | – | – | – | – | – | – | – | – | – | – | 10 | 410 | 1 | – | – | 1 | – | – | – | – | – | 20 | – |
| | 3.40 ,, | *16·2* | – | – | – | 15 | – | – | – | 2 | – | – | – | 4 | – | – | 1 | – | 10 | 870 | 2 | – | 10 | 6 | – | – | – | – | – | 50 | – |
| | 3.21 ,, | *23·4* | – | – | – | 8 | – | – | – | 7 | – | 1 | – | 5 | – | – | 1 | – | 20 | 1490 | 7 | 60 | – | 5 | – | – | 1 | – | – | 90 | – |
| | 2.58 ,, | *29·8* | – | – | 1 | 25 | – | 20 | 20 | 1217 | – | 2 | – | – | – | – | 1 | 1 | 100 | 2140 | 3 | 40 | – | 7 | 1 | – | 1 | – | 1 | 90 | – |
| | 2.35 ,, | *48·8* | 10 | – | – | 7 | – | 10 | – | 79 | – | – | – | 1 | – | – | – | – | 10 | 970 | 1 | 60 | – | – | 4 | – | 2 | – | – | 40 | – |
| DUSK. | 9.13 p.m. | *S.* | – | – | – | 117 | – | – | – | – | – | – | 1 | – | – | – | 21 | – | 70 | 200 | – | 10 | – | 4 | – | – | – | – | – | – | – |
| | 8.53 ,, | *5·4* | – | – | – | 55 | – | – | 20 | – | – | – | – | – | – | – | 11 | 1 | 60 | 600 | 2 | – | – | 1 | – | – | – | – | – | 50 | – |
| | 8.32 ,, | *14* | – | – | – | 16 | 10 | – | 10 | – | – | – | – | – | – | – | 4 | – | 40 | 1010 | 2 | – | – | 1 | – | – | – | – | – | 120 | – |
| | 8.13 ,, | *24·8* | – | – | – | 18 | 10 | – | 20 | 1 | 2 | – | – | – | – | – | 12 | 1 | 20 | 690 | – | 80 | – | – | – | – | – | – | – | 300 | – |
| | 7.50 ,, | *31·3* | 5 | – | | 12 | 80 | 20 | 100 | 251 | 37 | – | 1 | 2 | 1 | 1 | 10 | 3 | 60 | 640 | – | 220 | – | 2 | 3 | – | 1 | – | 1 | 880 | – |
| | 7.27 ,, | *38·6* | 5 | – | – | 2 | 20 | 20 | 110 | 36 | 6 | – | – | 6 | – | – | 2 | 1 | 30 | 510 | – | 110 | – | 1 | 7 | – | 2 | – | – | 210 | – |
| DARK. | 12.36 a.m. | *S.* | 2 | – | – | 1 | 10 | – | 190 | 20 | 25 | – | – | – | – | – | 24 | 2 | 960 | 1330 | – | 730 | 10 | 2 | 21 | 3 | 2 | 4 | – | 240 | – |
| | 12.15 ,, | *11·2* | – | – | – | 8 | 30 | – | 120 | 53 | 15 | – | 1 | – | – | – | 99 | 2 | 860 | 2850 | 1 | 150 | 80 | 2 | 68 | 11 | 9 | 1 | – | 190 | 1 |
| | 11.55 p.m. | *23* | – | – | – | 3 | 60 | – | 150 | 33 | 16 | 1 | – | – | – | – | 63 | 1 | 610 | 3520 | – | 120 | 30 | 3 | 84 | 8 | 7 | 1 | – | 150 | 1 |
| | 11.34 ,, | *26** | 10 | – | – | 17 | 20 | – | 120 | 52 | 32 | – | – | 1 | – | – | 12 | – | 350 | 1030 | 1 | 140 | 30 | 1 | 54 | 14 | 2 | 8 | 1 | 140 | 12 |
| | 11.11 ,, | *29* | 12 | – | – | 5 | 40 | – | 140 | 27 | 9 | – | – | – | – | – | 13 | – | 240 | 1050 | – | 190 | 20 | 3 | 153 | 14 | 2 | 10 | 1 | 60 | 14 |
| | †10.39 ,, | *49* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 382 | 7 | – | – | – | – | – |
| DAWN. | 4.19 a.m. | *S.* | – | – | – | 28 | 1 | 1 | 6 | – | – | 1 | – | – | – | – | 4 | – | 4 | 21 | – | 2 | – | 1 | – | – | – | – | – | 10 | – |
| | 3.59 ,, | *6* | – | – | – | 121 | 10 | – | 5 | – | 1 | 1 | – | – | – | – | 39 | – | 24 | 110 | – | 15 | – | 1 | – | – | – | – | – | 15 | – |
| | 3.40 ,, | *13* | – | – | – | 28 | 35 | 10 | 55 | 19 | – | – | – | – | – | – | 32 | 1 | 35 | 235 | 2 | 10 | – | 1 | – | – | – | – | – | 30 | – |
| | 3.19 ,, | *18* | – | – | – | 3 | 10 | – | 120 | 91 | 2 | – | – | – | – | – | 100 | 1 | 50 | 480 | 2 | 110 | 20 | – | 2 | – | – | – | – | 10 | – |
| | 2.58 ,, | *26·8* | 54 | – | – | 2 | 50 | 40 | 290 | 66 | 1 | – | 1 | 6 | – | – | 24 | – | 29 | 610 | 2 | 80 | 20 | 2 | 45 | 3 | – | – | – | 50 | – |
| | 2.36 ,, | *30* | 7 | – | – | 5 | 20 | – | 20 | 11 | – | – | – | 2 | 1 | – | 10 | – | 15 | 530 | 1 | 140 | – | 7 | 436 | 13 | – | – | – | 90 | – |

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DAYLIGHT, June 18th. | 9.3 a.m. | *S.* | – | – | – | 4 | – | – | – | – | – | – | – | – | – | – | – | – | 3 | – | – | – | – | – | – | – | – | – | – | – | – |
| | 8.45 ., | *3·2* | – | – | – | 4 | – | – | 40 | – | – | – | – | – | – | – | 1 | – | 6 | 7 | – | – | – | – | – | – | – | – | – | 1 | – |
| | 8.27 ,, | *7·5* | – | – | – | 15 | – | – | 50 | – | – | 1 | – | – | – | – | – | – | 17 | 175 | – | – | – | – | – | – | – | – | – | – | – |
| | 8.6 ,, | *9·9* | – | – | – | 7 | – | – | 45 | – | 1 | – | – | – | – | – | – | 1 | 6 | 285 | 1 | 15 | – | – | – | – | – | – | – | 5 | – |
| | 7.46 ,, | *20·8* | – | – | – | 17 | – | 5 | 50 | 1 | – | – | – | – | – | – | 2 | 2 | 7 | 620 | 2 | 20 | – | 4 | – | – | – | – | – | 15 | – |
| | 7.25 ,, | *31·4* | 6 | – | – | 4 | – | 25 | 40 | 18 | 2 | – | – | 2 | – | – | – | 5 | 13 | 330 | 2 | 5 | – | 1 | – | – | – | – | – | 25 | – |
| DUSK. | 9.6 p.m. | *S.* | – | – | – | 97 | – | 177 | 22 | – | – | – | – | – | – | – | 3 | 1 | 65 | 44 | – | 1 | – | 1 | – | – | – | – | – | – | – |
| | 8.49 ,, | *3·2* | – | – | – | 38 | – | 185 | 40 | 1 | – | – | – | – | – | – | 8 | – | 67 | 220 | 1 | – | – | – | – | – | – | – | – | – | – |
| | 8.31 ,, | *9·3* | – | – | – | 41 | 10 | 100 | 20 | 8 | 2 | – | – | – | – | – | 6 | – | 64 | 330 | 2 | – | – | 1 | – | – | – | – | – | 30 | – |
| | 8.11 ,, | *14* | – | – | 1 | 48 | 10 | 40 | 10 | 36 | – | – | – | – | – | – | 8 | 2 | 127 | 1160 | 3 | 20 | – | 3 | – | – | – | – | – | 40 | – |
| | 7.53 ,, | *19·4* | – | – | – | 70 | – | 40 | 10 | 30 | 3 | – | – | – | – | – | 8 | 10 | 88 | 1110 | 5 | 40 | – | 7 | – | – | – | – | – | 30 | – |
| | 7.30 ,, | *30·9* | – | – | – | 24 | 40 | – | 30 | 233 | 4 | – | – | 2 | – | – | – | 5 | 40 | 640 | – | 70 | 1 | – | 1 | – | – | – | 2 | 70 | – |
| DARK. | 12.13 a.m. | *S.* | 1 | – | – | 21 | – | – | 20 | 38 | 9 | – | – | – | – | – | 3 | 4 | 420 | 400 | – | 210 | – | 2 | 3 | – | 2 | 1 | 4 | 100 | – |
| | 11.55 p.m. | *5·2* | 4 | – | – | 23 | 10 | – | 160 | 42 | 9 | – | – | 1 | – | – | 49 | 1 | 820 | 1840 | 3 | 80 | 10 | 1 | 19 | 3 | 5 | 3 | 1 | 150 | 1 |
| | 11.36 ,, | *12·2* | 52 | – | – | 16 | – | – | 610 | 41 | 9 | – | – | – | – | – | 85 | 1 | 670 | 1230 | 4 | 30 | – | 1 | 19 | 8 | 4 | – | – | 110 | – |
| | 11.16 ,, | *16·6* | 33 | 1 | – | 16 | – | – | 570 | 44 | 24 | – | – | – | – | – | 61 | 3 | 640 | 1810 | 2 | 80 | 10 | 3 | 40 | 11 | 8 | 1 | 1 | 80 | – |
| | 10.55 ,, | *20·7* | 15 | 1 | 1 | 53 | – | – | 150 | 47 | 20 | – | – | – | 1 | 1 | 49 | 8 | 360 | 1330 | 1 | 60 | 10 | 1 | 25 | 20 | 1 | 2 | 1 | 90 | 1 |
| | 10.33 ,, | *25·8* | 26 | – | 1 | 62 | 10 | 20 | 260 | 113 | 25 | – | – | – | – | – | 33 | 11 | 260 | 2000 | 1 | 190 | – | 7 | 23 | 11 | 1 | 3 | – | 60 | 1 |
| DAWN. | 4.6 a.m. | *S.* | – | – | – | 134 | – | – | 4 | – | – | – | – | – | – | – | 2 | – | 29 | 45 | – | 1 | – | 1 | – | – | – | – | – | 6 | – |
| | 3.49 ,, | *3·6* | – | – | – | 39 | 10 | – | 30 | – | – | – | – | – | – | – | 11 | – | 63 | 465 | 1 | – | – | – | – | – | – | – | – | 7 | – |
| | 3.28 ,, | *8* | 1 | – | 1 | 50 | 10 | 30 | 40 | 4 | – | – | – | – | – | – | 59 | 1 | 90 | 460 | – | – | – | 5 | – | – | – | – | – | 60 | – |
| | 3.9 ,, | *13·9* | – | – | – | 19 | 30 | – | 80 | 65 | 2 | 1 | – | – | – | – | 84 | 1 | 64 | 340 | 1 | 160 | 10 | 6 | 2 | 1 | 1 | – | – | 40 | – |
| | 2.49 ,, | *23·7* | 4 | – | 5 | 21 | 120 | 30 | 290 | 25 | 2 | 1 | – | 5 | – | – | 8 | 1 | 131 | 360 | – | 100 | 10 | 3 | 9 | 2 | – | – | 1 | 20 | – |
| | 2.28 ,, | *27·5* | 13 | – | – | 16 | 10 | 120 | 40 | 2 | 4 | – | – | 2 | – | – | 13 | 12 | 70 | 800 | – | 50 | – | 1 | 229 | 6 | 1 | 2 | – | 40 | 3 |
| DAYLIGHT, June 19th. | 9.12 a.m. | *S.* | – | – | – | 1 | – | – | – | – | – | – | – | – | 1 | – | 1 | – | 5 | 12 | 9 | – | – | – | – | – | – | – | – | – | – |
| | 8.54 ,, | *4* | – | – | – | 4 | – | 11 | 23 | – | – | – | 1 | – | – | – | – | – | 32 | 314 | – | – | – | – | – | – | – | – | – | – | – |
| | 8.35 ,, | *11·1* | – | – | – | 58 | – | 155 | 110 | – | – | – | – | – | – | – | 3 | – | 57 | 1260 | – | – | – | – | – | – | 1 | – | – | – | – |
| | 8.16 ,, | *12·7* | – | – | – | 86 | – | 90 | 90 | 11 | – | 1 | – | – | – | – | 4 | 1 | 55 | 570 | – | 10 | – | 3 | – | – | – | – | – | 110 | – |
| | 7.56 ,, | *23·3* | 9 | 1 | 2 | 63 | – | 10 | 140 | 85 | 15 | – | – | – | – | – | 3 | 1 | 84 | 1410 | 4 | 20 | – | 6 | 1 | – | 2 | – | 2 | 270 | – |
| | 7.35 ,, | *28·5* | – | – | – | 13 | – | 20 | 100 | 32 | 2 | – | – | – | – | – | – | 5 | 79 | 1310 | 3 | 70 | – | 11 | – | – | 2 | – | – | 100 | – |

* Maximum depth, 31 m.: 26 m. given as possible average. † Net struck bottom.

## TABLE I—*continued.*

### June 17th, 18th, 19th, 1925.

| | Time. | *Depth in metres.* | Leander sp. larvæ. | Pandalid larvæ. | Alpheus larvæ. | Spirontocaris larvæ. | Crangonid larvæ. | Pontophilus larvæ. | Homarus larvæ. | Palinurus phyllosoma. | Galatheid larvæ. | Galatheid post-larvæ. | Upogebia larvæ. | Upogebia post-larvæ. | Callianassa larvæ. | Axius larvæ. | Pagurid larvæ. | Pagurid glaucothoë. | Porcellana zoea. | Ebalia sp. zoea. | Crab zoeas. | Crab megalopas. | Echinospira larvæ. | Limacina retroversa. | Tornaria larvæ. | *Total organisms.* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DAYLIGHT, June 17th. | 4.19 p.m. | *S.* | 1 | – | – | – | – | – | – | – | 4 | – | – | – | – | – | – | – | 62 | – | 496 | 361 | – | – | – | **965** |
| | 4.0 ,, | *4·5* | 2 | 10 | – | – | – | – | – | 2 | 60 | 10 | 110 | – | – | – | – | – | 710 | – | 2280 | 260 | – | – | – | **3,892** |
| | 3.40 ,, | *16·2* | 3 | 150 | – | – | – | – | – | – | 290 | 10 | 580 | – | – | – | 50 | – | 1090 | – | 3080 | 210 | 20 | 10 | – | **6,463** |
| | 3.21 ,, | *23·4* | 1 | 190 | – | – | – | – | – | 3 | 390 | – | 760 | – | 10 | – | 10 | – | 1550 | – | 2740 | 270 | 10 | 34 | – | **7,663** |
| | 2·58 ,, | *29·8* | – | 332 | – | – | 10 | 1 | – | 1 | 670 | 30 | 1700 | – | 10 | 1 | 80 | 1 | 2870 | – | 3640 | 470 | 10 | 10 | – | **13,506** |
| | 2.35 ,, | *48·8* | – | 123 | – | 20 | 20 | 1 | – | – | 130 | 30 | 230 | – | 10 | – | 40 | – | 830 | – | 1180 | 410 | – | – | – | **4,218** |
| DUSK. | 9.13 p.m. | *S.* | 5 | – | – | – | – | – | – | 52 | 40 | – | 30 | – | 10 | – | – | – | 180 | – | 1760 | – | 20 | – | – | **2,520** |
| | 8.53 ,, | *5·4* | 2 | 10 | 1 | – | – | – | – | 100 | 80 | – | 100 | – | 50 | – | 10 | – | 330 | – | 2180 | – | – | – | – | **3,663** |
| | 8.32 ,, | *14* | 4 | 51 | – | – | 10 | – | – | 72 | 140 | 20 | 280 | – | 30 | – | 60 | – | 380 | – | 2710 | 50 | 10 | – | – | **5,030** |
| | 8.13 ,, | *24·8* | – | 64 | – | – | – | 1 | – | 15 | 210 | – | 250 | – | 30 | – | 50 | – | 450 | – | 2910 | 90 | 10 | 4 | – | **5,238** |
| | 7.50 ,, | *31·3* | 5 | 325 | – | – | 70 | 5 | – | 7 | 360 | 70 | 170 | – | – | – | 260 | 4 | 380 | – | 6090 | 1100 | – | – | – | **11,176** |
| | 7·27 ,, | *38·6* | 1 | 311 | – | 10 | 40 | 2 | 1 | 3 | 380 | 50 | 170 | 1 | 20 | – | 240 | 5 | 380 | – | 3590 | 1480 | 10 | 1 | – | **7,773** |
| DARK. | 12.36 a.m. | *S.* | 1 | 20 | – | – | 50 | – | – | 12 | 350 | 20 | 400 | – | 50 | – | 140 | 2 | 5280 | – | 5370 | 1740 | – | – | – | **17,011** |
| | 12.15 ,, | *11·2* | 2 | 181 | – | – | 93 | – | – | 44 | 460 | 70 | 170 | – | 10 | 1 | 210 | 10 | 150 | – | 7800 | 450 | – | – | – | **13,202** |
| | 11.55 p.m. | *23* | 1 | 202 | – | – | 86 | 1 | – | 34 | 320 | 70 | 220 | – | – | – | 280 | 14 | 320 | – | 5830 | 320 | – | – | – | **12,559** |
| | 11.34 ,, | *26** | – | 110 | – | – | 123 | – | – | 7 | 170 | 60 | 170 | 1 | 10 | – | 150 | 31 | 250 | – | 1590 | 180 | 20 | – | – | **4,919** |
| | 11.11 ,, | *29* | – | 80 | – | – | 105 | 2 | – | 5 | 220 | 70 | 130 | – | 20 | – | 140 | 21 | 930 | – | 1480 | 310 | – | – | – | **5,516** |
| | †10.39 ,, | *49* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | (389) |
| DAWN. | 4.19 a.m. | *S.* | 3 | – | – | – | – | – | – | 3 | 1 | – | 1 | – | – | – | – | – | 11 | – | 133 | 58 | 1 | – | – | **290** |
| | 3.59 ,, | *6* | 4 | – | – | – | – | – | – | 3 | – | – | 25 | – | – | – | 5 | – | 145 | – | 410 | – | – | – | – | **934** |
| | 3.40 ,, | *13* | 2 | 5 | – | – | – | – | – | 11 | 25 | – | 130 | – | 15 | – | 10 | – | 455 | – | 820 | 80 | 15 | – | 10 | **2,071** |
| | 3.19 ,, | *18* | – | 20 | – | – | 10 | – | 1 | 14 | 90 | – | 330 | – | 20 | – | 50 | 1 | 1540 | – | 1850 | 120 | – | – | – | **5,047** |
| | 2.58 ,, | *26·8* | – | 50 | 1 | – | 10 | 1 | – | 4 | 380 | 100 | 220 | 2 | – | – | 140 | 29 | 2560 | – | 2470 | 320 | – | – | – | **7,662** |
| | 2.36 ,, | *30* | 1 | 140 | – | – | 66 | 2 | – | 11 | 310 | 170 | 230 | 5 | – | 1 | 130 | 43 | 3600 | – | 3350 | 720 | – | – | – | **10,087** |

| | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DAYLIGHT, June 18th. | 9.3 a.m. | *S.* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 5 | – | 47 | 15 | – | – | – | **74** |
| | 8.45 ,, | *3·2* | 2 | – | – | – | – | – | – | – | 4 | 2 | 5 | – | – | – | – | – | 33 | – | 317 | 63 | – | – | – | **485** |
| | 8.27 ,, | *7·5* | 4 | 5 | – | – | – | – | – | 1 | 5 | – | 75 | – | – | – | 10 | – | 410 | – | 665 | 125 | – | – | – | **1,558** |
| | 8.6 ,, | *9·9* | 4 | 5 | – | – | – | – | – | – | 40 | – | 170 | – | – | – | 5 | – | 405 | – | 390 | 185 | 5 | – | – | **1,580** |
| | 7.46 ,, | *20·8* | 4 | 30 | – | – | 5 | 1 | – | 1 | 90 | 10 | 190 | – | 10 | – | 20 | 1 | 1030 | – | 960 | 510 | 5 | – | – | **3,608** |
| | 7.25 ,, | *31·4* | 1 | 50 | – | – | 10 | 1 | – | 3 | 305 | 15 | 165 | – | 10 | – | 35 | – | 885 | – | 1180 | 320 | 5 | – | – | **3,458** |
| DUSK. | 9.6 p.m. | *S.* | 2 | – | – | – | – | – | – | – | – | – | 2 | – | 2 | – | - | – | 6 | – | 33 | 7 | 1 | – | 8 | **472** |
| | 8.49 ,, | *3·2* | – | – | – | – | – | – | – | 16 | – | – | 15 | – | 15 | – | - | – | 85 | – | 410 | – | 5 | – | – | **1,106** |
| | 8.31 ,, | *9·3* | 2 | 30 | – | – | – | – | – | 20 | 140 | – | 50 | – | 30 | – | 20 | – | 380 | – | 1490 | 10 | 30 | – | – | **2,516** |
| | 8.11 ,, | *14* | 11 | 140 | – | – | – | – | – | 42 | 670 | – | 560 | – | 60 | – | 80 | – | 840 | – | 4980 | – | 20 | – | 10 | **8,021** |
| | 7.53 ,, | *19·4* | 3 | 80 | – | – | – | – | – | 52 | 380 | – | 600 | – | 40 | – | 70 | – | 940 | – | 4080 | 70 | 60 | – | 20 | **7,828** |
| | 7.30 ,, | *30·9* | – | 132 | – | – | 1 | 1 | – | 16 | 150 | – | 180 | – | 10 | – | 10 | – | 820 | – | 1750 | 80 | 40 | – | 10 | **4,344** |
| DARK. | 12.13 a.m. | *S.* | – | 40 | – | – | 10 | – | – | 20 | 130 | 40 | 40 | – | – | – | 60 | 4 | 30 | – | 3370 | 900 | – | – | – | **5,882** |
| | 11.55 p.m. | *5·2* | 4 | 110 | – | – | 201 | – | – | 53 | 330 | 90 | 360 | – | 150 | – | 120 | 7 | 70 | – | 5140 | 630 | 10 | – | 10 | **10,520** |
| | 11.36 ,, | *12·2* | 2 | 80 | – | – | 60 | – | – | 16 | 330 | 50 | 210 | 1 | 90 | – | 50 | 9 | 310 | – | 4540 | 230 | 10 | – | 20 | **8,898** |
| | 11.16 ,, | *16·6* | 1 | 240 | – | – | 61 | 1 | – | 31 | 690 | 70 | 400 | 1 | 60 | – | 140 | 6 | 1150 | 110 | 6910 | 400 | 20 | – | 10 | **13,629** |
| | 10.55 ,, | *20·7* | 1 | 150 | – | – | 110 | 4 | – | 68 | 470 | 60 | 260 | 3 | 90 | – | 140 | 10 | 160 | 30 | 5210 | 390 | 40 | – | – | **8,444** |
| | 10.33 ,, | *25·8* | 2 | 80 | – | – | 51 | 3 | – | 8 | 320 | 50 | 360 | 2 | 20 | – | 150 | 21 | 310 | 10 | 3480 | 500 | 20 | – | – | **8,505** |
| DAWN. | 4.6 a.m. | *S.* | 3 | – | – | – | – | – | – | 1 | – | – | 3 | – | – | – | – | – | 10 | – | 51 | 1 | 1 | – | 2 | **294** |
| | 3.49 ,, | *3·6* | 4 | – | – | – | – | – | – | 4 | 10 | – | 22 | – | – | – | – | – | 80 | – | 755 | 10 | 10 | – | 10 | **1,531** |
| | 3.28 ,, | *8* | 2 | 20 | – | – | – | – | – | 13 | 50 | 20 | 330 | – | 30 | 2 | 20 | – | 480 | – | 1780 | 90 | – | – | 10 | **3,658** |
| | 3.9 ,, | *13·9* | 1 | 40 | – | – | – | – | – | 12 | 190 | 40 | 650 | – | 70 | 2 | 20 | 1 | 870 | – | 3130 | 300 | 10 | – | – | **6,243** |
| | 2.49 ,, | *23·7* | 4 | 40 | – | – | – | – | – | 7 | 340 | 120 | 180 | – | 10 | 1 | 100 | 5 | 1770 | – | 2230 | 330 | 30 | – | – | **6,315** |
| | 2.28 ,, | *27·5* | – | 130 | – | – | 30 | – | – | 3 | 480 | 160 | 270 | 6 | 10 | 4 | 120 | 20 | 1550 | – | 3070 | 460 | 10 | – | – | **7,757** |
| DAYLIGHT, June 19th. | 9.12 a.m. | *S.* | 1 | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | 4 | – | 119 | 22 | – | – | – | **176** |
| | 8.54 ,, | *4* | 1 | – | – | – | – | – | – | – | 1 | – | 3 | – | – | – | – | – | 12 | – | 239 | 19 | – | – | – | **660** |
| | 8.35 ,, | *11·1* | 1 | 35 | – | – | – | – | – | 1 | 30 | – | 195 | – | 45 | – | 5 | – | 115 | – | 1170 | 35 | 5 | – | – | **3,281** |
| | 8.16 ,, | *12·7* | 1 | 10 | – | – | – | – | – | 2 | 200 | – | 170 | – | 20 | – | 30 | – | 350 | – | 3420 | 70 | 30 | – | – | **5,384** |
| | 7.56 ,, | *23·3* | 1 | 170 | – | – | 60 | 1 | – | 9 | 440 | 10 | 300 | – | 20 | – | 40 | – | 1140 | 40 | 6330 | 140 | 30 | – | – | **8,849** |
| | 7.35 ,, | *28·5* | – | 250 | – | – | 20 | 1 | – | 32 | 650 | – | 480 | – | 50 | – | 120 | – | 1540 | 10 | 8850 | 360 | 40 | – | – | **14,150** |

* Maximum depth, 31 m.; 26 m. given as possible average. † Net struck bottom.

# A Net for Catching Plankton near the Bottom.

By
**F. S. Russell, D.S.C., B.A.**
*Assistant Naturalist at the Plymouth Laboratory.*

With 2 Figures in the Text.

In the course of the researches on the vertical distribution of plankton it became evident that a net was needed for sampling the water-layers very close to the sea bottom. While the net had to be efficient in capturing the plankton animals present in those layers, it was necessary that the catches should not be vitiated by the presence of bottom-living organisms which had been stirred up from the sea floor by the net itself.

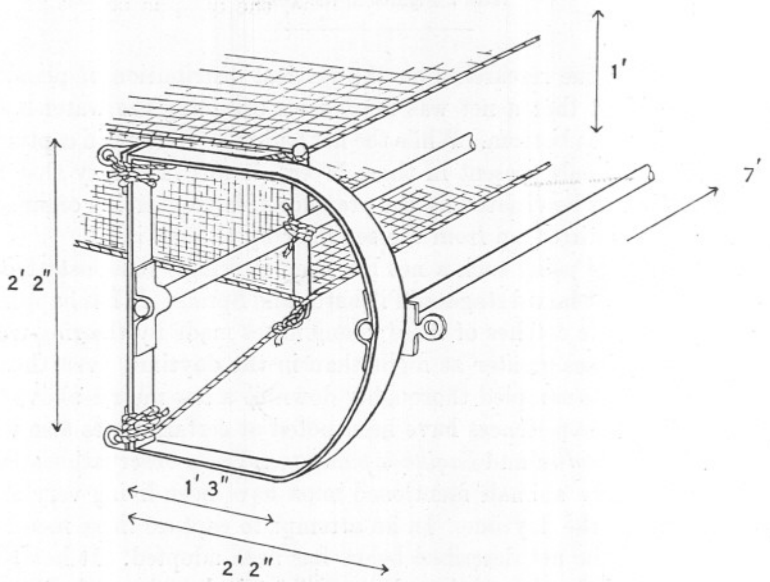
The necessity of using such a net has been strikingly demonstrated in the case of the post-larval stages of Pilchards and Sprats. It has happened repeatedly that the catches of these young fishes made by the ring-trawl are nearly ten times greater at night than in the daytime, even though the water-layers be sampled thoroughly down to a few metres above the bottom. Similar experiences have been noted at certain times also with *Tomopteris helgolandica* and *Sagitta bipunctata*. These observations point to the fact that the animals mentioned must have been living very close to the bottom in the daytime. In an attempt to capture these members of the plankton the net described below has been adopted. It has been shown in practice that it samples a layer about 7 inches above the bottom and 1 foot in thickness, capturing therefrom many plankton animals. Furthermore, the catches have been almost devoid of sand and gravel, or other bottom deposits, indicating that the capture of organisms stirred up from the bottom itself is probably very small.

## THE NET.

The net is made of " stramin," a Danish sacking made of threads of closely-spun hemp yarn, the meshes of which are merely interwoven and not knotted, with 15 to 16 strands to the inch. It has a rectangular mouth 4 feet in width and 1 foot in depth. It is 8 feet in length, and tapers to a circumference of 16 inches to take an ordinary tow-net bucket about 4 inches in diameter. The net is made in two main pieces, with two triangular gussets inset in front along the sides for a length of 3 feet

6 inches. The seams of the net are roped, as is also the edge of the mouth. The sides of the mouth are supported by round poles just over 1 foot in length. The net is, in fact, built on the same principle as the Young fish trawl Type A net described and figured by Clark (*Journ. Mar. Biol. Assoc.*, N.S., Vol. XII, No. 2, 1920, p. 163 and Fig. 1), except that the dimensions are different.

When fishing, the net is fixed to an Agassiz trawl frame (Fig. 1). Four short bridles from the stramin net are attached to the hind corners of the Agassiz shoes, care being taken to attach these bridles inside so that when the net is fishing they will not be chafed on the bottom. The two upright poles are then stopped to the rear horizontal bar of the Agassiz frame so as to keep the net central. The Agassiz trawl net itself is also fixed to the frame in the usual manner; the foot-ropes are, however, slacked off slightly so that, when fishing, they belly back behind the opening of the stramin net (Fig. 2).

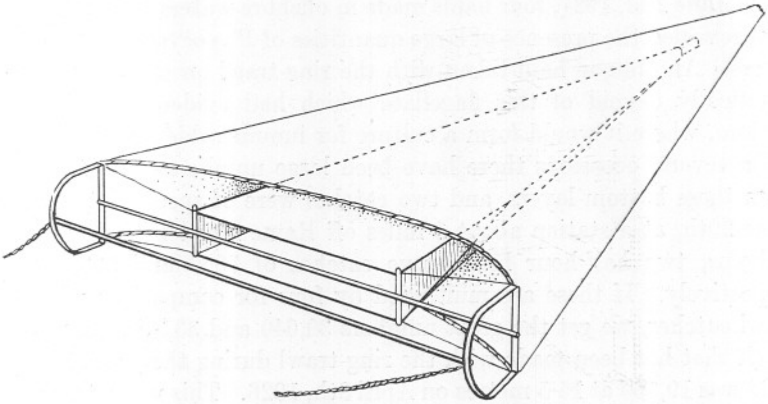


TEXT-FIG. 1.—Showing attachment of stramin net to Agassiz frame.

The Agassiz frame in use is of the following dimensions: Height of shoe, 2 feet 2 inches; length of flat part of shoe, 1 foot 3 inches; total length of shoe, 2 feet 2 inches. The iron of which the shoes are made is $\frac{3}{16}$ of an inch in thickness and $2\frac{1}{4}$ inches wide. The weight of each shoe is about 35 lbs.; the weight of the whole frame, with shackles, being nearly 1 cwt. The two shoes are held together by a pair of horizontal bars $1\frac{1}{4}$ inches in diameter and 7 feet in length.

If the stramin net is fixed centrally on the rear bar of the Agassiz it will have a clearance of 7 inches from the sea bottom, the height of the net being 1 foot and that of the Agassiz shoe 2 feet 2 inches. There will also be a clearance of 1 foot 6 inches at either end between the stramin net and the shoes: thus any matérial stirred up from the bottom by the shoes will be swept past the mouth of the net. At the same time, by slackening off the foot-ropes, one can ensure that the bottom is only stirred up by them behind the mouth of the net.

The cod-end of the Agassiz trawl net itself need not be tied up, so that any large spiny animals entering the net may pass out again and not damage the stramin net; at the same time, the net has been fished on several occasions with the cod-end tied up, thus effecting a dual purpose. The presence of the Agassiz trawl saves the stramin net from chafing on the sea floor.



TEXT-FIG. 2.—Showing method of fishing.

The net has now been in operation for over fifty hauls, each of half an hour's duration, and in every case the catches have been successful. The presence of sand or gravel in the catches is rare, and then only in such small quantities as to give the idea that it was already in suspension, due to tidal action rather than to disturbance caused by the net.

The net is towed with the engines going very slow, if anything slightly faster than for the ring-trawl, in order to prevent the shoes digging too deep into a soft bottom.

The dimensions of the opening (1 foot ×4 feet) give a fishing area similar to that of a metre tow-net, so that such a net can be adapted for the purpose. This area being almost exactly a quarter of that of the 2-metre ring-trawl, the catches made by the two nets may at once be roughly compared. Seeing that there will be a greater chance of animals avoiding the narrow mouth of the small net and that, owing to the presence of the rear bar of the Agassiz frame, its fishing capacity is probably not improved, one is justified in regarding a catch multiplied by four as being a minimum estimate of a catch made by a ring-trawl, if it had been used instead.

A further advantage of this net is that it could probably as easily be used on a beam-trawl frame if an Agassiz frame was not available. Improvements could be made by the building of a special frame to do away with the bar which lies immediately in the mouth of the net.

While it is as yet too early to discuss the results obtained by the net, mention may be made of one or two catches of interest.

On June 2nd, 1927, four hauls made in offshore waters in the Plymouth area revealed the presence of large quantities of Phæocystis in the bottom layers. An oblique haul taken with the ring-trawl on the same day was practically devoid of this flagellate which had evidently sunk to the bottom, where it would form a culture for innumerable small organisms.

On several occasions there have been large numbers of Sagitta taken from these bottom layers, and two catches were of special interest. On June 29th, at a station about 3 miles off Rame Head in a depth of 20 fathoms, two half-hour hauls gave catches of 7660 and 8330 Sagitta respectively. If these are multiplied by four for comparison with ring-trawl catches, we get the great numbers 30,640 and 33,320. The largest catch that has been made with the ring-trawl during the years 1925 and 1926 was 19,360 at 15·5 metres on April 9th, 1926. This was a ten-minute haul, or, to compare it with the half-hour catch of the bottom stramin net, 19,360 × 3 = 58,080. These great catches made in June near the bottom may well explain the great diurnal variation in number of Sagitta in the upper layers mentioned in a further paper on page 87 of this Journal. (*Journ. Mar. Biol. Assn.*, N.S., Vol. XV, No. 1, 1928, p. 81.)

As is to be expected, there are often many mysids in the catches, and Euphausiids are generally present in small numbers. On July 8th there was a large catch of 2210 mysids in a half-hour haul.

It is quite to be expected that in course of time many young stages of animals that have been rarely caught will appear in greater quantity in such collections. For instance, several young stages of the Squid up to a length of about 1¼ inches have already been taken. Such a net should prove of great use for capturing in good condition many of the smaller bottom-haunting animals in very deep waters.

I am much indebted to Mr. E. Ford for his assistance in drawing the figures.

# Studies of the Plymouth Brachyura. II. The Larval Stages of Ebalia and Pinnotheres.

By

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*Naturalist at the Plymouth Laboratory.*

With 2 Plates and one Figure in the Text.

FURTHER study of the larval crabs of the Plymouth district has resulted in the elucidation of many more life-histories. Amongst these perhaps some of the most interesting are Ebalia and Pinnotheres. These genera, placed by systematists in widely different groups, resemble one another closely in many details in their larval stages and are here purposely described together in order that a comparison may be made.

The genus Ebalia is the only one of the sub-tribe Oxystomata (using Borradaile's classification, 1907) represented in Britain, belonging to the family Leucosiidæ, sub-family Leucosiinæ. Pinnotheres is placed in the sub-tribe Brachygnatha, super-family Brachyrhyncha, family Pinnotheridæ.

The main form of the zoea of Ebalia is well known, having no dorsal spine to the carapace which is large and round, the rostral and lateral spines usually rudimentary and the telson hardly forked at all, but having the form of a flat plate slightly drawn out at each side and bearing six setæ in the emarginate centre. *Pinnotheres pisum,* the commonest and best-known British pea-crab, has no dorsal spine on the carapace, but the rostral and laterals are well developed, the latter bending down in a characteristic way. Figures of this zoea have been given by some of the earliest naturalists. The telson is peculiar in being three-lobed, with three setæ each side between the central and lateral lobes. *Pinnotheres veterum,* however, has all the spines of the carapace well developed, the telson being like *P. pisum.* Both Ebalia and Pinnotheres zoeae have a pronounced tendency to curl up in a ball, and a very important feature in both is the minute and very rudimentary antenna which is entirely without a spinous process.

There are three species of Ebalia at Plymouth—*Ebalia tuberosa* (Pennant), *E. Cranchii* Leach, and *E. tumefacta* (Montagu). Of these the first is much the commonest, and is the only one in which the whole life-history has been successfully worked out. This is described here completely for the first time. There are two species of Pinnotheres in the district, the "Common Pea-Crab," *Pinnotheres pisum* (Pennant), which occurs very frequently in mussels on the ground, also occasionally in cockles and ascidians, and the rare "Pinna Pea-Crab," *Pinnotheres veterum* Bosc. living in Pinna and other bivalves, the larva of which has hitherto only been known from a very incomplete description by Gourret (1882). The eggs of *P. pisum* have been hatched out in the aquarium, but it has not been possible to obtain adults of *P. veterum* during the last two years. Its larva occurs in the Plymouth plankton and has been reared as far as the megalopa. These larvæ are described here fully for the first time and are so different from those belonging to *P. pisum* that a revision of the adult characters may be necessary in order to determine whether *P. veterum* should not be placed in a separate genus. The investigations of Hyman (1924) on the larval forms of the Pinnotheridæ show, however, that these vary to a very large extent, especially with regard to the carapace and the telson.

## Genus **Ebalia.**

### *Ebalia tuberosa* (Pennant).

This crab is common in the usual dredging-grounds on sandy bottoms in the Sound. Berried females are to be found from January to June, but are commonest in the spring. The eggs are completely covered and hidden by the large abdomen which fits tightly under the carapace.

The larval forms of Ebalia so far described are not certainly identified. Cano (1892) gives a good figure of a late zoea (fourth and last) of an Ebalia, calling it Plagusia sp. and afterwards correcting this to Ebalia. He does not, however, identify the species. Williamson (1915) figures the first zoea of an Ebalia without giving the species. His description and figures closely resemble *Ebalia tuberosa* which is described here. He also mentions a third stage (number of setæ on the maxillipedes not ascertained) which he obtained from a second stage with six setæ. Miss Jorgensen (1925) describes larval Ebalia from North Sea plankton which she thinks probably belong to *E. Cranchii*, the commonest species on the Northumberland coast. It seems likely (as she herself suggests) that here are two species, *E. Cranchii* and *E. tuberosa*, for she figures four zoeae which apparently do not all belong to the same species. There appear to be six setæ on the maxillipedes in all the later stages. Possibly Fig. 8, which seems to be a fourth zoea, really has eight setæ instead of six. As her specimens were preserved there is no colour to guide us. She gives a drawing of a megalopa, probably *E. Cranchii*, which, although few details are shown, resembles that of *E. tuberosa*.

The eggs of *Ebalia tuberosa* are bright orange-red. These were hatched out into pre-zoeae in a small aërated aquarium in the Plymouth Laboratory in April, 1927. Egg, 0·28 mm. across when first extruded, 0·3 mm. across when ready to hatch. The pre-zoea cast the embryonic skin almost immediately and the first zoea appeared. Unfortunately these did not live, but others were obtained from the plankton, the second and third zoeae with six setæ to the maxillipedes, the fourth with eight. This last changed into the megalopa, and from the megalopa came the young crab. Thus we have the complete life-history of *Ebalia tuberosa*, and almost certainly the other species are very similar in their larval forms. The presence of six setæ on the maxillipedes of both the second and third zoeae is apparently a unique feature, for all the other genera of crabs known have normally six in the second zoea and eight in the third, whilst the fourth has ten. Thus the fourth zoea with eight setæ is only found in Ebalia so far as we know at present.

*Pre-zoea* (Plate I, Figs. 1–4), 1·2 mm. in length,* zoeal colours showing through the embryonic cuticle, orange, yellow, brown and black. Antennule and antenna each with two long setose spines; telson quite distinctly forked with the usual seven spines each side, six long setose and one short non-setose, the latter covering the spine representing the tip of the fork. These long antennal spines are specially interesting as the antenna of the zoea is only a rudimentary stump. The telson is also interesting as indicating the ordinary brachyuran type of larval telson, the forking becoming obliterated in the zoea whose very characteristic and peculiar telson is probably an adaptation to its mode of life.

*First zoea* (Plate I, Figs. 5, 6), 1·3 mm. in length. Usually curled up in a ball, and, although at first coming up to the top of the aquarium, it very soon descends to near the bottom. Carapace large, rounded, without dorsal spine, rostral and lateral spines rudimentary. Eyes sessile, antennules with two æsthetes and two spines; antennæ small uniramous stumps; mandible large with reticulated surface; first and second maxillæ of ordinary form; first and second maxillipedes, as always in the first zoea, with four setæ on the exopodites, endopodites of five and three joints respectively. Remaining thoracic appendages very rudimentary, hidden under carapace. Abdomen of five joints plus telson, second and third joints with lateral knobs, first joint with six hairs dorsally, the others with two each. Telson a triangular plate drawn out at each side to a small tooth, hind margin slightly emarginate with six setæ in centre. Colour of zoea when first hatched pale brownish with front pale yellow, an orange spot at the top of carapace; as it grows the colour becomes more red and the under part of thorax a brilliant crimson. The zoea moves about quickly, curling up its body by bringing

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* As in the previous paper (Lebour, 1927), the length is taken from the front of the head to the end of the telson.

the abdomen round tightly under the carapace. It is usually to be found near the bottom, and this is also the case in its natural surroundings. When Plankton samples are taken from surface, mid-water, and near the bottom, the Ebalia zoeae almost always occur, if present at all, in the samples from near the bottom but not in the others. Miss Jorgensen states that they rarely appear in the surface samples, and Russell (1927) also records them from the deeper layers only. Here it seems that we have a reason for the peculiar form ; the dorsal spine is not only superfluous but possibly actually in the way if the larva is not to live in the upper water layers. The forked telson with its long spines helps the ordinary crab larva to keep near the surface, but when this is not needed the telson tends to be flat and without long spines, and in this way it is wrapped round the body more easily to form a ball. The same reasoning may possibly apply to the antennæ, which have no long spinous process.

TEXT-FIG. 1.—Second zoea of *Ebalia tuberosa*, about 1·68 mm. long (Scale A).

*Second zoea* (Text-Fig. 1), about 1·68 mm. in length. Colours like the first. Eyes stalked, antennules, antennæ and mouth parts hardly altered, first and second maxillipedes with six setæ. Rudimentary legs under carapace. Abdomen and telson much the same as the first, no pleopods. Occurs in the plankton with the first zoea.

*Third zoea* (Plate I, Fig. 7), about 1·92 mm. in length. Colours like the first and second, but more intense crimson, and a large black chromatophore mixed with orange and red on the top of the carapace. Lateral spines slightly larger, sticking out from sides of carapace as pointed knobs. Antennules tending to be jointed, swollen at base, antennæ and mouth parts hardly altered, first and second maxillipedes with six setæ. Rudiments of other thoracic appendages slightly larger. Abdomen and telson much the same, but pleopods have appeared as short buds on second to fifth segments. Miss Jorgensen describes five pairs of pleopods. This third zoea is to be found in the bottom layers in the same way as the first and second.

*Fourth zoea* (Plate I, Figs. 8–13), about 3 mm. in length, obtained by the third zoea casting its skin. From the length of the pleopods and form and size of the rudimentary thoracic limbs it is clear that this is the last zoea. Colour the same as in the third zoea. Antennule, jointed, with small branch, antennæ little altered, palp on mandible, eight setæ on first and second maxillipedes. Thoracic legs slightly jointed, the first leg large with chela showing. Abdomen still with only five segments plus telson, and only four pairs of pleopods which are long. Knobs and hair on abdomen as before and telson hardly altered. The fourth zoea still keeps in the lower water layers, and changes into the megalopa. Thus there are four zoeal stages in *Ebalia tuberosa.*

Various foods were given to these zoeae. Even the first zoea was actually seen to eat early echinoderm larvæ and early Pomatoceros larvæ from artificial fertilisations, and their intestines often contained debris mixed with green cells and diatoms. Unfortunately they did not live. It was only the later stages, third and fourth zoea and megalopa, that lived any time and changed their skins. The megalopa was fed on small pieces of mussel.

*Megalopa* (Plate I, Fig. 14), obtained from fourth zoea, 3 mm. in length. Deep crimson with yellowish legs. Carapace nearly smooth without dorsal spine, almost straight in front, very slightly curved so that it protrudes in centre, but no rostrum. All legs functional, and maxillipedes now are mouth parts. Hind legs without feelers on last joint. Abdomen with six segments plus telson and five pairs of pleopods, the last pair with six setæ, the others with eleven. The hind legs without feelers resemble the Oxyrhyncha (Spider Crabs) and are unlike the Brachyrhyncha in this way, with the exception of Pinnotheres and probably its allies. The megalopa changed to the young crab (Plate I, Fig. 15), which was easily recognisable as Ebalia. This was no longer red but a pale yellowish colour. The second and third young stages from this were recognisable as *Ebalia tuberosa*, having the raised cross showing on the carapace. First young stage 1·9 mm. across carapace, second young stage 2·5 mm. across. Others grew to later stages but were not measured.

The following dates show the changes of skin from a megalopa obtained in the plankton 14/6/26 :—

First young stage 14/7/26.
Second ,, ,, 17/9/26.

These are probably much longer than is natural, as *Portunus puber* reared in comfortable conditions changed about once a week.

The life-history of *Ebalia tuberosa* is now complete, and we know that there are four zoeal stages and a megalopa before the first crab stage is reached, and that it is hatched as a pre-zoea.

## Genus **Pinnotheres.**

The larval forms of the Pinnotheridæ may differ to a large extent, even the species of Pinnotheres itself varying as to the number of spines on the carapace and form of telson. The larvæ of the two British species are so unlike that it seems improbable that they should belong to the same genus. There are, however, certain important characters which they have in common, such as the rudimentary antennæ, form of telson and abdomen, which show that they must be closely related.

### *Pinnotheres pisum* Leach.

The "Common Pea-Crab" occurs frequently in the Plymouth district inside the common mussel *Mytilus edulis* and is also occasionally found in *Modiola vulgaris* and in certain ascidians. The berried female occurs in the late spring and early summer, June being probably the best month, July slightly less so, and rare specimens may occur in August, after which the spawning is usually finished. A good figure of the berried crab is given by Miss Atkins (1927).

The eggs are an orange-red changing to a brownish colour when ready to hatch. The early eggs measure 0·27 mm., late eggs 0·3 mm. Berried females with eggs nearly ready to hatch taken from the mussels were put in plunger jars with some empty shells as shelter and the eggs hatched out as pre-zoeae, which almost immediately cast the embryonic skin and emerged as first zoeae. Unfortunately these did not live, and although similar specimens were obtained from the plankton no later stages were found. It is therefore impossible as yet to know the complete life-history. *Pinnotheres veterum* was found to have only two zoeal stages, but *P. pisum* probably has three or more, because the first zoea is much further backward in development compared with that of *P. veterum* and has no trace of pleopods. It is interesting that the first zoea of *P. pisum*, although at first rising to the surface, very soon went down to the bottom where it fed, the intestine being full of debris. There is no dorsal spine, and the zoea curls itself in a ball in a very similar way to Ebalia. The form in both seems to be adapted for life near the bottom.

Hyman (op. cit.) states that the only feature serving to distinguish the larvæ of the Pinnotheridæ is the minute size of the antenna, as the telson in some forms may be of the normal forked type and all the spines of the carapace may be present. As we have seen above, however, the antenna in Ebalia is also minute, but both British species of Pinnotheres are recognisable by the telson which has three lobes. This resembles *P. ostreum*, described by Hyman, which differs in having no spines at all on the carapace.

*Pre-zoea* (Plate II, Figs. 1, 2), 0·80 mm. long. Embryonic spines, antennules and antennæ so thin that it was impossible to secure them, and the first zoea appeared almost immediately. Taken from the egg nearly ready to hatch, the pre-zoea has a telson with two lateral teeth outside each of the lateral lobes.

*First zoea* (Plate II, Fig. 3–6), 0·96 mm. long. Minute and nearly always curled up in a ball. Colour greenish, made up of black, yellow, and orange chromatophores. No dorsal spine to carapace, but laterals and rostral well developed, all bending down. This is the stage given by Thompson (1835), the illustrations being copied by Bell (1853), therefore it is one of the earliest crab larvæ known. Eyes sessile, antennules short with two æsthetes and one spine, antenna minute, rudimentary stumps, mouth parts of the usual type. First and second maxillipides with four setæ on exopodites, endopodites of five and three joints respectively. Carapace large, rounded, no dorsal spine, laterals directed downwards and outwards, rostral curved downwards and slightly outwards. Abdomen of five segments plus telson, second and third segments with knobs, telson with three lobes, the central one rounded and slightly longer than the outer lobes which end in points. Outside outer lobes the margin is crenulated. Three spines each side between central and outer lobes. No trace of pleopods.

### *Pinnotheres veterum* Bosc.

Berried crab not obtained. This is a much rarer species, occurring in Pinna and occasionally in other mollusks. Zoeae occur in the plankton during late summer and early autumn (August to October). These appear indiscriminately from the surface to the bottom layers. Pre-zoea not seen, but first and second zoeae were obtained, the second being the last, which when kept in the Laboratory changed to the megalopa. A first zoea changed to the second, but it was not found possible to bring the megalopa to the crab stage. The zoea has the telson very much like that of *P. pisum*, but is much larger and has all the spines of the carapace present and well developed.

*First zoea* (Plate II, Figs. 7–8), about 1·52 mm. long. Colour pale brownish red merging into pale yellow with dark brown chromatophores on dorsal spine, carapace, antennæ, mandibles, lateral spines and abdominal segments. Eyes black, sessile. Dorsal spine 0·96 mm. long, slightly curved backwards and then straight. Lateral spines 0·65 mm. long, sticking out behind the body, slightly curved downwards and directed downwards, outwards and backwards. Rostral spine 0·72 mm. long, slightly curved inwards and outwards. Antennule with three æsthetes and one spine. Antenna a rudimentary stump. Mouth parts of the usual type. First and second maxillipedes with four setæ on the exopodites, endopodites with five and two joints respectively. Rudiments of other thoracic appendages hidden by carapace. Abdomen of five segments plus telson. Pleopods present as small knobs on segments two to five. Second and third segments with lateral knobs. Telson with central lobe shorter than laterals, the latter pointed with one short and thick tooth on its outer margin, but no crenulations as in *P. pisum*. The zoea has a decided tendency to curl up in a ball, but the spines probably enable it to keep in the upper water layers. They were always found singly and were never common. The telson is very like the figure given by Gourret for Pinnotheres sp. (1882), which he says is the same as *P. veterum*. Otherwise his very incomplete description tells us little. He obtained his specimen of *P. veterum* from *Pinna truncata*. In my previous paper (1927) it has been suggested that his figure of Pisa is probably *Pinnotheres veterum*. A comparison of this with the present illustrations will show how very likely this supposition is. That my specimens belong to a Pinnotheres is certain, and these are totally unlike any Spider Crab. In Gourret's figure of Pisa the rudimentary antennæ are shown, but the separate telson and antennæ which he depicts evidently really belong to Pisa and resemble Inachus and Macropodia. Being interpreted thus, Gourret's Fig. 3 (Plate II) should be *Pinnotheres veterum*, and Figs. 4 and 5 should be Pisa.

*Second zoea* (Plate II, Figs. 9–10), about 2 mm. long. Like the first in colouring and form. Eyes stalked. Six spines to maxillipedes. Antennules pointed and biramous. Antennæ as in the first zoea. Thoracic legs well developed but hidden under carapace; palp on mandible. Abdomen with still only five segments plus telson, knobs as before on second and third segments. Pleopods long, four pairs only. Telson unaltered. The second zoea changed into the megalopa, there are therefore only two zoeal stages in this species.

*Megalopa* (Plate II, Fig. 11), 1·68 mm. long. Greyish brown in colour. Carapace smooth without rostrum, the front slightly produced so as to form an undulating margin. Last pair of legs without feelers. Abdomen still with only five segments plus telson, and four pairs of pleopods. An interesting fact is that the megalopa swims very little and is so like a crab that one would almost describe it as the first crab stage if it were not that the setose pleopods are present and that the megalopa occasionally swims with them. More often it is seen with the abdomen tucked in under the body as in the crab. Now *Pinnixia Sayana* Stimpson has, according to Hyman (op. cit.), a zoea changing directly into a crab without any megalopa stage. This stage has also only four pairs of pleopods. The megalopa of *Pinnotheres veterum* seems to be intermediate between the ordinary megalopa and this form of young crab. Unfortunately it was not possible to rear these megalopæ any further, as they would not cast their skins nor enter the mollusks provided for them. It is possible, however, that had they been given young Pinna this might have been effected. As it was they lived some time without changing and then died.

The life-history of *P. veterum* must differ considerably from that of *P. pisum* as it has only two zoeal stages and is hatched in a very well-developed state, whilst *P. pisum* is much more backward and must almost certainly have three or more zoeal stages. Two such different larval forms should surely be an indication of distinct genera.

## Comparison of Pinnotheres and Ebalia.

It is interesting to compare the two types which in many ways are much alike, and yet the adults are placed so widely apart.

Perhaps the most important feature which these zoeae have in common is the rudimentary antenna which is merely a stump. This may be useful to a larva living near the bottom, but it is also present in those members of the Pinnotheridæ which have ordinary forked telson and all the spines of the carapace present.

In both Ebalia and the Pinnotheridæ there is a tendency to reduce the forks of the telson so that it becomes a more or less flat plate with the long spines shortened, and the abdomen usually curls in under the body so that a ball is formed. The habit of rolling into a ball seems obviously of advantage in keeping down below, but the curious form of the telson is probably derived from the ordinary forked type, and many of the Pinnotheridæ have this forked telson. We may perhaps look upon these peculiar variations in shape of telson as the most extreme deviations which are of advantage as an aid to curling up the body, those with ordinary telson being perhaps the more primitive.

Both Ebalia and the Pinnotheridæ have the abdominal segments less than the normal number in the later stages and a consequent reduction in the pleopods, and knobs are present on the second and third abdominal segment in all zoeal stages. It is difficult to see any meaning in the knobs, the number of which is, however, characteristic in certain groups, but a reduction in pleopods may possibly be because the zoea keeps to the lower layers of water. The megalopæ of both Ebalia and Pinnotheres are of the same type, having no rostrum, a comparatively smooth carapace without spines, and the last joint of the last legs being without feelers. These are the only megalopæ of all the British crabs known (and nearly all have now been observed by myself) which have no rostrum, and the absence of feelers on the last joint of the last leg is characteristic of the Oxyrhyncha, all the known megalopæ of the Brachyrhyncha with the exception of Pinnotheres having them. The megalopæ of Ebalia and

Pinnotheres are strikingly alike, the chief difference being that Ebalia has the normal number of abdominal segments (six plus telson) whilst Pinnotheres has only the five which were present in the zoea. Ebalia thus has added a segment in the megalopa whilst Pinnotheres still keeps to one less than the normal.

The resemblances in these larval crabs are interesting if at present not readily explainable, and the adult morphology might well be revised, for larval characters are of great importance and should be taken into account in any system of classification even if they are chiefly to be explained as special adaptations to environment.

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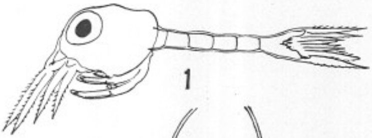
## EXPLANATION OF PLATES.

As in the previous paper, the figures are drawn to three scales, the pre-zoea and zoea to Scale A; the megalopa, young crab, and crab carapace to Scale B, half the Scale of A, and the appendages and various details to Scale C, three times the scale of A. All agree with those of the previous paper in scale.

## PLATE I. *Ebalia tuberosa.*

FIG. 1. Pre-zoea, 1·2 mm. long (Scale A).
FIG. 2. Antennule of Pre-zoea (Scale C).
FIG. 3. Antenna of same (Scale C).
FIG. 4. Telson of same (Scale C).
FIG. 5. First zoea, 1·3 mm. long (Scale A).
FIG. 6. First zoea, back view (Scale A).
FIG. 7. Third zoea, 1·92 mm. long (Scale A).
FIG. 8. Fourth zoea, about 3 mm. long (Scale A).
FIG. 9. Fourth zoea, abdomen (Scale A).
FIG. 10. Fourth zoea, back view of a more slender specimen (Scale A).
FIG. 11. Fourth zoea antennule (Scale A).
FIG. 12. Fourth zoea antenna (Scale A).
FIG. 13. Fourth zoea, cast skin, front portion showing rostrum (Scale A).
FIG. 14. Megalopa, 3 mm. long (Scale B).
FIG. 15. First crab stage, 1·9 mm. across carapace (Scale B).
FIG. 16. Second crab stage, 2·5 mm. across carapace (Scale B).

## PLATE I.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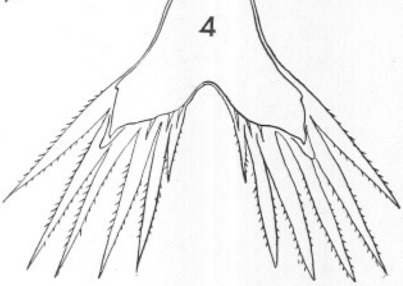
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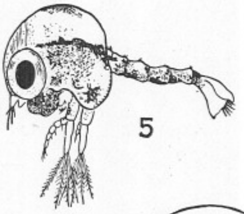
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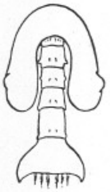
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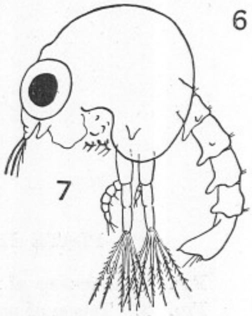
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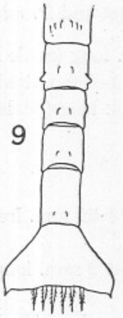
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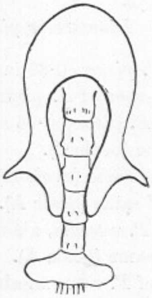
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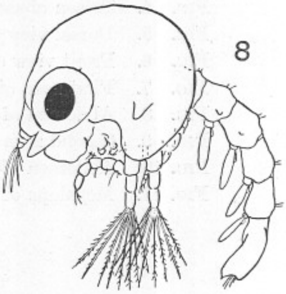
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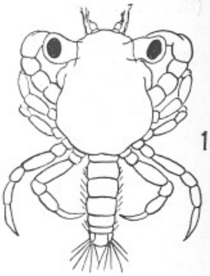
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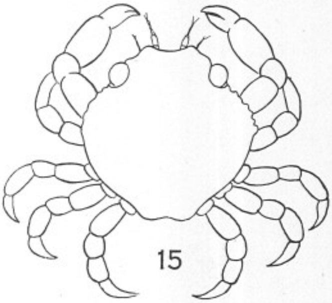
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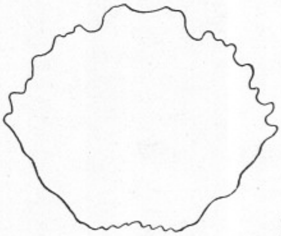
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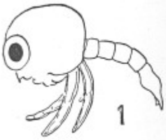
PLATE II. *Pinnotheres pisum* and *P. veterum*.

FIG. 1. Pre-zoea of *P. pisum*, 0·80 mm. long (Scale A).
FIG. 2. Telson of pre-zoea of *P. pisum* before hatching (Scale C)
FIG. 3. First zoea of *P. pisum*, 0·96 mm. long (Scale A).
FIG. 4. Telson of same (Scale C).
FIG. 5. Dorsal view of same (Scale A)
FIG. 6. Front view of same (Scale A).
FIG. 7. First zoea of *P. veterum*, about 1·52 mm. long (Scale A).
FIG. 8. Abdomen of same (Scale A).
FIG. 9. Second zoea of *P. veterum*, about 2 mm. long (Scale A).
FIG. 10. Abdomen of same (Scale A).
FIG. 11. Megalopa of *P. veterum*, 1·68 mm. long (Scale B).

PLATE II.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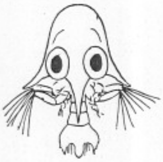
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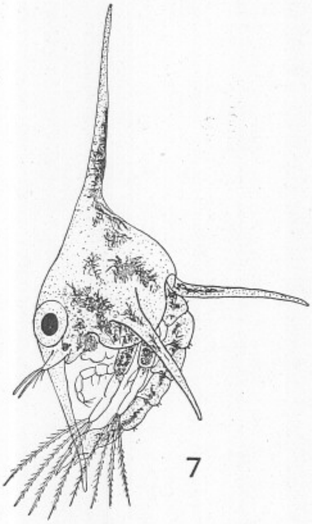
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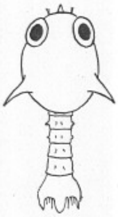
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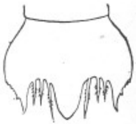
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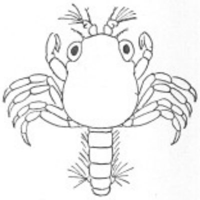
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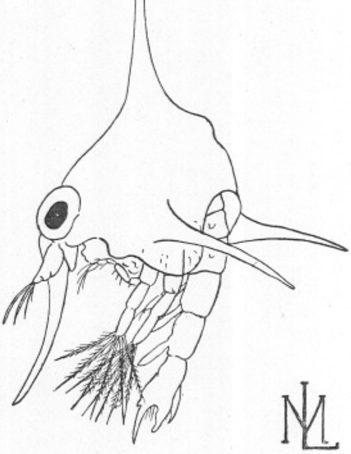
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# The Nauplius Larva of *Anelasma squalicola* (Lovén).

By

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With 4 Figures in the Text.

THE Cirripede *Anelasma squalicola* (Lovén) is parasitic on the smooth dogfish, *Etmopterus spinax* (Linnæus). These fish, which are caught at a depth of about 150–180 fathoms, were brought to the University of Liverpool as material for a chemical investigation by Professor Heilbronn and his colleagues. On finding that some of the fish were thus parasitised, Professor J. Johnstone and myself made a study of the general morphology of *Anelasma* (**3**).

During this research our interest was aroused by the presence of developing eggs and embryos contained in the " mantle cavity " of mature specimens, but no trace could be found of a completely developed larva ; thus no mention of it was made in the account of Anelasma.

Since the publication of the paper, however, Mr. C. F. Hickling has obtained specimens of the larvæ taken from adult parasites captured off the Flannan Islands, in the Western Hebrides region, in 270 fathoms of water. Owing to the peculiar structure of the adult organism, it was thought that the present description of the larval form would prove of interest.

There are very few references to the nauplius of Anelasma ; the oldest one is the paper by Koren and Danielssen in a Swedish publication of 1848 (**1**), and the account given there is summarised by Hoek in his paper on " Die Cirripidien " published in *Nordisches Plankton* (**2**).

Groom, in his well-known and detailed memoir on the " Early Development of the Cirripedia," makes no mention of this particular larva ; and although Darwin in his great monograph describes the adult animal, he has no reference to the early form.

While at sea, Mr. Hickling obtained the larvæ by dissecting out the " ovigerous lamellæ " from the " mantle cavity " ; he then hatched the eggs from these structures in a jar of sea-water and was thus able to make some interesting observations on the living animals.

When first hatched he noticed the nauplii moving actively by jerking movements of the antennæ. Later, the larvæ were even more vigorous, using now both legs and antennæ in a haphazard way in order to effect movement, and rolling over and over as they swam. The limbs themselves appeared to be very small in relation to the size of the body and, because of the uncoordinated way in which they were used, the nauplii made little progress. The form of the appendages and their functioning made a strong contrast with Balanus nauplii, where the appendages are comparatively large and their movements are rapid.

This contrast possibly may be correlated with the fact that these larvæ of Anelasma had been developed from eggs definitely removed for that purpose from the " mantle cavity " of the adult. Mr. Hickling suggests that under " natural " conditions the larvæ would still have been in the shelter of that " cavity " at this stage and would not be free-swimming at all (this may account for their peculiar movement).

After the above observations had been made, Mr. Hickling preserved nauplii of one and four days old and forwarded them to me. It is on these specimens that the following description is based.

## GENERAL APPEARANCE.

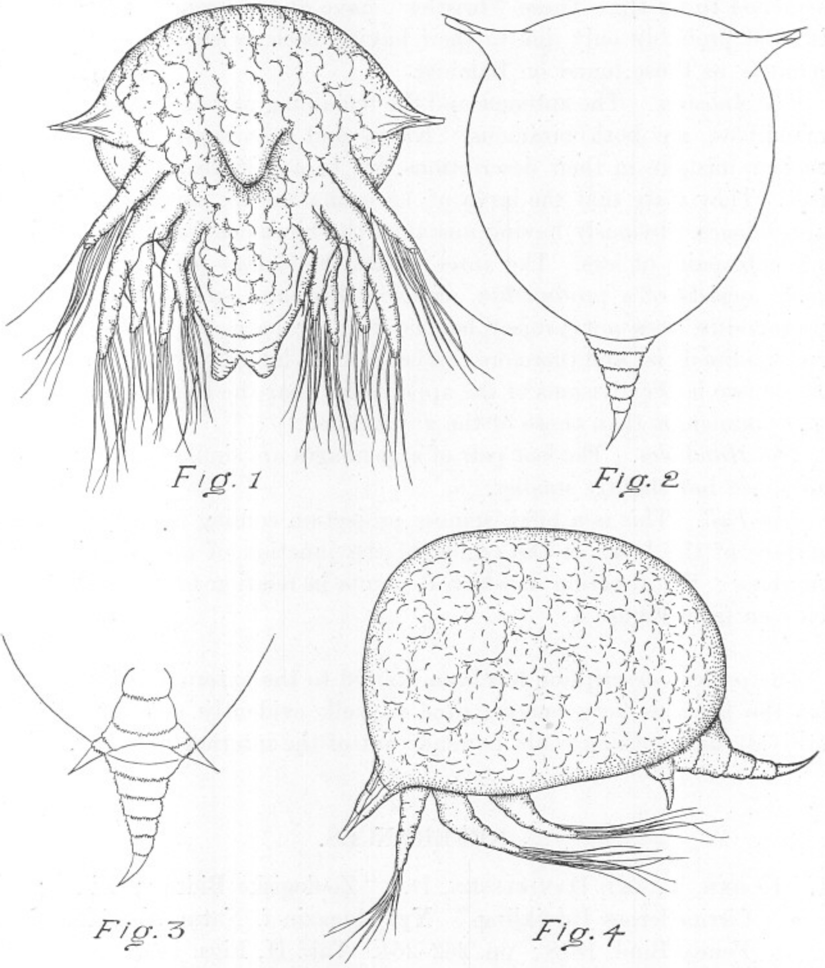
The uniformity of general appearance which characterises the Cirripede larvæ makes it easy, even from a cursory glance, to identify this nauplius as belonging to this class of Crustacea ; its specific characters are made out with closer study : it is small, being about ·665 mm. in length and about ·437 mm. at its widest part ; the length agrees with that given by Koren and Danielssen, but they give a much smaller measurement for the breadth ; the animal is just visible to the naked eye. It is opaque and colourless and has a general vacuolated appearance, which is due to the oil-laden cells.

The greater part of the body is covered by a dorsal, segmented carapace and this is produced at its antero-lateral extremities into two processes, the fronto-lateral horns so typical of all Cirripede nauplii. Each " horn " has a slight bifurcation at its distal end ; this really marks the opening of a minute passage which leads down into the " fronto-lateral gland " ; two processes, known as " fronto-lateral filaments," usually present in Barnacle larvæ are absent. No trace whatever could be found of that very typical structure, the nauplius eye. This fact is pointed out by Hoek, though he speaks of a small star-like speck which is to be seen on the dorsal surface ; this may, however, be only a pigment spot.

The main part of the body just described passes posteriorly into a five-segmented spine, ·115 mm. in length, whose chitinous covering is a continuation of the carapace. On looking down on the ventral surface of the animal a relatively large proboscis, or labrum, is seen bearing two small processes at its tip. It lies in such a way that it points slightly backwards and downwards in relation to the rest of the body ; in a lateral view it is not seen at all. In other nauplii the mouth would be found beneath this proboscis, but it has not been seen in Anelasma.

## THE APPENDAGES.

The appendages are best seen in a ventral view of the animal (Fig. 1). Laterally the distal ends are alone visible, and it is only possible, from the dorsal surface, to see the bristles attached to them. The appendages



FIGS. 1–4.—The nauplius of *Anelasma squalicola.*

(1) A nearly ventral view; (2) dorsal view; (3) the tail parts—ventral view (4) lateral view. The four drawings are all made from different larvæ.

*Dimensions.*—The nauplii are very nearly the same in length. The length of the one represented in Fig. 2 is 0·665 mm.; its breadth is 0·44 mm. The length of the caudal spine is 0·115 mm.

of most nauplii are segmented; those of Anelasma have curious "creasings" suggestive of incipient jointing, but definite segmentation seems absent. There are the three pairs of appendages typical of the nauplius.

*The Antennules.* The first pair of appendages which project forward, arise quite near, and slightly posterior to the "fronto-lateral horns." They are uniramous and beset with "bristles" or setæ, one of which comes off close to the tip of the appendage, whilst the remainder are attached to its tip. These "bristles" have an apparent jointing; this is most probably only due to their having been twisted; they are not plumose as those found on Balanus.

*The Antennæ.* The antennæ and the remaining pair of appendages, the mandibles, are both biramous. Koren and Danielssen have made a curious mistake in their descriptions due to a misinterpretation of this fact. They state that the larva of Anelasma has six pairs of uniramous appendages, obviously having mistaken the biramous formation for four separate pairs of legs. The antennæ are the largest pair of limbs, and each consists of a protopodite, an exopodite, and an endopodite. The protopodite does not project beyond the carapace, the exopodite and endopodite do so, and therefore can be seen in a lateral view of the animal. These two latter divisions of the appendages bear the bristles, longer and more numerous than those of the antennules.

*The Mandibles.* The last pair of appendages are similar in form to the antennæ, but slightly smaller.

*The Tail.* This is a bifid, spinose projection coming from the ventral surface of the body at the region of the junction of caudal spine and carapace; the direction in which it points in relation to the former can be seen from Figure 4.

The present description has been limited to the external features only, for the larva is very opaque (due to yolk evidently not yet entirely utilised), and nothing could be made out of the internal anatomy.

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2. Hoek, P. P. C. "Die Cirripedien"; Nordisches Plankton. Bd. 4. p. 304. 1909.

3. Johnstone, J., and Frost, W. E. 35th Annual Rept. Lancashire Sea-Fish-Laby. for 1926. (1927.)

# The Post-Larval Development of *Loimia medusa* Sav.

By
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*Student Probationer at the Plymouth Laboratory.*

With 2 Plates and 7 Figures in the Text.

## CONTENTS.

## 1. INTRODUCTION.

FOR many years a Terebellid larva, the genus and species of which were unknown to us, has been a conspicuous feature of spring plankton gatherings made in the Plymouth district. Immediately recognisable by its bulky gelatinous case it has frequently been a dominant form, and on account of its large tube has been responsible for increasing greatly the volume of the plankton samples obtained. It was of interest therefore to determine the species and to trace the main features of the development as far as this was possible. With this end in view a successful attempt was made to rear them, thus enabling the following contribution to our knowledge of larval Terebellids to be made.

## 2. METHODS.

On April 4th, 1927, and again on April 11th the plankton gatherings, particularly those made with the Young Fish Trawl, brought in by the s.s. *Salpa* from the neighbourhood of the Eddystone contained large numbers of this particular larva. Selected specimens in various stages of post-larval development were placed in a plunger-jar containing fresh unfiltered sea-water from outside the Breakwater and to this was added on two or three subsequent occasions a little Nitzschia from a pure culture kindly supplied by Dr. Allen. The jar was located in a window of north-westerly aspect, and in order to shield it from too much light a sheet of brown paper was tied round on the window side. On bright days a cardboard cover was placed on the top.

The larvæ were studied alive, the smaller forms in cavity-slips, the larger ones in open dishes. The drawings were made from these living larvæ while they were perfectly free to move about. This was done with the aid of a squared-net micrometer in the eyepiece, drawing in the first place on to squared paper. Care was taken to get the proportions as exact as possible, but on account of the constant movements and constrictions this was by no means an easy task. The different stages are illustrated at what was judged to be the mean of the varying degrees of contraction and all measurements likewise refer to this mean or resting condition. These drawings were subsequently checked, as far as was possible, by the examination of whole mounts of specimens narcotised with Menthol and fixed in Bouin. The uncini were drawn from larvæ flattened in Farrant's Medium.

## 3. PELAGIC STAGES.

### (a) *General Appearance.*

In general appearance the body is fusiform, but the shape is constantly changing as the larva moves about in its tube. Dilatations followed by constrictions repeatedly pass along the body in either direction, and the larva now elongates now shortens as it twists and turns in its tube. The latter is a large cylindrical gelatinous mass several times the size of the larva (Plate I, Fig. 1), perfectly transparent and, indeed, difficult to see until it is disfigured by the sticking on of debris to its outer surface. Through this mass there runs from one end to the other what can best be described as a tunnel. In this tunnel the larva lives, poking its head out at one end and stretching forth its tentacles as it drifts about in the water. Every now and then it turns round on itself, and crawling through the tunnel appears at the other end. As the larva grows the tube is increased in size, or the larva may make a new one. This frequently happens in the plunger-jar, the young worm deserting its old case and building another. The secretion of the jelly is rapid, and by the next day the larva is once more encased in a substantial mass. When free in the water the creature can swim forward by rapid, vigorous lateral undulations of the body, the tentacles being thrown out to both sides.

The larva possesses little pigment and is very transparent, and the internal organs are clearly visible. The prostomium is speckled with dark brown, and in the later stages this pigment also occurs on the ventral shields with some specks of it on the tentacles and upper lip. The gut is greenish yellow or brown, the tint varying according to its contents. This showing up through the transparent body-wall is the predominating colour of the larva.

The number and arrangement of the eye-spots varies slightly, there frequently being two dark brown spots, a large one with a smaller one below, on each side of the prostomium.

### (b) *The Development.*

The earliest larva seen was that shown in Plate I, Fig. 2. Just over a millimetre long it was already unmistakably a Terebellid. At this stage the median tentacle is budding forth in front of the prostomium above the great arch of the upper lip. Seven pairs of bristle-bundles are present, the first above the conspicuous statocyst, the last very small. Below each of the bundles, except the first, there is a long muscular process bearing distally a single uncinus of a larval type (Text-Fig. 4). These processes continue posteriorly, and five to six pairs are present behind the bundles. On the back there is a series of irregular nototrochs of short fine cilia, one nototroch to a segment. There is also a patch of cilia dorsally just behind the prostomium, a short lateral row below and anterior to the statocyst, and a scarcely visible row of very short fine cilia on the dorsal surface of the upper lip just in front of the eye-spots. A few rather short " sensory " cilia are present on the prostomium and around the anus. Similar cilia are also present on the tips of the tentacles of later stages.

The upper lip forms a kind of half-funnel at the bottom of which the mouth opens. Just inside the latter a prominent tongue-like process, really a thickening of the floor of the buccal cavity, is frequently turned forwards and downwards and then rotated back again. This organ is probably used in fashioning the tube. It is present in Lanice and is called by Elrington (**3**, p. 106) the " buccal organ." The œsophagus passes back to open into the stomach at which point an enlargement of the gut takes place. The first part of the stomach is thick-walled, and this is followed by a thinner-walled portion, which passes imperceptibly into the intestine. The gut is longer than the body, and is looped or thrown into folds in the body-cavity within which it is suspended by threads of tissue passing from the body-wall. These are indicated in the drawings of the two earliest stages.

Various other internal structures are visible ; these include the cerebral or dorsal glands behind the prostomium, the developing glands of the ventral shields, the heart, the muscles for moving the bristles, and just anterior to each statocyst a peculiar larval nephridium. This last is best seen at somewhat later stages (see Plate I, Fig. 3). It appears to open externally well up on the side of the body, but I have not paid any special attention to it. Later on (see Plate II, Fig. 1) it degenerates and disappears. This agrees with Meyer's view that the early larvæ of Terebellids possess a pair of temporary head-kidneys which ultimately degenerate and disappear (**11**, p. 662).

As development proceeds the larva increases in length and girth. The upper lip becomes relatively larger, the median tentacle elongates and the buds of others appear on each side. New tentacles usually arise alternately, first on one side and then on the other. This results in one side having one more tentacle than the other side, and its tentacles also are longer than the corresponding tentacles on the other side. This alternation may be either right or left, and in some cases it scarcely exists at all, the tentacles appearing simultaneously or almost simultaneously on each side. The tentacles become deeply grooved ventrally and the grooves ciliated. New segments are added posteriorly and these soon develop uncinigerous processes and irregularly broken nototrochs. New bristle-bundles arise behind those already formed and above the uncinigerous processes. Fig. 3, Plate I, shows a larva with five tentacles, eleven to twelve pairs of bristle-bundles and fifteen to sixteen pairs of processes bearing uncini. The other details are very similar to those already described for the earlier stage.

An important change now takes place. At about, or immediately after, the stage drawn in the last-mentioned figure the bristles above the statocysts are lost, and at the same time the uncinigerous processes below what was the second, but now becomes the first, pair of bristle-bundles also disappear.

Development then proceeds steadily, fresh segments are added on behind, new tentacles appear and the old ones elongate. Bristle-bundles are formed until seventeen pairs are present, and then the parapodia change their character and develop into the abdominal type. Before this happens, however, and at a stage with about twelve pairs of bristle-bundles and about seventeen pairs of uncinigerous processes (see larva 3 of diagram, Text-Fig. 7), the first pair of branchiæ appear above the statocysts a little dorsal to the position formerly occupied by the bristles which have been lost. About the same time swellings develop at the base of the uncinigerous processes, and a little later give rise to distinct tori as yet without uncini (see Text-Fig. 6).

Soon a fold grows out on each side just posterior to the statocyst and between it and the first thoracic chætæ. These folds develop into the fan-shaped flaps which are present below the second branchiæ in the adult. At about the same time a ridge arises ventrally just behind the mouth and passes up a little way on each side. This gradually grows out into a forwardly directed lamella to form the large post-oral platform so characteristic of the species (see larva 4 and subsequent stages in diagram, Text-Fig. 7). Uncini of the adult type (Text-Fig. 5) are now developing in the tori; these are dealt with in greater detail below (p. 139).

The second pair of branchiæ appear when all seventeen pairs of bristle-bundles are present (Larva 5 of diagram) and the first pair of branchiæ are beginning to branch. The four anal papillæ arise as swellings, and are soon distinct.

A little later stage is shown on Plate II, Fig. 1, and if this drawing is compared with that on Plate I, Fig. 3, several important differences will be noted. The branchiæ and the above-mentioned head-folds have, of course, appeared and the anal papillæ are prominent. All the thoracic parapodia are present, and with the exception of the first pair are now provided with tori in which uncini of the adult type have developed. The first six pairs of tori have each a single row of uncini, the latter facing forwards (i.e. teeth directed towards the head), while the posterior ten pairs have each a double row with the uncini back to back. The larval hooks and the long processes on which they were situated have disappeared. These thoracic parapodia are followed by about fourteen pairs of the abdominal type, the most posterior of which are still very small and scarcely differentiated. There are now two irregularly broken nototrochs of fine short cilia on every segment behind the first eight bristle-bundles, with the exception of the most newly acquired segments near the anus where there is only one to a segment. The gut is straighter than formerly and the larval nephridia are degenerating and ultimately disappear. The ventral shields are more prominent, and the tentacles longer and more numerous. The total length—including that of the longest tentacle—is now approximately 7·4 mm.

All this time the larva has been floating about in its case of transparent jelly. This it continues to do until it has reached a stage about equivalent to that indicated in larva 6 of the diagram (Text-Fig. 7). It is impossible to give the exact age at this stage as the larvæ put into the plunger-jar varied considerably in this respect. We can say, however, that in the plunger-jar it took roughly three months to pass from the earliest stage seen (Fig. 2, Plate I) to the stage at which they begin life on the bottom, because several of the larvæ placed in the jar on April 4th and April 11th were scarcely any older than the earliest one described and the last larva had settled down by July 14th. In the sea development is possibly much quicker, and there may be considerable variation depending on the amount of food each individual is able to obtain. In the plunger-jar they fed largely on diatoms.

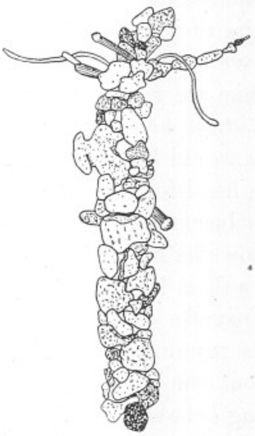
## 4. BOTTOM STAGES.

### (a) *The Building of the Sandy Tube.*

When the young worms reach the stage at which they are ready to settle on the bottom they exhibit an impulse to build, and if sand be denied them they will collect stray cotton hairs, fæcal matter, and other debris and attempt to build tubes on the sides of the jar. As soon as this was noticed in the older larvæ small pots of sterilised sand were placed in the plunger-jar, and those which had already settled down on the glass were carefully removed to these where they began to build at once. Subsequently other larvæ as they became ready to build settled in these pots, while others made use of scattered sand grains spilt on the bottom of the jar, or, if near enough, actually collected grains from the pots with their tentacles and so constructed tubes along the glass. The latter tubes were usually incomplete, the glass forming one side, but it was nevertheless coated over with the same cement as was used to stick the particles of sand together.

Larvæ would readily build in small dishes while under the microscope. As soon as it comes to rest on the bottom a larva stretches forth its tentacles and searches the immediate neighbourhood. Should the tentacles come into contact with sand grains these are immediately seized and conveyed towards the mouth. Sometimes the tentacles drag them along, often they cause them to travel down the deep grooves, a convenient edge of each piece sliding along in the groove. In this way a single tentacle may convey more than one grain at once, several sliding down its groove one after another. As much as possible of each is taken into the space between the upper lip and post-oral platform and into the mouth. If the piece is a flat one the upper lip and mouth are applied after the fashion of a sucker. The buccal organ is meanwhile seen to be working vigorously. After two or three seconds the piece, which has doubtless been coated with cement, is pushed or pulled into position by the head and anterior part of the body, the upper lip clinging tight hold all the time. As soon as it is in place it is released and another fragment is then immediately dealt with in the same way. When the grain is a large one the tentacles assist the lips to hold it. In this manner a length of sandy tube is rapidly constructed away from the mouth of the larval gelatinous case, and it is attached to whatever the substratum happens to be. As the sandy tube is lengthened the larva gradually quits its transparent case until it has left it altogether. Quite frequently after constructing a fair length of tube in one direction the worm will turn round and start building in the opposite direction from the other end of its old pelagic home.

There is very little selection of the grains used, few being discarded. This is different from *Lanice conchilega* Pallas (the larvæ of which I have also reared) which appears to be a little particular, taking greater care to make the pieces fit. Loimia takes less trouble over it, and uses a much wider range in size of fragments. Thus it leaves more and larger gaps between the pieces forming the wall of its tube, and through these gaps the worm can be seen. Its tube is also more pliable and fragile than that of Lanice, and the grains are not immovably cemented one to another; a considerable degree of bending can take place between them.



TEXT-FIG. 1.—Anterior portion of sandy tube constructed by an early juvenile of *Loimia medusa* Sav. (×5.)

TEXT-FIG. 2.—Anterior portion of a similar tube to that of Fig. 1, but with a more elaborate frill. (×5.)

In about half an hour a Loimia larva can construct a sandy tube about twice its own length (excluding the tentacles). During these building operations small fragments are sometimes accidentally swallowed, but they quickly pass along the gut and are voided at the anus.

The anterior end of one of these tubes is shown in Text-Fig. 1. At the time of drawing it was about one month from the larva having first settled down. At this age the tubes vary in length between twenty and thirty millimetres, and the young worms inside are similar to the stage shown in Fig. 2, Plate II. This particular tube was just getting a frill put on its anterior end, and in the figure two tentacles of the larva are seen protruding from the opening. A rather older tube with a fairly elaborate frill is illustrated in Text-Fig. 2. Small Echinus spines are largely used in its construction, and the frill, like the tube, is quite pliable. Note the wide range in size of the particles used in the formation of the tubes.

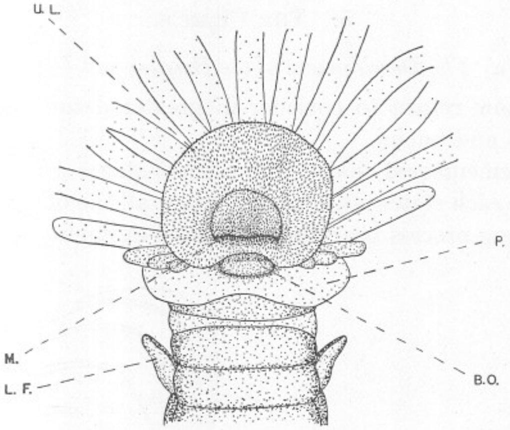
### (b) *The Early Bottom Stages.*

After settling down no marked change occurs in the sequence of development, it proceeds steadily as before. The young worm increases in size and acquires more and more abdominal segments, more bristles in each bundle, and more uncini. The first two pairs of branchiæ continue to branch and soon the third pair appears above the first pair of bristle-bundles and ramifies in its turn. The branchiæ are very contractile and are finely ciliated. Fig. 2, Plate II, shows a stage some little time after the appearance of the third pair. This larva would be about five weeks old after beginning life on the bottom. The head-folds grow until they reach adult proportions, the ventral shields become prominent, and a few more eye-specks appear on each side below the main eye-spot. Pigmentation remains as before, but the body-wall is less transparent and the integument wrinkled, rather strong transverse grooves and ridges being crossed by numerous fine wavy ridges running in a longitudinal direction. The nototrochs soon disappear, but the anterior dorsal part of the body behind the prostomium extending between the bases of the branchiæ downwards on each side to about the level of the parapodia and backwards to about the sixth pair of bristle-bundles has the appearance of being evenly ciliated. The short fine cilia may, however, be arranged in numerous close transverse rows, but of this it is extremely difficult to be certain. There are also patches of cilia on the prostomium.

A sketch of the ventral view of the head of the same specimen, as is shown in Fig. 2, Plate II, is given (Text-Fig. 3). This sketch shows the upper lip widely spread, and the fine cilia with which its inner surface is covered are indicated passing down into the œsophagus. The buccal organ is drawn back in the position of rest. Below is the post-oral platform, which rises as a forwardly projecting flap on either side of the head and passes downwards to form a broad shelf below the mouth. It is slightly indented in the middle line, and is finely ciliated on its outer surface. In the drawing it is represented as turned backwards. Behind are seen the ventral shields and the flap on each side below the second branchia. These flaps are also finely ciliated on their outer surfaces.

For a short time after first making a sandy tube the young worm can secrete a larval case if it be removed and placed in a dish where there is nothing for it with which to build. It soon loses this ability, and about this time the cerebral or dorsal gland degenerates and disappears. Elrington (**3**) has shown that in *Lanice conchilega* Pallas the dorsal gland is very probably that which furnishes the material for the formation of the larval tube, and that in that species also it disappears after the larvæ have settled down.

By the end of October several of the young Loimia worms were still living in the same plunger-jar without change of water, and were in a much more advanced condition than the oldest specimen illustrated. Their tubes averaged about ten centimetres long with posterior diameters of roughly two millimetres, widening gradually to about three millimetres at the anterior ends, which were adorned with large frills. The worms themselves were rather more than two and a half centimetres long (excluding the tentacles) and had about seventy chætigerous segments. The numerous tentacles were very slender and extensile, and could stretch out to a length two or three times that of the body. All the branchiæ were much branched and tree-like, the anterior pairs most so, and the pulsations of the red blood through their blood-vessels could be seen very distinctly. The body-wall was less transparent than formerly and of a very pale yellow colour by reflected light, but the general outline of the gut could still be seen through it though no internal detail was distinct. The speckled brown pigment had the same sort of distribution as before, and there were several rather irregular dark brown eye-spots



TEXT-FIG. 3.—Ventral view of the head region of the specimen drawn in lateral view on Plate II, Fig. 2. The upper lip is widely extended and stretched rather forwards and downwards (see p. 136). From life. (×32·5.)

B.O. Buccal organ.
L.F. Lateral head-fold.
M. Mouth.
P. Post-oral platform.
U.L. Upper lip.

in a transverse row on each side of the prostomium. The tori were longer in a dorso-ventral direction, and contained more uncini of the adult type; some of the hooks had six or seven teeth. There were four long anal papillæ.

The last remaining larva was fixed on December 5th. Without the tentacles it was approximately four centimetres long and correspondingly bulky, and it had eighty-one chætigerous segments. Its tube was twelve centimetres long with a posterior diameter of two millimetres and an anterior diameter of four millimetres. There were frills on both ends.

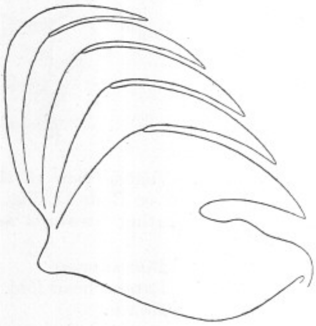
## 5. The Chætæ.

### (a) *The Development of the Bristles and Uncini.*

We must now return to consider in greater detail the development of the bristles and uncini.

It will be remembered that in the earliest stages a bristle-bundle was present above each statocyst, and that below all the other bristle-bundles there was a long process bearing at its distal extremity a single uncinus.

Text-Fig. 4.—Uncinus of Larval Type. (×2600.)

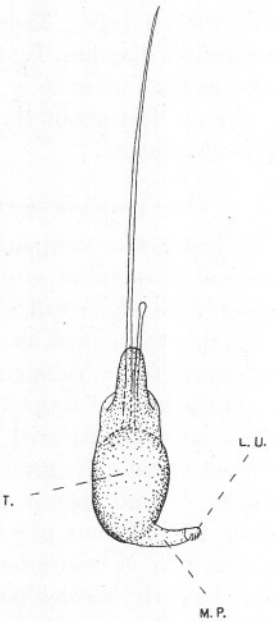


Text-Fig. 5.—Uncinus of Adult Type from an early bottom stage. (×2600.)

This uncinus is a larval kind (Text-Fig. 4) with longer and more slender teeth than that of the adult, but it is nevertheless distinctly of the Loimia pattern. Each bristle-bundle has two chætæ, the anterior one long, slender, and very pliable, the posterior short and with a swollen extremity (Text-Fig. 6). Each bundle as it develops acquires these two types of bristles until the eleventh (tenth adult) pair form, and then from there posteriorly only slender pointed bristles are produced.

It is interesting to watch the way in which these larval bristles are used. When a bundle is pressed against the wall of the tube the soft jelly is indented at that place. The long tapering bristle on account of its flexibility is bent into a curve until the knob of the other bristle also comes into contact with the jelly. This bristle does not bend, but the knob prevents it from piercing the tube wall. The jelly is now strongly indented, and in this way the bristles are doubtless able to get a pushing grip on the soft and presumably rather slippery internal wall of the tube.

While the bristle-bundles are thus pushing organs, the uncinigerous processes have exactly the opposite function. The hooks are used as anchors on the wall of the tube, and with them the larva can pull itself backwards. By adjusting the degree of antagonistic action between bristles and hooks the larva clings firmly to its floating home, and can safely stretch its head and tentacles out of one of the openings.



TEXT-FIG. 6.—An anterior thoracic parapodium from the left side of a post-larval *Loimia medusa* Sav. (×260.)

L.U. Uncinus of larval type.
M.P. Muscular process bearing uncinus.
T. Developing torus before appearance of uncini.

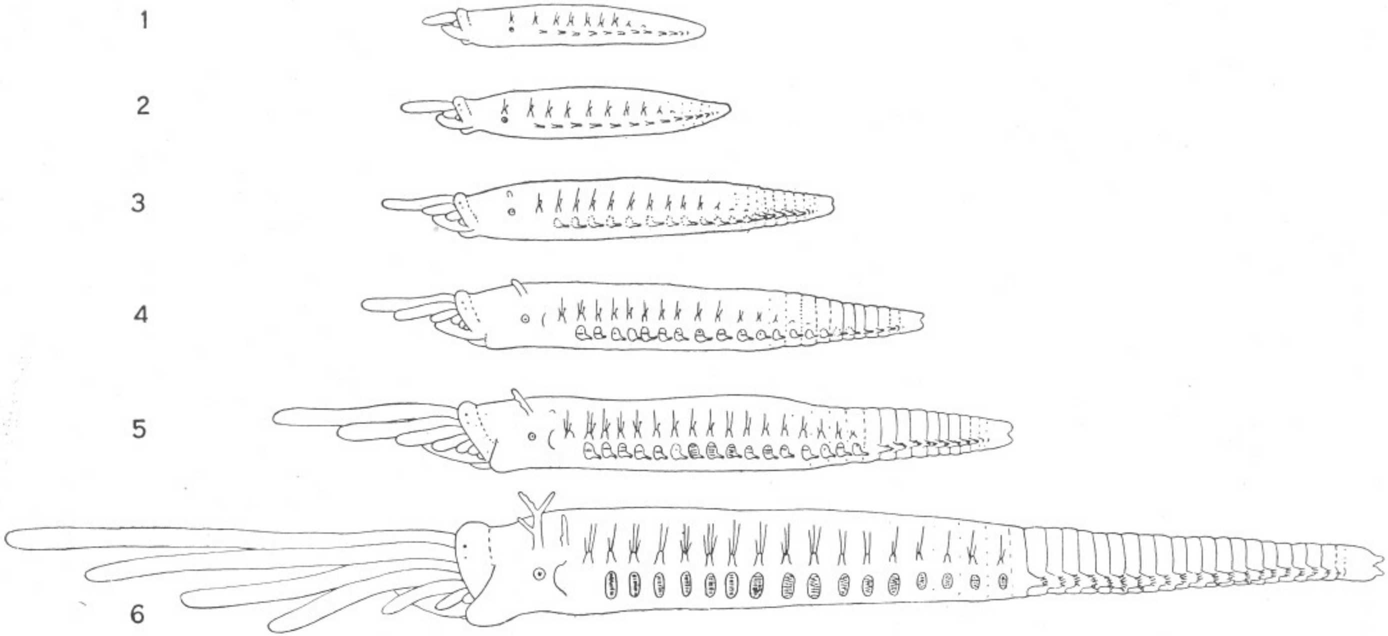
The disappearance of the first pair of larval bristle-bundles and uncinigerous processes has already been mentioned (see p. 132). As the larva grows older the tori gradually arise as swellings and increase in size, but are at first without uncini (Text-Fig. 6). They develop above the processes bearing the larval hooks, but in such a manner that these latter come to be seated at their lower extremities. At about the stage indicated in Larva 4 of the diagram (Text-Fig. 7) uncini first become visible in the tori, and it is interesting to note the order in which they develop. I have failed to trace a regularity comparable to that which Herpin (**9**, p. 204) found in *Nicolea zostericola* Œrsted sec. Grube, but certain generalities may be stated. The seventh and immediately succeeding pairs of tori rapidly acquire more hooks than the preceding six pairs. This is undoubtedly correlated with the fact that in the adult the first six pairs have only a single row, while the seventh and posterior pairs have each two rows of hooks. In the latter one or two hooks of the anterior row generally appear first and then those of the second row begin to appear. The hindermost tori lag behind possibly because they are the last to develop. By the time the larva is ready to abandon planktonic life the uncini in each torus are fairly numerous, there being approximately twelve to twenty in each of the six anterior pairs and ten or twelve in each row of those tori with double rows, except in the most posterior ones which have only about half that number. The double rows of uncini are opposed back to back. The abdominal feet have on an average four hooks each, but sometimes as many as six. All these uncini are of the adult type (Text-Fig. 5) and were the first definite proof of the identity of the species. The larval uncini and processes are lost shortly after the appearance of the second branchiæ.

While the hooks have been appearing so have new bristles of the adult winged type. These, as a rule, appear first in the most anterior bundles (see diagram, Text-Fig. 7), and gradually increase in numbers, but there does not seem to be any regular order of development. The larval bristles are lost about the same time as the larval hooks, before pelagic life is abandoned.

### (b) *Comparison with Nicolea zostericola Œrsted sec. Grube.*

An instructive comparison can now be made with the development of *Nicolea zostericola* as described by Herpin (**9**), and this will be made clearer if the reader will consult that writer's schematic figure of successive stages (p. 206) as well as my diagram (Text-Fig. 7). As has already been mentioned the development of the uncini is scarcely comparable, and it is to the history of the first three segments after the head that attention will be specially directed. In Loimia what may be regarded as the first segment behind the head possesses in the early stages a pair of bristle-bundles, but no uncini. Each bundle of the pair immediately following has an uncinigerous process situated below. These processes as well as the first pair of bristle-bundles are, it will be remembered, subsequently lost. In early Nicolea larvæ, on the other hand, the first two segments behind the head possess paired bristle-bundles, but no uncini, while the third segment carries a pair of bundles with a single uncinus below each. On further development the bundles on the first two segments and the uncini on the third segment are lost. It will be noticed that the important difference between the two forms is that Nicolea has two pairs of temporary bristle-bundles while Loimia has one. Which of these two pairs is homologous with the single pair of Loimia ?

Some indication of the probable answer to this question may be obtained by considering the position of the branchiæ. In Nicolea there are two pairs of these, and they arise on the first two segments near the positions formerly occupied by the temporary bristles. In Loimia there are three pairs, the first pair arising just dorsal to the position where the temporary bristles were situated, the second pair *between* these and the first pair of adult (second larval pair) thoracic bristles. The third pair arise above the latter. If we now make the very probable assumption that the



TEXT-FIG. 7.—Diagram of post-larval pelagic stages of *Loimia medusa* Sav. to show the development of bristles and uncini, tentacles, head-folds, branchiæ, and anal papillæ. Drawn from mounted specimens. (×19·5.) Explanation in the text.

branchiæ of Nicolea are homologous with the first two pairs of branchiæ of Loimia and that the corresponding segments on which they arise are homologous, we arrive at the interesting conclusion that in Loimia the second pair of larval bundles (first pair adult) are really homologous with the third larval pair of Nicolea, which are also the first adult pair of that worm. That this is so seems to be confirmed by the fact that these are the segments in both species which possess temporary uncini that are lost about the same time as the bristles. It seems probable then that Loimia, during its evolutionary history, has lost a pair of larval bristle-bundles between what are now its first and second larval pairs. At all events a segment does appear to exist between these two latter, for it is on this segment that the second pair of branchiæ and below them the lateral folds of the head arise.

## 6. Previous Records.

It remains to consider whether the larvæ of Loimia have been observed and described before. The most important record in this respect is undoubtedly that of Andrews (**2**) for the sea off the coast of North Carolina. In the systematic part of his paper he describes (p. 298) what he believes to be a new species of Loimia, which he found under stones on the shore near Beaufort. This species he named *L. turgida*. On Plate XVIII he gives a rough sketch (Fig. 46) of a Terebellid larva he found abundantly in the plankton and which he says is that of his *L. turgida*. By reason of the thick gelatinous tube indicated in this figure and the fact that the larva possessed a pair of prominent statocysts " anterior to the first pair of setæ " (p. 300) I have no doubt that he was correct. Unfortunately he gives no reasons for his identification, but it is possible that he may have observed the shape of uncini of the adult type in the later larval stages, but if so he makes no mention of the fact.

Fauvel (**4**, pp. 57 and 71) has made the suggestion that the Terebellid larva figured and described by Agassiz as the larva of *Terebella fulgida* Ag. (**1**, Plate VII, Fig. 19, and p. 320) is possibly identical with Andrews's *Loimia turgida* larva. This is quite possibly the case, but Agassiz's description is too meagre and his figure not detailed enough to be certain on the point. The fact that this larva possessed a pair of statocysts and showed alternate development of the tentacles suggests that it may possibly belong to this genus, but, on the other hand, Agassiz states that these larvæ " build their cases very late " (he does not say what kind of case) " and frequently leave them to climb about on eel-grass, piles, etc." Moreover, he states that " the first ring having dorsal setæ has also a row of hook-shaped bristles," which is not the case in *Loimia medusa* at least. He gives a figure of one of the hooks (Fig. 19a), and it certainly has some resemblance to the adult type of hook of *L. medusa*—as was pointed out by Fauvel—apart from the fact that he indicates no teeth beyond the large one next to the base. His figure rather suggests that he was doubtful about the existence of other teeth. He also states that " the eyes are still in prominent clusters and not yet formed into a ring round the collar, as they are arranged while gradually disappearing." This early clustered appearance is, I think, explained by the fact that the eye-spots, particularly the smaller ones, show little if any difference from the other pigment spots scattered over the prostomium, and as there is considerable variation among individuals in the way in which this pigment is distributed the clustered appearance could easily be produced. In the early stages only the large eye-spot on each side can be said to be really definite, and is still distinctly visible in stained and mounted specimens.

## 7. POINTS OF GENERAL INTEREST.

A few final points of general interest remain. McIntosh (**10**) separates our British Loimia from *Loimia medusa* Sav. because of a slight difference in the form of the uncinus from that of a Mediterranean specimen of the genus which he thinks is probably Savigny's species, and makes a new species *Loimia montagui*. The hooks of the latter " differ from those of the Mediterranean species, which have a process on the edge of the base beneath the main fang, and the curvatures also differ " (p. 149). Now if reference is made to my figure of the adult type of uncinus it will be observed that there is a rounded swelling in the same position as the process on the base of the uncinus of the Mediterranean specimen, as illustrated by McIntosh (**10**, Vol. IV, Plate CXXVI, Fig. 1b). It is true that it is by no means as pronounced a tooth as is shown in the latter figure and I have not seen one as prominent as is there illustrated, but it is an intermediate condition between the two types. Moreover, not all the uncini, even in the same torus, of the latest stage to which I have reared my larvæ bear even this slight swelling, in many the base below the great tooth is quite smooth like that of *L. montagui* McI. The uncini in other respects, such as curvature, also differ slightly one from another. The same remarks hold true for uncini from the same torus of an adult specimen I have examined. There again they vary from a smooth base to one with a tooth nearly as strongly developed as that shown in McIntosh's figure of a hook from *L. medusa* Sav. and the curvatures also vary slightly. Fauvel has pointed out (**5**, p. 146), from an examination of specimens from San Thomé, the Casamance, the Red Sea, and the Persian Gulf, that this basal tooth is less evident the larger the specimen and suggests that it disappears with wear. He further remarks on the danger of basing new species or varieties on such unimportant and variable characters. Under these circumstances I do not think that at present we can regard *L. montagui* McI. as a distinct species from *L. medusa* Sav., and for this reason I have retained the latter name in this paper. In any case the name *L. montagui* cannot be retained for this species as it has already been given by Grube (**8**, p. 224) to a Loimia from the Philippines.

Both Gravier (**7**, p. 224) and Fauvel (**4**, p. 70) have noticed that in young specimens of Loimia of about one or one and a half centimetres long the uncini have more than one row of teeth near the apex, whereas the adults have, of course, only one row. This is also the case with some, but by no means all, of the abdominal uncini of my specimens of about that size, but I have not observed it in thoracic hooks except in very early stages when uncini of the adult type were just appearing. All hooks of the larval type had the apical teeth in two or three rows. The figures of adult and juvenile hooks which Gravier gives (**7**, p. 224, Figs. 396–399) of specimens of *L. medusa* Sav. collected in the Red Sea, are rather different from the hooks of my adult and juvenile specimens. It must be noticed in connection with what has been said in the preceding paragraph that Savigny obtained his original specimens in the Red Sea. Gravier's figure of the adult hook differs from my specimens chiefly in the curvature ; he shows no process on the base below the great tooth, but indicates one in his figure of a hook from a young specimen. Gravier also mentions that in his young specimens there was a temporary lobe on the third segment that was not present in the adults. I have seen no such lobe in my specimens.

In this district Loimia usually lives in banks of shell-gravel below low-water mark, and is rarely found on the shore even at the lowest ebb of spring-tides. Portions of their wide (about 1 cm. in diameter) tubes are frequently brought up by the dredge, but the living animal itself is extremely rarely obtained. I have not, in fact, yet seen a living adult specimen, but Dr. Allen has kindly allowed me to examine and remove some of the uncini from a damaged preserved specimen obtained here many years ago. On the same dredging grounds the tops of the tubes of *Lanice conchilega* are also frequently obtained, but the worm itself very seldom. From this we can only conclude that the tubes penetrate down to at least a foot or more, and the worms at the least disturbance retreat to the bottom too deep for the dredge to get them.

While this paper has been in the press Fauvel has published the second part of his valuable work on the polychæte fauna of France (**6**), and in this part he describes the Terebellids. Unfortunately owing to his grave doubts (expressed on p. 293) as to the existence of Loimia near Plymouth he has omitted a description of this species. I immediately wrote to him, enclosing a copy of the MS. of this paper, and he kindly replied, stating, "I am sorry I did not include Loimia in my Fauna, for your letter furnishes me with the clear evidence which, till now, I wanted of the occurrence of Loimia near Plymouth."

In conclusion, it is a pleasure to express my thanks to Dr. Allen for his help and stimulating interest in this work, and to the Staff of the Laboratory also for many kindnesses. The major portion of this work was done while holding a Graduate Research Scholarship from Manchester University and a Maintenance Grant from the Department of Scientific and Industrial Research, and these institutions also I wish to thank.

## 8. SUMMARY.

1. The larva of a Terebellid which is very common in plankton from the Plymouth district during spring has been reared and proved to be the young of *Loimia medusa* Sav. This larva is characterised by its very large gelatinous tube.

2. The development of the external structures is described from a stage in which the first tentacle was just appearing to a juvenile stage in which all the main characters of the adult had been assumed.

3. The building of the first sandy tube on the bottom is described.

4. The development of the bristles and uncini are dealt with in some detail and a comparison made with the corresponding development in *Nicolea zostericola*. Evidence of the suppression of a pair of larval bristle-bundles in Loimia is indicated.

5. Previous records of Loimia larvæ are discussed.

6. McIntosh's separation of our British Loimia to a new species, *L. montagui*, is shown to be probably unjustified.

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## 10. DESCRIPTION OF THE PLATES.

### LIST OF REFERENCE LETTERS.

| | |
|---|---|
| $B^1$. | First pair of branchiæ. |
| $B^2$. | Second pair of branchiæ. |
| $B^3$. | Third pair of branchiæ. |
| B.O. | Buccal organ. |
| D.G. | Dorsal gland. |
| D.L.N. | Degenerating larval nephridium. |
| H. | Heart. |
| L.F. | Lateral head-fold. |
| L.N. | Larval nephridium. |
| M.P. | Muscular process bearing larval uncinus. |
| M.T. | Median tentacle. |
| N. | Nototroch. |
| P. | Post-oral platform. |
| S. | Statocyst. |
| S.G. | Ventral shield gland. |
| T. | Torus with uncini of adult type. |
| U.L. | Upper lip. |
| V.S. | Ventral shields. |

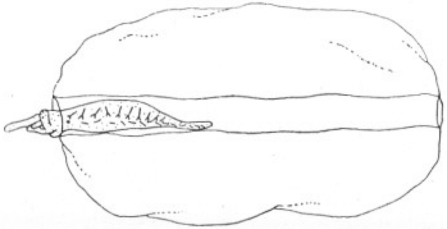
### PLATE I.

Fig. 1.—Early post-larva of *Loimia medusa* Sav. inside its gelatinous tube. (×9·75.)

Fig. 2.—The earliest post-larva seen (see p. 131). Lateral view from life. (×78.)

Fig. 3.—An early post-larva with a fairly long median tentacle and two lateral tentacle buds on each side (see p. 132). Lateral view from life. (×78.)

# PLATE I.



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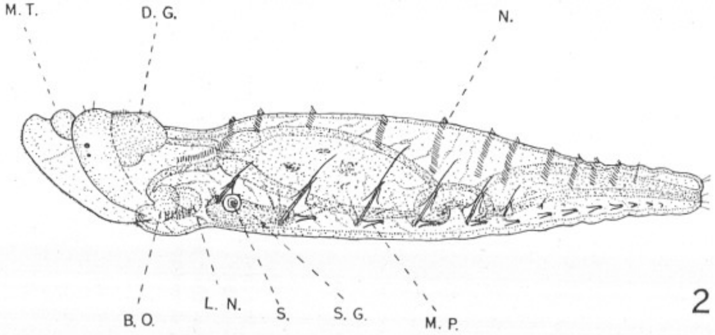

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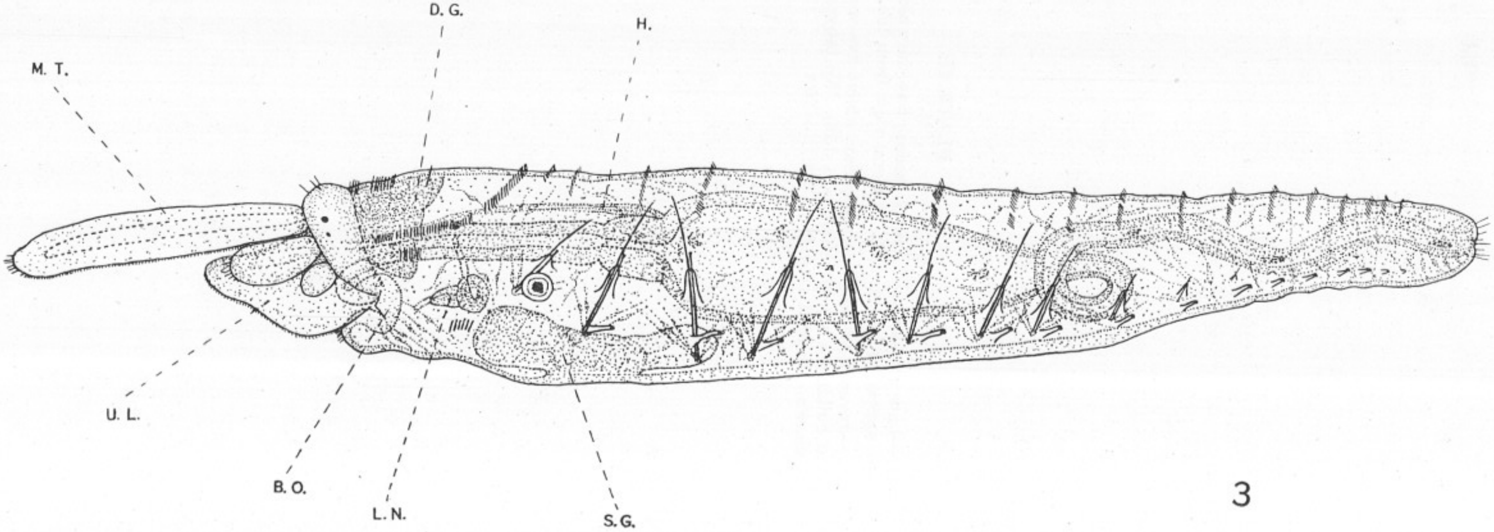

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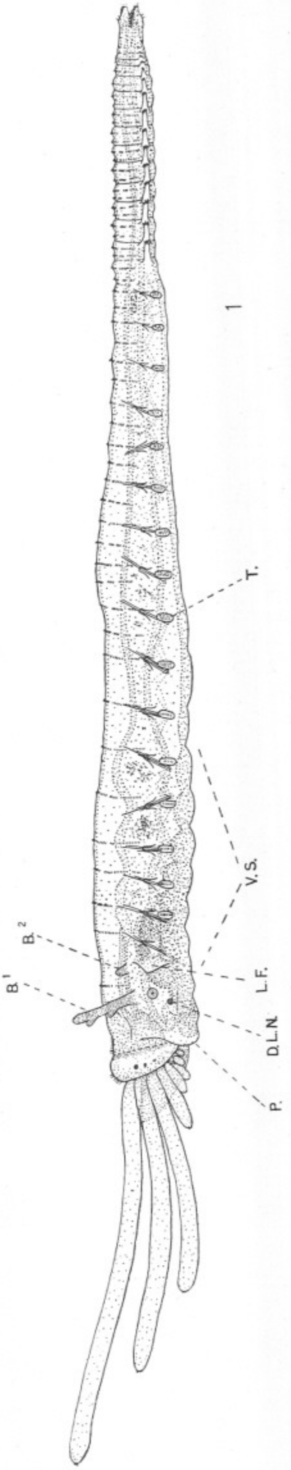
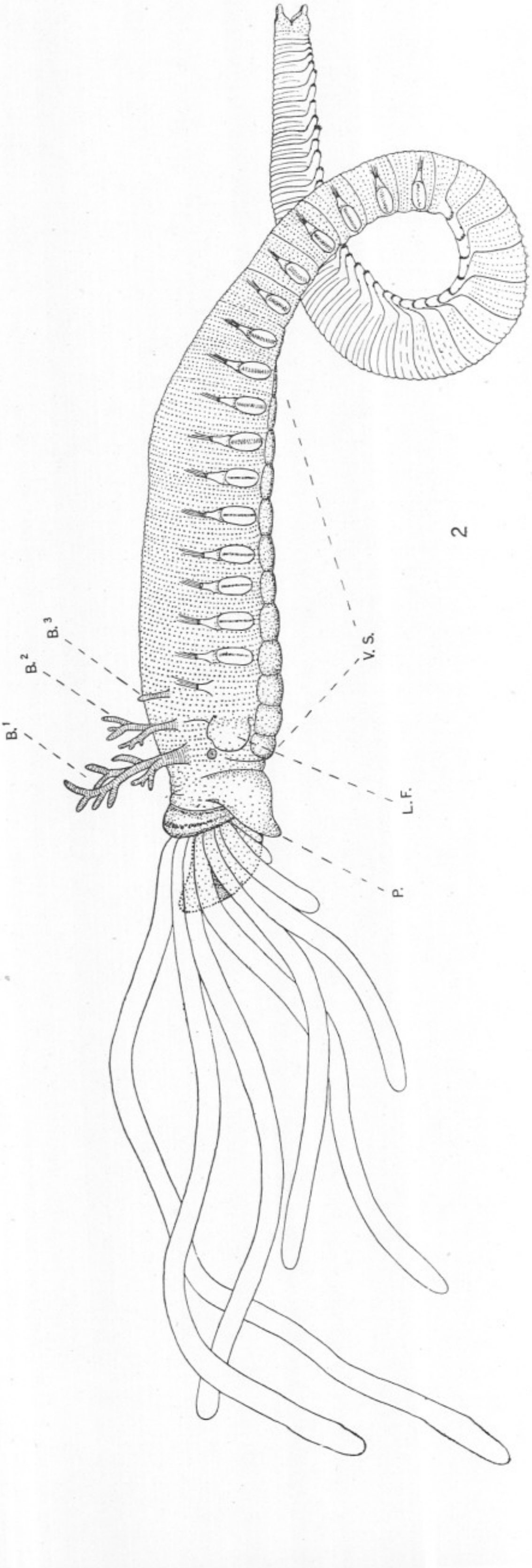
## PLATE II.

Fig. 1.—Late post-larva of *Loimia medusa* Sav. in which the first two pairs of branchiæ are appearing (see p. 133). Lateral view from life. (×26.)

Fig. 2.—Juvenile of *Loimia medusa* Sav. about five weeks after settling on the bottom and building a sandy tube (see p. 136). No internal structure except the statocyst is shown. Lateral view from life. (×26.)

PLATE II.





# Regeneration in the polychæt *Chætopterus variopedatus.*

By

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With 4 Figures in the Text.

THE members of the family Chætopteridæ are the most highly differentiated and most truly tubiculous among polychæt worms. In view of the ability to autotomise developed in connection with the tubicular habitat and the great specialisation of the different segments, a study of the phenomena of regeneration in this group becomes of special interest. *Chætopterus variopedatus*, the species most abundant and readily obtained in European waters, has been examined from this aspect.

This worm inhabits parchment-like semicircular tubes, which may or may not be buried in mud save for the two open extremities. It occurs from the low-water level to at least thirty fathoms, and may be found in extraordinarily large numbers. The morphology of this form has been investigated very thoroughly by Joyeux-Laffuie (1890), while the habits, general physiology, and development have been described by Enders (1909), but it is necessary for the present purpose to give a brief account of its structure and behaviour.

The body may be divided into three parts: anterior, middle, and posterior, the homologies of which have been well made out by Laffuie.

The anterior part, or so-called head, has been shown by him to consist of eleven segments, of which only the last nine are setigerous, and the whole forms a massive trowel-like structure with a terminal funnel-shaped mouth.

The middle region shows by far the greatest diversity of structure and consists of segments twelve to sixteen (see Fig. 1). Segment 12 bears a pair of large aliform notopodia, each possessing a ciliated furrow which unites with a furrow from the anterior region (see Fig. 4, A). The neuropodia are fused to form a powerfully adhesive disc, as also are those of segment 13.

Segment 13 is much elongated and contains the more dilated part of the green intestine, which undergoes peristalsis. The mid-dorsal part of the segment is greatly modified to form what Laffuie describes as a sucker, but which is said by Enders to be an accessory feeding organ.

This latter view is confirmed here, and never in several hundred cases has it been observed to act as a sucker. It is in the form of a cowl opening antero-dorsally, and is lined with cilia continuous with the dorsal ciliated furrow running forwards to that joined by the furrows of the aliform notopodia mentioned above. Segments 14, 15, and 16 have their dorsal parts expanded to form circular fan-like structures, which beat rhythmically. The ventral parts of each form an adhesive disc, though not so powerful as those of segments 12 and 13.

The posterior region may consist of as many as fifty segments, according to the age of the worm, and contains the sexual elements, male or female as the case may be. The segments of this region are all alike.

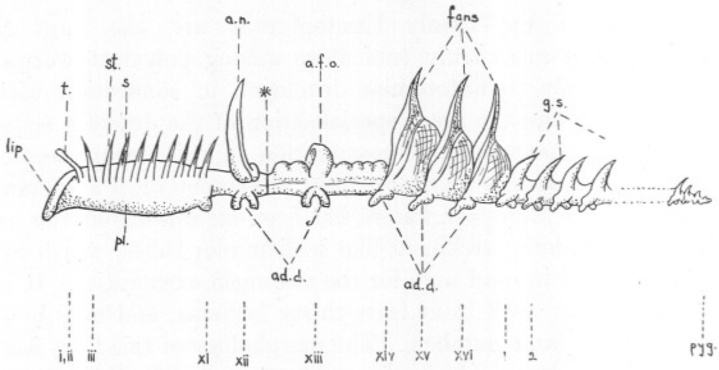

FIG. 1.—Diagram of Chætopterus showing order and types of segments: i–xvi–1–2, etc., segment numbers; *pyg.*, pygidium; *t*, tentacle; *pl.*, plastron; *st*, setigerous segment; *s*, stout setæ; *g.s*, genital segments; *a.n.*, aliform notopodia; *a.f.o.*, accessory feeding organ; *, autotomy level.

The animal normally lives completely within its tube, and the various specialised segments just described have been evolved for such an existence.

When undisturbed it lies along the base of the tube, so that the trowel-like " head " is closely opposed to one side, reducing the effective bore of the tube by about one-sixth. It is fixed in position by the especially stout setæ of the third setigerous segment. The rest of the body is held close to the side of the tube by the ventral suckers of the twelfth and thirteenth segments and to a less extent by those of the three succeeding segments. The large flattened notopodia of segment 12 extend dorsally along the side of the tube to meet above, thus forming an arch through which the water current produced by the rhythmically beating fan segments has to pass. The co-ordination of these fan segments has already been described (Berrill, 1927).

The animal feeds on planktonic and detrital matter brought in by the water current. This current passes over the ciliated mouth, between the aliform notopodia, the inner sides of which are ciliated, and converges on to the accessory feeding organ on the thirteenth segment, and thus altogether is exposed to extensive ciliary fields which carry forward to the mouth any particles that may have been brought in with the water. According to Enders there is a ciliary sorting mechanism for such particles in the region of the mouth.

While normally the worm lives completely within its tube, it not infrequently protrudes its anterior end, the white or creamy colour of which becoming a very obvious mark to any passing fish. This must be of such frequent occurrence in nature that autotomy has been developed and has a survival value for the species. When any sudden pull is made on the anterior " head " region, a local but very strong contraction of circular muscles of the body wall occurs between segments 12 and 13, cutting through all the more internal tissues and dividing the animal into two parts. In this way the genital and current-producing segments would be saved at the expense of the less valuable head region. The ability to autotomise and of the posterior piece so formed to regenerate the missing twelve anterior segments has long been known.

In most cases where regeneration has occurred, the regenerated tissues may readily be distinguished by their white delicate nature from the coarser cream or brownish tissues of the original piece. On this basis 10–15 per cent of a Chætopterus community will be found in various stages of regeneration of the anterior part. After two or three months, however, it becomes impossible to distinguish by colour between regenerated and non-regenerated segments, and the total percentage of worms that have regenerated missing parts cannot be determined.

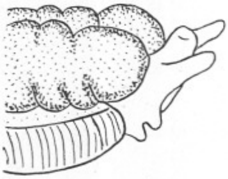
FIG. 2.—Anterior regeneration from segment 13 (autotomy) (see text).

Fig. 2 shows anterior regeneration from an animal that autotomised. The regenerated tissue is about 2 mm. in length, and consists of the rudimentary head with terminal mouth and the beginnings of the tentacles and first two setigerous segments.

The animals used for experiment were divided between various adjacent segments and the pieces kept in finger-bowls into which water was allowed to drip or over which to flow, thus ensuring a plentiful supply of oxygen and the removal of waste products. The greatest difficulty was experienced in maintaining alive the pieces consisting of genital segments alone, the more muscular tissues of the anterior part, and the beating of the fans of the middle part rendering those regions relatively hardy. The results of the last two out of four different sets of experiments are summarised in the tables given below.

## TABLE I.

Large Roman numerals, e.g. XI, denote original segments.
Small Roman numerals, e.g. xi, denote regenerated segments.
Arabic numerals, e.g. 3, denote number of genital segments.
O, lack of regeneration.
+, junction between regenerated and regenerating segments.
—, junction between adjacent segments of like nature.

### Regeneration after 95 Days at 10–11° C.

| | Pieces consisting of | Segments regenerated. | No. of cases. |
|---|---|---|---|
| Type a. | segments I–XII. | | |
| | | I–XII+xiii–xiv–xv–xvi–5 genital. | 1 |
| | | ,, ,, ,, 6 ,, | 1 |
| | | ,, ,, ,, 7 ,, | 3 |
| | | ,, ,, ,, 8 ,, | 1 |
| | | ,, ,, ,, 9 ,, | 1 |
| Type b. | ,, I–XIV. | | |
| | | I–XIV+xv–xvi–4 genital. | 2 |
| | | ,, ,, 6 ,, | 1 |
| | | ,, ,, 8 ,, | 1 |
| Type c. | ,, I–XVI. | | |
| | | I–XVI+5 genital. | 1 |
| Type d. | ,, XIII. | | |
| | | i–xii+XIII+xiv–xv–xvi–8 genital. | 1 |
| Type e. | ,, XIII–XIV. | | |
| | | i–xii+XIII–XIV+xv–xvi–5 genital. | 1 |
| Type f. | ,, XIII–XV. | | |
| | | i–xii+XIII–XIV+xvi–8 genital. | 2 |
| Type g. | ,, XIII–XVI. | | |
| | | i–xii+XIII–XVI+9 genital. | 5 |
| Type h. | ,, XIV. | | |
| | | i–x+XIV+xv–xvi–3 genital. | 1 |
| Type j. | ,, XV–XVI. | | |
| | | O+XV–XVI+5 genital. | 1 |
| Type k. | ,, XV–XVI–Genital complete. | | |
| | | O+XV–XVI–Genital complete. | 3 |
| Type m. | ,, XVI–Genital complete. | | |
| | | O+XVI Genital complete. | 3 |
| Type n. | ,, Genital complete. | | |
| | | O+Genital complete. | 2 |
| Type o. | ,, 12 Posterior Genital. | | |
| | | O+12 Posterior Genital. | 2 |

Regeneration after 45 Days at 10–11° C.

| Type | Pieces consisting of segments | Segments regenerated. | No. of cases. |
|---|---|---|---|
| Type d. | XIII. | i–xii+XIII+xiv–xv–xvi–4 genital. | 2 |
| Type i. | ,, XIV–XV. | i–xiii+XIV–XV+xvi–6 genital. | 1 |
| | | i–xi+XIV–XV+xvi–2 ,, | 1 |
| Type k. | ,, XV–XVI–Genital complete. | O+XV–XVI–Genital complete. | 2 |
| Type l. | ,, XVI–3 Genital. | O+XVI–3 genital+4 genital. | 2 |
| Type o. | ,, 12 Posterior Genital. | O+12 Posterior Genital. | 2 |
| Type p. | Numerous cases of regeneration of genital segments posteriorly from remaining genital regions. | | |

From these results two facts emerge. First, that while regeneration can take place posteriorly from any level, anterior regeneration is only possible from the fourteenth segment forwards; this level at which anterior regeneration ceases is very definite, for while regeneration may be completed from segment 14, there is none at all from segment 15 or any segment posterior to it. Secondly, where regeneration occurs at all, it is always complete, unless the original piece of tissue is too small to contain sufficient reserve food material. That is, since the majority of segments are perfectly recognisable by their peculiar structures, it appears very clearly that regeneration continues from any segment until that segment occupies in the new worm its original distinctive position (cf. Allen, 1921, p. 165). It is obvious, however, in the case of Chætopterus where regeneration occurs so commonly in nature, that had it been otherwise, striking diversities in structure of whole worms would long ago have been noted.

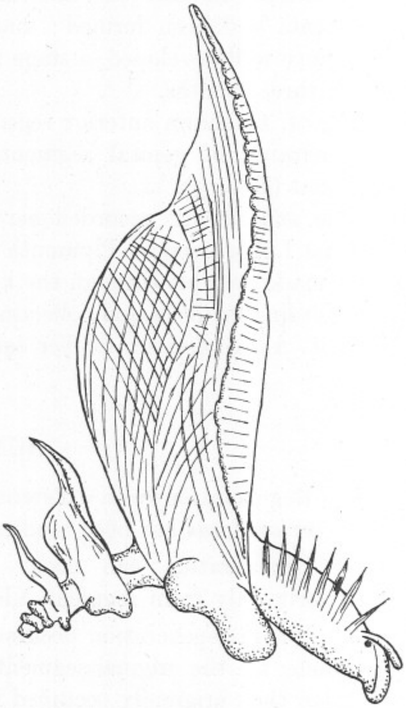

Fig. 3.—Anterior and posterior regeneration from (fan) segment 14.

Fig. 3 shows the first fan segment

(XIV) which was isolated ninety-five days before being drawn (see Type h in Table I). Posteriorly it has regenerated the remaining two fan segments and two to three genital segments, i.e. the zone of growth being terminal, the segments regenerated are already in their correct relative positions. Anteriorly, however, regeneration is not yet complete in that only the segments of the anterior part proper have been formed, segments xi, xii, and xiii being omitted. It may be noted that in this case the tissue comprising segment x merges directly with the muscular face of the fan segment and a zone of growth is ill-defined. That such a segment can regenerate forwards completely is shown by the first experiment recorded under Type b (Table I).

Fig. 4, A and B, shows regeneration posteriorly from the anterior piece resulting from autotomy, showing the characteristic flexure of the regenerated segments towards the ventral surface of the original part. Only in one instance was an autotomised " head " (Type a) found in a tube, which exhibited regeneration. This presumably had been kept healthy by the water current produced by the remainder of the animal in another region of the tube. Regeneration had occurred to a considerable extent, in that the thirteenth, fan segments, and twelve genital segments had been formed ; moreover, the green pigment in the gut was very well developed, a stage not reached by experimental cases even after three months.

Fig. 4, C, shows anterior regeneration from the autotomy level, and regeneration of genital segments posteriorly from the hindmost fan segment (Type g).

The experiments recorded here, and others, were carried out at the Marine Laboratory at Plymouth during the last three years, and were only made possible through the kindness of Dr. E. J. Allen and the staff in affording facilities and collecting the material. Thanks are also due to Mrs. T. A. Stephenson for her care of experiments during my absence.

## SUMMARY.

1. Regeneration from different levels in the polychæt worm *Chætopterus variopedatus* has been studied.

2. Regeneration can occur posteriorly from any segment, but anteriorly only from segment XIV forwards.

3. Where regeneration occurs at all, given sufficient time, it will be complete, i.e. the original segments occupy in the new worm the relative position they originally occupied in the old worm.

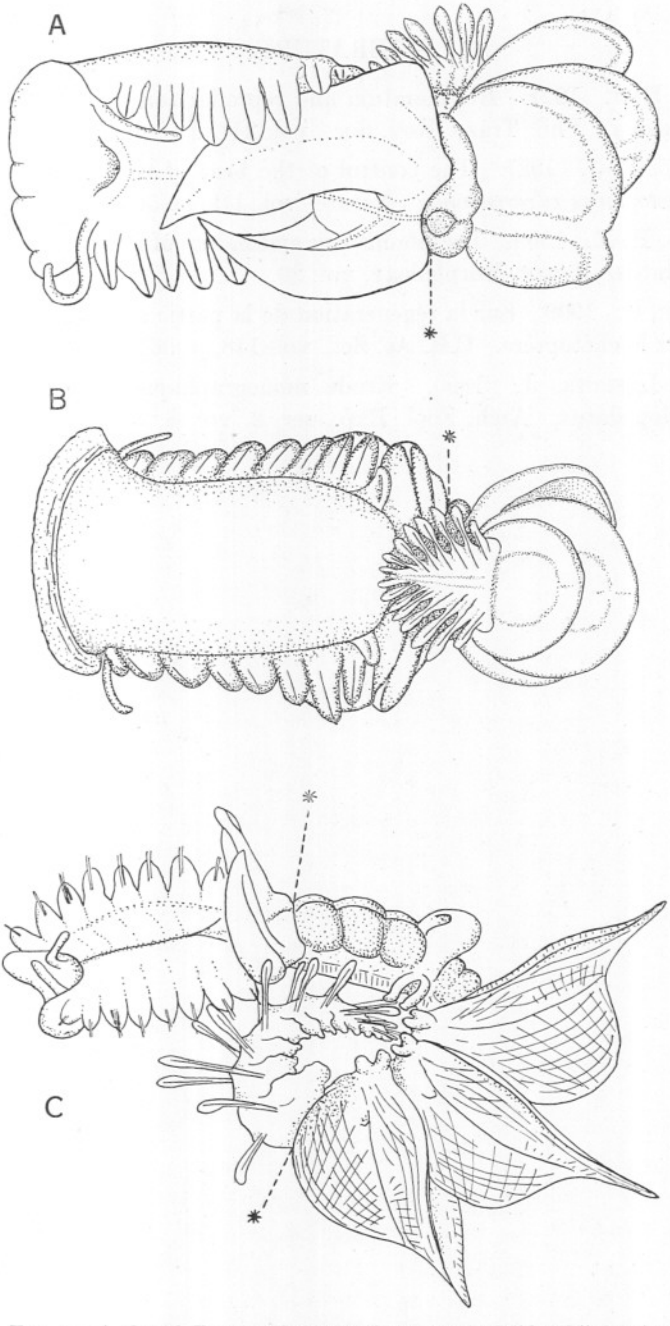

FIG. 4.—A, dorsal, B, ventral aspect of autotomised "head" showing posterior regeneration of fan and genital segments, reflected ventrally and anteriorly; C, segments XIII–XVI showing regeneration of "head" forwards from autotomy level and genital segments posteriorly from last fan segment.

* Junction of old and new segments.

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# The Identification and Validity of Certain Species of Ascidians.

By

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With 6 Figures in the Text.

## CONTENTS.

## INTRODUCTION.

THERE has existed in the past, and still does exist, considerable confusion both in the question of a satisfactory basis for the classification of ascidians and that of the validity of many species.

The principal orders and families are fairly stereotyped, and confusion and divergent opinion is mainly confined to the internal classification of the various families. These differences have a twofold origin, in that classifications have been constructed by various authors on three distinct bases, and that it is very difficult to distinguish between structures which are similar through relationship and those which are similar through convergent or parallel development. Further difficulty arises from the fact that authors describing a new species with a view to fitting it into one particular classification, have often given insufficient details for its accurate inclusion in another scheme. There is also divergent opinion as to the correct nomenclature that should be employed, but with that this paper is not concerned.

Briefly, the bases used for classificatory purposes within the families have been the characters of the branchial sac, of the gonads, and, to a lesser degree, of development; that this last has not been used to the extent that it might be has been due primarily to the relative difficulty in making the necessary observations.

This paper deals mainly with the family Molgulidæ (Cæsiridæ), but first a few points may be made concerning the classification of the class Ascidiacea as a whole.

The class has been divided by Seeliger and Hartmeyer (1909) into three orders: Ptychobranchia, Dictyobranchia, and Krikobranchia, each consisting of four families. This system was constructed with reference to adult structures alone, and is one of a series of such. Whether it is a natural division will only be known when yet more is known of the adult anatomy and of the development and physiology of the group.

One confirmation has been made by Huntsman (1915), who worked out the mode of formation of the developing protostigmata and found that the various types agree very closely with the classification mentioned above. The only exceptions are the families Tethyidæ and Styelidæ of the order Ptychobranchia, where this developmental evidence indicates a certain heterogeneity, and further revision of these families may become necessary. But, in addition to an extension of the observations made by Huntsman, developmental evidence of a different nature can be used; for example, most ascidian tadpoles possess both a pigmented eye and an otolith, but many possess an otolith alone. This type of variation is apparently confined to the order Ptychobranchia, and may become useful in determining the finer relationships of its component genera. Another variant in development is connected with the atrial syphon. This single syphon is usually and probably primitively formed by the independent invagination of a pair of atrial sacs, the openings of which later become involved in a single median dorsal invagination, but in many forms the invagination is median and single from the very beginning, though below the surface of the larva it bifurcates to form the two atrial sacs. Of the forms so far studied, all those belonging to the orders Dictyobranchia and Krikobranchia possess the first type of development, while those of the Ptychobranchia have the latter type; but the number of species investigated at present is insufficient to warrant an assertion that the fused type of development is universal in, and typical of, the Ptychobranchia. In any case, this variation in atrial development will be of use, either in confirming or correcting its subdivision. A table showing which species have at present been investigated is appended (p. 162).

The family Molgulidæ has been the subject of much discussion since 1870, when Lacaze-Duthiers first discovered that there were great differences in the development of its numerous species. Briefly, the species may be divided into two groups according to whether they possess a typical swimming larva with an otolith and fully formed tail, or whether these two structures have been eliminated from their development. This difference in development is very striking, and the results of a detailed investigation of it will be included in a later paper. Lacaze-Duthiers, however, considered that these larval differences were of more fundamental importance than adult anatomical differences and accordingly split the family into two genera, Molgula and Anurella, according to whether the larvæ possessed a tail or not. This scheme certainly brings together species which are ill-assorted from all other points of view, and has not been followed by other authors to any extent. That convergence has occurred to a considerable extent in connection with this modification of development will be shown in the paper mentioned above, and the types of development within this family do not afford a good basis for determining relationships. Hartmeyer (1909) and Van Name (1912) have used the details of the adult branchial sac as the chief diagnostic characters, while Huntsman (1922) considers that convergent parallel development may have occurred to a very great extent in that structure, and that the nature of the gonads and their related structures is much more indicative of relationship. But while it is considered that the one set of characters is as important as the other, it is not the purpose of this paper to discuss this question. Hartmeyer in his last work (1923–24), published posthumously, retains in the main his original point of view, but minimises the importance of many minor diagnostic characters and maintains that there are relatively few species of Molgulæ compared with those mentioned in his earlier account (1909) and that of Van Name (1912). In this connection he ignores developmental differences altogether, and many of his species described in 1923 contain forms whose development may be of either type. Even excluding developmental characters most of his enlarged species can be split into forms readily recognisable, especially in the living state, as other previously described species. Only in one case does the embryological evidence tend to confirm his grouping, and that is his inclusion of *Molgula ampulloides* under *Molgula manhattensis*.

The different characters that have been used in correcting or confirming his conclusions as to the synonymity of various species are of the organisation of the egg and the larval and post-larval development. Thus the egg can vary in size, and in the nature and number of its follicle cells and membranes. The tadpole stage may be completely eliminated, or if present the proportions and size of the tadpole may vary. The embryo may hatch through digestion of the egg membranes or through their rupture ; while another set of diagnostic characters is to be found in the arrangement and number of the extensions of the bodywall, ampullæ, forming a temporary respiratory and fixatory organ for the metamorphosing larva. Only those of the species Hartmeyer has grouped under one specific name, the validity of which is being reaffirmed, will be discussed. For the complete lists of his supposedly synonymous species the reader is referred to the original paper (1923).

TABLE TO SHOW CHARACTERS OF ASCIDIAN TADPOLES AND LARVÆ.

| | Otocyst. | Otocyst+Eye. | Atria fused. | Atria separate. |
|---|---|---|---|---|
| *Bostrichobranchus pilularis* | — | — | × | — |
| *Molgula manhattensis* | × | — | × | — |
| ,, *ampulloides* | × | — | × | — |
| ,, *simplex* | — | — | × | — |
| ,, *robusta* | — | — | × | — |
| ,, *oculata* | × | — | × | — |
| ,, *occulta* | — | — | × | — |
| ,, *citrina* | × | — | × | — |
| ,, *complanata* | × | — | × | — |
| ,, *canadensis* | × | — | × | — |
| ,, *bleizi* | — | — | × | — |
| ,, *retortiformis* | — | — | × | — |
| *Boltenia hirsuta* | — | × | × | — |
| *Tethyum pyriforme americanum* | — | × | × | — |
| *Styela partita* | — | × | × | — |
| *Styelopsis grossularia* | × | — | × | — |
| *Polycarpa rustica* | × | — | × | — |
| ,, *comata* | × | — | × | — |
| *Botryllus schlosseri* | × | — | × | — |
| ,, *(Botrylloides) rubrum* | × | — | × | — |
| *Corella parallelogramma* | — | × | — | × |
| *Ascidia mentula* | — | × | — | × |
| ,, *conchilega* | — | × | — | × |
| ,, *virginea* | — | × | — | × |
| ,, *obliqua* | — | × | — | × |
| ,, *prunum* | — | × | — | × |
| *Ascidiella aspersa* | — | × | — | × |
| ,, *scabra* | — | × | — | × |
| *Phallusia mammillata* | — | × | — | × |
| *Ciona intestinalis* | — | × | — | × |
| *Perophera listeri* | — | × | — | × |
| *Clavelina lepadiformis* | — | × | — | × |
| *Distaplia clavata* | — | × | — | × |
| *Amaroucium nordmanni* | — | × | — | ? |
| *Aplidium pallidum* | — | × | — | ? |
| *Diplosoma listerianum*, var. *gelatinosum* | — | × | — | × |

### *Molgula manhattensis* de Kay.

According to Hartmeyer this species should include amongst others *M. ampulloides* van Beneden, *M. socialis* Ald., *M. simplex* Ald., *M. macrosiphonica* Kupff., and *M. papillosa* (Huntsman). He also considered *M. robusta* van Name to be a variety of *M. manhattensis*, but A. M. Lucas (1927) has shown that *M. robusta* possesses an anural development while *M. manhattensis* produces typical tadpoles, and this difference in development merits at least a specific distinction.

*Molgula ampulloides* has a development similar in all respects to that of *M. manhattensis*. The eggs are of the same diameter, and have similar follicle cells and develop outside the parent. Both forms produce tadpoles with their characteristic otolith. Hatching is by digestion of the egg membrane, and in each case one long respiratory ampulla grows out four or five times the length of the body (see Fig. 1), while three or four shorter ampullæ develop later. Van Name (1912), after examining both forms, came to the conclusion they were not identical. Certainly the region of attachment and external appearance differ somewhat, but it is doubtful whether the differences are sufficiently great to justify the retention of *M. ampulloides* as a distinct species. But that the difference is such that a variety is justifiable is believed, and it is suggested that *M. ampulloides* be *M. manhattensis* v. *ampulloides*.

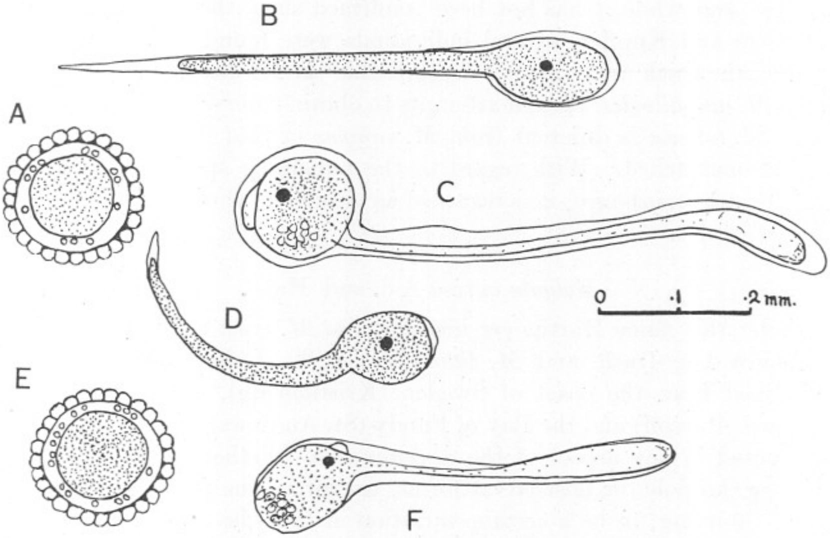

FIG. 1.—A, B, C, egg, tadpole, and metamorphosing tadpole with respiratory ampulla of *Molgula manhattensis*. E, D, F, do. *Molgula ampulloides*.

It should be noted that both these forms occur only in very shallow water, and may be found in the intertidal zone. *M. manhattensis* was described from the American coast, while *M. ampulloides* was described from the European coast.

*M. simplex* is in a different category. It has been described both by Lacaze-Duthiers (1877) and by Kupffer (1872) as possessing anural development, and while the anatomical differences between the adults are small, they are quite definite and the ensemble produces a difference in appearance which is very obvious. *Molgula simplex* has been recorded only from depths below 15 fathoms, and compared with *M. ampulloides* is more spherical and has much shorter syphons. The difference in development is sufficient, however, to maintain *M. simplex* as a distinct species, and while it has not been confirmed since the time of Lacaze-Duthiers and Kupffer, several individuals were found in the region of Plymouth which were readily recognisable as *M. simplex* and distinct from *M. ampulloides*, though attempts to obtain embryos were unsuccessful. *M. robusta* is different from *M. simplex* in that it is asymmetrical and is unattached. With regard to the remaining species, *M. socialis* and *M. macrosiphonica*, it is regarded as unproven whether they be valid species or not.

### *Molgula citrina* Ald. and Hanc.

Under this name Hartmeyer includes also *M. nana* Kupff., *M. echinosiphonica* Lac.-Duth. and *M. littoralis* Verrill. Individuals have been examined from the coast of Sweden (Kristineberg), from the English Channel (Roscoff) and the Bay of Fundy (St. Andrews), and no difference was noted in any aspect of the development, whether in the nature of the egg, tadpole, or post-larval forms, except in one particular. There seems, however, to be a certain variation in that the form described by Lacaze-Duthiers at Roscoff as *M. echinosiphonica* never attains the size reached by those in other regions, and in addition possesses well-developed test spines on the branchial syphon, spines which are developed hardly at all in the other forms.

The only variation that occurs in development is in connection with the hatching mechanism, and is of importance in that Caswell Grave (1926) has used it as a justification for maintaining the American *Molgula citrina* as a species distinct from the *M. nana* and *M. echinosiphonica* of European shores. All the forms are viviparous, and in every case the larva emerges by means of rupture of the egg membrane by the swelling larval test and respiratory ampullæ, and not by digestion of the membrane (see Fig. 2).

Grave describes the difference between the American and European forms as though it were a fundamental difference in development. Actually this difference is that while the tadpoles of the American form usually succeed in rupturing the egg membrane by the swelling of their anterior end, those of the European forms very often fail to do so at that stage, and rupture occurs later by the swelling larval test and outgrowing respiratory ampullæ, a stage where the tail has usually been absorbed. The swelling of the anterior part of the tadpole is of the same extent in both types, and all that is implied is that the egg membrane of the European forms on the average is tougher than that of the American form. Grave never found the second type of hatching among his material, and

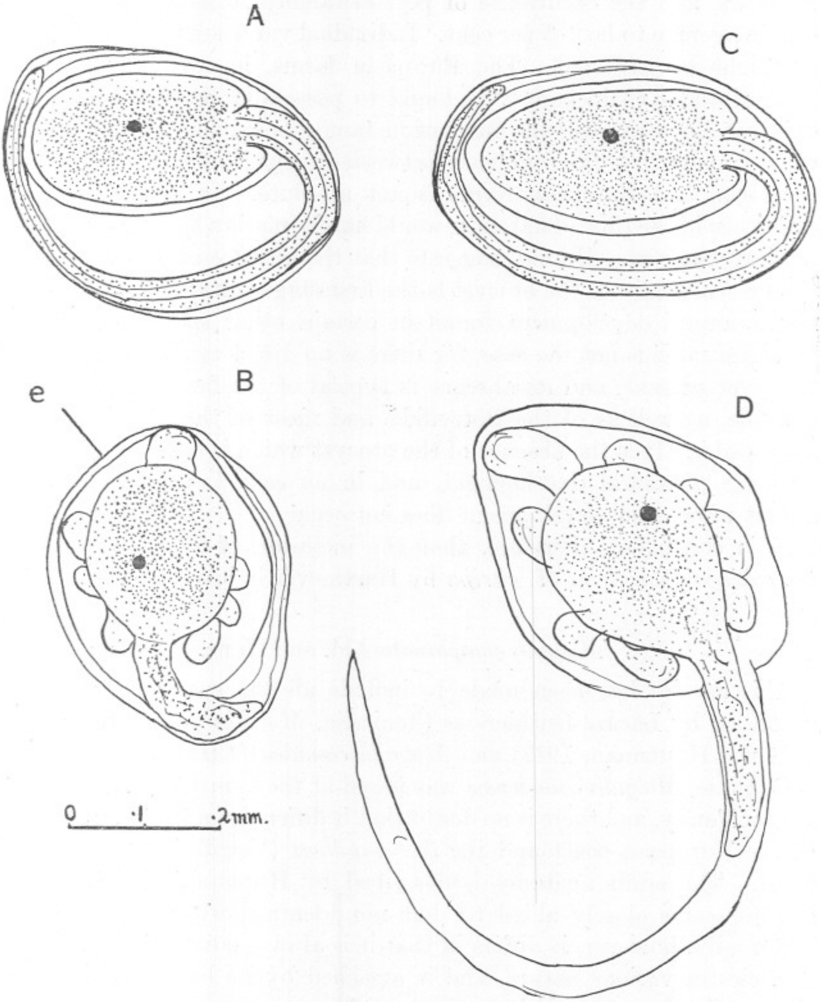

FIG. 2.—A, unhatched tadpole. B, same undergoing metamorphosis of *Molgula nana*. e, egg membrane. C, unhatched tadpole. D, hatched tadpole undergoing metamorphosis of *Molgula citrina*.

assumed also that the first type does not occur in the European forms. This is not the case. Several hundred individuals of *Molgula citrina*, containing altogether many thousand larvæ, were examined at St. Andrews, and the occurrence of post-metamorphic hatching was found on the average to be 2–3 per cent. Individual variation was considerable, as might be expected. The European forms, however, examined at Roscoff and Kristineberg were found to possess larvæ over 80 per cent of which hatched after the onset of metamorphosis, though by no means all did so, so that the difference between the method of hatching in the American and European forms is not absolute. In any case such a difference in the time of hatching would hardly merit a specific distinction, as Grave suggests He also suggests that the absence of a larval eye and the presence only of the otocyst is the first stage towards the acquisition of the anural development found in certain other species of Molgula. Obviously this is not the case, for there is no direct evidence that an eye was ever present, and its absence is typical of the family Molgulidæ as a whole, as well as of the Botryllidæ and most of the Styelidæ, of the same order. It is the absence of the otocyst which is correlated with the presence of anural development, and in no case has this been found absent where such development does not occur.

It is concluded, therefore, that the inclusion of *Molgula nana* and *M. echinosiphonica* in *M. citrina* by Hartmeyer is justifiable.

### *Molgula complanata* Ald. and Hanc.

This species has been made to include all the species of the genus described by Lacaze-Duthiers as Ctenicella, *Molgula papillosa* of Verrill (but not Huntsman, 1912) and *Molgula canadensis* Huntsman.

Of these, *Molgula canadensis* was found at the mouth of l'Etang River, Bay of Fundy, and there is no doubt that it differs from the *M. complanata* of the European coast and the *M. papillosa* (Verrill) of the American coast. The adult anatomy is described by Huntsman, 1912, and the species seems closely allied to, but not identical with, the other two. Externally, however, it differs in that it is always covered with adherent particles of various nature, and is attached by its base and not by its side, while the eggs and larvæ have different proportions from those of *M. complanata* (see Fig. 3).

How far Hartmeyer is justified in the case of his other inclusions it is difficult to say.

### *Molgula oculata* Forbes.

Under the name *Molgula oculata* are now included *M. occulta* (Kupff.), *M. roscovita* (Lac.-Duth.), *M. bleizi* (Lac.-Duth.), and *M. solenata* (Lac.-Duth.). Four of these were described by Lacaze-Duthiers (1874–1877), while *M. occulta* was described by Kupffer (1875). It is believed that *M. occulta* and *M. roscovita* are synonymous forms, and that in all probability they will be found to be identical with the Molgula described by Alder (1863) and Forbes (1848), and figured in Ald. and Hanc., 1907, under the name *Ascidia chonchilega*, and, if so, the name will have to be *M. chonchilega* Alder, but this cannot be determined until the type specimen is found. Thus under the single specific name "*oculata*" Hartmeyer will be shown to have included at least three valid species including *M. oculata* itself, and a probable fourth. It must be admitted in this case that the character of development of all these forms was thought to be anural at the time his account was written, though one anural species, *M. simplex*, he included elsewhere. The mistake was made in the first place by Lacaze-Duthiers himself in his original description of *Molgula oculata*, where he stated that development was direct, and that tailed tadpoles were not formed.

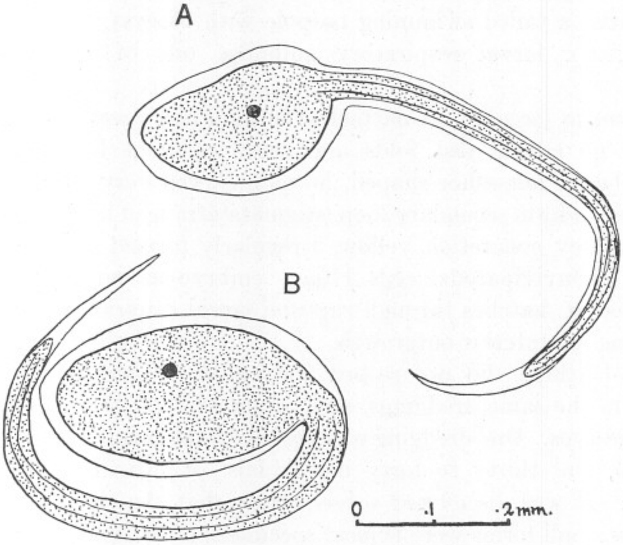

FIG. 3.—A, tadpole of *Molgula complanata*.
B, tadpole of *Molgula canadensis*.

In 1874 he described two species of Anurella (Molgula) from Roscoff, which were very similar in external appearance. The commonest to which he gave the name "*roscovita*" was found in large masses free in the sand at low water of high spring tides in the region of the Roche de Loup, and may still be found there in extraordinarily large numbers. The other he identified as the "*oculata*" of Forbes, and was and still may be found in dredgings from deeper water near the St. Pol River.

For detailed descriptions the reader is referred to the original paper, but as Hartmeyer considers them identical forms a brief account of their differences and resemblances is given here. A comparison of their development is given as well.

*Molgula oculata.* Unattached in sand and covered with adherent particles, test between syphons free from sand, syphons protected by lateral folds of test; dorsal tubercle horseshoe-shaped with horns very much incurved, gut loop not curved to form secondary loop, stigmata irregular, and spiral arrangement inconspicuous, kidney almost filled by purple concretion deposited in form of lamellæ; nonviviparous, eggs $110\mu$; larva a tailed swimming tadpole with otocyst, hatching through digestion, six larval respiratory ampullæ, one of which is always anterior.

*M. roscovita* (*occulta*). Unattached in sand and covered with adherent particles, no lateral test folds and sand adherent between syphons; dorsal tubercle horseshoe-shaped, horns incurved very slightly, gut loop not curved to form secondary loop, stigmata arranged in very conspicuous spirals, kidney concretion yellow, irregularly formed and by no means fills sac; nonviviparous, eggs $110\mu$; embryo at no time develops a tail or otocyst, hatches through rupture, larval respiratory ampullæ five, there being no anterior outgrowth.

Lacaze-Duthiers did not record finding *M. oculata* and *M. roscovita* together in the same dredgings, and he stated that *M. oculata* possessed anural embryos. One dredging was made from the same region in September, 1926, and thirty to forty individuals, of two distinct sizes, were included. It was discovered subsequently that the three large (5 cms.) and a few small forms were typical specimens of *M. oculata*, but that the remainder (3 cms.) were identical with *M. roscovita* in every respect. In the contracted state, however, apart from size, no external difference could be seen between them, and it is suggested that when Lacaze-Duthiers obtained his material from this region he examined the anatomy of the larger specimens and obtained his cultures from the smaller ones, without being aware that he had the two species present. In any case, whatever its origin, there seems to be no doubt that a mistake was made, for cultures made from all the individuals of *M. oculata* gave rise to typical urodele larvæ, while the others all produced anural larvæ, which differed in no detail from those of the shore-living *M. roscovita*.

A preserved collection from one dredging has since been found at the Marine Biological Laboratory at Plymouth, and there also were found the same two species of Molgula in close association, large individuals, up to 8 cms., only of *M. oculata*, and small individuals of both species. One to two hundred individuals were dredged near Kristineberg in 20 fathoms in the Koljö Fjord in 1926, which afterwards were determined to be identical with the species described as *M. roscovita* by Lacaze-Duthiers, though attempts at rearing larvæ were all unsuccessful.

In 1875 Kupffer described a species from the North Sea which he named *M. occulta*, and from his description this seems to be undoubtedly identical with *M. roscovita* rather than *M. oculata*, and while Lacaze-Duthiers had already published his account of the species, he did not name it until two years after Kupffer's publication, so that until it is shown that the *M. conchilega* of Forbes and Alder is a synonymous species it must be known as *Molgula occulta* Kupff.

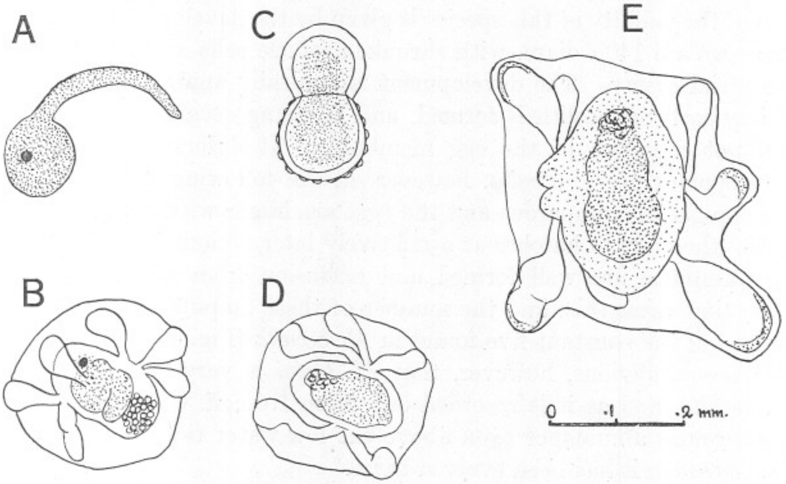

FIG. 4.—A, tadpole. B, metamorphosed larva of *Molgula oculata*. C, embryo hatching. D, equivalent stage to (B) of *Molgula occulta*. E, do. *Molgula bleizi*.

Lacaze-Duthiers described another anural species under the name *Anurella solenata*, which Hartmeyer includes as *M. oculata*. If this prove not to be a valid species, as it may well be, it will be synonymous not with *M. oculata*, but with *M. occulta*.

### *Molgula bleizi* Lac.-Duth.

The other species listed by Hartmeyer under the name *M. oculata* is *M. bleizi*, described by Lacaze-Duthiers, 1877. This form was said by him to possess anural development, which fact has been confirmed by myself and by Damas, 1902, and has not yet been discovered elsewhere than at Roscoff. It is a small form of average size, 5 mm., and was found attached side by side with *Molgula echinosiphonica* (*citrina*) on *Styelopsis* (*Dendrodoa*) *grossularia* in grottoes of the Roche de Loup and elsewhere.

The adult anatomy is well described by Lacaze-Duthiers, and it will be seen that the anatomical differences between this form and *M. oculata* and *M. occulta* are relatively small. Principally one must note, apart from the fixed habitat and great reduction in size, the smooth translucent test: it has a conspicuous spiral arrangement of the stigmata to form infundibula, as in *M. occulta*, and it differs from both *M. oculata* and *M. occulta* in that in these forms the vas deferens does not accompany the ovary and oviduct, while in *M. bleizi* it does. The most complete vindication of the validity of this species is given by the developmental evidence. The eggs are 140$\mu$ diam. with shrunken follicle cells and develop within the atrial cavity. The development is typically anural in that no tail of any sort nor otolith is formed, and hatching occurs through rupture and not digestion of the egg membrane. It differs from the anural development of *M. occulta*, however, in the following particulars: the development is viviparous and the eggs are larger with shrunken follicle cells; the embryo hatches at a relatively later period, when the respiratory ampullæ are well formed and extrusion from the parent occurs some time after this, and the number of these ampullæ is seven to nine instead of the constant five found in *M. occulta* (Fig. 4).

It seems obvious, however, that *M. bleizi* is very closely related to *M. occulta*, and as it is recorded only from Roscoff, where *M. occulta* is in enormous abundance even above the low-water tide level, it is more than possible it has been evolved there.

Of the relationship existing between *M. occulta* and *M. oculata* less can be said; it is significant, however, that their distribution is coextensive, and is confined to North European waters and to the northern parts of Mediterranean waters. The significance of the difference in development will be discussed elsewhere.

### *Ascidiella aspersa* Müll.

O. F. Müller, 1776, described from the Christiania fjord two species which he named *Ascidiella aspersa* and *Ascidiella scabra* respectively. Hartmeyer (1923) now considers them to be identical and retains the first name. This is considered to be unjustifiable as the two species, especially in the living condition, can be easily distinguished. In general structure there is very little difference, but in appearance and in some other respects they differ very markedly. *Ascidiella aspersa* is attached to the substratum by its posterior or basal end and can attain a length of 12–13 cms., while *Ascidiella scabra* is attached by its side and never attains a length of more than 4 cms. The atrial syphon of *A. scabra* is relatively nearer the anterior branchial syphon than is the case in *A. aspersa*. Internally, the renal vesicles are much less extensively distributed, and the red pigment is spread usually over most of the mantle in *A. scabra*, while in *A. aspersa* it is usually more localised near the syphons. Correlated with the difference in maximum size is a difference in the size at which the two species mature. *Ascidiella aspersa* is rarely mature until it exceeds 5 cms. in length, while *Ascidiella scabra* is mature when it reaches a length of 2 cms. Finally, there are very marked differences in the organisation of the living egg. This is shown most conspicuously when the eggs have lain in sea-water for an hour or two. *A. aspersa* possesses an incomplete investment of inner follicle or testa cells, and an outer investment of follicle cells of about $20\mu$ diameter. *A. scabra* has a complete investment of inner follicle cells and an outer investment of cells of the same size, i.e. $10\mu$ diameter ; further, the chorion on which the outer cells rest is lifted from the ovum surface to a much greater extent than is the case in *A. aspersa*. Finally, the egg of *A. aspersa* floats in sea-water of salinity 30 to $35^{\circ}/_{\circ\circ}$, and as far as is known is unique among Ascidian eggs in doing so (see Fig. 5).

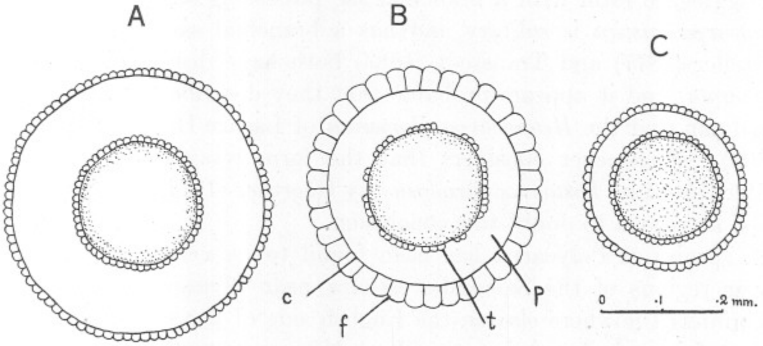

FIG. 5.—A, egg of *Ascidiella scabra*. B, of *Ascidiella aspersa*. C, of the small species of Ascidiella of Scandinavian waters. c, chorion. f, outer follicle cell. t. inner follicle cell. p, perivitelline jelly.

Both species are apparently confined to European waters, from the Norwegian Sea to the eastern Mediterranean. Hartmeyer, in his account of the distribution, does not distinguish between the two forms. They occur together abundantly in the coastal waters of S.W. England, but while the smaller *A. scabra* is abundant at Roscoff and Skagerak, the only individuals found of *A. aspersa* were three brought in at Kristineberg in 1926. But their range of distribution seems to be much the same, and in one district at least they occur side by side, so that their differences cannot be correlated with different environments. It has yet to be shown conclusively that the abundant small species of Ascidiella of the Swedish coast is absolutely identical with *A. scabra*. This form certainly differs in that it possesses a deep diffusely spread brown pigment, and has eggs which are semi-opaque instead of being translucent, and have a less extensive perivitelline space (see Fig. 5, C).

### *Polycarpa rustica* Lac.-Duth. and Del.

This species is not mentioned by Hartmeyer (1923). There is some confusion in that Herdman (1893) described a species from the Isle of Man, first under the mistaken impression that it was *Styela rustica*, and later as *Polycarpa glomerata*. When the monograph of Lacaze-Duthiers and Delage was published, Herdman suggested that the species there described as *Polycarpa rustica* was identical with his species *glomerata*, but this does not seem to be the case. *Polycarpa glomerata*, according to Herdman, is an aggregate form with a branchial sac possessing but three folds, while *Polycarpa rustica* is solitary and has a branchial sac with four folds.

Heller (1877) and Traustedt (1883) both have described a *Polycarpa glomerata*, and it appears probable that they describe the same form as Herdman and the *Heterocarpa glomerata* of Lacaze-Duthiers and Delage (1892); Hartmeyer considers that the form was originally described under the name *Distomus variolosus* by Gaertner (1774), and there seems to be no reason to doubt this conclusion.

A species of Polycarpa has been found to be very abundant in the upper regions of the Salcombe estuary near Plymouth, but has been encountered nowhere else on the English side of the Channel, though it occurs fairly commonly on the West Mersea oyster beds, according to information supplied by Dr. Orton. This form was thought at first to be identical with the *Polycarpa glomerata* of Herdman, but structurally it agrees perfectly with the *Polycarpa rustica* of Lacaze-Duthiers, and will therefore be recorded here as such for the English coast for the first time. It may be noted here that *Distomus variolosus* has since been shown to possess the faculty of budding (de Selys Longchamps, 1917), and also to possess eggs the diameter of which is in the region of ·5 mm., while *Polycarpa rustica* does not bud and has eggs of only ·15 mm. diameter. Both specimens are viviparous, but the embryos of *P. rustica* are very much more numerous.

### *Styelopsis grossularia* Bened.

This species is practically cosmopolitan, at least in the northern hemisphere, and ranges from the intertidal regions to below 200 fathoms, and therefore forms a good example of the extent to which the larval and post-larval characters discussed earlier in this paper may be influenced by normal changes in environmental factors.

Individuals from the intertidal regions of Plymouth and Roscoff in the English Channel have been examined, and these typically live in water of salinity $35\,^{\circ}/_{\circ\circ}$, temperature range 7–20° C., and periodical exposure to air. Others were examined at St. Andrews, Bay of Fundy. These live in water of salinity 31 °/$_{\circ\circ}$, temperature range 0–10° C., and occur mainly below the low-water mark.

In all these forms no difference was noted in the size or colour of the eggs, tadpoles, proportions of the tadpoles, nor in the nature of metamorphosis nor number of post-larval respiratory ampullæ.

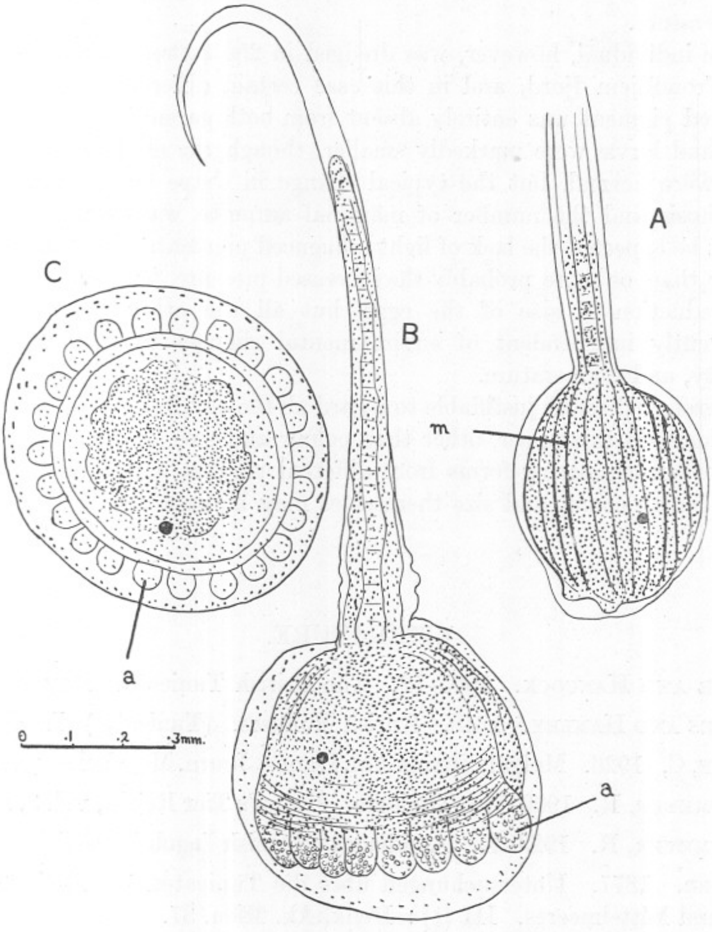

FIG. 6.—A, tadpole of *Styelopsis grossularia*. B, C, same undergoing metamorphosis. a, ampulla m, muscle band.

The adults and larvæ are all diffused with a deep red pigment, but when metamorphosis ensues, muscles in the trunk of the tadpole contract, and by the time the tail has been absorbed the trunk is transformed from an ovoid shape to a medusoid shape, while the colour changes to a yellow-orange. At the same time twenty-three to twenty-five respiratory ampullæ grow out to form a ring round the anterior end, i.e. round the margin of the medusoid body (see Fig. 6).

In the forms mentioned above all these characters were constant, implying independence of normal environmental changes in salinity and temperature.

One individual, however, was dredged in 250 fathoms at Galgenes in the Trondhjem fjord, and in this case certain differences were noted. The red pigment was entirely absent from both parent and larvæ. The eggs and larvæ were markedly smaller, though the chorion and follicle cells were normal, but the typical change in shape occurred at metamorphosis and the number of marginal ampullæ was 24 ; so that as might be expected the lack of light influenced pigmentation, and possibly either that, or more probably the increased pressure, was responsible for the reduction in size of the eggs, but all the other characters are apparently independent of environmental changes in light, pressure, salinity, and temperature.

Therefore it seems justifiable to regard all the developmental characters mentioned in this paper, other than colour and size, of diagnostic value even when comparing forms from different regions, and when from the same region colour and size themselves may be used with caution.

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# The Ascidian Fauna of the Plymouth Area.

By

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THE nomenclature followed is that used by Hartmeyer (**9**), in which account will be found identificattion keys and complete lists of the synonymous species, only the commoner of which are given below. That his conclusions in this respect are open to question has already been pointed out (see *Journ. Mar. Biol. Assoc.*, Vol. XV, p. 159).

For a description with figure of a species the reference number is placed after the name.

Those species common but widely scattered are denoted thus *, those common but local **.

Keys to localities : Aquarium tanks, *at.* Asia shoal, *a.* Bridge ground, *b.* Cawsand Bay, *c.* Duke Rock, *d.* Drake's Island, *dr.* Eddystone Grounds, *e.* Mewstone ledge, *f.* Millbay channel, *g.* Millbay Pier, *h.* New Grounds, *i.* Millbay Docks, *j.* Queen's Ground, *k.* Rame, *l.* Rame-Eddystone, *m.* Stoke Point, *n.* Salcombe (Castle Rocks), *o.* Salcombe (Salstone), *p.* Shore below Laboratory, *q.* Skerries, *s.* Torbay, *t.* Yealm River (hotel corner), *y.* Wembury, *w.* For outer western area stations (Crawshay, **3**), station number.

The months in which the different species are recorded to breed are denoted by Roman numerals, but the breeding season may in any case be of longer duration than that shown.

The records include those in the " Plymouth Invertebrate Fauna " (**1**), in the " Fauna of the Outer Western Area " (**3**), from collections in the museum of the Plymouth Laboratory identified (1911) by Hartmeyer, and those made by myself during the last four years.

## Molgulidæ,

EUGYRA ARENOSA Ald. (**14**). Deep water, free in sand or gravel. *m.*1.6.10.37.

MOLGULA MANHATTENSIS de Kay, var. AMPULLOIDES. =*M. ampulloides* Bened. (**14**). Low water, fixed. I–XII. *j.p.y.*

**MOLGULA OCULATA Forb. (**14**). Deep water, free in sand or gravel. VII–IX. *c.m.*11.33.46.

**MOLGULA OCCULTA Kupff. =*M. roscovita* Lac.-Duth. (**14**). ? +*M conchilega* Forb. In association with *M. oculata*. VII–IX. *c.m.* 11.33.46.

MOLGULA SIMPLEX Ald. (**14**). Deep water, fixed. V–VIII. *e.i.h.*1.3.7. 8.10.11.12.31.32.34.49.70.

MOLGULA COMPLANATA Ald. (**14**). Shallow water and intertidal, fixed. VII–IX. *a.o.*

### Tethyidæ.

PYURA TESSELLATA Forb. (**15**). =*Forbesella tessellata* Lac.-Duth. Shallow to deep water. VIII. *e.f.n.p.*

PYURA SQUAMULOSA Ald. (**10**). *f.*

PYURA SAVIGNYI Phil. (**15**). =*Pyura* (*Cynthia*) *morus* Forb. Shallow to deep water. VIII. *f.m.p.s.*3.4.8.15.34.43.

MICROCOSMUS CLAUDICANS Sav. (**15**). *t.f.*

### Styelidæ.

POLYCARPA POMARIA Sav. (**15**) (**7**). ?=*P. varians*+*P. tuberosa* Lac.-Duth. Deep water. VIII–IX. *e.f.g.k.y.*1.3.4.7.8.9.12.49.59.60.70.72.

POLYCARPA FIBROSA Stps. (**15**). =*P. comata* Ald. Shallow water. V–IX. *k.p.y.*1.4.10.31.53.

*POLYCARPA RUSTICA Lac.-Duth. (**15**). Shallow water. V–IX. *p.*

POLYCARPA GRACILIS Hell. =*P. tenere* Lac.-Duth. (**15**). Shallow water. *f.y.*

**STYELOPSIS (DENDRODOA) GROSSULARIA Bened. (**15**). Shallow water and intertidal. IV–X. *a.f.h.q.y.*

STOLONICA SOCIALIS Hartmr. (**15**). =*Thylacium aggregatum* (Ald.). Deep water. VIII–IX. *b.d.k.f.*

*DISTOMUS VARIOLOSUS Gaertn. (**15**). =*Heterocarpa glomerata* Lac.-Duth. Shallow water and intertidal. VII–IX. *a.c.f.k.*

### Botryllidæ.

*BOTRYLLUS SCHLOSSERI Pall., var. TYPICA (**6**). Shallow water and intertidal. VI–VIII. *g.k.l.m.o.q.*

BOTRYLLUS SCHLOSSERI, var. POLYCYCLUS (**4**). =*B. gigas*+*Polycyclus polycyclus*. Shallow to deep water. *a.e.f.*3.4.7.8.48.60.64.

*BOTRYLLUS LEACHII Sav. (**6**). =*Botrylloides vinosum*+*rubrum*, etc., Milne-Edw. Shallow water and intertidal. VIII–X. *i.q.p.*3·4.8.38.

### Rhodosamatidæ.

CORELLA PARALLELOGRAMMA Müll. (**7**). =*C. larvæformis* Hanc. Deep water. VIII. *b.d.e.g.f.*3.10.32.38.60.

### Ascidiidæ.

*ASCIDIA MENTULA Müll. (**4**). Deep water. II–XI. *f.g.h.n.p.*3.4.12.34.40.59.

ASCIDIA CONCHILEGA Müll. (**4**). =*A. depressa* (Ald.). Low water to deep water. I–XII. *h.e.g.p.*1.4.8.10.32.34.36.37.43.49.70.

ASCIDIA VIRGINEA Müll. (**7**). =*A. venosa* Traust. Deep water. VI–X. *h.e.*1.3.8.12.15.34.38.40.43.59.60.67.70.72.

**ASCIDIELLA ASPERSA Müll. (**12**). Intertidal to deep water. I–XII. *j.n.p.y.*

*ASCIDIELLA SCABRA Müll. (**12**). Shallow to deep water. V–IX. *e.g.k.m.n.y.*

*PHALLUSIA MAMMILLATA Cuv. (**18**). Low water to deep water. I–XII. *d.e.f.n.p.y.*

### Cionidæ.

*CIONA INTESTINALIS Linn. (**8**). =*C. fascicularis* Hanc. Low water to deep water. IV–X. *f.g.j.p.*3.4.10.12.34.40.44.49.59.67.70.

DIAZONA VIOLACEA Sav. (**4**). Deep water. *e.f.n.*

### Perophoridæ.

PEROPHORA LISTERI Forb. (**4**). Tidal pools and shallow water. VIII–X. *a.d.k.o.p.q.y.*

### Polycitoridæ.

**CLAVELINA LEPADIFORMIS Müll. (**4**). Low water and shallow water. VI–X. *dr.d.f.g.k.j.p.*

CLAVELINA AURILUCENS Garst. (**4**). =*Pycnoclavella aurilucens* Garst. Deep water. VIII–IX. *f.n.*

ARCHIDISTOMA AGGREGATUM Garst. (**5**). Shallow water. VI. *d.*

HOLOZOA (DISTAPLIA) ROSEA d. Valle. (**15**). Shallow to deep water. *k.d.*

### Synoicidæ.

SIDNYUM TURBINATUM Sav. (**6**). =*Circalium concrescens* Giard. Shallow water and intertidal. *b.dr.d.g.o.w.o.*

SIDNYUM ELEGANS Giard (**6**). =*Fragarium elegans* Giard. Shallow water. *d.g.i.*

AMAROUCIUM PUNCTUM Giard (**6**). Shallow to deep water. *b.f.k.j.n.*

*AMAROUCIUM NORDMANNI Milne-Edw. (**6**). Low water and shallow water. VI–IX. *k.m.p.w.*

AMAROUCIUM DENSUM Giard (**6**). *f.t.*

APLIDIUM PALLIDUM Verrill. (**6**). =*A. zostericola* Giard+*A. lacteum* Huit. Kaas.+*Amaroucium pall.* Verrill. Shallow to deep water. *d.l.i.k.*

*MORCHELLIUM ARGUS Milne-Edw. (**10**). =*Morchelloides alderi* (Herd.). Intertidal and shallow water. VI–IX. *a.b.d.g.h.i.j.o.p.y.*

POLYCLINUM AURANTIUM Milne-Edw. (**6**). =*P. sabulosum* Giard+ *Glossoforum sabulosum* Giard+*Aurantium aurantium* Lah. Shallow to deep water. *k.l.i.*

### Didemnidæ.

*DIPLOSOMA LISTERIANUM M.E., var. GELATINOSUM M.E. (**16**). =*Didemnum gelatinosum*+*Leptoclinum gelatinosum* M.E. Shallow to deep water. *at.a.g.i.h.n.*1.3.4.5.9.

TRIDIDEMNUM TENERUM Verrill. (**7**). =*Didemnopsis variabile* Hartmr.+ *Didemnum cereum* Giard. Intertidal to deep water. *d.f.h.i.m.n.o.y.*

### Doliolidæ.

DOLIOLUM NATIONALIS Borgert. (**2**). In tow-nettings, Aug., Sept., 1893. Abundant 1895. A few S. of Eddystone, Nov., 1904.

### Salpidæ.

SALPA FUSIFORMIS Cuv. (**13**). Aggregated form at surface, N. of Eddystone, Aug., 1901.

SALPA MUCRONATA Forskal. (**13**). Large shoals in Sound, 1893, in June and July. VIII–X.

### Appendicularia.

OIKOPLEURA DIOICA Fol. (**17**). Tow-nettings. III–IV.

FRITILLARIA BOREALIS (**17**). Tow-nettings.

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# Nitrate in the Sea. II.

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*Hydrographer at the Plymouth Laboratory.*

With 3 Figures in the Text.

In any attempt to analyse the factors controlling the fertility of extensive areas of the sea, the first and most definite fact which presents itself is the entire dependence of all marine animals upon the phytoplankton. The animals dissipate energy in the course of their metabolic processes during their whole lifetime, and utilise the energy of the carbon compounds in the food they consume to balance this loss, while the plants absorb radiant energy during photosynthesis and store it in the carbon compounds they build. If we define fertility as the quantity of organically combined carbon present in the living organisms inhabiting a particular and extensive area of the sea, it is the plants alone which can add *de novo* to this quantity. In consequence the fertility, in the above sense, will be limited by those factors which limit plant growth—by the intensity and duration of a sufficient supply of radiant energy from light and by the lack of any one nutrient salt. Of the latter there is an ample supply except, at times, of phosphate or of nitrate.

Subsequent to the publication in March, 1926, of an account of a rapid method for the approximate estimation of nitrate in sea-water and the data obtained over a period of nine months, observations in the English Channel have been continued at frequent intervals.

These have confirmed the picture which it was then possible to draw concerning the almost complete utilisation of this nutrient salt in the upper water layers during the outburst of diatom growth in spring.

## SEASONAL VARIATION IN THE ENGLISH CHANNEL.

The nitrate content of the water in the English Channel between February, 1926, and May, 1927, is shown in Table I (which is a continuation of Table VIII, *Journ. Mar. Biol. Assoc.*, **14**, p. 81).

## TABLE I.

NITRATE CONTENT IN MILLIGRAMS OF NITRATE-$N_2$ PER CUBIC METRE AT VARIOUS DEPTHS (IN METRES, M.) OF WATER IN THE ENGLISH CHANNEL ON THE LINE PLYMOUTH-USHANT.

| | In Plymouth Sound Station $L_1$ | Off west end of Plymouth Breakwater Station $L_2$ | 9 miles S 21° W (true) from Plymouth Hoe Station $L_1$ | 22 miles S 21° W (true) from Plymouth Hoe Station $E_1$ | 59½ miles S 21° W (true) from Plymouth Hoe Station $E_2$ | 115½ miles S 21° W (true) from Plymouth Hoe Station $E_3$ |
|---|---|---|---|---|---|---|
| Feb. 3rd, 1926 | — | 0 m. **120** | 0 m. **73** | 5 m. **83** | — | — |
| | — | — | — | 25 m. **64** | — | — |
| | — | — | 40 m. **64** | 50 m. **64** | — | — |
| | — | — | — | 70 m. **64** | — | — |
| Mar. 11th & 12th | 0 m. <**190** | — | 0 m. **73** | 5 m. **68** | 5 m. **53** | 5 m. **75** |
| | — | — | — | 25 m. **68** | 25 m. **56** | — |
| | — | — | — | 50 m. **68** | — | 50 m. **75** |
| | — | — | — | 70 m. **78** | — | — |
| | — | — | — | — | 85 m. **52** | — |
| | — | — | — | — | — | 105 m. **75** |
| April 10th | 0 m. **135** | — | 0 m. **110** | 0 m. **75** | — | — |
| | — | — | — | 5 m. **50** | — | — |
| | — | — | 40 m. **79** | 25 m. **76** | — | — |
| | — | — | — | 50 m. **76** | — | — |
| | — | — | — | 70 m. **76** | — | — |
| May 17th & 18th | 0 m. **11** | — | 0 m. **5** | 0 m. **4** | 0 m. **30** | 0 m. **62** |
| | — | — | — | 5 m. **6** | 5 m. **32** | 5 m. **54** |
| | — | — | — | 25 m. **6** | — | — |
| | — | — | 40 m. **10** | 50 m. **6** | 50 m. **32** | — |
| | — | — | — | 70 m. **6** | — | — |
| | — | — | — | — | 90 m. **30** | — |
| | — | — | — | — | — | 105 m. **54** |
| July 8th & 9th | 0 m. **24** | — | 0 m. **5** | 0 m. <**5** | — | — |
| | — | — | — | 5 m. <**5** | 5 m. <**5** | 5 m. **6** |
| | — | — | — | 20 m. **9** | 25 m. **24** | 108 m. **35** |
| | — | — | — | 40 m. **10** | 50 m. **21** | 50 m. **35** |
| | — | — | — | 70 m. **11** | — | — |
| | — | — | — | — | 90 m. **36** | 108 m. **35** |
| Aug. 16th | 0 m. **20** | — | 0 m. **8** | 0 m. **10** | — | — |
| | — | — | — | 5 m. **12** | — | — |
| | — | — | — | 15 m. **12** | — | — |
| | — | — | — | 25 m. **14** | — | — |
| | — | — | — | 50 m. **20** | — | — |
| | — | — | — | 70 m. **20** | — | — |
| Sept. 22nd | 0 m. **17** | 0 m. **15** | 0 m. **7** | 0 m. **5** | — | — |
| | — | — | — | 5 m. **5** | — | — |
| | — | — | — | 25 m. **12** | — | — |
| | — | — | 40 m. **14** | 50 m. **13** | — | — |
| | — | — | — | 70 m. **14** | — | — |
| Nov. 24th | 0 m. <**300** | — | 0 m. **92** | 0 m. **100** | — | — |
| | — | — | — | 5 m. **100** | 5 m. **180** | 5 m. **57** |
| | — | — | — | 25 m. **92** | 25 m. **180** | — |
| | — | — | 40 m. **92** | 50 m. **83** | 50 m. **180** | 50 m. **65** |
| | — | — | — | 70 m. (**75**) | — | — |
| | — | — | — | — | 90 m. **195** | — |
| | — | — | — | — | — | 105 m. **75** |

TABLE I—*continued*.

| | In Plymouth Sound Station $L_1$ | Off west end of Plymouth Breakwater Station $L_2$ | 9 miles S 21° W (true) from Plymouth Hoe Station $L_4$ | 22 miles S 21° W (true) from Plymouth Hoe Station $E_1$ | 59½ miles S 21° W (true) from Plymouth Hoe Station $E_2$ | 115½ miles S 21° W (true) from Plymouth Hoe Station $E_3$ |
|---|---|---|---|---|---|---|
| Dec. 13th | 0 m. <**250** | — | 0 m. **95** | — | — | — |
| | — | — | — | 5 m. **65** | — | — |
| | — | — | 40 m. (**73**) | — | — | — |
| | — | — | — | 70 m. **62** | — | — |
| Dec. 31st | 0 m. **190** | — | — | 5 m. **68** | — | — |
| | — | — | — | 70 m. **61** | — | — |
| Feb. 15th & 16th, 1927 | 0 m. **100** | — | 0 m. **86** | 5 m. **55** | 0 m. **66** | 0 m. **27** |
| | — | — | 40 m. **71** | 50 m. **38** | — | 50m. **38** |
| | — | — | — | 70 m. **83** | — | — |
| | — | — | — | — | 92 m. **81** | — |
| | — | — | — | — | — | 109 m. **64** |
| April 20th | — | — | — | 0 m. **12** | — | — |
| | — | — | — | 5 m. **15** | — | — |
| | — | — | — | 25 m. **44** | — | — |
| | — | — | — | 50 m. **75** | — | — |
| | — | — | — | 70 m. **75** | — | — |
| May 23rd | — | — | — | 5 m. **7** | — | — |
| | — | — | — | 25 m. **7** | — | — |
| | — | — | — | 50 m. **7** | — | — |
| | — | — | — | 70 m. **7** | — | — |

During the spring of 1926 utilisation of nearly all the nitrate available for the growth of diatoms and other phytoplankton occurred between April 10th and May 17th. On April 22nd, 1925, considerable utilisation of the nitrate had taken place above 25 metres, and on April 20th, 1927, a partial utilisation had taken place in the upper strata. About the end of September—rather earlier in 1925 than in 1926—the rate at which nitrate is being utilised is greatly exceeded by the rate at which it is regenerated from the summer crop of plankton organisms which mostly die out towards the beginning of September.

Fig. 1 shows the seasonal variation in the upper 5-metre stratum of water 22 miles south-west of Plymouth. For the values relating to the phosphate in the water I am indebted to Dr. W. R. G. Atkins. The curves indicate that, during the summer months, plant life is at times limited by lack of nitrate and at times by lack of phosphate: when limited by phosphate (July, 1925, August, 1926) the nitrate tends to increase and vice versa (June and August, 1925, June and July, 1926).

Fig. 2 shows the seasonal variation in the bottom stratum of water. Here the utilisation by plant life is not so rapid as near the surface, owing to lack of light. From the data presented in the previous communication it was concluded that the final stage of the regeneration of nitrate takes place in the deeper water, and does not proceed in the surface layer during the summer. The curves in Fig. 2 indicate that an increase in phosphate tends to occur during the summer when plant life is limited by lack of nitrate (August, 1925, May–June, 1926).

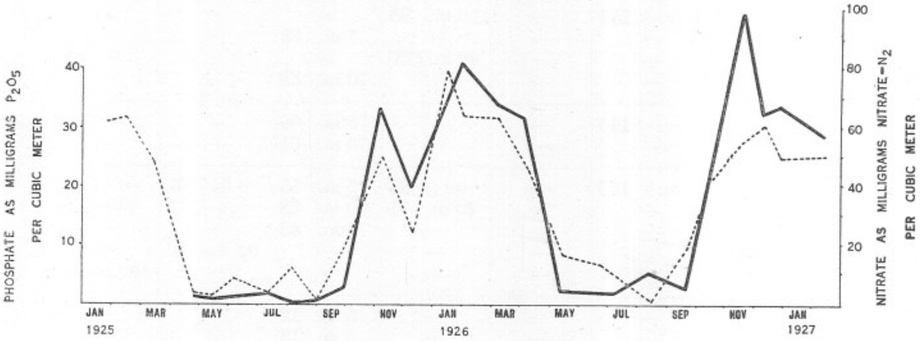

FIG. 1.—The seasonal variation of nitrate and of phosphate (Atkins) in the upper 5-metre stratum of water as shown by observations made at position E1, 22 miles south-west of Plymouth. The nitrate is represented by a thick line and the phosphate by a dotted line.

Inflowing oceanic water has an effect upon the nitrate and phosphate content of the water at position E3, lying north of Ushant. Between March 12th and May 18th, 1926, the water (*circa* 35·1 $^{\circ}/_{\circ\circ}$ S.) was replaced by more saline water (*circa* 35·3 $^{\circ}/_{\circ\circ}$ S.) containing more phosphate and almost as much nitrate, in spite of the fact that during this period a great outburst of diatom growth occurs. Meanwhile the nitrate and phosphate in the water at E1, 22 miles south-west of Plymouth, had both been largely used up by the phytoplankton. The conditions on the two dates are shown in the sectional diagrams in Fig. 3.

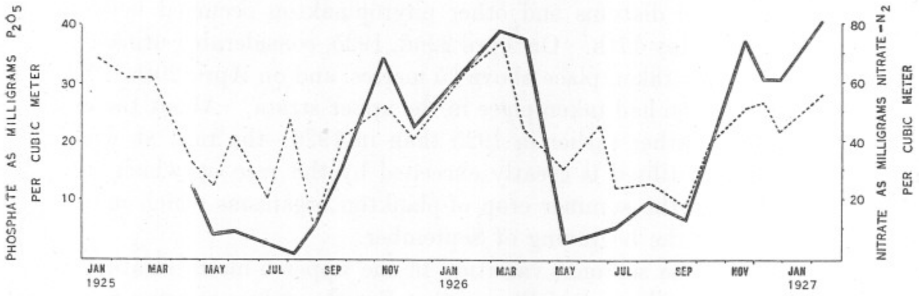

FIG. 2.—Seasonal variation in the nitrate and phosphate (Atkins) in the bottom water at *circa* 70 metres depth at position E1, 22 miles south-west of Plymouth. The nitrate is represented by a thick line and the phosphate by a dotted line.

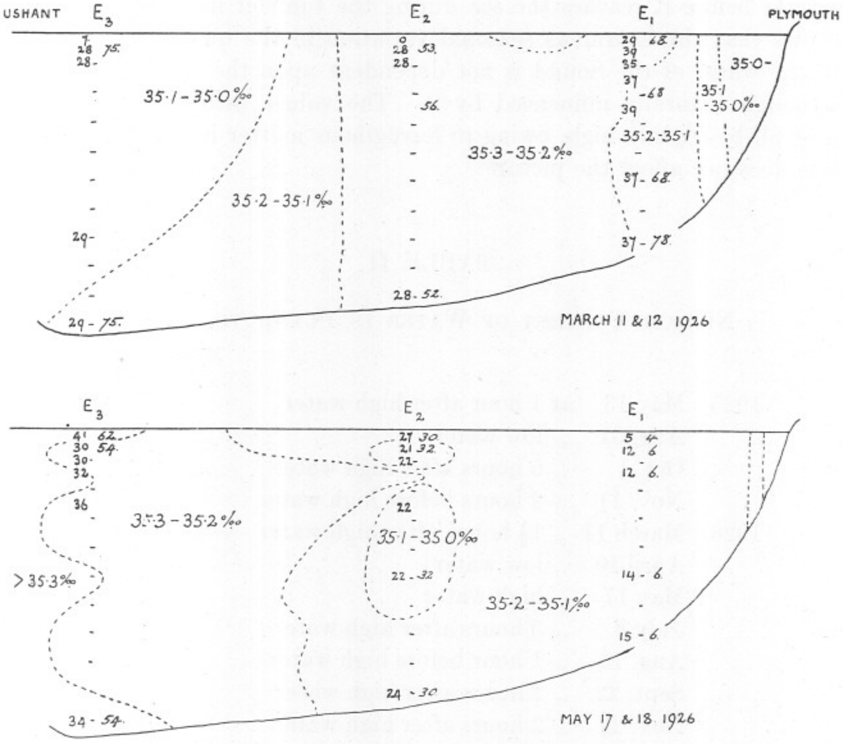

FIG. 3.—Sections across the English Channel between Plymouth and Ushant showing the distribution of salinity (°/$_{oo}$), of nitrate (slanting figures show milligrams of nitrate–$N_2$ per cubic metre), and of phosphate (upright figures show milligrams of $P_2O_5$ per cubic metre) as observed in March and May, 1926.

## EFFECT OF LAND DRAINAGE UPON THE FERTILITY OF COASTAL AREAS.

The nitrate content of the water in Plymouth Sound into which rivers and the sewage of a large town drains, is of particular interest, because it shows that plant growth in the rivers and estuary uses up most of the nitrate before it reaches the sea during the summer months. Table II shows that the enormous seasonal variation in the quantity of nitrate in the water of the Sound is not dependent upon the state of the tide although naturally influenced by it. The values throughout the year may all be slightly high, owing to ferruginous matter in suspension, but this does not affect the picture.

### TABLE II.

NITRATE CONTENT OF WATER IN PLYMOUTH SOUND.

| | | | Milligrams nitrate-$N_2$ per cubic metre. |
|---|---|---|---|
| 1925. | May 13 | at 1 hour after high water | (14) |
| | Aug. 31 | ,, low water | 9 |
| | Oct. 1 | ,, 5 hours after high water | 112 |
| | Nov. 11 | ,, 2 hours before high water | 176 |
| 1926. | March 11 | ,, $1\frac{1}{2}$ hours after high water | >190 |
| | April 10 | ,, low water | 135 |
| | May 17 | ,, high water | 11 |
| | July 8 | ,, 5 hours after high water | 24 |
| | Aug. 16 | ,, 1 hour before high water | 20 |
| | Sept. 22 | ,, 2 hours after high water | 17 |
| | Nov. 24 | ,, 2 hours after high water | >300 |
| | Dec. 13 | ,, 3 hours before high water | >250 |
| | Dec. 31 | ,, 5 hours before high water | 190 |
| 1927. | Feb. 15 | ,, 5 hours after high water | 100 |

An inspection of Table I, the table of which the latter is a continuation (*op. cit.*, **14**, p. 81), and of the data for phosphates in the inshore waters between September, 1923, and December, 1924, given in Table III, indicates that the effect of land drainage is not marked beyond a few miles offshore even during the winter months. It is masked by the large quantity of nutrient salts regenerated from dead organisms, which almost totally eclipses the quantity draining from the land into the broad waters of the English Channel.

## TABLE III.

MILLIGRAMS OF PHOSPHATE AS $P_2O_5$ PER CUBIC METRE IN THE SURFACE WATER AT VARYING DISTANCES OFFSHORE (ATKINS).

| In Plymouth Sound. | 2 miles S 21°W (true) from Plymouth Break-water. | Off Eddy-stone Light-house. | 19 miles S 21°W (true) from Plymouth Break-water. | 56½ miles S 21°W (true) from Plymouth Break-water. | Date. |
|---|---|---|---|---|---|
| 23 | 18 | 9 | 0 | — | Sept. 13, 1923. |
| 12 | 17 | 15 | 22 | — | Oct. 15, 1923. |
| 23 | 32 | 36 | 38 | — | Jan. 2, 1924. |
| 35 | 30 | 35 | 32 | 31 | Feb. 15, 1924. |
| 3 | 2 | 3 | 2½ | — | June 17, 1924. |
| 3 | 2 | 0 | 2½ | 4* | July 9, 1924. |
| 13½ | 8 | 1½ | 1½ | — | Aug. 7, 1924. |
| 28 | 28 | 15 | 12 | — | Sept. 3, 1924. |
| 19 | 21 | 33 | 14 | 12 | Nov. 12, 1924. |
| 35 | 35 | 33 | 32 | — | Dec. 9, 1924. |

* At 5 metres.

### NITRATE IN THE WATER OF THE ATLANTIC.

Samples collected from the surface in the tropical waters of the Atlantic in April were found to be poor in nitrate, as previously found in samples collected in September on the same route.

| Date collected. | Temperature. | Lat. | Long. | Nitrate-$N_2$ in milligrams per cubic metre. |
|---|---|---|---|---|
| April 16, 1926 | 27·4°C. | 0° 03′N. | 47° 00′W. | 3 |
| ,, 16 | 27·2°C. | 1° 27′N. | 45° 32′W. | 2 |
| ,, 17 | 26·1°C. | 6° 20′N. | 41° 18′W. | 3 |
| ,, 19 | 25·0°C. | 11° 08′N. | 37° 13′W. | 7 |
| ,, 20 | 23·6°C. | 17° 28′N. | 31° 36′W. | 3 |
| ,, 23 | 20·3°C. | 26° 52′N. | 22° 44′W. | 9 |

Samples from the west coast of Ireland, collected in August and analysed two months later, yielded the following results :—

Collected 17/8/26, at 50°34′N., 11°17′W.

| Depth. | Temperature. | Nitrate-$N_2$ in milligrams per cubic metre. |
|---|---|---|
| Surface | 17·1°C. | 9 |
| 100 metres | 11·13°C. | 170 |
| 770 metres | 9·18°C. | 180 |

Collected 12/8/26, at 49°20′N., 9°00′W.

| Depth. | Temperature. | Nitrate-$N_2$ in milligrams per cubic metre. |
|---|---|---|
| Surface | 18·25°C. | 84 |
| 146 metres | 10·26°C. | 110 |

## THE METHOD OF ESTIMATION.

The preparation of the reagent has proved to be somewhat capricious. A batch prepared in the manner described (*ibid.*, **14**, pp. 72–76) has sometimes been tinted pink owing to impurities in the reagents used, has sometimes developed a pink tint during storage, and an apparently satisfactory batch has sometimes given a yellowish pink tint on adding to sea-water poor in nitrate and proved unsuitable for quantitative estimation. The most generally satisfactory batches were made as follows: 0·5 gms. strychnine sulphate dissolved in 30 c.c. boiling distilled water were added to 4 square inches of amalgamated zinc foil (free from iron) in a shallow evaporating basin on an electrically heated water bath. 30 c.c. concentrated hydrochloric acid were run in, about 5 c.c. at a time, over a period of 6 hours. A little distilled water was also added from time to time, evaporation never proceeding quite to dryness. After removal of the remains of the zinc, and cooling, 200 c.c. of concentrated sulphuric acid was slowly poured in, stirred, and after the zinc sulphate had settled, the clear reagent poured off.

Although, from the numerous concordant results, it is apparent that the method gives good approximate values in dealing with water from the open sea and shows clearly the very considerable variations in nitrate content which occur from place to place and during the passage of the seasons, it appears that the values obtained in certain cases are low (in the bottom water at E1, in November, 1925, and probably again in 1926). For the examination of nitrate in inshore waters containing suspended particles of iron oxide the method is obviously unsuitable.

## SUMMARY.

1. Observations made subsequent to December, 1925, confirm the conclusion that the nitrates in the water of the English Channel, twenty-two miles south-west of Plymouth, are almost entirely utilised by phytoplankton in the summer, and are reformed in early autumn at a greater rate than they are utilised.

2. Movements of the water masses are shown to affect the quantity of nutrient salts available for phytoplankton in the waters immediately north of Ushant.

3. The effect of land drainage on the quantity of nitrate in the sea is not apparent beyond a few miles to seaward from Plymouth Sound, being masked by the nitrate which is regenerated from dead marine organisms.

4. The nitrate in the river and estuarine waters entering Plymouth Sound is nearly all utilised by plants in the rivers and estuaries themselves before reaching the open sea during summer.

# Seasonal Variations in the Phosphate and Silicate Content of Sea Water during 1926 and 1927 in Relation to the Phytoplankton Crop.

By

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Matthews (1916, 1917) was the first to observe that in early summer the surface water of the sea just outside Plymouth Breakwater is almost completely devoid of phosphate, owing to its utilization by algæ, fixed and planktonic. Brandt (1916–20) using Raben's (1916–20) analyses noted, in the Baltic especially, a minimum phosphate content in June, but this minimum was far from denoting complete exhaustion.

Later, Atkins (1923,'25,'26), using methods of analysis entirely different from those employed by Matthews or by Raben, obtained results in close agreement with those of Matthews, and showed that even twenty miles out to sea, at the International Hydrographic Station E1, the surface water was entirely deprived of phosphate in summer. As the season advanced the deeper water became at first very much poorer in phosphate and later on rather richer again, according as this salt was used up by the phytoplankton and then regenerated by the decay of animal and plant cells and by the excretion of animals. It was further shown by Atkins and Wilson (1927) that Brandt's curve did not indicate complete exhaustion of phosphate because the method of analysis employed included arsenic, originally present as arsenite, but oxidised to arsenate and precipitated with the phosphate. Reasons were adduced for the belief that the amount of arsenic present in the sea as arsenate is very minute and is all used up in summer by the algæ. It is doubtful whether any analyses yet made have distinguished the trace of arsenate, if indeed it exists, from phosphate.

Since the phosphate content of the various species of the phytoplankton, mainly diatoms, may be assumed to be similar, a study of the phosphate changes affords a measure, in an inverse ratio, of the production of the algal crop, and indicates from year to year the variations that occur in its seasonal waxing and waning. Such studies have shown that between the spring outbursts of activity as much as two months' difference may be noted in successive years. The variations observed here in the phosphate content showed a general correlation with the early spring daily sunshine average. When sunshine reached about three hours daily the increase in diatoms, as indicated by decrease in phosphate, became marked. Marshall and Orr (1927), however, found a remarkable constancy in the date of the vernal diatom outburst in the Clyde area. Their phosphate observations were checked by estimations of the diatom chains, a good agreement being found. They consider the length of the day, rather than the amount of sunshine, to be the most important factor. Working with a muffed glass receiving surface mounted over a photoelectric cell, Poole and Atkins (1926) found that in September—which may be considered as more or less comparable to April—the ratio of the reading with the cell exposed horizontally to full sunlight to that obtained when the direct rays of the sun were cut off, so that the cell received diffuse light only, was about 3·5 under clear conditions, falling to about two with weak sunlight and hazy or cloudy sky, so that the diffused light was high. These figures are not accurate measures of the ratio of total light to diffuse light, since the average obliquity of the diffuse light was not identical with that of the sun's rays, but it serves well as a comparison. It appears then that the effect of full sunshine is to raise the general illumination by three hundred or three hundred and fifty per cent with respect to a horizontal surface, and since a diatom may be considered as set at the most advantageous angle to the incident light the effect must be even greater. In any case an hour of direct sunlight is at least equivalent to two hours of the diffuse light of a sunny day, and it may be equivalent to three hours or more. On a grey day a specially dark cloud has been observed to reduce the general illumination to one-sixth within a period of three minutes, so it may be realized that it is not easy to correlate either sunshine or length of day with diatom growth, even assuming that the latter were to act as a reliable integrating agent. Ångström (1924), however, has found that the following formula fits in well* with the data obtained at Washington and Stockholm for daily sunshine, length of day and total solar radiation, direct or indirect.

Where S = the proportion of the actual to the possible hours of sunshine during the day,

$Q_o$ = the solar radiation corresponding to a perfectly clear day,

$Q_s$ = the solar radiation recorded at the place of observation (mean value for each month),

then $Q_s = Q_o\ (0{\cdot}25 + 0{\cdot}75\ S)$.

From the form of the equation it is clear that on a clear day (or month)

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* Haines (1925) found that the variation at Rothamsted was on the whole of the same order as that found by Ångström at Stockholm, but the general tendency was to give too low values at Rothamsted.

$Q_s = Q_o$, and the ratio S becomes unity; accordingly under these conditions the fact that the equation is a fairly good representation of the observed data shows that the diffuse radiation is one-third of the direct sunlight, for the figures inside the bracket are now unity. On the other hand, with a ten-hour day and one hour sunshine the relative values for diffuse and direct radiation become 0·25 and 0·075. With $3\frac{1}{3}$ hours of sunshine and a ten-hour day the diffuse and direct radiation become equal; with a twelve-hour day the ratio would be unity with four hours sunshine daily. It is more or less under these conditions, a ten–twelve-hour day—before the vernal equinox—and about three hours a day sunshine that the diatom outburst appears; so from the above considerations it seems that the sunshine effect, for the few hours it lasts, must be about equal to that of the diffuse radiation. Since the length of the day at the same season is, of course, the same from year to year it is to the sunshine effect* that one must look for the large amount of extra energy necessarily used up in the vernal diatom outburst, which may come earlier one year than another.

Three other factors, however, may affect the illumination to which the diatoms are exposed, though the factors are not necessarily or even probably unrelated. Firstly, the turbidity of the water in a given locality may vary at the same season in different years due to difference in plankton content or to suspended inorganic matter, whether occasioned by a variation in currents or to stirring up of bottom deposits. Secondly, the amount of light reflected at the surface may vary, photoelectric measurements having shown that on a calm day with glassy surface as little as five per cent is lost at the water surface, whereas with a wind causing waves to break the loss may amount to thirty-one per cent and doubtless to more under stormy conditions. Thirdly, since diatoms multiply by continued doubling when under suitable conditions as regards illumination, nutrient salts and temperature, it is clear that, starting with a small number of diatoms some time must elapse before any depletion of phosphate can be detected. Assuming for simplicity that the doubling occupies one day under certain conditions, and that at the detectable limit, 1 mg. per cubic metre of phosphate, reckoned as $P_2O_5$, is used up in one day. The next day 2 mg. will be used, then 4, 8, 16 in the succeeding days, so that in five days 31 mg. would have been consumed, namely, the surface water would have been reduced from its winter maximum of 36–40 mg. down to 5–9 mg. Such a rapid falling off, within a month or even probably a fortnight—possibly less—has been observed. The fall taking place in a fortnight would correspond to a doubling in three days. If, however, when the diatoms have reached

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* It is of course obvious that the energy received on earth from one hour's sunshine depends both on the time of the day and upon the season.

the 1 mg. per day (or per three days) stage in the surface metre under good illumination, stormy weather ensues, with, we will suppose, the result that the water mass—which in spring is isothermal—becomes well mixed to a considerable depth, it is obvious that the number of diatoms at the surface will have become reduced far below the detectable limit of action. If the water has been thoroughly mixed to 16 metres the average number of diatoms will have been reduced to one-sixteenth, and when good lighting conditions are restored at the surface at least five days—on the one-day doubling rate, or fifteen on the three-day rate—must elapse before the detectable limit of phosphate consumption is again reached. It might be supposed accordingly that in calm weather a diatom outburst could take place under conditions of illumination inadequate when stormy.

In order to test this hypothesis the meteorological records for Plymouth (Cattewater) were examined for the periods in 1923–1925, during which the vernal diatom outbursts were most marked. Table 1 shows the velocity of the wind, on the Beaufort Scale (0–12), on which three denotes 8–12 statute miles per hour, four 13–18, five 19–24, six 25–31, and seven 32–38. No records above seven were found during the periods. Our vessel, the *Salpa*, has carried out hydrographic work at Station E1 with wind five on the scale. It is at once obvious that there is no connection between the date of the outburst and the average value for the wind. Neither can any correlation be made out between the date of the outburst and the delaying action of strong winds—over five on the scale. Since wind from the southerly sector, between east and west, inclusive, is more potent at E1 in bringing about a heavy sea than is wind from the northerly sector the percentages of the total observations with south sector winds are shown in column 6, and the percentage of strong south sector winds in column 7. The only relation that may possibly be made

TABLE 1.

SHOWING PHOSPHATE CONSUMPTION AS MILLIGRAMS $P_2O_5$ PER $M^3$. IN THE SURFACE WATER AT STATION E1, AND THE STRENGTH AND DIRECTION OF THE WIND FROM PLYMOUTH RECORDS.

| | | | | Percentages of total observations. | | |
|---|---|---|---|---|---|---|
| Year. | Period. | Phosphate consumption. | Beaufort Scale. | Wind 5 or over. | Wind in S sector. | Wind in S sector 5 or over. |
| 1923 | Mar. 7th–Apl. 24th | 13 | 3·3 | 14 | 65 | 10 |
| ,, | Apl. 25th–May 22nd | 21 | 3·7 | 36 | 60 | 18 |
| 1924 | Feb. 16th–Mar. 10th | 20 | 3·5 | 29 | 38 | 19 |
| 1925 | Mar. 15th–Apl. 22nd | 22 | 3·6 | 23 | 58 | 14 |

out is that in 1924, when the outburst came very early, north sector winds predominated, though within the same period rough weather from the south was at its highest with 19 per cent five or over. The relation works back to the sunny weather and clear skies associated with northerly winds. The results of this comparison show that at an open station, such as E1, the strength of the wind is not a factor of any importance in bringing about differences in the dates of the vernal diatom outbursts. It cannot accordingly be effective in mixing the water in the manner supposed so as to carry down the diatoms into regions of inadequate illumination; it may be remarked that the light that does penetrate into the water is about halved at 5 metres depth at E1. The agreement between the sunshine record and the diatom outburst dates still seems to indicate that direct sunlight with the general good lighting conditions that accompany it is the one factor most potent in bringing about diatom multiplication in open water rich in nutrient salts. The sunshine records are shown in Fig. 5 (Atkins, 1926, Phosphate III). It may be explained that the concluding sentence of the legend under Fig. 5 should be deleted, as it belongs to the legend of Fig. 3 and has been repeated in error. For the present, therefore, no explanation can be given of the discrepancy between the E1 results and those for the Clyde area, where the length of the day appears to control the date of the vernal diatom outburst (Marshall and Orr, Fig. 9). Wind and tide are admittedly effective in their area as regards vertical mixing, but that hardly makes the solution of the problem any easier. Herdman, Scott, and Dakin (1910) have also correlated the early spring sunshine with the diatom outburst at Port Erin, 1907 having an unusually early diatom crop following, with a lag, a high value for February sunshine.

In autumn the surface cooling sets up convection currents and produces a very thorough mixing of the water. While this is in progress diatoms multiplying near the surface will be carried down into regions of lesser illumination, so it is unlikely that an outburst will occur till after the water has become isothermal.

Data already presented (Atkins, 1926, 1 and 2; Harvey, 1926) have traced the changes in silicate, phosphate and nitrate over periods of one or more years. The results now published extend these, and an attempt is being made to correlate the variations in these minor constituents of sea-water, which are of special importance to the phytoplankton.

## SEASONAL CHANGES IN PHOSPHATE AND SILICATE CONCENTRATION.

The data recorded in Table 2 merely confirm previous results as to the generally insignificant effect of land drainage upon phosphate content, though at L1, under the Laboratory, an occasional high value is found.

This series has been discontinued, save for the surface and bottom (40 m.) observations at L4, half-way between Rame Head and the Eddystone. Here, as at E1, during the autumn and early winter the surface values are sometimes in excess of the bottom, due apparently to regeneration of phosphate from bodies either floating or suspended in the upper layers. No corresponding silicate estimations were made, as it had already been shown that there was a fairly steep gradient from the Sound to L4 or sometimes to E1, from which on to E3 (Ushant) there was but little change.

In Table 3 are shown the seasonal changes in phosphate and silicate, also the temperatures for 1926 to March 1927, from which time the analyses were discontinued on account of illness. The phosphate series had been unbroken from March 1923, for four years. In 1926 a rapid fall in phosphate, extending to the bottom, took place at the end of March or early in April, rather earlier than in 1925, and going deeper, rather later than in 1924, though deeper than then also ; 1923 was a very late year since the fall did not occur till May. The results are plotted in Fig. 1 for the upper 5 m., and Fig. 2 (of the accompanying paper by H. W. Harvey, *Journ. Mar. Biol. Assoc.*, Vol. XV, p. 186) for the bottom, 70 m., together with those for nitrate, and are further discussed together with the nitrate analyses in Harvey's paper.

The silica analyses for E1 were all carried out upon water collected in large bottles coated internally with paraffin wax to meet the haunting suspicion that an occasional high result might be due to silicate from the bottle. A number of other results were obtained, using water from the ordinary green glass spring clip milk bottles in vogue for sea-water samples in general. These gave no reason for thinking that their use was illegitimate for short periods of storage—a conclusion reached before (Atkins, 1923). However, the waxed bottles provide a large sample conveniently and with absolute certainty that storage can add no silica save in so far as suspended matter may dissolve.

It must be pointed out, however, that these waxed bottles are not suitable for water destined for the analysis of phosphate, but they may give results in perfect accord—if the bottle has been freshly waxed it seems. Thus values such as 26 in glass, 26 in wax, and 20 in glass, 19 in wax were obtained in two comparisons. The waxed bottles usually, however, give lower results, such as 32 in glass, 25 and again 25 in wax. Two possibilities presented themselves, firstly that the uncoated bottles had contained floating matter rich in phosphate or had been accidentally contaminated—but the consistence with which such high values appeared only in the uncoated bottles ruled this out in time ; secondly, that the large waxed bottles, which usually had one sample standing in them till taken to sea for another, afforded a resting-place for moulds which,

## TABLE 2.

Phosphate Content of Surface Samples (also 40 M. for L4) at Stations from the Laboratory to E1 from Feb., 1926–March, 1927, expressed as Mg. per $M^3$. of $P_2O_5$. "A" indicates date on which the Analyses were made.

| | Feb. 3rd. | Mar. 11th. | Apl. 10th. | May 17th. | June 24th. | July 8th. | Aug. 16th. | Sept. 22nd. | Oct. 19th. | Nov. 24th. | Dec. 14th. | Dec. 31st. | Feb. 15th. | Mar. 21st. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| L1 | 38 | — | — | — | — | — | 100 | — | — | — | — | — | — | — |
| L2 | — | — | — | — | — | — | 29 | — | — | — | — | — | — | — |
| L3 | 33 | — | — | — | 7 | — | 24 | — | — | — | — | — | — | — |
| L4 | 39 | 25* | — | 9* | 5 | — | 10 | 17 | 29 | 43 | 32 | 34 | 52 | 25 |
| L40 m. | 33 | 40 | — | 12 | 30 | — | 8 | 11 | 17 | 19 | 33 | 22 | 31 | 28 |
| L5 | 33 | — | — | — | 4 | — | 28 | 22 | 27 | 26 | — | — | — | — |
| L6 | — | — | — | 7 | — | — | 2 | 14 | 36 | — | — | — | — | — |
| E1 | 30 | 25 | 10* | 5 | 4 | 7 | 0 | 15 | 26 | 41 | 32 | 27 | 24 | 25 |
| A | 5/2 | 13/3 | 26/4 | 19/5 | 25/6 | 13/7 | 18/8 | 4/10 | 20/10 | 26/11 | 15/12 | 3/1/27 | 24/2 | 22/3 |

## TABLE 3.

Station E1, February 1926–March 1927. Phosphate as $P_2O_5$ and Silicate as $SiO_2$, in Milligrams per Cubic Metre. The values for Silica are only shown for 0 and 70 M. "A" indicates the date on which the Analyses immediately above were made. Temperatures are shown at the bottom of the Table.

| M | Feb. 3rd. | Mar. 11th. | Apl. 10th. | May 17th. | June 24th. | July 8th. | Aug. 16th. | Sept. 22nd. | Oct. 19th. | Nov. 24th. | Dec. 13th. | Dec. 31st. | Feb. 15th. | Mar. 21st. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 30 | 25* | 10* | 5* | 4 | 7 | 0 | 15 | 26 | 41 | 32 | 27 | 24 | 41 |
| 5 | 34 | 39 | — | 12 | 10 | 4 | 0 | 5 | 17 | 24 | 30 | 23 | 28 | 27 |
| 10 | 33 | 35 | — | — | 10 | 4 | 0 | 0 | — | — | 25 | — | — | — |
| 15 | — | 37 | — | 12 | 11 | 7 | 2 | 0 | — | — | — | — | — | — |
| 20 | — | — | — | — | 12 | 11 | 14 | 1 | — | — | — | — | — | — |
| 25 | — | 39 | — | 12 | 17 | 13 | 14 | 15 | 17 | — | 29 | 20 | — | 28 |
| 30 | — | — | — | — | 20 | — | — | 13 | — | — | — | — | — | — |
| 50 | — | 37 | — | 14 | — | 12 | 14 | 10 | — | — | 29 | — | — | — |
| 70 | 33 | 37 | 9 | 15 | 23 | 12 | 13 | 9 | 20 | 26 | 27 | 22 | 28 | 30 |
| A | 5th | 13th | 26th | 19th | 25th | 13th | 18th | 1st | 20th | 26th | 15th | 3rd | 24th | 22nd |
| 0 | 175 | 80 | — | 40 | 55 | 75 | 36 | 70 | 94 | 263 | 168 | 104 | 260 | 144 |
| 70 | — | 90 | — | 40 | 55 | — | 44 | 130 | 108 | 134 | 168 | 104 | 260 | 250 |
| A | 6th | 14th | — | 20th | 28th | 14th | 18th | 6th | 21st | 27th | 17th | 4th | 3rd | 24th |
| 0 | 9·5 | 9·5 | 10·2 | 10·9 | 14·3 | 16·9 | 17·1 | 16·7 | 14·4 | 12·2 | 11·7 | 10·3 | 9·4 | 9·4 |
| 70 | 9·4 | 9·4 | 9·6 | 10·5 | 11·3 | 11·8 | 12·6 | 13·5 | 14·5 | 12·2 | 11·7 | 10·3 | 9·4 | 9·0 |

* All values for phosphate in March, April and May may be too high, as the standard had deteriorated and the correction applied is only an approximation. The figures for each month are, however, consistent among themselves.

owing to the wax, could not be seen. Evidence in support of the mould theory was afforded when the sample, which had previously given 25 mg. per m$^3$. twice, was shaken up and again analysed when the values 16 and 15 were obtained, showing clearly that phosphate had been removed from the lower portion of the bottle to a greater extent than from the top—yet this sample had only stood one day. The moulds were, of course, already developed, and had remained over from the previous contents of the bottle. Such growths have been clearly seen in uncoated bottles allowed to stand, and the risk of getting low results owing to moulds was pointed out by Matthews as a reason for analysing freshly drawn samples. The wax, however, appears to afford an anchorage for these growths. A third possibility, that the glass gave off phosphate, was tested at the start of the phosphate work and was negatived—nevertheless one batch of white soda glass bottles sent here for the analysis of sea-water samples did give off a little on prolonged standing. The changes in phosphate content of water stored for an appreciable time have recently (1927) been studied by Gill, but the discrepancies noted between the waxed and unwaxed bottles were obtained with samples within one or two days of their collection. That the silicate results are unaffected, whereas the phosphate results are too low, is due to the fact that the moulds take up no silicate. This leads on to a point of importance, the comparison of the seasonal changes in silicate and in phosphate. Neither the Phæocystis outburst nor those of species of Dinoflagellates result in a diminution of silicate, though phosphate is taken up. It is accordingly not surprising to note that there are discrepancies between the silicate and phosphate curves. Moreover, the silicate winter maximum varies from year to year far more than does the phosphate ; thus for the former the following maxima were obtained : 1923–'24, 200 mg. per m$^3$. ; 1924–'25, 240 mg. ; 1925–'26, 175 mg. ; 1926–'27, 260 mg. for the surface water at E1 ; for phosphate the corresponding values were : March, 1923, 36 mg. ; 1923–'24, 38 mg. ; then 33, 40, and 32 respectively, neglecting a high surface value where the water was not homogeneous. Moreover, a high silicate year, 1926–'27, 260 mg. may be a low phosphate year, 32 mg. As shown by salinity results and by the silicate analyses previously given (1926), water at E1 is but little affected by the outflow from the rivers flowing into Plymouth Sound. That enrichment from fresh water has nothing to do with these high values for silicate at E1 is shown by the fact that the surface value of November 24th, 1926, was 263 mg., the bottom 134 mg., yet the respective salinities were 35·26 and 35·28 $^\circ/_{\circ\circ}$. On February 15th silica, after falling to 104 on December 31st, had risen to 260 at surface and bottom, the respective salinities being 35·37 and 35·32 $^\circ/_{\circ\circ}$. There is perhaps some indication that water of high salinity may also be high in silicate, for a 10-metre sample from E2 on November 24th had 144 mg. and 35·21 °/₀₀, the values for E3 at the same time and depth being 379 mg. and 35·31 °/₀₀. On the whole it must be concluded that no entirely satisfactory explanation can be reached as to the large variations in silicate shown by successive yearly maxima. The data available reveal a reasonably close correspondence between the vernal decrease in silicate and in phosphate, but in 1925 and to a lesser extent in 1926 silicate rose again in July, whereas phosphate remained low. The plotting of the silicate results beside those of phosphate and nitrate brings out the similarities and the differences between the behaviour of silicate and of the other two, between which the similarities largely predominate. In order, however, not to confuse the representation of the phosphate and nitrate analyses the silicate data have been omitted from the figures in the accompanying paper by Harvey. It is hoped that further work may afford an insight into the causes of the peculiar behaviour of the silicate.

In Table 4 are shown the phosphate analyses from four cruises to Ushant, also the surface and bottom temperatures. Perhaps the most striking result is the removal of phosphate from the surface water between E1 and E3, the E2 value being zero, although at 5 m. it was 28 mg. per m$^3$. By May, however, E1 has experienced an outburst of phytoplankton, resulting in a large fall in phosphate extending to the bottom; the accompanying rise in temperature shows that the water has undergone mixing. E2, however, has risen, and E3 is higher again; this may indicate an influx of phosphate rich water—the nitrate values obtained by Harvey undoubtedly do—but owing to the uncertainty of the correction for the deterioration in the standard solution, which unfortunately affected these results, too much reliance cannot be placed upon them. Since, however, in March the phosphate content at E2 was almost identical with that at E3 the differences noted in May do seem to indicate enrichment from an external source. Two very curious results were obtained in the July series, namely, 3 mg. at E2 bottom and 12 mg. at E3, with much higher values above. One is loath to attribute two unexpected results to analytical error, especially when they both happen to be bottom samples; but the nitrate gradient as found by Harvey was normal, and the salinity results show an almost isohaline column at the two stations, that for E2 (and E1) being slightly under 35·1, that for E3 over 35·3 °/₀₀.

Table 5 records the phosphate content of deep water off the south-west coast of Ireland. For these samples and the temperature readings the author is indebted to Mr. G. P. Farran.

## TABLE 4.

Phosphate as $P_2O_5$ in Milligrams per Cubic Metre on the Plymouth–Ushant Line. "A" indicates the date on which the Analyses immediately above were made. Temperatures are shown at the bottom of the Table, B denoting greatest depth.

|  | 11th of March, 1926. |  |  |  |  | 17th of May. |  |  |  |  | 8th of July. |  |  |  |  | 24th of November. |  |  | 15th of Feb., 1927. |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| m. | E1 | Mid. | E2 | Mid. | E3 | E1 | Mid. | E2 | Mid. | E3 | E1 | Mid. | E2 | Mid. | E3 | E1 | E2 | E3 | E1 | E2 | E3 |
| 0 | 25† | 11 | 0 | 5 | 7 | 5† | 14 | 27 | 42 | 41 | 7 | 25 | 11 | 4 | 12 | 28 | 30 | 20 | 24 | 13 | 24 |
| 5 | 39 | – | 28‡ | – | 28 | 12 | – | 21 | – | 30 | 4 | – | 4 | – | 12 | 24 | 23 | 20 | 28 | 29 | 24 |
| 10 | 35 | – | 28 | – | 28 | – | – | 22 | – | 30 | 4 | – | 6 | – | 17 | – | – | – | – | – | – |
| 15 | 37 | – | – | – | – | 12 | – | – | – | 32 | 7 | – | 11 | – | 17 | – | – | – | – | – | – |
| 20 | – | – | – | – | – | – | – | – | – | – | 11 | – | 20 | – | – | – | – | – | – | – | – |
| 25 | 39 | – | – | – | – | 12 | – | 22 | – | 36 | 13 | – | 29 | – | 20 | – | – | – | – | – | – |
| 30 | – | – | – | – | – | – | – | – | – | – | – | – | 30 | – | – | – | – | – | – | – | – |
| 50 | 37 | – | – | – | – | 14 | – | 22 | – | – | 12 | – | 24 | – | 20 | – | – | – | – | – | – |
| 70 | 37 | – | – | – | 29 | 15 | – | – | – | – | 12 | – | 24 | – | 21 | 26 | – | – | 28 | – | – |
| 90 | * | – | 28 | – | – | * | – | 24 | – | – | * | – | 3 | – | – | * | 22 | – | * | 29 | – |
| 110 | * | * | * | * | 29 | * | * | * | * | 34 | * | * | * | * | 12 | * | * | 20 | * | * | 24 |
| A | 13/3 | do. | do. | do. | do. | 19/5 | do. | do. | do. | do. | 13/7 | do. | do. | do. | do. | 26/11 | do. | do. | 24/2 | do. | do. |
| 0 | 9·5 | 9·8 | 10·4 | 10·3 | 10·3 | 10·9 | 11·3 | 11·1 | 11·7 | 11·4 | 16·9 | 17·2 | 16·9 | 17·4 | 14·5 | 12·2 | 12·0 | 12·2 | 9·4 | 9·8 | 10·0 |
| B | 9·4 | – | 10·0 | – | 10·3 | 10·5 | – | 10·8 | – | 11·1 | 11·8 | – | 12·2 | – | 12·3 | 12·2 | 12·0 | 12·3 | 9·4 | 9·8 | 10 1 |

† As previously noted, values for March and May may be high.
Mid. = midway sample.
‡ Temp. = 10·1°.
* Indicates bottom has been reached before depth shown.

## TABLE 5.

Phosphate as $P_2O_5$ in Milligrams per Cubic Metre and Temperature off the S.W. Coast of Ireland at 50°34′, 11°17′W., and 49°20′N., 9°00′W. respectively. "A" denotes date on which Analysis was performed.

| | Aug. 17th, '26. | | Feb. 19th, '27. | | | Aug. 12th, '26. | | Feb. 18th, '27. | |
|---|---|---|---|---|---|---|---|---|---|
| m. | t° | $P_2O_5$ | t° | $P_2O_5$ | m. | t° | $P_2O_5$ | t° | $P_2O_5$ |
| 0 | 17·1 | 0 | 10·7 | 24 | 0 | 18·2 | 0 | 10·0 | 16 |
| 100 | 11·1 | 38 | — | — | 141 | — | — | 9·9 | 27 |
| 402 | — | — | 10·5 | 38 | 146 | 10·9 | 35 | — | — |
| 768 | 9·2 | 51 | — | — | * | * | * | * | * |
| 860 | — | — | 9·3 | 48 | | | | | |
| A | — | 4/10 | — | 3/3 | A | — | 4/10 | — | 3/3 |

The analyses show clearly that the deep water is very well supplied with phosphate, and more so in summer than in winter when the equalisation of temperature points to mixing with the surface water, the latter being thereby enriched. The figures are probably subject to some error due to storage, but not enough to invalidate the conclusions. The complete removal of phosphate from the surface water in summer is noteworthy. Harvey, in his nitrate paper, records 9 mg. nitrate nitrogen per m$^3$. for the deep-water station in August and 84 mg. for the corresponding surface sample in the shallower station, so in these waters nitrate appears to be in excess of phosphate. The phosphate results are quite in accord with those for 1924 (Atkins, 1925, Table 13) and for 1925 (1926, Table 10) for the same region.

## TABLE 6.

Phosphate as $P_2O_5$ in Milligrams per m$^3$. in the Atlantic, Para to Liverpool route, Surface Samples taken by R.M.S. *Hildebrand* during 1926–'27. "A" denotes date on which Analyses were performed. The Figures are Averages between the Latitudes and Longitudes given.

| Lat. N. | Long. W. | Apl. 16th–29th. | June 24th–July 8th. | Aug. 19th–Sept. 2nd. | Dec. 24th–Jan. 6th. |
|---|---|---|---|---|---|
| 0°–5° | 47°–43° | 11 | 23 | 17 | 6 |
| 5°–15° | 43°–34° | 19 | 16 | 3 | 3 |
| 15°–25° | 34°–24° | 16 | 17 | 9 | 3 |
| 25°–35° | 24°–14° | 12 | 7 | 6 | 3 |
| 35°–48° | 14°–7° | 23 | 3 | 9 | 5 |
| Mean of all | | 16 | 12 | 8 | 4 |
| No. analysed | | 21 | 18 | 17 | 14 |
| | A | 21/5 | 20/7 | 4/10 | 17/1 |

Table 6, which is a continuation of Table 12 (1926) recording results for 1925, shows the values obtained for surface samples on the Para–Liverpool route. The analyses are subject to an unknown storage error, but seem to indicate that the highest values occur in April, especially near the eastern end, but in June at the western end. The lowest values were found in August and December. On the whole the results are higher than for 1925.

## THE ESTIMATION OF PHOSPHATE IN SEA-WATER.

The method of Denigès, which has been in use in this laboratory since 1923, has recently been compared with other methods involving the use of organic reducing agents instead of stannous chloride. The conclusion was reached (Atkins and Wilson, 1926) that in delicacy and rapidity Denigès' method was superior to the others. Trouble due to the appearance of a yellow tint, converting the clear blue of the reduced phosphomolybdate into a greenish colour, has been reported. The remedy for this consists in adding only one drop of the stannous chloride reagent instead of five. The method has been criticised on the score that the measurement of the stannous chloride by drops is not an exact measure, also that as ordinarily made up the strength of the latter is only roughly constant, about 0·1 grm. of tin dissolved and made up to 10 cubic centimetres. With the quantities of phosphate found in natural waters the addition of one drop of this reagent means that a very large excess is present, so that the ratio of phosphate to reagent is quite unaffected, for practical purposes, by any such variation in the strength of the reagent. The method standardised in Meyerhof's laboratory (Lohmann and Jendrassik, 1926) in which eikonogen, suitably purified, is used as the reducing agent has not been tried for sea-water, because the necessity of boiling the water for five minutes would add too greatly to the time required for dealing with large numbers of samples in view of the fact that Denigès' method has been found reliable and rapid. It may here be noted that Wattenberg (1926) attributes the method to E. G. Moberg, who appears to have used it in the Pacific some years after Denigès' papers led to the method being used elsewhere for sea-water.

## THE ESTIMATION OF SILICATE IN SEA-WATER.

The colorimetric method of Diénert and Wandenbulcke (1923) was used, adding 2 c.c. of ten per cent ammonium molybdate, followed by four drops of fifty per cent (by volume) sulphuric acid to 100 c.c. of sea-water. The limit detectable is close to 0·04 mg. per litre $SiO_2$. Though this is so, above the detectable limit much smaller differences than 0·04 can be distinguished. Thus a value 0·094 mg. p.l. or 94 mg. per $m^3$.

was obtained for a surface sample and 108 mg. for a bottom sample. To make sure that the difference was a real one the colorimeter column was altered, and it was found that a reading 100 mg. was definitely too light, 128 was clearly too high, 120 was a near match, but too high. The value first found, 108, was therefore correct, and a difference of 10 mg. per m$^3$., or 0·01 mg. p.l., can be distinguished. This is only about one-tenth the delicacy of the Denigès' phosphate reaction.

In order to see whether exceptionally high phosphate values could affect the accuracy of the silicate estimations a solution of $KH_2PO_4$ equivalent to 100 mg. p.l. $P_2O_5$ was analysed as if it were silicate; the yellow tint it gave was only equivalent to 0·3 mg. p.l. $SiO_2$. As the solution of phosphate taken was over 2000 times as concentrated as is sea-water with respect to this salt, it is obvious that its presence is quite without effect upon silica estimations.

## SUMMARY.

1. A comparison of the strength of the wind, Beaufort Scale, and of its direction during the periods when the vernal diatom outburst caused phosphate depletion of the surface water, has failed to indicate that there is any connection between either strength or direction and the date of the outburst. The spring sunshine still appears to be the important factor at E1.

2. The sequence of the years studied as regards the main spring diatom outburst deduced from phosphate depletion at Station E1 is as follows: 1924, early March; 1926, late March to early April; 1925, early April; 1923, early May.

3. Phosphate regeneration may take place at or near the surface more rapidly than at the intermediate depths. The bottom is the most important source of phosphate, but its regeneration throughout the whole water column takes place to a lesser extent.

4. In 1926 the surface water at the mid-Channel station, E2, had become completely void of phosphate by March 11th, while this salt was still abundant at E1 and not exhausted at E3. A diatom outburst need not therefore originate near the coast, but may take place where local conditions are favourable.

5. Waxed bottles, used for storing water for silicate analysis, may harbour moulds which rapidly reduce the phosphate content of the water sample.

6. The vernal fall in phosphate and in silicate shows good agreement, but a summer rise in silicate has been observed while phosphate has

remained low. Since Phæocystis and the Peridineæ take up no silicate the two radicles should only vary together when diatoms are the main constituent of the phytoplankton.

7. There is a considerable difference between the yearly maxima for silicate at E1, and a high silicate year may be a low phosphate year; the variations in the latter are, however, less.

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# The Relationship between State of Maturity and Chemical Composition of the Whiting, *Gadus merlangus* L.

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With 2 Figures in the Text.

THIS research was undertaken at the instigation of Mr. E. Ford, who, during other investigations, had noticed great fluctuations in the relative size of the liver in the whiting. It is likely that the results obtained are representative of gadoids generally, when subject to similar conditions. In an account of the Irish Sea Cod Fishery, 1921–3, by Johnstone, Smith and Fleming (**1**), a series of analyses are given, which, though showing wide variation, indicate that there is no seasonal variation in the composition of the Manx cod—contrary to the authors' expectations. There are in addition, several accurate, detailed descriptions of correlated tissue changes in other fishes, notably the herring, salmon and eel, and it should be economically valuable to have a similar record of all the staple food fishes.

For the whiting, such a study needs more preliminary data than are at present available.

Age determination in this species, by means of scales, has, in these waters, been found difficult, though in Icelandic waters, where there is a very well marked bi-annual seasonal change of conditions, it is, according to Saemundsson (**2**), quite possible. In the present investigation it has not been attempted.

The effect of food at different stages of digestion is another unknown factor exerting probably a large influence, and requiring a systematic enquiry. Whiting have usually the habit of ejecting the whole of their stomach contents, when caught in the trawl, and it is difficult to get an accurate idea of the food they may have recently consumed. When any food was found present, its amount and nature was noted. (See Appendix to Table 4, p. 218).

Lastly, so far as I know, no one has given a description of the developmental changes in the ripening gonads. I have therefore drawn up the following arbitrary scheme of the various stages, which agrees very closely with that given by Graham (**3**) for the Cod.

## DEFINITIONS OF MATURITY STAGES.

(a) *Females.*

As in the cod, a classification can be drawn up based mainly on changes in colour of the ovary. The following stages have been adopted :—

I. Immature fish. Ovaries not more than 2·5 cm. × 0·5 cm.—frequently a narrow ribbon, only with difficulty to be distinguished from testis in a similar stage. Eggs microscopic. Colour, whitish or pinkish : becomes orange before maturing.

II. Mature fish, in normal resting condition, after complete recovery from previous spawning (if any). Ovaries approximately 5 cm. × 1 cm. Eggs microscopic. Colour, dull to bright orange.

IIA. "Spents." Ovaries pinkish white, flaccid, shrunken, with perhaps a few undischarged, degenerating eggs.

III. Mature fish, ripening. Ovaries enlarging, not less than 5 cm. × 1 cm. Eggs visible to the naked eye : opaque. Colour, buff, pinkish-buff, or flesh.

IV. Ovaries much enlarged and distended—almost ripe. Eggs nearly all transparent. Colour, dark to light cream.

V. Spawning fish. No examples obtained.

(b) *Males.*

These are far more difficult to classify than the females.

I. Immature fish. Testes very minute ; a very thin, narrow translucent, whitish ribbon. Invariably characteristic of fish in the first year of life, and of older fishes not previously spawned or approaching spawning.

II. Mature fish in normal resting condition. Testes slightly lobed and only lightly coiled : much less translucent than I., with a few opaque, whitish patches.

IIA. "Spents." Indistinguishable from II., and therefore not used in practice.

III. Mature fish ripening. Testes more pronounced, more strongly coiled, and lobes fatter. Colour mainly opaque-white. Rarely less than 5 cm. × 1·25 cm.

IV. Testes strongly lobed and much convoluted, with a completely opaque, milky-white appearance.

V. Spawning. Milt running. No examples obtained.

## PREPARATION OF MATERIAL.

The fish used were caught off Plymouth by the Research Steamer *Salpa*, landed usually between 3.0 p.m. and 5.0 p.m., and brought at once to the chemical laboratory. If a large number of fish were landed, an adequate sample was taken of the various sizes represented, whilst if a small collection only was obtained, the whole was utilised.

The fish were wiped free from all adherent moisture and slime, immediately measured, and weighed. The livers and gonads were dissected out, freed from superficial body fluid and blood by means of blotting-paper, and weighed at once. For the analysis of the flesh, the whole of one side of the fish was used, after separating the muscle substance from the vertebral column and skin. Except in the very largest fish, the full amount of this flesh was used, so that there is no question of errors in sampling—even supposing these to be significant in flesh so homogeneous as that of the whiting.

Fish of similar size and like state of maturity were picked out from the sample and grouped together in the manner shown in Table 4. The analyses of liver and flesh were made upon each group of fish, taken collectively, and treated as one.

## METHODS OF ANALYSIS.

These need not be given in detail, as they differed little from standard practice, but a few notes are necessary.

*Water.* The weighed portions, representing usually 15–20 grms., but frequently more or less, were dried in tared beakers at 100°C. to a constant weight. This required from 36 to 48 hours—muscular tissue requiring much less time than the liver. The loss of weight was checked by weighing the solids after extraction with ether.

*Fat.* The quantity remaining after drying was extracted with 250 c.c. anhydrous ether in a 100 c.c. Soxhlet extraction apparatus for 6 to 8 hours. The ether was distilled off from the ethereal extract and the residue dried at 100°C. in a current of dry $CO_2$ to a constant weight, taking the usual precautions. The error arising from oxidation, though by no means negligible in accurate work, is sufficiently small to be neglected here, in view of the errors inherent in sampling fresh tissues.

*Protein.* This is here regarded as total nitrogen × 6·25.

The Kjeldahl-Gunning method was followed with only minor variations. Estimations were made on 0·2 or 0·5 grm. of the dried, fat-free material remaining after the drying and subsequent extraction with ether.

Several workers on biological problems have doubted the validity of the factor 6·25, when applied to fish protein, though their views are very conflicting. Atwater, Johnstone, Bruce (**4**) and others contribute to the discussion. The factor 6·25 is used here, however, in the belief that it is sufficiently correct for our purpose, and it must be stated that most of the arguments put forward against its use are not very convincing. For instance, in the *Report of the Lancashire Sea Fisheries Laboratory*, Vol. 37, page 120, it is regarded as too high, on the ground that the totals, " water, fat, ash and proteid (N. × 6·25)," came to considerably more than 100%, when it would be much more reasonable to cast doubt on the larger variables, water and fat.

Bruce (**4**), on the other hand, mentions that there is some uncertainty about the application of the factor 6·25, in the conversion of total nitrogen into *fish* protein, but does not deal with it from the point of view of protein constitution, which is the real issue.

In using carbon tetrachloride for the extraction of fats, some proteid matter is carried through, and he mainly confines his discussion to the correction of this loss. With the use of this fat-solvent and his procedure, which is similar to Johnstone's, he therefore suggests a higher factor. The remedy would be the use of a different fat-solvent : e.g. ether.

Plimmer (**5**), however, states that this conversion factor is correct, or nearly so, for the proteins of the muscular tissue of fishes, but not for those derived from other sources. Until it is known what proteins are present in the livers and tissues of the fishes concerned, it seems futile to argue about the bearing of unexpected analytical results on the application of this factor for the conversion of total nitrogen into fish protein. This is particularly so with the herring, in view of the possibility that clupein, whose percentage of nitrogen is 31·68, and which is normally found in ripe sperms, may be present in other parts. Likewise, in any fish, the presence of protamines would necessitate a change in the factor.

*Ash.* Non-volatile mineral matter left on ignition of the dried, fat-free material at bright red heat.

*Carbohydrates.* These were not estimated, owing to the impossibility of carrying out large numbers of estimations in the time available. It is probable that the " undetermined " is mainly carbohydrates, though this has not been confirmed. Accepting this as true for practical purposes, it would seem that the amount in the liver varies more or less haphazardly, and, as suggested by Kilburn and Macleod (**6**), very likely varies with the season, feeding conditions, and possibly with many other factors.

## THE RESULTS.

The results are expressed in the form of a comprehensive table (Table 4, p. 216), which includes all the relevant information : males, females, and " very small " fish being separately treated. Besides the material there presented, the relationships of length and weight of fish respectively to weight of liver were also worked out; in both cases the correlation is very slight. Neither is there any strong relationship between the ratio $\frac{\text{weight of fish}}{\text{weight of liver}}$ and the state of maturity.

The results in the whiting thus agree with those in the cod—although Graham (**3**) argues, albeit with insufficient data, that an increase in the value of K, the "condition constant" of the fish, should in general be accompanied by an increase in the "condition constant" of the liver, i.e.—100 × wt. of liver : length of fish$^3$.

The main point of interest that the results show, however, is that whereas in the trade category "fatty" fish, salmon, herring, etc., most of the material necessary for gonad formation seems to be derived from the longitudinal muscles of the body wall, in the whiting, the composition of the muscular tissue remains remarkably constant, and it is the liver which undergoes great changes in composition, as may be clearly seen by a study of Table 4. Even the isolated analysis of the flesh given by Plimmer (**5**), referring to a fish from unknown locality, is very similar to the analyses given by me, of which the average values are shown in the table below:—

## TABLE 1.

### COMPOSITION OF WHITING MUSCLE.

| | Plimmer. | Average of results of present investigation. *Females.* | *Males.* | *Very small. Sex doubtful.* Av. size 12·4 cm. |
|---|---|---|---|---|
| Water . . | 80·4 | 80·5 | 80·0 | 80·2 |
| Fat . . . | 0·2 | 0·3 | 0·3 | 0·3 |
| Protein . . | 17·7 | 16·4 | 17·1 | 16·7 |
| Ash . . . | 1·1 | 1·3 | 1·4 | 1·3 |
| Undetermined . | 0·6 | 1·5 | 1·2 | 1·5 |
| | 100·0 | 100·0 | 100·0 | 100·0 |

In the whiting then, it appears that there is a direct relationship between the state of maturity and the gross chemical composition of the liver. This is best illustrated by giving the ratio of fat to water in the liver, and the following table gives the mean value of this figure corresponding to the various stages in development of the gonads. It is depicted graphically in Fig. 1, and it will be noted that there is some difference in the sexes, both with regard to the percentage of fat generally, and the rate at which its increase and decrease in the liver takes place.

## TABLE 2.

### The Relationship between the Stage of Maturity and Amount of Fat in the Liver of the Whiting.

| Maturity stage. | I. | I–II. | II. | II–III. | III. | III–IV. | IV. | IV–V. | IIA. |
|---|---|---|---|---|---|---|---|---|---|
| (a) *Females.* | | | | | | | | | |
| % Fat (means) . | 34·1 | 42·7 | 56·2 | 56·6 | 58·2 | 63·2 | 61·2 | 40·6 | 43·2 |
| Ratio Fat : water (means) | 0·67 | 0·94 | 1·68 | 1·66 | 1·98 | 2·31 | 2·22 | 0·87 | 0·98 |
| (b) *Males.* | | | | | | | | | |
| % Fat (means) . | 29·9 | 46·3 | 48·8 | 67·0 | – | 67·5 | – | – | – |
| Ratio Fat : water (means) | 0·53 | 1·25 | 1·24 | 2·79 | – | 2·85 | – | – | – |
| (c) *Very small.* (Aver. 12·4 cms.). | | | | | | | | | |
| % Fat (means) . | 14·1 | – | – | – | – | – | – | – | – |
| Ratio Fat : water (means) | 0·21 | – | – | – | – | – | – | – | – |

As the numerical designation of the maturity stages is artificial, it is only natural that there should be a wide variation within the classes. For instance, in the IIA class, the ratio would depend on how far the fish had recovered from spawning, which by ordinary observation is not ascertainable.

The ratios in the respective classes of immature Stage I, immature female Stage I–II, and the female in normal resting condition Stage II, must obviously overlap greatly—depending on the precocity, retardation of development, or nutrition of the fish. The only other figure (amongst the females) calling for comment is the ratio of 1·577 in Stage III–IV (February 1st, 1927). It is quite reasonable to suppose that the fishes which gave this figure were in a much later stage than that in which they were placed—a point of view that is quite permissible from Fulton's statement (**7**) that the eggs mature in successive crops, which, as they mature, are shed.

I have already mentioned the difficulty of classifying the maturity stages of the males, so that here also it is not surprising to find an occasional exceptional figure: indeed, even in quite immature fish functional sperms are present. The testes do not undergo so great a development as the ovaries—a fact which is reflected in the higher percentage of fat in the liver at the stages when ripening is initiated. But as the testes become relatively much enlarged and convoluted, the fat content of the liver becomes gradually reduced, and although it seems impossible to separate " Spents " from " Normal resting males," a loss of fat seems to occur in much the same way as is shown more clearly in the female. The ratio fat : water of 0·21 given by the immature fish, is made the first point on the graphs of both sexes.

The results appear to indicate that with growth both in size and maturity the quantity of fat in the liver becomes relatively greater, reaching its maximum a little time after the gonads have begun to ripen—i.e. about Stage III. Thereafter, as the gonads increase in size, and the drain in metabolism becomes felt, the fat in the liver becomes rapidly less, reaching a minimum in spent fish : the cycle being then repeated as before. On the other hand, the muscle substance remains approximately unchanged—which, of course, accounts for the palatability of the flesh in recently spawned fishes not being impaired.

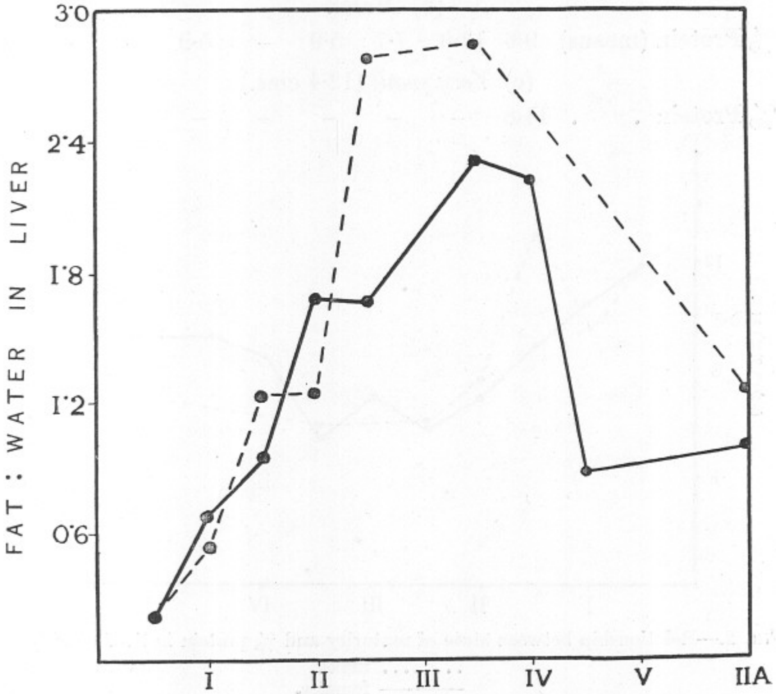

Fig. 1.—Relationship between state of maturity and ratio of fat : water in the liver of the whiting.

........ males.
———— females.

Of the other substances in the liver it is noticeable that the amount of protein is also correlated with age and maturity, but that, unlike the fat content, it becomes less with increasing stages of maturity. The average value of the protein content of the liver for each maturity class is shown in the following table, and is indicated graphically in Fig. 2.

## TABLE 3.

### Average Protein Content of the Liver of the Whiting in Relation to Maturity.

| Maturity stage. | I. | I–II. | II. | II–III. | III. | III–IV. | IV. | IV–V. | IIA. |
|---|---|---|---|---|---|---|---|---|---|
| (a) *Females.* | | | | | | | | | |
| % Protein (means) | 10·4 | 8·8 | 6·8 | 5·7 | 7·0 | 5·5 | 8·4 | 9·3 | 9·3 |
| (b) *Males.* | | | | | | | | | |
| % Protein (means) | 9·6 | 13·0 | 7·7 | 5·9 | – | 5·9 | – | – | – |
| (c) *Very small* (12·4 cms.) | | | | | | | | | |
| % Protein . . | 11·8 | – | – | – | – | – | – | – | – |

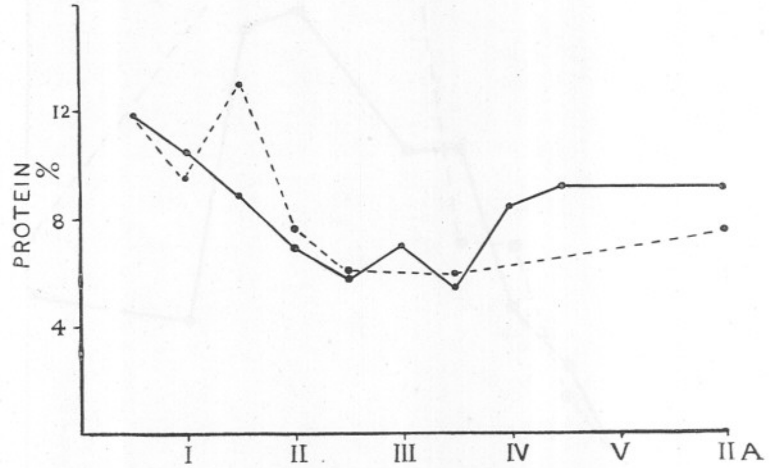

Fig. 2.—Relationship between state of maturity and % protein in liver of whiting.
........ males.
———— females.

It appears quite definite then, that immature fishes have a decidedly higher protein content in the liver than mature fishes. This diminishes until commencement of ripening, and then becomes gradually higher, reaching its highest amongst mature fishes in the "Spent" stages.

The changes undergone by the liver, as outlined above, are almost parallel to those recorded by Bruce in the muscle of the herring. He also found a like decrease in fat content of the liver of the herring correlated with the growth of the gonads, and states that the liver of the male, as in the case of whiting, is richer in fat than that of the female.

He concludes that the metabolic demands of the developing gonads are met, in the first instance, by the fatty reserves of the liver. There is no doubt whatever that this occurs also in the whiting.

Other species of fish investigated up to the present have not yielded much evidence upon this point, so that it cannot as yet be stated that it is general amongst fishes. Storage, and subsequent metabolic transference of materials, especially those contributing to the structure of lecithins, may occur in other parts of the digestive tract besides the liver.

I wish to thank my wife for her valuable help, and Dr. E. J. Allen, Dr. W. R. G. Atkins, and Mr. E. Ford for their helpful criticism.

## SUMMARY.

In the whiting, no significant changes occur in the composition of the *muscle substance*, either throughout the year, or with increasing age, or during ripening of the gonads.

The amount of fat in the *liver* is very low in immature fishes, increasing greatly with age, and reaching its maximum just after the commencement of the ripening of the gonads. It then falls off, reaching its lowest value amongst mature fishes in the " Spent " stages. Males are richer in liver fat than females.

Immature fish have a decidedly higher protein content in the liver than have mature fish.

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## TABLE 4.

### PARTICULARS OF FISH TAKEN FOR ANALYSIS, AND THE COMPLETE ANALYSES THEREOF.

| Date of capture. | No. of fish in sample analysed. | Mean length, cms. | Mean weight, grms. | Mean weight of liver, grms. | Maturity stage. | *Analysis of Liver.* | | | | | *Analysis of Muscle.* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | $H_2O$. % | Fat. % | Protein. % | Ash. % | Undet. % | $H_2O$. % | Fat. % | Protein. % | Ash. % | Undet. % |
| (a) *FEMALES.* | | | | | | | | | | | | | | | |
| 1926. | | | | | | | | | | | | | | | |
| January 4 | 1 | 38·0 | 635 | 26·6 | III. | 29·5 | 58·2 | 7·0 | 0·7 | 4·6 | – | – | – | – | – |
| ,, 21 | 2 | 39·0 | 555 | 40·0 | III–IV. | 24·8 | 65·5 | 5·4 | 0·5 | 3·8 | – | – | – | – | – |
| February 11 | 1 | 36·0 | 427 | 34·3 | IV. | 27·2 | 66·8 | 3·7 | 0·4 | 1·9 | – | – | – | – | – |
| April 20 | 1 | 25·0 | 113 | 5·3 | I–II. | 39·5 | 50·7 | 7·7 | 0·6 | 1·5 | 80·6 | 0·3 | 17·2 | 1·3 | 0·6 |
| May 20 | 1 | 52·0 | 836 | 23·0 | IIA. | 54·2 | 34·2 | 10·2 | 0·8 | 0·6 | 83·3 | 0·2 | 13·6 | 1·2 | 1·7 |
| ,, | 1 | 34·0 | 349 | 13·3 | IIA. | 39·4 | 50·6 | 7·3 | 0·5 | 2·2 | 81·1 | 0·2 | 15·1 | 1·4 | 2·2 |
| ,, | 5 | 26·7 | 149 | 3·4 | I. | 51·1 | 35·1 | 9·2 | 0·8 | 3·8 | 81·1 | 0·3 | 15·8 | 1·3 | 1·5 |
| July 27 | 6 | 26·2 | 122 | 2·8 | I. | 40·1 | 46·4 | 9·0 | 0·6 | 3·9 | 80·0 | 0·2 | 16·8 | 1·3 | 1·7 |
| September 6 | 4 | 32·3 | 256 | 6·8 | II. | 28·3 | 60·7 | 7·4 | 0·6 | 3·0 | 79·7 | 0·2 | 16·3 | 1·4 | 2·4 |
| ,, | 4 | 29·4 | 181 | 3·8 | I–II. | 35·9 | 53·6 | 6·9 | 0·5 | 3·1 | – | – | – | – | – |
| ,, | 2 | 23·8 | 88 | 1·3 | I. | 70·0 | 13·4 | 10·6 | 0·8 | 5·2 | 80·0 | 0·3 | 17·3 | 1·3 | 1·1 |
| October 14 | 6 | 25·6 | 110 | 1·7 | I. | 54·7 | 33·0 | 8·5 | 0·6 | 3·2 | – | – | – | – | – |
| ,, 21 | 4 | 38·2 | 424 | 9·1 | II. | 36·5 | 53·7 | 6·8 | 0·5 | 2·5 | 80·3 | 0·2 | 16·9 | 1·3 | 1·3 |
| December 3 | 3 | 35·3 | 339 | 8·4 | II. | 38·8 | 51·7 | 6·9 | 0·5 | 2·4 | – | – | – | – | – |
| ,, 7 | 4 | 39·9 | 519 | 24·5 | II. | – | – | – | – | – | 80·2 | 0·3 | 17·2 | 1·4 | 0·9 |
| ,, 14 | 5 | 40·6 | 616 | 41·2 | II. | 22·8 | 68·2 | 5·9 | 0·4 | 2·7 | 80·6 | 0·4 | 16·2 | 1·1 | 1·7 |
| ,, 16 | 2 | 37·7 | 264 | 9·0 | II. | 40·6 | 46·8 | – | 0·6 | – | – | – | – | – | – |
| 1927. | | | | | | | | | | | | | | | |
| January 11 | 1 | 28·6 | 199 | 13·7 | IV. | 27·7 | 55·6 | 13·1 | 1·0 | 3·3 | – | – | – | – | – |
| ,, | 2 | 21·0 | 73 | 2·2 | I. | 55·2 | 31·1 | 10·3 | 0·7 | 2·7 | – | – | – | – | – |
| January 20 | 2 | 40·0 | 532 | 27·0 | II–III. | 34·5 | 55·6 | 5·7 | 0·5 | 3·7 | – | – | – | – | – |
| ,, | 3 | 33·1 | 298 | 14·0 | ,, | 33·6 | 57·5 | 5·6 | 0·6 | 2·7 | – | – | – | – | – |
| ,, | 8 | 22·1 | 80 | 2·2 | I. | 46·2 | 41·7 | 7·7 | 0·6 | 3·8 | – | – | – | – | – |
| February 1 | 3 | 33·0 | 328 | 19·0 | III–IV. | 34·5 | 54·4 | 6·8 | 0·6 | 3·7 | 78·9 | 0·4 | 18·3 | 1·3 | 2·1 |
| ,, 3 | 1 | 45·5 | 909 | 80·5 | ,, | 25·3 | 67·5 | 4·2 | 0·4 | 2·6 | – | – | – | – | – |
| ,, 8 | 2 | 20·9 | 72 | 2·1 | I–II. | 45·6 | 42·5 | 7·6 | 0·4 | 3·9 | – | – | – | – | – |
| March 10 | 1 | 45·5 | 916 | 49·8 | IV–V. | 41·0 | 46·3 | 9·6 | 0·4 | 2·7 | – | – | – | – | – |
| ,, | 1 | 41·3 | 692 | 38·0 | ,, | 37·1 | 50·8 | 7·1 | 0·6 | 4·4 | – | – | – | – | – |
| March 15 | 5 | 23·8 | 98 | 3·4 | I. | 39·5 | 45·4 | 12·0 | 0·6 | 2·5 | – | – | – | – | – |
| ,, | 10 | 20·7 | 63 | 1·7 | I. | 33·0 | 51·9 | 10·7 | 0·9 | 3·5 | 81·0 | 0·4 | 16·6 | 1·3 | 1·7 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| April 5 | 5 | 19·8 | 53 | 1·0 | I. | 55·5 | 31·3 | 9·5 | 0·6 | 2·1 | – | – | – | – | – |
| ,, | 3 | 26·3 | 129 | 4 2 | I–II. | 39·8 | 47·3 | 10·7 | 0·7 | 1·6 | – | – | – | – | – |
| ,, | 2 | 28·0 | 154 | 4·7 | IV–V. | 61·8 | 24·7 | 11·2 | 0·6 | 1·7 | – | – | – | – | – |
| April 27 | 3 | 17·9 | 38 | 0·4 | I. | 64·0 | 14·5 | 17·0 | 1·1 | 3·4 | – | – | – | – | – |
| ,, | 5 | 25·2 | 113 | 2·1 | I. | 54·2 | 31·7 | 10·2 | 0·8 | 3·1 | – | – | – | – | – |
| May 4 | 3 | 27·2 | 142 | 1·9 | I–II. | 66·0 | 19·3 | 10·9 | 0·7 | 3·1 | – | – | – | – | – |
| ,, 5 | 1 | 40·8 | 485 | 15·2 | IIA. | 47·0 | 43·2 | 7·5 | 0·6 | 1·6 | – | – | – | – | – |
| ,, 13 | 4 | 33·9 | 283 | 6·5 | IIA. | 38·3 | 45·0 | 12·4 | 0·8 | 3·5 | – | – | – | – | – |
| (b) *MALES.* | | | | | | | | | | | | | | | |
| 1926. | | | | | | | | | | | | | | | |
| January 4 | 1 | 27·0 | 264 | 8·7 | II–III. | 18·9 | 72·6 | 3·8 | 0·4 | 4·3 | – | – | – | – | – |
| ,, 21 | 1 | 28·3 | 204 | 11·8 | ,, | 18·0 | 69·7 | 9·4 | 0·8 | 2·1 | – | – | – | – | – |
| ,, | 1 | 27·0 | 139 | 6·1 | ,, | 22·6 | 71·2 | 5·0 | 0·2 | 1·0 | – | – | – | – | – |
| February 11 | 1 | 21·0 | 74 | 1·7 | II. | 31·1 | 44·1 | – | – | – | – | – | – | – | – |
| ,, | 1 | 30·5 | 236 | 11·9 | III–IV. | 25·1 | 68·6 | 4·2 | 0·4 | 1·7 | – | – | – | – | – |
| April 20 | 6 | 20·0 | 69 | 1·6 | I. | 52·2 | 34·2 | 7·8 | 0·7 | 5·1 | 80·7 | 0·5 | 15·9 | 1·3 | 1·6 |
| June 24 | 10 | 24·8 | 108 | 2·4 | I. | 47·5 | 39·9 | 8·5 | 0·7 | 3·4 | 80·1 | 0·2 | 16·6 | 1·4 | 1·7 |
| July 27 | 1 | 23·8 | 99 | 3·4 | I. | 40·1 | 46·4 | 9·0 | 0·6 | 3·9 | 80·0 | 0·2 | 17·2 | 1·3 | 1·1 |
| ,, | 2 | 28·7 | 198 | 11·8 | II. | 43·6 | 44·6 | 5·4 | 0·5 | 5·9 | 79·8 | 0·2 | 17·1 | 1·2 | 1·7 |
| September 6 | 2 | 24·0 | 88 | 2·0 | I. | 70·0 | 13·4 | 10·6 | 0·8 | 5·2 | 80·0 | 0·3 | 17·3 | 1·3 | 1·1 |
| October 13 | 6 | 32·6 | 256 | 10·2 | II. | 18·9 | 72·0 | 5·7 | 0·3 | 3·1 | 79·7 | 0·4 | 17·4 | 1·4 | 1·1 |
| ,, 21 | 1 | 39·3 | 443 | 7·9 | II. | 36·5 | 53·7 | 6·8 | 0·5 | 2·5 | 80·3 | 0·2 | 16·9 | 1·3 | 1·3 |
| December 3 | 4 | 31·8 | 231 | 4·8 | II. | 42·0 | 41·7 | 11·3 | 0·8 | 4·2 | – | – | – | – | – |
| ,, 7 | 5 | 29·8 | 176 | 6·6 | II–III. | – | – | – | – | – | 80·2 | 0·5 | 16·7 | 1·5 | 1·1 |
| ,, | 5 | 18·6 | 44 | 0·9 | I. | 56·8 | 29·4 | 10·1 | 0·7 | 3·0 | 81·0 | 0·4 | 14·7 | 1·5 | 2·4 |
| ,, 16 | 3 | 24·5 | 99 | 1·8 | I–II. | 36·9 | 46·3 | 13·0 | 0·8 | 3·0 | – | – | – | – | – |
| 1927. | | | | | | | | | | | | | | | |
| January 11 | 5 | 27·4 | 165 | 5·9 | II–III. | 35·2 | 53·3 | 6·7 | 0·5 | 4·3 | – | – | – | – | – |
| ,, | 6 | 21·1 | 70 | 1·6 | I. | 55·2 | 31·1 | 10·3 | 0·7 | 2·7 | – | – | – | – | – |
| ,, 20 | 5 | 30·3 | 233 | 16·3 | II–III. | 25·4 | 68·0 | 4·5 | 0·3 | 1·8 | – | – | – | – | – |
| February 1 | 1 | 34·6 | 368 | 15·6 | III–IV. | 23·9 | 63·3 | 9·0 | 0·7 | 3·1 | 77·5 | 0·5 | 19·6 | 1·5 | 0·9 |
| ,, 3 | 3 | 27·2 | 175 | 13·3 | III–IV. | 22·1 | 70·6 | 4·5 | 0·2 | 2·6 | – | – | – | – | – |
| ,, 8 | 4 | 21·2 | 80 | 2·9 | II. | 38·5 | 51·3 | 4·7 | 0·5 | 5·0 | – | – | – | – | – |
| March 15 | 6 | 20·3 | 61 | 1·2 | I. | 60·9 | 25·2 | 9·2 | 0·7 | 4·0 | 81·0 | 0·4 | 16·6 | 1·3 | 0·7 |
| May 4 | 3 | 26·5 | 129 | 2·4 | I. | 66·0 | 19·3 | 10·9 | 0·7 | 3·1 | – | – | – | – | – |
| ,, 13 | 2 | 33·7 | 271 | 9·0 | II. | 35·4 | 53·9 | 8·5 | 0·4 | 1·8 | – | – | – | – | – |
| (c) *VERY SMALL. SEX DOUBTFUL.* | | | | | | | | | | | | | | | |
| 1926. | | | | | | | | | | | | | | | |
| July 5 | 23 | 13·1 | 16·8 | 0·35 | | 60·1 | 23·3 | 10·4 | 0·8 | 5·5 | 79·7 | 0·3 | 17·0 | 1·3 | 1·7 |
| September 7 | 10 | 11·1 | 9·5 | 0·09 | | 76·8 | 4·9 | 13·1 | 1·0 | 4·3 | 80·6 | 0·3 | 16·4 | 1·4 | 1·3 |

## APPENDIX TO TABLE 4.

### STOMACH CONTENTS.

Number of stomachs containing each item given in brackets.

| | | |
|---|---|---|
| (a) *Females.* | Stages I and I–II. | 76 Specimens.<br>Empty (51), "Fish"* (18), Sprat (1), *Gobius minutus* (1), Mysids (1), Upogebia sp. (2), Larval Gadoids (1). |
| | Stages II–V. | 55 Specimens.<br>Empty (28), "Fish" (18), *Gadus minutus* (2), *G. merlangus* (2), Clupeoids (4), Upogebia (1), Carcinus (1). |
| (b) *Males.* | Stages I and I–II. | 50 Specimens.<br>Empty (43), Mysids (4), Upogebia (2), Larval Gadoids (8). |
| | Stages II–V. | 62 Specimens.<br>Empty (43), "Fish" (8), Clupeoids (4), Callionymus sp. (2), *Upogebia deltura* (1), Squid (1), Nereis sp. (1). |
| (c) *Very small.* | Average size 12·4 cms. | 33 Specimens.<br>All with larval gadoids.<br>(*Gadus minutus* and *merlangus*.) |

* "Fish" denotes unidentifiable fish remains.

# The Preservation of Fishing Nets by Treatment with Copper Soaps and Other Substances.

By

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In previous papers (1925, 1926) the writer published confirmations of the work of Taylor and Wells (1923), who had introduced to America the use of copper oleate dissolved in benzene or petrol. Within the last year a summary (1927, 1) of the results of further tests was published, also (1927, 2) a series of popular articles urging the adoption of certain of the methods tried. The object of the present paper is to set forth the details of the methods and the results, especially the tensile tests, obtained by a continuation of the work.

To avoid confusion in the nomenclature of the organic liquids used as solvents for the copper oleate (or other copper soap) it may be explained that by benzene the more or less impure mixture of benzene, $C_6H_6$, with toluene, $C_6H_5.CH_3$, is meant. This is a gas-works by-product and has a light brownish yellow colour. It is the best cheap solvent for these copper soaps, much better indeed than is pure benzene. The term petrol is reserved for the lighter portion of the petroleum distillate such as is used in motor-cars; it is known as gasoline in U.S.A. and elsewhere. This is a complex mixture of straight chain hydrocarbons with compounds having the benzene ring. Petrol from Sumatra has a larger proportion of the latter than has American petrol and may accordingly be expected to be a rather better solvent for the copper soaps. The heavier petroleum distillate, such as is used in lamps, is known in England as paraffin oil, in America as kerosene.

Copper oleate was not, however, used in the tests here once it had been established that a mixed copper soap was as effective, or more so. The latter has now been put on the market in Great Britain and contains stearates, palmitates, and oleates in the proportions in which they exist in a commercial product utilized in its manufacture. It is sold ready mixed with the 10 per cent of mineral lubricating oil recommended by Taylor and Wells to prevent the soap from creeping out of the fabric as the solvent evaporates.

Later on Taylor and Wells (1926) tried to improve their method by incorporating various binding agents with the soap. Trials on these lines have been in progress here, also experiments with "Cuprinol" alone and with binding agents. The writer is indebted to Dr. A. C. Johansen for having brought "Cuprinol" to his notice. This is not copper oleate, nor is it a mixture of fatty acid soaps such as the English product. It appears to be a preparation of copper salts of naphthenic acids derived from petroleum and is more soluble in petrol than are the fatty acid copper salts.

In view of the widespread use of cutch in net preservation it seemed advisable also to include it in the comparative tests, as though single treatments are much less durable than single treatments with copper oleate as shown by Taylor and Wells, it seemed possible that current practice was not as inadequate as has been imagined—the nets being cutched at intervals. Trials were also made according to Dr. Olie's Dutch method, in which after cutch the nets are immersed in ammoniacal copper sulphate.

The various methods of preservation tried were compared by placing the nets, usually about a metre square, in a jar of sea-water and allowing them to rot, the water being changed three times a week. The tests are truly comparable, though obviously the conditions do not approximate to those under which the nets are used, save as regards pound nets. Nets used from boats are, however, rarely quite dry, and rotting proceeds continuously in a slightly damp net. The rotting test is, however, more severe than practice, inasmuch as the damp net is not having the preservative leached out all the time ; it is less severe because the net, when in use, is subjected to a stream of water, so that removal of the preservative is more rapid than under the conditions of the experiments ; again, the net in practice undergoes wear and tear to which the nets kept in the jars are not exposed.

In the first experiments made the strands of the nets were tested by hand. It was usually possible to tear the net about one month after the strands could thus be broken. When the net could be torn its serviceable life was considered at an end. In later work tensile tests were carried out upon the strands, using a spring balance. When the strands had deteriorated so as to be "too weak to test," the net was considered unserviceable. On the balance this corresponds to a strength of under four pounds. The condition of the net is then such that it can be torn and would be condemned by the hand test also.

In the course of the work certain facts bearing on all such tests became apparent :—

1. That it is always necessary to include an untreated net in each series, or when comparing two treatments to carry out the comparison simultaneously. This is rendered necessary by the different rates of

rotting in summer and in winter or occasioned by differences in the water used.

2. That it is necessary to compare nets in jars of equal size.

3. That the purity of the water used has a very considerable effect upon the rate of rotting. Pure sea-water—" outside water "—being relatively poor in phosphates and nitrates, is not such a good medium for bacterial growth on the fibres as is water from the Aquarium tanks. In the early work outside water was used. Later on—and without at the time realizing how great was the difference—tank water was used on account of the large volume required by the numerous experimental jars. Tank water exerts its full effect upon the untreated controls. The nets treated with a good preservative are not affected at all till the preservative has been leached out, and there is no evidence that tank water does this any more rapidly than outside water. Tank water is, however, a nearer approach to having the nets fouled by fish than is outside water, so its use is advantageous. Since the damage due to fouling is occasioned by bacterial fermentation, leading to the production of heat in piled nets, it is obvious that so long as the net fibres are coated with an efficient preservative, namely, an antiseptic, the fermentation of fish slime, etc., on the outside can have relatively little effect on the net itself. Once the preservative has been leached out, however, such conditions lead to the very rapid decay of the net.

A short account will now be given of the methods of preservation employed, and the results will then be shown in tables.

### TREATMENT WITH COPPER OLEATE.

The soap, a greasy greenish blue solid, is dissolved in benzene preferably ; but petrol was used for the experiments, as it is sufficiently soluble in it to make up a 10 per cent solution at room temperature, 15° C. This was made 1 per cent with respect to mineral oil. The net was dipped in the solution till thoroughly wetted and then hung up to dry. The petrol evaporates quickly.

### TREATMENT WITH MIXED COPPER SOAPS.

(Pilot protective copper soap, manufactured by Messrs. Ogston and Tennant, Renfrew.)

Being less soluble than the oleate, this was at first used in 5 per cent solution in petrol. It is sold with the mineral oil already incorporated. This concentration is, however, far from being a saturated solution, and a 10 per cent solution was subsequently used in warm weather. Finally, as a standard mixture, one pound (454 grm.) to an Imperial gallon (4·54 litres) was adopted. This is close to a 12 per cent solution. It is most conveniently prepared by melting the soap by standing the tin in hot water and then adding a little petrol and mixing till the whole can be poured out. The petrol should be slightly warmed by hot water*; this is necessary in cool weather, much under 15° C., and is always an advantage. The nets should be immersed in the solution till the liquid has penetrated into the knots fairly well. This object is attained when the whole appears thoroughly wetted and has stood five to ten minutes, though a longer immersion is recommended, when practicable. On hanging up to dry the petrol evaporates quickly. The treatment is best carried out in the open air, both to minimise risk of fire and because the vapour from petrol or benzene is apt to produce headache. For this reason a breezy day is most suitable with, if possible, sun to dry the nets. Care should be taken to do this thoroughly so that they may not give off inflammable vapour when piled up in a heap. Half an hour or an hour usually suffices for the drying.

## TREATMENT WITH CUTCH.

Cunningham (1902) showed that the portion of the cutch most effective as a preservative was that which was insoluble in cold water, but soluble in boiling water. Nets were accordingly boiled for half an hour in a 2 per cent infusion of cutch, using enough liquid completely to cover the nets. The nets were allowed to stand in the solution, after boiling, for twenty-four hours. They were then dried and re-treated with cutch in the same way as before. The cutch used was that sold for the purpose in Plymouth, "Caller Herrin'" brand (Bakau Co.). Experiments with cutch and a review of the literature are given by Taylor (1921) and need not be repeated here.

## DR. OLIE'S (THE DUTCH) TREATMENT.

The nets are first treated with cutch as already described, two boilings. When finally dried they are placed in a solution of ammoniacal copper sulphate. This is prepared by adding to a 1 per cent solution of the sulphate enough ammonia solution to re-dissolve the precipitate first formed, leaving a clear deep blue solution. The addition of 4 c.c. of strong (sp. gr. 0·88) ammonia solution to a litre† of the copper salt produces the desired effect. The nets are placed in this solution for not more than fifteen minutes. The solution is largely decolorized by the nets. The substances used are cheap and the treatment is simple and rapid. Care should be taken not to breathe the gas given off from the strong ammonia solution and to keep it from the eyes.

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* A miner's safety lamp with absolutely intact gauze might also be used to keep the petrol warm, but it has not been tried here.

† Namely, four volumes of ammonia solution to one thousand of copper solution.

### TAR, ANTI-FOULING PAINT, RESIN.

The tar used was the coal-distillation product. This varies somewhat in composition, which may account for the superior results given by certain experiments in which it was used as compared with others. It is stirred into the petrol solution containing copper soap, and mixes well, up to the maximum proportion used, one pound to the gallon.

The anti-fouling paint used was a red copper oxide preparation obtained from Messrs. Foster, Mason, and Harvey. It was stirred into the petrol solution of copper soap. The ounces mentioned are by weight (1 ounce = 28·3 grams).

The difficulty that resin is insoluble in petrol was surmounted by melting it with the copper soap and then stirring up with petrol. Using one pound of resin to one of soap and a gallon of petrol a solution of low viscosity was obtained; this in time becomes thicker. The netting treated with this mixture dries readily and handling is a relatively clean business, which is not the case with nets freshly treated with the soap-tar or soap-paint mixtures.

### CUPRINOL.

This is sold in liquid form. It is a mixture of 50 parts of the copper salts of crude acids separated from Russian or Galician petroleum dissolved in 36 parts of volatile petroleum (boiling range 85°–250°) with 14 parts of heavy mineral oil.* It is manufactured by Aktieselskabet Kymeia, Glentevej 61, Copenhagen. A five kilogram tin costs, when delivered in Plymouth, 16·25 Danish kroner. For use the manufacturers recommend that it should be diluted with an equal volume of solvent naphtha, petrol ("gasolin"), or mineral paint oil. One kilogram of net consumes about half its weight of mixed cuprinol. The 5 kg. tin (roughly 5 litres), diluted with an equal volume of petrol (say, sp. gr. 0·8), gives 9 kg. of mixture, which suffices for 18 kg. of net at a cost of 16·25 kroner plus one gallon approximately of petrol (fifteen pence), total 19 shillings. The cost is therefore roughly one shilling per kilogram of net treated.

Cuprinol received a gold medal award in the International Fishery Exhibition at Copenhagen in 1912, and in spite of the danger of fire, urged as an objection to the use of copper soaps, it is still manufactured and used in Denmark. An English firm preparing a tender for tarpaulin covers for the Danish State Railways found that the specification embodied the use of Cuprinol.

On the same consumption basis, one half-kilogram of solution to one of net, using Pilot protective copper soap, at fifteen pence a pound with petrol at the same price per gallon, the cost of treating a 35 lb. herring-net would be as follows: Half weight of net, say 18 lbs., equivalent to

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* Private communication.

2 lbs. soap plus two gallons of petrol, cost 5/– or $3\frac{1}{3}$ pence per pound of net, which is much cheaper than cuprinol. However, for the actual treatment of one such net, to soak it properly, a larger volume of solution is required, up to about seven gallons, at a total cost of 17/6. Much of the solution is, however, left—it is not all consumed. Neglecting the cost of labour, the treatment is estimated to add one shilling in the pound, or 5 per cent, to the cost of a cotton net.

Taking a herring net 55 yards long and 17 score meshes deep, $32\frac{1}{2}$ rows to the yard, made up with ropes and floats, ready cutched, to be worth £5 5s. and to weigh 39 lbs., and assuming that it completely uses up the seven gallons of soap solution, at 17/6 the cost is still under 18 per cent on that of the net, whereas the life is much prolonged. On the above basis there can be no gain in the treatment unless the life of the net is prolonged by over 20 per cent; but to say that the cost is prohibitive —as has been said—when the life of the net is doubled or trebled or preserved even longer is scarcely correct mathematics.

## THE DETERIORATION OF UNTREATED NET.

Table 1 shows how quickly the untreated controls, used in the preservation tests, became rotten. Outside sea-water is less severe than is tank water. There is no great difference between the rate at which hemp and cotton rot: in summer both are rotten in under two months, in winter in five to six.

### TABLE 1.

Showing the time required for materials, having the initial tensile strength per strand of net as shown in column No. 2, to become unserviceable; the date of immersion is shown in column No. 4.

| No. | lbs. | Material. | Immersed. | Till unserviceable, months. | Medium. |
|---|---|---|---|---|---|
| 7 | 14 | Hemp | 16/9/'24 | 7 | Outside sea-water. |
| 10 | 14 | ,, | 26/9/'25 | 5 | Aquarium tank water. |
| 28 | 18 | ,, | 17/3/'26 | 2 | ,, ,, |
| 10A | 22 | Cotton | 26/9/'25 | $5\frac{1}{2}$ | ,, ,, |
| 15A | 19 | ,, | 7/11/'25 | $4\frac{1}{2}$ | ,, ,, |
| 34A | 18 | ,, | 20/10/'26 | $5\frac{1}{2}$ | ,, ,, |
| 24A | 12 | ,, | 17/3/'26 | 2 | ,, ,, |

## PRESERVATION WITH MIXED COPPER SOAP AND WITH COPPER OLEATE.

In Table 2 it may be seen that the commercial copper soap, with mixed fatty acids, is at least as good as is pure copper oleate. There is an indication that the former is considerably better since the life of the net was about the same, though only half as concentrated a dip was used. It will be noted that the control perished under the cooler winter conditions—about two months would have sufficed in summer.

### TABLE 2.

Hemp young fish trawl-net rotting in outside sea-water for seven months, then in aquarium tank water. Initial strength 14 lbs. per strand.

| No. | Treatment. | Immersed. | Till unserviceable, months. |
|---|---|---|---|
| 7 | Untreated | 16/9/'24 | 7 |
| 6 | Copper oleate, 10% | ,, | 14 |
| 5 | Mixed copper soaps, 5% | 4/9/'24 | 13½ |
| 8 | As No. 5. Re-treated with 12% mixed soaps after 11, 17, 21, and 24 months | ,, | Still two-thirds of original strength after 27 months, 4/12/'26. |

## PRESERVATION WITH MIXED COPPER SOAPS (PILOT PROTECTIVE COPPER SOAP) REINFORCED WITH ANTI-FOULING PAINT, TAR OR RESIN.

Tables 3 and 4 show the results obtained with hemp ; 5, 6, and 7 with cotton. Resin gives a net which is very clean to handle, using it pound for pound with soap, which is the best proportion of those tried ; it is an improvement, up to about 50 per cent on soap alone on hemp ; on cotton, however, it is well over twice as good as soap alone. It was feared at one time that the use of resin, favourable under water, might result in weakening of the fibre in nets exposed to air and light to dry. Direct tests using fabrics continuously exposed on the roof fortunately disproved this. The soap-resin mixture leaves the net green in colour and very pliable.

Anti-fouling paint enormously increases the life of the net, even using a few ounces to each pound of soap. It leaves the net a red colour, very pliable and greasy, soiling the hands for months in the pound for pound proportion. On the score of cleanliness and cost half a pound or less might be used.

Tar, too, has given excellent results in the pound for pound proportion (see Nos. 14 and 14A). This amount does not make the net any way stiff, for the soap is a thick grease.

The experiments in Table 7, designed to show the best small proportion of tar, have unfortunately proved inconclusive, for all perished simultaneously. Moreover, the pound for pound mixture, No. 51A, had a life of only 11 months, whereas No. 14A, similarly treated, has maintained its original strength after 26 months. One can but suggest some difference in the tar ; probably it was a tar in which distillation had been pushed too far, leaving a brittle product on drying.

## TABLE 3.

Hemp net rotting in Aquarium tank water; initial strength, average of sets of six, 13½ lbs. and 14¾ lbs. dry; after soaking for three hours, 12½ lbs. Immersed 26/9/'25.

| No. | Treatment. | Till unserviceable, months. | Percentage life of net. |
|---|---|---|---|
| 10 | Untreated | 5 | 100 |
| 11 | Copper soaps, 12% | 9 | 180 |
| 12† | Do. with resin 1 lb. per gallon (12%) | 11 | 220 |
| 13 | Do. with anti-fouling paint, 12% | 26+x | 500+y* |
| 14 | Do. with tar, 12% | 26+x′ | 500+y′‡ |

* Half strength, still serviceable, looks as new.

† The soap and resin, paint, or tar respectively were mixed, so that only one dip was required.

‡ Slightly under half strength, still serviceable, looks as new.

## TABLE 4.

Hemp net rotting in Aquarium tank water; initial strength, dry, 14 lbs. Immersed 17/10/'25.

| No. | Treatment. | Till unserviceable, months. | Percentage life of net.† |
|---|---|---|---|
| 15 | Copper soap 1 lb., resin ¼ lb. per gallon | 12* | 240 |
| 16 | Do. ,, ,, ½ lb. ,, | 12 | 240 |
| 17 | Do. ,, ,, 1 lb. ,, | 14½ | 290 |

† Taking No. 10, immersed 26/9/'25 as control, life 5 months.

* Nos. 15 and 16 were 8¼ lbs. and 11 lbs. respectively after 11½ months, but were too weak to test after 12½. No. 17, which was 11½ lbs. after 11½ months, decreased gradually to 5 lbs. after 14½ months, so was perhaps serviceable up to 15 months.

## TABLE 5.

Cotton net rotting in Aquarium tank water; initial strength, dry, 19½ lbs. Immersed 26/9/'25.

| No. | Treatment. | Till unserviceable, months. | Percentage life of net. |
|---|---|---|---|
| 10A | Untreated | 5½ | 100 |
| 11A | Copper soaps, 12% | 10¼ | 190 |
| 12A† | Do. with resin 1 lb. per gallon (12%) | 26+x | 470+y |
| 13A‡ | Do. with anti-fouling paint, 12% | 26+x′ | 470+y′ |
| 14A* | Do. with tar, 12% | 26+x″ | 470+y″ |

† No. 12A is still over half strength, 10 lbs.

‡* Nos. 13A and 14A look as new, neither paint nor tar now soil the hands. They are stronger than before treatment, 26 and 24 lbs. respectively; this may be partly due to cementation of the fibres, partly to inequality in strength of the strands.

## TABLE 6.

Cotton net rotting in Aquarium tank water; initial strength, dry, 19½ lbs. Immersed 7/11/'25, in smaller jars than in the other tests.

| No. | Treatment. | Till unserviceable, months. | Strength after 23 months. |
|---|---|---|---|
| 15A | Untreated | 4½ | 0 |
| 16A | Copper soaps 1 lb. per gallon (12%) | 23+x | 16½ |
| 17A | Do. with anti-fouling paint, 8 oz. per gallon | ,, | 17½ |
| 18A | Do. ,, ,, 4 oz. ,, | ,, | 19½ |
| 19A | Do. ,, ,, 2 oz. ,, | ,, | 22½ |
| 20A | Do. ,, ,, 1 oz. ,, | ,, | 29 |

## TABLE 7.

Cotton net rotting in Aquarium tank water; initial strength, dry, 12 lbs. Immersed 18/11/'26. Life, eleven months.

| No. | Treatment. | Strength, 12/10/'27. | Strength, 8/11/'27. |
|---|---|---|---|
| 48A | Copper soap 1 lb. and tar 2 oz. per gallon | 12 | Too weak to test |
| 49A | Do. ,, , tar 4 oz. ,, | 10 | ,, ,, |
| 50A | Do. ,, ,, tar 8 oz. ,, | 12 | ,, ,, |
| 51A | Do. ,, ,, tar 16 oz. ,, (1 lb.) | 12½ | ,, ,, |

### PREPARATION OF COPPER SOAP FOR ISSUE IN A LIQUID FORM.

A pound of soap (as supplied, ready mixed with one-tenth its weight of mineral oil) was melted and a pound of powdered resin or of tar was stirred in. To the mixture a pound and a half of carbon tetrachloride was added. The result is a mobile liquid which becomes thicker when cold, or even gelatinous if left overnight at 10° C. It becomes liquid in a warm room at 15° C. Carbon tetrachloride is non-inflammable—it is used in fire extinguishers—but is volatile and gives off a heavy vapour similar to chloroform in its action when breathed. It was chosen on account of its non-inflammable nature and because it is the cheapest suitable solvent, costing about one shilling per pound. Since the copper soap coats only fifteen pence per pound, the use of the liquid preparation more than doubles the cost, but it can of course be mixed with the main solvent, petrol or benzene, very readily.

### USE OF PARAFFIN INSTEAD OF PETROL AS SOLVENT.

With the object of producing a mixture that could be used and stored under conditions of comparative safety against fire, under "fool-proof" conditions, paraffin oil of high flash-point, such as used in lamps, was used as solvent with the carbon tetrachloride liquid soap mixtures mentioned in the last section. The results show that the increase in the life of the net is not nearly as good as when petrol is used as solvent (see Table 8). These poor results need not be attributed to the use of carbon tetrachloride, for it evaporates quickly, leaving no residue.

## TABLE 8.

Cotton net rotting in Aquarium tank water. Immersed 5/1/'26. Solvent for the melted mixture of soap with resin or tar, first carbon tetrachloride, $1\frac{1}{2}$ lbs., followed by one gallon (about 8 lbs.) of paraffin oil.

| No. | Treatment. | Till unserviceable, months. | Percentage life of net.* |
|---|---|---|---|
| 21A | Copper soap 1 lb, resin 1 lb. | 6 | 150 |
| 22A | Copper soap 1 lb, tar 1 lb. | $7\frac{1}{2}$ | 190 |

* Taking untreated as 4 months, average winter-summer value.

### A COMPARISON OF TREATMENT WITH CUTCH, CUTCH AND AMMONIA COPPER SULPHATE (OLIE'S METHOD), AND COPPER SOAP ALONE AND WITH CUTCH.

Tables 9 and 10 set forth the results. Firstly, it may be seen that cutch is more effective upon hemp than on cotton. Secondly, it is established that the further treatment with ammonia copper sulphate is a great improvement upon cutch alone; it brings the treatment up to the level of that with copper soap alone (short dip) for cotton, and surpasses it for hemp. Olie's method is rapid and cheap. It has much to recommend it, though it is nothing like as effective as copper soap with tar or anti-fouling paint on cotton. A comparison of Nos. 31 and 32 shows that treatment with cutch before copper soap is an advantage with hemp, though Nos. 27A and 28A give no indication that it is any advantage with cotton. Fillon (1925), however, considers it an advantage on cotton also. In this series No. 30A is by far the best; though soap and resin may be inferior to soap alone (Nos. 32 and 33) when the latter is allowed to soak thoroughly, or much better (Nos. 11A, 12A, 11 and 12), yet a first dip in soap, followed by a second in soap and resin, undoubtedly gives excellent results. The cost is, of course, about doubled, since the solvent is the chief item; but as compared with soap and tar or soap and anti-fouling paint there is the great advantage of a net which is quite clean to handle.

As regards the duration of soaking in copper soap solution, No. 28A compared with No. 11A shows the percentage life of the net to be 250 and 190 respectively, which is in favour of the longer time of soaking. (The actual life of the net 11A was longer, twice as long as that of 28A, but the former was rotting in winter and was an 18 lb. strand as against a 12 lb.) With hemp the improvement is more marked, a single treatment with 3 hours' soaking having preserved the net for 19 months.

## TABLE 9.

Hemp net rotting in Aquarium tank water ; initial strength, dry, averages of sets of six tests each, 15¼, 15¾, 18½ ; maximum single strand 21, minimum 12½. Immersed 17/3/'26.

| No. | Treatment. | Till un-serviceable, months. | Percentage life of net. |
|---|---|---|---|
| 28 | Untreated | 2½ | 100 |
| 29 | Cutch 2% infusion, two boilings | 6 | 240 |
| 30 | Do. followed by Olie's treatment, ammonia copper sulphate | 20+x | 800+y |
| 31 | As 29, followed when dry by 12% copper soap | 20+x′ | 800+y′ |
| 32 | Copper soap, 12%, but soaked for three hours | 19 | 760 |
| 33 | Copper soap 12% with 1 lb. resin per gallon | 13½ | 540 |
| 34* | Copper soap, 12% followed when dry by No. 33 treatment | 20+x″ | 800+y″ |

* After 20 months Nos. 30, 31, and 34 are respectively 8⅓, 8¼, and 8 lbs., about half strength.

## TABLE 10.

Cotton net rotting in Aquarium tank water ; initial strength, dry, 12 lbs. Immersed 17/3/'26.

| No. | Treatment. | Till un-serviceable, months. | Percentage life of net. |
|---|---|---|---|
| 24A | Untreated | 2 | 100 |
| 26A | Cutch, 2% infusion, two boilings | 3 | 150 |
| 25A | Do. followed by Olie's treatment, ammonia copper sulphate | 5 | 250 |
| 27A | As 26A, followed when dry by 12% copper soap | 5 | 250 |
| 28A | Copper soap, 12%, soaked three hours | 5 | 250 |
| 29A | Do. with 1 lb. resin per gallon | 5 | 250 |
| 30A | As 28A, followed when dry by 29A dip | 20+x* | 1000+y |

* Colour all gone by 17/11/'27, strength 7½ lbs.

### RE-TREATMENT OF NETS WITH CUTCH AND BY OLIE'S METHOD.

The results of the above treatments having proved better on hemp than on cotton nets, it seemed advisable to select the latter for a study of the effect of repeated treatments, especially as cutch is so largely used. The cutch bichromate method, introduced by Cunningham, was not tried at all since Taylor and Wells (1923) showed conclusively that it was inferior to the Dutch method with ammonia copper sulphate, though considerably superior to cutch alone. Taylor and Wells also showed that the various coal tar and pine tar treatments were inferior to copper soap. A summary of their most recent work (1926) is included at the end of this paper.

Table 11 contains the results of one year's immersion tests. It may be seen that by boiling again with cutch every two or three months the original strength has been retained, or very nearly so. Two re-treatments with cutch and ammoniacal copper sulphate in the course of the year suffice to keep the net quite sound. These nets, however, feel rather harsh to the hand, and the cutched nets give a very clean break in the tensile test. The nets have not the softness and pliability of those treated with copper soap with or without tar or anti-fouling paint.

### TABLE 11.

Cotton net rotting in Aquarium tank water ; initial strength, dry, 18 lbs. Immersed 20/10/'26.

| No. | Treatment. | Number of times re-treated. | Strength after 12 months. |
|---|---|---|---|
| 37A | Untreated, life 5½ months | — | 0 |
| 35A* | Cutch, two boilings | 4 | 16⅓ |
| 36A | Do. | 3 | 18 |
| 37A | Do. followed by ammonia copper sulphate (Olie's method) | 2 | 22½ |

* No. 35A was re-treated every two months, irregularly, viz. on 20/12/'26, 3/3/'27, 3/5/'27, 23/8/'27, 20/10/'27. No. 36A was re-treated every three months, viz. 20/1/'27, 20/4/'27, 20/8/'27 one month late. No. 37A was re-treated on 3/3/'27 and 20/8/'27.

### Comparison of Copper Soap (Pilot Protective Copper Soap) with Cuprinol, with and without Tar, in Fresh and in Salt Water.

Tables 12 and 13 record the results of one year's immersion on nets treated as shown. Nos. 35, 37, 40, and 42 prove that Cuprinol is better than the fatty acid soap mixture for preserving hemp in both salt and fresh water. As regards cotton, there are indications that Cuprinol will prove to be the better ; even though No. 45A is somewhat below the others in strength the preservative is still on it all over ; the lower tensile values may be due to variation in the net. As far as results extend, tar and fatty acid copper soap are about as good as Cuprinol alone, and a mixture of the two soap products is also good. Longer periods are required to differentiate between these mixtures and Cuprinol with tar.

### TABLE 12.

Hemp net Nos. 35–39 rotting in Aquarium tank water ; Nos. 40–44 in fresh water. Immersed 25/11/'27. Initial strength, dry, 16½ lbs.

| No. | Treatment. | Strength after 12 months.* |
|---|---|---|
| 35 | Copper soap, 12% | 5⅓ green all gone. |
| 36 | Do. with tar as No. 14 | 14⅓ good brown. |
| 37 | Cuprinol with equal volume of petrol | 12⅓ green in patches. |
| 38 | As No. 37 with 1 lb. tar per gallon of mixture | 16⅓ light black. |
| 39 | Copper soap as No. 35, Cuprinol as No. 37, equal volumes of solution | 13 green in patches. |
| 40 | As No. 35 | 7 green all gone. |
| 41 | As No. 36 | 9 good brown. |
| 42 | As No. 37 | 14 good green all over. |
| 43 | As No. 38 | 13½ good brown. |
| 44 | As No. 39 | 12 good green all over |

* Tested, 16/11/'27.

## TABLE 13.

Cotton net Nos. 38A–42A rotting in Aquarium tank water ; Nos. 43A–47A in fresh water. Immersed 25/11/'26. Initial strength, 18½ lbs., done on 40A before treatment, 17½ lbs. done on 45A similarly, average 18 lbs.

| No. | Treatment. | Strength after 12 months.* |
|---|---|---|
| 38A | Copper soap, 12% | 22 green colour gone. |
| 39A | Do. with tar as in 14A | 11† good dark brown. |
| 40A | Cuprinol with equal volume of petrol | 25 green colour retained in patches. |
| 41A | Cuprinol as 40A with tar, 1 lb. per gallon of mixture | 25 colour a light black. |
| 42A | Copper soap as 38A, Cuprinol as 40A, equal volumes of solution | 25⅓ green colour all gone. |
| 43A | As 38A | 22 green in patches. |
| 44A | As 39A | 21 good black. |
| 45A | As 40A | 16½ good green all over. |
| 46A | As 41A | 21 good black. |
| 47A | As 42A | 26 good green all over. |

* Tested 16/11/'27.

† Evidently a weak piece of the original fibre, for when repeated on 18th the average of the six tests was 18⅓ lbs.

### RESULTS OBTAINED BY TAYLOR AND WELLS.

The following quotations from the 1926 paper of these American workers will serve to bring their extensive series of tests to the notice of net users in this country.

" The tests were made in salt water at two places in the Atlantic Ocean, one place in the Pacific, and in fresh water at four places."

" The principal results and conclusions drawn from the present work are as follows :—

1. The combination of copper oleate with coal tar was the best preservative of tensile strength of those used.
2. Both the proprietary waterproofing material and the proprietary wood preservative did some good as preservatives, but neither one was as effective as copper oleate or coal tar.
3. At all places where tests were made linen lines, both treated and untreated, were completely rotten in less than two months.
4. Azulmic acid, a dye tested as a preservative, proved to be of no value for this purpose.
5. The combination of rare earths and copper oleate was very little better than copper oleate used alone.
6. Combinations of copper oleate with paraffin, boiled and raw linseed oil did not preserve tensile strength any better than copper oleate alone.
7. The copper oleate and linseed oil combinations appeared to wash out less rapidly than copper oleate alone, but did not prevent fouling by marine growth as well.
8. With the exception of the quercitron-ammoniacal copper sulphate treatment, the effectiveness of the several preservatives is of the same order on hemp as on cotton.
9. For hemp lines the copper oleate coal tar mixture was the best preservative of tensile strength, copper oleate coming second at all places except Fairport, Iowa, where coal tar was second best.
10. The quercitron-ammoniacal copper sulphate treatment (L) did not make as good a showing on cotton samples in the 1923 tests as it did in 1922. We do not know of any cause for this other than that due to the variation in water conditions at different localities and in the same locality from one year to another.
11. The quercitron-ammoniacal copper sulphate treatment (L) made a very poor showing on hemp samples. The hot-water solution of quercitron seems to damage hemp, causing an exceedingly large diminution in tensile strength, and probably is the cause of the poor results of this treatment on hemp.

12. In fresh water of the Mississippi River at Fairport, Iowa, sample lines suffered more rapid deterioration than at any other point where tests were made. Coal tar preserved cotton lines at Fairport for three months. Lines treated by all other methods were completely rotten after two months' exposure.

13. Twine that is removed from the water every 30 days, dried, and treated with copper oleate lasts more than twice as long as that which is treated but once.

14. In fresh water at Put in Bay, Ohio, results with copper oleate were more satisfactory than in the previous series there.

15. The results at Put in Bay, Ohio, indicate that the rate of deterioration of nets not only varies from one locality to another, but differs in different years in the same locality.

(L) Quercitron and ammoniacal copper sulphate (called Dutch method in former paper). The lines were steeped in a hot solution of quercitron, 1 lb. to 2 gallons of water, until the solution was cold, dried, again steeped in the same way, and again dried. They were then immersed for a few minutes in an ammoniacal solution of copper sulphate containing one pound of copper sulphate and 3 pounds of 25 per cent ammonia for every 12½ gallons of water. For a full description of this method see Olie (1918)."

The following section is also quoted from Taylor and Wells: " Results of Practical Application of Copper Oleate by Fishermen."

" During the 1923 season between 60,000 and 100,000 pounds of copper oleate were used by fishermen. In order to determine whether these practical trials had produced satisfactory results, we visited the fishermen along the New England and middle Atlantic coasts, examined their nets, and obtained from them their observations and opinions. Lobster and pound-net fishermen from Maine to Long Island have, with few exceptions, had excellent results. At the time the survey was made copper oleate had been tried on but a very few gill nets in this region.

Those fishermen who used copper oleate found that it was an excellent anti-fouling agent and preservative as long as it remained in the twine. The length of time during which it remained in the twine varied from 14 days to 5 or 6 months. In those cases where it washed out in 14 days the fishermen believe the grade of copper oleate used was very poor.

Various combinations of copper oleate with other substances were tried by the fishermen. One of the most successful of these was a mixture of a small amount of copper paint with the kerosene solution of copper oleate. This is reported as being an excellent preservative for use on pound nets.

The fishermen were about equally divided in their opinions as to whether gasoline or kerosene [namely, petrol or paraffin oil] gave better results as a solvent. Gasoline seems to give a more uniform distribution of oleate through twine, drys more rapidly, and leaves twine less oily than kerosene. On the other hand, kerosene is cheaper than gasoline and also safer, because it is not inflammable. It was also found that in most cases better results were obtained when the net or webbing was allowed to steep in the solution for several hours, preferably over night, instead of 5 or 10 minutes, as was first recommended.

The principal suggestions from users of copper oleate were as follows :—

1. Steps should be taken to prevent copper oleate from washing out of the webbing as rapidly as it now does.

2. There is need for some substance which, when combined with copper oleate, will give it more body, so that the webbing will be better protected from mechanical wear.

3. When copper oleate is used on seines, some substance should be added to prevent the slipping of knots when the seine is hauled.

With respect to the first of these suggestions, one must remember that if copper oleate is to prevent growth successfully it is necessary for it to be at least slightly soluble in water. An entirely insoluble substance would not preserve at all. It is doubtful, therefore, if it would be advisable to decrease the solubility of copper oleate to any great extent. We have conducted experiments that have indicated that if the solubility is appreciably decreased by such substances as linseed oil or paraffin, copper oleate is less effective as an anti-fouling agent.

In regard to the second and third suggestions, it has been found from our experiments that a mixture of copper oleate and coal tar makes an excellent preservative ; in fact, one of the most effective tested. Where considerable increase in weight and stiffness is objectionable, such a treatment, of course, would not be permissible. This treatment would also eliminate the slipping of knots."

## GENERAL DISCUSSION.

As regards Taylor and Wells' conclusion that copper oleate and coal tar treatment is excellent as a preservative the writer is in complete agreement, but less tar was used here. It should be noted, however, that the soap used here was not—save at first—oleate, but a mixture containing oleate. There is no doubt that with this petrol secures better penetration than does paraffin. To use paraffin is a very false economy. It must be pointed out also that quercitron, though a tanning agent, is not the same as the cutch (from acacia) used by Olie, nor did they boil the solution. Fillon (1925) has obtained very good results with Olie's ammonia copper sulphate method, particularly using a second treatment with one cutching followed by the copper dip. Fillon gives the following figures for the percentage increase in weight after various treatments: Cutching followed by ammoniacal copper sulphate, double application 30%; copper oleate and coal tar (oleate 1, benzene 8, tar 8), 65%—it should be noted that the mixture used here contains tar 1, not 8; copper oleate alone (15% in petrol), 18%; coal tar diluted with an equal part of benzene, 68%. The results obtained here in which copper soaps with tar were superior to Olie's method were carried out with less tar than were those of Fillon or of Taylor and Wells. However, a second initial treatment was not given. Particularly good results were obtained here using Olie's method on hemp. This is in direct contradiction of the finding of Taylor and Wells using quercitron. It is curious also that their linen lines rotted so quickly, for though linen line rots in less than two months in Aquarium water in summer in tap water (which is, however, pure) it lasts several times as long.

As regards the slipping of the knots in nets treated with copper soap, this may be avoided by pulling them tight by hand before treatment—a general practice hereabouts before nets are used—or they may be cutched first and then treated with copper soap and tar. As regards the oleate remaining "in the twine" for 14 days to 5 or 6 months, it seems obvious that the shorter period recorded was due to poor penetration occasioned probably by treatment of nets which were not thoroughly dry, or in very cold weather. Moreover, although nets may look quite colourless, they are not necessarily devoid of copper soap. This is shown by the fact that they remain intact for two or three months longer and finally become black as they rot, the black being copper sulphide produced from the remainder of the soap. Untreated nets never become black in this way.

The writer has been informed that the cutch and bichromate method in one locality replaced that with ammonia copper sulphate. This, according to Olie's results, is a retrograde move, and no results in the literature show the bichromate method to be at all as good as the latter. The two were not compared here, as the question was regarded as finally decided in favour of Olie's method. For this treatment, double application, Fillon gives the increase in weight as 30%, that for oleate alone being 18%; the copper soap and tar (1 lb. to 1 lb.) used here would therefore give about 30%, for only the soap and tar remain on the net. Using less tar or anti-fouling paint the weight might be reduced to 20–25%. Since less water is taken up by a net already impregnated with the greasy soap-tar mixture, the actual increase in the hauling weight must be small.

## SUMMARY.

1. Under the conditions of the tests cotton and hemp nets became rotten in Aquarium tank water in two months or less in summer, in 4½–5½ months in winter.

2. A mixed copper soap, containing oleate, stearate, and palmitate, is as good, probably rather better, than is copper oleate as a net preservative.

3. "Cuprinol," a petroleum acid copper soap, is better than the fatty acid soaps, both in fresh and in salt water. It is more than three times as expensive, however.

4. The following specially good results have been obtained: Mixed fatty acid copper soap, 1 lb. with 1 lb. of coal tar or anti-fouling paint in a gallon of petrol, hemp nets about half strength, cotton nets full strength, after 26 months. Also copper soap 1 lb. to gallon, followed by a dip in copper soap 1 lb., resin 1 lb., petrol 1 gallon, hemp net about half strength, cotton net the same, after 20 months. The controls perished in 2½ and 2 months respectively. In this series cutch and copper soap and Olie's method did well, half strength after 20 months, on hemp, but lasted only 5 on cotton. A repetition of Olie's treatment twice in the course of the year was, however, found to preserve the cotton well. Fillon recommends a double Olie treatment at the very start and shows that nets so treated were sound after 18 months, as were also those cutched before copper oleate and coal tar treatment.

5. From the experiments carried out here it may be concluded that by far the best initial treatment for nets is one with a copper soap reinforced with anti-fouling paint or coal tar. On the score of shrinking the knots, as well as for preservation, a preliminary cutching appears to be advantageous. It is, however, doubtful whether Olie's ammoniacal copper sulphate treatment, repeated from time to time, may not be more suitable on account of its low cost.

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# Herring Investigations at Plymouth. I. Methods of Collection and Treatment of Data.

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With 5 Figures in the Text.

## CONTENTS.

## GENERAL INTRODUCTION.

Towards the end of the year 1924, the present writer commenced a statistical study of random samples from commercial landings of herrings at Plymouth, in order to obtain information on the two following questions :—

(*a*) Upon what year-class or year-classes of herring was the season's fishery of 1924–25 concentrated ?

(*b*) Did the fishes landed throughout that season appear to conform to a single morphological type ?

Throughout the work the size of the sample and the number of characters studied had to be such that all observations could be made by one investigator with the help of a single Laboratory Assistant. It was found by experience that if the sample did not greatly exceed one hundred fishes, the following routine procedure could be followed for each fish of two or three samples per week :—

(*a*) Take a measurement of length.

(*b*) Clean and mount three scales on a numbered glass slide.

(*c*) Open up the body-cavity, note the sex and degree of maturity of the roe or milt.

(*d*) Attach a linen label to the head of the fish by means of a safety pin.

(*e*) When all the fishes had been treated as above, boil in lots of about fifty, and prepare clean skeletons to be dried for a subsequent determination of the number of vertebræ.

The results for the season showed quite definitely that herrings with five summer growth-zones and five winter-rings to the scale greatly predominated in the catches throughout the season November, 1924, to March, 1925. On the other hand, all observations seemed to suggest that the conception of a single " type " of herring for Plymouth was untenable. In the light of these results it appeared advisable to examine herrings from other areas, there being the possibility that, elsewhere, " types " would be recognised which would, in the event of their coming to Plymouth to spawn, produce a complex population similar to that observed in 1924–25. Accordingly, in addition to a series of samples from the Plymouth catches during each of the two following seasons, 1925–26 and 1926–27, samples from Milford Haven, Padstow, Newlyn, Mevagissey, Brixham, Brighton, and Lowestoft were studied.

This extensive sampling resulted in the accumulation of a formidable mass of statistical data from which the writer has been able to extract information outside the original scope of the research. The most convenient way of presenting this information is in the form of a series of separate papers each of which deals with one particular section of the work done.

In the present part an endeavour has been made to provide the reader with a general account of the uses and limitations of the various statistical data collected for the study of the life-history of the herring. It is freely admitted that the larger portion of the subject-matter may make little or no appeal to the technical expert—it is not intended for him. It is hoped, however, that it may prove helpful to the general biological worker in assisting him to recognise the peculiar usefulness and importance of the statistical method of approach to the problems of herring biology. Probably in the case of no other economically valuable fish are we so dependent upon indirect evidence for our knowledge of its life and habits. If, then, the conclusions based on indirect evidence derived from statistical data are to carry conviction, it is essential that the general mathematical principles underlying the statistical treatment should be made clear. Since this report was prepared, the British Association Committee on Biological Measurements has issued a leaflet (British Association Report, Section D, Leeds, 1927), making recommendations for the taking and presentation of biological measurements. This leaflet should prove most helpful to all biologists whose work necessitates the compilation and interpretation of statistical data.

Acknowledgments for special services rendered will be made at times appropriate during the series of papers, but the writer is pleased here to record his thanks to Mr. F. J. Warren, Laboratory Assistant at Plymouth, who has acted as recorder throughout and rendered help generally in the collection of the data.

## THE USES AND LIMITATIONS OF THE STATISTICAL DATA COLLECTED.

### LENGTH OF FISH.

The standard measurement adopted was identical with character 9 of Orton (**18**, p. 73), viz. " from the tip of the snout to the distal end of the longest ray in the dorsal fluke of the caudal fin, when the fluke is placed so that its dorsal margin lies parallel to the line of measurement." The actual measurement was made to the " nearest 1 mm. below " ; thus, a fish whose length exceeded 25·5 cm. but was less than 25·6 cm. was recorded as of length 25·5 cm. When for statistical purposes it became necessary to group fishes into classes according to length, the grouping was made to the " nearest 1 cm. below " ; thus, all fishes of length 25·0 cm. to 25·9 cm. both inclusive, were included in the 25 cm. group.

A convenient method of comparing samples with regard to the length of the fishes is by means of the calculated values known as the *median* and the *upper and lower quartiles*. An illustration will serve to demonstrate the nature and significance of these statistical values. Imagine one hundred fishes arranged in serial order of length from the shortest in the first position to the longest at the end of the series. Note the lengths of the 25th and 26th fishes of the series ; then the value lying midway between these two lengths is the *lower quartile*, ($Q_1$). The value midway between the lengths of the 50th and the 51st fishes is the *median*, ($Q_2$), while that between the lengths of the 75th and 76th is the *upper quartile*, ($Q_3$). In other words, the values of $Q_1$, $Q_2$, $Q_3$ merely indicate the lengths below which lie 25%, 50%, and 75% of the series.

An alternative method for comparison between samples is to calculate the values of the statistics known as the *arithmetic mean* and the *standard deviation* for each sample. Consideration of these two mathematical constants is given in the section of this paper which deals with the treatment of data on the number of vertebræ (page 256.)

If samples appear to differ with regard to the length of fish it is necessary to determine the extent to which the observed difference can be attributed to each of the following causes :—

1. Errors, unavoidable or accidental, either in the actual determinations of length, or in the subsequent calculation of constants.
2. Errors of sampling due to the limitation of the size of the statistical sample.
3. Some form of selective action on the part of the apparatus used for the collection of the sample, which action has operated differently in the cases under comparison.
4. Real differences in population sampled.

The causes under heading 1 need not be enlarged upon, and those under headings 2 and 4 can be more conveniently dealt with at a later stage. Some observations on heading 3 are given in the sub-section which follows.

### *Selective Action of Fishing Nets.*

It is important to remember that while random samples from commercial landings may give an excellent picture of the sizes of herring forming the mainstay of the local fisheries, they must be treated with the utmost caution as evidence concerning the actual herring *stock* on the grounds.

The outlook of the fisherman is entirely economic—he fishes for the maximum financial yield—so that in designing his nets he endeavours to obtain an apparatus which will catch the maximum quantity of fish of the best-paying sizes which can be caught in his local area. There seems little reason to doubt that the fisherman himself is by far the best judge of the most profitable size of mesh required in his own district, even if we contend that past custom may have influenced him in his choice. Unlike the biologist, however, he has no reason to be disturbed by the fact that the mesh of his net allows smaller fishes to escape and may be too small to capture the largest, nor by the knowledge that the mesh of his net differs from that used in another area. When, therefore, the biologist wishes to compare the herring *stock* in one area with that in another, he must remember that the data for random samples from commercial catches are subject to correction for differences in mesh used in the two areas (*vide* Bjerkan, **1**).

## AGE AND GROWTH FROM SCALES.

As a rule, three scales from each fish, separately picked with forceps from the anterior region of the body near the tip of the pectoral fin, were cleaned between finger and thumb in water and mounted on a numbered glass slide, using a mixture of egg-albumen and glycerine as the adhesive.

### *Estimations of Age from Scale-readings.*

The methods of scale-reading which have been followed so persistently and carefully by the Norwegians are based upon three important premises :—

1. That for each winter passed through by a fish subsequent to the first formation of scales, a definite winter-ring is recorded on the scale.
2. That the scale-reader is able to distinguish between winter-rings and secondary-rings, the latter of which may not be in any way connected with age.
3. That the scale-reader has reliable information on the age of the fish when the first winter-ring was laid down.

The first of these three premises is obviously the most vital, and its proof has been derived from a study of the edge of the scale at different times of the year. The researches of Dahl (**3**), Lea (**15**), and later Hodgson (**7**) have shown that the herring scale grows by a definite annual cycle consisting of an initial phase of active growth (the physiological summer) followed by one of rest from growth (the physiological winter), and that the character of the edge of the scale changes accordingly. Thus all herrings caught during the summer have scales which exhibit a typical growing or " summer " edge, while those caught during the winter have scales which exhibit an equally typical resting or " winter " edge. The commencement of the growing phase of every annual cycle is recorded on the scale as a definite winter-ring.

The second premise, while it serves to impress the fact that some practical experience in scale-reading and interpretation is necessary, is intended rather to emphasize the truth that scale-readings are, to some extent, *personal estimates of age.* In this connection the words of Johansen (**11**, p. 23) may be usefully repeated, although, in the writer's opinion, these are somewhat too severe. He says :—

> " . . . Erroneous determinations are probably frequent, and mainly on account of the fact that the winter-rings are often not more distinct than the ' secondary-rings,' which have nothing to do with the winter-rings. Each naturalist forms his own praxis in his distinction between the two sorts of rings. He may be able to count the number of ' winter-rings ' approximately in the same way at different times, but this is not a sufficient proof that the counting is correct. There is some evidence that the first winter-ring is often feeble or wanting, and in old specimens it is usually the case that there is an outer zone with more or less indistinct rings which are lying very close to each other. In this zone the distinction between winter-rings and secondary-rings becomes highly arbitrary. . . ."

Although it is true that " each naturalist forms his own praxis " in his distinction between true and false rings, tests have shown that two skilled scale-readers independently examining the same sample of scales arrive at very similar results. Lea (**12**, p. 17) provides two instances of this. The age of each of one hundred herrings was estimated from their scales by himself and Knut Dahl in turn, and the final results compared. There was a discrepancy of one year in three instances where there was only one scale available for examination, but absolute agreement in all cases where three scales were available. The second test was conducted by Lea and Hjort. Their separate age estimates for several hundreds of herrings agreed in every case but one, in which Lea had undoubtedly made a mistake. But, even this agreement between independent observers does not dispose of the possibility of false rings being so similar in appearance to true winter-rings that they defy detection in the routine inspection of scales. The remarkable Norwegian results over an unbroken period of many years (Lea, **16**), however, surely constitute a striking argument in favour of the view that the unavoidable personal error in age estimation from scales cannot, on the whole, be regarded as unduly large.

That reliable information on the time of formation of the first winter-ring is essential for accurate age estimations from scales will be realised from the study of the problem presented to the Scottish investigators (**20**). Two broods of herring larvæ occur annually, the one in the spring with its maximum in April, and the other in the autumn, at its height in September. The members of the spring brood and a proportion of the autumn brood are fully scaled by the end of the year. But a large—if not the larger—proportion of the autumn brood is carried over the winter months still in the unscaled condition It is at once seen that when these latter fishes acquire their first winter-ring, their more advanced relatives of the same autumn spawning, as well as those spawned in the previous spring, will be recording their *second* winter-ring. A preliminary report on the growth of winter-spawned herrings at Plymouth is given in Part 4 of this series (see p. 305), in which this question is more fully considered. It will be sufficient here to state that in the Plymouth estimates of age for fish of the south-western area, the first winter-ring was in all cases regarded as formed during the first winter following that of birth.

### *The Part of the Body from which Scales are taken.*

At a meeting of the Herring Committee of the International Council (**2**, p. 34) held in Oslo, June, 1923, a recommendation was made regarding the part of the body from which scales for age-estimation should be taken. When the rings on the scale are distinctly marked and few in number, it is of little importance from which part of the body the scales are taken; on the other hand, when the rings are many and closely set, accurate counting becomes more and more difficult as one proceeds from scales taken from the anterior region of the body near the tip of the pectoral fin, to those either from the posterior part of the body or on the dorsal surface. When, therefore, the object is to count the maximum number of rings, those scales (viz. those from the anterior part of the body near the tip of the pectoral fin) should be chosen which show the fullest development of the rings.

### *Methods of Recording Estimates of Age.*

The manner in which scale-readings may be recorded needs some consideration. Hodgson (**7**, p. 13) differentiates between three annual phases in the appearance of the edge of the scale. During the physiological winter the edge is in the "A" phase with a clear margin continuous around the scale. At the onset of new growth the scale-striæ are seen to extend right to the margin at the "top" of the scale, i.e. at the edge furthest from the base-line, leaving on the inside the first indications of a new winter-ring. On each side, however, the clear margin of the "A" phase persists. This is the "B" phase. In the height of the physiological summer, the striæ extend to the margin throughout the whole of the edge, and the new winter-ring is left behind in its complete form. This is the "C" phase. A concise record of an age-estimate, therefore, would include not only the number of completed winter-rings, but also some indication of the phase of the edge. Thus, the common practice in scale-recording of referring fishes to appropriate " age-groups " according to the number of completed winter-rings inside the edge of the scale does not differentiate between scales which are in different phases of edge. At Plymouth it has been found convenient to consider an " A " phase edge as a *completed winter-ring*, and to record scale-readings in the form of a double entry of the number of summer zones and winter-rings. The following tabular illustration will serve to demonstrate the method adopted :—

| Phase of scale edge. | No. of completed winter rings inside edge. | Plymouth record of age. | |
|---|---|---|---|
| | | Summer zones. | Winter rings. |
| C | 3 | 4 | 3 |
| A | 3 | 4 | 4 |
| B | 3 | 4 or 5* | 4 |
| C | 4 | 5 | 4 |

An alternative method of procedure is to assign fishes to " year-groups " (Lea, **15**, p. 104). When a fish is placed in, say, the 1920 year-group, this means that the fish in question formed its first summer zone on the scale in the year 1920. For all fishes spawned in the spring, the date of the year-group will be identical with that of the year of birth, but in the case of those spawned during the latter part of the year, such is not necessarily so. It has been shown on page 243 above that although some of the autumn-spawned Scottish herrings definitely acquire scales and so form a summer zone during the calendar year of birth, a greater proportion of them are carried over the winter still in the unscaled condition, so that the first summer zone is not formed until the calendar year following that of birth. Thus the Scottish herrings spawned in the autumn of 1920 would be assigned partly to the 1920 year-group and partly to the 1921 year-group. In a place like Plymouth, where the maximum spawning takes place during the months of December and January, fishes born in two calendar years will obviously form part of the same year-group. For example, the offspring of the spawning of December, 1919–January, 1920, formed their first summer zone in 1920, and therefore belong to the 1920 year-group.

During actual scale-reading it is often convenient to create a number of " interval age groups," which allow the inclusion of fishes of doubtful age in their approximately correct position in the series of age groups. For instance, an observer may feel certain that a scale is either 6-zoned 6-ringed or 7-zoned 7-ringed, but is unable to decide which ; by assigning

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* Personal judgment would be exercised in light of particular circumstances.

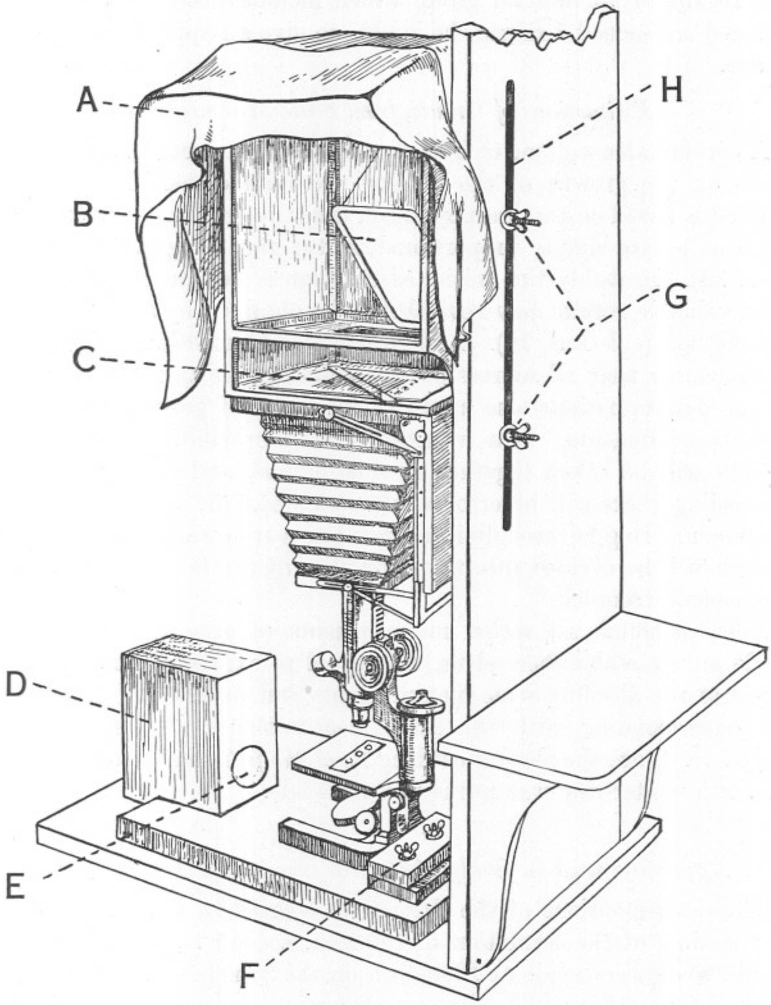

FIG. 1.—Vertical projector used at Plymouth.

A. Black cloth hood spread over wire framework.
B. Mirror set at 45°.
C. Measuring plate of ground glass. See Fig. 2 for details.
D. Lamp-box sheltering 100-watt electric lamp.
E. 200-c.c. flask acting as condenser. It is filled with distilled water to which has been added :—

5 drops of ·04% Sol. of Brom-thymol blue.
5 drops of ·04% Sol. of Brom-cresol purple.
2 drops of N/Sodium bicarbonate.

F. Wooden clamp for securing microscope stand.
G. Thumb-screws on bolts for raising or lowering projector.
H. Slot in vertical stand to allow passage of G.

this record to an interval group which includes fishes of age, 6-zoned 6-ringed *or* 7-zoned 7-ringed, he is able to give an approximate estimate of age.

### *Estimations of Growth from Scale Measurements.*

A considerable volume of information has been accumulated in recent years on the growth of the herring, from scale measurements. The method is based on the presupposition that the growth of the scale takes place at a rate simply proportional to the rate of growth of the fish (Lea, **12**). Probably this initial assumption is not entirely correct, but most valuable results may nevertheless be obtained by a cautious use of the method (*vide* Lea, **14**). As Lea points out, however, it is necessary to remember that all sources of error which make themselves apparent in age determinations also apply to estimates of growth derived from scale measurements. If a winter-ring be overlooked, then two years' growth will be taken together as that of one, and the growth of the succeeding years will be erroneously reckoned. If, on the other hand, a secondary-ring be wrongly interpreted as a true winter-ring, the year's growth will be divided into two, and that of the following years again erroneously recorded.

Now, although all actual measurements of growth increments are made on the scales themselves, it is usual to express the results not in terms of the absolute scale measurements, but in terms of the *length of fish* corresponding with the scale measurements. Thus, the values $l_1, l_2 \ldots l_x$ are the theoretical lengths *of the fish* when the first, second . . . xth winter-ring was formed on the scale.

### *Apparatus used in Study of Growth from Scale Measurements.*

The determinations of the theoretical lengths $l_1, l_2 \ldots l_x$ of a fish at the time of the formation of the first, second . . . xth winter-ring on the scale were made at Plymouth on the principle of the Norwegian method (Lea, **15**, p. 103); but by projecting the image of the scale on to a ground-glass plate fitted with a movable swing-arm, the use of slips of paper was avoided, and the values of $l_1, l_2 \ldots l_x$ read off direct. The general features of the simple home-made projector used for this purpose may be gathered from the accompanying Figs. 1 and 2 and their legends, without further comment.

### *Growth "Types" from Scale Measurements.*

If in a given sample all the fishes of a particular age-group agreed closely in their values of $l_1$, $l_2$, etc., it would be reasonable to suspect that they had lived and grown up under similar growth conditions.

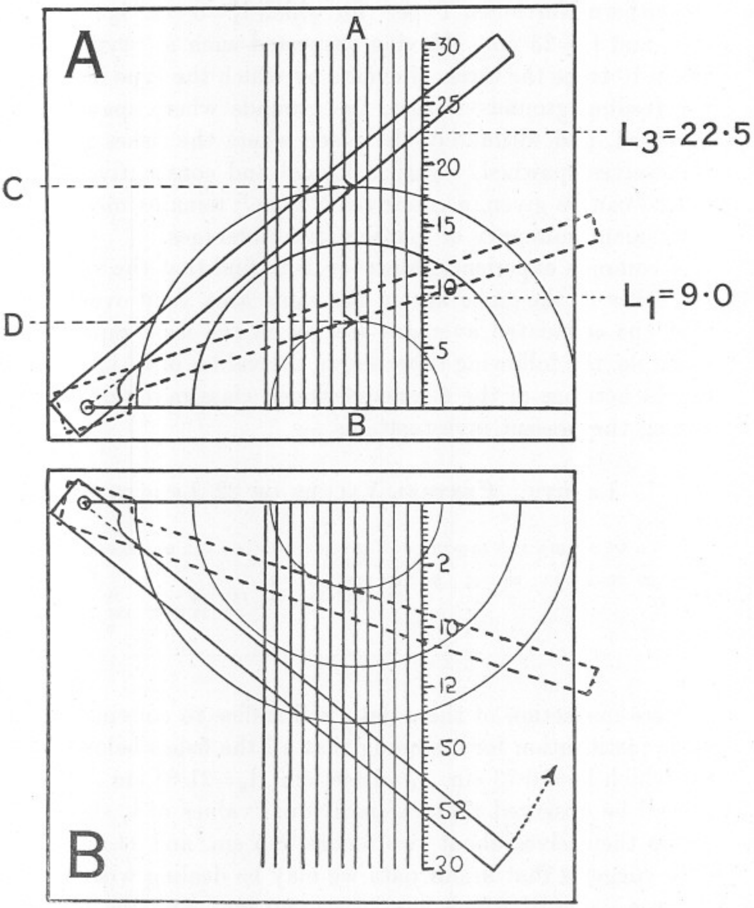

FIG. 2.—Diagrams illustrating method of using measuring-plate (Fig. 1–C).

B. The actual plate with its movable swing-arm, and the projection of a herring-scale from a fish of length 22·5 cm.

A. The reflected view of B as seen by the observer in the mirror (Fig. 1–B). The swing-arm is first adjusted to register 22·5 cm. The measuring-plate is then moved until its base-line coincides with the base-line of the herring-scale, and one of its vertical lines, A B, passes through the scale-origin B, while the edge of the herring-scale is in register with the swing-arm at point C. To determine "$l_1$" for the fish, all that is necessary is to move the swing-arm until it is in register at point D along the line A B with the first ring of the herring-scale, and then read off the value ($l_1$= 9·0 cm.).

Under such circumstances it would be permissible to use the average values of $l_1$, $l_2$, etc., as a " type " representing the stock of the particular age in the sampling area. In this way, Hodgson (**8**, p. 16) arrived at his " Southern North Sea Type," for which $l_1=8$ cm., $l_2=16$ cm., $l_3=20$–$21$ cm., and $l_4=23$ cm. Having suspected such a " type " steps must be taken to trace the series of events by which the type has been built up—the feeding grounds visited, the grounds where spawning, if any, has occurred, and ultimately the place where the fishes of that type were themselves spawned. Until a logical and consecutive account of these events can be given, a conceived " type " remains merely a more or less convenient summary of mathematical averages.

A common experience, however, is to find that the values of $l_1$, $l_2$, etc., for fishes of the same age in the same area vary over so wide a range that the calculated averages are not in the least representative.* For example, the following table shows the values of $l_1$, $l_2$, $l_3$, and $l_4$ for each of 374 herrings of the 4-zoned 4-ringed class taken off the Sussex Coast during the present investigations :—

| | LENGTH. CENTRAL VALUES OF 22 LENGTH CLASSES. CM. | | | | | | | | | | | | | | | | | | | | | | Arith. Mean. CM. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5·5 | 6·5 | 7·5 | 8·5 | 9·5 | 10·5 | 11·5 | 12·5 | 13·5 | 14·5 | 15·5 | 16·5 | 17·5 | 18·5 | 19·5 | 20·5 | 21·5 | 22·5 | 23·5 | 24·5 | 25·5 | 26·5 | |
| $l_1$ | 1 | 3 | 24 | 70 | 54 | 53 | 69 | 47 | 26 | 12 | 11 | 3 | 1 | – | – | – | – | – | – | – | – | – | 10·73 |
| $l_2$ | – | – | – | – | – | – | – | – | 2 | 11 | 28 | 58 | 64 | 111 | 64 | 27 | 8 | 1 | – | – | – | – | 18·04 |
| $l_3$ | – | – | – | – | – | – | – | – | – | – | – | – | – | 2 | 11 | 56 | 127 | 134 | 37 | 6 | 1 | – | 21·89 |
| $l_4$ | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 9 | 74 | 160 | 111 | 16 | 3 | 23·65 |

Mere inspection of these data will suffice to convince us that there is little justification for assuming that all the fishes belong to one " type " for which $l_1=10{\cdot}73$ cm., $l_2=18{\cdot}04$ cm., $l_3=21{\cdot}89$ cm., and $l_4=23{\cdot}65$ cm. It will be observed that the individual values of $l_1$ show a tendency to group themselves about two modes, 8·5 cm. and 11·5 cm., respectively. This suggests that in our data we may be dealing with a mixture of two " types," one of which has $l_1=$ca. 8·5 cm., and the other, $l_1=$ca. 11·5 cm. ; but as there is no definite indication of " bimodality " in the corresponding values of $l_2$, $l_3$, or $l_4$, it is not possible from the data, as they stand, to make further progress in the definition of the two conceivable types.

If we analyse the data more closely and ascertain for each individual value of $l_1$—the corresponding values of $l_2$, $l_3$, and $l_4$—we find that fishes with the smaller values of $l_1$ tend on average to add relatively greater annual increments of length in subsequent years than those with the

---

* The reliability of the average may be tested by calculation of its " standard error." See page 259 for a consideration of this statistic. Also consult Lea (**15**, p. 133) for an account of the use of the standard error of the mean in this connection.

larger values of $l_1$. In illustration of this point, the following is a table correlating the values of $l_2$ with observed values of $l_1$ :—

### Correlation Table.

Length $l_1$. Central Values of 13 Length Classes.

| Length $l_2$. Central values of 10 length classes. CM. | CM. 5·5 | 6·5 | 7·5 | 8·5 | 9·5 | 10·5 | 11·5 | 12·5 | 13·5 | 14·5 | 15·5 | 16·5 | 17·5 | Totals. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 13·5 | – | – | 2 | – | – | – | – | – | – | – | – | – | – | 2 |
| 14·5 | 1 | 2 | 3 | 5 | – | – | – | – | – | – | – | – | – | 11 |
| 15·5 | – | 1 | 6 | 11 | 7 | 3 | – | – | – | – | – | – | – | 28 |
| 16·5 | – | – | 7 | 27 | 16 | 6 | 3 | – | – | – | – | – | – | 58 |
| 17·5 | – | – | 5 | 15 | 16 | 16 | 11 | 1 | – | – | – | – | – | 64 |
| 18·5 | – | – | 1 | 10 | 13 | 22 | 36 | 25 | 3 | 1 | – | – | – | 111 |
| 19·5 | – | – | – | 2 | 2 | 5 | 17 | 13 | 16 | 5 | 3 | 1 | – | 64 |
| 20·5 | – | – | – | – | – | 1 | 3 | 8 | 5 | 5 | 5 | – | – | 27 |
| 21·5 | – | – | – | – | – | – | – | – | 2 | 1 | 3 | 2 | – | 8 |
| 22·5 | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 |
| Totals | 1 | 3 | 24 | 70 | 54 | 53 | 69 | 47 | 26 | 12 | 11 | 3 | 1 | 374 |
| Mean $l_2$ | 14·5 | 14·83 | 16·04 | 16·79 | 17·26 | 17·93 | 18·59 | 19·10 | 19·73 | 20·00 | 20·50 | 20·83 | 22·5 | |
| Mean $l_2-l_1$ | 9·0 | 8·33 | 8·54 | 8·29 | 7·76 | 7·43 | 7·09 | 6·60 | 6·23 | 5·50 | 5·00 | 4·33 | 5·00 | |

We observe from the values of the character (mean $l_2-l_1$) shown at the foot of the table that there is a steady decrease from left to right, which is to say that the smaller values of $l_1$ have added larger increments of length than the greater values of $l_1$ have done. In a similar manner it could be shown that fishes with the smaller $l_2$ added larger increments of length, in attaining the length $l_3$, than did the fishes with the greater $l_2$ ; and similarly those with the smaller $l_3$ in growing to the length $l_4$.

If the mean values of $l_2$ for successive values of $l_1$ be plotted graphically as in Fig. 3, it will be found that they conform reasonably well with a straight line AB, except at the extremes where the number of observations is small. It is possible to determine a mathematical equation representing the straight line which best fits the data, and it is :—

$$l_2 = \cdot 59\, l_1 + 11\cdot 70 \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

How nearly this equation fits the data may be seen when the observed values and the calculated values are tabulated in conjunction, thus :—

| | $l_1$ | 5·5 | 6·5 | 7·5 | 8·5 | 9·5 | 10·5 | 11·5 | 12·5 | 13·5 | 14·5 | 15·5 | 16·5 | 17·5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $l_2$ | observed. | 14·50 | 14·83 | 16·04 | 16·79 | 17·26 | 17·93 | 18·59 | 19·10 | 19·73 | 20·00 | 20·50 | 20·83 | 22·50 |
| | $l_2 = \cdot 59\, l_1 + 11\cdot 7$ | 14·94 | 15·53 | 16 12 | 16·71 | 17·30 | 17·89 | 18·48 | 19·07 | 19·66 | 20·25 | 20·84 | 21 43 | 22·02 |

In a similar way it can be shown that the values of $l_3$ and $l_2$ are "positively correlated" according to a straight line equation, and also those of $l_3$ and $l_4$, the two equations being :—

$$l_3 = \cdot 504\, l_2 + 12\cdot 80 \ldots\ldots\ldots\ldots\ldots (2)$$
$$l_4 = \cdot 774\, l_3 + 6\cdot 71 \ldots\ldots\ldots\ldots\ldots (3)$$

It is equally possible to calculate two further equations, the one linking $l_1$ and $l_3$, and the other $l_1$ and $l_4$ :—

$$l_3 = \cdot 277\, l_1 + 18 \cdot 92 \dots\dots\dots\dots\dots (4)$$
$$l_4 = \cdot 221\, l_1 + 21 \cdot 28 \dots\dots\dots\dots\dots (5)$$

From the above we thus learn that instead of endeavouring to segregate the fishes into two growth "types" based on average values of $l_1$, $l_2$, $l_3$, and $l_4$, we can summarise the data in the form of five simple equations (1 to 5 above), from which we can calculate the length reached by a fish of any given value of $l_1$ at the end of any subsequent growth period.

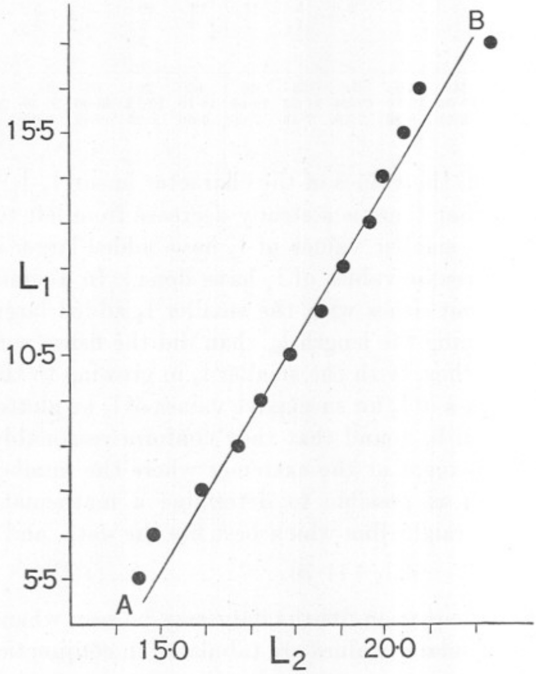

FIG. 3.—Mean values of $l_2$ for observed values of $l_1$ (cm.). Fishes from Sussex Coast.

### *Comparisons between Samples from different Areas.*

Equations 1 to 5 above enable us to compare the growth of the Sussex fishes with that of similar aged fishes from other places. Supposing, for example, that we wished to compare the growth of the Sussex fishes as indicated by equations 1 to 5 with that of fishes taken at Grimsby. Hjort (**6**) has given data on 141 herrings obtained from Grimsby on September 30th, 1906 (Collection, Nr. 26, p. 151), which may be used as an illustration. These 141 herrings were of a similar age to, and for all practical purposes otherwise comparable with, the Sussex fishes. The average values of $l_1$, $l_2$, $l_3$, and $l_4$ given by Hjort are :—

cm.

| $l_1$ | $l_2$ | $l_3$ | $l_4$ |
|---|---|---|---|
| 9·2 | 17·1 | 21·6 | 24·1 |

The corresponding values for the Sussex fishes are :—

cm.

| $l_1$ | $l_2$ | $l_3$ | $l_4$ |
|---|---|---|---|
| 10·73 | 18·04 | 21·89 | 23·65 |

Now we wish to learn how the growth of the Grimsby herrings from $l_1$ to $l_2$, from $l_2$ to $l_3$, and from $l_3$ to $l_4$ compares with that of the Sussex herrings for the corresponding periods. Let us turn to our equation (1) and calculate the length $l_2$, which would be reached by a *Sussex* fish commencing at a length $l_1=9{\cdot}2$ cm., equal to the average value of $l_1$ for the *Grimsby* fishes :—

$$\begin{aligned} l_2 &= {\cdot}59\,l_1+11{\cdot}70 \ldots\ldots\ldots\ldots\ldots (1) \\ &= {\cdot}59\,(9{\cdot}2)+11{\cdot}70 \\ &= 17{\cdot}13 \text{ cm. (Compare with Hjort's observed average } l_2=17{\cdot}1 \text{ cm.)} \end{aligned}$$

Again, let us determine from our equation (2) the length $l_3$ which would be reached by a *Sussex* fish commencing at a length $l_2=17{\cdot}1$ cm., which is the average value of $l_2$ for the *Grimsby* fishes :—

$$\begin{aligned} l_3 &= {\cdot}504\,l_1+12{\cdot}80 \ldots\ldots\ldots\ldots (2) \\ &= {\cdot}504\,(17{\cdot}1)+12{\cdot}80 \\ &= 21{\cdot}42 \text{ cm. (Compare with Hjort's observed average } l_3=21{\cdot}6 \text{ cm.)} \end{aligned}$$

Finally, from our equation (3) let us calculate the length $l_4$ which would be reached by a *Sussex* fish commencing at a length $l_3=21{\cdot}6$ cm., the average value of $l_3$ for the *Grimsby* fishes :—

$$\begin{aligned} l_4 &= {\cdot}774\,l_3+6{\cdot}71 \ldots\ldots\ldots\ldots\ldots (3) \\ &= {\cdot}774\,(21{\cdot}6)+6{\cdot}71 \\ &= 23{\cdot}42 \text{ cm. (Compare with Hjort's observed average } l_4=24{\cdot}1 \text{ cm.)} \end{aligned}$$

From these results we are surely justified in suspecting that the Sussex fishes and the Grimsby fishes had, for the two years in which they grew from $l_1$ to $l_3$, been under growth conditions of a closely similar nature. In their fourth year, however, when changing from $l_3$ to $l_4$, it would seem that the Grimsby fishes had experienced slightly the more favourable conditions for growth.

The fact that the average value of $l_1$ is greater for the Sussex fishes than for those from Grimsby shows that fishes with the greater values of $l_1$ were relatively more numerous on the Sussex ground than on the Grimsby ground at the time of sampling.

A more critical method for comparing these two sets of data would have been to determine equations for the Grimsby fishes similar to equations 1 to 5 and then make a comparison between corresponding equations. It does not seem necessary, however, here to do this as the above is sufficient to illustrate the usefulness of the equations in this instance.

### *Differences of Growth as Evidence of Migrations.*

One further important application of these equations must be considered. Storrow (**21**, p. 13), following the earlier observations of Lea, has endeavoured to trace the movements of herring shoals by a study of the differences in the yearly increments of growth as exhibited on the scale. If we imagine a herring which, say, for the first three years of its life had remained within a region where unduly large growth does not occur, and assume that it migrates at the end of the third year to a region where it can grow at a relatively faster rate than hitherto, then its scale would show an unusually wide zone of growth for the latter period. Storrow has followed this conception and thereby endeavoured to trace the movements of herrings from " narrow seas " to " oceanic " conditions, and vice versa. Now, although there appears to be nothing inherently wrong with this principle, the study of our growth equations shows most clearly that care must be exercised in interpreting the differences between annual increments of growth as shown by the scales. Every difference must be considered in its relation *to the actual lengths of the fishes at the commencement of the growth period in which the difference arose,* for we have seen that fishes which are smaller at the beginning of any one growth period will add a greater increment of length by the end of that period than those which are larger.* Thus, if in an Area, A, three-year-old fishes were found to have added 2 cm. during the fourth year, while in a second area, B, similar-aged fishes were found to have added 3 cm. during the same period, it is incorrect to accept this observation as evidence of better growing conditions in area B unless it can be demonstrated that at the beginning of the fourth year the average size was the same in the two areas.

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* Watkin (**22**, Part V, p. 59) refers to this phenomenon as " compensatory growth." See also D'Arcy Thompson, " Growth and Form " (p. 79).

## THE NUMBER OF VERTEBRÆ.

### *Preparation of Skeletons.*

At an early stage of the work a number of records were lost due to three causes :—

1. Identification labels became unreadable as the result of boiling.
2. Identification labels became detached during boiling or subsequent cleaning.
3. An undue amount of breakage of skeletons occurred during cleaning.

The first of these difficulties was overcome by writing the serial number of the fish in marking ink, sold under the commercial name of "Melanyl," on linen tape. The second was overcome by securing the safety-pin through the skull behind the eyes. Breakage of skeletons was reduced to a minimum by commencing with the fish immersed in cold water and raising almost but not quite to the boiling point. In this way the flesh was just set and came away easily and cleanly, leaving the skeleton intact with all the vertebræ secure. A final cleaning with a tooth-brush in cold water ensured a skeleton in excellent condition for counting vertebræ when dried.

### *Use of Radiograms.*

An alternative method for determining the number of vertebræ has been tried, which promises to be useful and convenient when the fishes are too small to be boiled. Radiograms are taken and counts of the vertebræ made direct from them. Dr. J. B. Stauffer, of Devonport, was good enough to arrange for a trial of the method at the Royal Albert Hospital, and more recently Dr. H. A. Harris, of the Institute of Anatomy, University College, London, provided me with a series of most beautiful negatives of herrings ranging from about 35 mm. to 80 mm. in length.

### *The Vertebral Count made.*

The actual count of the "number of vertebræ" was identical with that of Orton (**18**, p. 80) ; that is to say, *exclusive* of the terminal ossicle. Fig. 4, reproduced from Johansen (**10**, p. 6, Fig. 4), may be used to demonstrate the difference between the count made at Plymouth and that adopted by Johansen. At Plymouth the count concluded with the vertebra marked 2, whereas Johansen included No. 1 in his count. Thus, all Plymouth records of the total number of vertebræ need to be increased by one before they become comparable with those of Johansen.

A sample of one hundred fishes usually included one which exhibited an abnormality in the vertebral column (see Ford and Bull, **5**). Such abnormal specimens were not used for the statistical count.

### *The Chances of drawing truly Representative Samples from a known Population.*

If a random sample of herrings be taken and the number of vertebræ in each determined, a " frequency " table can be drawn up to show the number of fishes having *a*, *b* . . . *x* vertebræ respectively. Now it is no more reasonable to expect this table to depict an exact representation of the proportions in the population sampled than it would be to expect to draw the ace of spades from a pack of cards in a single trial. Either event might, of course, occur, but the " chances " are against it. In the case of the pack of cards which we know to consist of 52 dissimilar cards, we say that the " chance " of cutting the ace of spades at a single trial is $\frac{1}{52}$, for any one of the pack is equally likely to turn up. Similarly, if we knew the exact proportions of fishes having *a*, *b* . . . *x* vertebræ in a population of herrings, we could calculate the chance of drawing a sample of any given size and of any given composition. For example, let us assume a very large population of herrings having 57, 56, or 55 vertebræ, the proportions of the three classes being :—

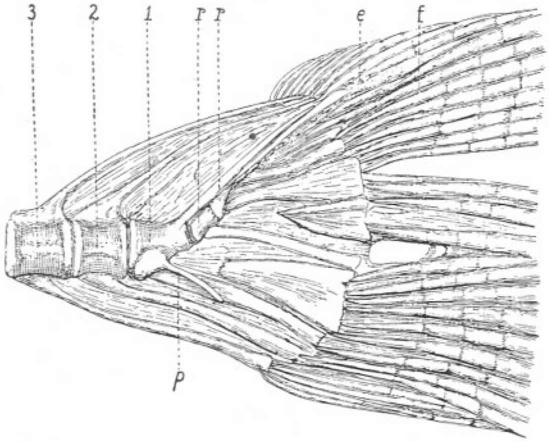

Fig. 4.—Caudal bones of a herring of 75 mm., Limfjord, Jutland, Jan. 1916 (after Johansen).

| Johansen. | Orton and Ford. |
|---|---|
| 1. Vertebra regarded as the last. | 1. Not included. |
| 2. Vertebra regarded as the last but one. | 2. Vertebra regarded as the last. |

| | |
|---|---|
| Fishes with 57 vertebræ . . . | 10% |
| ,, ,, 56 ,, . . . | 60% |
| ,, ,, 55 ,, . . . | 30% |

The formula given in the footnote below* enables us to calculate the chance of drawing a sample of one hundred fishes in which the proportions of the vertebral classes are of a particular value. In the following table the values of the chance for nine conceivable samples are given :—

SAMPLES.

| No. of Vertebræ | $A_1$ | $A_2$ | $A_3$ | $A_4$ | $A_5$ | $A_6$ | $A_7$ | $A_8$ | $A_9$ |
|---|---|---|---|---|---|---|---|---|---|
| 57 | 1 | 1 | 5 | 5 | 10 | 15 | 15 | 20 | 20 |
| 56 | 78 | 58 | 60 | 70 | 60 | 50 | 60 | 60 | 40 |
| 55 | 21 | 41 | 35 | 25 | 30 | 35 | 25 | 20 | 40 |
| $n$ | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| Value of Chance | $\frac{8}{10,000,000}$ | $\frac{6}{1,000,000}$ | $\frac{2}{1,000}$ | $\frac{1}{1,000}$ | $\frac{1}{100}$ | $\frac{1}{1,000}$ | $\frac{2}{1,000}$ | $\frac{3}{10,000}$ | $\frac{9}{10,000,000}$ |

It is seen that sample $A_5$ is more likely to occur than any one of the others. This illustrates the general fact that in taking a random sample from a population, the one most likely to occur is that which is a faithful representation of the population sampled. The values of the chance also show that the nearer the sample approaches the true representation the better its chance of being drawn. The values of the chance for samples $A_1$ and $A_9$ which exhibit proportions of the vertebræ classes appreciably different from those of the population are, thus, extremely small.

The value of the "chance" is materially affected by an increase in the number of fishes comprising the sample. This important fact may be illustrated by comparing the values of the chance for samples constructed as follows :—

SAMPLES.

| Percentage No. of fishes with | Series 1. | Series 2. | Series 3. |
|---|---|---|---|
| 57 vertebræ | 10% | 10% | 20% |
| 56 ,, | 40% | 60% | 60% |
| 55 ,, | 50% | 30% | 20% |
| Value of chance when n=100 | ·000001 | ·012 | ·00003 |
| n= 50 | ·000208 | ·023 | ·00114 |
| n= 20 | ·008245 | ·056 | ·01555 |

---

* The "chance" of a random sample of n articles giving $a_1$ of the first kind, $a_2$ of the second . . . $a_s$ of the last kind is given by :— $\frac{\underline{|n}}{\underline{|a_1}\;\underline{|a_2}\;\ldots\;\underline{|a_s}}\,p_1^{a_1}\,p_2^{a_2}\cdots p_s^{a_s}$. where $p_1\,p_2\ldots p_s$ are the "probabilities" that a single item drawn from the population is of the 1st, 2nd . . . sth kind (*vide* Fisher, **4**, p. 66).

It will be seen that the effect of increasing (n) from 20 to 100 has been to lessen the absolute value of the chance in each of the series, but that the degree of lessening is very much more marked in series 1 and 3 than in series 2. In other words, although we have actually lessened our chance of drawing an *exact* representation of the population (series 2), we have at the same time reduced to a far greater degree the chance of drawing an "outside" sample (series 1 and 3). Thus, in practice, by making our statistical sample as large as possible, we very materially add to our chances of gaining a close approximation to the composition of the population sampled.

In the foregoing illustrations, however, we have been dealing with samples from a *population of known composition*, whereas normally we have to do with samples which come from a population whose composition we never can know, but concerning which we wish to obtain information. Having taken a sample, no matter how large, we are bound to admit that in our very first trial we may have drawn an "outside chance" of composition quite different from that of the population. But while this fact must not be overlooked, we are entitled to regard this event as highly improbable, and to suspect that the sample is a not unreasonable approximation to the true proportions in the population.

### *The Arithmetic Mean and the Standard Deviation.*

The characterisation of a population in the form of a frequency table showing the proportions of its component vertebræ classes is somewhat unhandy for statistical purposes. As an alternative it has been found more convenient to specify the composition of a population in terms of certain purely mathematical characters or "parameters" (Fisher, **4**, p. 7). There are two "parameters" which we need to consider at this stage, viz. the Arithmetic Mean Number of vertebræ (M) and the Standard Deviation ($\sigma$). Let us consider a sample of 363 Shetland herrings examined by Johansen (**11**, p. 8) :—

| No. of Vertebræ | 51 | 54 | 55 | 56 | 57 | 58 | 59 |
|---|---|---|---|---|---|---|---|
| No. of Fishes | 1 | 1 | 10 | 170 | 163 | 17 | 1 |

Let us imagine 363 exactly similar weights suspended from a graduated rod in their appropriate positions, according to the above distribution, as in Fig. 5. Obviously there is but one point on the rod at which the latter could be supported so that this system of weights would remain in an exact state of "balance." This point is in the region of 56·504.

That this is so is shown by the fact that if we multiply the number of weights at each point of suspension by their distance from 56·504, the sum of the products to the left is approximately equal to that of the products to the right :—

| Left. | Right. |
|---|---|
| 1 × 5·504 = 5·504<br>1 × 2·504 = 2·504<br>10 × 1·504 = 15·040<br>170 × ·504 = 85·680 | 163 × ·496 = 80·848<br>17 × 1·496 = 25·432<br>1 × 2·496 = 2·496 |
| Sum = 108·728 | Sum = 108·776 |

The value, 56·504, is the Arithmetic Mean Number of Vertebræ for the sample. This statistic is, thus, simply and solely a numerical value representing the centre point of the distribution of the fishes among the several vertebræ classes ; it has no concrete counterpart in nature.

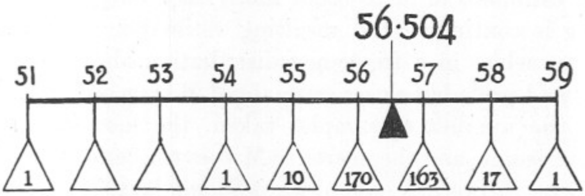

FIG. 5.—Diagram illustrating the nature and significance of the "Arithmetic Mean" (see text, p. 256).

But, just as there are many ways of redistributing the 363 weights along the rod while still retaining balance at point 56·504, so are there many different frequency distributions having the same value for the Arithmetic Mean. We therefore need some further character which will serve to specify the extent of the scattering or dispersion of individuals about the mean. One way of doing this is to add together all the individual deviations from the mean, irrespective of their + or − sign, and divide by the total number of individuals. The result is the *average* or *mean deviation.* Its value for the above sample is ·599. A more convenient character, however, is the *standard deviation*, which, like the average deviation, is a form of average of individual deviations from the Arithmetic Mean, but derived in a different manner. Instead of ignoring the positive and negative signs of these deviations, the deviations are squared, thereby bringing all of them to the same positive sign. An average of these squares is then taken. The square-root of this mean square is the standard deviation. Its value for the above sample is ±0·718.

### *Errors due to Sampling.*

From the data for a sample (A) of 363 fishes, Johansen thus arrived at estimates $m_a$ (=56·504) and $\sigma_a$ (=±0·718) of the parameters M and $\sigma$ for the particular population he had sampled. Now, it is almost certain that if Johansen had been able to analyse a second sample (B), also of 363 fishes and *taken from the same population*, he would have arrived at a second pair of estimates, $m_b$ and $\sigma_b$, which differed from $m_a$ and $\sigma_a$, notwithstanding the fact that both samples had been taken from the same population. The estimates $m_a$ and $m_b$ (and similarly $\sigma_a$ and $\sigma_b$) are, as we say, subject to "errors due to sampling," and it is necessary for us next to consider the question of the magnitude of such "errors." We have already seen that in drawing a single sample from a population, the chances are all in favour of its being one which fairly faithfully depicts the true composition of the population sampled. If, then, we proceed to draw a number of similar samples in succession, we may expect near estimates of M to occur more frequently than outside ones. As sampling is continued, the resulting estimates $m_a$, $m_b \ldots m_x$ tend to group themselves in a frequency distribution about a central value, itself a new and probably closer estimate of M than any one of the series. The larger the number of samples taken, the more regular does the distribution become, and the nearer to M does the central value approach. In the extreme theoretical case of an *infinitely* large number of samples, the distribution is perfectly symmetrical and of a particular mathematical type, known as the "normal," while the central value is identical with M. The standard deviation ($\sigma_M$) of this normal distribution of estimates of M is a convenient measure of the average amount by which individual sample estimates differ from M itself. Moreover, the amount ($m_x-M$) by which any one particular sample estimate differs from M can be expressed in terms of the average ($\sigma_M$). Now Fisher (**4**, p. 46) tells us that ($m_x-M$) exceeds twice $\sigma_M$ about once in 22 trials, thrice $\sigma_M$ only once in 370 trials, while nearly a thousand million trials are needed for ($m_x-M$) to exceed $\sigma_M$ sixfold. With these results in mind, statisticians have formally agreed to assume that a random sample, drawn from a population whose arithmetic mean number of vertebræ is M, is not likely to yield an estimate of M, which falls outside the range ($M-2\ \sigma_M$) and ($M+2\ \sigma_M$). But, as we have seen, $\sigma_M$ is a purely theoretical value representing the standard deviation of the distribution of an infinite series of estimates of M, so that until we can obtain some knowledge of its probable value, the above formal agreement is of little practical use. Obviously we cannot obtain the exact value of $\sigma_M$, but fortunately we can derive an *estimate* of it from sample data. This estimate of $\sigma_M$ is known as the *standard error of the mean* ($\sigma_m$).*

Returning now to Johansen's sample of 363 fishes, we have an estimate of M ($m_a = 56{\cdot}504$) and an estimate of $\sigma_M$ ($\sigma_{m_a} = \pm 0{\cdot}0377$), so that we may say that the value of M lies most likely between $56{\cdot}504 - 2(0{\cdot}0377)$ and $56{\cdot}504 + 2(0{\cdot}0377)$.

## *Comparisons between Samples.*

Supposing that, in practice, we have analysed two samples and arrived at the following estimates :—

| | Sample 1. | Sample 2. |
|---|---|---|
| No. of Fishes . . . . . | $n_1$ | $n_2$ |
| Arithmetic Mean No. of Vertebræ . . | $m_1$ | $m_2$ |
| Standard Deviation . . . . | $\sigma_1$ | $\sigma_2$ |
| Standard Error of the Mean . | $\sigma_{m_1} = \frac{\sigma_1}{\sqrt{n_1}}$ | $\sigma_{m_2} = \frac{\sigma_2}{\sqrt{n_2}}$ |

We observe that there is a difference ($m_1 - m_2$) between the means. How can we decide whether this difference is one which might reasonably arise between two samples from the same type of population, or is due to the fact that we have sampled different populations ? If the two samples had been taken from the same population, the probability is that neither $m_1$ nor $m_2$ would have been greatly different from the parameter (M) of the population. From this it follows that their difference ($m_1 - m_2$) would not have been large. Here again, by formal agreement, we say that probably ($m_1 - m_2$) would not have exceeded twice its own standard error, viz. $\sqrt{\sigma_{m_1}^2 + \sigma_{m_2}^2}$.† If then we find that the difference ($m_1 - m_2$) does actually exceed twice its own standard error, we suspect that the samples had been taken from different populations.

It will be instructive here to return to the question of the number of fishes (n) in our statistical sample. We have seen (p. 255) from the study of the "chance" for each of a series of similar composed samples in which (n) is 20, 50, and 100 respectively that the value of the chance is very materially affected by the value of (n). This same fact may be

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* The standard error of the mean ($\sigma_{m_x}$) is calculated by $\sigma_{m_x} = \pm \frac{\sigma_x}{\sqrt{n}}$

where $\sigma_x$ = standard deviation of sample.
n = number of individuals in sample.

The mathematical argument for using the value of $\sigma_{m_x}$ as an estimate of $\sigma_M$ may be found in a standard textbook. See table of Notations and Formulæ on page 261.

† See table of Notations and Formulæ on page 261.

demonstrated by comparing the values of (m) and of their standard errors for samples of different sizes from two populations A and B : –

| Number of Fishes with | Population A. Sample $a_1$ | Sample $a_2$ | Population B. Sample $b_1$ | Sample $b_2$ |
|---|---|---|---|---|
| 57 vertebræ | 10 | 40 | 15 | 60 |
| 56 ,, | 60 | 240 | 60 | 240 |
| 55 ,, | 30 | 120 | 25 | 100 |
| n | 100 | 400 | 100 | 400 |
| Arithmetic Mean No. of Vertebræ (m) | $55{\cdot}80 = m_1$ | | $55{\cdot}90 = m_2$ | |
| Standard Deviation ($\sigma$) | $0{\cdot}60 = \sigma_1$ | | $0{\cdot}62 = \sigma_2$ | |
| Standard Error of Mean $\sigma_m = \frac{\sigma}{\sqrt{n}}$ | 0·060 | 0·030 | 0·062 | 0·031 |
| $\sigma_m{}^2$ | 0·0036 | 0·00090 | 0·0039 | 0·000975 |

Comparing samples $b_1$ and $a_1$ : $(m_2 - m_1) = 0{\cdot}10$ ;

$$\text{standard error of } (m_2 - m_1) = \sqrt{\sigma_{m_2}^2 + \sigma_{m_1}^2} = 0{\cdot}087.$$

Comparing samples $b_2$ and $a_2$ : $(m_2 - m_1) = 0{\cdot}10$ ;

$$\text{standard error of } (m_2 - m_1) = \sqrt{\sigma_{m_2}^2 + \sigma_{m_1}^2} = 0{\cdot}043.$$

For the samples of 100, viz. $b_1$ and $a_1$, the difference $(m_2 - m_1)$ does not exceed twice its own standard error. Therefore we should not suspect any material difference in type between the two populations B and A. But when the samples are increased to 400, as in samples $b_2$ and $a_2$, then the difference $(m_2 - m_1)$ does exceed twice its own standard error, and we should be led to suspect a significant difference in composition between the two populations.

An alternative method of ascertaining whether or no two samples may be regarded as representative of distinct populations, is to apply a "test of independence" explained by Fisher (**4**, p. 77), in which the value of an "index of dispersion," $\chi^2$ is calculated, and its significance noted from a table of "goodness of fit" (Fisher, p. 98). The reader is referred to Fisher for an explanation of these terms, and of the details of the test itself. One example, worked out in detail, will, however, illustrate the method :—

| | No. of Vertebræ. | | | No. of Fishes. |
|---|---|---|---|---|
| | 57 | 56 | 55 | |
| Sample C | 10 | 40 | 50 | 100 |
| Sample D | 15 | 78 | 27 | 120 |
| Totals | 25 | 118 | 77 | |

CLASS 57.

$$\begin{aligned} 10 \times 120 &= 1{,}200 \\ 15 \times 100 &= 1{,}500 \\ \text{Difference} &= 300 \\ \text{Diff.)}^2 &= 90{,}000 \\ \text{Discrepancy} = \frac{(\text{diff.})^2}{25} &= 3{,}600 \end{aligned}$$

CLASS 56.

$$\begin{aligned} 40 \times 120 &= 4{,}800 \\ 78 \times 100 &= 7{,}800 \\ \text{Difference} &= 3{,}000 \\ (\text{Diff.})^2 &= 9{,}000{,}000 \\ \text{Discrepancy} = \frac{(\text{diff.})^2}{118} &= 76.300 \end{aligned}$$

CLASS 55.

$$\begin{aligned} 50 \times 120 &= 6{,}000 \\ 27 \times 100 &= 2{,}700 \\ \text{Difference} &= 3{,}300 \\ (\text{Diff.})^2 &= 10{,}890{,}000 \\ \text{Discrepancy} = \frac{(\text{diff.})^2}{77} &= 141{,}400 \end{aligned}$$

$$\text{Total discrepancy} = (3{,}600 + 76{,}300 + 141{,}400) = 221{,}300$$

$$\therefore \; \chi^2 = \frac{221.300}{100 \times 120} = 18.44$$

From Table III (Fisher, **4**, p. 99) it is seen that the " chance " of such a discrepancy is less than one in a hundred ; $\chi^2$ may thus be regarded as significant of a difference in type of population sampled.

### *Table of Notations and Formulæ.*

It has not been thought necessary to include in preceding paragraphs the proofs of the formulæ given below. Such proofs can be found in standard textbooks. A recommended list of suitable works of reference are given on page 12 of the leaflet issued by the British Association on Biological Measurements (British Association, Section D, Leeds, 1927).

Standard Deviation $\sigma = \pm \sqrt{\dfrac{\Sigma p\alpha^2}{(n-1)}}$

where $p$ = number of variates in the separate classes.
$\alpha$ = deviation of a variate from the mean (m).
$n$ = total number of variates.

Standard Error of the mean m, calculated by $\sigma_m = \pm \dfrac{\sigma}{\sqrt{n}}$

Standard Error of the Standard Deviation, calculated by $\sigma_\sigma = \dfrac{\sigma}{\sqrt{2n}}$

Standard Error of a difference $(m_1 - m_2)$, calculated by $\sqrt{\sigma_{m_1}^2 + \sigma_{m_2}^2}$

## BIOLOGICAL SIGNIFICANCE OF STATISTICAL RESULTS.

The preceding paragraphs were devoted to a survey of the nature and collection of sample data, and, in them, an endeavour was made to explain the methods of treatment utilised. It is now necessary to consider how these raw statistical data serve to advance our knowledge of those vital events in the life-cycle of herrings upon which the great commercial fisheries are so completely dependent.

The annual life-cycle of an adult herring may be said to consist essentially of a movement inshore to a spawning ground, followed by an outward movement to a feeding ground. On the spawning ground the fish sheds its ova or milt, thereby playing its part in the determination of the morphological characters of a batch of larvæ which in due course will themselves become adult. It is not yet known, however, to what extent the morphological characters of the larvæ are due to heredity or to environmental influences. On a feeding ground the fish feeds and grows and records on its scale an index of the increase in length. There is no reason to suppose that the number of vertebræ of an adult fish, which was definitely fixed at a very early stage in its life, undergoes any subsequent change. Thus the scales of a fish will tell us what happened during its stay on a *feeding* ground, whereas the number of vertebræ in itself tells us nothing of its adult life, but gives us a clue to the combined effect of parental influence, and environmental influence soon after it was born. It will be appreciated, therefore, that by an organised scheme of intensive sampling carried out for a sufficient time, it should ultimately be possible from the study of scales to link up feeding grounds with spawning grounds, and from the study of the number of vertebræ to determine whether given feeding grounds and spawning places are visited by distinct herring stocks, as well as the extent to which this occurs. For instance, from the comparison of scale measurements of fishes spawning at Plymouth during the winter of 1925–26 with those of fishes taken during the feeding period in the deeper waters off the south-west coast of Cornwall in 1926, it would seem reasonable to suspect that some of the latter had come to Plymouth to spawn ; on the other hand, the data on the average number of vertebræ for the same samples showed that in both these areas more than one type of stock occurred. The interpretation of these undoubtedly different types of stock as revealed by the study of such characters as the average of vertebræ, the number of keeled scales or bony fin-rays, presents many difficulties. Without the slightest doubt, the averages for any one of these characters often differ from sample to sample in the same sampling area, and from area to area, by amounts appreciably exceeding those which can be wholly attributed to errors due to sampling. In an endeavour to demonstrate the difficulties of the problem presented, we will imagine an egg spawned by a herring having 56 vertebræ to be fertilised by milt from a male also having 56 vertebræ. What number of vertebræ will the resulting offspring possess? We will consider this question under two hypotheses :—

*Hypothesis* (1) :—

*That the average number of vertebræ is a character strictly inherited and thus unaffected by environmental conditions prevailing at the time of its fixation.*

Under this hypothesis, the average number of vertebræ for our larval brood would invariably be 56·00.

*Hypothesis* (2) :—

*That the average number of vertebræ is a character entirely decided by environmental conditions prevailing at the time of its fixation and thus not in the least dependent upon the parental number of vertebræ.*

In this instance we should require to know the particular environmental conditions under which the vertebræ of the larvae were developed before we could state what the average number of vertebræ for the total brood would be.

Let us next enquire how, under these two hypotheses, we should interpret a marked difference between the average number of vertebræ for herrings in one area A and that for herrings in a second area B? Under hypothesis (1) it would seem quite reasonable to suspect that areas A and B were populated by different "genetic races" of herrings, each "race" carrying out an independent life-cycle within definite limits of distribution, and retaining its identity from generation to generation by the processes of heredity. This being so, herrings from area A, if transported to area B, would carry with them their distinct racial potentialities and react accordingly. Under hypothesis (2), however, it would be held that the observed differences in average number of vertebræ between the herrings in area A and those in area B were entirely due to the fact that the larvæ developed their vertebræ under different environmental conditions. Fishes from area A if transplanted to area B would subsequently react to the new environmental conditions in precisely the same way as the normal inhabitants of the area did.

Now Johansen by comparing the values of the average number of vertebræ, keeled scales, and fin-rays for samples of herrings from different parts of the North Sea, and noting the magnitude of the differences, has created a considerable number of "races" which he regards as true races, the characters of which are due to heredity (**11**, p. 90). He has expressed the view, however, that smaller differences, such as those between the "Scotch Summer Herring" and the "Dogger Bank Herring" and between the " Scotch Spring Herring " and the " Icelandic Summer Herring " may not be of a hereditary nature. Johansen would thus seem to take a standpoint which is in the nature of a compromise between our hypotheses 1 and 2 above.

It seems to the present writer that until more definite knowledge of the respective parts played by heredity and environment in the establishment of the number of such characters as vertebræ, keeled scales, and fin-rays is gained, it is doubtful whether, in directing our sample analyses towards the immediate recognition of possible " races," we are following the method most likely to lead to a correct interpretation of observed sample differences. We are not without indications that environment can, and does, play its part in the establishment of the number of vertebræ, keeled scales and fin-rays.

Schnakenbeck (**19**, p. 192), by utilising the values of the average number of vertebræ for no less than twenty-eight of Johansen's races of herrings, has shown that the value increases from areas of low salinity to those of higher salinity. Schmidt (*vide* Johansen, **11**, p. 89) has demonstrated by direct experiment that temperature and salinity materially affect the average value of the above morphological characters in *Zoarces viviparus* L., *Lebistes reticulatus* Regan., and *Salmo trutta* L. Johansen (**11**, p. 90) suggests that the herring is a less " plastic " species than those studied by Schmidt, but there is, as yet, no experimental proof of this.

In accepting appreciable differences between sample averages as evidence for differences in " racial " composition, we are, in practice, forced to conclude that racial admixture is of frequent occurrence (*vide* Part 2, p. 275). In a new area of observation the knowledge that such admixture may occur renders it most difficult to decide what races are actually represented. If, too, mixture of races, particularly if it occurs at spawning time, is a common feature, then it is not easy to understand how the distinctive characters of the different races are retained from one generation to the next.

As an alternative to the study of sample averages as " racial " characters, it is suggested that they should be examined as the defining morphological characters of *temporary populations*, regardless of " race," and used in conjunction with the data on age and growth from scale measurements as clues to the movements of shoals which brought about those temporary populations. Having established a working knowledge of these movements, the recognition of " races," if such are shown to exist, would follow as a natural sequence.

It is not proposed further to pursue this matter at this stage ; the present object is to impress the case for the fullest possible study of the morphological differences which the statistical study of random samples has amply demonstrated. Sampling in a given area must be frequent and continuous. Experience in the south-western area has shown most conclusively that it is very dangerous to attempt to draw conclusions as to the herring populations frequenting an area from the results of a few isolated samples. Furthermore, it becomes increasingly evident that one of the most desirable and urgent pieces of research is the study by experiment of the number of vertebræ in herrings reared from eggs of known parentage under controlled environmental conditions.

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# Herring Investigations at Plymouth. II. The Average Number of Vertebrae for Herrings from the English Channel and South-East of Ireland.

By

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With a Chart and 1 Figure in the Text.

## CONTENTS.

## THE HERRINGS OF THE ENGLISH CHANNEL AND SOUTH-EAST OF IRELAND.

THE published observations of other workers, on samples of herrings taken from the area under consideration, whether they relate to the study of such morphological characters as the number of vertebræ and keeled scales, or are chiefly concerned with the examination of the growth of the fishes as indicated by their scales, demonstrate very clearly that the eastern, central and western sectors of the area are visited by herrings which differ in character. It will be convenient to summarise the opinions of these workers under the headings of the statistical regions in which the samples were taken. The reader is referred to the chart on page 269, which shows the geographical extent of the regions dealt with.

### *Statistical Region VIId (English Channel, East).*

Johansen (**4**), Hodgson (**2** and **3**) and le Gall (**5**) have made interesting contributions to our knowledge of fishes caught in this region. On the one hand we have Johansen who, on the evidence of samples examined by Sauvage and Canu, Cligny, Delsman and Redeke, postulates the existence of a race of herrings which he calls "Channel Sea Herring" to include the winter-spawning fish of both the eastern end of the English Channel and of the south-western corner of the North Sea. On the other hand, both Hodgson and le Gall, from their studies of scales, oppose this view, and draw distinction between the herrings of the Southern Bight ("Southern North Sea Type" of Hodgson) and those of the Channel proper. They admit that shoals of the Southern North Sea Type enter the Channel to spawn, but contend that after spawning they return to the North Sea. In contrast with this, they hold that the fish of the Channel proper are essentially Channel fish, quite distinct from the Southern North Sea Type, which carry out the whole of their migratory cycle within the confines of the Channel itself. On a line running approximately from Newhaven on the English side to Cap d'Antifer on the French, shoals of the two forms may intermingle, with the result that mixed catches are liable to be made in this vicinity.

### *Statistical Region VIIe (English Channel, West).*

It will suffice for the present purpose to restrict attention to observations made on fishes caught off Plymouth. Here we find that Johansen, on the evidence of the results of Orton (**6**), considers the Plymouth fish to belong either to one race or a mixture of races quite distinct from his Channel Sea Herring found to the eastward. Schnakenbeck (**8**), however, examined three samples from Plymouth, and came to the conclusion that two of the samples could be considered representative of such a new race, but that the third appeared similar to Johansen's Channel Sea Herring. Le Gall's view is that the Plymouth fish belong to what he terms "Hareng type Atlantique, variété côtière." He believes that all along the English and French coasts of the English Channel, westwards of a line from Newhaven to Cap d'Antifer, the herrings belong to one coastal type of herring which carry out the whole of their migratory cycle within the English Channel. Watkin (**10**) has also examined fishes from Plymouth and compared them with those from still more westerly waters, and he tends to the view that there is a general relationship between them.

### *Statistical Regions VIIf and VIIg (Bristol Channel and South-East of Ireland).*

The published work on herrings from these two regions is limited in extent. The work of Heldt (**1**) was, until recently, the chief evidence used as reference by others. Heldt regarded the "Smalls" trawled herrings as forming yet another distinct race, and his finding is quoted and accepted by Johansen and Schnakenbeck. In the

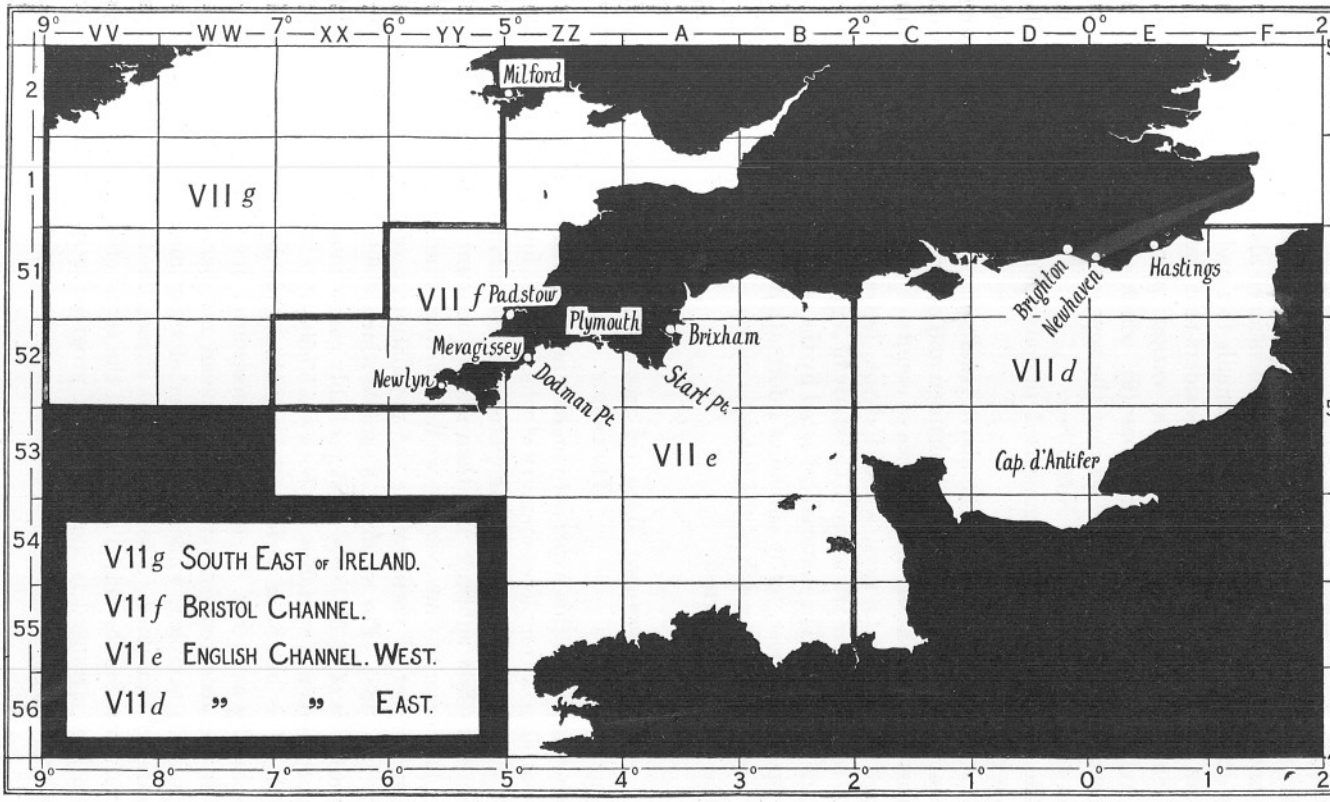

CHART SHOWING STATISTICAL REGIONS DEALT WITH IN THIS PAPER.

case of le Gall, we find that he proffers the name of "race Atlantique variété du large," thereby suggesting some difference from and yet some relationship between the Smalls fish and his "variété côtière" from the Channel. Watkin, as has already been mentioned above, does not favour any distinction of race between the Smalls fish and those taken off the coasts of Devon and Cornwall, but considers that the former after leaving the Smalls grounds come to spawn at various places in the latter area. He refers to Storrow's observations (**9**), which are broadly similar in import, and emphasizes the fact that the western fishes are much larger than those of the Southern North Sea.

The foregoing may be summarised in convenient tabular form. (See table on opposite page.)

It is to be observed that the above results have been reached by two distinct methods of approach. Johansen and Schnakenbeck have arrived at their conclusions on the evidence of counts of the number of vertebræ, keeled scales and fin-rays, while Hodgson, le Gall, Watkin and Storrow have confined their attention to the study of "growth facies" by measurements of scales. The material collected by the present writer is, therefore, of especial interest, for it embodies information on both the number of vertebræ and the growth of the fishes as indicated by their scales, in each of the regions concerned.

## NEW PLYMOUTH DATA ON THE AVERAGE NUMBER OF VERTEBRÆ.

The purpose of this paper is to present new data on the average number of vertebræ, a complete summary of which will be found in Table I at the end of this paper. If to the calculated average number of vertebræ for a sample we first subtract and then add an amount equal to twice the standard error of that average, we fix arbitrary limits between which the mean number of vertebræ for the population most probably lies (*vide* Part I, p. 258). For example, a sample which yields an average number of vertebræ of $55{\cdot}50 \pm 0{\cdot}06$ most probably came from a population whose mean number of vertebræ lay between $55{\cdot}50-(2\times0{\cdot}06)$ and $55{\cdot}50+(2\times0{\cdot}06)$. This has been performed for each sample and the results plotted graphically as in Fig. 1; each short horizontal line in the diagram indicates the accepted estimate of the mean number of vertebræ for the population sampled, while the number of such lines shows the number of samples examined. The centre point of each line is the average number of vertebræ for the actual sample, and the serial order in which the lines have been arranged is merely one of progressive increase in the value of these sample means.

## Statistical Regions.

| Investigator. | VIId. | VIIe. | VIIg. |
|---|---|---|---|
| Johansen | Channel Sea Herring<br>Average No. of vertebræ = 55·57*<br>(Cligny)<br>Average No. of keeled scales = 14·23<br>(Sauvage) | Separate race or admixture of races<br>Average No. of vertebræ = 55·77*<br>(Orton)<br>Average No. of keeled scales = 14·71<br>(Orton) | Separate race<br>Average No. of vert. = 56·49*<br>(le Danois and Heldt) |
| Schnakenbeck | | (*a*) Separate race<br>Average No. of vertebræ = 55·85*<br>Average No. of keeled scales = 14·37<br>(*b*) Channel Sea Herring (Johansen)<br>Average No. of vertebræ = 55·64*<br>Average No. of keeled scales = 13·85 | |
| Hodgson | (*a*) Southern North Sea Type<br>$l_1 = 8$ cm.<br>$l_2 = 16$ cm.<br>$l_3 = 20–21$ cm.<br>$l_4 = 23$ cm.<br>(*b*) Channel Type—<br>$l_1 = 12$ cm. | | |
| le Gall | (*a*) Southern North Sea Type<br>(Hodgson)<br>(*b*) Race Atlantique<br>variété côtière | Race Atlantique<br>variété côtière | Race Atlantique<br>variété du large |
| Watkin | | Fishes related in these regions. | |

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* It should be noted that the average is here expressed according to the Plymouth method of recording, and not necessarily as given in the original work (*vide* Part I, p. 253).

### *Populational Differences within the same Statistical Region.*

In the first place it will be seen that in each of the statistical regions there is a large range of variation in the average number of vertebræ. Comparisons between pairs of estimates show that the differences may be large enough to suggest that more than one type of population had been sampled. This may be exemplified by giving the values of the highest estimate and the lowest for each region together with the results of the tests of significance applied to the difference between them :—

| Statistical Region. | Highest estimate $M_h$. | Lowest estimate $M_l$. | Difference $(M_h-M_l)$. | Standard error of difference |
|---|---|---|---|---|
| VIId | 55·86 ± ·071 | 55·62 ± ·066 | 0·24 | 0·090 |
| VIIe<br>Plymouth area only | 55·91 ± ·061 | 55·57 ± ·056 | 0·34 | 0·083 |
| VIIh<br>Padstow | 55·882 ± ·056 | 55·645 ± ·067 | 0·24 | 0·087 |
| VIIg<br>Smalls trawled | 55·97 ± ·048 | 55·63 ± ·078 | 0·34 | 0·091 |
| VIIg<br>Drift fishery | 55·99 ± ·072 | 55·48 ± ·053 | 0·51 | 0·090 |

In each case the difference $(M_h - M_l)$ easily exceeds twice its own standard error, and may be regarded as indicative of real populational difference.

The importance of the observation that undoubted populational differences occur within one and the same statistical region cannot be overemphasized. The suggestion given in Part I (p. 265) that it is unsafe to draw conclusions as to the herring populations frequenting an area unless sampling has been frequent and continuous, is amply demonstrated by the above results. In each and every statistical region the results raise big difficulties regarding the various " races " postulated from an earlier study of a few samples. For instance, in region VIIg, instead of having to account for a single high value of 56·49 (Race Atlantique variété du large), we have to deal with a whole series of sample averages down to as low as 55·48.

### *Tendency for Average Number of Vertebræ to rise from East to West.*

Now although there is a large range of variation in the average number of vertebræ among samples taken within the same statistical region, the data shown in Fig. 1 also suggest that there is a general tendency for the average number of vertebræ to rise from east to west. The average of the individual sample averages for the same region may be used to demonstrate this tendency :—

| | STATISTICAL REGION. | | | | |
|---|---|---|---|---|---|
| | VIId (Sussex). | VIIe (Brixham). | VIIe (Plymouth). | VIIf (Padstow). | VIIg. |
| Average of Sample averages | 55·70 | 55·74 | 55·78 | 55·75 | 55·84 |

This second observation, unlike the first, is in general agreement with the earlier results. Thus Johansen's "Channel Sea Herring" to the eastward have the low average of 55·57 vertebræ ; the Plymouth averages (Orton, 55·77, and Schnakenbeck, 55·64 and 55·85) occupy an intermediate position, while to the westward Heldt's fishes from the Smalls have the high average of 56·49 vertebræ.

Schnakenbeck (**8**), using Johansen's data, has shown that the average number of vertebræ is low in areas of low salinity and high in areas of high salinity. It is of interest, therefore, to note that the general tendency for the average to rise from east to west in the English Channel is a repetition of Schnackenbeck's observation. Schmidt (**7**) has shown, also, that populations of *Zoarces viviparus* have a lower number of vertebræ in the inner parts of the fiords than in the outer parts, and that the salinity shows a gradation which corresponds strikingly with the gradation in the average number of vertebræ. As Schmidt points out, however, we are not justified in interpreting the upward trend of the average number of vertebræ as the direct effect of the upward change in salinity, but we are entitled to regard the coincidence of the two phenomena as an expression of the importance of environment.

## SAMPLE AVERAGES AS INDICATIONS OF "RACIAL" COMPOSITION.

If we presuppose that distinct "races" of herrings do actually exist, and accept the average number of vertebræ for a random sample as an indication of the "racial" composition of the stock sampled, we meet with the greatest difficulty in arriving at a satisfactory interpretation of the above sample data. In the first place, unless we are prepared to work on the hypothesis that the average number of vertebræ is independent of environment, we must take into account the age-composition of the sample. An annual variation in environment may induce an annual alteration in the average number of vertebræ, *within the same race,* so that the average for a random sample composed of fishes of several year-classes, is liable to variation from this cause. But the considerable variation in sample averages in the same statistical

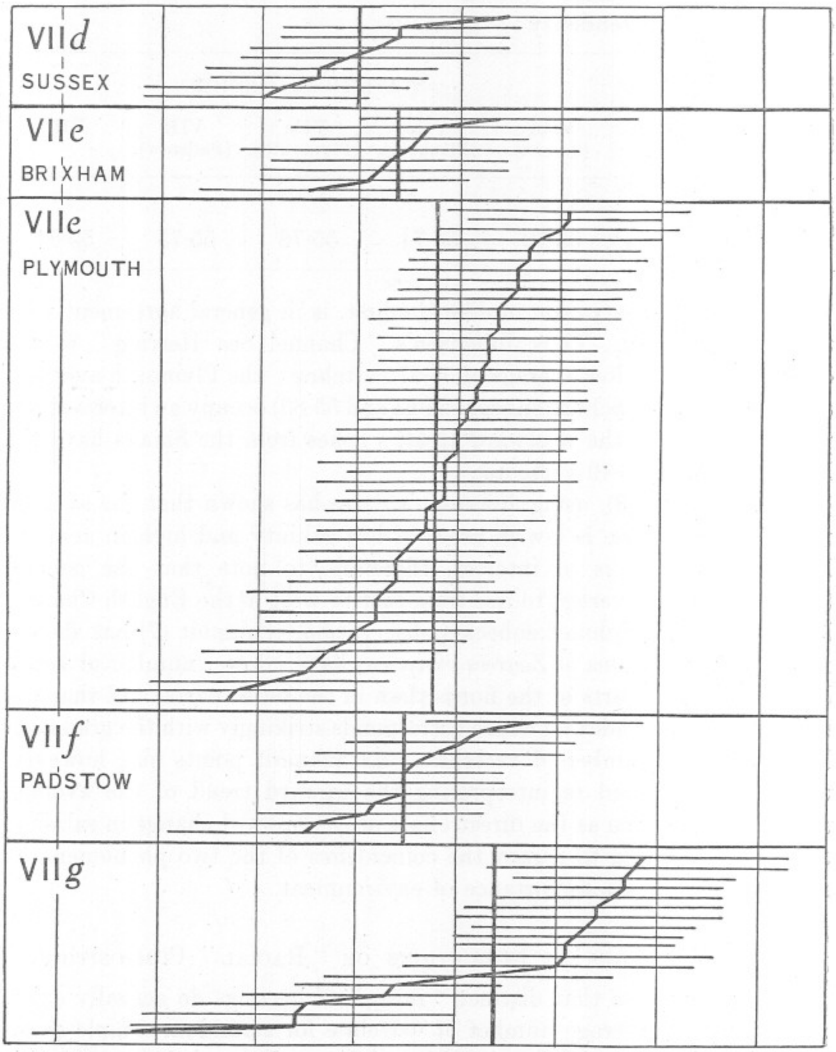

Fig. 1.—Number of vertebræ from samples taken in south and south-western waters. For explanation see text, p. 270.

region cannot, under the "racial" hypothesis, be regarded as entirely due to the annual variations in environment just mentioned, so that, in the second place, we must admit that more than one race may occur within the same statistical region. Indeed, at times, it is necessary to assume an admixture of races at one and the same time. Moreover, neighbouring regions exhibit equally pronounced mixture. It is easily seen that the sorting out of our fishes into "races" is, under these circumstances, at best, highly speculative.

As stated in Part I (p. 264), therefore, it has been considered advisable, in the first instance, not to study the average number of vertebræ as an indication of "racial" composition, but to use it, as we use the other sample data, strictly as a character of a population of herrings frequenting a given region at the time of sampling.

## SAMPLE AVERAGES AS CHARACTERS OF TEMPORARY POPULATIONS.

If the fishes of a particular year-class in a sample A were found to agree with those of a similar age in a second sample B in the average of vertebræ, it would be logical to argue that the fishes of the two samples had, in their early larval life, developed their vertebræ under identical influences. If, also, they agreed in their growth characters as indicated by scale measurements, then it would be reasonable to suspect that from their earliest days until the time of sampling, the fishes of the two samples had lived and grown under similar conditions.

The above paragraph illustrates the general principle upon which it is proposed to consider sample data. That is to say, the average number of vertebræ will be used as an index of the conditions under which the vertebræ were actually developed, while the growth data derived from measurements of scales will be utilised as an index of the conditions prevailing after the vertebræ number was definitely established. Used in conjunction, the two sets of data should enable the investigator eventually to discover the system of movements of shoals by which the different herring populations (as indicated by his samples) observed in his region were brought about.

It will be apparent to the reader that if herring "races" do exist, the knowledge of the local movements of herrings acquired by the method suggested would reveal the particular "races" represented. But the advantage of the method lies in the fact that in the initial study of the movements, work may proceed without any thought of "races" or "racial" composition.

Further study of the actual data on average number of vertebræ must thus be deferred until an account has been given of the sample data on age and growth for fishes in the statistical regions dealt with.

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## TABLE I.

| Statistical Region. | Fishing Ground. | Method of Fishing. | Port of Landing. | Date of Sample. | No of fishes in 6 Vertebræ Classes | | | | | | Total No. of Fishes in sample (n). | Arith. Mean No. of Vertebræ (m). | Standard Deviation σ | Standard Error of m $\frac{\sigma}{\sqrt{n}}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 53 | 54 | 55 | 56 | 57 | 58 | | | | |
| VIIg | "Smalls" | Trawl | Milford Haven | Aug. 19th, 1925 | 1 | – | 25 | 55 | 19 | – | 100 | 55·91 | 0·73 | 0·073 |
| | | ,, | | Sept. 1st, 1925 | – | – | 19 | 65 | 11 | – | 95 | 55·92 | 0·56 | 0·056 |
| | | ,, | ,, | Sept. 14th, 1925 | – | – | 25 | 99 | 19 | 1 | 144 | 55·97 | 0·58 | 0·048 |
| | | ,, | ,, | Sept. 30th, 1925 | – | 1 | 19 | 61 | 13 | 1 | 95 | 55·94 | 0·65 | 0·066 |
| | | ,, | ,, | Oct. 19th, 1925 | – | – | 29 | 87 | 23 | 1 | 140 | 55·97 | 0·63 | 0·054 |
| | | ,, | ,, | July 28th, 1926 | – | 1 | 39 | 41 | 9 | – | 90 | 55·64 | 0·68 | 0·076 |
| | | ,, | ,, | Aug. 10th, 1926 | – | 2 | 33 | 50 | 11 | – | 96 | 55·73 | 0·69 | 0·070 |
| | | ,, | ,, | Aug. 18th, 1926 | – | 3 | 36 | 37 | 10 | – | 86 | 55·63 | 0·73 | 0·078 |
| | | ,, | ,, | Aug. 24th, 1926 | – | – | 30 | 49 | 18 | 1 | 98 | 55·90 | 0·72 | 0·073 |
| | | ,, | ,, | Sept. 2nd, 1926 | – | – | 25 | 53 | 19 | – | 97 | 55·94 | 0·67 | 0·068 |
| | | ,, | Plymouth | Sept. 7th, 1926 | – | – | 22 | 73 | 17 | – | 112 | 55·955 | 0·59 | 0·056 |
| | | ,, | Milford Haven | Sept. 28th, 1926 | – | 2 | 22 | 51 | 10 | – | 85 | 55·81 | 0·85 | 0·072 |
| | | ,, | | Nov. 15th, 1926 | – | 1 | 31 | 82 | 19 | 1 | 134 | 55·91 | 0·65 | 0·056 |
| VIIg | Between English and Irish Coasts southwards of latitude 52° N. | Drift Nets | Newlyn | April 24th, 1926 | – | 1 | 19 | 58 | 16 | 2 | 96 | 55·99 | 0·70 | 0·072 |
| | | | Milford Haven | April 26th, 1926 | – | 3 | 63 | 77 | 14 | – | 157 | 55·65 | 0·67 | 0·053 |
| | | ,, | | June 16th, 1926 | – | – | 29 | 78 | 18 | 1 | 126 | 55·93 | 0·63 | 0·057 |
| | | ,, | ,, | June 23rd, 1926 | – | – | 24 | 50 | 20 | 1 | 95 | 55·98 | 0·71 | 0·073 |
| | | ,, | Newlyn | June 23rd, 1926 | – | 3 | 38 | 80 | 10 | – | 131 | 55·74 | 0·62 | 0·053 |
| | | ,, | Milford Haven | July 13th, 1926 | – | 5 | 79 | 63 | 7 | 1 | 155 | 55·48 | 0·67 | 0·053 |
| VIIf (ZZ 51) | Port Isaac Bay and Vicinity | Drift Nets | Padstow | Nov. 5th, 1925 | – | 2 | 24 | 79 | 14 | – | 119 | 55·88 | 0·61 | 0·056 |
| | | | ,, | Nov. 11th, 1925 | – | 1 | 34 | 77 | 6 | – | 118 | 55·75 | 0·56 | 0·051 |
| | | ,, | ,, | Nov. 17th, 1925 | – | 1 | 35 | 68 | 14 | – | 118 | 55·805 | 0·64 | 0·059 |
| | | ,, | ,, | Nov. 25th, 1925 | – | – | 37 | 74 | 7 | – | 118 | 55·75 | 0·56 | 0·051 |
| | | ,, | ,, | Dec. 11th, 1925 | – | 2 | 30 | 70 | 13 | – | 115 | 55·82 | 0·64 | 0·060 |
| | | ,, | ,, | Nov. 10th, 1926 | – | 1 | 35 | 67 | 8 | – | 111 | 55·75 | 0·60 | 0·057 |
| | | ,, | ,, | Nov. 16th, 1926 | – | 1 | 37 | 67 | 7 | – | 112 | 55·715 | 0·59 | 0·056 |
| | | ,, | ,, | Nov. 24th, 1926 | – | 3 | 44 | 58 | 11 | – | 116 | 55·66 | 0·68 | 0·064 |
| | | ,, | ,, | Nov. 29th, 1926 | – | 1 | 32 | 71 | 4 | – | 108 | 55·72 | 0·54 | 0·052 |
| | | ,, | ,, | Dec. 7th, 1926 | – | – | 35 | 61 | 10 | – | 106 | 55·76 | 0·61 | 0·059 |
| | | ,, | ,, | Dec. 20th, 1926 | – | – | 40 | 62 | 13 | 1 | 116 | 55·78 | 0·67 | 0·062 |
| | | ,, | ,, | Dec. 28th, 1926 | – | 2 | 47 | 49 | 12 | – | 110 | 55·645 | 0·70 | 0·067 |
| VIIe (YY 52 & 53) | Mounts Bay | Trawl | Plymouth | Mar. 9th, 1926 | – | 3 | 51 | 53 | 6 | – | 113 | 55·55 | 0·64 | 0·060 |
| | | ,, | ,, | Mar. 17th, 1926 | – | 1 | 32 | 74 | 9 | 1 | 117 | 55·80 | 0·62 | 0·057 |
| | | ,, | ,, | Mar. 22nd, 1926 | – | 1 | 38 | 84 | 9 | – | 132 | 55·76 | 0·57 | 0·051 |
| VIIe (ZZ 52) | Mevagissey Bay, 6 miles E.S.E. of Mevagissey | Set-Nets | Mevagissey | Oct. 26th, 1925 | – | 3 | 42 | 83 | 6 | 1 | 135 | 55·69 | 0·62 | 0·052 |
| | | Drift | ,, | Jan. 8th, 1926 | – | – | 22 | 65 | 8 | – | 95 | 55·85 | 0·55 | 0·056 |
| VIIe (ZZ 52) A 52) | Area covered by local fishery at Plymouth | Set-Nets<br>Seine<br>Drift Nets | Plymouth | Nov. 20th, 1924 | – | 1 | 31 | 77 | 6 | – | 115 | 55·77 | 0·55 | 0·051 |
| | | | ,, | Dec. 3rd, 1924 | – | – | 31 | 62 | 6 | – | 99 | 55·75 | 0·56 | 0·056 |
| | | | ,, | Dec. 9th, 1924 | – | 2 | 23 | 64 | 8 | – | 97 | 55·80 | 0·60 | 0·061 |
| | | | ,, | Dec. 16th, 1924 | – | – | 26 | 65 | 9 | – | 100 | 55·83 | 0·57 | 0·057 |
| | | | ,, | Jan. 5th, 1925 | – | – | 25 | 63 | 10 | – | 98 | 55·85 | 0·58 | 0·059 |
| | | ,, | ,, | Jan. 8th, 1925 | – | 2 | 27 | 61 | 10 | – | 100 | 55·79 | 0·64 | 0·064 |
| | | ,, | ,, | Jan. 13th, 1925 | – | – | 28 | 59 | 10 | 1 | 98 | 55·84 | 0·64 | 0·064 |
| | | ,, | ,, | Jan. 20th, 1925 | – | – | 23 | 62 | 14 | – | 99 | 55·91 | 0·61 | 0·061 |
| | | ,, | ,, | Jan. 27th, 1925 | – | – | 26 | 62 | 9 | – | 97 | 55·825 | 0·57 | 0·059 |
| | | ,, | ,, | Feb. 2nd, 1925 | – | 1 | 31 | 59 | 4 | – | 95 | 55·695 | 0·58 | 0·058 |
| | | ,, | ,, | Feb. 9th, 1925 | – | – | 25 | 62 | 12 | – | 99 | 55·87 | 0·60 | 0·060 |
| | | ,, | ,, | Feb. 18th, 1925 | – | – | 22 | 66 | 10 | 1 | 99 | 55·90 | 0·60 | 0·060 |
| | | ,, | ,, | Feb. 20th, 1925 | – | – | 33 | 58 | 6 | – | 97 | 55·72 | 0·57 | 0·058 |
| | | ,, | ,, | Mar. 2nd, 1925 | – | 2 | 24 | 65 | 6 | – | 97 | 55·77 | 0·59 | 0·060 |
| | | ,, | ,, | Oct. 25th, 1925 | – | 3 | 49 | 62 | 4 | – | 118 | 55·57 | 0·61 | 0·056 |
| | | ,, | ,, | Nov. 1st, 1925 | – | 1 | 48 | 53 | 5 | – | 107 | 55·58 | 0·60 | 0·058 |
| | | ,, | ,, | Nov. 4th, 1925 | – | 1 | 29 | 80 | 9 | 1 | 120 | 55·83 | 0·61 | 0·056 |
| | | ,, | ,, | Nov. 18th, 1925 | – | 2 | 37 | 63 | 5 | – | 107 | 55·66 | 0·59 | 0·057 |
| | | ,, | ,, | Nov. 20th, 1925 | – | – | 46 | 66 | 5 | – | 117 | 55·65 | 0·56 | 0·052 |
| | | ,, | ,, | Dec. 1st, 1925 | – | 2 | 29 | 70 | 15 | 1 | 117 | 55·86 | 0·65 | 0·060 |
| | | ,, | ,, | Dec. 6th, 1925 | – | 1 | 31 | 77 | 10 | – | 119 | 55·81 | 0·59 | 0·054 |
| | | ,, | ,, | Dec. 15th, 1925 | – | 1 | 34 | 74 | 6 | – | 115 | 55·74 | 0·56 | 0·052 |
| | | ,, | ,, | Dec. 21st, 1925 | – | 1 | 28 | 71 | 14 | – | 114 | 55·86 | 0·62 | 0·058 |
| | | ,, | ,, | Dec. 23rd, 1925 | – | 2 | 25 | 82 | 8 | 1 | 118 | 55·84 | 0·60 | 0·055 |
| | | ,, | ,, | Jan. 1st, 1926 | – | – | 38 | 70 | 10 | – | 118 | 55·76 | 0·59 | 0·055 |
| | | ,, | ,, | Jan. 6th, 1926 | – | 1 | 30 | 74 | 8 | – | 113 | 55·79 | 0·57 | 0·054 |
| | | ,, | ,, | Jan. 10th, 1926 | – | 1 | 34 | 71 | 12 | – | 118 | 55·80 | 0·62 | 0·057 |
| | | ,, | ,, | Jan. 14th, 1926 | – | – | 36 | 74 | 9 | – | 119 | 55·77 | 0·57 | 0·052 |
| | | ,, | ,, | Jan. 18th, 1926 | – | 1 | 31 | 69 | 13 | – | 114 | 55·825 | 0·63 | 0·059 |

TABLE I—*continued.*

| Statistical Region. | Fishing Ground. | Method of Fishing. | Port of Landing. | Date of Sample. | No of fishes in 6 Vertebræ Classes. | | | | | | Total No. of Fishes in sample (n). | Arith. Mean No. of Vertebræ (m). | Standard Deviation σ | Standard Error of m $\frac{\sigma}{\sqrt{n}}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 53 | 54 | 55 | 56 | 57 | 58 | | | | |
| VIIe (ZZ 52 A 52) | Area covered by local fishery at Plymouth | Set Nets Seine Drift Nets | Plymouth | Jan. 25th, 1926 | – | 2 | 25 | 81 | 7 | 1 | 116 | 55·83 | 0·59 | 0·055 |
| | | | ,, | Jan. 28th, 1926 | – | 2 | 28 | 74 | 11 | – | 115 | 55·82 | 0·61 | 0·057 |
| | | | ,, | Feb. 2nd, 1926 | – | – | 26 | 73 | 10 | 1 | 110 | 55·87 | 0·59 | 0·056 |
| | | | ,, | Feb. 4th, 1926 | – | 1 | 23 | 82 | 9 | – | 115 | 55·86 | 0·54 | 0·051 |
| | | | ,, | Feb. 10th, 1926 | – | – | 23 | 82 | 12 | – | 117 | 55·91 | 0·54 | 0·050 |
| | | ,, | ,, | June 8th, 1926 | – | 3 | 27 | 53 | 9 | – | 92 | 55·74 | 0·68 | 0·071 |
| | | ,, | ,, | Oct. 18th, 1926 | – | – | 50 | 51 | 8 | – | 109 | 55·615 | 0·62 | 0·061 |
| | | ,, | ,, | Oct. 21st, 1926 | – | – | 32 | 71 | 9 | 1 | 113 | 55·81 | 0·61 | 0·057 |
| | | ,, | ,, | Oct. 25th, 1926 | 1 | 3 | 25 | 70 | 11 | – | 110 | 55·79 | 0·69 | 0·066 |
| | | ,, | ,, | Nov. 3rd, 1926 | – | – | 33 | 77 | 8 | – | 118 | 55·79 | 0·55 | 0·051 |
| | | ,, | ,, | Nov. 4th, 1926 | – | – | 30 | 72 | 10 | – | 112 | 55·82 | 0·58 | 0·054 |
| | | ,, | ,, | Nov. 15th, 1926 | – | 2 | 28 | 64 | 11 | – | 105 | 55·80 | 0·62 | 0·060 |
| | | ,, | ,, | Nov. 23rd, 1926 | 1 | 1 | 31 | 66 | 7 | – | 106 | 55·73 | 0·68 | 0·067 |
| | | ,, | ,, | Nov. 30th, 1926 | – | – | 39 | 71 | 8 | – | 118 | 55·74 | 0·58 | 0·053 |
| | | ,, | ,, | Dec. 6th, 1926 | – | 2 | 28 | 70 | 14 | – | 114 | 55·84 | 0·64 | 0·060 |
| | | ,, | ,, | Dec. 20th, 1926 | – | – | 28 | 65 | 13 | 1 | 107 | 55·88 | 0·64 | 0·062 |
| | | ,, | ,, | Dec. 20th, 1926 | – | 2 | 37 | 73 | 6 | 1 | 119 | 55·72 | 0·62 | 0·057 |
| | | ,, | ,, | Dec. 30th, 1926 | – | 3 | 42 | 62 | 12 | – | 119 | 55·70 | 0·69 | 0·063 |
| | | ,, | ,, | Dec. 30th, 1926 | – | – | 26 | 69 | 5 | – | 100 | 55·79 | 0·52 | 0·052 |
| | | ,, | ,, | Jan. 4th, 1927 | – | 2 | 38 | 62 | 9 | 1 | 112 | 55·72 | 0·67 | 0·063 |
| | | ,, | ,, | Jan. 19th, 1927 | – | 4 | 41 | 62 | 10 | – | 117 | 55·67 | 0·68 | 0·062 |
| VIIe (A 52) | River Dart Great West Bay | Seine Set Nets and Drift | Brixham | Dec. 10th, 1925 | – | 1 | 32 | 53 | 11 | – | 97 | 55·76 | 0·66 | 0·068 |
| | | | ,, | Nov. 10th, 1925 | – | 1 | 17 | 51 | 7 | – | 76 | 55·84 | 0·59 | 0·068 |
| | | | ,, | Nov. 26th, 1925 | – | 3 | 37 | 65 | 11 | – | 116 | 55·72 | 0·67 | 0·062 |
| | | | ,, | Dec. 16th, 1925 | – | 1 | 28 | 58 | 5 | – | 92 | 55·73 | 0·58 | 0·060 |
| | | | ,, | Jan. 4th, 1926 | – | – | 24 | 32 | 8 | – | 64 | 55·75 | 0·66 | 0·083 |
| | | ,, | ,, | Oct. 27th, 1926 | – | 2 | 28 | 71 | 6 | – | 107 | 55·76 | 0·58 | 0·056 |
| | | ,, | ,, | Nov. 23rd, 1926 | – | – | 40 | 70 | 6 | – | 116 | 55·71 | 0·56 | 0·052 |
| | | ,, | ,, | Dec. 14th, 1926 | – | 2 | 44 | 67 | 6 | – | 119 | 55·65 | 0·61 | 0·055 |
| VIId (D 51 E 51) | Off Sussex Coast | Set Nets or Drift | Plymouth | Dec. 9th, 1924 | – | 2 | 26 | 54 | 16 | – | 98 | 55·86 | 0·70 | 0·071 |
| | | | Brighton | Oct. 19th, 1925 | – | 1 | 46 | 67 | 10 | – | 124 | 55·69 | 0·63 | 0·056 |
| | | | ,, | Nov. 10th, 1925 | – | 2 | 30 | 58 | 7 | – | 97 | 55·72 | 0·65 | 0·066 |
| | | ,, | ,, | Dec. 1st, 1925 | 1 | 4 | 44 | 62 | 6 | 1 | 118 | 55·62 | 0·72 | 0·066 |
| | | ,, | ,, | Nov. 1st, 1926 | – | 3 | 42 | 66 | 8 | – | 119 | 55·66 | 0·64 | 0·059 |
| | | ,, | ,, | Nov. 5th, 1926 | – | 1 | 30 | 59 | 7 | – | 97 | 55·74 | 0·60 | 0·061 |
| | | ,, | ,, | Dec. 2nd, 1926 | – | – | 36 | 58 | 3 | – | 97 | 55·66 | 0·54 | 0·054 |
| | | ,, | Hastings | Dec. 10th, 1926 | – | 2 | 37 | 65 | 11 | – | 115 | 55·74 | 0·65 | 0·061 |
| | | ,, | Brighton | June 29th, 1927 | – | 3 | 37 | 56 | 3 | – | 99 | 55·60 | 0·56 | 0·056 |

# Herring Investigations at Plymouth. III. The Plymouth Winter Fishery during the seasons 1924–25, 1925–26, and 1926–27.

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With 6 Figures in the Text.

## CONTENTS.

## The Plymouth Winter Fishery.

Although locally caught drift herrings may be landed at Plymouth from the end of September onwards until the beginning of March, the fishery only assumes economic importance during the months of December and January, when a large number of visiting drifters from both Cornwall and East Anglia are making daily fishing trips, using Plymouth as their temporary base. The composition of the fishing fleet in each of the seasons from 1918–19 onwards is shown in the following table kindly supplied by Mr. E. G. Nelder, and published by the courtesy of the Sutton Harbour Improvement Company :—

*Boats fishing for Herrings from Plymouth during Winter Herring Seasons.*

| Season. | East Country steamers. | West Country (Cornish) motor drifters. |
|---|---|---|
| 1918–19 | 33 | 139 |
| 1919–20 | 30 | 156 |
| 1920–21 | 26 | 182 |
| 1921–22 | 31 | 155 |
| 1922–23 | 68 | 142 |
| 1923–24 | 59 | 161 |
| 1924–25 | 86 | 176 |
| 1925–26 | 153 | 158 |
| 1926–27 | 129 | 169 |

The average number of Plymouth boats fishing for herrings is 10. Some years during the above period there were only 3, but in 1925–26, twenty-five.

### *Port Facilities for the Fishery.*

It is to be observed, first, that during the past two seasons the total visiting fleet numbered about 300 vessels, of which nearly one-half were steamers. This considerable increase in the number of vessels participating in the fishery has sorely taxed the available accommodation within Sutton Harbour, and the landing and packing operations have been conducted under most congested conditions. The harbour is a tidal one, so that movements of large fishing vessels within it, as well as arrivals and departures, can only be performed during from four to six hours around the time of high-water. The fish-market itself is small, and comparatively little surrounding ground is available for the packing of fish landed and for the storage of boxes and barrels ; the quayside accommodation adjacent to the market is limited in extent. It is only natural that boats should prefer to land their catches at the market quays, with the result that congestion is particularly manifest in this area. Much valuable work is performed by one or two skilled servants of the Harbour Company in directing the assembly at, and departure of, vessels from these quays ; but despite their efforts much delay in landing catches is caused and there is always a risk of damage to vessels. Obviously, too, no movements of ships can be carried out during unfavourable tidal conditions. Some further improvement may possibly be brought about by continuance of the present efforts to divert part of the landings to other sites within the harbour. The alternative of decentralising the fishery so that some landings could be made at places outside Sutton Harbour would seem to necessitate the withdrawal or modification of the present Parliamentary Act which states that " all fish brought or carried to the harbour of Sutton Pool or to any part of the Borough of Plymouth and whether by sea or land and whether in ships boats carts trucks vans boxes or otherwise for sale shall be sold only by public auction and in the fish market."

A second point to be observed from the above table is that there has been a notable rise in the number of Lowestoft and Yarmouth steamers during recent years. Their presence has led to a great increase in the total quantity of fish landed in the season, as the following official statistics show :—

| Season. Dec.–Jan. | Total quantity Herrings landed. cwt. | Landings by steamers only. cwt. | % weight landed by steamers. |
|---|---|---|---|
| 1918–19 | 8,624 | 7,628 | 88·4 |
| 1919–20 | 29,425 | 12,728 | 43·3 |
| 1920–21 | 40,263 | 20,973 | 52·1 |
| 1921–22 | 16,922 | 10,494 | 62·0 |
| 1922–23 | 54,839 | 40,941 | 74·6 |
| 1923–24 | 98,684 | 57,519 | 58·4 |
| 1924–25 | 113,585 | 83,647 | 73·7 |
| 1925–26 | 105,643 | 82,780 | 78·3 |
| 1926–27 | 63,138 | 45,932 | 72·7 |

The percentages shown on the right of the above table demonstrate the fact that the East Anglian fleet are landing practically three-quarters of the season's catch. Now it has to be remembered, that a large fleet of steamers attracts important outside buyers. The presence of these buyers must tend to keep the purchase price at a steadier higher level. When few buyers are present, particularly if their requirements are limited, the price is apt to fluctuate very considerably from day to day, and always to drop heavily when supplies are good. The steadying influence of a large number of big buyers benefits not only the steamers, but the local motor-drifters as well. Any circumstance, therefore, which tends to discourage the annual visit of the steamers must most seriously affect the annual yield of the winter fishery at Plymouth.

### *A Comparison between Motor-driven and Steam-driven Fishing Vessels.*

The presence of two comparatively large fleets of drifters, the one composed of steamers and the other of motor-propelled craft, renders possible several interesting comparisons of performance. During the nine consecutive seasons from Dec. 1918–Jan. 1919 to Dec. 1926–Jan. 1927, the steamers made 13,625 landings with an average of 26·6 cwt. per landing ; in the same period, motor-vessels (irrespective of size) made 7,781 landings, with an average of 22·1 cwt. per landing. Thus, landing for landing, the steamers do not seem to have exhibited a very marked superiority in density of catch per boat, although by reason of their sea-going advantages they were able to fish over a wider area from as far east as off Berry Head to as far west as Dodman Point. But it is in the actual number of landings made that the steamers reaped the advantage. It is to be remembered that the fishery coincides with the time of most severe weather. In some seasons the whole of the motor fleet may be forced to remain in harbour for days on end, owing to adverse weather conditions, whereas the steamers, or at any rate a number of them, are yet able to work with satisfactory results. A study of the daily landings, also shows that landings by motor craft are rarely, if ever, made on Sundays, Christmas Days, or Boxing Days, although steamers continue to work on these days. The following table gives statistics of daily landings during the five seasons, 1922–23 to 1926–27 (Dec. and Jan. only), when fish was landed by steamers only :—

| Season Dec.–Jan. | No. days when fish was landed by steamers only. | | | No. landings by steamers on these days. | Total weight of fish landed by steamers cwt. on these days. | Total landing by motors throughout *whole season* cwt. |
|---|---|---|---|---|---|---|
| | Sundays, Xmas, & Boxing Day. | Other Days. | Total. | | | |
| 1922–23 | 9 | 13 | 22 | 740 | 22,980 | 13,898 |
| 1923–24 | 6 | 9 | 15 | 383 | 11,154 | 41,165 |
| 1924–25 | 8 | 14 | 22 | 540 | 20,696 | 29,938 |
| 1925–26 | 10 | 20 | 30 | 1,510 | 30,909 | 22,863 |
| 1926–27 | 6 | 13 | 19 | 523 | 10,939 | 17,206 |

It is seen from the above table that an appreciable amount of fish was landed by the steamers on the days when there were no landings by motor craft, and that in the seasons 1922–23 and 1925–26 this amount exceeded the weight of fish landed throughout the whole of the two months of December and January by the motor-fleet.

### *General Features of the Fishery.*

The fishery itself presents peculiar features. It is always liable to serious interruption by incursions of dogfish (*Squalus acanthias*). These fish may be so numerous on some parts of the ground that shooting drift-nets involves risk of total loss of or severe damage to gear. Some skippers elect to shoot only a very limited number of nets, hauling and reshooting at frequent intervals during the hours of fishing. The catches of dogfish are not always saleable, particularly when they are plentiful, owing to the limited commercial demand for this class of fish. The fishery, again, is characterised by the fact that the herrings appear to be present in shoals of limited size, there being little in the nature of " banks " of herrings. It is generally the case, also, for shoals of mackerel and pilchards to be present in the neighbourhood more particularly to the westward. As a result of these circumstances, individual landings on the same day from boats working in close association may differ to a striking degree, in total quantity, quality, and class of fish. Thus, one boat may land a fine clean catch of excellent full herrings, while a second may have only a few herrings, perhaps spent, together with a quantity of mackerel or pilchards or both. In an individual boat, the nets of the fleet may differ to a similar extent in the class of fish they have captured. Under these conditions it is not surprising that there is a big difference between the boats at the end of the season with regard to their earnings, or that the general average landing is by weight not very high.

### *French Trawling Activities.*

Before leaving the subject of the practical fisheries, some remarks may be made concerning the operations of French steam trawlers off the Devon coasts between Start Point and the Eddystone. It is, perhaps, only natural that the presence of, say, from twenty to thirty powerful steamers within sight of home should arouse grave misgivings in the minds of the local trawlermen lest the grounds should be so depleted of fish as to render their fishing unprofitable. It is true, of course, that the grounds lie in international waters where the French have as much right to fish as our local men. If, therefore, the French by reason of a sound knowledge of the local movements of fish and satisfactory fishery organisation can maintain a commercial steam fishery off our shores, they are entitled to do so. But, at the same time, the present writer is of the opinion that the feelings of our local fishermen are not to be regarded as due merely to a spirit of resentment towards " outside " participation in a local fishery. One has only to observe the thorough manner in which an area is swept by the French trawls to sympathise with the smacksman or motor-trawler whose living is made on that ground, and to believe that the local fishery is seriously affected by the French activities.

The question considered in relation to the drift-fishery for herrings is also of importance. Le Gall (**3**) states that the French trawlers working in the " Baie de Plymouth " take some herrings at all times of the year. From July to September to the south and south-west of the Eddystone, and in September in the region of the Start, good catches are made. In the months of January, February, and March, " spent " herrings are caught within the same area. Le Gall inclines to the view that these are the same herring which come to spawn off the south coasts of Devon and Cornwall, and which form the stock for the winter drift-fishery at Plymouth. Now in the first weeks of November, 1927, some thirty to forty French trawlers were intensively engaged by day on grounds where a few hours later the Plymouth drifters were shooting their nets for herring. It is neither illogical nor unreasonable to suspect that the trawling had a material effect on the prospects for the subsequent drifting.

From the above it would seem that in purely local considerations the possible effects of French trawling activities must not be overlooked.

## THE CHARACTERS OF THE FISHES LANDED.

From what has been said concerning the fishery, it will be appreciated that a small sample taken at random from a commercial catch conveys only a very rough estimate of the herring population present at the time of sampling. A second sample taken from another boat might easily differ appreciably from the first. A series of such samples, however, taken at intervals during a season, does provide a much better picture than just one or two isolated samples, no matter how big the latter may be.

### *Condition of Gonads (Roes and Milts).*

In using the data on the state of the gonads of fishes in the series of samples as a guide to the progress of spawning, a good deal of irregularity would be expected; but in spite of this they do provide a clear idea of the general situation. Table I (at the end of this paper) and Fig. 1 show for each sample taken during the season 1924–25 the proportions of females in the following classes :—

1. Full fish.—Ovaries filling the body cavity, but eggs opaque and not mature.
2. Fish ready to spawn or spawning.—Ova quite transparent and ready to be shed from the ovaries.
3. Spent fish or recovering spents.

It is seen from Fig. 1 that during November and the early part of December the catches largely consisted of unripe fishes (Class I, above). In the latter part of December and throughout January ripe fishes predominated, while from the end of January until the end of the season, spent fishes were most in evidence. The data also show that while some spent fishes were caught early in December, some 12% of a sample taken on March 2nd, 1925, were still unripe. In the following season, an earlier start with sampling was possible, and fishes ready to spawn were taken towards the end of September. It is interesting to record that this early run of ripe fishes was detected in samples taken from catches by stop-nets within Plymouth Sound, during September and October, 1925, and again in October, 1926. The same early spawners were also present among catches of seine-caught sprats from the River Tamar. During these same months, however, fishes caught outside Plymouth Breakwater in the open sea were all in an unripe condition.

The duration of the spawning time in the Plymouth area is of

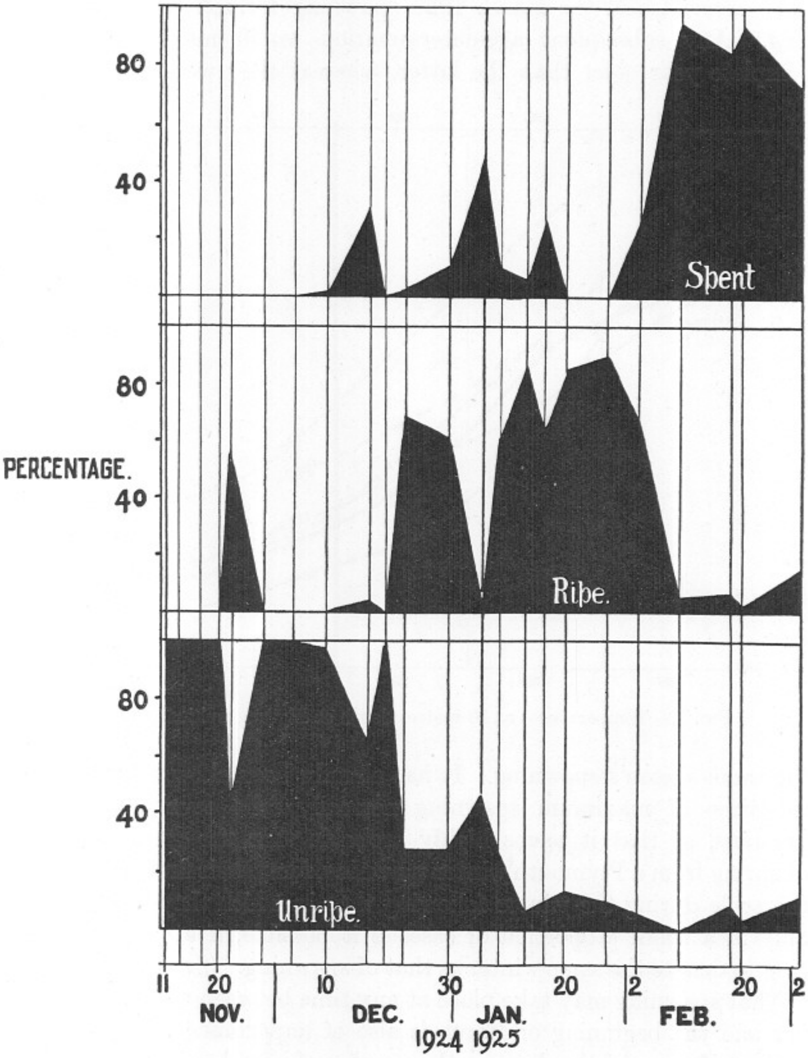

Fig. 1.—Condition of Ovaries (roes) in herrings landed at Plymouth during season 1924–25. Percentage of each class marked off along vertical lines erected at dates when the samples were taken.

importance when considering the question of the significance of the first winter-ring on the scales of adult fishes. The offspring from the fish which spawned in September, 1925, obviously had over five calendar months in which to grow before the offspring spawned in March, 1926, had appeared. It has yet to be determined whether the September spawned fish acquired scales by the end of the year 1925; but if they did, then in the winter of 1926–27 they formed their *second* winter-ring, while their associates of the March 1926 spawning formed their *first* winter-ring. Any subsequent age-determination would make the former a complete year older than the latter, whereas they were the product of the same season's spawning. It has already been shown, however, that the time of maximum spawning normally falls over December and January, so that it seems highly probable that the great bulk of the offspring from a Plymouth winter spawning, form their first winter-ring on the scale during the winter following that in which they were spawned; only in a small proportion of cases is it possible, if at all, for the first ring to denote the same winter as that of spawning. (See Part IV, p. 313.)

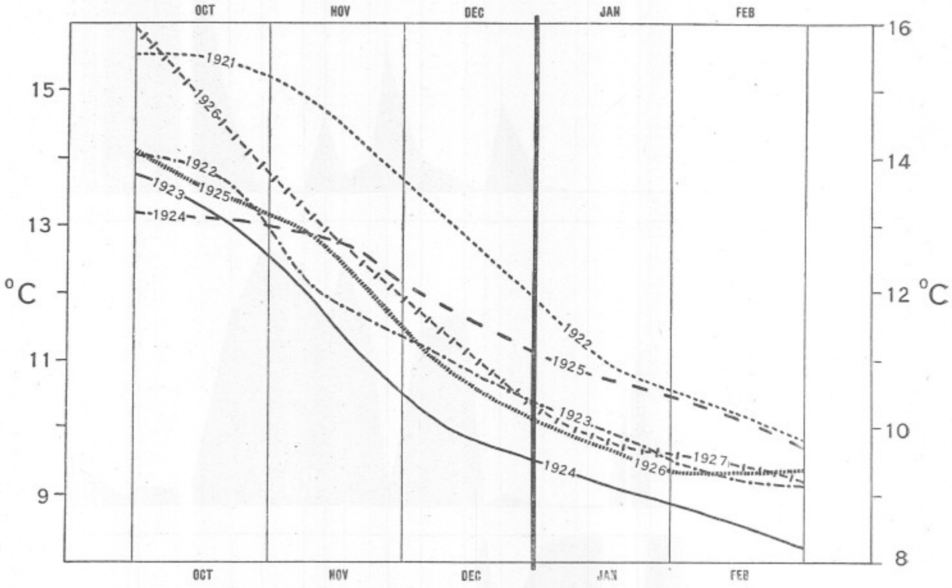

Fig. 2.—Temperatures at 10 metres depth at Hydrographical Station $E_1$.

That spawning may take place at any time between the end of September and the beginning of March is also of importance when considering the significance of the data on the number of vertebræ. If the "racial" theory be true, it is possible that the earlier spawning fishes are of different racial origin from those which spawn later. On the other hand, if the number of vertebræ is materially influenced by environmental conditions prevailing at the critical period, the fishes spawning, say, in October, would give rise to larvæ having on average a different number of vertebræ from those spawned by the December or January spawners. The temperature conditions prevailing during spawning cannot be stated with exactitude, but Fig. 2, depicting the temperature at a depth of 10 metres at hydrographical station E1 (situated some 10 miles S.W. of the Eddystone), kindly supplied by my colleague, Mr. H. W. Harvey, may be used as a close approximation. Probably on the coastal region where spawning takes place, the total range is somewhat greater, and the temperatures slightly lower. It will be seen that maximum spawning coincides with a temperature of, say, from 9° C. to 11° C. It is also apparent that the total possible range of spawning from October to March covers an appreciable range of temperature even when allowance is made for probable annual fluctuation in spawning time.

### *Average Length.*

The data on length, taken in the three successive seasons, 1924–25, 1925–26, and 1926–27, serve to indicate the length groups upon which the fishery is chiefly centred. In Table II on page 301 the values of the median ($Q_2$), quartiles ($Q_1$ and $Q_3$) and the upper and lower limits of size of fishes of samples taken from commercial landings during the three seasons, are given. These same values are recorded graphically in Fig. 3. The range in size of the middle 50% ($Q_3$–$Q_1$) of each sample may be used as a convenient index of the sizes occurring most frequently. It is seen that the value of the lower quartile ($Q_1$) dropped below 25 cm. on two occasions only (both during the season 1926–27), while on all but three occasions (one in each of the three seasons) the value of the upper quartile ($Q_3$) was under 29·0 cm. Thus, it may be taken that the fishery is centred chiefly upon fishes of the 25, 26, 27, and 28 cm. groups (i.e. roughly 10 in. to 11 in.).

Comparing season with season, however, it is seen that there was an appreciable and general depression of length during the season 1926–27. It will be shown later that this was due to an influx of younger fishes. It should be noted for future reference that samples of the " Smalls " trawled fishes during the autumn of 1925, and also those of the " drift " fishes caught at Padstow in November and December of 1925 showed a similar increase in the percentage of fishes of shorter length.

The data for the Plymouth samples of 1924–25 were analysed according to the locality in which the fishes were captured to determine whether or no the statistics would confirm the view of local fishers that the " Bay " herring caught inshore to the eastward of the port are a smaller " class "

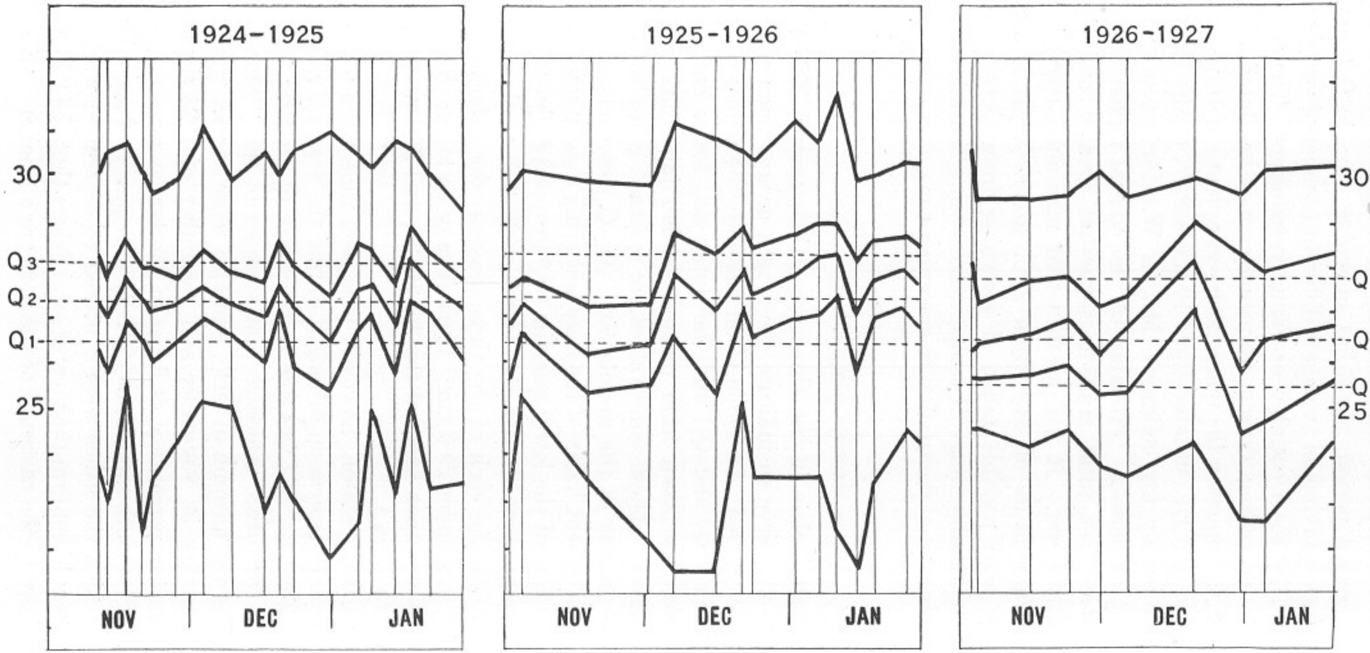

Fig. 3.—Length of fishes landed at Plymouth.

Vertical lines indicate the dates when samples were taken. For each sample the following values are shown :—

Upper limit of length.
Upper Quartile ($Q_3$).
Median ($Q_2$).
Lower Quartile ($Q_1$).
Lower limit of length.

of herring than those taken to the westward. Accordingly, samples were grouped into three classes dependent on whether they were taken from (*a*) eastward, (*b*) off harbour, or (*c*) to the westward. The divisions were admittedly rough, but only a rough comparison could be made under the circumstances. The rearranged data on length are shown in Fig. 4 in convenient form to demonstrate differences between the values of $Q_1$, $Q_2$, and $Q_3$ in the three areas. It is interesting to observe that these values show a general tendency to be lowest to the eastward, intermediate off the harbour, and greatest to the westward. It would not be advisable to stress this indication, but that it may have some significance will become apparent at a later date when the samples landed at the neighbouring port of Brixham are under review.

### *Age Composition of Shoals.*

As stated on page 243 of Part I of this series, the first winter-ring on the scales of the Plymouth fishes was assumed to have been laid down during the winter following that in which the fish was born. It has also been shown on page 284 of the present paper that the spawning period overlaps two calendar years. If, therefore, we follow the principle of referring fishes to " year-groups " named after the calendar year in which the first summer zone was formed on the scale, it means that we shall have to include fishes born in two calendar years within one and the same year-group. For instance, the year-group 1920 would include fishes derived both from the spawning of November and December, 1919, and from that of January and February, 1920. Although this may not be the most convenient method of recording age, it has been followed in the present work because it permits of more ready comparison of results with those of other workers in other areas.

The age-composition of the samples taken in the three seasons 1924–27 is given in the form of percentages in Table III on page 303 and graphically in Fig. 5 in terms of the actual age at the time of sampling. It is seen that fishes of the 1920 year-class formed a dominant element of the samples in all three seasons. During the season 1924–25, as 5-zoned 5-ringed fishes they comprised more than half of many samples. In the following season, as 6-zoned 6-ringed fishes they still greatly outnumbered those of any other year-group. In the third season (1926–27), when 7-zoned 7-ringed, although not so heavily represented as previously, they yet formed an important constituent.

In contrast with the importance of the 1920 year-class, the relative insignificance of the proportion contributed by the 1921 year-class is to be noted. In the seasons 1924–25 and 1925–26 it was completely overshadowed by the 1920 class, while during the season 1926–27 it was

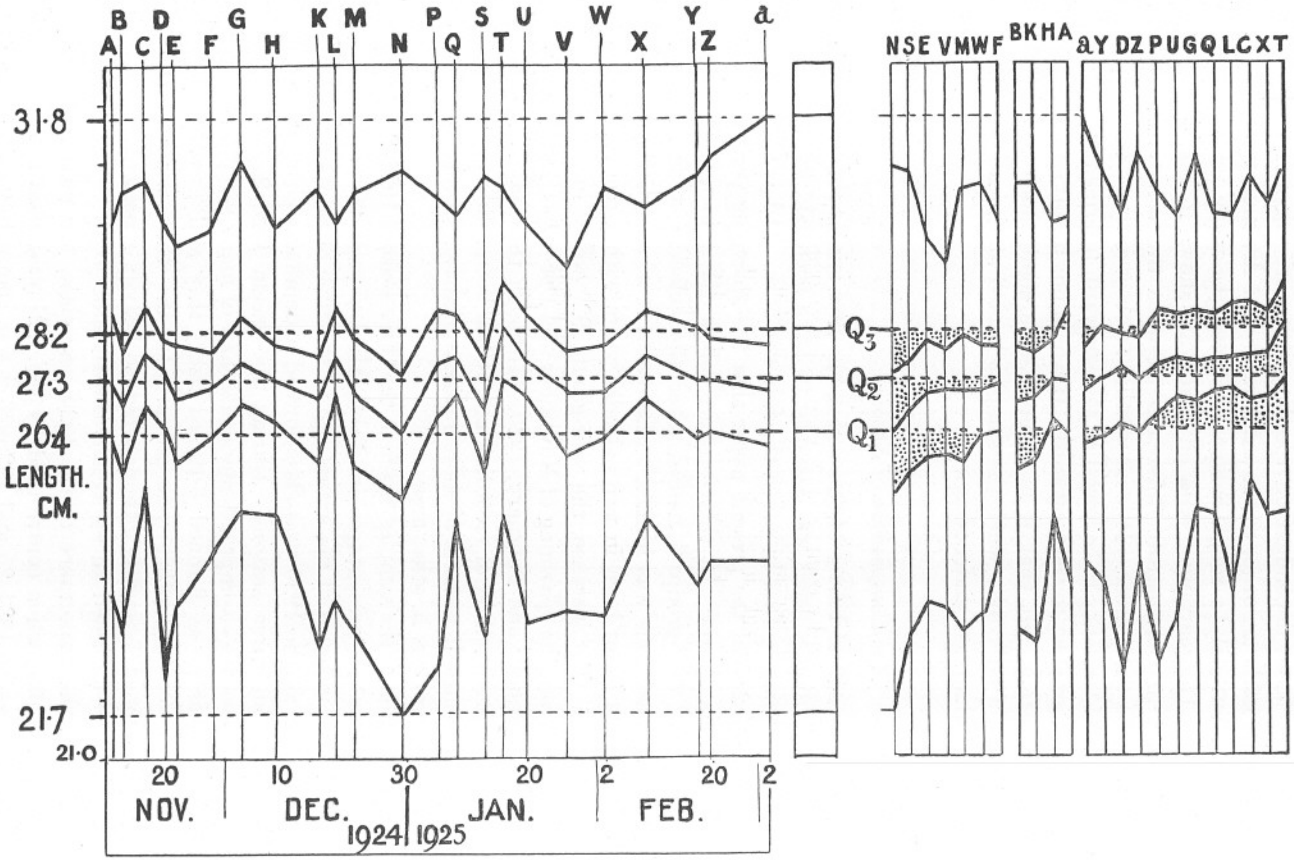

FIG. 4.—Length of fishes landed at Plymouth during season 1924–25.

On left, data shown as in Fig. 3. On right, samples arranged according to locality :—

Samples N, S, E, V, M, W, F . . . . . East Bay.
Samples B, K, H, A . . . . . . Off Harbour.
Samples a, Y, D, Z, P, U, G, Q, L, C, X, T . Westward samples.

The order of the samples in the three areas is according to the magnitude of $(Q_2)$.
The dotted areas indicate the deviations from the mean values.

even less in evidence than the two immediately younger classes of 1922 and 1923.

It is seen from the 1926–27 results that the 1920 class showed definite signs of a decline in intensity, and that the 1921 class gave no signs that it would ever become important, while of the younger classes, that of 1923 was the most promising. It would, therefore, seem reasonable to expect that in the coming season of 1927–28, the samples will show a fair proportion of the 1923 class as 5-zoned 5-ringed fishes. Whether or not the 1923 class will prove to be the dominant element depends, of course, on the extent to which still younger fishes arrive.

### *Dominance of the* 1920 *Year-class.*

The fact that the 1920 year-class constituted a large proportion of the samples at Plymouth in at least three consecutive seasons is worthy of especial comment. Storrow (**4**, p. 10) shows that in samples examined by him during January, February, and March, 1924, from about the Shetlands, the North of Scotland, Eyemouth, and the north-west of Ireland, there was a strikingly high percentage of fishes with four winter-rings (i.e. the 1920 year-class). Two of his samples from Wick were composed almost entirely of this one year-class; in the one sample of 211 fishes there were 208 with four winter-rings, and in the other of 214 fish, 203 showed four winter-rings. In the following year (1925) the same year-class was again of first importance in the samples from Wick and yielded a large percentage in the samples from off Flugga, Eyemouth, and the north-west of Ireland (Storrow, **5**, p. 9). In 1926, Storrow (**6**, pp. 11 and 14) reported that in the north of Scotland and north-west of Ireland, the 1920 year-class was still abundant.

Watkin (**7**), also supplies data which shows the dominance of the 1920 class in samples taken off the Welsh and Cornish coasts during the winters of 1923–24 and 1924–25.

The above results are sufficient to show that the richness of the 1920 year-class was a widely-spread phenomenon. Its observance at Plymouth must therefore not be stressed as evidence of the return year after year of the same body of fish. The likelihood of this latter fact can only be estimated after the examination of the growth and morphological characters of the fishes of the same year-class which came each year.

### *Variation in Length among Fishes of same Sample.*

Differences in length between fishes of the same sample may be due to the fact that the fishes are not all of the same age, for obviously we should not expect the younger fishes normally to be so large as their older associates, although there is evidence that the larger members of

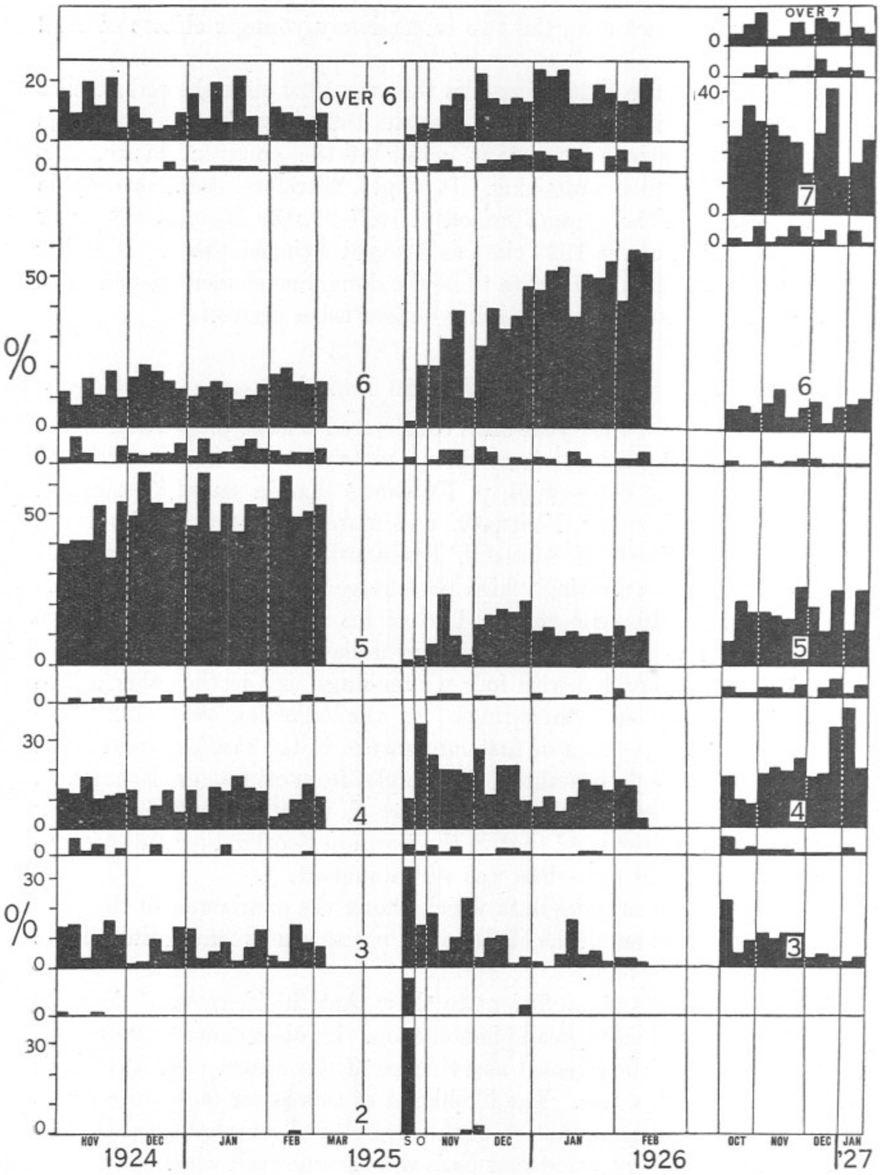

FIG. 5.—Age composition of samples of Plymouth fishes.

Sample percentages are shown as small vertical blocks. The age classes are as follows :—

| | |
|---|---|
| 2 | 2-zoned 2-ringed. |
| 3 | 3-zoned 3-ringed. |
| 4 | 4-zoned 4-ringed. |
| 5 | 5-zoned 5-ringed. |
| 6 | 6-zoned 6-ringed. |
| 7 | 7-zoned 7-ringed. |

The " interval " classes are obviously 2 or 3, 3 or 4, 4 or 5, etc.

a younger year-class do swim with the smaller members of an older class. But it is found that the individuals of the same year-class themselves vary in length over a considerable range, and such differences must be attributed to one or both of the following causes :—

1. Some of the individuals were spawned earlier in the season than others.
2. Some of the individuals had experienced better conditions for growth than others during the whole or part of their life.

The study of the growth in length of the Plymouth fish from measurements of their scales has shown that fishes of the same year-class vary to a most perplexing degree in the lengths $l_1$, $l_2$ . . . etc., attained at the end of the 1st, 2nd . . . etc., year of life. Whereas, ordinarily, the annual increments of length become successively smaller as the fish gets older, it is frequently seen that some fishes have grown more in a late year than during a preceding one. We have, therefore, to determine how this complex state of affairs has been brought about by the operation of causes (1) and (2) above.

### *Length for Age.*

In the following table the average length and individual variation of fishes of different ages are given :—

| Age. | Season. | No. fishes in each of 11 Length groups (cm.). | | | | | | | | | | | Total No. | Average length. cm. | Year-class. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | |
| 3-zoned 3-ringed | 1924–25 | – | 3 | 19 | 39 | 68 | 36 | 15 | 3 | 1 | – | – | 184 | 25·5 | 1922 |
| | 1925–26 | 2 | 10 | 9 | 32 | 44 | 13 | 3 | – | – | – | – | 113 | 24·9 | 1923 |
| | 1926–27 | – | – | 4 | 11 | 33 | 27 | 12 | – | – | – | – | 87 | 25·9 | 1924 |
| 4-zoned 4-ringed | 1924–25 | – | – | 6 | 13 | 34 | 67 | 72 | 53 | 10 | 2 | – | 257 | 27·0 | 1921 |
| | 1925–26 | – | 4 | 11 | 33 | 59 | 94 | 87 | 22 | – | – | – | 310 | 26·4 | 1922 |
| | 1926–27 | – | 2 | 13 | 59 | 88 | 46 | 19 | 14 | 2 | – | – | 243 | 25·7 | 1923 |
| 5-zoned 5-ringed | 1924–25 | – | – | – | 11 | 96 | 304 | 481 | 251 | 33 | 4 | 1 | 1181 | 27·4 | 1920 |
| | 1925–26 | – | – | – | 10 | 35 | 58 | 79 | 37 | 12 | 2 | – | 233 | 27·1 | 1921 |
| | 1926–27 | – | – | 3 | 21 | 54 | 65 | 48 | 25 | 2 | – | – | 218 | 26·5 | 1922 |
| 6-zoned 6-ringed | 1924–25 | – | – | 1 | 2 | 12 | 59 | 140 | 65 | 26 | – | – | 305 | 27·6 | 1919 |
| | 1925–26 | – | – | – | 6 | 37 | 106 | 250 | 304 | 97 | 6 | – | 806 | 27·9 | 1920 |
| | 1926–27 | – | – | – | 4 | 10 | 21 | 34 | 18 | 9 | 2 | – | 98 | 27·4 | 1921 |
| 7-zoned 7-ringed | 1926–27 | – | – | – | – | 8 | 32 | 90 | 116 | 62 | 3 | – | 311 | 28·1 | 1920 |

The data as they stand suffice to illustrate the three following points :—

(*a*) Fishes of the same age vary considerably in length.

(*b*) The younger fishes are on average smaller than their older associates.

(*c*) The average length for fishes of the same age is not constant from season to season.

The data may be rearranged to show the successive average lengths for fishes of the same year-class, thus :—

| Year-class. | Average Length in cm. during following seasons. 1924–25. | 1925–26. | 1926–27. |
|---|---|---|---|
| 1919 . . | 27·6 | — | — |
| 1920 . . | 27·4 | 27·9 | 28·1 |
| 1921 . . | 27·0 | 27·1 | 27·4 |
| 1922 . . | 25·5 | 25·4 | 26·5 |
| 1923 . . | — | 24·9 | 25·7 |
| 1924 . . | — | — | 25·9 |

It is seen that each year-class, on average, tends to increase in length, but that the absolute increases exhibited cannot be accepted as reliable estimates of the actual increments of growth added.

### *Length at Formation of First Winter-ring.*

As already stated, there is a lack of uniformity in the length $l_1$, at which the first winter-ring is formed on the scale. The following table shows the value of $l_1$ for each of a total of 1122 fishes of the 5-zoned 5-ringed class (1920 year-class) taken during the season 1924–25 :—

$L_1$. Central Values of 13 Classes (cm.).

| 6·5 | 7·5 | 8·5 | 9·5 | 10·5 | 11·5 | 12·5 | 13·5 | 14·5 | 15·5 | 16·5 | 17·5 | 18·5 | Total. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 14 | 39 | 56 | 100 | 170 | 210 | 174 | 159 | 129 | 57 | 11 | 2 | 1122 |

Average Value of $L_1$ = 12·86 cm.
Standard Deviation $\sigma$ = 2·13 cm.

It is seen from the total range of variation (6·5 cm. to 18·5 cm.) and from the standard deviation ($\sigma$=2·13 cm.) that the value of $l_1$ varies very considerably from fish to fish. The magnitude of the mean $l_1$ (=12·86 cm.) merely indicates that fishes with $l_1$ between, say, 11·5 cm. and 14·5 cm. are the most common. These results, in conjunction with those of Hjort (**1**), Storrow (**4**, **5**, **6**), Watkin (**7**), Hodgson (**2**), and Le Gall (**3**), clearly show that wide individual variation in the value of $l_1$ is a general feature among fishes of the English Channel and to the south-west. Moreover, they show that values of $l_1$ of 12 cm. and over are most common. It is, therefore, of the greatest importance to determine the relative ages of the fishes at the time when the first winter-ring was formed. This question is considered in Part IV (p. 313).

### *Growth subsequent to Formation of First Winter-ring.*

As was shown in Part I (p. 252), the increment of length added during any one season of growth is dependent upon the length of the fish at the commencement of that season. Thus, having shown above that there is a great amount of variation in the length $l_1$, it is essential that we should make due allowance for this fact when considering any subsequent growth. The following table shows the calculated values of $l_1$, $l_2$, $l_3$, and $l_4$ from scale measurements for a total of 244 fishes of the 4-zoned 4-ringed class taken during the season 1924–25 at Plymouth :—

Central Values of 23-length Classes. (cm.).

| | 8·5 | 9·5 | 10·5 | 11·5 | 12·5 | 13·5 | 14·5 | 15·5 | 16·5 | 17·5 | 18·5 | 19·5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $l_1$ | 2 | 7 | 19 | 25 | 26 | 37 | 46 | 48 | 26 | 8 | – | – |
| $l_2$ | – | – | – | – | – | – | – | – | 2 | 8 | 19 | 39 |
| $l_3$ | – | – | – | – | – | – | – | – | – | – | – | – |
| $l_4$ | – | – | – | – | – | – | – | – | – | – | – | – |

| | 20·5 | 21·5 | 22·5 | 23·5 | 24·5 | 25·5 | 26·5 | 27·5 | 28·5 | 29·5 | 30·5 | Mean (cm.) | $\sigma$ (cm.) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $l_1$ | – | – | – | – | – | – | – | – | – | – | – | 13·88 | 2·04 |
| $l_2$ | 52 | 45 | 51 | 21 | 6 | 1 | – | – | – | – | – | 21·03 | 1·68 |
| $l_3$ | 1 | 6 | 37 | 48 | 47 | 41 | 46 | 17 | 1 | – | – | 24·68 | 1·61 |
| $l_4$ | – | – | – | 6 | 13 | 33 | 61 | 69 | 52 | 9 | 1 | 27·02 | 1·33 |

The successive values of the coefficient of correlation (r) between the values $l_1$ and $l_2$, $l_2$ and $l_3$, and $l_3$ and $l_4$ ; and the regression equations linking these values are :—

$l_1$ and $l_2$....$r = {\cdot}82$ ; $l_2 = {\cdot}675\ l_1 + 11{\cdot}68$ .......... i.
$l_2$ and $l_3$....$r = {\cdot}91$ ; $l_3 = {\cdot}871\ l_2 + 6{\cdot}36$ .......... ii.
$l_3$ and $l_4$....$r = {\cdot}88$ ; $l_4 = {\cdot}727\ l_3 + 9{\cdot}07$ ..........iii.

From equations i to iii it is possible to determine how much a fish of given length will grow during the next season. The following results as calculated from the equations are shown in conjunction with the actual observations :—

Values of $l_1$ (cm.).

| | 8·5 | 9·5 | 10·5 | 11·5 | 12·5 | 13·5 | 14·5 | 15·5 | 16·5 | 17·5 |
|---|---|---|---|---|---|---|---|---|---|---|
| Values of $l_2$— | | | | | | | | | | |
| Observed | (18·5) | 17·93 | 18·87 | 19·58 | 20·15 | 20·82 | 21·22 | 22·29 | 22·69 | (24·0) |
| $l_2 = {\cdot}675\ l_1 + 11{\cdot}68$ | 17·42 | 18·09 | 18·77 | 19·44 | 20·12 | 20·79 | 21·46 | 22·14 | 22·81 | 23·49 |
| Growth $(l_2 - l_1)$— | | | | | | | | | | |
| Observed | (10·0) | 8·43 | 8·37 | 8·08 | 7·65 | 7·32 | 6·72 | 6·79 | 6·19 | (6·50) |
| Calculated | 8·92 | 8·59 | 8·27 | 7·94 | 7·62 | 7·29 | 6·96 | 6·64 | 6·31 | 5·99 |

Values of $l_2$ (cm.).

| | 16·5 | 17·5 | 18·5 | 19·5 | 20·5 | 21·5 | 22·5 | 23·5 | 24·5 | 25·5 |
|---|---|---|---|---|---|---|---|---|---|---|
| Values of $l_3$— | | | | | | | | | | |
| Observed | 21·0 | 21·87 | 22·76 | 23·50 | 24·02 | 25·06 | 26·11 | 26·79 | (27·33) | 28·5 |
| $l_3 = {\cdot}871\ l_2 + 6{\cdot}36$ | 20·73 | 21·60 | 22·47 | 23·34 | 24·22 | 25·09 | 25·96 | 26·83 | 27·70 | 28·57 |
| Growth $(l_3 - l_2)$— | | | | | | | | | | |
| Observed | 4·5 | 4·37 | 4·26 | 4·00 | 3·52 | 3·56 | 3·61 | 3·29 | (2·83) | 3·00 |
| Calculated | 4·23 | 4·10 | 3·97 | 3·84 | 3·72 | 3·59 | 3·46 | 3·33 | 3·20 | 3·07 |

VALUES OF $l_3$ (CM.).

| | 20·5 | 21·5 | 22·5 | 23·5 | 24·5 | 25·5 | 26·5 | 27·5 | 28·5 |
|---|---|---|---|---|---|---|---|---|---|
| Values of $l_4$— | | | | | | | | | |
| Observed | (23·50) | (24·17) | 25·53 | 26·39 | 26·97 | 27·55 | 28·22 | 28·97 | (30·5) |
| $l_4 = {\cdot}727\, l_3 + 9{\cdot}07$ | 23·97 | 24·70 | 25·43 | 26·15 | 26·88 | 27·61 | 28·34 | 29·06 | 29·79 |
| Growth ($l_4$–$l_3$)— | | | | | | | | | |
| Observed | (3·00) | (2·67) | 3·03 | 2·89 | 2·47 | 2·05 | 1·72 | 1·47 | (2·0) |
| Calculated | 3·47 | 3·20 | 2·93 | 2·65 | 2·38 | 2·11 | 1·84 | 1·56 | 1·29 |

It is seen from the above, first, that the equations are a reasonable practical " fit " to the data ; and, second, that during any one growth-period, the smaller fish adds the larger increment.

Now if we accept equations i to iii and the values of the means as roughly representative of the 4-zoned 4-ringed fishes which visited Plymouth during the season 1924–25, and compare them with the corresponding data for similar-aged fish taken off the Sussex coast (*vide* Part I, p. 248), we find that there is an appreciable difference. In the following table the mean values for $l_1$, $l_2$, $l_3$, and $l_4$ in the two cases, and the regression equations are shown together, and in Fig. 6 the differences for individual values of $l_1$, $l_2$, and $l_3$ are demonstrated graphically :—

| | Plymouth Sample. | Sussex Sample. |
|---|---|---|
| Mean $l_1$ (cm.) | 13·88 | 10·73 |
| Mean $l_2$ (cm.) | 21·03 | 18·04 |
| Mean $l_3$ (cm.) | 24·68 | 21·89 |
| Mean $l_4$ (cm.) | 27·02 | 23·65 |
| Regression Equations | $l_2 = {\cdot}675\, l_1 + 11{\cdot}68$ | $l_2 = {\cdot}59\, l_1 + 11{\cdot}70$ |
| | $l_3 = {\cdot}871\, l_2 + 6{\cdot}36$ | $l_3 = {\cdot}504\, l_2 + 12{\cdot}80$ |
| | $l_4 = {\cdot}727\, l_3 + 9{\cdot}07$ | $l_4 = {\cdot}774\, l_3 + 6{\cdot}71$ |

It is clear that the Plymouth fish had made a superior growth throughout. This suggests that the Plymouth fish had frequented grounds more favourable for growth than had the Sussex ones, and in seeking to discover grounds where such superior conditions prevail, we naturally look to the more open waters to the south-west. As an immediate working hypothesis, therefore, let us accept the Plymouth regression equations as representative of a life spent in the more open westerly waters, and the Sussex regression equations as representative of a life spent in the enclosed waters of the English Channel. Under this hypothesis we should say that the 4-zoned 4-ringed Plymouth fish had spent all their life in westerly conditions, while those from the Sussex coast had always remained under Channel conditions. So far as is known at present, however, there is no reason to insist that a fish after spawning necessarily returns to the same feeding area from which it came. That is to say, we need not insist that a fish coming from the open west to spawn at Plymouth shall return to the westward again—it may possibly elect to spend the next feeding season within the confines of the enclosed Channel. Here it will be subject to Channel conditions of growth, and on its next return to Plymouth to spawn, if such return happens to take place, it will be of an inferior length to that shown by a western migrant. If this same process was repeated year by year, it is easily seen that the growth characters of the spawning stock at Plymouth would yearly become more and more complicated.

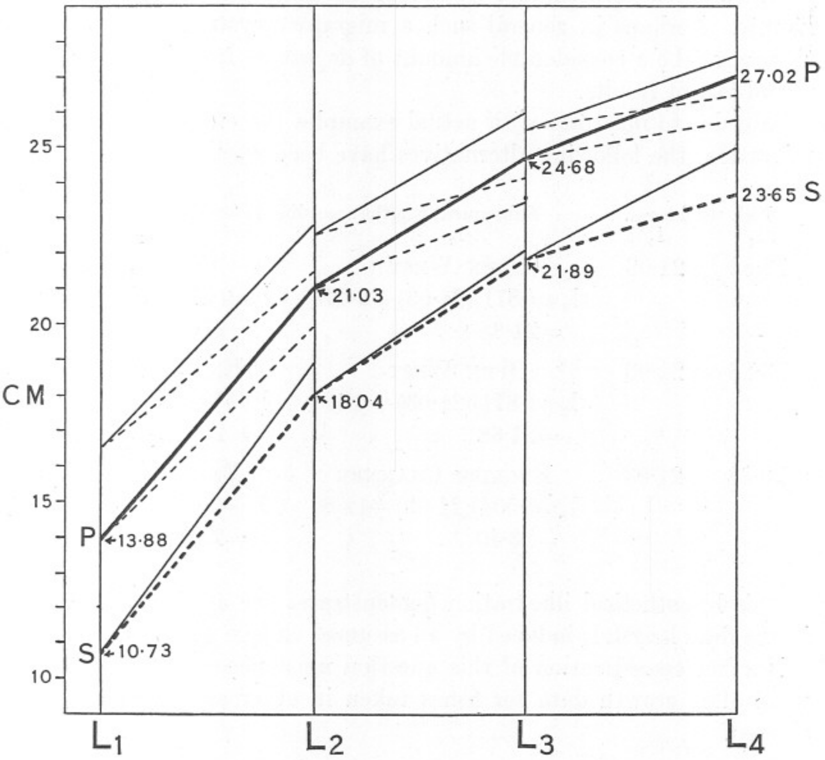

FIG. 6.—Comparison between growth of 4-zoned 4-ringed fishes from Plymouth (1924–25) and from the Sussex Coast.

Continuous line PP . . Mean values for Plymouth fish.
Continuous dotted line SS . ,, ,, ,, Sussex fish.

The Plymouth and Sussex values for given values of $l_1$, $l_2$, and $l_3$ are calculated from the regression equations given in the text on opposite page.

But it may also be said that we have, as yet, no proof that a fish invariably returns to the same ground to spawn. Thus, a fish coming from the westward to spawn at Plymouth might then proceed to the eastward for a season's feeding there and then move off to spawn, not at Plymouth, but on a spawning ground, say, at the east end of the Channel off the

French coast. This process in operation would also tend to produce a complex spawning population.

The above may be criticised by some as highly speculative, but it must be remembered that the spawning stock under investigation at Plymouth seems so mixed that it is almost impossible to believe that it may be explained in terms of some simple uniform unaltered annual movement from one feeding area to a spawning ground and a return to former haunts. Perhaps in general such a migratory system does apply, but there must be a considerable amount of departure from it to account for the observed results.

In order to illustrate with actual examples the effects of a change of migration, the following alternatives have been worked out :—

| Fish considered. | | Subsequent lengths according to feeding-area visited. | |
|---|---|---|---|
| $l_1$ | $l_2$ | $l_3$ | $l_4$ |
| 13·88 | 21·03 | OPEN WEST<br>$l_3=(\cdot 871)(21\cdot 03)+6\cdot 36$<br>$=24\cdot 68$ | OPEN WEST<br>$l_4=(\cdot 727)(24\cdot 68)+9\cdot 07$<br>$=27\cdot 02$ |
| 13·88 | 21·03 | OPEN WEST<br>$l_3=(\cdot 871)(21\cdot 03)+6\cdot 36$<br>$=24\cdot 68$ | ENGLISH CHANNEL<br>$l_4(\cdot 774)(24\cdot 68)+6\cdot 71$<br>$=25\cdot 82$ |
| 13·88 | 21·03 | ENGLISH CHANNEL<br>$l_3=(\cdot 504)(21\cdot 03)+12\cdot 80$<br>$=23\cdot 40$ | ENGLISH CHANNEL<br>$l_4=(\cdot 774)(23\cdot 40)+6\cdot 71$<br>$=24\cdot 82$ |

This hypothetical illustration demonstrates the appreciable difference in the final length $l_4$ induced by an assumed change in migration.

Further consideration of this question must necessarily be postponed until after growth data for fishes taken in other areas have been considered.

### *The Average Number of Vertebræ.*

Details of the sample averages obtained for the Plymouth fishes have already been given in Part II of this series (see Table I on p. 277). Little may be added at this stage to what was given in Part II, save to emphasize the need for study of the effect on the average number of vertebræ of the possible change of spawning and feeding grounds by a fish from one year to the next. A change of feeding ground may result in significant differences in average number of vertebræ among samples taken in the feeding area, while a change in spawning ground may similarly result in significant differences in average number of vertebræ among samples taken on that spawning ground.

### *Movements of Shoals.*

From what has been said in the preceding paragraphs it will be evident that the writer favours the hypothesis that the shoals which visit Plymouth for the winter spawning arrive both from the English Channel and from the more open waters off the south-west coast. The fishes coming from the west show a better increment of growth for the previous summer than those arriving from the east. After spawning, neither easterly nor westerly migrants necessarily return to the feeding grounds from whence they came. The general situation on the spawning grounds may be further complicated by reason of the presence of fish which in other years had spawned elsewhere. But as the distance over which a herring migrates during any one season is not likely to be excessively large, fishes will tend to remain roughly centralised about the spawning area in which they themselves were spawned.

The above must, however, be regarded purely as a working hypothesis until the data for samples in other areas have been discussed. With regard to the Plymouth samples already obtained it would provide a feasible explanation of the mixed populations experienced, and it would account for the fact that French trawlers can capture herrings during the summer months in the English Channel. It would also account for the similarity in growth between fishes caught off the south-west coast of Cornwall and those at Plymouth, as recorded by Watkin (**7**).

## ACKNOWLEDGMENTS.

I thank Mr. T. Edser, of the Statistical Department, Ministry of Agriculture and Fisheries, for his kindness in giving me free access to statistical returns relating to the western fisheries, and Mr. A. J. Smith, of the Laboratory staff at Plymouth, for keeping a most helpful diary of the daily landings of herrings at the fish markets. I would also like to express my gratitude to those members of the local and visiting fleets who have so kindly volunteered information concerning their catches and the fishery in general.

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## TABLE I.

### Condition of Ovary (Season 1924–25 at Plymouth).

| Sample. | Date. | Total No. fishes examined. | Percentage No. of Specimens with Ovaries in following condition. Unripe. | Mature. | Spent. |
|---|---|---|---|---|---|
| | 1924 | | | | |
| A | Nov. 11 | 51 | 100 | – | – |
| B | Nov. 13 | 55 | 100 | – | – |
| C | Nov. 17 | 70 | 100 | – | – |
| D | Nov. 20 | 65 | 100 | – | – |
| E | Nov. 22 | 39 | 44 | 56 | – |
| F | Nov. 28 | 57 | 100 | – | – |
| G | Dec. 3 | 58 | 100 | – | – |
| H | Dec. 9 | 53 | 98 | – | 2 |
| K | Dec. 16 | 55 | 65 | 4 | 31 |
| L | Dec. 19 | 51 | 100 | – | – |
| M | Dec. 22 | 71 | 28 | 69 | 3 |
| N | Dec. 30 | 65 | 28 | 60 | 12 |
| | 1925 | | | | |
| P | Jan. 5 | 64 | 47 | 3 | 50 |
| Q | Jan. 8 | 54 | 28 | 61 | 11 |
| R | Jan. 8 | 50 | 30 | 48 | 22 |
| S | Jan. 13 | 68 | 7 | 87 | 6 |
| T | Jan. 16 | 49 | 10 | 63 | 27 |
| U | Jan. 20 | 65 | 14 | 86 | – |
| V | Jan. 27 | 40 | 10 | 90 | – |
| W | Feb. 2 | 68 | 6 | 66 | 28 |
| X | Feb. 9 | 84 | – | 5 | 95 |
| Y | Feb. 18 | 57 | 9 | 7 | 84 |
| Z | Feb. 20 | 65 | 3 | 3 | 94 |
| a | Mar. 2 | 66 | 12 | 15 | 73 |

## TABLE II.

| | | | LENGTH DISTRIBUTION (CM.). | | | | |
|---|---|---|---|---|---|---|---|
| Sample. | Date. | Total No. of Fishes. | Lower Limit. | Lower Quartile $Q_1$. | Median $Q_2$. | Upper Quartile $Q_3$. | Upper Limit. |
| | 1924 | | | | | | |
| A | Nov. 11 | 100 | 23·7 | 26·3 | 27·3 | 28·5 | 30·0 |
| B | Nov. 13 | 100 | 23·0 | 25·7 | 26·9 | 27·8 | 30·5 |
| C | Nov. 17 | 119 | 25·5 | 26·9 | 27·8 | 28·6 | 30·7 |
| D | Nov. 20 | 116 | 22·3 | 26·5 | 27·4 | 28·0 | 30·0 |
| E | Nov. 22 | 112 | 23·5 | 25·9 | 27·0 | 27·9 | 29·6 |
| F | Nov. 28 | 117 | 24·4 | 26·4 | 27·2 | 27·8 | 29·9 |
| G | Dec. 3 | 124 | 25·1 | 26·9 | 27·6 | 28·4 | 31·0 |
| H | Dec. 9 | 115 | 25·0 | 26·6 | 27·3 | 27·9 | 29·9 |
| K | Dec. 16 | 134 | 22·8 | 25·9 | 27·0 | 27·7 | 30·5 |
| L | Dec. 19 | 106 | 23·6 | 27·1 | 27·7 | 28·6 | 30·0 |
| M | Dec. 22 | 173 | 23·0 | 25·8 | 27·1 | 28·0 | 30·5 |
| N | Dec. 30 | 136 | 21·7 | 25·3 | 26·4 | 27·4 | 30·9 |
| | 1925 | | | | | | |
| P | Jan. 5 | 121 | 22·5 | 26·7 | 27·6 | 28·5 | 30·4 |
| Q | Jan. 8 | 123 | 25·0 | 27·1 | 27·7 | 28·4 | 30·1 |
| R | Jan. 8 | 115 | 24·5 | 27·0 | 27·75 | 28·7 | 30·5 |
| S | Jan. 13 | 126 | 23·0 | 25·7 | 26·8 | 27·6 | 30·8 |
| T | Jan. 16 | 118 | 25·0 | 27·3 | 28·2 | 29·0 | 30·6 |
| U | Jan. 20 | 126 | 23·2 | 27·0 | 27·6 | 28·4 | 30·0 |
| V | Jan. 27 | 97 | 23·4 | 26·0 | 27·1 | 27·8 | 29·2 |
| W | Feb. 2 | 124 | 23·3 | 26·3 | 27·1 | 27·9 | 30·6 |
| X | Feb. 9 | 140 | 24·9 | 27·0 | 27·7 | 28·5 | 30·2 |
| Y | Feb. 18 | 119 | 23·8 | 26·3 | 27·3 | 28·2 | 30·8 |
| Z | Feb. 20 | 123 | 24·2 | 26·4 | 27·3 | 28·0 | 31·1 |
| a | Mar. 2 | 119 | 24·2 | 26·2 | 27·1 | 27·9 | 31·8 |
| | 1925 | | | | | | |
| b | Sept. 2 | 53 | 21·4 | 22·6 | 23·5 | 25·1 | 26·7 |
| e | Oct. 25 | 121 | 23·4 | 25·1 | 26·0 | 27·1 | 29·2 |
| f | Nov. 1 | 110 | 23·2 | 25·6 | 26·7 | 27·6 | 29·6 |
| g | Nov. 4 | 121 | 25·2 | 26·6 | 27·3 | 27·8 | 30·1 |
| h | Nov. 18 | 110 | 23·4 | 25·3 | 26·1 | 27·2 | 29·9 |
| k | Dec. 1 | 119 | 22·1 | 25·5 | 26·3 | 27·2 | 29·8 |
| l | Dec. 6 | 120 | 21·5 | 26·6 | 27·9 | 28·8 | 31·1 |
| m | Dec. 15 | 116 | 21·5 | 25·3 | 27·1 | 28·3 | 30·8 |
| n | Dec. 21 | 115 | 25·1 | 27·2 | 28·0 | 28·9 | 30·5 |
| o | Dec. 23 | 119 | 23·5 | 26·5 | 27·4 | 28·4 | 30·3 |

## TABLE II—*continued.*

| | | | LENGTH DISTRIBUTION (CM.). | | | | |
|---|---|---|---|---|---|---|---|
| Sample. | Date. | Total No. of Fishes. | Lower Limit. | Lower Quartile $Q_1$. | Median $Q_2$. | Upper Quartile $Q_3$. | Upper Limit. |
| | 1926 | | | | | | |
| p | Jan. 1 | 120 | 23·5 | 26·9 | 27·8 | 28·7 | 31·2 |
| q | Jan. 6 | 117 | 23·5 | 27·0 | 28·2 | 29·0 | 30·7 |
| r | Jan. 10 | 119 | 22·2 | 27·4 | 28·3 | 28·9 | 31·8 |
| s | Jan. 14 | 120 | 21·5 | 25·7 | 27·0 | 28·1 | 29·9 |
| t | Jan. 18 | 117 | 23·4 | 26·9 | 27·8 | 28·6 | 30·0 |
| u | Jan. 25 | 116 | 24·5 | 27·2 | 28·0 | 28·7 | 30·3 |
| v | Jan. 28 | 116 | 24·1 | 26·75 | 27·7 | 28·5 | 30·3 |
| w | Feb. 2 | 112 | 23·3 | 27·2 | 27·9 | 28·6 | 30·5 |
| x | Feb. 4 | 120 | 23·5 | 26·8 | 27·7 | 28·5 | 29·9 |
| y | Feb. 10 | 119 | 24·5 | 27·1 | 27·8 | 28·7 | 30·0 |
| | 1926 | | | | | | |
| AA | Oct. 18 | 111 | 24·5 | 26·5 | 27·7 | 28·95 | 30·5 |
| BB | Oct. 21 | 115 | 23·7 | 27·1 | 27·8 | 28·6 | 30·9 |
| CC | Oct. 25 | 115 | 23·3 | 26·5 | 27·7 | 28·6 | 30·2 |
| DD | Nov. 3 | 119 | 24·5 | 25·6 | 26·2 | 28·1 | 30·5 |
| EE | Nov. 4 | 117 | 24·5 | 25·6 | 26·4 | 27·2 | 29·5 |
| FF | Nov. 15 | 110 | 24·1 | 25·7 | 26·6 | 27·75 | 29·5 |
| GG | Nov. 23 | 110 | 24·5 | 25·9 | 26·9 | 27·8 | 29·6 |
| HH | Nov. 30 | 120 | 23·7 | 25·3 | 26·1 | 27·2 | 30·1 |
| JJ | Dec. 6 | 115 | 23·5 | 25·3 | 26·6 | 27·4 | 29·5 |
| LL | Dec. 20 | 110 | 24·3 | 27·1 | 28·2 | 29·0 | 29·9 |
| MM | Dec. 20 | 120 | 23·0 | 24·4 | 25·4 | 26·9 | 29·8 |
| NN | Dec. 30 | 203 | 22·5 | 24·4 | 25·7 | 27·3 | 29·5 |
| | 1927 | | | | | | |
| OO | Jan. 4 | 117 | 22·5 | 24·7 | 26·4 | 27·9 | 30·1 |
| PP | Jan. 19 | 120 | 24·3 | 25·6 | 26·6 | 28·3 | 30·2 |

## TABLE III.

### PERCENTAGE AGE COMPOSITION.

| Sample. | Date. | 2 | 2–3 | 3 | 3–4 | 4 | 4–5 | 5 | 5–6 | 6 | 6–old. | Older than 6. | Total No. of Fish in Sample. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1924 | | | | | | | | | | | | |
| A | Nov. 11 | – | 1·0 | 13·5 | – | 13·5 | – | 41·7 | 1·0 | 12·6 | – | 16·7 | 96 |
| B | Nov. 13 | – | – | 14·4 | 5·2 | 12·4 | 1·0 | 42·3 | 8·2 | 7·2 | – | 9·3 | 97 |
| C | Nov. 17 | – | – | 2·6 | ·9 | 17·1 | – | 41·8 | 2·6 | 15·4 | – | 19·6 | 117 |
| D | Nov. 20 | – | ·9 | 10·6 | 2·7 | 9·8 | ·9 | 53·9 | – | 10·6 | – | 10·6 | 113 |
| E | Nov. 22 | – | – | 15·7 | – | 11·1 | – | 35·2 | – | 17·6 | – | 20·4 | 108 |
| F | Nov. 28 | – | – | 10·7 | 1·9 | 11·7 | 1·9 | 55·4 | 4·9 | 9·7 | – | 3·9 | 103 |
| G | Dec. 3 | – | – | 1·0 | – | 13·7 | 2·1 | 52·6 | 3·2 | 15·8 | – | 11·6 | 95 |
| H | Dec. 9 | – | – | 2·0 | – | 4·1 | – | 65·3 | 2·0 | 19·4 | – | 7·2 | 98 |
| K | Dec. 16 | – | – | 9·4 | 3·1 | 8·3 | – | 55·3 | 3·1 | 17·7 | – | 3·1 | 96 |
| L | Dec. 19 | – | – | 5·2 | – | 13·5 | 2·1 | 54·2 | 3·3 | 14·6 | 2·1 | 5·2 | 96 |
| M | Dec. 22 | – | – | 13·5 | – | 5·8 | – | 53·8 | 5·8 | 11·5 | – | 9·6 | 104 |
| N | Dec. 30 | – | – | – | – | NO DATA. | | – | – | – | – | – | – |
| | 1925 | | | | | | | | | | | | |
| P | Jan. 5 | – | – | 13·1 | – | 13·1 | 1·0 | 46·5 | 2·0 | 9·1 | 1·0 | 14·2 | 99 |
| Q | Jan. 8 | – | – | 3·0 | – | 6·0 | 2·0 | 64·0 | 7·0 | 12·0 | – | 6·0 | 100 |
| R | Jan. 8 | – | – | 4·7 | – | 14·0 | 1·2 | 44·2 | 2·3 | 14·0 | 1·2 | 18·6 | 86 |
| S | Jan. 13 | – | – | 8·1 | 3·0 | 13·1 | 1·0 | 53·6 | 3·0 | 12·1 | 1·0 | 5·1 | 99 |
| T | Jan. 16 | – | – | 2·0 | – | 17·0 | 2·0 | 44·0 | 5·0 | 8·0 | 1·0 | 21·0 | 100 |
| U | Jan. 20 | – | – | 6·0 | – | 14·0 | 3·0 | 53·0 | 7·0 | 9·0 | 1·0 | 7·0 | 100 |
| V | Jan. 27 | – | – | 12·4 | – | 13·4 | 3·1 | 52·6 | 4·1 | 13·4 | – | 1·0 | 97 |
| W | Feb. 2 | – | – | 4·3 | – | 4·3 | 1·0 | 58·5 | 3·2 | 17·0 | – | 11·7 | 94 |
| X | Feb. 9 | – | – | 2·0 | – | 5·0 | – | 63·0 | 2·0 | 18·0 | 1·0 | 9·0 | 100 |
| Y | Feb. 18 | 1 | – | 14·1 | – | 10·1 | – | 49·6 | 3·0 | 14·1 | 1·0 | 7·1 | 99 |
| Z | Feb. 20 | – | – | 8·0 | 1·0 | 15·0 | 2·0 | 51·0 | 3·0 | 13·0 | 1·0 | 6·0 | 100 |
| a | Mar. 2 | – | – | 7·1 | – | 11·1 | 1·0 | 53·6 | 4·0 | 14·1 | – | 9·1 | 99 |
| | 1925 | | | | | | | | | | | | |
| b | Sept. 2 | 36 | 12 | 32 | – | 10 | – | 2 | 2 | 2 | – | 2 | 50 |
| e | Oct. 25 | – | – | 14 | 2 | 35 | – | 3 | – | 21 | 1 | 6 | 100 |
| f | Nov. 1 | – | – | 18 | 4 | 22 | 1 | 7 | 1 | 21 | 2 | 4 | 100 |
| g | Nov. 4 | – | – | 5 | 1 | 19 | 2 | 24 | 4 | 30 | 3 | 12 | 100 |
| h | Nov. 18 | 1 | – | 10 | 3 | 19 | 2 | 10 | 4 | 39 | 1 | 16 | 100 |
| j | Nov. 20 | 3 | 3 | 23 | – | 18 | – | 4 | – | 10 | – | 5 | 100 |
| k | Dec. 1 | – | – | 3 | – | 27 | 1 | 13 | 5 | 27 | 2 | 21 | 100 |
| l | Dec. 6 | – | – | 9 | – | 12 | 1 | 16 | 3 | 40 | 3 | 14 | 100 |
| m | Dec. 15 | – | – | 10 | 2 | 22 | – | 18 | – | 34 | 3 | 11 | 100 |

TABLE III—*continued.*

| Sample. | Date. | 2 | 2–3 | 3 | 3–4 | 4 | 4–5 | 5 | 5–6 | 6 | 6–old. | Older than 6. | Total No. of Fish in Sample. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| n | Dec. 21 | – | – | 1 | 2 | 22 | – | 17 | 2 | 38 | 4 | 14 | 100 |
| o | Dec. 23 | – | – | 3 | 1 | 10 | – | 21 | 1 | 48 | 4 | 12 | 100 |
| | 1926 | | | | | | | | | | | | |
| p | Jan. 1 | – | – | 2 | – | 8 | 2 | 11 | 2 | 47 | 5 | 23 | 100 |
| q | Jan. 6 | – | – | – | – | 11 | – | 12 | 1 | 53 | 4 | 18 | 100 |
| r | Jan. 10 | – | – | 4 | – | 6 | – | 9 | – | 54 | 3 | 23 | 100 |
| s | Jan. 14 | – | – | 16 | 1 | 11 | 1 | 11 | 3 | 38 | 7 | 11 | 100 |
| t | Jan. 18 | – | – | 4 | 1 | 17 | – | 9 | 1 | 51 | 6 | 11 | 100 |
| u | Jan. 25 | – | – | 5 | 1 | 15 | 1 | 10 | – | 50 | – | 18 | 100 |
| v | Jan. 28 | – | – | 2 | – | 13 | – | 9 | – | 55 | 4 | 15 | 100 |
| w | Feb. 2 | – | – | 3 | – | 17 | 3 | 12 | 1 | 42 | 7 | 13 | 100 |
| x | Feb. 4 | – | – | 3 | – | 15 | – | 9 | 1 | 59 | 1 | 12 | 100 |
| y | Feb. 10 | – | – | 1 | – | 4 | – | 11 | 3 | 58 | 3 | 20 | 100 |

| | 1926 | 2 | 2-3 | 3 | 3–4 | 4 | 4–5 | 5 | 5–6 | 6 | 6–7 | 7 | 7-old. | Older than7. | Total No. of Fish in Sample- |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AA | Oct. 18 | – | – | 22 | 5 | 17 | 3 | 8 | 2 | 7 | 2 | 26 | – | 4 | 100 |
| BB | Oct. 21 | – | – | 4 | 1 | 9 | 1 | 22 | – | 8 | 1 | 36 | 1 | 7 | 100 |
| CC | Oct. 25 | – | – | 8 | 2 | 8 | 1 | 18 | – | 6 | 6 | 31 | 4 | 11 | 100 |
| DD | Nov. 3 | – | – | 11 | 1 | 18 | 3 | 18 | 2 | 9 | 1 | 30 | 1 | 2 | 100 |
| FF | Nov. 15 | – | – | 9 | 1 | 20 | 3 | 17 | 1 | 14 | 3 | 26 | – | 3 | 100 |
| GG | Nov. 23 | – | – | 11 | 1 | 19 | 1 | 16 | 2 | 5 | 6 | 24 | 2 | 8 | 100 |
| HH | Nov. 30 | – | – | 11 | – | 23 | 4 | 26 | 3 | 8 | 3 | 14 | 2 | 4 | 100 |
| JJ | Dec. 6 | – | – | 3 | – | 17 | – | 20 | 3 | 10 | 2 | 27 | 6 | 9 | 100 |
| LL | Dec. 20 | – | – | 4 | – | 18 | 3 | 11 | 1 | 3 | 5 | 42 | 2 | 8 | 100 |
| MM | Dec. 20 | – | – | 3 | – | 34 | 6 | 25 | 1 | 8 | – | 13 | 3 | 3 | 100 |
| | 1927 | | | | | | | | | | | | | | |
| OO | Jan. 4 | – | – | 2 | 2 | 40 | 1 | 12 | 1 | 9 | 5 | 17 | 2 | 6 | 100 |
| PP | Jan. 19 | – | – | 3 | – | 20 | 4 | 25 | 1 | 11 | 1 | 25 | – | 4 | 100 |

# Herring Investigations at Plymouth. IV. The Growth of Young Herrings in the Neighbourhood of Plymouth.

By

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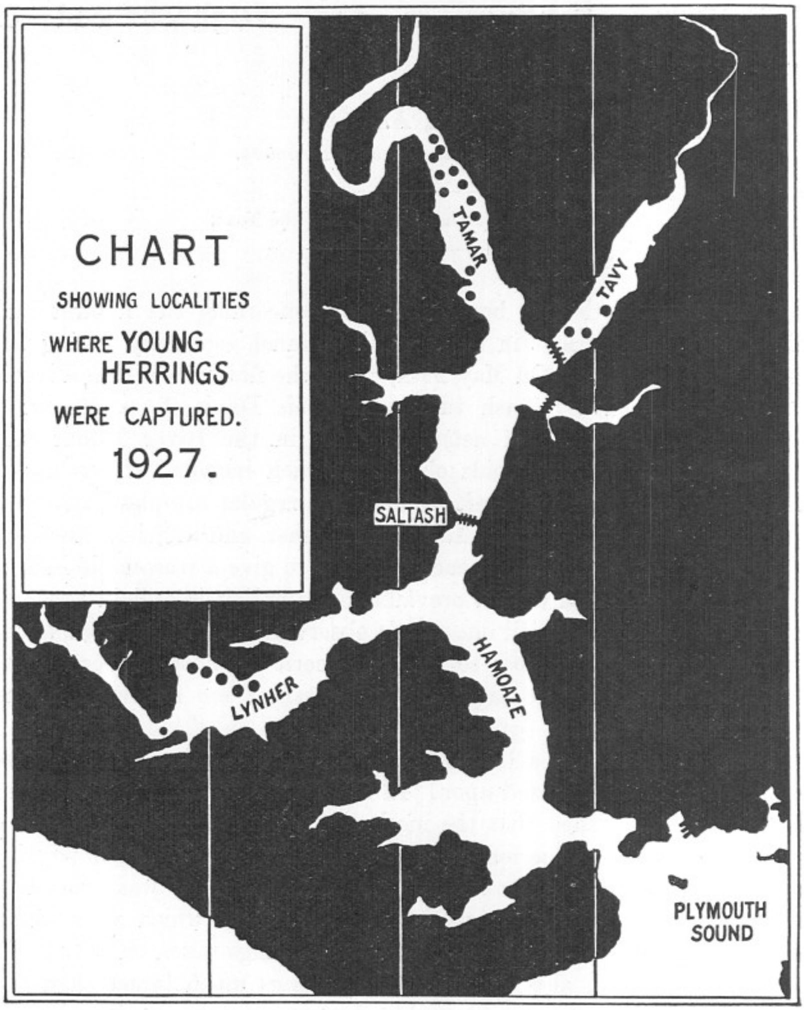
With 1 Chart and 4 Figures in the Text.

Comparatively little has been published concerning the habitat and growth of young herrings in the English Channel, especially during the first year of their life. On May 26th, 1927, the first of a series of hauls with a small-meshed Saltash tuck seine (*vide* Davis, **1**, p. 70, for a description of this type of net) was made in the River Tamar and a fine haul of young clupeoids obtained, which included the young of the herring, sprat and pilchard. Since then, regular samples have been taken from the rivers Tamar, Tavy and Lynher, and sufficient numbers of young herrings collected on each occasion to give a reasonable indication of the length-distribution prevailing. Sampling is still in progress and will be continued until one year's observation has been completed, but sufficient data are now to hand to merit an initial report. The localities from which the samples were obtained are indicated in the accompanying chart.

Before proceeding to a discussion of the data obtained, one or two facts need to be commented upon. In the first place it may be accepted as definitely established that the mesh of the seine used was of such a size that no question of serious selectivity among the " 0 " group populations during the period of sampling can arise. The net was proved to be capable of capturing young sprats in quantity which were much smaller than the great bulk of the smallest herrings taken on May 26th, 1927, while it could also capture older herrings much larger than the largest of the " 0 " group. Probably, however, in the coming months of, say, March and April and even early in May, 1928, the selective action of the net will need to be taken into account. The second fact, apart from its explanation, is of immediate interest because of its effect on the choice of a standard measurement of length. A regular experience throughout the sampling has been to find that a large proportion of the young herrings had an incomplete caudal fin. The condition of the tail in such specimens presented an appearance which suggested that it had been "nibbled." Slightly affected cases had only a small portion of one fluke missing, but in the more severe cases the caudal peduncle alone remained. This tail affection obviously made it impossible to determine the total length from the tip of the snout to the end of the dorsal fluke of the tail. To have discarded all affected specimens would have meant the sacrifice of the major portion of every haul, and rather than do this it was thought better to adopt some other standard of length. It was therefore decided to use the *body* length from the tip



of the snout to the end of the *caudal peduncle*, instead of the *total* length to the end of the *caudal fin*. This standard of length, although perfectly satisfactory in practice, has the disadvantage that it is not in common use, so that the data on growth are expressed in terms unfamiliar to other workers. To meet this objection so far as is possible, both the body length and the total length have been determined for each of a large number of normal-tailed specimens covering the whole range in size, and a correlation table drawn up from which it is possible to read off the total lengths corresponding with given body lengths (see p. 309).

As a rule hauls of the seine were kept separate, and a sufficient number of hauls taken on each occasion to give as good a representation as possible of the stock present. It was found that hauls taken at the same place during the same visit differed to some extent in their size composition, due, one believes, to the tendency on the part of the fish to segregate into shoals according to size. By increasing the number of hauls and adding together the data for the day, the effects of this segregation were probably fairly well overcome. The actual measurements of length were made to the " nearest 5 mm. below," and the data grouped into 5 mm. classes. For example, all fishes from 65 mm. to 69 mm. were included in the 65 mm. class. Particulars and data for each sample are given in the tables at the end of this paper.

It became evident at an early stage that there was an appreciable difference in size distribution between the normal-tailed and the abnormal-tailed specimens of the same sample, the proportion of the smaller sizes being greater among the latter. There was also an indication that among the abnormal-tailed specimens themselves, size distribution was dependent upon the degree to which the tail was affected. This may be illustrated by an analysis of a sample taken on October 20th, 1927, in which the abnormal-tailed specimens were grouped into two classes, according to a rough standard of severity in tail affection as shown in the photographs in Fig. 1 :—

| | | Body Length. 12 length groups. mm. | | | | | | | | | | | | | Median $Q_2$. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Types | 80 | 85 | 90 | 95 | 100 | 105 | 110 | 115 | 120 | 125 | 130 | 135 | Totals | mm. |
| Abnormal-tailed specimens. | 1–3 | 5 | 14 | 25 | 30 | 21 | 23 | 14 | 11 | 5 | – | 1 | – | 149 | 100·2 |
| | 4–7 | – | – | 3 | 14 | 33 | 34 | 25 | 18 | 14 | 7 | 4 | 1 | 153 | 109·0 |

The Saltash fishermen assert that a big flow of fresh water down the rivers, as the result of heavy rains, drives fish downstream into the lower reaches of the estuary. Now if, as seems possible, the bigger fishes are more susceptible to a marked freshening of the water than are the smaller ones, then samples taken during the periods of such freshening would show a resultant lower average size. When the fresh water " dried up," as the fishermen would say, the bigger fish would return to their usual haunts upstream, with the result that the sample average would rise again. Such a phenomenon would tend to cause some irregularity in the general upward trend of the average size as calculated from sample data.

As the immediate purpose of this paper is to describe the broad features of the growth of the general stock of young herrings in the area, the summarised data, as shown in Tables V and VI (p. 319), may be used. It will be realised, however, from what has been said above, that the estimates of growth derived from these summaries are subject to correction for the reasons stated. It is at once seen that throughout the period of sampling there was always a considerable range in size among the individuals of any one sample. The difference in size between the fishes of the first sample (May 26th, 1927) is believed to be due, in the main, to a difference in the time at which the fishes were

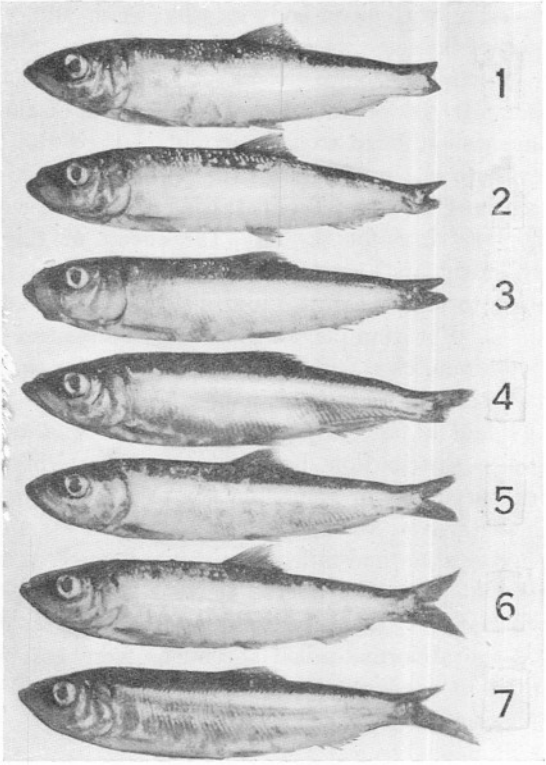


FIG. 1.—Seven examples of young herrings from Tamar with abnormal tails. Body length 95 mm. 1927. (*ca.* × $\frac{4}{7}$).

spawned. Between 200 and 300 of the specimens in this sample had not yet completed their metamorphosis; these may be regarded as the final contribution from the winter spawning season of 1926–27, which, as was shown in Part III (see p. 284), may have commenced as early as October, 1926, and finished as late as March, 1927. The question of the difference in size directly attributable to a difference in time of birth can only be approached with confidence, however, when samples taken during the early months of the year 1928 become available. The extent of the range in size within the sample showed no tendency to diminish as time went on; if anything, the later samples showed an even greater range. It is quite feasible that abnormality of the tail reduces the general efficiency for hunting food, with the result that badly affected specimens are less fortunate than their healthier associates and, in consequence, grow less. Certainly, as has already been shown, abnormal-tailed specimens were on average smaller than normal-tailed ones, and the more severe the affection, the less the average size.

## PROPORTIONATE LENGTH OF THE TAIL.

The *body* length and the *total* length were determined for each of 1305 specimens with unaffected tails, and the data are shown in the form of a correlation table (Table II, on p. 316). There is an almost perfect correlation between the two measurements, and it may be taken that for any value ($L_B$) of the body length, the corresponding total length ($L_T$) is approximately 7/6 $L_B$. It is interesting to observe that this proportion holds good to a strikingly close degree for a total of 1075 adult herrings measured at Plymouth by Orton (2). The latter data are given in Table I, p. 315, but the following summary may be used to demonstrate the observation:—

PLYMOUTH "O" GROUP FISHES.

| (mm.) Observed $L_B$ | 32·5 | 37·5 | 42·5 | 47·5 | 52·5 | 57·5 | 62·5 | 67·5 | 72·5 | 77·5 | 82·5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Average $L_T$ | 37·5 | 43·0 | 49·1 | 55·3 | 59·7 | 66·4 | 72·3 | 77·6 | 82·9 | 89·1 | 95·1 |
| $L_T = 7/6\, L_B$ | 37·9 | 43·5 | 49·6 | 55·4 | 61·2 | 67·1 | 72·9 | 78·7 | 84·5 | 90·4 | 96·2 |

| 87·5 | 92·5 | 97·5 | 102·5 | 107·5 | 112·5 | 117·5 | 122·5 | 127·5 | 132·5 | 137·5 | 142·5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100·2 | 106·8 | 112·7 | 119·0 | 124·2 | 129·4 | 135·5 | 141·5 | 148·2 | 153·5 | 159·0 | 162·5 |
| 102·1 | 107·8 | 113·7 | 119·6 | 125·4 | 131·2 | 137·0 | 142·9 | 148·7 | 154·6 | 160·4 | 166·2 |

ORTON'S ADULT FISHES.

| (cm.) $L_B$* | 18·5 | 19·5 | 20·5 | 21·5 | 22·5 | 23·5 | 24·5 | 25·5 | 26·5 |
|---|---|---|---|---|---|---|---|---|---|
| $L_T$* | 21·9 | 23·0 | 24·1 | 25·2 | 26·3 | 27·5 | 28·5 | 29·75 | 31.5 |
| $L_T = 7/6\, L_B$ | 21·6 | 22·75 | 23·9 | 25·1 | 26·2 | 27·4 | 28·6 | 29·74 | 30·9 |

* $L_B$ is Orton's character $7_b$ and $L_T$ is Orton's character 9.

## Tamar Samples

The data for the Tamar samples are given in Tables III and V on pp. 317 and 319, and shown graphically in Fig. 2. If the curve AB be accepted as a reasonable approximation to the general upward trend of the median body length ($L_B$), then it is seen that the average growth from month to month may be expressed as follows :—

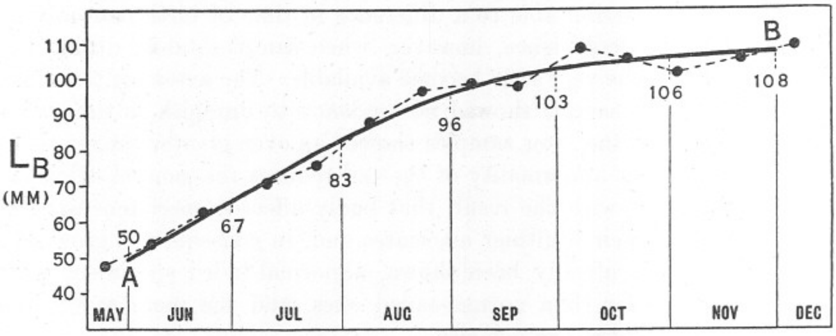


Fig. 2.—Median body length ($L_B$) for samples of young herrings caught in Tamar, 1927. The curve A B is a freehand curve indicating the general upward trend of the median. The values of the median on the first day of each month is shown.

| Date. 1927. | Median Body Length. $L_B$. mm. | inches. | Median Total Length. $L_T = 7/6\ L_B$. mm. | inches. | Median Total Length. Monthly increments. mm. | inches. |
|---|---|---|---|---|---|---|
| June 1st | 50 | 2·0 | 58·3 | 2·3 | | |
| July 1st | 67 | 2·6 | 78·1 | 3·1 | June, 19·8 | 0·78 |
| Aug. 1st | 83 | 3·3 | 96·8 | 3·8 | July, 18·7 | 0·74 |
| Sept. 1st | 96 | 3·8 | 112·0 | 4·41 | Aug., 15·2 | 0·60 |
| Oct. 1st | 103 | 4·06 | 120·1 | 4·73 | Sept., 8·1 | 0·32 |
| Nov. 1st | 106 | 4·17 | 123·6 | 4·87 | Oct., 3·5 | 0·14 |
| Dec. 1st | 108 | 4·25 | 126·0 | 4·96 | Nov., 2·4 | 0·09 |

Thus, the median length increased most rapidly during June and July, less and less rapidly during August, September, and October, until during November it remained almost stationary. Fig. 3 will convey a good impression of the alteration in appearance of the fish as growth proceeds. Some idea of the growth by weight may be obtained by using the values of the cubes of the successive total lengths as functions of the weights as shown on page 312.

It is seen that whereas in the case of length, the monthly increment added falls continuously from June onwards, the increment of weight increases from June to the maximum in August, and then subsequently falls away, arriving at the minimum in November.

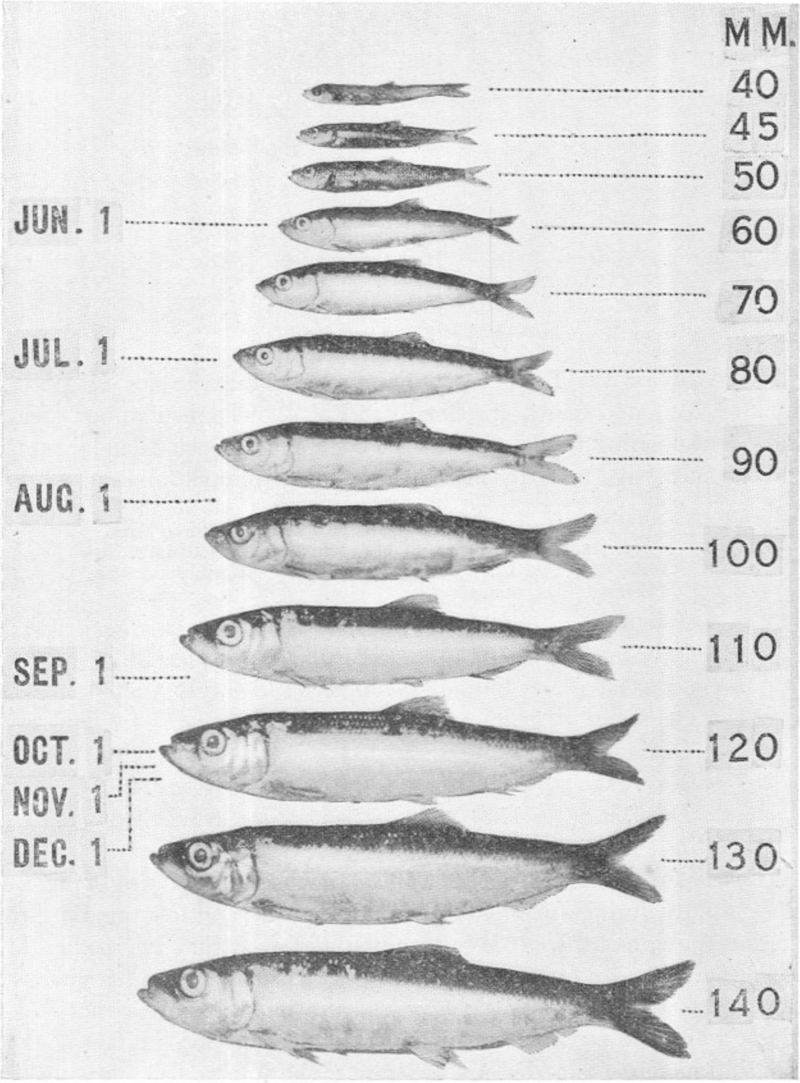


FIG. 3.—Photograph to illustrate the average growth made by the Tamar fish from June 1st to December 1st, 1927. The total lengths $L_T$ are shown. (*ca.* × ½).

| Date. 1927. | Median Total Length. $L_T$ mm. | $\left(\frac{L_{T_x}}{L_{T_1}}\right)^3$ | $\left(\frac{L_{T_x}}{L_{T_{\;\;1}}}\right)^3$ | Monthly increments of weight. $=K\left\{L_{T_x}^3 - L_{T_{x-1}}^3\right\}$ |
|---|---|---|---|---|
| June 1st | $58{\cdot}3=L_{T_1}$ | 1·0 | — | |
| July 1st | $78{\cdot}1=L_{T_2}$ | 2·4 | 2·40 | June $=K\times10^4\times27{\cdot}83$ |
| Aug. 1st | $96{\cdot}8=L_{T_3}$ | 4·6 | 1·94 | July $=K\times10^4\times43{\cdot}07$ |
| Sept. 1st | $112{\cdot}0=L_{T_4}$ | 7·1 | 1·55 | Aug. $=K\times10^4\times49{\cdot}78$ |
| Oct. 1st | $102{\cdot}1=L_{T_5}$ | 8·7 | 1·23 | Sept. $=K\times10^4\times32{\cdot}70$ |
| Nov. 1st | $123{\cdot}6=L_{T_6}$ | 9·5 | 1·09 | Oct. $=K\times10^4\times15{\cdot}60$ |
| Dec. 1st | $126{\cdot}0=L_{T_7}$ | 10·1 | 1·06 | Nov. $=K\times10^4\times11{\cdot}30$ |

### LYNHER SAMPLES.

The data for the Lynher samples are given in Tables IV and VI (pp. 318, 319), and shown graphically in Fig. 4. The median body length and corresponding total length at the beginning of each calendar month, and the successive monthly increments added, were as follows :—

| Date. 1927. | Median Body Length. $L_B$. mm. | Median Total Length. $L_T$. mm. | Median Total Length. Monthly increments. mm. |
|---|---|---|---|
| June 1st | 59 | 68·8 | |
| July 1st | 75 | 87·5 | June, 18·7 |
| Aug. 1st | 89 | 103·8 | July, 16·3 |
| Sept. 1st | 99 | 115·5 | Aug., 11·7 |
| Oct. 1st | 105 | 122·5 | Sept., 7·0 |
| Nov. 1st | 109 | 127·1 | Oct., 4·6 |
| Dec. 1st | 111 | 129·5 | Nov., 2·4 |

Thus, as for the fishes from the Tamar, the median total length increased most rapidly during June and July, and then less and less rapidly during the remaining months. It is to be noted, however, that the median total length on June 1st for the Lynher fishes was some 10 mm. greater than the corresponding Tamar value. This initial difference, whatever its cause, would, to some extent at any rate, account for the fact that the monthly increments added are different ; the Tamar fish, starting from the smaller June length of 58·3 mm., adding the larger increment of 19·8 mm. during June, while the Lynher fish starting from the larger June length of 68·8 mm., adding the smaller increment of 18·7 mm. during June.

The superior median length of the Lynher fish at the commencement of the period of observation was undoubtedly due in a marked degree to the fact that the proportion of normal-tailed individuals was very much higher than in the Tamar during the same period. Thus, the first Lynher sample, taken on June 13th, 1927, included only 98 abnormal-tailed specimens in a total of 613, whereas a Tamar sample of 884 taken on June 23rd, 1927, included 602 abnormal-tailed specimens. We have already seen (p. 307) that on average the normal-tailed specimens of a sample were larger than the abnormal-tailed.

## GROWTH DURING FIRST SEASON IN SCALED CONDITION.

In all estimations of age and growth of adult fishes from scale readings, it is essential that the investigator should possess precise knowledge of the significance of the first winter-ring (see Part I, p. 242). From the above results it may be concluded that by the end of November, 1927, practically all growth for the season had been made, although some subsequent slight increase in length during the winter may yet be possible, especially on the part of the smaller specimens. Taking the Tavy sample of December 5th as an approximation to the final position, it is seen that there is a range in *body* length from about 80–140 mm., with a median value of approximately 110 mm. Expressed as *total* length, the range is thus from about 90–160 mm., with a median total length of approximately 130 mm. Now it may be accepted that the great bulk of the small herrings captured on May 26th, 1927 (the first of the series of samples), had either acquired their scales or were in actual process of doing so in the *calendar year* 1927. Their subsequent growth to the median length of 130 mm. by December thus represents the first season's growth in the scaled condition. When, therefore, these fish eventually grow to adults, they will show a first winter-ring at a length $l_1$ of approximately 130 mm. on average, but with

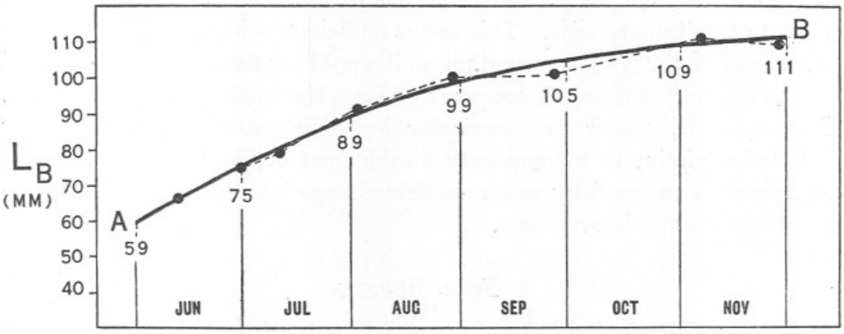


FIG. 4.—Median body length ($L_B$) for samples of young herrings caught in Lynher, 1927. Details as in Fig. 2.

a range of variation of from 90–160 mm. It is of interest and importance to note that the calculated values of $l_1$ for adult fishes visiting Plymouth during the winter season compare quite favourably with those for the young fishes taken from the Tamar and Lynher. Thus, in 1924–25, a total of 244 " 4-zoned 4-ringed " fishes showed a range in $l_1$ from 85 mm. to 175 mm., with an average of 138·8 mm. A total of 1122 fishes of the " 5-zoned 5-ringed " class of the same season varied from 65 to 185 mm. in their value of $l_1$, the average value being 128·6 mm. That the scales of the young fish under discussion will actually show a winter-ring is proved by the fact that in the later samples the well-marked clear " winter-edge " was beginning to appear, and was well established in the last samples.

The reason for the amount of variation in the length $l_1$ appears to be twofold. In the first place, the time of spawning undoubtedly plays its part. On May 26th, 1927, while many were fully scaled and growing well, there was an appreciable number of individuals still in the early stages of metamorphosis. This seems sufficient evidence of a difference in time of birth. In the second place, it would appear that fishes spawned at the same time may not necessarily attain the same ultimate length, $l_1$. For example, under the particular local circumstances, a fish may become a victim to a temporary disablement of the tail and therefore not grow so successfully as its unaffected associate until (if such occurs) the tail affection is overcome.

## Food Supply

A detailed analysis of the stomach contents of the fishes has not yet been completed, but from the observations so far made it is abundantly evident that the fully-scaled fishes were feeding throughout with great avidity almost entirely on mysids. The rivers abound with mysids, and the stomachs examined during the summer were always well filled.

## Acknowledgments.

I am greatly indebted to Mr. J. H. Blake, of Saltash, both for constructing the successful small-meshed seine and for his skilful superintendence of the actual fishing operations. I wish also to thank Mr. W. Searle, of the Laboratory staff, for his willing and valuable services in the collection of the samples.

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2 Orton, J. H. "An Account of the Researches on Races of Herrings carried out by the Marine Biological Association at Plymouth, 1914–15." Journ. Mar. Biol. Assoc., Vol. XI, No. 1, 1916.

## TABLE I.

### Correlation Table. Body Length and Total Length (Orton's Samples of Adult Fishes).

### 1914–15.

| Body Length. Central values for 9 length groups, (cm.) | Total Length. Central values for 11 length groups (cm.) | | | | | | | | | | | | Arith. means. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 21·5 | 22·5 | 23·5 | 24·5 | 25·5 | 26·5 | 27·5 | 28·5 | 29·5 | 30·5 | 31·5 | Totals | |
| 18·5 | 3 | 2 | | | | | | | | | | 5 | 21·9 |
| 19·5 | | 19 | 23 | | | | | | | | | 42 | 23·0 |
| 20·5 | | | 50 | 88 | | | | | | | | 138 | 24·1 |
| 21·5 | | | | 62 | 171 | 1 | | | | | | 234 | 25·2 |
| 22·5 | | | | | 64 | 294 | 7 | | | | | 365 | 26·3 |
| 23·5 | | | | | | 20 | 156 | 19 | | | | 195 | 27·5 |
| 24·5 | | | | | | | 4 | 73 | 6 | | | 83 | 28·5 |
| 25·5 | | | | | | | | | 9 | 3 | | 12 | 29·75 |
| 26·5 | | | | | | | | | | | 1 | 1 | 31·5 |
| Totals | 3 | 21 | 73 | 150 | 235 | 315 | 167 | 92 | 15 | 3 | 1 | 1075 | |

# TABLE II.

## CORRELATION TABLE. BODY LENGTH AND TOTAL LENGTH. YOUNG HERRINGS, PLYMOUTH, 1927.

TOTAL LENGTH. Central Values for 26 length groups (5 mm.).

| BODY LENGTH. Central Values for 23 length groups (5 mm.). | 37·5 | 42·5 | 47·5 | 52·5 | 57·5 | 62·5 | 67·5 | 72·5 | 77·5 | 82·5 | 87·5 | 92·5 | 97·5 | 102·5 | 107·5 | 112·5 | 117·5 | 122·5 | 127·5 | 132·5 | 137·5 | 142·5 | 147·5 | 152·5 | 157·5 | 162·5 | Totals. | Arith. Means. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 32·5 | 66 | | | | | | | | | | | | | | | | | | | | | | | | | | 66 | 37·5 |
| 37·5 | | 58 | 7 | | | | | | | | | | | | | | | | | | | | | | | | 65 | 43·0 |
| 42·5 | | | 11 | 5 | | | | | | | | | | | | | | | | | | | | | | | 16 | 49·1 |
| 47·5 | | | | 22 | 28 | | | | | | | | | | | | | | | | | | | | | | 50 | 55·3 |
| 52·5 | | | | | 51 | 40 | | | | | | | | | | | | | | | | | | | | | 91 | 59·7 |
| 57·5 | | | | | | 13 | 35 | 2 | | | | | | | | | | | | | | | | | | | 50 | 66·4 |
| 62·5 | | | | | | | 15 | 107 | 10 | | | | | | | | | | | | | | | | | | 132 | 72·3 |
| 67·5 | | | | | | | | 27 | 195 | 33 | | | | | | | | | | | | | | | | | 255 | 77·6 |
| 72·5 | | | | | | | | | 4 | 57 | 10 | | | | | | | | | | | | | | | | 71 | 82·9 |
| 77·5 | | | | | | | | | | | 43 | 20 | | | | | | | | | | | | | | | 63 | 89·1 |
| 82·5 | | | | | | | | | | | | 25 | 28 | | | | | | | | | | | | | | 53 | 95·1 |
| 87·5 | | | | | | | | | | | | | 23 | 27 | | | | | | | | | | | | | 50 | 100·2 |
| 92·5 | | | | | | | | | | | | | | 5 | 30 | | | | | | | | | | | | 35 | 106·8 |
| 97·5 | | | | | | | | | | | | | | | 8 | 42 | 10 | | | | | | | | | | 60 | 112·7 |
| 102·5 | | | | | | | | | | | | | | | | 2 | 51 | 25 | | | | | | | | | 78 | 119·0 |
| 107·5 | | | | | | | | | | | | | | | | | | 53 | 28 | | | | | | | | 81 | 124·2 |
| 112·5 | | | | | | | | | | | | | | | | | | 2 | 43 | 32 | | | | | | | 77 | 129·4 |
| 117·5 | | | | | | | | | | | | | | | | | | | | 22 | 27 | | | | | | 49 | 135·5 |
| 122·5 | | | | | | | | | | | | | | | | | | | | | 6 | 28 | 1 | | | | 37 | 141·5 |
| 127·5 | | | | | | | | | | | | | | | | | | | | | | | 13 | 2 | | | 15 | 148·2 |
| 132·5 | | | | | | | | | | | | | | | | | | | | | | | | 4 | 1 | | 5 | 153·5 |
| 137·5 | | | | | | | | | | | | | | | | | | | | | | | | | 3 | 1 | 4 | 159·0 |
| 142·5 | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 2 | 162·5 |
| Totals | 66 | 58 | 18 | 27 | 79 | 53 | 50 | 136 | 209 | 90 | 53 | 45 | 51 | 32 | 38 | 44 | 61 | 80 | 71 | 54 | 35 | 28 | 14 | 6 | 4 | 3 | 1305 | |

# TABLE III.

## Samples from Tamar and Tavy.

| Date, 1927. | Condition of Tail. | Body Length. 5 mm. Groups. | | | | | | | | | | | | | | | | | | | | | | | | Total No. of Fishes. | Grand Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | 80 | 85 | 90 | 95 | 100 | 105 | 110 | 115 | 120 | 125 | 130 | 135 | 140 | | |
| May 26th | Normal and Abnormal | 3 | 136 | 96 | 181 | 700 | 383 | 56 | 27 | 32 | 19 | 5 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | 1639 | 1639 |
| June 8th | Normal and Abnormal | – | 13 | 26 | 20 | 85 | 146 | 102 | 77 | 39 | 12 | 11 | 2 | 1 | – | – | – | – | – | – | – | – | – | – | – | 534 | 534 |
| June 23rd* | Normal | – | – | 2 | – | 3 | 10 | 42 | 68 | 81 | 50 | 21 | 5 | – | – | – | – | – | – | – | – | – | – | – | – | 282 | 884 |
| | Abnormal | – | 1 | 1 | 1 | 15 | 65 | 161 | 170 | 91 | 44 | 23 | 21 | 6 | 3 | – | – | – | – | – | – | – | – | – | – | 602 | |
| July 11th | Normal | – | – | – | – | 7 | 4 | 4 | 4 | 14 | 24 | 38 | 45 | 28 | 4 | 3 | – | – | 1 | – | – | – | – | – | – | 176 | 1061 |
| | Abnormal | – | – | 2 | 16 | 19 | 31 | 94 | 164 | 143 | 135 | 131 | 88 | 44 | 12 | 3 | 2 | 1 | – | – | – | – | – | – | – | 885 | |
| July 25th | Normal | – | – | – | – | – | – | 1 | 3 | 5 | 4 | 13 | 29 | 44 | 30 | 19 | 4 | – | 1 | – | – | – | – | – | – | 153 | 996 |
| | Abnormal | – | – | – | 2 | 19 | 25 | 40 | 75 | 137 | 156 | 120 | 114 | 68 | 57 | 17 | 9 | 3 | 1 | 2 | – | – | – | – | – | 843 | |
| Aug. 9th* | Normal | – | – | – | – | – | – | – | 1 | 1 | 6 | 17 | 27 | 22 | 49 | 31 | 13 | 4 | 1 | – | – | – | – | – | – | 172 | 543 |
| | Abnormal | – | – | – | – | – | – | 2 | 2 | 12 | 36 | 57 | 61 | 63 | 49 | 49 | 21 | 15 | 3 | 1 | – | – | – | – | – | 371 | |
| Aug. 23rd | Normal | – | – | – | – | 1 | – | – | – | 1 | 2 | 3 | 14 | 16 | 33 | 62 | 93 | 33 | 8 | 2 | 1 | – | – | – | – | 269 | 1225 |
| | Abnormal | – | – | – | – | 2 | 1 | 1 | 10 | 30 | 53 | 122 | 156 | 147 | 128 | 145 | 84 | 45 | 19 | 9 | 3 | – | 1 | – | – | 956 | |
| Sept. 7th | Normal | – | – | – | – | – | – | – | 1 | 1 | 1 | 2 | 6 | 2 | 12 | 20 | 35 | 20 | 24 | 6 | – | – | – | – | – | 130 | 1035 |
| | Abnormal | – | – | – | – | – | – | – | – | – | 6 | 19 | 53 | 111 | 129 | 199 | 163 | 99 | 78 | 37 | 8 | 3 | – | – | – | 905 | |
| Sept. 20th | Normal | – | – | – | – | – | – | – | – | 2 | – | 1 | 1 | 1 | 4 | 7 | 13 | 19 | 25 | 12 | 3 | – | – | – | – | 88 | 566 |
| | Abnormal | – | – | – | – | – | – | – | 1 | 3 | 13 | 15 | 32 | 74 | 87 | 75 | 53 | 58 | 48 | 15 | 2 | – | – | – | – | 478 | |
| Oct. 7th | Normal | – | – | – | – | – | – | – | – | 1 | – | – | – | 4 | 4 | 16 | 13 | 20 | 30 | 26 | 17 | 2 | 2 | – | 1 | 136 | 538 |
| | Abnormal | – | – | – | – | – | – | – | – | – | 1 | 1 | 9 | 15 | 30 | 44 | 62 | 68 | 58 | 55 | 43 | 13 | 3 | – | – | 402 | |
| Oct. 20th | Normal | – | – | – | – | – | – | – | – | – | 1 | 1 | 2 | 3 | 9 | 5 | 13 | 16 | 18 | 15 | 9 | 4 | – | 1 | – | 97 | 483 |
| | Abnormal | – | – | – | – | – | – | – | – | 1 | – | 1 | 9 | 24 | 35 | 59 | 64 | 71 | 52 | 32 | 25 | 7 | 5 | 1 | – | 386 | |
| Nov. 3rd | Normal | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 1 | 1 | 1 | 5 | 2 | 2 | 1 | – | – | – | – | 14 | 123 |
| | Abnormal | – | – | – | – | – | – | – | – | – | 1 | 3 | 8 | 11 | 14 | 14 | 19 | 17 | 11 | 5 | 4 | – | 2 | – | – | 109 | |
| Nov. 21st | Normal | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 3 | – | 1 | – | – | – | – | – | 4 | 86 |
| | Abnormal | – | – | – | – | – | – | – | – | – | – | – | 1 | 6 | 4 | 16 | 13 | 17 | 8 | 10 | 3 | 1 | 3 | – | – | 82 | |
| Dec. 5th* | Normal | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | 1 | – | 2 | 4 | 2 | – | – | 1 | – | – | 11 | 97 |
| | Abnormal | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 5 | 11 | 15 | 14 | 14 | 16 | 5 | 3 | 1 | – | 1 | 86 | |

* Tavy samples.

## TABLE IV.

### SAMPLES FROM LYNHER.

| Date, 1927. | Condition of Tail. | Body Length. 5 mm. Groups. | | | | | | | | | | | | | | | | | | | | | | | | Total No. of Fishes. | Grand Total. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | 80 | 85 | 90 | 95 | 100 | 105 | 110 | 115 | 120 | 125 | 130 | 135 | 140 | | |
| June 13th | Normal | – | – | – | 1 | 2 | 12 | 23 | 132 | 255 | 69 | 13 | 4 | 2 | 1 | 1 | – | – | – | – | – | – | – | – | – | 515 | 613 |
| | Abnormal | – | – | – | – | 1 | 13 | 31 | 20 | 19 | 6 | 3 | 3 | 2 | – | – | – | – | – | – | – | – | – | – | – | 98 | |
| July 1st | Normal | – | – | – | – | – | 2 | 2 | 11 | 52 | 159 | 173 | 70 | 10 | – | – | – | – | – | – | – | – | – | – | – | 479 | 748 |
| | Abnormal | – | – | – | – | – | 3 | 6 | 23 | 43 | 64 | 71 | 43 | 12 | 4 | – | – | – | – | – | – | – | – | – | – | 269 | |
| July 12th | Normal | – | – | – | – | – | – | – | 1 | 6 | 16 | 29 | 23 | 7 | 1 | – | – | – | – | – | – | – | – | – | – | 83 | 183 |
| | Abnormal | – | – | – | 1 | – | – | – | 1 | 4 | 17 | 35 | 24 | 11 | 7 | – | – | – | – | – | – | – | – | – | – | 100 | |
| Aug. 3rd | Normal | – | – | – | – | – | – | – | 1 | – | 4 | 11 | 32 | 98 | 118 | 82 | 23 | 2 | – | – | – | – | – | – | – | 371 | 879 |
| | Abnormal | – | – | – | – | – | – | – | – | 4 | 14 | 23 | 83 | 103 | 136 | 108 | 29 | 6 | 2 | – | – | – | – | – | – | 508 | |
| Aug. 30th | Normal | – | – | – | – | – | – | – | 1 | 1 | 1 | 1 | 4 | 7 | 17 | 40 | 58 | 46 | 16 | 5 | 1 | – | – | – | – | 198 | 947 |
| | Abnormal | – | – | – | – | – | – | – | 2 | 6 | 9 | 19 | 40 | 69 | 103 | 141 | 155 | 119 | 61 | 19 | 5 | 1 | – | – | – | 749 | |
| Sept. 28th | Normal | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | 1 | – | – | – | 1 | – | – | – | 3 | 131 |
| | Abnormal | – | – | – | – | – | – | – | 3 | – | 2 | 1 | 11 | 18 | 9 | 16 | 20 | 18 | 14 | 10 | 1 | 2 | 2 | 1 | – | 128 | |
| Nov. 7th | Normal | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | 1 | 3 | 3 | 4 | 2 | 2 | 2 | – | – | – | 18 | 147 |
| | Abnormal | – | – | – | – | – | – | – | – | – | 1 | 2 | – | 3 | 8 | 11 | 18 | 18 | 18 | 17 | 19 | 9 | 3 | 1 | 1 | 129 | |
| Nov. 29th | Normal and Abnormal | – | – | – | – | – | – | – | – | – | 2 | – | 1 | 11 | 12 | 33 | 54 | 87 | 76 | 54 | 25 | 7 | 1 | – | – | 363 | 363 |

## TABLE V.

### Samples from the Tamar and Tavy, 1927.

| Date. 1927. | Total No. of Fishes. | Body-Length, Distribution. Deciles, Quartiles, and Median (cm.). | | | | |
|---|---|---|---|---|---|---|
| | | $d_1$. | $Q_1$. | $Q_2$. | $Q_3$. | $d_9$. |
| May 26th | 1639 | 3·63 | 4·48 | 4·79 | 5·30 | 5·47 |
| June 8th | 534 | 4·36 | 4·99 | 5·42 | 6·06 | 6·66 |
| June 23rd | 884 | 5·43 | 5·80 | 6·30 | 6·86 | 7·45 |
| July 11th | 1061 | 5·64 | 6·26 | 7·09 | 7·90 | 8·47 |
| July 25th | 996 | 6·09 | 6·80 | 7·63 | 8·54 | 9·27 |
| Aug. 9th | 543 | 7·44 | 8·01 | 8·80 | 9·53 | 10·09 |
| Aug. 23rd | 1225 | 8·09 | 8·83 | 9·67 | 10·48 | 11·00 |
| Sept. 7th | 1035 | 8·56 | 9·20 | 9·90 | 10·57 | 11·26 |
| Sept. 20th | 566 | 8·33 | 8·99 | 9·80 | 10·77 | 11·34 |
| Oct. 7th | 538 | 9·42 | 10·06 | 10·89 | 11·68 | 12·15 |
| Oct. 20th | 483 | 9·07 | 9·77 | 10·59 | 11·34 | 12·08 |
| Nov. 3rd | 123 | 8·47 | 9·23 | 10·20 | 10·93 | 12·04 |
| Nov. 21st | 86 | 9·21 | 9·83 | 10·59 | 11·34 | 11·97 |
| Dec. 5th | 97 | 9·62 | 10·18 | 10·97 | 11·65 | 12·22 |

## TABLE VI.

### Samples from the Lynher, 1927.

| Date. 1927. | Total No. of Fishes. | Body-Length, Distribution. Deciles, Quartiles, and Median (cm.). | | | | |
|---|---|---|---|---|---|---|
| | | $d_1$. | $Q_1$. | $Q_2$. | $Q_3$. | $d_9$. |
| June 13th | 613 | 5·80 | 6·23 | 6·63 | 6·91 | 7·29 |
| July 1st | 748 | 6·64 | 7·10 | 7·52 | 7·90 | 8·29 |
| July 12th | 183 | 7·10 | 7·50 | 7·86 | 8·29 | 8·71 |
| Aug. 3rd | 879 | 8·12 | 8·57 | 9·13 | 9·59 | 9·93 |
| Aug. 30th | 947 | 8·57 | 9·32 | 10·03 | 10·61 | 11·09 |
| Sept. 28th | 131 | 8·33 | 8·94 | 10·12 | 10·97 | 11·74 |
| Nov. 7th | 147 | 9·49 | 10·24 | 11·11 | 12·03 | 12·56 |
| Nov. 29th | 363 | 9·66 | 10·30 | 10·90 | 11·48 | 11·98 |

# The Photosynthesis of Diatom Cultures in the Sea.

By

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With 24 Figures in the Text.

Photosynthesis in the open sea is due mainly to two groups of organisms, the diatoms and the dinoflagellates. In British seas the diatoms are so much more numerous that the chemical changes which are due to photosynthetic activity can be almost entirely ascribed to their influence. Recent work on these chemical changes has shown that they do not extend deeper than about 30 metres. Of the external limiting factors light is among the most important and the depth to which photosynthesis can go on must, of course, depend on the light intensity. In the study of the phytoplankton under natural conditions the results are complicated by the interaction of many other factors such as temperature, viscosity, or lack of food salts, so that it is difficult to come to definite conclusions on the effect of light alone.

Early experimental work on the effect of light at different depths was carried out at Monaco by Regnard (1891), who germinated seeds of cress and radish at different depths, and found that little chlorophyll was formed at 30 metres. He also estimated the oxygen production of Ulva over a day, and found that this was too low to measure at 8 and 10 metres. His method, however, was not a delicate one. Jönsson (1903), in the Oslo fjord, using the moss *Climacium dendroides*, found that photosynthesis fell off rapidly from the surface, and was not appreciable below 17–27 metres. More recently Gaarder and Gran (1927), using samples of sea-water rich in diatoms, found that photosynthesis was considerably less below than at the surface, and that at about 10 metres photosynthesis and respiration just balanced each other. Considering the methods used, and the differences in latitude and season there is probably no real discrepancy in the results of these different observers.

While the results of Gaarder and Gran probably give a true picture of what goes on in the sea in the course of a diatom increase they are still dependent on a combination of factors, and in addition such experimental work is limited to the times when diatoms are sufficiently rich in the sea. By using cultures of diatoms, however, it is possible to control several of these factors and to work at any time throughout the year. The effect of light can then be discussed with greater certainty. The following experiments, carried out chiefly with cultures of diatoms prepared as described by Allen and Nelson (1910), and partly with the diatoms in the sea, had this as their object.

A persistent culture of *Coscinosira polychorda* was used. A " persistent culture " was defined by Allen and Nelson as a culture in which only one species of diatom was present, although there might be bacteria and a small number of other organisms such as flagellates. In our cultures there were always bacteria, and in old cultures minute flagellates were sometimes seen. Coscinosira is not noted as occurring commonly here or in the North Sea, but it is very similar to species of Thalassiosira, and may have been counted along with them by mistake. Gran (1912) states that its occurrence agrees with that of *T. nordenskioldi*, but says it may have been confused with Thalassiosira sp. It has its maximum in March. The number of cells per c.c. of culture was estimated for each experiment, so that the results could be expressed as the amount of oxygen produced by a million diatoms. A young culture will, however, produce more oxygen per million cells than an old one, and even two cultures of the same age grown under the same conditions do not always behave exactly alike, so that the actual amounts of oxygen in different experiments may not be strictly comparable. As far as possible cultures of about the same age and cell content were used in these experiments.

Considering the importance of light for photosynthesis it would have been desirable to estimate its intensity in conjunction with the experiments. There is as yet, unfortunately, no suitable method for the continuous measurement of light intensity at different depths in the sea. Of several methods tried, the recent one of Anderson and Robinson (1925) was found suitable for continuous measurement of the intensity in the air, but not for measurements below the surface. This method depends on the decomposition of oxalic acid in the presence of traces of a uranium salt when exposed to light and measures the intensity of wave-lengths shorter than 4,500 Å, although even then absorption by the solution is only partial. The amount of absorption increases as the extreme violet end of the spectrum is approached. There are two objections to the use of the method in the sea. As decomposition goes on, gases are evolved, causing an increase in pressure which inhibits the reaction and in addition there is superimposed the pressure of the column of sea-water overlying the tube. In the second place absorption of light of very short wave-length by sea-water is rapid and the results obtained below the surface are low. The wave-lengths measured are not those generally thought to be responsible for photosynthesis. By this method, in default of a better one, results are obtained in air which are of use in comparison with photosynthesis. Some of them are shown in conjunction with later experiments.

Photosynthesis was measured by the oxygen production as estimated by Winkler's method. This is a very reliable method in most cases, but when the solution was highly supersaturated small bubbles were often formed and duplicate samples did not then agree well. As a rule, short experiments gave more accurate results. No special precautions were taken to keep the bottles at the same temperature until they were titrated, and according to Ruud (1926) this decreases the accuracy of the method.

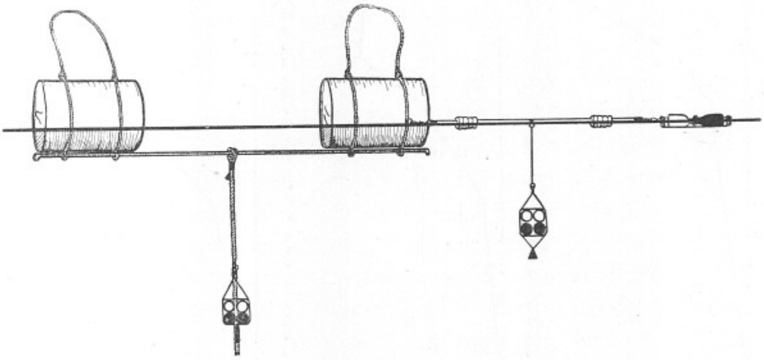

FIG. 1.—Arrangement of apparatus in the sea.

The diatom culture was enclosed in ordinary white glass reagent bottles of about 150 c.c. capacity with well-ground stoppers, and these were arranged in cages of wide-mesh wire-netting, so that the long axes of the bottles lay horizontally. A buoy (Fig. 1) was anchored in the position chosen, and the cages were then hooked on to the buoy rope at various depths, a heavy weight being attached below the bottom cage to keep the rope vertical. For the surface bottles a small float was made which was attached to the end of a stick, the other end of which was hooked on to the buoy, and from this stick the half-metre cage was also suspended to avoid the buoy's shadow. To reduce shadow effects the buoy used was double, two drums being connected by a rigid bar to the middle of which the rope was attached. In each cage there were two bottles in the light (these being uppermost), and one bottle painted black and enclosed in a dark cloth bag. The presence of the dark cloth prevented the reflection of any light from below. The oxygen produced in the two lighted bottles measured photosynthesis minus respiration, while the fall in oxygen content of the dark bottles measured respiration alone. By adding this oxygen loss to the oxygen production in the light bottles, the total photosynthesis could be calculated. It was found that the results from all the dark bottles in an experiment were very nearly the same, and any differences showed no relation to increasing depth or temperature. The average was therefore used in calculating photosynthesis. The experiments were carried out as far as possible while the sea was free from diatoms. Greenwich Mean Time is used throughout.

The early experiments (Figs. 2, 3, 4, and Tables I, II, III, on p. 343) were carried out in March, 1927, in Loch Striven,* and the photosynthesis over 24 hours measured at depths of 0, 5, 10, 20, and 40 metres. Fig. 2 shows graphically the oxygen produced by a million diatoms at these depths on March 18th–19th. The sky was overcast and there was no sunshine. Sea temperature was low throughout, about 7° C. with a slight fall to the surface. Photosynthesis showed a marked maximum at the surface decreasing rapidly in deeper water. At 5 metres the difference in oxygen content between the original culture and the lighted bottles fell within experimental error, i.e. the amount of oxygen produced by photosynthesis was just equal to the amount of oxygen used up by respiration. The light intensity at which this occurs is called the compensation point. Below this photosynthesis may still go on, but there is a continuous loss of oxygen and life becomes impossible.

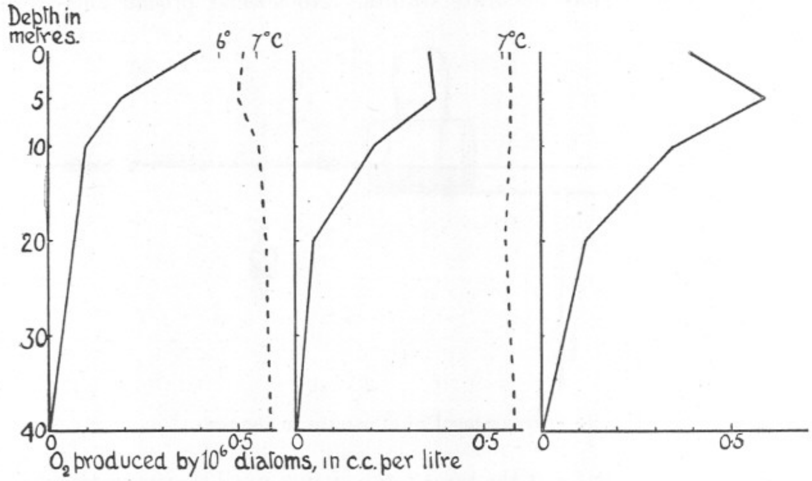

Fig. 2.—Oxygen production per $10^6$ diatoms in Loch Striven. 18–19/3/27.

Fig. 3.—Oxygen production per $10^6$ diatoms in Loch Striven. 28–29/3/27.

Fig. 4.—Oxygen production per $10^6$ diatoms in Loch Striven. 31/3–1/4/27.

——— oxygen production ; . . . . . . temperature.

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* On old charts this is spelled Strivan, but the current use is Striven.

Fig. 3 shows the type of curve obtained during brighter weather about the same date, March 28th–29th. There were 5 hours 50 minutes sunshine during this experiment. The temperature was not taken on this occasion, but the curve for March 26th is given and this is not likely to have altered much. The loch was homothermic, about 7° C. The most interesting features of the photosynthesis curve are that the compensation point is much deeper, 10–20 metres, and that photosynthesis instead of rising all the way to the surface has stopped increasing above 5 metres. It is possible that in the brighter weather of this experiment, temperature and not light was the limiting factor above 5 metres, i.e. the vertical part of the curve represents the maximum amount of photosynthesis possible at that particular temperature. Fig. 4, however, shows that another explanation is more probable. This experiment was carried out on March 31st–April 1st, when there were 5 hours 15 minutes sunshine. The compensation point is still between 10 and 20 metres, but as can be seen from the curves the production at 10 metres is considerably greater than in the previous experiment. Above 5 metres there is a sharp fall in oxygen production, a fall which cannot be accounted for by temperature, and which must be due to the strong light at the surface. The fact that there was almost the same amount of sunshine during these two experiments makes the difference between them surprising, but as will be seen later not only sunshine, but also bright diffuse light can be supraoptimal for diatom photosynthesis. The weather was brighter during this experiment than during the previous one, and this is probably the cause of the difference between the two curves. With one exception other experiments done about the same time showed similar results, an increase to the surface on dull days and a decrease on sunny days. The exception was on April 5th–6th in rather dull weather with numerous intervals of sunshine amounting altogether to 8 hours 35 minutes. On this day oxygen production rose steadily all the way to the surface, reaching a high value there.

In the middle of March when the spring diatom increase was at its height, very low values were obtained for depths below the surface, the compensation point lying between the surface and 5 metres. The weather was dull, but it is certain that a good deal of light was cut off by the enormous number of diatoms suspended in the water.

When diatoms are exposed to too strong illumination the chromatophores contract and collect in the middle or at one side of the cell. This condition of "systrophe" was described by Schimper (Karsten, 1905), who supposed that the light optimum for most species lay below the surface and for the main bulk of diatoms at a depth of 40–60 metres. Whipple (1914) found by experiment that photosynthesis was more active at a depth of 6 inches than at the surface, because of the strong light there. Ruttner (1926) carried out a number of experiments in the Lunzer See on photosynthesis in Elodea and other fresh-water plants, and found that in sunny weather the light became too strong at the surface and photosynthesis decreased there. Gran (1927) also mentions the injurious effect of strong light on diatoms, and considers that at a depth of 5 metres the diatoms are under optimal conditions. In several experiments we exposed samples at a depth of 18 cm., and the harmful effect was still noticed but to a much less degree than at the surface, indicating that the part of the spectrum responsible for this adverse effect is rapidly absorbed.

Light of short wave-length has been shown to have a harmful effect on the growth of land plants, and since the violet part of the spectrum is rapidly absorbed by sea-water it seemed possible that this might account for the decreased amount of photosynthesis at the surface. Ordinary glass absorbs this short wave-length light, but Uviol glass (made by Schott and Co., Jena) allows it to pass. Several comparisons were, therefore, made with bottles of the two types of glass at different depths in the sea. Except in one sample, however, the differences between them were within experimental error.

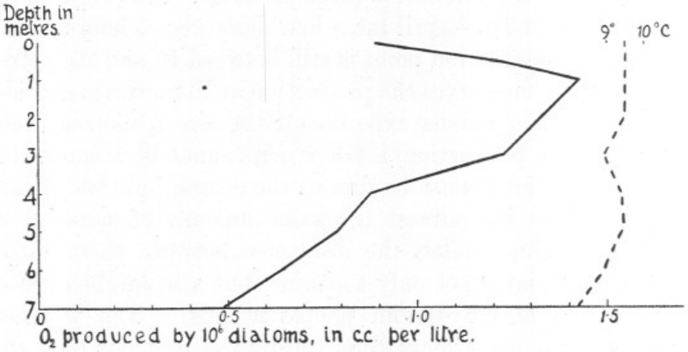

FIG. 5.—Oxygen production per $10^6$ diatoms in Loch Striven, 18–19/5/27.
. . . . . . Temperature.

Several experiments were then carried out with cages at 0, ½, 1, 2, 3, 4, 5, 6, and 7 metres to find the position of optimal light intensity. The result of one such experiment is shown in Fig. 5 and Table IV. Here the maximum is at 1 metre with a rapid fall both above and below this depth. On this day there were 5 hours 55 minutes sunshine. On another day with 5 hours 5 minutes sunshine, a similar experiment showed the maximum at half a metre.

As summer approaches photosynthesis goes deeper. Fig. 6 and Table V give the results of an experiment down to 60 metres on a sunny day near midsummer. Unfortunately the surface and half-metre samples were lost, and so the fall in photosynthesis to the surface is not shown. There is a rapid and fairly regular fall from 1 metre down to 20 metres when the decrease slows off. The compensation point lies between 20 and 30 metres. This curve also brings out clearly the much greater amount of photosynthesis possible in the sea during the long summer days than in the short days of early spring.

Since the optimal depth depends so closely on the light intensity, its position must vary during the course of the day. McLean (1920) and Yap (1920) have shown that the rate of photosynthesis of sugar-cane in the Philippines increases rapidly from about 7.30 a.m. to 9.30 a.m. and falls slightly in the middle of the day, rising again to a maximum about 5 p.m. An experiment was carried out to find the actual course of photosynthesis in the sea on a sunny day. Cages were sunk to 0, $\frac{1}{2}$, 1, 2, 3, 4, and 6 metres, and were changed every 3 hours over 24 hours. The diatom culture used (about 30 litres) was the same throughout, and the number of cells counted at the beginning and end of the experiment. It did not increase, probably because the culture was old enough for its rate of increase to have fallen to a figure within the limit of error of the

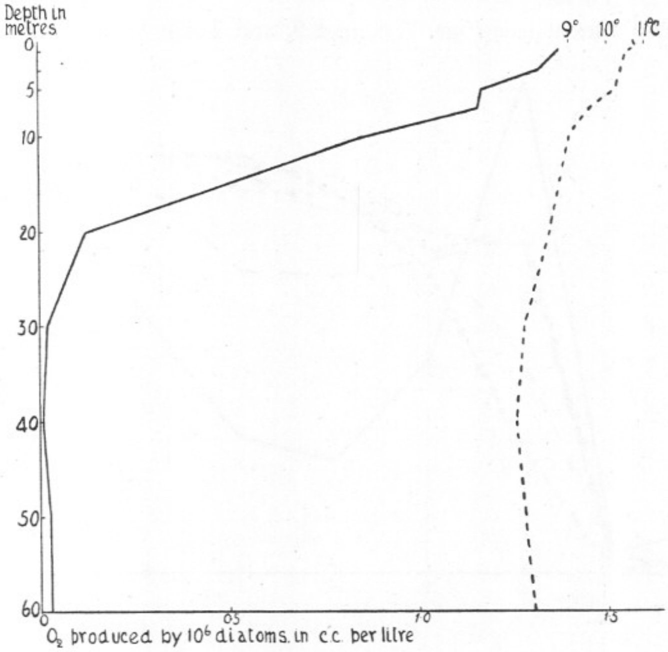

Fig. 6.—Oxygen production per $10^6$ diatoms in Loch Striven. 13–14/6/27.
. . . . . . Temperature.

counting method (10%). It will be noticed that the initial samples do not agree closely, and this is probably due to inefficient mixing. Mechanical stirring was carried on 15 minutes before as well as during the filling of the bottles, one initial sample being drawn off first, the other after filling the experimental bottles. In a subsequent experiment where mixing went on during the whole 24 hours duplicates agreed more closely. This, however, does not affect the final results at all. The buoy was anchored in about 9 metres off Farland Point, a few minutes distant from the Marine Station.

The experiment (see Figs. 7, 8, and 9, and Table VI) was carried out near midsummer and a bright day chosen. The length of the day was 17 hours 22 minutes (sunset and sunrise are marked on the figure by arrows), and there were 15 hours 5 minutes sunshine during the experiment. The light was also measured by Anderson and Robinson's method and from the half-hourly readings the curve (Fig. 13) constructed. The experiment was begun at 6 a.m. on June 9th, and carried on till 6 a.m., June 10th, but for convenience the curves are drawn as from 12 midnight. The mornings were equally calm and cloudless, and there is probably no error involved in doing this. It was scarcely dark all night, the darkest hours being from midnight till 3 a.m. During these hours the

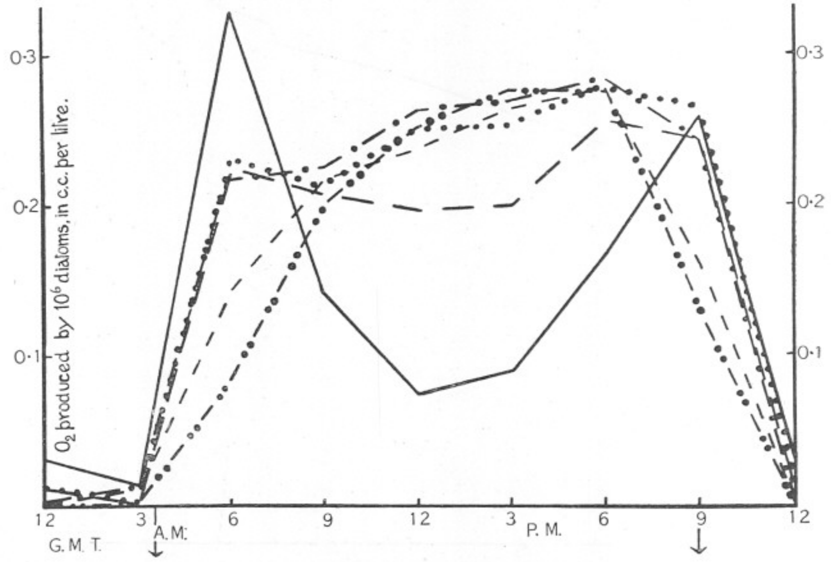

FIG. 7.—Photosynthesis over 3-hour intervals during a sunny summer day. 15 hours 5 minutes sunshine. June 9–10. Sun's meridian altitude, 57° 10′.
———— surface, —— —— ½ metre, . . . . 1 metre,
—— —— 2 metres, — — — 4 metres, —— · · —— 6 metres.

oxygen production at all depths was negligible. From 3–6 a.m. the surface curve reaches its maximum and the maximum production for any depth during the day. This was followed by a rapid fall from 6–9 a.m. and a further fall from 9 a.m. till 12 noon. After this there was a slight but gradual increase till 9 p.m. where the curve shows another peak, though not so high as the morning one. Photosynthesis then fell rapidly because of lack of light. From 9 p.m. till 12 midnight there was still a slight production of oxygen, but only at the surface. The half-metre samples show a similar curve, with the morning and evening peaks flattened off and the midday depression less marked. The curves for the other depths are very like each other from 9 a.m. till 6 p.m., showing a gradual rise to a maximum at 6 p.m. Before 9 a.m. and after 6 p.m. the curves for the layers below the surface separate from one another, the 4- and 6-metre curves falling off more rapidly than the others. It should be noticed that no curve follows that for light intensity shown in Fig. 13.

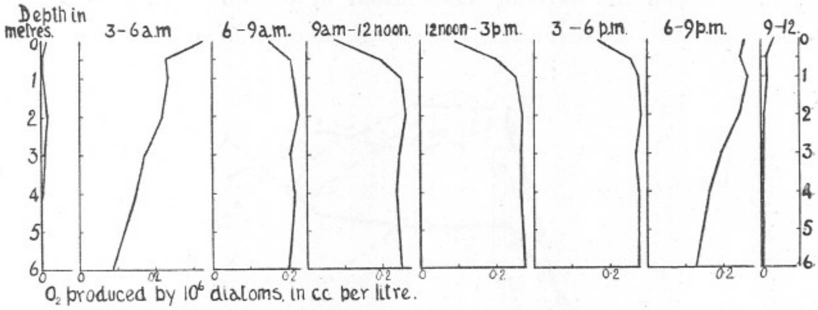

FIG. 8.—Vertical curves showing photosynthesis every 3 hours (June 9–10).

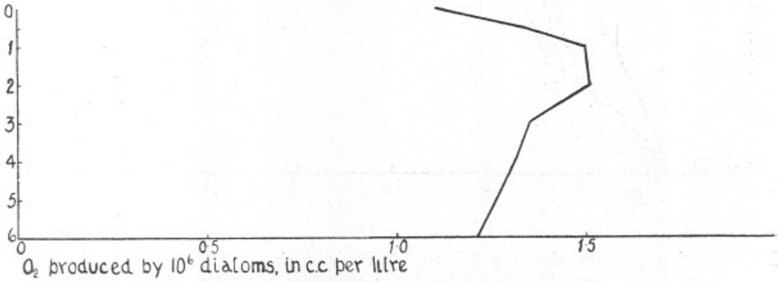

FIG. 9.—Composite curve showing total photosynthesis from the above curves (in Fig. 8).

This decrease in photosynthesis in deeper water may be due partly to the total reflection of the sun's rays in the morning and evening and partly to the diffuse light being sub-optimal below the surface. The loss of light by reflection even in summer is variable, depending on the height of the sun, the clouds, and the surface of the sea. Poole and Atkins (1926) have found reflection to vary from 5–31%. With fresh water, according to Schmidt (quoted by Ruttner, 1926), reflection is from 0–6% when the angle of incidence is from 0–60°, is 13% at 70°, 35% at 80°, and 100% at 90°. The variation in reflection between midday in summer and midday in winter is 12%. This is for the direct rays of the sun, while of diffuse light about 17% is reflected. These figures vary, of course, with the latitude, and from day to day with the weather.

Fig. 8 shows the vertical distribution of photosynthesis over each 3-hour period, and Fig. 9 the curve obtained by adding the separate values for each depth together. The latter can be compared with the all-day curves. The maximum over the day is at 1 or 2 metres, the fall above and below these depths being rapid. This curve can only be an approximation to the truth, because the values for each three hours are those given by a fresh uninjured diatom culture, and not by diatoms which have remained all day in the strong light. That recovery can take place was shown by an experiment carried out over 48 hours on land in which the bottles were all put outside at the beginning and two taken in each three hours. Although the bottles were exposed only to strong diffuse light the resulting curve showed a deep midday depression and

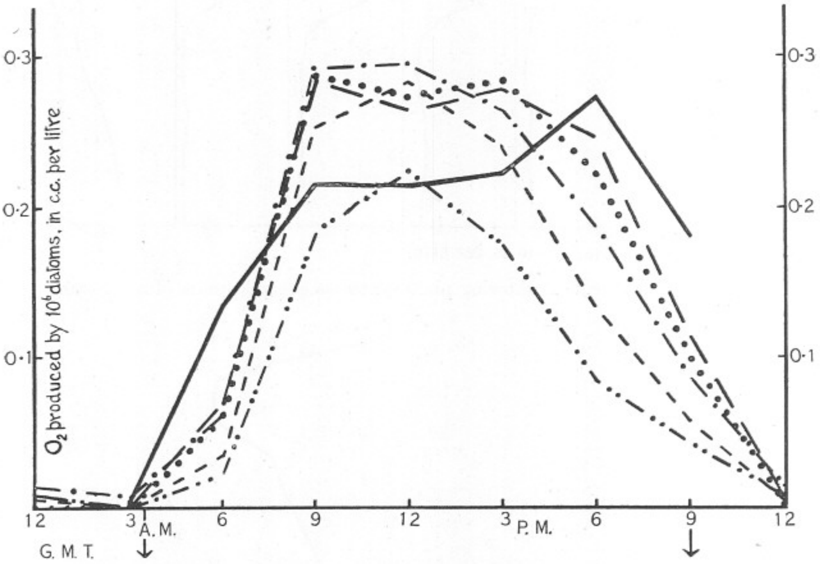

FIG. 10.—Photosynthesis over 3-hour intervals during a dull summer day. No sunshine. June 28. Sun's meridian altitude, 57° 34′.

——— surface, —— —— ½ metre, . . . . 1 metre,
— · — 2 metres, — — — 4 metres, — . . — 6 metres.

a morning and evening peak. On the other hand, experiments have shown that whereas in sub-optimal light it is possible to add the results of two successive 3-hour exposures together and obtain the same result as for a 6-hour exposure, in strong light this cannot be done. The stronger the light the more marked is the injury. In one case where a culture cooled by running water was exposed to the direct sun all day, the majority of the diatoms were killed and the culture showed only a slight recovery after 6 days. From this it is clear that the greatest amount of photosynthesis at or near the surface takes place in the early morning in sunny weather.

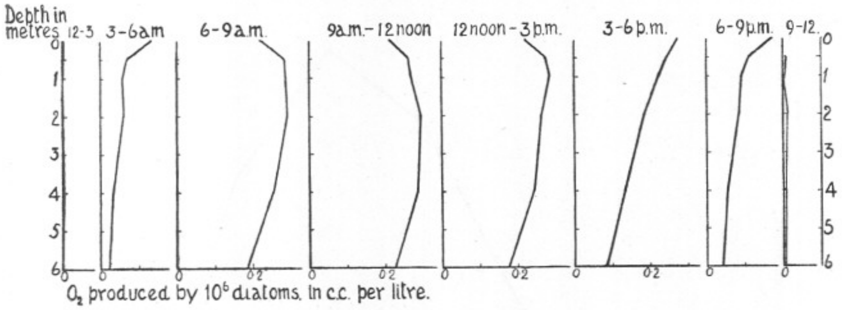

FIG. 11.—Vertical curves showing photosynthesis every 3 hours (June 28).

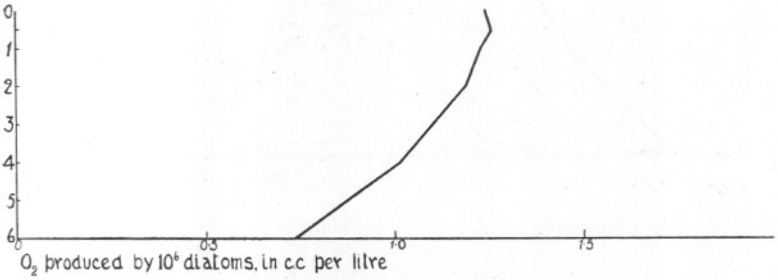

FIG. 12.—Composite curve showing total photosynthesis from the above curves.

It was felt that a comparison of this experiment with a similar one carried out on a dull day would provide interesting results. For this only the 0, $\frac{1}{2}$, 1, 2, 4, and 6 metres were worked. The experiment was started at midnight, June 27th–28th, and continued for 24 hours. The day was 17 hours 30 minutes long and there was no sunshine. The sky was heavily overcast most of the day, but there was no rain till the evening of the 28th. The results are shown in Figs. 10, 11, 12, and 13 and Tables VII and XIII. When we compare the curves in Fig. 10 with those for the previous experiment striking difference sre aseen. The surface curve shows no morning peak, but photosynthesis rises gradually from 3–6 a.m. and from 6–9 a.m., when it remains almost constant till a rise to the evening maximum at 6 p.m., not 9 p.m. as before. After this the curve falls sharply. Unfortunately the surface samples for 9 p.m.–12 midnight were lost because of rough weather, but it is certain that the curve would have fallen to a low value. The ½-, 1-, and 2-metre curves again resemble one another, the ½ and 1 metre each showing a slight midday depression. The 4- and 6-metre and to a less extent the 2-metre curves are symmetrical, rising steadily to a maximum at midday and falling off thereafter. If we compare them with Fig. 13 we see that the 4- and 6-metre curves agree precisely with the light curve for the day. The inhibitory effect of the high light intensity had disappeared somewhere between 2 and 4 metres on the dull day, whereas it affected every depth investigated on the sunny day. Photosynthesis began later and fell off earlier, and the maximal values are found from 9 a.m. till 3 p.m. The vertical curves (Fig. 11) show this clearly, but although the composite curve shows that the total amount of photosynthesis was greater even at ½ metre on the sunny than on the dull day, it is not safe, as has already been mentioned, to conclude that this was really the case. The curves in the morning and evening are further apart than they were on the sunny day. These two

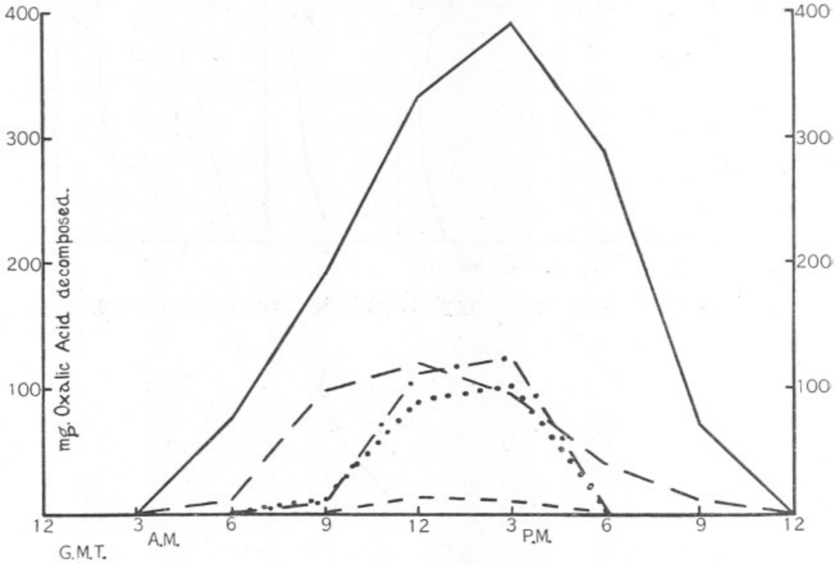

FIG. 13.—Light intensity.

——————— 9–10/6/27.
——— ——— 28/6/27.
—— · —— 29/11/27.
· · · · · · 9/11/27.
— — — 7/12/27.

experiments show that the curves for earlier experiments can be analysed, so as to bring out the effect of a number of separate factors. The steep fall in photosynthesis in deeper layers is due largely to the morning and evening fall-off in intensity as well as to the sub-optimal light, while the surface fall is a cumulative effect over the brighter part of the day.

Similar experiments were carried out in winter in sunny, bright, and dull weather. The results of these are shown in Figs. 14–22 and Tables VIII, IX, X, and XIII. The results obtained on a sunny day (Nov. 29th) are shown in Figs. 14, 15, and 16 and Table VIII. The day was 7 hours 25 minutes long, and the sun shone all the time, although only 6 hours were recorded. The Secchi disc reading was 7¾ metres, but this low reading is probably due to the turbidity following a S.W. wind the previous day. It was quite dark before 6 a.m. and after 6 p.m. Values were low at all depths from 6 a.m. to 9 a.m., but by noon had risen rapidly and the surface had reached its maximum for the day, the surface ½, 1, and 2 metres having almost the same values. The 4- and 6-metre layers were much lower. By 3 p.m. the surface layer had fallen considerably, owing to the strong sunlight while there was a further rise at ½, 1, and 2 metres. The 4- and 6-metre layers showed little change. By 6 p.m. photosynthesis had fallen to a low value everywhere except at

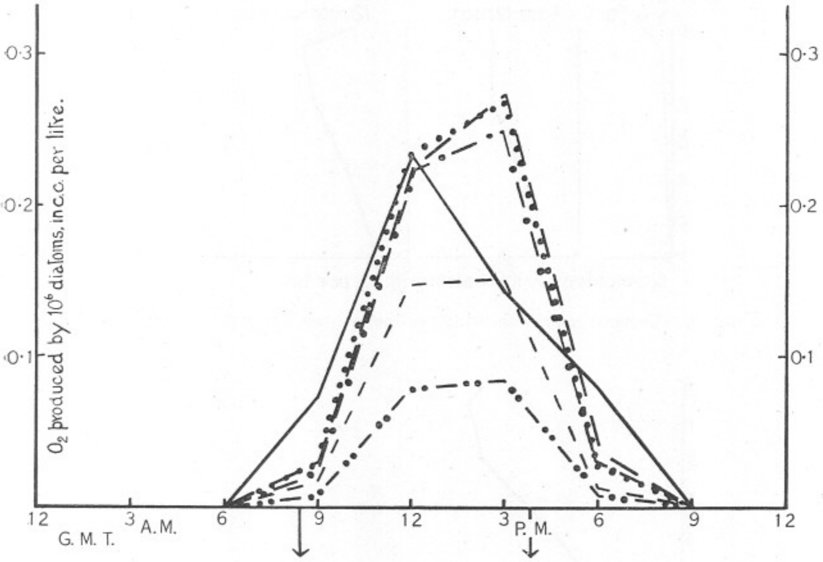

FIG. 14.—Photosynthesis over 3-hour intervals during a sunny winter day. 6 hours sunshine. November 29. Sun's meridian altitude, 12° 53′.

———— surface, —— —— ½ metre, · · · 1 metre,
—— · —— 2 metres, — — — 4 metres, — · · · — 6 metres.

the surface, and by 9 p.m. it had stopped completely. The light curve for the day (see Fig. 13 and Table XIII) agrees well with the depths below the surface, while the greatest injury at the surface coincides with the peak of the light curve.

In Figs. 17, 18, and 19 and Table IX are shown the results obtained on a bright day in winter. The day was 8 hours 38 minutes long, and there were 2 hours 55 minutes sunshine recorded. The day was bright, but there were rapidly moving high clouds which frequently obscured the sun. The experiment took place on November 9th, and is very similar to the last in results. Between 12 noon and 3 p.m. there were 2 hours of uninterrupted sunshine, which accounts for the injury at the surface shown then. There is a greater separation of the curves for the layers below the surface on this day than on the sunny day. This is due, no doubt, to the lower light intensity on this day as well as to the visibly greater turbidity of the water. Unfortunately no Secchi disc reading was taken. Figs. 16 and 19 are the composite curves for these two experiments. In each case the maximum is at ½ metre and the curves fall off steeply in deeper water.

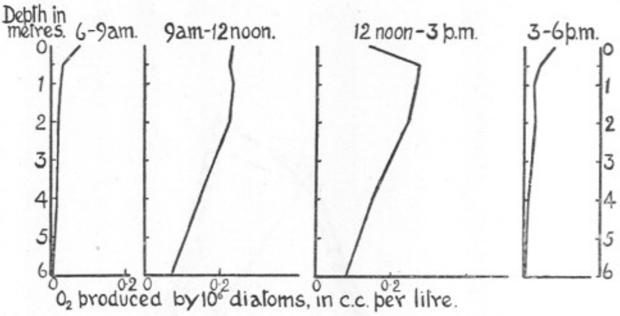

FIG. 15.—Vertical curves showing photosynthesis every 3 hours (Nov. 29).

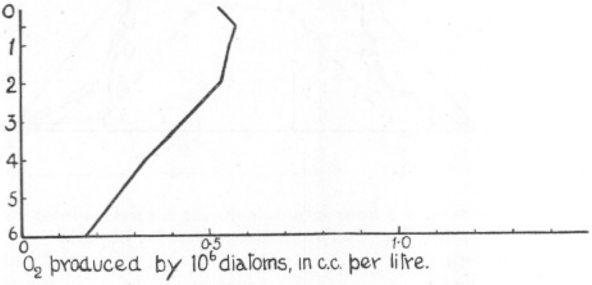

FIG. 16.—Composite curve showing total photosynthesis from the above curves.

The dull day chosen, December 7th, is represented in Figs. 20, 21, and 22 and Table X. The sky was quite overcast, and there was a certain amount of low-lying fog. The day was 7 hours 7 minutes long and there was no sunshine. The Secchi disc reading was 8½ metres. The light intensity for the day is shown in Fig. 13 and Table XIII, and is extremely low. Light on this day never reached an optimal value at the surface, and there is a regular fall in photosynthesis from depth to depth throughout the day. The respiration over a 3-hour period is too low for experimental error to be negligible, so to find the depth of the compensation point samples were kept in the dark for 24 hours. The compensation point lay between 4 and 6 metres. On a very foggy day (Nov. 30th–Dec. 1st) an experiment in the sea showed the compensation point to be at about 2 metres, which is the least depth we have found.

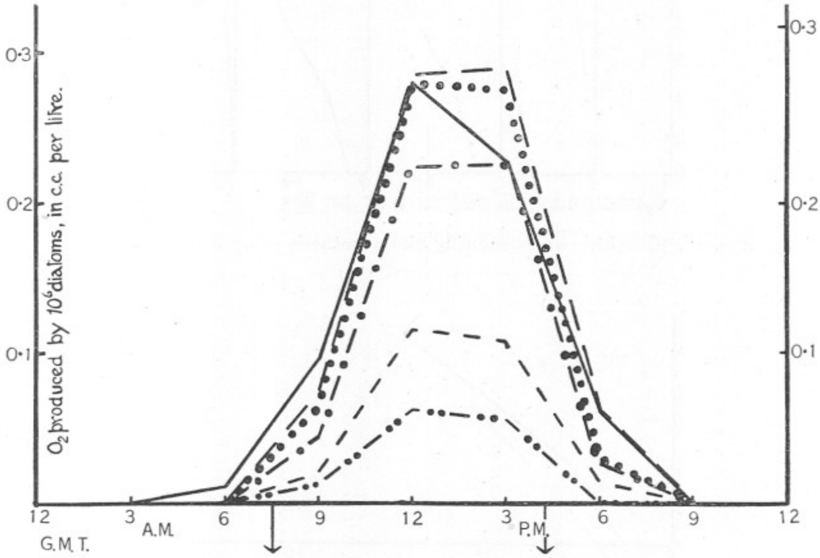

FIG. 17.—Photosynthesis over 3-hour intervals during a bright winter day. 2 hours 55 minutes sunshine. November 9. Sun's meridian altitude, 17° 35′.
———— surface, ——— ——— ½ metre, · · · · · 1 metre,
—— · —— 2 metres, — — — 4 metres, — · · — 6 metres.

In comparison with the summer curves the most striking difference is the short time available for photosynthesis. There is also a much more rapid falling off with depth which agrees with the lower curves for light, and is probably due in part to the greater obliquity of the sun's rays and possibly also to the greater turbidity of the sea in winter. The amount of photosynthesis taking place at the surface and ½ metre in the middle hours of the day is not very different from what takes place in summer. As might be expected the winter sun has less effect than the summer sun, and injury does not appear to extend much beyond the surface layer.

It may be suggested that the inhibitory effect of strong light was not caused by the light itself, but by the increasing temperature which accompanies sunlight. At the time of the summer experiments showing diurnal variation, the surface temperature was about 12° C., and there was probably a difference of several degrees between the surface and 6-metre layers, although the diurnal variation would be small. During the winter experiments the temperature was about 10° C. Experiments in the laboratory have shown that an increase of temperature up to 15° C. does not injure the diatoms, although a temperature of 25° C. does. The temperature therefore cannot be the cause of the diurnal variations in photosynthesis. As has already been mentioned, respiration figures showed no significant variation at different depths.

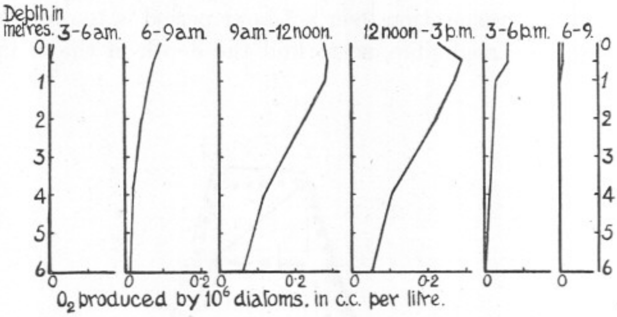

FIG. 18.—Vertical curves showing photosynthesis every 3 hours (Nov. 9).

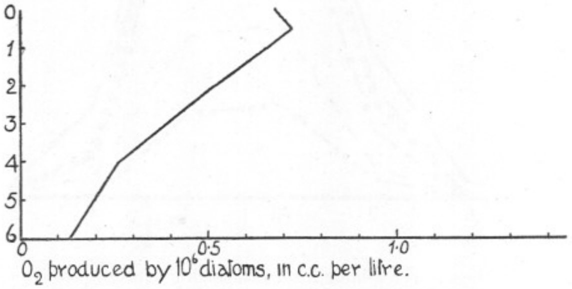

FIG. 19.—Composite curve showing total photosynthesis from the above curves.

It seemed possible that different species of diatoms would show a different relation to light of varying intensity since some are characteristically summer forms and others winter or spring forms. Fig. 23 and

Table XI show a comparison of photosynthesis in cultures of Coscinosira and Chætoceros (probably *C. cinctum*) over 24 hours in bright weather. The Chætoceros species used has much smaller cells than Coscinosira, so the amount of oxygen produced by a million cells of each is not comparable and the total oxygen produced is shown as well. The unexpected result is obtained that Chætoceros, which is here a summer form, is much more sensitive to light than the spring diatom Coscinosira. In the surface layer Chætoceros lost oxygen instead of producing it, and photosynthesis remained almost the same from 1–4 metres. This experiment gave similar results on the three separate occasions on which it was tried. A curious irregularity is shown in the photosynthesis curve at 4 metres, particularly with Coscinosira. Such irregularities, sometimes even more marked, appeared occasionally for no obvious reason. It is interesting to note that on July 18th, when diatoms were rich in the sea (mainly *Chætoceros cinctum*, *Skeletonema costatum*, and *Thalassiosira gravida*), the percentage showing systrophe at the surface was as follows : *C. cinctum*, 33% ; *S. costatum*, 8% ; *T. gravida*, 0%.

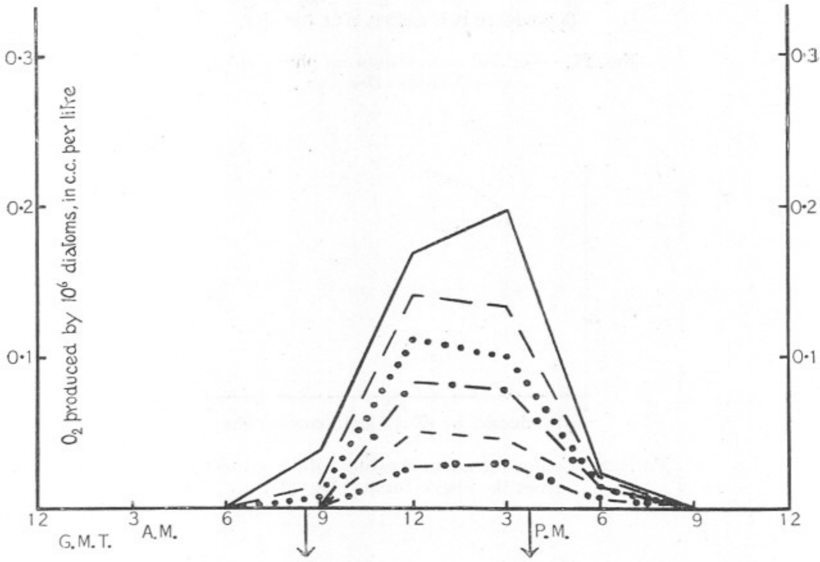

FIG. 20.—Photosynthesis over 3-hour intervals during a dull winter day. No sunshine. December 7th. Sun's meridian altitude, 11° 42′.

——— surface, —— —— ½ metre, · · · · · 1 metre,
— · — · — 2 metres, — — — 4 metres, — · · — 6 metres.

The cultures were grown in a north window and were never exposed to full daylight. It therefore seemed possible that the inhibitory effect of strong light might be due to this fact alone (i.e. growth in weak light),

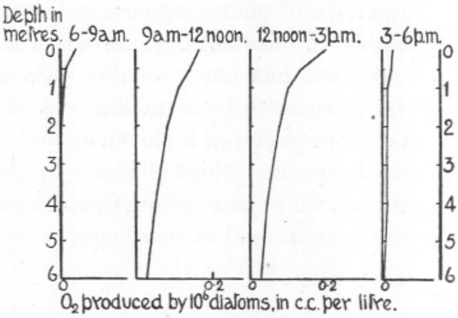

FIG. 21.—Vertical curves showing photosynthesis every 3 hours (Dec. 7th).

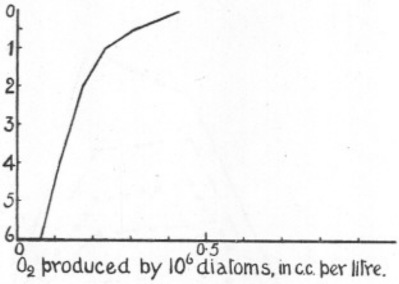

FIG. 22.—Composite curve showing total photosynthesis from the above curves (Fig. 21).

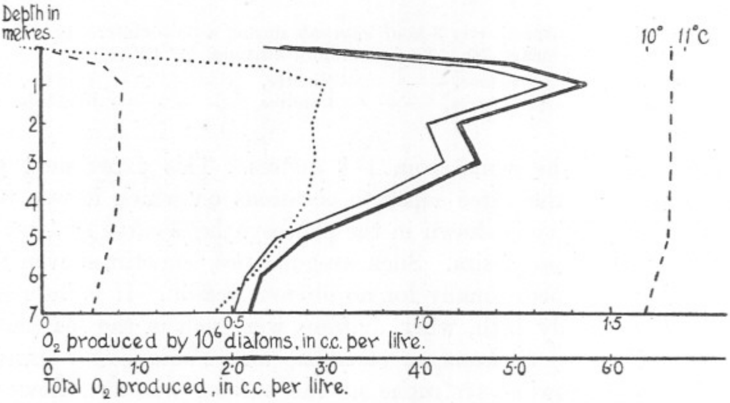

FIG. 23.—Comparison of different species of diatoms. Loch Striven. 27–28/5/27.

Coscinosira. Total oxygen produced. ————
Oxygen produced per $10^6$ diatoms. ▬▬▬
Chætoceros. Total oxygen produced. . . . . . . .
Oxygen produced per $10^6$ diatoms. — — — —

and that the results were not applicable to diatoms in the sea. In March, during the spring diatom increase, samples of sea-water were sunk at various depths along with diatom culture. The oxygen production was usually lower than that of the culture, and was generally low except at the surface and occasionally at 5 metres. It is possible that these results are complicated by a lack of nutrient salts. By March 27th diatoms had almost disappeared and these experiments were discontinued. In July, however, a diatom increase (referred to above) began, and samples of the rich surface water were used for an experiment on July 18th. Fig. 24 and Table XII show the results for a sunny 5-hour period in the middle of the day down to 15 metres. The general shape of the curve is the same as those for culture experiments. At the surface and ½ metre the sunlight was injurious, while below 2 metres there was a gradual falling away. This makes it clear that strong light has an inhibitory effect on diatoms grown under natural conditions as well as on those grown artificially.

When we compare the results of the experiments recorded above with the observations available on the vertical distribution of diatoms in the sea we find considerable disagreement. Phytoplankton has been found as deep as 1000 metres, and "maxima" have been recorded from depths ranging from the surface to 70 or 80 metres. Lohmann (1908) first described how after a diatom increase the cells sank gradually to the bottom, so that the greatest number may be found at any intermediate depth, and Gran (1912) has shown that some of the "maxima" are due to a holding up of the diatoms in their fall when a denser layer of water is reached. He concluded from a survey of the plankton production in North European waters that the light optimum for plant growth in the sea was probably less than 10 and never deeper than 30 metres. As has already been mentioned, this has been confirmed (Atkins, 1926b;

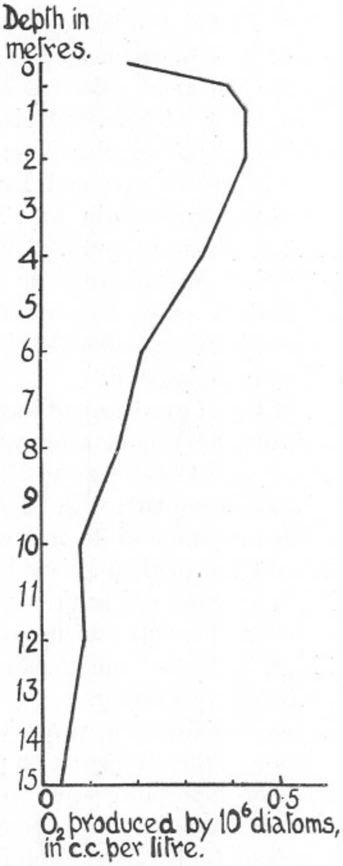

FIG. 24.—Oxygen produced per $10^6$ diatoms off Hunterston Perch, 18/7/27.

Harvey, 1926 ; Marshall and Orr, 1927) by examining throughout the year the chemical changes set up by photosynthesis.

A comparison of the depths to which diatoms can grow with the distribution of the fixed algæ is interesting. Since diatoms are brown they correspond, in colour at least, to the shallower fixed algæ. In northern waters the lower limit for the algæ varies from about 20 metres (in the Baltic) to about 50 metres (off Iceland), while in the Mediterranean it is as much as 130 to 160 metres (see Gran, 1912 ; Atkins, 1926a). The great difference between the two is no doubt due not only to the lower latitude, but also to the more transparent waters of the Mediterranean. Similar differences are to be expected in the phytoplankton distribution and have often been found. Lohmann (1902), working off Syracuse in May, found coccolithophores and diatoms much more abundant at a depth of 50 metres than at the surface. Sleggs (1927) states that in California the phytoplankton production of the upper 20 metres is comparatively small, and that most takes place from 25 to 55 metres. It is possible that these results are complicated by the sinking of the phytoplankton.

A factor of great importance is the length of day at different depths. Regnard (1891) made a few observations in clear weather in March off Madeira and found that at 20 metres the length of day was reduced to 7 hours as compared with 11 at the surface, at 30 metres it was reduced to 5 hours, while at 40 metres it only lasted for a few minutes. The photographic method he used, however, measures mainly the blue end of the spectrum, and so these results cannot be directly related to photosynthesis. The effect of shortening of the day with depth is well shown in Figs. 7, 10, 14, and 17, and is naturally much more marked in dull than in sunny weather.

Even at midwinter, photosynthesis is greater than respiration at the surface and the compensation point is always at a depth of some metres. This is of importance when we consider the causes of the spring diatom increase. Little is known about the amount of reserve material necessary before a diatom divides, but it is difficult to believe that in the lengthening days of February and March light can act as a limiting factor for growth in the sea.

## CONCLUSIONS AND SUMMARY.

Experiments have been carried out on the photosynthesis of diatom cultures at different depths in the sea. The results of these lead to the conclusion that the compensation point in this latitude in inshore waters lies at a depth of from 20 to 30 metres in summer. As we approach the surface the increasing light enables more photosynthesis to take place, but this increase only goes on up to a certain depth. There is no point which can be considered as the optimum, but a range extending over 2 or 3 metres. Above this light is too strong and photosynthesis falls off again. Even at midwinter the midday sun is injurious at the surface. These depths naturally depend on the season and also to a large extent on the kind of weather. The compensation point sinks gradually from a position close to the surface in winter to a depth of 20 to 30 metres in summer. This applies, of course, to coastal water which has more detritus in suspension (cf. Poole and Atkins, 1926), and as we go further from land this depth will increase.

We are indebted to the Royal Society for a grant to cover publication of figures and plates in this and our previous paper (1927).

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We desire also to thank Mr. Elmhirst and members of the staff for their help throughout.

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## TABLE I.

Loch Striven, 18–19/3/27. No sunshine.
Diatom culture of Oct. 18th—2,300 cells per c.c.
12.15 p.m. to 11.15 a.m. Initial $O_2$ content $\left.\begin{matrix}6\cdot43\\6\cdot46\end{matrix}\right\}6\cdot45.$

| Depth in metres. | Light. | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. | Temperature °C. |
|---|---|---|---|---|---|---|
| 0 | 1.6·94 | 1.5·90 | 6·02 | +0·92 | 0·40 | 6·64 |
| 5 | 1.6·44 | 1.5·96 | 6·02 | +0·44 | 0·19 | 6·50 |
| 10 | 1.6·26 | 1.6·06 | 6·02 | +0·24 | 0·10 | 7·05 |
| 20 | 1.6·19 | 1.6·08 | 6·02 | +0·17 | 0·07 | 7·23 |
| 40 | 1.6·06 | 1.6·06 | 6·02 | +0·04 | — | 7·35 |

## TABLE II.

Loch Striven, 28–29/3/27. Sunshine—5 hrs. 50 mins.
Diatom culture of February 21st—3,500 cells per c.c.
11–40 a.m. to 12 noon. Initial $O_2$ content 6·56.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 0 | 1.7·34<br>2.7·46<br>3.7·41 | 7·40 | 1.6·14 | 6·14 | +1·26 | 0·36 | 7·1 |
| 5 | 1.7·38<br>2.7·47 | 7·43 | 1.6·10 | 6·14 | +1·29 | 0·37 | 7·20 |
| 10 | 1.6·84<br>2.6·88 | 6·86 | 1.6·17 | 6·14 | +0·72 | 0·21 | 7·18 |
| 20 | 1.6·32<br>2.6·32 | 6·32 | 1.6·13 | 6·14 | +0·18 | 0·05 | 7·02 |
| 40 | 1.6·13<br>2.6·11 | 6·12 | 1. | 6·14 | — | — | 7·30 |

## TABLE III.

Loch Striven, 31/3–1/4/27. Sunshine—5 hrs. 15 mins.
Diatom culture of February 21st—2,800 cells per c.c.
12 noon to 11–30 a.m. Initial $O_2$ content 6·55.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·14<br>2.7·17 | 7·15 | 1.6·02 | 6·05 | +1·10 | 0·39 |
| 5 | 1.7·68<br>2.7·75 | 7·71 | 1. | 6·05 | +1·66 | 0·59 |
| 10 | 1.7·03<br>2.7·02 | 7·02 | 1.6·06 | 6·05 | +0·97 | 0·35 |
| 20 | 1.6·41<br>2.6·35 | 6·38 | 1.6·07 | 6·05 | +0·33 | 0·12 |
| 40 | 1.6·10 | 6·10 | 1. | 6·05 | — | — |

## TABLE IV.

Loch Striven, 18–19/5/27. 5 hrs. 55 mins. sunshine (all on 18th).
Diatom culture of May 3rd—3,400 cells per c.c.
11.25 a.m. to 11 a.m. Initial $O_2$ content $\left.\begin{matrix}1.7{\cdot}02\\2.7{\cdot}12\end{matrix}\right\}7{\cdot}07.$

| Depth in metres | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. | Temperature °C. |
|---|---|---|---|---|---|---|---|
| 0 | 1. 9·59<br>2. 9·18 | 9·38 | 1.6·28 | 6·36 | +3·02 | 0·89 | 9·47 |
| ½ | 1. 9·96<br>2.10·66<br>3.10·94 | 10·52 | 1.6·38<br>2.6·31 | 6·36 | +4·16 | 1·22 | — |
| 1 | 1.11·28<br>2.11·14 | 11·21 | 1.6·28 | 6·36 | +4·85 | 1·43 | 9·46 |
| 2 | 1.10·87<br>2.10·88 | 10·88 | 1.6·31 | 6·36 | +4·52 | 1·33 | 9·45 |
| 3 | 1.10·53<br>2.10·56 | 10·55 | 1.6·34 | 6·36 | +4·19 | 1·23 | 8·92 |
| 4 | 1. 9·30<br>2. 9·43 | 9·36 | 1.6·39 | 6·36 | +3·00 | 0·88 | 9·38 |
| 5 | 1. 9·06<br>2. 9·06 | 9·06 | 1.6·41 | 6·36 | +2·70 | 0·79 | 9·40 |
| 6 | 1. 8·58 | 8·58 | 1.6·39 | 6·36 | +2·22 | 0·65 | 8·92 |
| 7 | 1. 7·99<br>2. 8·04 | 8·01 | 1.6·35 | 6·36 | +1·65 | 0·49 | 8·26 |

## TABLE V.

Loch Striven, 13–14/6/27. Sunshine—16 hrs. 5 mins.
Culture of May 29th—3,700 cells per c.c.
11 a.m. to 10.50 a.m. Initial $O_2$ content $\left.\begin{matrix}1.6{\cdot}95\\2.6{\cdot}93\\3.6{\cdot}92\end{matrix}\right\}6{\cdot}93.$

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 1 | 1.12·05<br>2.11·63 | 11·84 | 1. — | 6·78 | +5·06 | 1·37 | 10·58 |
| 3 | 1.11·76<br>2.11·59 | 11·68 | 1.6·77 | 6·78 | +4·90 | 1·32 | 10·38 |
| 5 | 1.11·10<br>2.11·12 | 11·11 | 1.6·73 | 6·78 | +4·33 | 1·17 | 10·23 |
| 7 | 1.11·11<br>2.11·04 | 11·08 | 1.6·77 | 6·78 | +4·30 | 1·16 | 9·59 |
| 10 | 1. 9·97<br>2. 9·96 | 9·96 | 1.6·77 | 6·78 | +3·18 | 0·86 | 9·00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 20 | 1. 7·21<br>2. 7·20 | 7·21 | 1.6·79 | 6·78 | +0·43 | 0·12 | 8·50 |
| 30 | 1. 6·87<br>2. 6·85 | 6·86 | 1.6·76 | 6·78 | +0·08 | 0·02 | 7·78 |
| 40* | 1. 6·80 | 6·80 | 1.6·88 | 6·78 | +0·02 | 0·01 | 7·58 |
| 50 | 1. 6·87<br>2. 6·92 | 6·90 | 1.6·78 | 6·78 | +0·12 | 0·03 | 7·82 |
| 60 | 1. 6·87<br>2. 6·89 | 6·88 | 1.6·81 | 6·78 | +0·10 | 0·03 | 8·07 |

## TABLE VI.

Farland Point, 9–10/6/27. Sunshine—15 hrs. 5 minutes.
Diatom cultures of May—3.600 cells per c.c.

12.3 A.M. TO 3 A.M.

Initial $O_2$ content—$\left.\begin{array}{l}1.5{\cdot}86\\2.5{\cdot}87\end{array}\right\}$ 5·86.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.5·81<br>2.5·81 | 5·81 | 1.5·82 | 5·76 | +0·05 | 0·014 |
| ½ | 1.5·77<br>2.5·75 | 5·76 | 1.5·69 | 5·76 | — | — |
| 1 | 1.5·75<br>2.5·78 | 5·77 | 1.5·76 | 5·76 | +0·01 | 0·003 |
| 2 | 1.5·83<br>2.5·78 | 5·81 | 1.5·75 | 5·76 | +0·05 | 0·014 |
| 3 | 1.5·79<br>2.5·78 | 5·78 | 1.5·78 | 5·76 | +0·02 | 0·006 |
| 4 | 1.5·76<br>2.5·84 | 5·80 | 1.5·81 | 5·76 | +0·04 | 0·011 |
| 6 | 1.5·75<br>2.5·76 | 5·76 | 1.5·71 | 5·76 | — | — |

3 A.M. TO 6 A.M.

Initial $O_2$ content $\left.\begin{array}{l}1.\ 5{\cdot}79\\2.\ 5{\cdot}86\end{array}\right\}$ 5·83.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·92<br>2.6·95 | 6·93 | 1.5·81 | 5·75 | +1·18 | 0·328 |
| ½ | 1.6·53<br>2.6·59 | 6·56 | 1.5·79 | 5·75 | +0·81 | 0·225 |
| 1 | 1.6·61<br>2.6·56 | 6·58 | 1.5·81 | 5·75 | +0·83 | 0·231 |
| 2 | 1.6·55<br>2.6·51 | 6·53 | 1.5·68 | 5·75 | +0·78 | 0·217 |

---

* Remains of Cyanea found on cage.

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 3 | 1.6·34<br>2.6·37 | 6·35 | 1. | 5·75 | +0·60 | 0·167 |
| 4 | 1.6·26<br>2.6·28 | 6·27 | 1.5·68 | 5·75 | +0·52 | 0·144 |
| 6 | 1.6·08<br>2.6·03 | 6·05 | 1.5·74 | 5·75 | +0·30 | 0·083 |

### 6.5 A.M. TO 8.50 A.M.

Initial $O_2$ content 1. 7·63
2. 7·67 7·65.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·94<br>2.8·03 | 7·99 | 1.7·58 | 7·48 | +0·51 | 0·142 |
| ½ | 1.8·23<br>2.8·23 | 8·23 | 1.7·50 | 7·48 | +0·75 | 0·208 |
| 1 | 1.8·34<br>2.8·15 | 8·25 | 1.7·48 | 7·48 | +0·77 | 0·214 |
| 2 | 1.8·35<br>2.8·23 | 8·29 | 1.7·48 | 7·48 | +0·81 | 0·225 |
| 3 | 1.8·21 | 8·21 | 1.7·45 | 7·48 | +0·73 | 0·203 |
| 4 | 1.8·32<br>2.8·20 | 8·26 | 1.7·39 | 7·48 | +0·78 | 0·217 |
| 6 | 1.8·26<br>2.8·13 | 8·20 | 1.7·48 | 7·48 | +0·72 | 0·200 |

### 9 A.M. TO 11.55 A.M.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·53<br>2.7·56 | 7·54 | 1.7·37 | 7·27 | +0·27 | 0·075 |
| ½ | 1.8·03<br>2.7·91 | 7·97 | 1.7·06 | 7·27 | +0·70 | 0·195 |
| 1 | 1.8·19<br>2.8·14 | 8·17 | 1.7·30 | 7·27 | +0·90 | 0·250 |
| 2 | 1.8·24<br>2.8·18 | 8·21 | 1.7·31 | 7·27 | +0·94 | 0·262 |
| 3 | 1.8·18<br>2.8·12 | 8·15 | 1.7·21 | 7·27 | +0·88 | 0·244 |
| 4 | 1.8·14<br>2.8·11 | 8·12 | 1.7·26 | 7·27 | +0·85 | 0·236 |
| 6 | 1.8·19<br>2.8·15 | 8·17 | 1.7·19 | 7·27 | +0·90 | 0·250 |

12 NOON TO 2.57 P.M.

Initial $O_2$ content $\left.\begin{array}{l}1.\ 7{\cdot}33\\ 2.\ 7{\cdot}16\end{array}\right\}7{\cdot}25.$

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·38<br>2.7·36 | 7·37 | 1. | 7·05 | +0·32 | 0·089 |
| ½ | 1.7·81<br>2.7·73 | 7·77 | 1.7·08 | 7·05 | +0·72 | 0·200 |
| 1 | 1.7·91<br>2.8·01 | 7·96 | 1.7·04 | 7·05 | +0·91 | 0·253 |
| 2 | 1.8·05<br>2.7·99 | 8·02 | 1.7·01 | 7·05 | +0·97 | 0·270 |
| 3 | 1.8·05<br>2.7·96 | 8·01 | 1.7·06 | 7·05 | +0·96 | 0·267 |
| 4 | 1.8·06<br>2.7·93 | 8·00 | 1.7·07 | 7·05 | +0·95 | 0·264 |
| 6 | 1.8·10<br>2.7·98 | 8·04 | 1.7·03 | 7·05 | +0·99 | 0·275 |

3 P.M. TO 5.55 P.M.

Initial $O_2$ content $\left.\begin{array}{l}1.\ 6{\cdot}80\\ 2.\ 7.02\end{array}\right\}6{\cdot}91.$

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·15<br>2.7·40 | 7·27 | 1. | 6·67 | +0·60 | 0·167 |
| ½ | 1.7·60<br>2.7·58 | 7·59 | 1.6·69 | 6·67 | +0·92 | 0·256 |
| 1 | 1.7·68<br>2.7·66 | 7·67 | 1.6·69 | 6·67 | +1·00 | 0·278 |
| 2 | 1.7·69<br>2.7·69 | 7·69 | 1.6·68 | 6·67 | +1·02 | 0·283 |
| 3 | 1.7·67<br>2.7·62 | 7·64 | 1.6·64 | 6·67 | +0·97 | 0·270 |
| 4 | 1.7·66<br>2.7·68 | 7·67 | 1.6·62 | 6·67 | +1·00 | 0·277 |
| 6 | 1.7·67<br>2.7·65 | 7·66 | 1.6·71 | 6·67 | +0·99 | 0·275 |

6 P.M. TO 8.53 P.M.

Initial $O_2$ content $\left.\begin{array}{l}1.\ 6{\cdot}45\\ 2.\ 6{\cdot}32\end{array}\right\}6{\cdot}38.$

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·25<br>2.7·18 | 7·22 | 1.6·43 | 6·29 | +0·93 | 0·258 |
| ½ | 1.7·15<br>2.7·20 | 7·17 | 1.6·41 | 6·29 | +0·88 | 0·244 |

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 1 | 1.7·21<br>2.7·27 | 7·24 | 1.6·32 | 6·29 | +0·95 | 0·264 |
| 2 | 1.7·16 | 7·16 | 1.6·28 | 6·29 | +0·87 | 0·242 |
| 3 | 1.7·01<br>2.6·98 | 6·99 | 1.6·20 | 6·29 | +0·70 | 0·195 |
| 4 | 1.6·89<br>2.6·85 | 6·87 | 1.6·19 | 6·29 | +0·58 | 0·161 |
| 6 | 1.6·92<br>2.6·61 | 6·77 | 1.6·19 | 6·29 | +0·46 | 0·128 |

### 8.57 p.m. to 12 midnight.

Initial $O_2$ content $\left.\begin{matrix}1.\ 6{\cdot}09\\ 2.\ 6{\cdot}04\end{matrix}\right\}6{\cdot}06.$

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·02<br>2.6·01 | 6·01 | 1.6·01 | 5·90 | +0·11 | 0·031 |
| ½ | 1.5·96<br>2.5·92 | 5·94 | 1.5·91 | 5·90 | +0·04 | 0·011 |
| 1 | 1.5·97<br>2.5·93 | 5·95 | 1.5·93 | 5·90 | +0·05 | 0·014 |
| 2 | 1.5·91<br>2.5·91 | 5·91 | 1.5·90 | 5·90 | +0·01 | 0·003 |
| 3 | 1.5·89<br>2.5·91 | 5·90 | 1.5·88 | 5·90 | — | — |
| 4 | 1.5·87<br>2.5·89 | 5·88 | 1.5·84 | 5·90 | — | — |
| 6 | 1.5·87<br>2.5·85 | 5·86 | 1.5·85 | 5·90 | — | — |

### Composite Curve.

| | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|
| Surface | +3·97 | 1·103 |
| ½ m. | +4·82 | 1·339 |
| 1 m. | +5·42 | 1·505 |
| 2 m. | +5·45 | 1·514 |
| 3 m. | +4·86 | 1·350 |
| 4 m. | +4·72 | 1·311 |
| 6 m. | +4·36 | 1·212 |

## TABLE VII.

Farland Point, 28/6/27. No sunshine.
Diatom cultures of June 2nd–June 13th—3,700 cells per c.c.

12.10 A.M. TO 3.3 A.M.

Initial $O_2$ content 1.6·78, 2.6·69 } 6·73.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·69<br>2.6·64 | 6·66 | 1.6·67 | 6·65 | +0·01 | 0·003 |
| ½ | 1.6·66<br>2.6·63 | 6·64 | 1.6·67 | 6·65 | — | — |
| 1 | 1.6·66<br>2.6·63 | 6·65 | 1.6·59 | 6·65 | — | — |
| 2 | 1.6·67<br>2.6·67 | 6·67 | | 6·65 | +0·02 | 0·005 |
| 4 | 1.6·65 | 6·65 | 1.6·67 | 6·65 | — | — |
| 6 | 1.6·65<br>2.6·62 | 6·63 | 1.6·66 | 6·65 | — | — |

3.3 A.M. TO 5.57 A.M.

Initial $O_2$ content 1.6·11, 2.6·14 } 6·12.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·61<br>2.6·57 | 6·59 | 1.6·12 | 6·09 | +0·50 | 0·135 |
| ½ | 1.6·34<br>2.6·36 | 6·35 | 1.6·10 | 6·09 | +0·26 | 0·070 |
| 1 | 1.6·28<br>2.6·33 | 6·31 | 1.6·04 | 6·09 | +0·22 | 0·060 |
| 2 | 1.6·33<br>2.6·31 | 6·32 | 1.6·12 | 6·09 | +0·23 | 0·062 |
| 4 | 1.6·23<br>2.6·20 | 6·22 | 1.6·08 | 6·09 | +0·13 | 0·035 |
| 6 | 1.6·18<br>2.6·16 | 6·17 | 1.6·09 | 6·09 | +0·08 | 0·022 |

5.57 A.M. TO 9.0 A.M.

Initial $O_2$ content 1.5·97, 2.5·94 } 5·96.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·70 | 6·70 | 1.5·94 | 5·90 | +0·80 | 0·217 |
| ½ | 1.6·96<br>2.6·94 | 6·95 | 1.5·89 | 5·90 | +1·05 | 0·284 |

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 1 | 1.6·98<br>2.6·95 | 6·96 | 1.5·87 | 5·90 | +1·06 | 0·287 |
| 2 | 1.6·98 | 6·98 | 1.5·91 | 5·90 | +1·08 | 0·292 |
| 4 | 1.6·84<br>2.6·85 | 6·84 | 1.5·88 | 5·90 | +0·94 | 0·254 |
| 6 | 1.6·60<br>2.6·57 | 6·58 | 1.5·89 | 5·90 | +0·68 | 0·184 |

9 A.M. TO 12 NOON.

Initial $O_2$ content $\left.\begin{array}{l}1.6{\cdot}17\\2.6{\cdot}19\end{array}\right\}$ 6·18.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·85<br>2.6·88 | 6·87 | 1.6·14 | 6·08 | +0·79 | 0·214 |
| ½ | 1.7·03<br>2.7·08 | 7·06 | 1.6·07 | 6·08 | +0·98 | 0·265 |
| 1 | 1.7·07<br>2.7·12 | 7·09 | 1.6·04 | 6·08 | +1·01 | 0·273 |
| 2 | 1.7·17 | 7·17 | 1.6·09 | 6·08 | +1·09 | 0·295 |
| 4 | 1.7·14<br>2.7·11 | 7·13 | 1.6·09 | 6·08 | +1·05 | 0·284 |
| 6 | 1.6·89<br>2.6·93 | 6·91 | 1.6·09 | 6·08 | +0·83 | 0·224 |

12 NOON TO 3.5 P.M.

Initial $O_2$ content $\left.\begin{array}{l}1.6{\cdot}05\\2.6{\cdot}06\end{array}\right\}$ 6·05.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·84<br>2.6·71 | 6·77 | 1.5·96 | 5·95 | +0·82 | 0·222 |
| ½ | 1.6·98<br>2.6·99 | 6·98 | 1.5·93 | 5·95 | +1.03 | 0·278 |
| 1 | 1.7·00<br>2.7·00 | 7·00 | 1.5·91 | 5·95 | +1·05 | 0·284 |
| 2 | 1.6·93 | 6·93 | 1.5·98 | 5·95 | +0·98 | 0·265 |
| 4 | 1.6·85<br>2.6·83 | 6·84 | 1.5·96 | 5·95 | +0·89 | 0·241 |
| 6 | 1.6·62<br>2.6·59 | 6·60 | 1.6·22 | 5·95 | +0·65 | 0·176 |

3.5 P.M. TO 5.55 P.M.

Initial $O_2$ content 1.5·86, 2.5·89 } 5·87.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·79<br>2.6·76 | 6·78 | 1.5·75 | 5·77 | +1·01 | 0·273 |
| ½ | 1.6·68<br>2.6·67 | 6·68 | 1.5·74 | 5·77 | +0·91 | 0·246 |
| 1 | 1.6·56<br>2.6·63 | 6·59 | 1.5·75 | 5·77 | +0·82 | 0·222 |
| 2 | 1.6·53<br>2.6·39 | 6·46 | 1.5·79 | 5·77 | +0·69 | 0·187 |
| 4 | 1.6·24<br>2.6·29 | 6·27 | | 5·77 | +0·50 | 0·135 |
| 6 | 1.6·06<br>2.6·13 | 6·09 | 1.5·82 | 5·77 | +0·32 | 0·086 |

5.55 P.M. TO 9 P.M.

Initial $O_2$ content 1.5·83, 2.5·84 } 5·83.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·46<br>2.6·37 | 6·42 | 1.5·79 | 5.76 | +0·66 | 0·178 |
| ½ | 1.6·18<br>2.6·18 | 6·18 | 1.5·71 | 5·76 | +0·42 | 0·114 |
| 1 | 1.6·12<br>2.6·12 | 6·12 | 1.5·72 | 5·76 | +0·36 | 0·097 |
| 2 | 1.6·08 | 6·08 | 1.5·79 | 5·76 | +0·32 | 0·086 |
| 4 | 1.5·99<br>2.5·96 | 5·97 | 1.5·80 | 5·76 | +0·21 | 0·057 |
| 6 | 1.5·93<br>2.5·91 | 5·92 | 1.5·77 | 5·76 | +0·16 | 0·043 |

9 P.M. TO 12 MIDNIGHT.

Initial $O_2$ content—1.5·90 5·90.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1. Lost.<br>2. Lost. | | 1.5·77 | 5·78 | Lost. | Lost. |
| ½ | 1.5·80<br>2.5·82 | 5·81 | 1.5·77 | 5·78 | +0·03 | 0·008 |
| 1 | 1.5·74<br>2.5·77 | 5·75 | 1.5·74 | 5·78 | — | — |
| 2 | 1.5·83 | 5·83 | 1.5·79 | 5·78 | +0·05 | 0·014 |
| 4 | 1.5·80 | 5·80 | 1.5·78 | 5·78 | +0·02 | 0·005 |
| 6 | 1.5·80<br>2.5·82 | 5·81 | 1.5·82 | 5·78 | +0·03 | 0·008 |

COMPOSITE CURVE.*

| | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|
| Surface | +4·58 | 1·238 |
| ½ m. | +4·64 | 1·254 |
| 1 m. | +4·52 | 1·222 |
| 2 m. | +4·39 | 1·187 |
| 4 m. | +3·72 | 1·006 |
| 6 m. | +2·72 | 0·735 |

## TABLE VIII.

Farland Point, 29/11/27. Sunshine—6 hours.
Diatom culture of October 8th, 18th, 26th, 27th—6,000 cells per c.c.

6.20 A.M. TO 9.10 A.M.

Initial $O_2$ content—1.7·32 7·32.

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^5$ diatoms. |
|---|---|---|---|---|---|---|
| 0 | 1.7·70 | 7·70 | 1.7·31 | 7·26 | +0·44 | 0·073 |
| ½ | 1.7·44<br>2.7·43 | 7·44 | 1.7·25 | 7·26 | +0·18 | 0·030 |
| 1 | 1.7·44<br>2.7·41 | 7·43 | 1.7·21 | 7·26 | +0·17 | 0·029 |
| 2 | 1.7·40<br>2.7·42 | 7·41 | 1.7·28 | 7·26 | +0·15 | 0·025 |
| 4 | 1.7·35<br>2.7·37 | 7·36 | 1.7·27 | 7·26 | +0·10 | 0·017 |
| 6 | 1.7·30<br>2.7·30 | 7·30 | 1.7·24 | 7·26 | +0·04 | 0·007 |

9.10 A.M. TO 12 NOON.

Initial $O_2$ content—$\left.\begin{matrix}1.6\cdot63\\2.6\cdot60\end{matrix}\right\}$ 6·62.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.8·00<br>2.7·96 | 7·98 | 1.6·59 | 6·59 | +1·39 | 0·232 |
| ½ | 1.7·92<br>2.7·95 | 7·94 | 1.6·55 | 6·59 | +1·35 | 0·225 |
| 1 | 1.8·00<br>2.8·00 | 8·00 | 1.6·50 | 6·59 | +1·41 | 0·235 |

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* Figures from 9 p.m.–12 midnight and 12 midnight–3 a.m. omitted because all results were within experimental error, and the surface lights were lost in the latter experiment.

| | | | | | | |
|---|---|---|---|---|---|---|
| 2 | 1.7·91<br>2.7·95 | 7·93 | 1.6·66 | 6·59 | +1·34 | 0·223 |
| 4 | 1.7·50<br>2.7·45 | 7·48 | 1.6·63 | 6·59 | +0·89 | 0·148 |
| 6 | 1.7·06<br>2.7·05 | 7·05 | | 6·59 | +0·46 | 0·077 |

12 NOON TO 3 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}46\\2.6{\cdot}48\end{matrix}\right\}$ 6·47.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·44<br>2.7·00 | 7·22* | 1.6·34 | 6·36 | +0·86 | 0·143 |
| ½ | 1.8·00 | 8·00 | 1.6·34 | 6·36 | +1·64 | 0·273 |
| 1 | 1.7·97<br>2.7·98 | 7·97 | 1.6·33 | 6·36 | +1·61 | 0·268 |
| 2 | 1.7·83<br>2.7·87 | 7·85 | 1.6·40 | 6·36 | +1·49 | 0·248 |
| 4 | 1.7·27<br>2.7·28 | 7·27 | 1.6·35 | 6·36 | +0·91 | 0·151 |
| 6 | 1.6·87<br>2.6·86 | 6·87 | 1.6·42 | 6·36 | +0·51 | 0·085 |

3 P.M. TO 6 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}20\\2.6{\cdot}19\end{matrix}\right\}$ 6·20.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·71<br>2.6·63 | 6·67 | 1.6·19 | 6·19 | +0·48 | 0·080 |
| ½ | 1.6·44<br>2.6·44 | 6·44 | 1.6·17 | 6·19 | +0·25 | 0·042 |
| 1 | 1.6·38<br>2.6·31 | 6·35 | 1.6·16 | 6·19 | +0·16 | 0·027 |
| 2 | 1.6·38 | 6·38 | 1.6·25 | 6·19 | +0·19 | 0·031 |
| 4 | 1.6·22<br>2.6·32 | 6·27 | 1.6·17 | 6·19 | +0·08 | 0·013 |
| 6 | 1.6·24<br>2.6·22 | 6·23 | 1.6·23 | 6·19 | +0·04 | 0·007 |

6 P.M. TO 9.3 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}07\\2.6{\cdot}06\end{matrix}\right\}$ 6·06.

| | | | | | |
|---|---|---|---|---|---|
| 0 | 1.6·03 | 6·03 | 1.6·02 | 6·02 | +0·01 |
| ½ | 1.6·03<br>2.6·04 | 6·04 | 1.6·05 | 6·02 | +0·02 |

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* It is probable that these bottles have been interchanged, which would make the readings 7·22 and 7·21.

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 1 | 1.6·02<br>2.5·96 | 5·99 | 1.5·97 | 6·02 | — | |
| 2 | 1.6·02<br>2.6·07 | 6·05 | 1.6·05 | 6·02 | +0·03 | |
| 4 | 1.6·04<br>2.6·05 | 6·04 | | 6·02 | +0·02 | |
| 6 | 1.6·05<br>2.6·02 | 6·04 | 1.6·01 | 6·02 | +0·02 | |

### Composite Curve.

| | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|
| Surface | +3·17 | 0·528 |
| ½ m. | +3·42 | 0·570 |
| 1 m. | +3·35 | 0·558 |
| 2 m. | +3·17 | 0·533 |
| 4 m. | +1·98 | 0·330 |
| 6 m. | +1·05 | 0·175 |

## TABLE IX.

Farland Point, 9/11/27. Sunshine—2 hours, 55 minutes.
Diatom culture of October 1st–October 18th—5,600 cells per c.c.

### 3.5 A.M. TO 6.0 A.M.

Initial $O_2$ content—1.7·29 7·29.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·30 | 7·30 | 1. | 7·24 | +0·06 | 0·011 |
| ½ | 1.7·26<br>2.7·29 | 7·27 | 1.7·24 | 7·24 | +0·03 | — |
| 1 | 1.7·31<br>2.7·26 | 7·29 | 1.7·24 | 7·24 | +0·05 | — |
| 2 | 1.7·21<br>2.7·19 | 7·20 | 1.7·24 | 7·24 | — | — |
| 4 | 1.7·24<br>2.7·26 | 7·25 | 1.7·23 | 7·24 | +0·01 | — |
| 6 | 1.7·26<br>2.7·22 | 7·24 | 1.7·25 | 7·24 | — | — |

6.5 A.M. TO 9.0 A.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}70\\2.6{\cdot}61\end{matrix}\right\}$ 6·65.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·27 | 7·27 | 1.6·74 | 6·73 | +0·54 | 0·096 |
| ½ | 1.7·15<br>2.7·15 | 7·15 | 1.6·72 | 6·73 | +0·42 | 0·075 |
| 1 | 1.7·10<br>2.7·08 | 7·09 | 1.6·72 | 6·73 | +0·36 | 0·064 |
| 2 | 1.6·97<br>2.7·00 | 6·98 | 1.6·70 | 6·73 | +0·25 | 0·045 |
| 4 | 1.6·84<br>2.6·86 | 6·85 | 1.6·71 | 6·73 | +0·12 | 0·021 |
| 6 | 1.6·81<br>2.6·82 | 6·81 | 1.6·76 | 6·73 | +0·08 | 0·014 |

9.0 A.M. TO 12 NOON.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}57\\2.6{\cdot}48\end{matrix}\right\}$ 6·53.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.8·11 | 8·11 | 1.6·55 | 6·55 | +1·56 | 0·279 |
| ½ | 1.8·12<br>2.8·18 | 8·15 | 1.6·52 | 6·55 | +1·60 | 0·286 |
| 1 | 1.8·12<br>2.8·11 | 8·11 | 1.6·57 | 6·55 | +1·56 | 0·279 |
| 2 | 1.7·79<br>2.7·84 | 7·81 | 1.6·57 | 6·55 | +1·26 | 0·225 |
| 4 | 1.7·23<br>2.7·18 | 7·20 | 1.6·56 | 6·55 | +0·65 | 0·116 |
| 6 | 1.6·90 | 6·90 | 1.6·55 | 6·55 | +0·35 | 0·063 |

12 NOON TO 3 P.M.

Initial $O_2$ content—1.6·63 6·63.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.7·73<br>2.7·71 | 7·72 | 1.6·49 | 6·45 | +1·27 | 0·227 |
| ½ | 1.8·10<br>2.8·07 | 8·08 | 1.6·32 | 6·45 | +1·63 | 0·291 |
| 1 | 1.7·98<br>2.8·00 | 7·99 | | 6·45 | +1·54 | 0·275 |
| 2 | 1.7·67<br>2.7·74 | 7·71 | 1.6·51 | 6·45 | +1·26 | 0·225 |
| 4 | 1.7·07<br>2.7·04 | 7·05 | 1.6·49 | 6·45 | +0·60 | 0·107 |
| 6 | 1.6·80<br>2.6·75 | 6·77 | | 6·45 | +0·32 | 0·057 |

3.10 P.M. TO 6.0 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}22\\2.6{\cdot}18\end{matrix}\right\}$ 6·20.

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 0 | 1.6·54<br>2.6·52 | 6·52 | 1.6·17 | 6·18 | +0·34 | 0·061 |
| ½ | 1.6·53<br>2.6·51 | 6·52 | 1.6·20 | 6·18 | +0·34 | 0·061 |
| 1 | 1.6·36<br>2.6·34 | 6·35 | 1.6·17 | 6·18 | +0·17 | 0·030 |
| 2 | 1.6·32<br>2.6·33 | 6·33 | 1.6·20 | 6·18 | +0·15 | 0·027 |
| 4 | 1.6·26<br>2.6·26 | 6·26 | 1.6·17 | 6·18 | +0·08 | 0·014 |
| 6 | 1.6·08 | 6·08 | 1. | 6·18 | — | — |

COMPOSITE CURVE.

| | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|
| Surface | +3·80 | 0·679 |
| ½ m. | +4·05 | 0·723 |
| 1 m. | +3·68 | 0·657 |
| 2 m. | +2·92 | 0·521 |
| 4 m. | +1·46 | 0·261 |
| 6 m. | +0·75 | 0·134 |

## TABLE X.

Farland Point, 7/12/27. No sunshine.
Diatom culture of November 11th and 13th—4,100 cells per c.c.

6.10 A.M. TO 9.3 A.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6{\cdot}79\\2.6{\cdot}66\end{matrix}\right\}$ 6·72.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·86<br>2.6·83 | 6·85 | 1.6·79 | 6·69 | +0·16 | 0·039 |
| ½ | 1.6·76<br>2.6·74 | 6·75 | 1.6·72 | 6·69 | +0·06 | 0·015 |
| 1 | 1.6·71<br>2.6·73 | 6·72 | 1.6·67 | 6·69 | +0·03 | 0·007 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 2 | 1.6·66<br>2.6·72 | 6·69 | 1.6·68 | 6·69 | — | — |
| 4 | 1.6·69<br>2.6·69 | 6·69 | 1.6·63 | 6·69 | — | — |
| 6 | 1.6·69<br>2.6·67 | 6·68 | 1.6·66 | 6·69 | — | — |

### 9.7 A.M. TO 12.4 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.6\cdot00\\2.5\cdot91\end{matrix}\right\}$ 5·95.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·63<br>2.6·62 | 6·63 | 1.5·95 | 5·94 | +0·69 | 0·168 |
| ½ | 1.6·51<br>2.6·53 | 6·52 | 1.5·95 | 5·94 | +0·58 | 0·142 |
| 1 | 1.6·51<br>2.6·53 | 6·40 | 1.5·93 | 5·94 | +0·46 | 0·112 |
| 2 | 1.6·28<br>2.6·29 | 6·28 | 1.5·98 | 5·94 | +0·34 | 0·083 |
| 4 | 1.6·14<br>2.6·16 | 6·15 | 1.5·88 | 5·94 | +0·21 | 0·051 |
| 6 | 1.6·04<br>2.6·05 | 6·05 | 1.5·99 | 5·94 | +0·11 | 0·027 |

### 12.4 P.M. TO 3 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.5\cdot96\\2.5\cdot91\end{matrix}\right\}$ 5·93.

| | | | | | | |
|---|---|---|---|---|---|---|
| 0 | 1.6·72<br>2.6·72 | 6·72 | 1.5·92 | 5·91 | +0·81 | 0·198 |
| ½ | 1.6·47<br>2.6·46 | 6·46 | 1.5·93 | 5·91 | +0·55 | 0·134 |
| 1 | 1.6·31<br>2.6·33 | 6·32 | 1.5·91 | 5·91 | +0·41 | 0·100 |
| 2 | 1.6·20<br>2.6·26 | 6·23 | 1.5·91 | 5·91 | +0·32 | 0·078 |
| 4 | 1.6·12<br>2.6·08 | 6·10 | 1.5·91 | 5·91 | +0·19 | 0·046 |
| 6 | 1.6·02<br>2.6·03 | 6·03 | 1.5·91 | 5·91 | +0·12 | 0·029 |

### 3 P.M. TO 6 P.M.

Initial $O_2$ content—$\left.\begin{matrix}1.5{\cdot}85\\2.5{\cdot}79\end{matrix}\right\}$ 5·82.

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 0 | 1.5·85<br>2.5·86 | 5·85 | 1.5·74 | 5·76 | +0·09 | 0·022 |
| ½ | 1.5·85<br>2.5·83 | 5·84 | 1.5·74 | 5·76 | +0·08 | 0·020 |
| 1 | 1.5·81<br>2.5·80 | 5·81 | 1.5·72 | 5·76 | +0·05 | 0·012 |
| 2 | 1.5·82<br>2.5·80 | 5·81 | 1.5·80 | 5·76 | +0·05 | 0·012 |
| 4 | 1.5·81<br>2.5·82 | 5·81 | 1.5·74 | 5·76 | +0·05 | 0·012 |
| 6 | 1.5·77<br>2.5·79 | 5·78 | 1.5·80 | 5·76 | +0·02 | 0·005 |

### COMPOSITE CURVE.

| | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|
| Surface | +1·75 | 0·427 |
| ½ m. | +1·27 | 0·310 |
| 1 m. | +0·95 | 0·232 |
| 2 m. | +0·71 | 0·173 |
| 4 m. | +0·45 | 0·110 |
| 6 m. | +0·25 | 0·061 |

## TABLE XI.

Loch Striven, 27–28/5/27. Sunshine—11 hours 10 minutes.
Culture of Coscinosira, May 4th and 10th—3,700 cells per c.c.
Culture of Chætoceros May 2nd, 13,900 cells per c.c.

10.35 a.m. to 10.10 a.m. Initial $O_2$ content—$\left.\begin{matrix}\text{1.Ch.5·27}\\ \text{2.Ch.5·27}\end{matrix}\right\}$ 5·27.
$\left.\begin{matrix}\text{1.Co. 6·04}\\ \text{2.Co. 6·05}\end{matrix}\right\}$ 6·05.

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. Ch. | Total $O_2$ produced. Co. | $O_2$ produced by $10^6$ diatoms. Ch. | $O_2$ produced by $10^6$ diatoms. Co. | Temperature. °C. |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 1.Ch. 4·41 | 4·41 | 1.Ch.5·05 | 4·66 | −0·25 | +2·33 | −0·018 | +0·63 | 10·62 |
| | 2.Co. 7·69 | 7·69 | 2.Co.5·33 | 5·36 | | | | | |
| ½ | 1.Ch. 6·99 | 7·01 | 1.Ch.4·60 | 4·66 | +2·35 | +4·59 | +0·169 | +1·24 | |
| | 2.Ch. 7·02 | | 2.Co.5·21 | 5·36 | | | | | |
| | 3.Co. 9·95 | 9·95 | | | | | | | |
| 1 | 1.Ch. 7·64 | 7·64 | 1.Ch.4·58 | 4·66 | +2·98 | +5·34 | +0·214 | +1·44 | |
| | 2.Co.10·70 | 10·70 | 2.Co.5·34 | 5·36 | | | | | |
| 2 | 1.Ch. 7·52 | 7·52 | 1.Ch.4·66 | 4·66 | +2·86 | +4·08 | +0·206 | +1·10 | 10·59 |
| | 2.Co. 9·47 | 9·44 | 2.Co.5·37 | 5·36 | | | | | (2·5 |
| | 3.Co. 9·42 | | | | | | | | metres) |
| 3 | 1.Ch. 7·55 | 7·54 | 1.Ch.4·73 | 4·66 | +2·88 | +4·24 | +0·207 | +1·15 | |
| | 2.Ch. 7·52 | | 2.Co.5·34 | 5·36 | | | | | |
| | 3.Co. 9·60 | 9·60 | | | | | | | |
| 4 | 1.Ch. 7·46 | 7·46 | 1.Ch.4·65 | 4·66 | +2·80 | +3·43 | +0·201 | +0·93 | |
| | 2.Co. 8·79 | 8·79 | Co. | 5·36 | | | | | |
| 5 | 1.Ch. 7·22 | 7·22 | 1.Ch.4·71 | 4·66 | +2·56 | +2·56 | +0·184 | +0·69 | 10·52 |
| | 2.Co. 7·77 | 7·92 | 2.Co.5·50 | 5·36 | | | | | |
| | 3.Co. 8·08 | | | | | | | | |
| 6 | 1.Ch. 6·88 | 6·88 | 1.Ch.4·65 | 4·66 | +2·22 | +2·16 | +0·160 | +0·58 | |
| | 2.Co. 7·52 | 7·52 | 2.Co.5·40 | 5·36 | | | | | |
| 7 | 1.Ch. 6·49 | 6·49 | 1.Ch.4·68 | 4·66 | +1·83 | +2·02 | +0·132 | +0·55 | 9·91 |
| | 2.Co. 7·39 | 7·39 | Co. | 5·36 | | | | | |

## TABLE XII.

Off Hunterston Perch, 18/7/27. 10.50 a.m.–3.50 p.m. All sunshine. Water sample contained about 200 chains per c.c., mostly Skeletonema, Thalassiosira, and Chætoceros. Average number of cells per chain, 5.

$$\text{Initial } O_2 \text{ content—}\left.\begin{matrix}1.7{\cdot}09\\2.7{\cdot}07\\3.7{\cdot}08\end{matrix}\right\} 7{\cdot}08.$$

| Depth in metres. | Light. | | Dark. | | Total $O_2$ produced. | $O_2$ produced by $10^6$ diatoms. |
|---|---|---|---|---|---|---|
| 0 | 1.7·31<br>2.7·25 | 7·28 | 1.7·08 | 7·10 | +0·18 | 0·18 |
| ½ | 1.7·49<br>2.7·49 | 7·49 | 1.7·08 | 7·10 | +0·39 | 0·39 |
| 1 | 1.7·51<br>2.7·54 | 7·53 | 1.7·10 | 7·10 | +0·43 | 0·43 |
| 2 | 1.7·53<br>2.7·53 | 7·53 | 1.7·09 | 7·10 | +0·43 | 0·43 |
| 4 | 1.7·45<br>2.7·44 | 7·44 | 1.7·04 | 7·10 | +0·34 | 0·34 |
| 6 | 1.7·30<br>2.7·33 | 7·31 | 1.7·11 | 7·10 | +0·21 | 0·21 |
| 8 | 1.7·26<br>2.7·26 | 7·26 | 1.7·12 | 7·10 | +0·16 | 0·16 |
| 10 | 1.7·21<br>2.7·16 | 7·18 | 1.7·12 | 7·10 | +0·08 | 0·08 |
| 12 | 1.7·18<br>2.7·20 | 7·19 | 1.7·10 | 7·10 | +0·09 | 0·09 |
| 15 | 1.7·15<br>2.7·13 | 7·14 | 1.7·15 | 7·10 | +0·04 | 0·04 |

## TABLE XIII.

### LIGHT INTENSITY.

mg. Oxalic Acid decomposed.

| Time. | 9–10/6/27. | 28/6/27. | 29/11/27. | 9/11/27. | 7/12/27. |
|---|---|---|---|---|---|
| 12 midnight–3 a.m. | 1·0 | 0 | 0 | 0 | 0 |
| 3 a.m.–6 a.m. | 77·2 | 10·7 | 0 | 0 | 0 |
| 6 a.m.–9 a.m. | 191·7 | 97·8 | 8·5 | 11·8 | 0·7 |
| 9 a.m.–12 noon | 333·4 | 119·8 | 113·0 | 89·2 | 12·5 |
| 12 noon–3 p.m. | 390·4 | 94·7 | 123·6 | 102·0 | 10·4 |
| 3 p.m.–6 p.m. | 285·3 | 39·9 | 4·5 | 2·6 | 1·0 |
| 6 p.m.–9 p.m. | 70·0 | 12·0 | 0 | 0 | 0 |
| 9 p.m.–12 midnight | 0·5 | 0·7 | 0 | 0 | 0 |

# Arthur Everett Shipley.

By the death of Sir Arthur Shipley, G.B.E., F.R.S., Master of Christ's College, Cambridge, and, from June, 1906, to June, 1927, Chairman of the Council of the Marine Biological Association, the Association has lost one of its most active and enthusiastic supporters and one who in recent years has contributed largely to its success. His clear judgment, his firm faith in scientific method as a chief instrument in human progress, and his ready wit, combined with a considerable knowledge of administration, made him an excellent Chairman of a Council composed both of scientific men and of men of business. His wide influence outside the usual scientific circles was also a great asset to the Association, and was especially valuable at those times when it was necessary to appeal for funds for the extension of the buildings at Plymouth.

To the Staff at the Laboratory the late Chairman was a kind and considerate friend, always anxious to help their work in every possible way. Realising that the practical applications of science must always depend upon the fruit of research into fundamental problems, it was ever his aim that such problems should receive their due share of attention. This broad-minded and helpful attitude made us look forward, with satisfaction and pleasure, to his frequent visits to Plymouth.

Sir Arthur Shipley's scientific interests were very wide, and as a zoologist he was attracted to many groups of the animal kingdom. He had a special fondness for marine animals, and this, no doubt, led him to take such an active part in the work of the Laboratory. He died on September 22nd, 1927, at the Master's Lodge, Christ's College, at the age of sixty-six.

E. J. A.

# Walter Campbell De Morgan.

Many of those who have worked at the Plymouth Laboratory during the last twenty years will learn with regret that Mr. W. C. De Morgan died in the West of Ireland on October 13th, 1927, in his seventy-sixth year.

On his retirement from the Indian Public Works Department De Morgan took up the serious study of Zoology, a subject in which he had always been interested. He attended the general course in that subject given by the late Professor E. A. Minchin at University College, London, including the practical laboratory work.

After completing this preliminary training in the subject, he came to Plymouth in February, 1906, and commenced research work at the Marine Biological Laboratory. His original intention was to remain in Plymouth for a few weeks only, in order to collect material which he could take back with him to London and investigate there. But he was so attracted by the study of the living marine animals that from that date until April, 1926, he spent the greater part of each year at Plymouth and worked at the Laboratory as keenly and diligently as any member of the professional staff. He was an excellent observer, and acquired great skill as a draughtsman in representing the animals he was studying. His first published paper (1910*a*), written in co-operation with the late G. Harold Drew, which described some experimental work on the scallop, *Pecten maximus*, was really an attempt to study the fundamental problems at the back of cancer research, as was also a later paper (1914*b*) with the same collaborator. During this period he was also working at crustacea, and some of his results were recorded in the paper (1910*b*) on species of the burrowing prawn Upogebia.

De Morgan then turned to the group of Echinoderms (sea-urchins), and what is perhaps his best-known work is recorded in the series of papers with Shearer and Fuchs on the hybridization of Echinoids (1911, 1912, 1914*a*), the last one being published in the Philosophical Transactions of the Royal Society. The larger portion of the experimental work on which these papers were written was done by him, as were also many of the illustrations.

During the war period and after it he was working on marine protozoa. This work he did quite independently, and the brilliant series of papers recording it (1924, 1925, 1926), with the excellent drawings with which he illustrated them, are a really remarkable testimony to his great powers of work, his skill, and his ability, more especially when it is remembered that they were written when he was about seventy years of age and at the end of a long and busy life.

De Morgan was a man of charming and vigorous personality, and it was a great pleasure to have him associated with the Laboratory. His interests were very wide, he was a great reader on almost every subject, and kept up his interest in the classics to the last. Homer was his special study and he read him practically every day. His engineering experience had been very varied and was often of use to him, as well as to the Laboratory in general. His disposition was kindly and helpful, and all those who came in contact with him feel themselves the poorer by the loss of an exceptionally broad-minded and sympathetic friend.

E. J. A.

## PAPERS BY MR. W. DE MORGAN.

1910*a*. Drew, G. H., and De Morgan, W. The Origin and Formation of Fibrous Tissue produced as a Reaction to Injury in *Pecten maximus*. (Quart. Journ. Micro. Sci., Vol. LV, 1910, pp. 595–610.)

1910*b*. De Morgan, W. On the Species *Upogebia stellata* and *Gebia deltura*. (Journ. Mar. Biol. Assoc., Vol. VIII, 1910, pp. 475–478.)

1911. Shearer, C., De Morgan, W., and Fuchs, H. M. Preliminary Notice on the Experimental Hybridization of Echinoids. (Journ. Mar. Biol. Assoc., Vol. IX, 1911, pp. 121–141.)

1912. Shearer, C., De Morgan, W., and Fuchs, H. M. On Paternal Characters in Echinoid Hybrids. (Quart. Journ. Micr. Sci., Vol. LVIII, 1912, pp. 337–352.)

1913. De Morgan, W. The Echinoderms collected by the *Huxley* from the North Side of the Bay of Biscay in August, 1906. (Journ. Mar. Biol. Assoc., Vol. IX, 1913, pp. 530–541.)

1914*a*. Shearer, C., De Morgan, W., and Fuchs, H. M. On the Experimental Hybridization of Echinoids. (Phil. Trans. Roy. Soc., Lond., Ser. B, Vol. CCIV, 1914, pp. 255–362.)

1914*b*. De Morgan, W., and Drew, G. H. A Study of the Restitution Masses formed by the Dissociated Cells of the Hydroids, *Antennularia ramosa* and *A. antennina*. (Journ. Mar. Biol. Assoc., Vol. X, 1914, pp. 440–463.)

1924. De Morgan, W. Foettingeria actiniarum (parasitic in Anemones). (Quart. Journ. Micr. Sci., Vol. LXVIII, 1924, pp. 343–360.)

1925. De Morgan, W. Some Marine Ciliates living in the Laboratory Tanks at Plymouth, with a Description of a New Species, *Holophrya coronata*. (Journ. Mar. Biol. Assoc., Vol. XIII, 1925, pp. 600–658.)

1926. De Morgan, W. Further Observations on Marine Ciliates living in the Laboratory Tanks at Plymouth. (Journ. Mar. Biol. Assoc., Vol. XIV, 1926, pp. 23–53.)

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All correspondence should be addressed to the Director, The Laboratory, Plymouth.

# OBJECTS

## OF THE

# Marine Biological Association

## OF THE UNITED KINGDOM.

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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,
nd amongst the speakers in support of the project were the late Duke of ARGYLL, the
ate Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr.
ARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY,
he late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combina-
ion of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons,
re specially interested in the great sea fisheries of the United Kingdom. It is universally
dmitted that our knowledge of the habits and conditions of life of sea fishes is very small,
nd insufficient to enable either the practical fisherman or the Legislature to take measures
alculated to ensure to the country the greatest return from the "harvest of the sea."
aturalists are, on the other hand, anxious to push further our knowledge of marine life
nd its conditions. Hence the Association has erected at Plymouth a thoroughly efficient
aboratory, where naturalists may study the history of marine animals and plants in general,
nd where researches on food-fishes and molluscs may be carried out with the best
ppliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000,
nd from that time until 1926 a sum of over £6,500 has been spent on additional buildings.
hroughout this period investigations, practical and scientific, have been constantly pursued
t Plymouth. Practical investigations upon matters connected with sea-fishing are carried on
nder the direction of the Council; in addition, naturalists from England and from abroad
ave come to the Laboratory, to carry on their own independent researches, and have made
aluable additions to zoological and botanical science, at the expense of a small rent for the
se of a working table in the Laboratory and other appliances. The number of naturalists
ho can be employed by the Association in special investigations on fishery questions, and
efinitely retained for the purpose of carrying on those researches throughout the year,
ust depend on the funds subscribed by private individuals and public bodies for the
urpose. The first charges on the revenue of the Association are the working of the sea-
ater circulation in the tanks, stocking the tanks with fish and feeding the latter, the
ayment of servants and fishermen, the maintenance of a research steamer and other
ollecting boats, and the salaries of the Resident Director and Staff. At the commencement
f 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
national in character and constitution, and its affairs are conducted by a representative
ouncil, by an Honorary Secretary and an Honorary Treasurer, without any charge upon
s funds, so that the whole of the subscriptions and donations received are devoted
bsolutely to the support of the Laboratory and the prosecution of researches by aid of
s appliances. The reader is referred to page 4 of the Cover for information as to
embership of the Association.