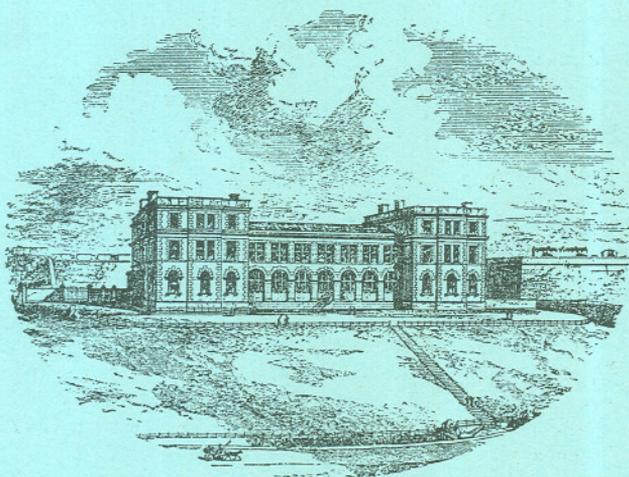


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The Vertical Distribution of Marine Macroplankton.
 V. The Distribution of Animals Caught in the
 Ring-trawl in the Daytime in the Plymouth Area.

By

F. S. Russell, D.S.C., B.A.,

Assistant Naturalist at the Plymouth Laboratory.

With 11 Figures in the Text.

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INTRODUCTION.

BETWEEN April 2nd and August 6th, 1925, a number of serial collections were made with the ring-trawl to determine the vertical distribution of the pelagic young of teleostean fish. The details of the young fish distribution have already been published (23), and it is with the remaining plankton animals taken in these collections that this paper deals.

I should like to take this opportunity of expressing my thanks to Dr. E. J. Allen, F.R.S., and other members of the staff of this Laboratory, for much helpful criticism and advice, especially to Dr. M. V. Lebour for assistance in the identification of many species. I also wish to thank Capt. V. Lord and the crew of the s.s. *Salpa* for their unflinching help when collecting at sea.

METHODS OF COLLECTING.

The details of methods of fishing have been given in the previous paper (23, p. 102). It is only necessary to repeat here that the net employed was a non-closing, stramin ring-trawl (diameter at mouth, 2 metres; length, 6 metres), with depth-recorder attached. All the stations were made in depths of 50 metres or over. The positions of stations, details of fishing times, weather conditions, etc., are to be found in the Appendix to the above-mentioned paper (23, pp. 145-151). Results of one station made with a closing metre-net of silk (mesh, 40 strands to the inch; length, 2 metres 60 cm.) are also given here.

POSSIBLE ERROR DUE TO THE EMPLOYMENT OF A
NON-CLOSING NET.

As stated above, the net employed for these researches was not fitted with a closing device. It is therefore necessary to obtain some idea of the error that is likely to be met with in the catches from the deeper layers due to the organisms that must be caught as the net is being hauled to the surface. I have accordingly attempted to estimate the possible errors for the catches made on one day, July 16th, 1925. On this occasion there were large numbers of *Calanus finmarchicus* taken, and it is for this species that I have made the estimations: on this date also the depths at which the net fished and times taken to haul it in were most suitable for making the calculations as simple as possible.

In Fig. 1 I have given the percentage vertical distribution of *Calanus* on July 16th as obtained without applying any corrections for possible

errors (unbroken lines) : in the same figure I have also superimposed the vertical distribution that is given when corrections have been made for errors due to the non-closing of the net (broken lines). It can at once be seen that the uncorrected distribution diagram differs slightly from that obtained after the application of corrections in that, as is to be expected, the corrected percentages in the upper layers are slightly larger than the uncorrected, and, conversely, slightly smaller in the deeper layers. At the same time it is also obvious that the differences are in no degree great

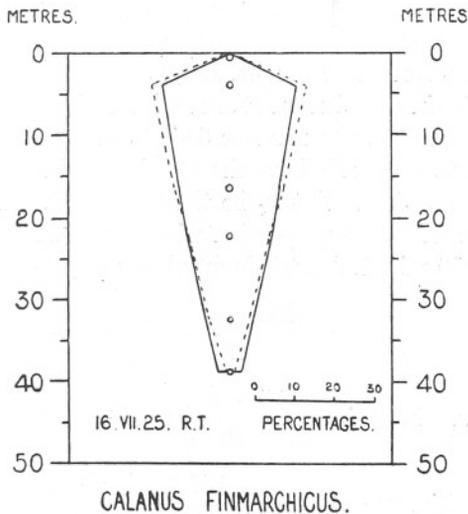


FIG. 1.—Diagram showing percentage vertical distribution of *Calanus finmarchicus* on July 16th, 1925. In this figure the unbroken line (—) represents the vertical distribution, as shown by the actual catches, and the broken line (...) the same after correction for possible error due to the employment of a non-closing net.

enough to alter the true significance of the vertical distribution, as shown by uncorrected figures. To correct all catches for all species would, therefore, involve unnecessary waste of time and labour ; in consequence all the distribution diagrams and tables are composed of the actual catches made by the net, and I think we can safely conclude that any errors due to the non-closing of the net are for our purposes negligible, at any rate when the animals are fairly numerous.

I give below the method by which the corrections given in Fig. 1 were obtained : in this case it was necessary to assume that the curves between each depth point on a distribution diagram are straight lines.

ACTUAL UNCORRECTED RESULTS.

Average depth at which hauls were made, in metres.	Approximate time taken to haul in net, in minutes.	Total catches of Calanus caught in 10 minute hauls plus time taken to reach the surface.	
Surface	0 minutes	157	0.9%
4	$\frac{1}{4}$ "	5450	33.4%
16.5	1 "	4140	25.4%
22	$1\frac{1}{2}$ "	3420	21.1%
32	2 "	2070	12.7%
38	$2\frac{1}{2}$ "	1040	6.4%

At the surface the number caught, 157, is correct, because the haul is exactly 10 minutes in duration and the net immediately leaves the water.

At 4 metres, however, the number 5450 is incorrect, the net having fished for $\frac{1}{4}$ minute over and above the 10 minutes, in the layers between 4 metres and the surface. Let x_4 be the true catch. If the number of Calanus increase in direct proportion with depth between the surface and 4 metres, a 10 minutes' catch in any layer above 4 metres would be

$$\frac{157 + x_4}{2}$$

$$\therefore \text{ in } \frac{1}{4} \text{ minute } \frac{157 + x_4}{2 \times 10 \times 4} \text{ would be taken.}$$

$$\text{Now } x_4 = 5450 - \left(\frac{157 + x_4}{80} \right) = 5381.$$

The number caught, therefore, between the surface and 4 metres as the net is hauled up is

$$5450 - 5381 = 69.$$

Again, let $x_{16.5}$ represent the true catch obtained at 16.5 metres. The net took 1 minute to reach the surface; it was, then, fishing approximately for $\frac{3}{4}$ minute between 16.5 and 4 metres, and for $\frac{1}{4}$ minute between 4 metres and the surface.

We have already found that in $\frac{1}{4}$ minute between 4 metres and the surface 69 specimens would be caught; it is necessary, therefore, to find now how many would be taken between 16.5 and 4 metres in $\frac{3}{4}$ minute.

$$\text{This will be } \left(\frac{5381 + x_{16.5}}{2 \times 10} \right)^{\frac{3}{4}}$$

$$\therefore x_{16.5} = 4140 - \left(\frac{5381 + x_{16.5}}{2 \times 10} \right)^{\frac{3}{4}} - 69 = 3729.$$

Let x_{22} be the true catch at 22 metres: the net took $1\frac{1}{2}$ minutes to reach the surface; say—for convenience— $\frac{1}{2}$ minute between 22 and 16.5 m. and 1 minute between 16.5 m. and the surface. Between 16.5 m. and the surface we saw from the previous haul that in 1 minute 4140—3729=411 specimens were caught.

Now between 22 and 16.5 m. in $\frac{1}{2}$ minute $\left(\frac{3729+x_{22}}{2 \times 10}\right) \frac{1}{2}$ would be taken

$$\therefore x_{22} = 3420 - \left(\frac{3729+x_{22}}{2 \times 10}\right) \frac{1}{2} - 411 = \mathbf{2845}.$$

Similarly let x_{32} be the correct catch at 32 m., and say that the net on its upward journey took $\frac{1}{2}$ minute from 32–22 m. and $1\frac{1}{2}$ minutes from 22 m. to the surface. Then,

$$x_{32} = 2070 - \left(\frac{2845+x_{32}}{2 \times 10}\right) \frac{1}{2} - (3420-2845) = \mathbf{1389}.$$

Similarly at 38 m., allowing $\frac{1}{2}$ minute to haul from 38 to 32 m., the whole period to the surface being $2\frac{1}{2}$ minutes, we find

$$x_{38} = 1040 - \left(\frac{1389+x_{38}}{2 \times 10}\right) \frac{1}{2} - (2070-1389) = \mathbf{316}.$$

So that the approximate corrected figures will be:—

Surface	157	1.1 %
4 metres	5381	39.0 %
16.5 "	3729	27.1 %
22 "	2845	20.6 %
32 "	1389	10.0 %
38 "	316	2.2 %

FISHING DEPTHS.

The graphic depth-recorder, kindly lent by Admiralty authorities, was employed to obtain the depths at which the net was fishing. The records obtained on April 8th and 29th, May 19th, June 17th, 18th, and 19th, have already been published (**23**, p. 104, and **24**, pp. 392, 393). I give here in Fig. 2 tracings obtained on five further dates, July 1st (i.) and (ii.), 16th, and 29th, and August 6th, 1925.

The average depths for each haul have been obtained by taking the depths at 10 or more equidistant points along each curve and finding the mean. In Station 26, July 29th, after haul Number VI the bucket containing the catch was lost: another haul was therefore taken, but the clock was not wound up, so that the maximum depth of the haul only was recorded, i.e. 31 m. In the tables the average depth of this haul has been put at about 29 metres.

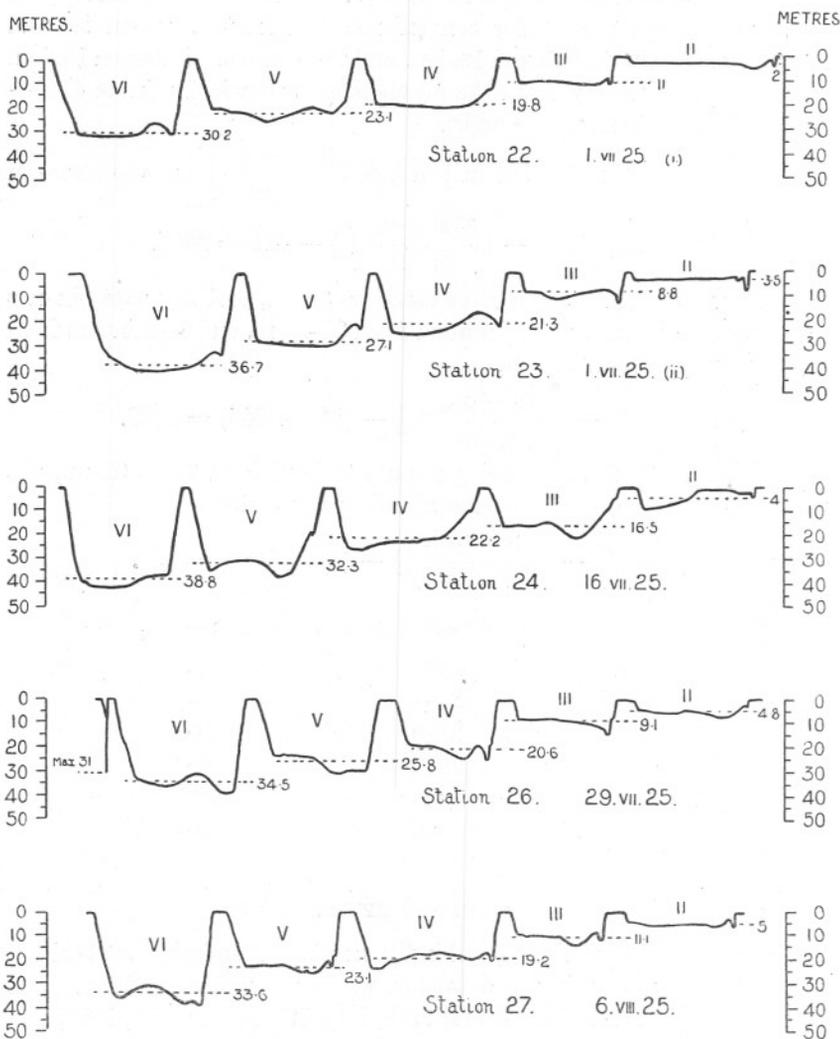


FIG. 2.—Five series of curves, obtained on the dates given, showing the path of the net through the water for each haul. (The surface hauls are not included.) The net enters the water on the right-hand side of each curve. The dotted lines indicate the calculated "average depth." (The differences in the lengths of the curves are due to irregularities in the speed of the recorder clock and not to errors in timing.)

EXAMINATION OF MATERIAL.

Before any sorting was undertaken each catch was placed in a tall measuring jar and the volume noted after being allowed to settle for 24 hours. From each catch were then picked out all species that on

account of their size, or shape, or colour, could be easily distinguished : at the same time those species that were comparatively rare and only occurred in small numbers were picked out as carefully as possible, because the error in sampling might tend to obscure the true distribution of these species when their numbers were so small. The following species were dealt with in the above manner, and all numbers given in the tables for these species are therefore obtained by complete counts :—

Turris pileata, *Cosmetira pilosella*, *Saphenia gracilis*, *Cyanea capillata*, *Aurelia aurita*, *Slabberia halterata*, *Liriope* sp., *Peachia* sp., *Anomalocera Patersoni*, *Caligus rapax*, *Leander* sp. larvæ, *Alpheus ruber* larvæ, *Pontophilus spinosus* larvæ, *Palinurus vulgaris* Phyllosoma larvæ, Pagurid sp. *Glaucothoe* larvæ, *Axius styrhinchus* larvæ, *Nyctiphanes Couchii* adults and young, Mysids, Hyperiid amphipods, *Squilla Desmaresti* Alima larvæ, *Tomopteris helgolandica*, *Pæcilocheetus serpens* larvæ, *Arachnactis* larvæ.

The remaining species were sampled by the method described in a previous publication (22, p. 776), the catch being made up to 5000 c.c. in a wide-mouthed bell-jar and 500 c.c. removed while the mass was being stirred. In a few cases when the catches were unusually small they were only made up to 2500 c.c. and 500 c.c. samples withdrawn, so that $\frac{1}{5}$ instead of $\frac{1}{10}$ of the whole catch was counted. In extremely small catches, such as occurred at times in the surface layers, all the organisms were counted without sampling.

GENERAL RESULTS.

I give in the last column of Tables III and IV (at end of paper) the actual volumes of each catch obtained by allowing them to settle for 24 hours : although very misleading on account of the different-sized animals that compose the collections, these volumes show on the whole the fact that the preponderance of the plankton sampled by the ring-trawl occurred in the deeper layers, the main exceptions being on April 8th and May 19th (i.), when it can be seen that the large surface volumes are caused by swarms of zoeas and megalopas of *Corystes cassivelaunus*. In the last column but one of Tables III and IV are given the total numbers of organisms caught on each occasion, and their percentage vertical distribution is given in Fig. 11, p. 600. These figures show clearly that generally in the daytime, at any rate during the months of May, June, and July, the general mass of the plankton animals sampled by the ring-trawl live in the deeper layers around 25 to 30 metres, and that a gradual lessening in numbers is shown from this depth towards the surface, the upper 5 or 10 metres being very sparsely populated. At the same time there are indications that in early April, and in August under foggy weather conditions, there are nearly

as many organisms to be found close to the surface as in the deeper levels; the number of observations made at these times of the year are, however, too few to warrant one to draw conclusions. Now this impression is, of course, that of the vertical distribution of all the animals together, and is, in fact, the sum of a number of different types of vertical distribution shown by the various individual species.

From the information so far obtained it is not safe to make absolutely definite conclusions, but general indications would appear to give probability to the following statements:—

1. Some species have an optimum depth at which the majority of that species live, while a certain vertical range of distribution is shown within the confines of which the same species more or less keeps. These depths may vary for different aged animals and for the two sexes in the same species.

2. Certain species can be chosen that, when compared, will give a gradual descending series of the region of their maximum abundance. During May, June, and July a marked consistency is shown in the order of this variation of depth distribution, so that from day to day the species exhibit the same differences in the region of their maximal abundance with relation to each other.

3. The actual depths at which the regions of greatest abundance occur may vary for each species from day to day. Fig. 3, for instance, shows that *Calanus finmarchicus*, *Upogebia* larvæ, and *Turris pileata*, had their regions of maximum abundance confined within the limits of 6.5 and 22 metres on May 19th, 11.4 and 34 metres on June 4th, and 3 and 22.5 metres on July 16th, but at the same time the sequence shown by these three species in the order of their depth distribution did not vary.

4. Certain species may exhibit sudden marked changes in the depth of their maximum abundance; *Sagitta bipunctata*, while preferring the deeper layers below 20 or 25 metres in April, May, and June, suddenly appeared more abundantly much nearer the surface at the end of July and beginning of August. Similarly, *Tomopteris helgolandica*, while apparently living very close to the bottom during April, May, and June, like *Sagitta*, came up into the upper water layers at the end of July and beginning of August. The significance of this behaviour is not known. The weather in July and August when the change was apparent was extremely foggy, which very probably may have had an influence: at the same time, with *Tomopteris* at any rate, there seems a possibility that spawning may have been a factor of importance. Many more observations of this kind are required before the behaviour can be understood.

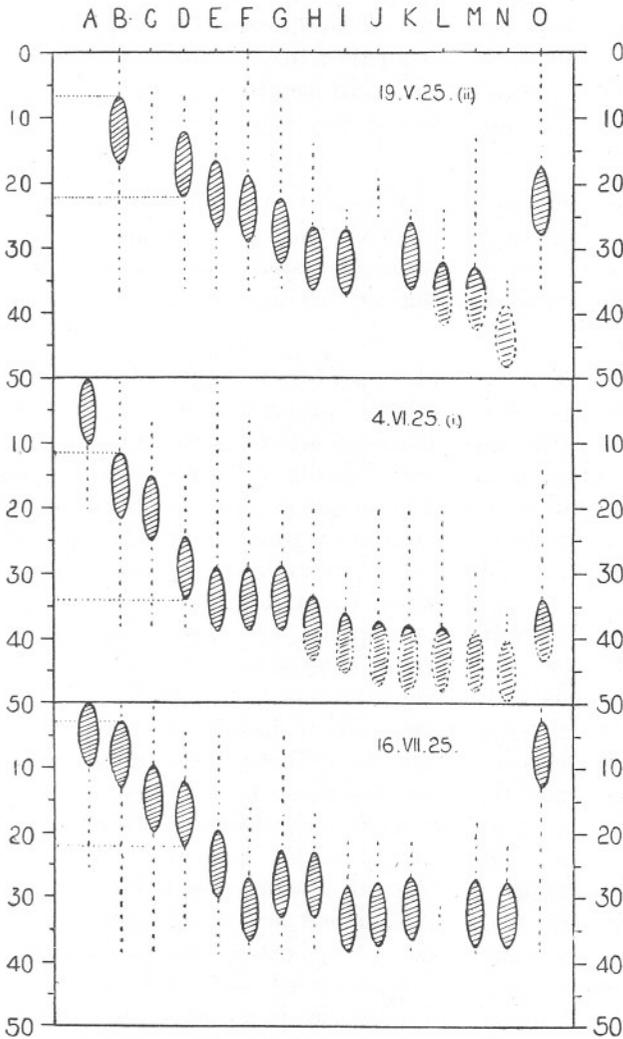


FIG. 3.—Diagram to show the vertical distribution of the undermentioned animals on the three dates given. The shaded ellipses show the region of maximum abundance and the vertical broken lines the total range of vertical distribution for each species. The depths are in metres.

A. *Anomalocera Patersoni*. B. *Calanus finmarchicus*. C. *Upogebia* sp. larvæ.
 D. *Turris pileata*. E. *Porcellana* sp. zoea. F. Galatheid larvæ. G. Pandalid larvæ.
 H. Pagurid larvæ. I. *Cosmetira pilosella*. J. *Candacia armata*. K. Crangonid
 larvæ. L. *Pontophilus spinosus* larvæ. M. *Apherusa* sp. N. *Tomopteris helgo-
 landica*. O. *Sagitta bipunctata*.

5. Other species, such as *Phialidium*, appear very inconsistent in their vertical distribution, being most abundant one day at one depth and the next day at a very different level, without any apparent important change occurring in the external factors. Whether such signifies their indifference to the various physical factors met with at different depths, or whether distribution of food may control their movements remains to be discovered.

6. The majority of the species met with in the ring-trawl collections showed a preference for the layers from about 20 metres downwards in sunny weather, the species that appeared to like the surface and upper highly illumined layers being very few in number.

It is obviously not possible to put forward any scheme to cover broadly the various types of vertical distribution shown by the different species, dealt with in this paper, based on actual depth units, as we have seen that these vary from day to day. In Fig. 3 I have shown diagrammatically the vertical distribution for 15 species on three different days, May 19th, June 4th, and July 16th. In this diagram the vertical range of any one species is given by a broken line, and the region of maximal abundance, as near as it can be estimated, is indicated by a shaded ellipse. From the actual catches of certain species, e.g. *Pontophilus spinosus* larvæ, Crangonid larvæ, etc., it seems permissible to assume that the region of maximal abundance lies below the depth at which the deepest haul was made, and that the upper limits of its distribution alone were sampled: in these cases I have indicated by dotted ellipses the probable depth at which their region of greatest abundance may be located. The diagram, then, shows very strikingly that as one goes deeper so new animals become abundant. I have also inserted in this figure the vertical distribution of *Sagitta bipunctata*, showing the apparent change that occurred in the depth at which it was most abundant between June 4th and July 16th. In a previous publication (25, p. 416) I gave the actual percentage vertical distribution for ten species on June 4th, July 1st, and July 16th. In that diagram I placed certain species in a slightly different order from that given in Fig. 3 of this paper. The species in question were Crangonid larvæ, *Candacia armata*, and *Cosmetira pilosella*; the point is, however, of slight importance, as from the few observations obtained it is difficult to state whether these three species show any difference in their vertical distribution. Careful study of the question points to the fact that Crangonid larvæ probably occur slightly deeper than either *Cosmetira* or *Candacia* when the actual numbers rather than percentages are judged.

Although I have pointed out that one cannot base a scheme for the

vertical distribution of different species on actual depth units, I give below a list showing their vertical distribution with arbitrary depth units inserted, in order to make possible an impression of the distribution of many of the different animals taken in the ring-trawl with relation to each other. It must, however, be firmly understood that these depths are not fixed, and that we are here dealing only with the species captured by the ring-trawl and the various sizes of those species that it samples, for the months, end of April, May, June, July, and beginning of August.

Surface. *Anomalocera Patersoni* (but deeper on August 6th).

Corystes cassivelaunus, late zoeas and megalopas on occasion.

Leander sp. larvæ (as well as in deeper layers).

Abundant below 10 metres. *Calanus finmarchicus*.

„	„	12	„	Upogebia sp. larvæ : <i>Alpheus ruber</i> larvæ ; <i>Squilla Desmaresti</i> alima larvæ.
„	„	15	„	<i>Turris pileata</i> : <i>Axius styrhinchus</i> larvæ.
„	„	18	„	Porcellana sp. zoea.
„	„	20	„	<i>Caligus rapax</i> ; Galatheid sp. larvæ : Pandalid larvæ ; <i>Callianassa subterranea</i> larvæ.
„	„	25	„	<i>Saphenia gracilis</i> ; <i>Cosmetira pilosella</i> ; <i>Sagitta bipunctata</i> (until end of July and beginning of August) ; <i>Candacia</i> <i>armata</i> ; <i>Apherusa</i> sp. ; Pagurid larvæ.
„	„	30	„	<i>Steenstrupia rubra</i> ; <i>Tomopteris helgo-</i> <i>landica</i> (until end of July and beginning of August) ; Crangonid larvæ ; <i>Ponto-</i> <i>philus spinosus</i> larvæ : <i>Palinurus vul-</i> <i>garis</i> phyllosoma larvæ ; Galatheid post-larvæ ; Upogebia post-larvæ ; Pa- gurid glaucothoë larvæ.

Occurring irregularly at all depths : *Phialidium* sp. ; *Obelia* sp. ;
Pleurobrachia pileus (?).

I would emphasize again that the above scheme is not to be taken too literally, as it is obviously extremely difficult to draw hard and fast lines between the distributions of many species ; it is, however, in the writer's opinion, a fairly correct impression gained by repeated sorting of material and careful perusal of the figures. There are, of course, many species not mentioned above occurring in the catches, but generally in too small numbers to draw conclusions from. Crab zoeas also are not included, as

they comprise such a variety of species; identification of certain species, e.g. *Ebalia*, has shown that the various species that go to make up the mass of crab zoeas have different vertical distributions, as, indeed, is only to be expected.

No attempt is made in this paper to correlate results with the factors that may control the vertical distribution of the animals dealt with. It is merely intended as a description of the actual distribution exhibited by the various species in this region on certain days between April and August as revealed by catches obtained with the ring-trawl. Although containing apparently a very large mass of information, it must be remembered that for each species the observations are few, being confined mostly to two or three in each month. In 1926 a similar series of observations has been made, and it may be possible that with the combined results of the two years, 1925 and 1926, correlations may make themselves apparent.

One or two points are indicated, the evidence for which may or may not, as yet, be sufficient to be significant. It is noticeable that in many cases the deeper an animal normally lives the less change it seems to show in its vertical distribution under changing seasonal and weather conditions. As an example we may cite *Calanus finmarchicus*, *Upogebia* larvæ, Pandalid larvæ, *Cosmetira pilosella*, and Crangonid larvæ. While *Calanus* and *Upogebia* larvæ show quite distinct alterations in level under sunny or dull conditions (Figs. 5 and 9), Pandalid larvæ show a much less marked change (Fig. 9), and *Cosmetira* and Crangonid larvæ show apparently no alterations in level (Figs. 4 and 9). The occurrence of many species at the surface on May 19th, when a large swarm of *Corystes megalopas* was in the upper layers, is also of interest.

In the succeeding pages the different species are dealt with in detail, and short notes are also appended on the seasonal distribution of certain species. Taken on the whole the ring-trawl collected plankton reached a very high value on May 19th, and was then somewhat scarce until, towards the end of July, there was a further great increase in numbers, due especially to large swarms of *Calanus* and *Sagitta*. It is interesting that these two peaks in the abundance of plankton appear slightly before two small increases in the phosphate content in the summer of that year.

In order to save space the actual figures for each species on the different days are given in the Tables 2, 3, and 4 at the end of the paper. The species caught in the metre net (Table 2) are arranged roughly in the order in which they become abundant as the net fishes deeper, and the Table thus emphasizes the gradual appearance of certain species in the lower layers, which were absent nearer the surface.

CŒLEENTERATA.

ANTHOMEDUSÆ.

STEENSTRUPIA RUBRA Forbes.

This medusa did not appear in the collections until June. From then onwards it was not common; but occurred as follows:—

June	4th,	20 individuals	at 31·8 metres.
	„	17th, 10	„ 48·8 „
	„	18th, 6	„ 31·4 „
	„	19th, 9	„ 23·3 „
	July	16th, 2	at 22·2 m. : 1 at 32·3 m. : and 1 at 38·8 m.

From the above figures it would appear that *Steenstrupia* was a deep-living member of the plankton in this region, occurring always below 20 metres and generally below 30 metres, and being absent in the layers above these depths. On July 15th and 16th, 1924, this species was also taken mostly below 20 metres in the daytime, none being caught above a depth of 18 m. (22, p. 781). The fact that in July, 1924, the numbers increased at night, a phenomenon repeated during experiments made on two nights in June, 1925 (not yet published), would suggest that generally they were mostly distributed in deeper layers than those sampled by the net in the daytime.

Seasonal distribution. In Tables 3 and 4 it can be seen that none of these medusæ were captured until June 4th, and that after July 1st no more were taken. There is, however, risk in drawing conclusions for this species, because, as indicated above, it is possible that they live mostly in the deeper unsampled layers.

SLABBERIA HALTERATA Forbes.

This medusa occurred only once, on June 19th, when one specimen was caught in the haul at 23·3 metres.

STOMATOCA DINEMA L. Agassiz.

Only seven specimens of this medusa were obtained. On June 17th, one at 29·8 m.; on June 19th, two at 23·3 m.; on July 1st, one at 21·3 m. and one at 27·1 m.; on July 16th, one at 4 m.; and on July 29th, one at 29 metres. This species would appear then usually to have preferred the layers below 20 metres.

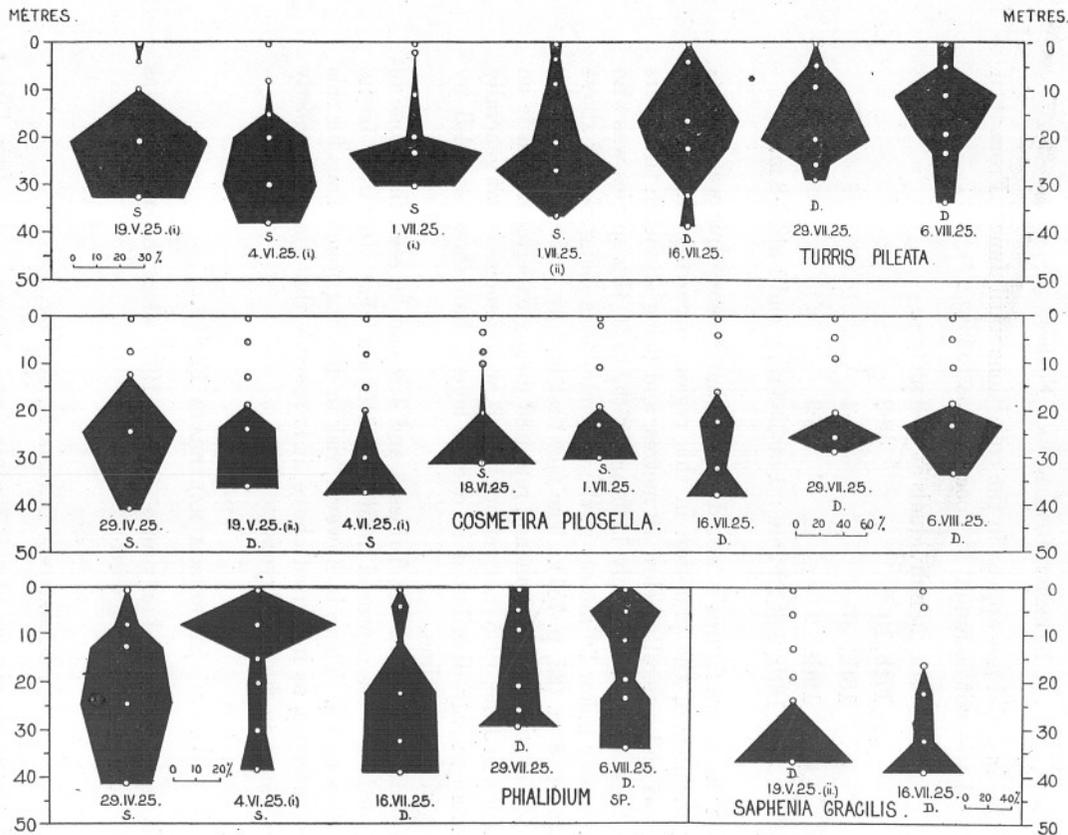


FIG. 4.—The percentage vertical distribution of *Turris pileata*, *Cosmetira pilosella*, *Phialidium* sp., and *Saphenia gracilis* on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull. Note that the percentage scale for *Saphenia* and *Cosmetira* is half that of the other two species.

TURRIS PILEATA (Forsk.)

Turris pileata became abundant in the plankton in May.

From then until July 1st its region of maximum abundance on sunny days, at position A, lay between 20 and 30 metres. It was comparatively rare in the hauls above 20 metres. At the Station L4, however, which is about 4 miles nearer the shore, they were slightly higher in the water on May 19th, June 4th, and July 1st.

On July 16th and 29th, and August 6th, they were considerably higher in the water at position A than earlier in the year (Fig. 4). This may have been correlated with the fact that on these days the weather was very dull and foggy. On June 19th, 1925, nearer L4 than A, the vertical distribution was almost identical with that on July 15th and 16th, 1924. (See 25, Fig. 6, p. 432, and 22, Fig. 2, p. 783.)

Seasonal distribution. *Turris* was present on almost all the days on which collections were made, but was most abundant in May, June, and July and the beginning of August. The largest catches occurred on May 19th at L4, but on the same day at A the numbers taken were very much smaller, showing that at L4 a swarm was probably encountered. The next largest catch occurred on July 1st.

BOUGAINVILLEA sp.

When present these medusæ were very rarely caught in the water layers above 18 metres, the region of maximum abundance lying at about 25 to 30 metres on June 4th and July 16th, on which days it was most numerous.

LEPTOMEDUSÆ.

OBELIA sp.

The occurrence of this species, probably *Obelia nigra*, was somewhat irregular. On the occasions on which it was present it did not appear to show any definite preference for different levels in its vertical distribution. Although from the ring-trawl collections it would appear to have been most numerous below 20 metres, on July 16th, when the ring-trawl catches showed the greatest number at 22.2 metres, hauls in the same locality with the silk closing metre net showed the largest catch at 6.5 metres, indicating that the species is not consistent in its depth distribution, unless there was size selection by the two nets, the catches of the ring-trawl representing the largest medusæ. This, however, was unfortunately not noticed at the time, and the samples have since been thrown away.

Seasonal distribution. Swarms were apparently met with on April 22nd, July 16th and 29th; on the remaining days on which collections were made few or none were caught in the ring-trawl.

PHIALIDIUM sp.

The vertical distribution of this species, probably mostly *P. hemisphericum*, was very irregular, the region of maximum abundance lying sometimes up at the 10-metre level and at other times considerably deeper (Fig. 4). Like *Obelia*, this species was shown to be most abundant below 20 metres with the ring-trawl on July 16th, and yet the largest catch occurred at 2.7 metres with the silk metre net.

Seasonal distribution. *Phialidium* was present in most catches throughout the period of collecting, but there was a very pronounced maximum of abundance on July 16th, and the species was still very numerous on July 29th and August 6th.

COSMETIRA PILOSELLA Hartlaub.

This medusa is evidently a deep-living member of the plankton community in this locality in the daytime. Its region of maximum abundance always lay below the 20-metre level and generally deeper (Fig. 4). The type of distribution shown by this species, which apparently lives within a very narrow vertical range, has been discussed in a previous paper (25, pp. 423 and 428). So consistent is this form in its vertical distribution and so rarely is it taken in the layers above 20 metres, and then only in very small numbers, that its existence in fair abundance in a day time catch in offshore waters would seem to be a very reliable indication that the net has been fishing below 20 metres. On account of its very distinctive appearance and large size it gives a very characteristic aspect to collections from the deeper levels.

Seasonal distribution. *Cosmetira* was present throughout the collecting period, except on April 2nd and 8th.

SAPHENIA GRACILIS (Forbes and Goodsir).

This medusa was never very abundant; the majority were, however, caught from below 20 metres (Fig. 4).

Seasonal distribution. *Saphenia* was present in small numbers in almost all the collections between April and August; the largest catch occurred on July 16th.

ÆQUOREA FORSKALEA Péron and Lesueur.

Very young representatives of this species, between $\frac{1}{4}$ and $\frac{3}{4}$ -inch in diameter, occurred occasionally. When present they were always taken from below 20 metres.

TRACHYMEDUSÆ.

AGLANTHA ROSEA Browne.

This species only occurred on two days, April 8th, when one was caught at 16.5 m. and one at 25.3 m. ; and on April 22nd at 22.1 metres.

LIRIOPE sp.

This species appeared only in the catches on August 6th, when 8 specimens were captured at 11.1 m. ; one at 19.2 m., and one at 23.1 m. None were taken either at the surface or at 5 metres.

SCYPHOMEDUSÆ.

CYANEA CAPILLATA Eschscholtz.

Small specimens of *Cyanea* between $\frac{1}{2}$ and $3\frac{1}{2}$ inches in diameter were caught occasionally. They usually came from below 15 metres.

CTENOPHORA.

PLEUROBRACHIA PILEUS Fab.

This ctenophore when present appeared rather inconsistent in its vertical distribution, being more or less irregularly distributed from the surface downwards. On the day on which most were caught, July 1st, the region of maximum abundance lay apparently between the surface and 15 metres.

Seasonal distribution. While being very scarce up till May 19th, from June 4th onwards *Pleurobrachia* was relatively abundant.

ZOANTHARIA.

PEACHIA sp. larvæ.

These larval anemones were not common in the collections. Their distribution is probably governed by the medusæ that carry them. It is a curious fact, however, that on May 19th 10 occurred in the surface haul, but there were no medusæ except for 5 *Turris*. There was, however, at the time a very large shoal of *Corystes* zoeas at the surface, which seemed to attract many other species to the surface.

ARACHNACTIS BOURNEI Fowl.

These, the larvæ of *Cerianthus Lloydii* Gosse, occurred on two or three occasions generally below 20 metres.

ANNELIDA.

POLYCHÆTA.

TOMOPTERIS HELGOLANDICA Greef.

Tomopteris was frequent at times in the collections. Individuals varied in size from about 4 mm. upwards in length. McIntosh, in a recent paper (19), discusses the specificity of the small Tomopteris found in the North Sea. These forms, less than 12 mm. in length, are characterised by the possession of a pair of small setigerous frontal cirri in front of the pair normally present in the full-grown *T. helgolandica*; in all other respects they apparently accurately resemble this latter species. McIntosh quotes Carpenter and Claparède, who state that the young forms of *T. helgolandica* possess this additional pair of small cirri, the setigerous portions of which are thrown off when the development of the caudal region takes place, and the tubercle remaining gradually disappears. McIntosh says: "Some of the small forms, again, which were placed as undisputed examples of *T. Catherina* (*T. helgolandica*), presented a knob or stump on the site of the first cirrus, so that the remarks of Carpenter and Claparède rest on fact, viz. that the first cirrus may occasionally be removed, though further investigations are necessary." McIntosh is, however, inclined to identify this small form with *T. kefersteini* of Greef, and, having seen an ovigerous female with two pairs of cirri, says, "On the whole, the evidence leans to the separation of *T. kefersteini* up to date, and it is a form widely distributed in European waters."

When discussing the vertical distribution it is necessary to know whether two species are being dealt with. I have accordingly examined a large number of Tomopteris with the following result:—

With two pairs of cirri, ca. 3–10 mm. long	163
With knob on site of 1st cirrus, 10 mm. and over	38
Without first cirrus or knob, over 10 mm.	650

In view of the fact that I have never seen a specimen less than about 10 mm. in length without the additional pair of cirri, and that I have found so many carrying small knobs or tubercles, indicating that the cirrus is caducous, I have regarded all individuals as belonging to one species, *Tomopteris helgolandica* Greef. Malaquin and Carin regard it as characteristic of many young forms to possess this first pair of cirri which are larval characters only in many species. They say (20, p. 4): "L'organe est rudimentaire et il manque chez la forme adulte d'un certain nombre d'espèces." And again (p. 18): "D'autres caractères ne sont

applicables qu'à des individus âgés, par exemple la présence ou l'absence de la première paire d'appendices sétigères, . . . En effet, si le Tomoptère étudié est suffisamment jeune on observa la première paire d'appendices sétigères, même si le type adult n'en comporte pas."

I only obtained Tomopteris in abundance, in the daytime, on July 16th and 29th and August 6th : on all other occasions it occurred either singly or in very small numbers ; most, however, were taken below 20 metres. On July 16th, when they were numerous, the majority also occurred below 20 metres, the maximum catch being at 32 metres. On July 29th the maximum was at 29 m. ; the water below this depth was, however, not sampled : on this occasion Tomopteris was far more numerous also in the upper layers, above 20 metres, than previously (Fig. 5). It was noteworthy that the catch at 29 metres contained many very small specimens. On August 6th they were abundant at all depths from 33.6 metres up to 5 metres, but only one was captured right at the surface.

From an examination of these day results one would conclude that until July 16th Tomopteris was not abundant in the Plymouth region at all. On the nights of June 17th-18th and 18th-19th, however, similar series of observations were made, with the following results :—

JUNE 17th-18th.		JUNE 18th-19th.	
10.37 p.m.-12.46 a.m.		10.31 p.m.-12.33 a.m.	
<i>Surface</i>	24	<i>Surface</i>	3
<i>11.2 m.</i>	99	<i>5.2 m.</i>	49
<i>23</i> ,,	63	<i>12.2</i> ,,	85
<i>26</i> ,,	12	<i>16.6</i> ,,	61
<i>29</i> ,,	13	<i>20.7</i> ,,	49
		<i>25.8</i> ,,	33

Thus, while on any day between April 2nd and July 16th the total of six catches never exceeded 34 (i. vii. 25 (i.)) in the daylight, on two nights in the middle of June the total numbers caught were 211 (5 hauls only) and 280. These two catches, then, represent the same population as the 252 caught on July 16th, 300 on July 29th, and 290 on August 6th. This is somewhat disturbing, as it indicates that, in mid-June at any rate, although the daytime catches showed that Tomopteris was absent from the plankton, it was certainly present in the locality. On June 17th, on the afternoon before the night catches of 211 were made, only 3 specimens of Tomopteris were caught : on this occasion none were taken in the deepest haul, during which the net fished to a maximum depth of 52 metres, with an average of 48.8 m., the bottom itself being at most at about 56 metres. From these results only one conclusion can be drawn :

that is, that, on this day at any rate, *Tomopteris* was either lying on the bottom, or in the water layers immediately adjacent.

Until further observations are forthcoming then it would appear that from April until mid-July *Tomopteris helgolandica* lives in the daytime either on or very close to the bottom, and that in mid-July and August it comes up into the midwater layers with the rest of the plankton. It should be noted, however, that on the three days in July and August when *Tomopteris* was abundant in the midwater layers the weather was extremely dull and foggy, which may signify that the lighting conditions, rather than the time of year, were responsible for their appearance above the bottom. A further observation of interest is, also, that on July 16th and 29th some of the worms were seen to be carrying eggs. The actual numbers were :—

16.vii.25.	A.	R.T.	<i>Tomopteris</i> with eggs :	22.2 metres=	6
			“ “ “	32.3 “	=26
			“ “ “	38.8 “	=10
16.vii.25.	A.	C.M.N.	“ “ “	25.8 “	= 3
				41.7 “	=11
29.vii.25.	A.	R.T.	“ “ “	4.8 “	= 3
			“ “ “	9.1 “	= 1
			“ “ “	20.6 “	= 6

It may be possible, then, that this appearance in the upper layers of *Tomopteris* in July is in some way connected with their spawning habits. It is interesting to find that on July 15th and 16th, 1924, when they were also numerous in the plankton in the daytime (22, p. 788), I had made a note that many were carrying eggs.

For the deep waters off the Irish coast, Southern (27) says : “ With reference to the vertical distribution of *T. helgolandica*, there are no signs of any correlation between its occurrence at certain depths and such factors as temperature, hour of the day, state of sexual maturity, etc. It has been taken at all depths from the surface to below 1000 fathoms.”

Gough (8) says that on July 1st, 1903, “ during the hottest part of the day the bulk of the *Tomopteris* was found near the bottom at 70 metres, only a very few being at 30 metres.”

Seasonal distribution. The above results are of great importance when we consider the seasonal distribution of the species : it would appear that it is not possible to draw conclusions from day hauls only ; these must be supplemented by collections made at night. As stated, the species would appear to be relatively scarce in this region until mid-July, if it were not for the fact that night collections made in June demonstrated

that they were in reality present here. Southern (27) states that off the coast of Ireland collections indicated a maximum in late autumn, especially from August to November; he also says: "Whilst the number of individuals varies with the season of the year, their distribution in space remains very uniform, and there is no seasonal migration." He abstracted the results of the Plankton Investigations of the International Council in the English Area, including the English Channel and the Bristol Channel, and the results agreed with his findings in showing a maximum in the autumn and a minimum in the spring. He states that the breeding season takes place between May and August.

Lebour (17), for the Plymouth Sound region, says that this species begins in the middle of June, and is very common in July and rare in September and October.

McIntosh (19, p. 17) says, "Autumn seems to be the period in British waters when Tomopterids occur most abundantly, the maximum being in October."

LARVÆ OF PÆCILOCHÆTUS SERPENS Allen.

These polychæte larvæ were never abundant. On no occasion were any caught at the surface or in the layers above 12 metres. It would, therefore, seem that Pæcilochætus larvæ normally live in the deeper layers in the daytime.

CHÆTOGNATHA

SAGITTA BIPUNCTATA Quoy and Gaimard.

From April 8th until July 1st the majority of Sagitta were captured from the deeper layers below 20 or 25 metres at the outer station, A. At L4, however, which is closer inshore, on May 19th, June 4th, and July 1st they were considerably higher in the water than at A on the same dates.

On July 16th and 29th and August 6th, all three foggy days, Sagitta was abundant from 4 or 5 metres downwards and fairly evenly distributed throughout the layers, except on August 6th, when they were apparently concentrated between 10 and 25 m. (Fig. 5).

It was noted that very often the smaller stages were most prevalent in the upper layers, and on this account measurements are being taken of the Sagitta present in this year's (1926) collections.

Seasonal distribution. While present in small numbers in April, May, and June, Sagitta showed an enormous increase in the middle of July; on July 29th the numbers taken on the 16th were nearly doubled, while these were again doubled by the catch on August 6th.

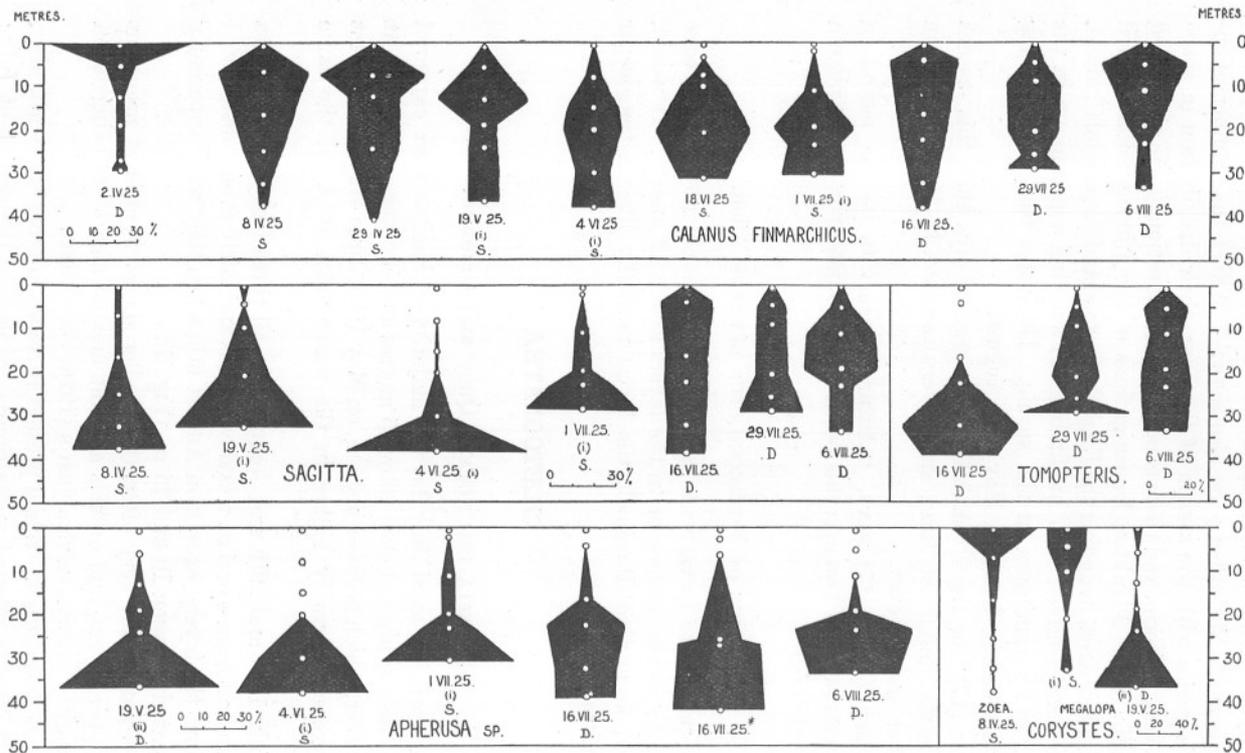


FIG. 5.—The percentage vertical distribution of *Calanus finmarchicus*, *Sagitta bipunctata*, *Tomopteris helgolandica*, *Apherusa* sp., and *Corystes cassivelaunus* zoetas and megalopas on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull. Asterisk (*)=closing metre net. Note that the percentage scale for *Corystes* zoetas and megalopas is half that of the other species. (In the case of *Calanus*, the date 19.v.25 (i.) should read 19.v.25 (ii.).)

CRUSTACEA.

BRANCHIOPODA.

EVADNE NORDMANNI Lovén.

Although this species is too small to be normally retained by the ring-trawl, I have one observation on its vertical distribution that was made with the silk closing metre net on July 16th. On this day (Table II), although it cannot be said to have been abundant, the largest catch occurred at 25.8 metres. It was absent from the actual surface, but was present in the catch from 2.7 m.

PODON INTERMEDIUS Lillj.

This species, again, like *Evadne*, was only obtained when the silk net was used on July 16th. It was quite abundant on this occasion, and showed a marked maximum at 25.8 metres, though actually it may have been higher in the water because unfortunately there is no haul between 6.5 and 25.8 m. (Table II).

COPEPODA.

CALANUS FINMARCHICUS (Gunner).

In discussing the vertical distribution of this copepod it is desirable to know with which stages of development we are dealing. In the life-history of *Calanus finmarchicus* there are 12 stages—6 larval nauplius stages, 5 post-larval copepodid stages, and the adult—which have been described by Krøyer, Grobben (10), Lebour (16), and With (28). It is only the copepodid stages that concern us here, the nauplius stages being far too small to be retained by the net used. It has already been noted by previous workers that the younger individuals are at times higher in the water than the older. For instance, Gran (9, p. 64) remarks: “. . . im Sommer sind die Jungen hauptsächlich in den oberen, erwärmten Schichten zu finden, während die älteren oft vereinzelt in der Tiefe umherschwimmen.” Damas (4, p. 18) says also: “Verticalement, les stades sont répartis de telle sorte que les individus jeunes prédominent à la surface et les adultes vers la profondeur. Il est probable que les *Calanus* gagnent vers la profondeur en avançant en âge.”

Farran (5, p. 84), for the smaller southern form, gives as an example the following figures showing a preponderance of young forms at the surface and adult forms deeper: the locality was on the west coast of

Ireland, 30 miles west of Cleggan Co. Galway, and the time of year, May in 1904 :—

Stages.	♂ ♀	V.	IV.	III.	II.	I.	
Surface	2	9	32	27	24	6	Percentage present.
35 fathoms	73	14	6	3	4	—	„ „

In view of these differences in vertical distribution noticed for the various stages of development, I have made observations in order to find out which stages are mostly caught by the ring-trawl.

On July 16th, 1925, horizontal hauls were made at six different depths with a closing net, 1 metre diameter at mouth and silk with a mesh of ca. 40 strands to the inch. The catches consisted of large numbers of *Calanus* chiefly composed of the last three stages—Adult, V, and IV. Measurements were made of the total length (furcal setæ excluded), and of the thorax only, of 394 individuals. Similar measurements were made of a sample of *Calanus* collected by the ring-trawl on July 15th, 1924. The results are given in Table I. It can be seen that whereas the silk net took large quantities of post-larvæ of Stages IV and V, as well as adults (VI), the composition of the ring-trawl catches was made up mostly of adults with only a small proportion of Stage V and hardly any of Stage IV, the percentage composition being—

Adults . . .	84.8%
Stage V . . .	12.5%
Stage IV . . .	2.7%

This agrees well with the conclusions of Paulsen (21, p. 11), who says : “ These Young fish trawl samples contain only specimens of Stage II* of the Juniores, younger stages pass through the meshes.” The young fish trawl is made of the same material—stramin—as the ring-trawl.

As an example I quote some of his figures :—

	♂	I.	II.	III.	IV.	V.	VI.
Young Fish trawl	1	89	5	5	—	—	—
Young Fish trawl	—	77	16	7	—	—	—
Silk net, Gauze 20	—	13	6	32	16	22	11
Silk net, Gauze 20	—	44	10	30	16	—	—

I have also tested five further samples taken on April 9th, 1926, from five different depths, with the following results :—

Adults.	V.	IV.
94.8 %	5.2 %	—
91 „	9 „	—
87 „	13 „	—
83 „	15 „	2 %

* Paulsen's stages are numbered in the reverse order : this, therefore, corresponds to my Stage V.

It can, I think, then, be safely stated that the observations given below on the vertical distribution of *Calanus* relate almost exclusively to the adult stages, with also a few of the last copepodid stage.

It is, however, unfortunate that it is not possible to say which sex we

TABLE I.

Mm.	Total Length.						Mm.	Length of Thorax.					
	Silk Net. Stage.			Ring-trawl. Stage.				Silk Net. Stage.			Ring-trawl. Stage.		
	IV.	V.	VI.	IV.	V.	VI.	IV.	V.	VI.	IV.	V.	VI.	
1.76	1	-	-	-	-	-	1.43	4	-	-	-	-	
1.815	3	-	-	-	-	-	1.485	3	-	-	-	-	
1.87	3	-	-	-	-	-	1.54	13	-	-	-	-	
1.925	8	-	-	-	-	-	1.595	10	-	-	-	-	
1.98	11	-	-	-	-	-	1.65	14	-	-	1	-	
2.035	11	-	-	1	-	-	1.705	10	1	-	1	-	
2.09	8	-	-	-	-	-	1.76	2	-	-	-	-	
2.145	6	1	-	-	-	-	1.815	2	4	-	-	-	
2.2	6	1	-	1	-	-	1.87	-	5	-	-	-	
2.255	-	1	-	-	-	-	1.925	-	13	-	-	-	
2.31	1	3	-	-	-	-	1.98	-	16	-	1	-	
2.365	-	4	-	1	-	-	2.035	-	21	-	-	-	
2.42	-	7	-	-	-	-	2.09	-	24	-	-	1	
2.475	-	14	-	-	-	-	2.145	-	17	-	-	2	
2.53	-	16	-	-	-	-	2.2	-	25	2	-	3	
2.585	-	23	-	-	-	-	2.255	-	30	3	-	3	
2.64	-	15	-	-	1	-	2.31	-	38	5	-	3	
2.695	-	15	-	-	1	-	2.365	-	4	15	-	1	
2.75	-	17	-	-	4	-	2.42	-	-	21	-	1	
2.805	-	21	-	-	1	-	2.475	-	-	28	-	-	
2.86	-	33	-	-	2	-	2.53	-	-	33	-	-	
2.915	-	27	6	-	1	-	2.585	-	-	20	-	-	
2.97	-	-	8	-	2	-	2.64	-	-	12	-	-	
3.025	-	-	20	-	2	4	2.695	-	-	2	-	-	
3.08	-	-	20	-	-	2	2.75	-	-	-	-	-	
3.135	-	-	22	-	-	4	2.805	-	-	-	-	6	
3.19	-	-	24	-	-	9	2.86	-	-	-	-	2	
3.245	-	-	15	-	-	14	2.915	-	-	-	-	1	
3.3	-	-	18	-	-	17							
3.355	-	-	4	-	-	15							
3.41	-	-	1	-	-	15							
3.465	-	-	-	-	-	9							
3.52	-	-	-	-	-	2							
3.575	-	-	-	-	-	2							
3.63	-	-	-	-	-	1							
3.685	-	-	-	-	-	1							

are dealing with. When first undertaken, this research was intended for examination of the depth distributions of the young, pelagic stages of fish, and the plankton was also examined in order to get a general idea of the distribution of some of the other constituents of the animate environment in relation to that of the young fish. It seems, however,

desirable later that the distribution of each single species be examined in detail.

Nevertheless I can give the vertical distribution of the two sexes for two separate occasions, July 16th, 1925, and April 9th, 1926. The results are given in the following table :—

JULY 16TH, 1925. A. CLOSING METRE NET.				
Depth.	♂	♀	% ♂	% ♀
<i>Surface</i>	196	6,804	1.1	14.1
<i>2.7 metres</i>	66	9,295	0.3	19.3
<i>6.5</i> ,,	6,970	20,804	39.8	43.1
<i>25.8</i> ,,	3,680	3,006	21.2	6.2
<i>26.8</i> ,,	5,240	6,541	30.0	13.5
<i>41.8</i> ,,	1,339	1,895	7.6	3.8
			<u>100.0</u>	<u>100.0</u>

APRIL 9TH, 1926. A. RING-TRAWL.				
<i>Surface</i>	5	60	0.5	0.7
<i>2 metres</i>	31	812	3.4	9.4
<i>7</i> ,,	55	2,456	6.1	28.0
<i>15.5</i> ,,	438	2,738	48.6	35.4
<i>22.4</i> ,,	146	958	16.3	12.3
<i>32.4</i> ,,	225	1,047	25.1	14.2
			<u>100.0</u>	<u>100.0</u>

It can be seen from these figures that on both occasions there was a difference in the vertical distribution of the two sexes, the males exhibiting a greater tendency to avoid the surface layers than the females. This is shown very clearly in Fig. 6. At the same time it is to be noticed that on these two occasions the females so preponderated in numbers over the males that the distribution of the two sexes together did not differ essentially from that of the females alone (Fig. 6). There is therefore a possibility that the distributions shown by my collections may depict that of the females, if on each occasion the males formed as small a proportion of the whole as they did on the two days dealt with above.

Before proceeding with an account of the actual vertical distribution of *Calanus* in the daytime, in 1925, a further fact of interest shown by Table 1 is worthy of mention; this is the variation in actual size of the adults. We note that while in 1925 the majority lay within the limits of 3.025 and 3.3 mm. in length—with a maximum of 3.4—in 1924 they were obviously considerably larger, most of them being between 3.19 and 3.465 mm. in length, and one even reaching 3.685 mm. Although it is true that the smaller adults may have passed through the meshes of the

ring-trawl, thus giving the impression of a larger lower-limit than that shown by the silk net, it is unlikely that the silk net would have failed to catch the largest forms and so produce the opposite effect. It seems, therefore, quite probable that in July, 1924, the *Calanus* population sampled consisted of larger individuals than that sampled in July, 1925; this is also borne out by the fact that the few Stage V specimens retained

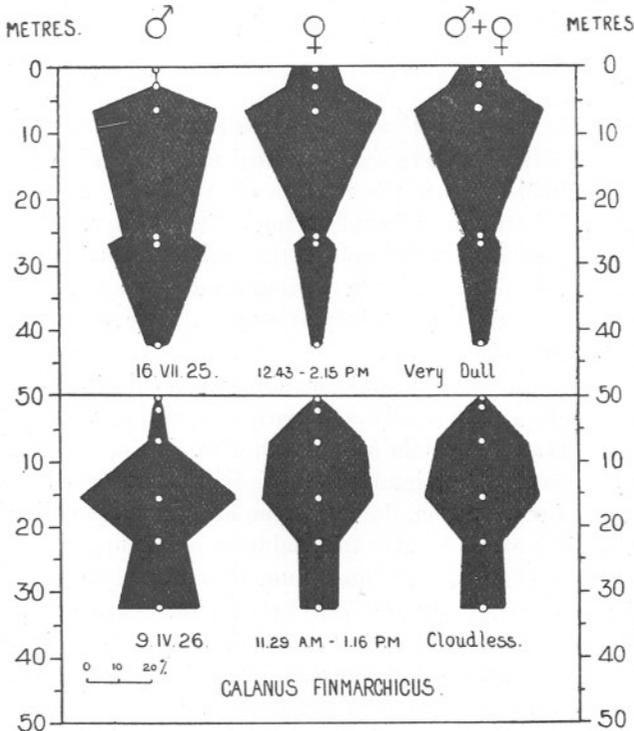


FIG. 6.—Percentage vertical distribution of male and female *Calanus finmarchicus* on July 16th, 1925, and April 9th, 1926, showing—

- (i.) The preference of the males for deeper layers than the females.
- (ii.) Owing to the preponderance of females over males the combined distribution resembles that of the females.

by the ring-trawl in 1924 were evidently of a larger size than those of the corresponding stage caught in July, 1925.

Such variations in size in the same locality have already been noted by Gran (9, pp. 60 and 64), who says that the sizes for each stage differ according to season, and also that a raising of the temperature accelerates development, but produces smaller forms.

The same has also been noted by Kraefft (15, p. 76) for the copepod *Paracalanus parvus*. In view of these observations it is interesting to note that, presuming the adult *Calanus* in question to have been born in the

spring, those born in 1925 would have developed under conditions at least 1° C. higher than those born in the spring of 1924, which might explain the smaller size of the adults in 1925. The actual temperatures were:—

	1924.	1925.
February	8.67° C	10.01° C
March	7.90°	9.19°
April	8.15°	9.47°
May	9.55°	10.3°

As regards the actual vertical distributions shown by *Calanus finmarchicus* (which we have seen consisted mostly of adults) during the daytime in 1925, between the months of April and August, in Fig. 5 are given the distributions found on ten different days. The shapes of some of these distribution figures and the apparent descent of the region of maximum abundance between April and mid-June have already been discussed in a previous paper (25) as regards their possible correlation with the intensity of the light.

Calanus exhibits a very wide vertical range in its distribution, occurring fairly abundantly at almost all depths early in April, but gradually avoiding the actual surface layers as the season advances. It would, however, appear to have a pronounced optimum level of abundance, which varies from day to day. In this region, during the months in which collections were made in 1925, it was evidently an inhabitant of the upper more brightly illuminated layers, the region of maximum abundance lying almost always above the 20-metre level; the depth of the region of maximum abundance showed a marked seasonal change descending from about 5 metres early in April to just below 20 metres in mid-June. Daily changes in this level were also shown, the copepods being higher in the water on dull than on bright days, cf. April 2nd and 8th, and July 1st and 16th.

Seasonal distribution. *Calanus* was present in all the collections, but showed a very great increase in numbers on July 16th, 29th, and August 6th. Whether these represent individuals transported into this area or whether they were the 1925 brood grown to a sufficient size to be captured by the ring-trawl cannot be said.

Farran (5, p. 85), says that the Channel is not to "be regarded as one of the areas in which the annual presence of vast swarms is normal. Such an area lies, however, immediately off its mouth, and large shoals are frequently carried into the western half of the Channel."

ANOMALOCERA PATERSONI Tempkt.

The specimens of this copepod dealt with in these collections were probably all adults, the sexes, however, have unfortunately not been

noted. From Fig. 7 it can be seen that between April 2nd and July 1st *Anomalocera* showed a decided preference for the actual surface layers above 10 m., at the times at which collections were made. It is noticeable, however, that after July 1st a change appears to have taken place in the way in which they were distributed. On July 16th they were still numerous at the surface, but were also taken in relatively large numbers even as deep as 22 metres. On July 29th a large catch was made at 29 m., while on August 6th there were many taken from a depth of 33 m., but on this date the area of maximum abundance appeared to be in the region of 20 m.

With so few observations it is not possible to attempt an explanation of this apparent change in behaviour. Suffice it to say that on these days the weather was very dull; one should also keep in mind the fact that at

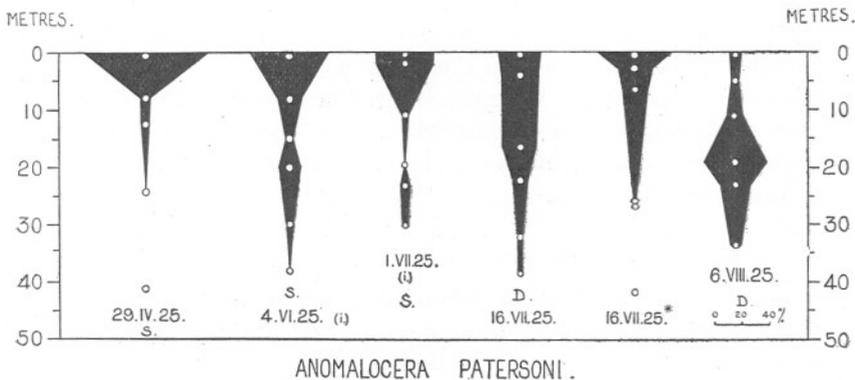


FIG. 7.—The percentage vertical distribution of *Anomalocera Patersoni* on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull. Asterisk (*)=closing metre net.

this time of year the surface layers are reaching their maximum temperature (25, p. 437).

The collections made on July 16th with the closing metre net do not give quite similar results to those taken with the ring-trawl on the same date: the presence in these samples of many young stages and also the absence of a sample from between the depths of 6 and 25 m. will probably account for this.

From a study of observations by previous workers on the distribution of this species the general conclusion is that it is a surface living form, though it may occur occasionally in deeper layers. Gough's remark (8, p. 336)—“*A. Patersoni* is usually found at the surface, very rarely descending to 10 metres. In August, however, a few specimens . . . were found in a sample from 110 metres”—may have some significance in view of the fact that it is at the beginning of August that *Anomalocera*

occurred deepest in my collections. Farran (6, p. 292) reports the occurrence of this copepod in the 100-fathom nets in the Biscayan plankton collections; he remarks that they ". . . may possibly have been taken while these nets were being hauled to the surface; but they occurred more often than might have been expected if this were the case."

In 1924 in mid-July I took this species chiefly on the surface on July 15th, but at all depths down to 30 metres on July 16th; there was a marked massing at 9 and 16 metres at 2.50 to 4.16 a.m. on July 16th (22, p. 795).

Wolfenden (29, p. 140) remarks: "For long it has been considered that *Anomalocera Patersoni* was a purely surface species, but the capture of an adult male example in a bottom scraping at 400 fathoms, in perfect condition, shows that it can sometimes descend to considerable depths."

In records given by Savage (26, p. 33) for the North Sea this species occurred only in surface hauls in July, 1922.

Seasonal distribution. *Anomalocera* was never very abundant; the largest catch was made on August 6th. The main centre of distribution probably lies very much farther to the westward of this locality, and we only just touch the fringe.

CANDACIA ARMATA (Boeck.).

This copepod, mostly adults, showed a decided preference for the layers below a depth of 20 metres in the daytime, as indicated by collections made between April 2nd and July 29th, 1925; on August 6th, however,

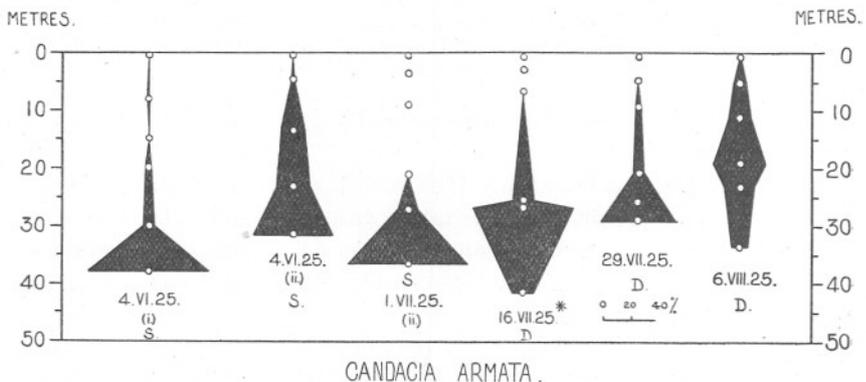


FIG. 8.—The percentage vertical distribution of *Candacia armata* on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull. Asterisk (*)=closing metre net.

they occurred in considerable numbers much higher up in the water, the majority occurring at about 20 metres (Fig. 8).

Lebour (18, p. 403) says that in the winter this copepod, which is an important constituent of the food of Herring, is taken "usually from the lower layers."

Seasonal distribution. This copepod was present throughout the period in which collections were made, but became more abundant at the beginning of June: the largest catch was on August 6th.

CENTROPAGES TYPICUS Kröyer.

This copepod, although occurring occasionally in the ring-trawl catches, has not been counted. On account of its small size the majority most certainly pass through the meshes, and results given by the few that are retained cannot be relied on.

I have, however, in Table II, p. 608, given the results of catches made on July 16th with the silk closing net. From these numbers and a figure previously published (25, p. 425) it can be seen that the majority occurred in the 10-metre region on this date.

TEMORA LONGICORNIS (Müller).

As with *Centropages* catches of *Temora* obtained by the ring-trawl cannot be relied upon. On July 16th this copepod was also numerous in the closing net collections, and it can be seen from Table 2 and the previously published figure (25, p. 425) that the majority occurred on this occasion below 25 metres.

Savage (26), working in the North Sea, off the mouth of the Tyne, found in July that in the daytime the majority of this species were in the bottom layers, and he has drawn charts showing the distribution of *Temora* over a given area that bring this out in a very striking manner.

ISIAS CLAVIPES Boeck.

This species only occurred in the catches made with the silk closing net on July 16th, and then they were present only in small numbers. The figures obtained by sampling the catches showed that none occurred at the surface or at 2.7 metres; at 6.5 m. there were 40 specimens; at 25.8 m., 40; at 26.8 m. and at 41.8 m., 20.

METRIDIA LUCENS Boeck.

This copepod only occurred occasionally in the ring-trawl; it is possible that it is just small enough for the majority to pass through the meshes of the ring-trawl; this locality is also probably far from the main area of

its distribution which lies in deeper water farther to the west. On the three dates on which any were found in the collections, April 22nd, June 17th, and August 6th, none were taken from above 15 metres. It was also present in the silk metre net collections on July 16th, when it occurred only in the three deeper hauls.

CALIGUS RAPAX Milne Edwardes.

Free-swimming males and females of this species occurred in small numbers on each day on which collections were made. They were always most numerous below a depth of 18 to 20 metres. In fact, between April 2nd and June 4th none were captured in the layers above this depth.

Seasonal distribution. *Caligus rapax* showed a decided increase in abundance in the middle of June and remained abundant for the rest of the period, during which observations were made; the largest catches were made on August 6th.

MYSIDACEA.

Mysids live in the daytime generally either on or very close to the bottom, and it is natural that they were very rare in my collections. The largest catches occurred on June 4th, when 41 were taken at 30 metres and 125 at 38.

It is, however, of interest to record the presence of extremely young mysids in the plankton, on July 16th, in the catches of the metre net. It can be seen in Table II that while of the adults 1 was caught at 26.8 m. and 21 at 41.8 m., the very young stages were quite numerous at 25.8 and 26.8 m., although the majority were at 41.75 m.

EUPHAUSIACEA.

NYCTIPHANES COUCHII (Bell).

Both adults and young (including the later Cyrtopia stages) kept apparently nearly always to the deeper layers below 20 metres in the daytime. On July 16th collections made by the closing metre net gave a definite indication that the Furcilia stages were abundant higher in the water—up to the 6-metre level—than the adults, although they were also abundant in the deeper layers, the numbers being as follows :—

	Surface.	2.7 m.	6.5 m.	25.8 m.	26.8 m.	41.8 m.
Furcilia stages	.	—	—	100	140	40
Adults	.	—	—	—	4	25
					63	

Lebour (18, p. 404) states that "the adults and older larvæ all appear to live very near the bottom in the daytime, . . . although the young larvæ seem to keep near the surface." Also (p. 411), "the younger larval stages, especially the Calyptopis, were nearly always at the surface or midwater, the post-larvæ near the bottom. . . ."

A curious exception to the apparently normal behaviour of adult *Nyctiphanes* occurred on June 4th, when besides being abundant below 25 metres they were very numerous right at the surface during bright sunshine.

AMPHIPODA.

APHERUSA sp.

There are possibly several species of *Apherusa* included in the collections. On account of the labour that would be involved in carrying out the identifications they are here dealt with together. Examination of a certain number has shown that besides *Apherusa clevei* G. O. Sars, there were also present many *A. ovalipes* Norman and Scott; in fact, the impression gained was that of the two *A. ovalipes* was the commoner.

These amphipods on almost all occasions were absent from the surface, and did not become abundant until the 20-metre level was reached (Fig. 5). On two occasions (19.v.25 (i.) and 1.vii.25 (ii.)) they occurred at the surface: I am inclined to feel, however, that this may have been accidental, as these amphipods have a habit of sticking very strongly to the material of the net, and it may well be that they were left over on the surface of the net from the previous deep hauls.

HYPERIID sp.

Hyperiid amphipods were very rare in the collections, and always occurred below 19 or 20 metres when present.

DECAPODA.

DECAPOD LARVÆ.

In the period during which these observations were made the decapod larvæ form a very important constituent of the catches made by the ring-trawl. The identification of many of the larval decapods is a matter of considerable difficulty, and consequently I have assigned to the actual species only those that are at once distinguishable even with the naked eye, the remainder being placed together under the families or groups to which they belong. The following scheme shows the result of the final sorting:—

MACRURA.

Palæmonidæ.	<i>Leander serratus.</i> } <i>L. squilla.</i> }	Grouped together as Leander sp.
Pandalidæ.		
Hippolytidæ.	<i>Pandalus montagui.</i> } <i>Pandalina brevirostris.</i> }	Grouped under the head- ing : Pandalid larvæ (the larvæ of <i>Spirontocaris</i> were very scarce).
Processidæ.	<i>Spirontocaris Cranchi.</i> }	
Alpheidæ.	<i>Processa canaliculata.</i> }	
Crangonidæ.	<i>Alpheus ruber.</i>	Identified.
	<i>Crangon allmanni.</i> } <i>C. vulgaris.</i> } <i>Cheraphilus nanus.</i> } <i>C. trispinosus.</i> }	Grouped under the head- ing : Crangonid larvæ.
Nephrosidæ.	<i>Pontophilus spinosus.</i>	Identified.
Palinuridæ.	<i>Homarus vulgaris.</i>	Identified.
	<i>Palinurus vulgaris.</i>	Identified.
Galatheidæ.	<i>Galathea dispersa.</i> } <i>G. intermedia.</i> } <i>G. squamifera.</i> } <i>G. strigosa.</i> }	Grouped under the head- ings : Galatheid larvæ and Galatheid post- larvæ.
Callianassidæ.	<i>Upogebia stellata.</i> } <i>U. deltura.</i> }	Grouped under the head- ings : Upogebia larvæ and Upogebia post-larvæ.
	<i>Callianassa subterranea.</i>	
Axiidæ.	<i>Axius styrhinchus.</i>	Identified.
Paguridæ.	<i>Eupagurus bernhardus.</i> } <i>E. cuanensis.</i> } <i>E. Prideauxi.</i> } <i>E. sculptimanus.</i> } <i>Diogenes varians.</i> } <i>Anapagurus lævis.</i> }	Grouped under the head- ings : Pagurid larvæ and Pagurid Glaucothoë.

BRACHYURA.

Porcellanidæ.	<i>Porcellana longicornis</i> . <i>P. platycheles</i> .	} Grouped under the headings : Porcellana zoea and Porcellana post-larvæ.
Leucosiidæ.	<i>Ebalia Cranchi</i> . <i>E. tuberosa</i> . <i>E. tumefacta</i> .	} Grouped under the headings : Ebalia zoea and Ebalia megalopa.
Corystidæ.	<i>Corystes cassivelaunus</i> .	Identified—zoea and megalopa.

All remaining brachyura (crabs) were separated into zoeas and megalopas and grouped together : by far the most abundant are probably *Portunus* spp., together with *Cancer pagurus*, *Carcinus mœnas*, Inachidæ and Maiidæ.

The various decapod larvæ show marked differences in their types of vertical distribution, the details of which are given in the ensuing pages.

For instance, while *Leander* sp. larvæ were evenly distributed from the surface downwards with a slight preference for the surface layers, *Upogebia* larvæ had their region of maximum abundance a few metres beneath the surface, *Porcellana* zoeas were slightly deeper, *Galatheid* and *Pandalid* larvæ (including the larvæ of *Processa canaliculata*) deeper still, then *Pagurid* larvæ, and deepest of all, *Crangonid* larvæ and *Pontophilus spinosus* larvæ. Of Brachyuran larvæ many zoeas frequented the surface layers as well as greater depths, notably *Corystes cassivelaunus* and probably *Portunus* sp. : *Ebalia* sp. zoea, on the other hand, when identified, were much deeper in the water.

Savage, in the North Sea, in July, 1922, as a result of one serial collection had indications of differences in the behaviour of decapod larvæ. On p. 13 (26) he remarks : " It was noted above that *Portunus* spp. were the only decapod larvæ that were more abundant at the surface than in other layers, and the comparative absence of these species from this station left the surface waters practically devoid of decapod larvæ. *Galathea intermedia* was the most abundant form, and it had a big maximum at 25 fathoms, where 50 per cent of its total number was taken, the majority of the remainder were below this depth. *Pandalus brevirostris* and *Eupagurus bernhardus* were almost wholly in the bottom hauls (35-45 fathoms) particularly the latter. *Crangon allmanni* was only found between 25 and 35 fathoms."

In this order of their depth distribution the decapod larvæ follow fairly closely my own results. Savage's results differ in the position of *Crangon allmanni*, but possibly the actual numbers caught were rather low to draw conclusions from.

LEANDER sp. LARVÆ.

It is probable that these larvæ consist mostly of *L. serratus* and *L. squilla*. Gurney says (13, p. 101): "Owing to the difference in the breeding period, any *Leander* larvæ found off the British Coasts from December to nearly the end of June may confidently be assigned to *L. serratus*"; and (*ibid.*, p. 105), "From then onwards the larvæ probably comprise both *L. serratus* and *L. squilla*, whose larvæ probably appear in the plankton in July."

The stages of development dealt with here are mostly late ones: the actual percentages of different stages in the collections are:—

Stage.	I.	II.	III.	IV.	V.
Percentage	1	3.5	15.5	26	54

No post-larval stages were met with.

In a previous paper (22, p. 799) I have given the vertical distribution for these decapod larvæ for July 15th and 16th, 1924, showing that on that occasion they were more abundant in the surface layers. In 1925 they were also comparatively numerous in the upper layers from the surface down to about 10 metres: at the same time they occurred also in the deeper layers, so that their vertical distribution would appear to have been somewhat indiscriminate. Between the surface and 10 m. in the whole collections 63 individuals occurred out of 35 hauls in those layers: between 10 and 20 m. there were 30 specimens out of 14 hauls: between 20 and 30 m. 33 out of 19 hauls, and between 30 and 40 m. 14 individuals out of 11 hauls. So that the average numbers of specimens per haul in the different layers were:—

Surface to 10 m.	.	.	.	1.8
10-20 m.	.	.	.	2.14
20-30 m.	.	.	.	1.73
30-40 m.	.	.	.	1.27

This points to a fairly even distribution with a tendency for greater abundance between 10 and 20 m.: the numbers are, however, really too low to be significant.

Seasonal distribution. These larvæ were present in fairly equal numbers from mid-April until the beginning of August, when collecting ceased.

PANDALID LARVÆ.

Included amongst these larvæ are mostly *Pandalus Montagui** Leach, *Pandalina brevirostris* (Rathke), and *Processa canaliculata* Leach. Larvæ

* It is here necessary to point out an error that I made in my first paper (22, p. 800), where I called this species by mistake *P. borealis*, a northern species that has never been recorded in this locality.

of *Spirontocaris Cranchi* (Leach) were also occasionally present, but only in extremely small numbers.

Practically all the stages captured by the ring-trawl were of stages 4 and 5 or older.

Fig. 9 shows that throughout the months April to August in 1925 these larvæ avoided the surface and upper layers, only becoming abundant below the 15-metre level, in the daytime. It was noted that on April 2nd only *Processa* larvæ were present. Gurney (12, p. 263) criticises the fact that *Processa* is usually placed so near to the Crangonidæ; his argument being that the larval characters differ so markedly from those of Crangonid larvæ. It is interesting therefore to note that in their habits also the larvæ of *Processa* differ from Crangonid larvæ. While *Processa* larvæ on April 2nd were present in the water layers from about 15 metres downwards, Crangonid larvæ, as always, were only abundant below 25 metres: in this all Crangonid larvæ, including those of *Pontophilus spinosus*, appear to be very consistent (see Fig. 9).

Seasonal distribution. These Pandalid larvæ were very numerous in the plankton from the end of April to the end of July. In April they were less numerous; and it has been mentioned that all those examined on April 2nd, and also most of those in the catches of April 22nd, proved to be *Processa canaliculata*. After this date the samples were not sorted.

LARVÆ OF ALPHEUS RUBER Milne-Edwards.

These larvæ were only taken in the daytime on July 29th and August 6th, 1925, when their numbers were:—

JULY 29TH, 1925.	A.	R.T.	AUGUST 6TH, 1925.	A.	R.T.
Surface	.	—	Surface	.	—
4.8 m.	.	—	5 m.	.	—
9.1 "	.	—	11.1 "	.	27
20.6 "	.	4	19.2 "	.	23
25.8 "	.	7	23.1 "	.	12
29 "	.	3	33.6 "	.	11

From this it will be seen that they avoided the uppermost layer above about 10 metres: both these days were, however, very dull and foggy.

CRANGONID LARVÆ.

Larval Crangonids, including probably most of the local species, with the exception of *Pontophilus spinosus*, and with *Crangon Allmanni* as the most common, showed a consistent preference for the deeper layers below 20 and 25 metres (Fig. 9). In July, 1924, the indications were also

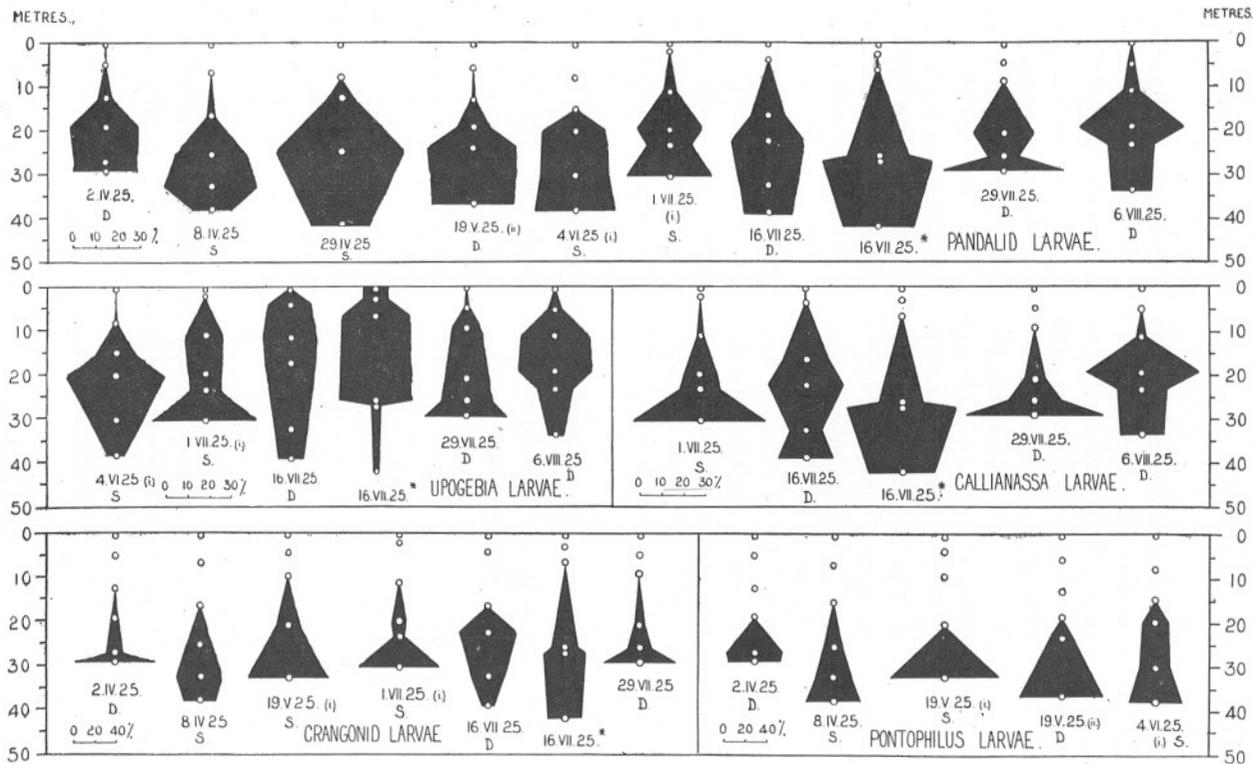


FIG. 9.—The percentage vertical distribution of Pandalid larvæ; *Upegebia* sp. larvæ, *Callianassa subterranea* larvæ; Crangonid larvæ and *Pontophilus spinosus* larvæ, on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull. Asterisk (*)=closing metre net. Note that the percentage scale for Crangonid and Pontophilus larvæ is half that of the other species.

that they were deep living forms (22, p. 801). Not a single specimen was caught above 12 metres in 1925, and only six above 19 metres, out of a total of 1909 caught.

Seasonal distribution. Crangonid larvæ were present in the catches in greater or less numbers throughout the period of collecting.

LARVÆ OF PONTOPHILUS SPINOSUS Leach.

Like other Crangonid larvæ, *Pontophilus* exhibited a decided preference for the layers below 20 or 25 metres, being practically entirely absent above 20 metres (Fig. 9). All stages of development were represented in the catches, though the later stages were most abundant.

Seasonal distribution. *Pontophilus* larvæ were most numerous between April 2nd and June 4th, after which time they were rarely caught.

LARVÆ OF HOMARUS VULGARIS Milne-Edwards.

Only 6 of these larvæ were captured: 1 on May 19th, at the surface; 1 on July 1st, at 21.3 m.; 2 on July 16th, at the surface; and 2 on July 29th, at 29 metres.

PHYLLOSOMA LARVA OF PALINURUS VULGARIS Latreille.

These Phyllosoma larvæ probably mostly belonged to *Palinurus vulgaris*, though there is a slight possibility that one or two *Scyllarus arcturus* may have been present, as the adult of that species is occasionally, though somewhat rarely, taken in this locality. These larvæ were most common below 16 metres and very rarely occurred above 10 metres. The largest catch, of 75 specimens, was made at 36.7 m. on July 1st. There are indications that the region of maximum abundance may normally have lain deeper than the net fished on most occasions, because on June 17th, 18th, and 19th in the daytime the total catches were 6, 5, and 44, while on the two nights between these days they were 102 and 196.

Cunningham (3, p. 147) says: ". . . some hundreds may be taken in about an hour in the neighbourhood of the Eddystone in July, with a net whose meshes are about 2 mm. in diameter, and whose mouth is 8 feet by 6 feet area. On the two occasions on which I obtained the larvæ, I captured them only when towing the net at the surface, not when it was sunk to some depth." These results are opposed to mine, but it may be that the catches were made much nearer the Eddystone rocks, where upwelling currents might upset the normal distribution of the plankton in more quiet waters. The exact positions were not given, but were "a little to the north of the Eddystone" and "to the south of the Eddystone."

Seasonal distribution. It is evident that the larvæ were present throughout the months April to August; I have noted, however, that up till the end of June they were all small early stages; on July 1st, 2 "large" specimens were caught; on July 16th, 1 "large"; July 29th, 10 "large"; and August 4th, 4 "large." From this it would appear that metamorphosis into the "Puerulus" stage would occur mostly after June in July and August, my "large" stages being stages 7, 8, and 9 of Bouvier. This agrees with Bouvier (1, p. 191), who says that the last stage but one (avant-dernier stade) is very common at the end of July and during the month of August.

GALATHEID LARVÆ.

Fig. 10 shows the vertical distribution for Galatheid larvæ on most of the days when collections were made between April and August. They usually showed a sudden increase in abundance between about 15 and 20 metres, and occasionally deeper. In their distribution then they were very similar to the Pandalid larvæ. On April 2nd they were abundant at the surface, and then the numbers decreased until below 20 metres, when they again became abundant. It is curious that on this day many forms which usually live deeper down were present at the surface.

Seasonal distribution. Although occurring on all days on which collections were made, Galatheid larvæ were most numerous on May 19th and June 4th.

GALATHEID POST-LARVÆ.

These post-larvæ were never very abundant, but when they did occur in fair numbers, e.g. June 4th, they were most numerous below 30 metres. Probably the majority live still deeper in the layers close to the bottom; this has been indicated by the increase in numbers caught at night (22, p. 803). It is possible that included among these may be a few post-larvæ of *Porcellana* before July 1st, after which date the presence of *Porcellana* post-larvæ was noted.

UPOGEBIA spp. LARVÆ.

Larval forms of *Upogebia*, including probably both *U. deltura* Leach, and *U. stellata* (Montagu), showed a tendency to be distributed higher in the water than most species of decapod larvæ. On June 4th they became abundant at a depth of about 15 metres below the surface at position A, and just below 10 metres at L4. On the other days from July 1st to August 6th they only avoided the actual surface layers, and were found abundantly at 10 or even 5 metres (Fig. 9).

Seasonal distribution. Upogebia larvæ were practically absent from the catches until June 4th; at this date it was noticed that they were all in the early stages of development without the possession of uropods. By June 17th later stages, in which uropods were present, were caught. Another batch of young stages occurred on August 6th. All larvæ became very much more numerous by July 16th, and the numbers were still increasing on August 6th.

UPOGEBIA spp. POST-LARVÆ.

These post-larvæ were very scarce in the collections; when present they were nearly always below 20 metres. Probably this stage is almost bottom living. The post-larvæ of both *U. deltura* and *U. stellata* were noticed.

LARVÆ OF CALLIANASSA SUBTERRANEA Leach.

Larvæ of this decapod were most numerous below 20 metres, except on August 6th, when they were slightly higher in the water (Fig. 9). Like the zoeas of Porcellana, on July 1st at L4, Callianassa larvæ were extremely abundant at 36.7 m., while at all depths above they were relatively scarce.

Seasonal distribution. Callianassa larvæ did not appear at all in the collections until June 17th. The numbers were very much increased on July 16th and 29th.

LARVÆ OF AXIUS STYRHINCHUS Leach.

These larvæ were only caught on three days in the daytime. On June 17th one at 29.8 m.; on July 1st at L4 one was taken at 27.1 m. and 3 at 36.7 m.; on August 6th two specimens were caught at each of the following three depths respectively, 19.2, 23.1, and 33.6 metres. This slight evidence then points to their preference for the layers below a depth of 15 metres.

PAGURID LARVÆ.

Fig. 10 shows that these larvæ lived generally deep down, below the 20-metre level, and from the shapes of most of the distribution diagrams it would appear that the upper portion only of their vertical distribution region was sampled. They thus lie slightly deeper in the water than the Galatheid larvæ, whose numbers can be seen from Fig. 10 mostly to be decreasing in the deepest hauls.

Seasonal distribution. Pagurid larvæ were present in all the collections, the largest catch occurring on May 19th.

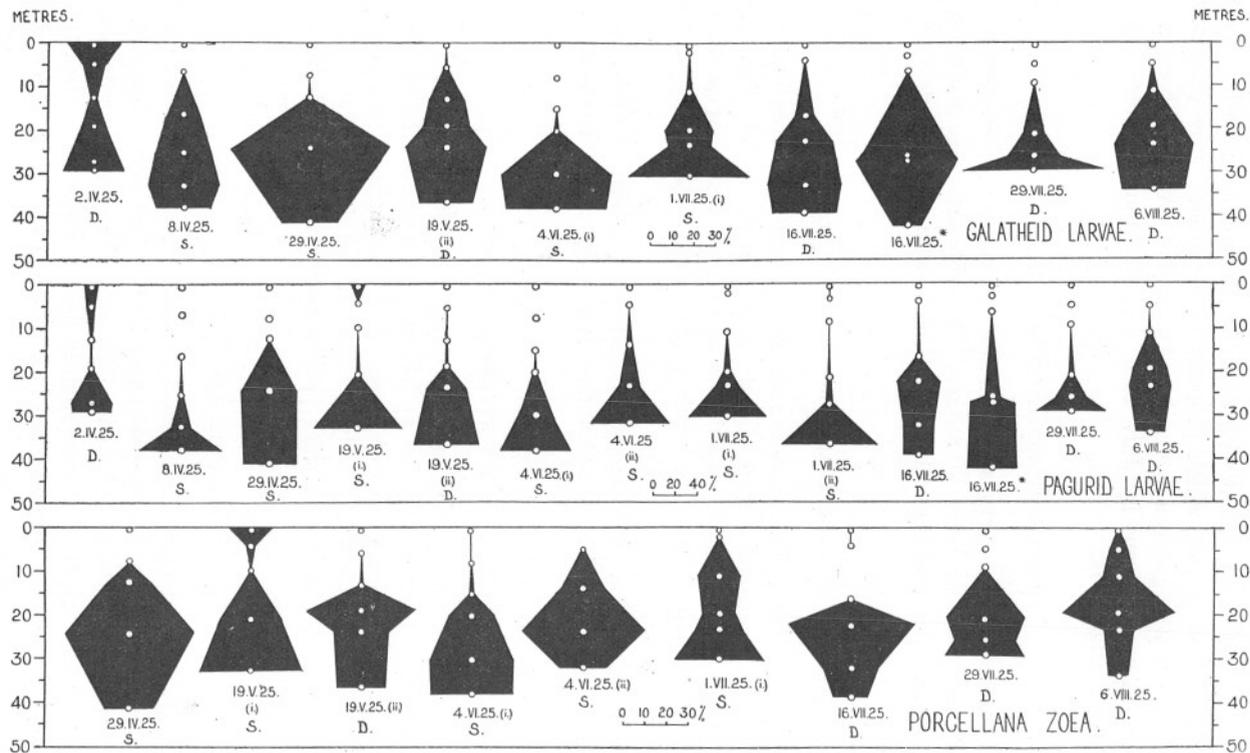


FIG. 10.—The percentage vertical distribution of Galatheid larvæ, Pagurid larvæ, and Porcellana sp. zoeae, on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull. Asterisk (*) = closing metre net. Note that the percentage scale for Pagurid larvæ is half that of the other two species.

GLAUCOTHOË LARVÆ OF PAGURIDS.

These post-larval stages of the hermit crabs were not very numerous, when they did occur, however, it was nearly always below 22 metres. The largest catches were on May 19th, at L4, when 12 were taken at 23.7 metres and 62 at 36.5 m.

It seems probable, however, that generally this stage lives actually on, or very near to, the bottom in the daytime, as the numbers in the deeper layers always increase at night, apparently indicating that the animals have come from still deeper levels; this occurred in July, 1924 (22, p. 805), and also again in June, 1925, but the results on this occasion are not yet published.

PORCELLANA spp. ZOEÆ.

The zoeas of *Porcellana*, probably *P. platycheles* (Pennant) and *P. longicornis* (Linnæus), were very abundant at most of the stations. In Fig. 10 it can be seen that in the majority of cases they show an increase in numbers below 15 metres, being comparatively scarce in the upper layers.

It is noticeable that on May 19th at Station A there were large quantities at the surface itself; in this they agree with many other of the plankton organisms on this occasion, the surface catch being characterised by a large mass of *Corystes* zoeas. Worthy of note also is the catch made at 36.7 m. on July 1st at L4, in which the enormous number of 62,820 *Porcellana* zoeas were present, while at all depths above this they were comparatively scarce.

Seasonal distribution. *Porcellana* zoeas were absent in the catches on April 2nd and April 8th, but had become very numerous by May 19th, after which date they remained abundant throughout the period of collecting.

PORCELLANA spp. POST-LARVÆ.

Post-larval stages of *Porcellana* from July 1st onwards always occurred below the 20-metre level. It is possible that like the Galatheid post-larvæ these may be more numerous in the water layers adjacent to the bottom. Before July 1st there may possibly have been some of these post-larvæ included with those of *Galathea*, as it is from this date only that I started to separate the two post-larvæ; in any case they cannot have been numerous as the numbers given for the Galatheid post-larvæ are low.

CRAB ZOEAS.

All the Crab zoeas are here treated together except for the later stages of *Corystes cassivelaunus*, and, after June 19th, the zoeas of *Ebalia* sp., which are dealt with separately below. It can, however, be fairly safely

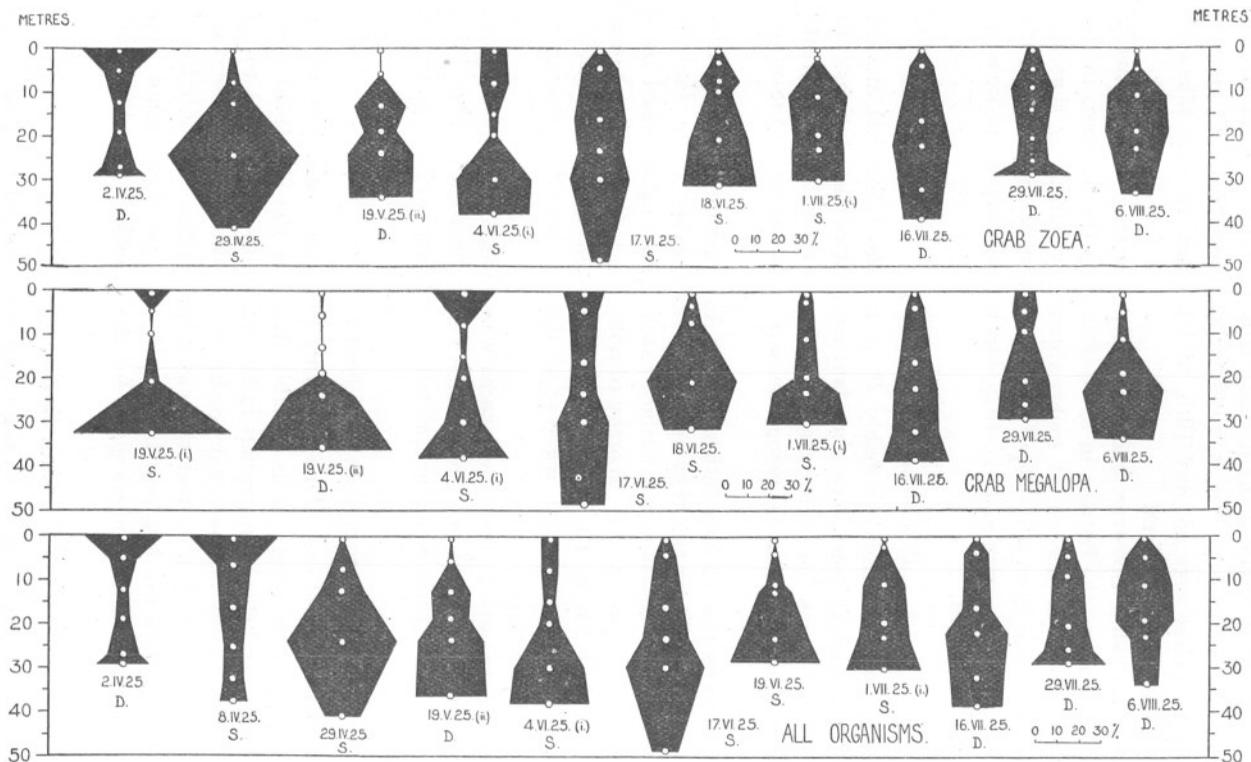


FIG. 11.—The percentage vertical distribution of Crab zoeae, Crab megalopas, and all organisms taken by the ring-trawl on the dates given. The white spots and black circles indicate the average depths at which hauls were taken. S=Sunshine. D=Dull.

said that the majority will be those of *Portunus* spp., these being by far the commonest in this locality. It is likely that different species of crabs will exhibit different behaviour, and, indeed, such is indicated by the zoeas of *Ebalia* sp., and in the 1926 material there are indications that *Hyas* sp. prefer the deeper layers: there is a strong possibility, however, that the *Portunus* spp. zoeas will on almost all occasions be present in such an overwhelming majority that the presence of other species may not significantly upset the true picture of their vertical distribution: I am not in a position to state this for certain. Of the *Portunus* spp. present near Plymouth, *P. depurator* (Linn.) is the most prevalent.

Fig. 11 shows the percentage vertical distribution of Crab zoeas throughout the period of collecting. It will be noticed that while, usually, they avoided the actual surface layers, they were frequently numerous right up to within 5 metres of the surface. It is interesting to find that Savage (26, p. 10) noted in the North Sea in July that "*Portunus* spp. (principally *P. depurator* and *P. holsatus*) . . . differed from the *Macrura* and the *Anomura* in that the greatest numbers were found in the surface hauls."

Seasonal distribution. Crab zoeas, although numerous in all collections, were by far the most abundant on May 19th. The very large catch of 87,060 at position A in the haul at 32.6 m. is noteworthy.

CRAB MEGALOPAS.

These include all species except *Corystes cassivelaunus* and, after July 16th, *Ebalia* sp. From a study of Fig. 11 it can be seen that there is a tendency for Crab megalopas to be slightly deeper in the water than the zoeas. On the other hand, there were occasions when they were relatively numerous actually at the surface itself.

Seasonal distribution. These megalopa stages of crabs were most abundant on May 19th and June 4th.

EBALIA sp. ZOEAE.

Until June 19th these zoeas were not separated from the main mass of Crab zoeas. On and after this date they were identified, and it was noticeable that they preferred the deeper layers, being absent always above 20 metres. On July 16th many of these zoeas, which are very small, were retained in the catches of the silk metre net, when the largest catch occurred at 41.75 m. (see Table II).

EBALIA sp. MEGALOPAS.

These were only identified from the remaining Crab megalopas on and after July 16th, when they occurred only in small numbers, generally in the deeper layers.

ZOEAE OF *CORYSTES CASSIVELAUNUS* (Pennant).

Corystes zoeas, mostly stages 3 and 4, on the two occasions on which they were taken appeared to show a preference for the surface layers. On April 8th a very thick shoal was encountered, and Fig. 5, p. 578, shows that the majority were located right at the surface. This swarm was very visible from the deck of the ship, and we were well in the middle of it when the first three hauls at the surface, 6.9 and 16.5 metres were made. No swarm was, however, visible, the ship having moved out of the area, when the deeper hauls at 25.3, 32.5, and 37.8 metres were made, so that it might be said that there was not evidence that in the centre of the swarm the zoeas were not just as numerous in the deeper layers as at the surface; the results for the upper three depths, however, when we were well in the shoal, point to a marked decrease in numbers from the surface downwards.

Seasonal distribution. After May 19th no *Corystes* zoeas were seen: it is evident that the majority of later stage zoeas were to be found in early April. Gurney, in 1902, observed the same. He says (11): "Occurring first on February 21st, the larvæ were obtained in small numbers fairly regularly from that time onwards. Advanced stages occurred first on March 15th, and in considerable numbers. The tow-net collections of April 14th, taken in the West Channel, were remarkable for the extraordinary abundance of the zoea stages of *Corystes*. They abounded on that date to the almost complete exclusion of all other zoeas, nearly all the specimens being at an advanced stage of development. Since April 14th the zoeas have continued to occur, but very few have been found in the early stages."

MEGALOPA OF *CORYSTES CASSIVELAUNUS* (Pennant).

On April 8th one megalopa was taken at the surface, and on April 22nd one at 51.4 metres. On May 19th *Corystes* megalopas were very abundant: on this day two stations were made, one at L4 and the other at A. It is interesting that at A, where they were very numerous, they were mostly located at the surface, while at L4, where their numbers were considerably smaller, the majority were in the deeper layers (Fig. 5, p. 578). The actual numbers were:—

19.v.25 (i.)	<i>Surface.</i>	4.3	9.9	20.8	32.6 metres.	
A.	4050	3970	2110	153	1214	
19.v.25 (ii.)	<i>Surface.</i>	5.6	12.9	18.9	23.7	36.5 metres.
L4.	34	8	5	25	59	430

It was noted that at A, where the great shoal of megalopas was located, the diatom *Rhizosolenia* was extremely abundant, whereas at L4 it was comparatively rare. Examination of stomachs, however, did not show that the megalopas were feeding on the diatom. The presence of many other species of plankton organisms at the surface amongst these *Corystes* megalopas was marked (see Table III); certain young fish which normally live deep down were also on the surface on this occasion (23, p. 109). Gurney says (11, p. 464) that the megalopa does not seem to be a pelagic form properly speaking, and was only once obtained in the tow-net, and then within a fathom or so of the bottom, in deep water.

Seasonal distribution. It is obvious from the above results that *Corystes* megalopas were most abundant in mid-May; after May 19th none were captured.

It would be interesting to know whether this was the same shoal that was met with on April 8th, when the *Corystes* were then in the later zoea stages. It is, at any rate, an indication that the larvæ must have some considerable powers of keeping together if, when they have passed through all the stages of their pelagic existence, they can form so large a shoal as that met with on May 19th, 1925. Gurney (14, p. 39) says: "It is not very unusual to find swarms of the larvæ of one species in different stages of development, which seems to indicate a power of keeping together from hatching onwards, or of collecting in a suitable locality." He mentions such a swarm of *Corystes* zoeas at Plymouth.

STOMATOPODA.

ALIMA LARVÆ OF *SQUILLA DESMARESTI* Risso.

These larvæ were present on two days, July 29th and August 6th, the catches being—

JULY 29TH, 1925.		A.	R.T.	AUGUST 6TH, 1925.		A.	R.T.
<i>Surface</i>	.	.	—	<i>Surface</i>	.	.	—
4.8 m.	.	.	—	5 m.	.	.	—
9.1 "	.	.	—	11.1 "	.	.	12
20.6 "	.	.	3	19.2 "	.	.	16
25.8 "	.	.	1	23.1 "	.	.	9
29 "	.	.	—	33.6 "	.	.	4

Thus it is seen that the larvæ, which consisted of stages 1, 2, 3, and 4 (Giesbrecht, 7) in equal numbers and of one stage 5, appeared to have their maximum abundance between 10 and 25 metres, being absent from the surface and 5-metre layers.

Giesbrecht (7, p. 226), in connection with the vertical distribution of this species in the Mediterranean, says that the pelagic larvæ of *Squilla* sp. (*Alima*) were only occasionally met with in the surface catches, most of them occurring in the collections made with nets with 50 to 200 metres of wire out. According to Chun (2, p. 29) *Alima* stages were chiefly at a depth of 40–100 m. It is to be expected that in this region they would be higher in the water than in the Mediterranean.

MOLLUSCA.

ECHINOSPIRA LARVÆ OF LAMELLARIA sp.

Echinospira larvæ, when present, always occurred below a depth of 10 metres. They were never captured at levels above this depth.

PURPURA LAPILLUS (Linnæus).

Young stages of this species occurred once in the plankton, when nine were taken at 22.1 metres on April 22nd, at E1.

LIMACINA RETROVERSA (Flemm.).

When present *Limacina* were taken from depths below 10 metres.

Paulsen (21 a, p. 57) says, "As a whole, *L. retroversa* is a surface-organism, found most frequently at or near the surface of the sea. In many cases it is common from the surface to a depth of about 50 m." He also gives records from greater depths, and he further remarks, "When the sun is high in the sky, the species is sometimes not met with at the surface in great quantities, but lives in a depth 5–75 m., but when the sun is low large shoals can be taken at the very surface."

PHORONIDEA.

ACTINOTROCHA LARVÆ OF PHORONIS sp.

Actinotrocha larvæ occurred in the collections at E1 on April 22nd, when 4 were taken at 22.1 m., 3 at 51.4, and 2 at 61.4 metres.

VERTEBRATA.

PISCES.

Pelagic eggs of Teleostean fishes occurred in fair quantities, but on account of the difficulty of identifying preserved eggs they have not been dealt with. The vertical distribution shown by the pelagic young of teleostean fishes has been dealt with in a previous paper (23).

SUMMARY.

1. The vertical distribution of many species in daylight in the Plymouth area is shown, as a result of the examination of a number of serial hauls taken with the stramin ring-trawl between the dates April 2nd and August 6th, 1926.

2. It is shown that probably the errors introduced by the employment of a non-closing net are for the present purpose negligible.

3. The indications are that most species have an optimum level at which they live, in the daytime, the actual depth varying from day to day according to weather and other conditions.

4. A few species appear to show no preference, being present equally abundantly at all depths or showing marked changes in the region of greatest abundance from day to day.

5. A provisional list is given on page 567, showing the order in which many of the different species appear in greatest abundance from the surface downwards.

6. The vertical distribution appears to differ for the two sexes of *Calanus finmarchicus*, the males tending to avoid the surface layers more than the females.

7. The presence of the medusa *Cosmetira pilosella* in fair numbers in a catch in the daytime in the Plymouth region would seem to be a reliable indication that the net has been fishing below 20 metres.

8. A catch of *Calanus finmarchicus* made by the stramin ring-trawl consists nearly always of over 80 per cent adults.

9. No attempt has been made definitely to correlate behaviour with external factors: more observations are to be desired.

10. Brief notes are given on the seasonal distribution of various species. The danger of drawing conclusions about seasonal abundance from daylight hauls only is shown by the results for *Tomopteris helgolandica* (p. 575).

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TABLE II.
SHOWING TOTAL NUMBERS OF ORGANISMS IN 10-MINUTE
HAULS AT EACH DEPTH.

July 16th, 1925.	Closing Metre Net.					
	Surface.	A. 2·7 m.	6·5 m.	25·8 m.	26·8 m.	41·8 m.
<i>Anomalocera Patersoni</i>	291	123	101	12	6	3
<i>Leander</i> sp. larvæ	2	4	—	—	—	—
<i>Calanus finmarchicus</i>	17,640	28,540	59,220	13,900	21,680	6,880
Crab zoeas	5,740	1,920	3,860	2,280	2,380	4,320
<i>Upogebia</i> sp. larvæ	900	840	2,300	2,380	380	180
Crab megalopa	380	60	60	120	100	60
<i>Centropages typicus</i>	5,860	11,560	21,680	6,980	6,080	1,840
<i>Sagitta bipunctata</i>	1,080	5,860	8,460	10,940	15,360	21,280
<i>Pleurobrachia pileus</i>	81	11	27	28	36	25
<i>Phialidium</i> sp.	60	6,520	3,760	780	20	2,940
<i>Obelia</i> sp.	—	160	2,720	2,040	—	180
<i>Turris pileata</i>	—	1	2	29	293	125
<i>Podon intermedius</i>	—	60	420	2,720	1,460	760
<i>Evadne Nordmanni</i>	—	40	80	200	40	20
<i>Isias clavipes</i>	—	—	40	40	20	20
<i>Pandalid</i> larvæ	—	—	20	360	960	620
<i>Nyctiphanes furcilia</i>	—	—	100	140	40	100
<i>Porcellana</i> sp. zoea	—	—	—	140	120	420
<i>Galatheid</i> larvæ	—	—	—	700	740	220
<i>Callianassa</i> larvæ	—	—	—	1,520	3,760	2,280
<i>Cosmetira pilosella</i>	—	—	—	110	14	108
<i>Candacia armata</i>	—	—	—	40	180	40
<i>Apherusa</i> sp.	—	—	—	3,480	6,480	6,940
<i>Pagurid</i> larvæ	—	—	—	180	480	540
<i>Saphenia gracilis</i>	—	—	—	11	—	32
Young mysids	—	—	—	200	100	840
<i>Tomopteris helgolandica</i>	—	—	—	14	17	169
<i>Crangonid</i> larvæ	—	—	—	80	120	100
<i>Ebalia</i> sp. zoea	—	—	—	140	200	720
<i>Metridia lucens</i>	—	—	—	20	20	20
<i>Temora longicornis</i>	40	40	—	5,820	11,320	29,820
<i>Nyctiphanes Couchii</i>	—	—	—	4	25	63
<i>Palinurus phyllosoma</i>	—	—	—	1	1	6
<i>Galatheid</i> post-larvæ	—	—	—	20	—	—
<i>Porcellana</i> sp. post-larva	—	—	—	60	40	80
<i>Upogebia</i> sp. post-larva	—	—	—	1	1	4
Young <i>Æquorea</i> <i>Forskalia</i>	—	—	—	3	—	1
Adult mysids	—	—	—	—	1	21
<i>Caligus rapax</i>	—	—	—	—	2	2
<i>Bougainvillea</i> sp.	—	—	—	—	—	4
<i>Ebalia</i> sp. megalopa	—	—	—	—	—	40
<i>Pagurid glaucothoë</i>	—	—	—	—	—	3
<i>Pœciloætus</i> larvæ	—	—	—	—	—	2

The Phosphorus and Arsenic Compounds of Sea-Water.

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THE first estimations of phosphate in sea-water, in which sufficiently accurate analytical methods were adopted, were carried out more or less simultaneously by Matthews (1916, 1917) and by Raben (1916-20) working independently. Matthews used the colorimetric method of Pouget and Chouchak (1909, 1911), and precipitated the phosphate from 500 c.c. of sea-water by means of ferric chloride. Pouget and Chouchak checked their method using the gravimetric method of Posternak, weighing the barium phosphomolybdate obtained. Values similar to those obtained by Matthews were obtained in the Government Chemist's Laboratory, London, upon samples sent from Plymouth, and the seasonal variation in the phosphate content of sea-water as found by one of us (1923) is in close agreement with the analyses recorded by Matthews—although an entirely different method was used, that of Denigès, which is colorimetric.

Raben analysed sea-water from many sources and from various depths, but his results and those of his co-workers are uniformly much higher than those of Matthews and Atkins (1925, 1926) for surface water; moreover, these results as plotted by Brandt (1920) never indicate that lack of phosphate may set a limit to the algal plankton, for the minimum value found was close to 50 mg. of phosphate, as P_2O_5 per m.³, whereas Matthews and Atkins found the surface water to be almost entirely devoid of phosphate in summer. As has previously been pointed out by one of us (1926) a serious discrepancy exists, though Raben tested his analytical methods upon known minute amounts of phosphate in the presence of the salts of sea-water, and his results leave nothing to be desired so far as their accuracy is concerned and within the limits of the conditions of his test.

Matthews, however, found that with the ammonium phosphomolybdate precipitate a little molybdic acid was liable to be thrown down, and he considered the colorimetric method to be the preferable. He also found

that after oxidising with permanganate or nitric acid larger yields were obtained. He arrived at the conclusion that "the analyses as a whole, however, do not allow more to be stated with certainty than that there is a soluble phosphorus compound present other than phosphoric acid, that it is probably not a lower acid of phosphorus, owing to the comparative difficulty with which it is oxidised, and that it is probably an organic compound." Now Raben's ordinary routine involved evaporation with nitric acid, so the results obtained are comparable rather with Matthews' results for phosphate plus phosphate from organically combined phosphorus than for his values for phosphate alone. The writers do not wish to deny that a portion of the phosphorus present in sea-water may exist in an organic combination, since it is built up into such compounds as lecithin (choline distearyl-glycerophosphate) and others of similar or greater complexity. Such a body as lecithin* is, however, hydrolysed, and not oxidised to phosphate.

While not denying that some of the phosphorus of sea-water may be in solution as a complex phosphate, or as some other complex phosphorus compound, the writers are of the opinion that the results obtained by Matthews can be equally well explained, on a qualitative basis, by taking into account the presence of arsenic in sea-water. The quantitative analyses available show, moreover, that arsenic, calculated as As_2O_3 , may be present in amount equal to, or greater than, that of phosphate, as P_2O_5 . The suggestion is also put forward that Raben's high values for phosphate are due to his method of analysis (though reliable for phosphate alone) including arsenate; the latter would be produced from arsenite originally present, by oxidation with nitric acid as carried out in the course of his method of analysis.

With the object of testing these points, a study of the behaviour of various methods of analysis of phosphate, arsenate and arsenite, was undertaken, the results being published elsewhere (1926). It was found that Denigès reaction for phosphates is given by arsenates also, but not by arsenites. Values for phosphate in sea-water, thus obtained, will accordingly include arsenate, if any; both these radicles would therefore be quantitatively removed from surface waters in early summer. Now algæ are known to contain small amounts of arsenic, as will be mentioned later, so it is possible that a little arsenate is present in sea-water, and is removed by the plankton simultaneously with the removal of phosphate. Arsenic up to 25 mg. As_2O_3 per m.³ is, however, present in water of the English Channel in November (Orton, 1924). This was ascertained by the electrolytic modification of Marsh's apparatus in the Government Chemist's Laboratory, London. It accordingly records

* Stoklasa (1896) showed by a culture experiment with *Avena sativa* in a sterile solution, to which lecithin was added as the only source of phosphorus, that the plant was able to take up lecithin and utilise it.

only the presence of arsenic, without indicating its state of combination. The arsenic, if present as arsenite, would therefore only be detected by Denigès reaction after oxidation. Similarly it was found that Bell and Doisy's method for phosphates was applicable to arsenates also, but arsenites behaved irregularly. This method is, however, less sensitive than that of Denigès, and was not used for sea-water.

Pouget and Chouchak's method, used by Matthews, was also examined; it gives with phosphates either an immediate opalescence in the cold or, if very dilute, on standing; with arsenates in equimolecular quantities no opalescence is obtained in the cold—or at most a very faint opalescence, though on warming the normal opalescence and yellow colour appear; with arsenites only a very faint opalescence appears on warming, due probably to slight oxidation to arsenate. Matthews' results obtained after oxidation appear therefore to be, in part at least, due to the oxidation of arsenite, present in sea-water, to arsenate; the irregularity of the figures obtained, upon which Matthews comments specially, seems to have been due to the uncertain amount of arsenate yielding the opalescence in a solution, not actually warmed, but probably warm from its previous treatment, and to the difficulty of oxidising the arsenite quantitatively to arsenate by either nitric acid or permanganate.

Again, in Raben's work the phosphate was precipitated as ammonium phosphomolybdate, and by using an artificial sea-water made up from pure chemicals Raben demonstrated that the accuracy was not impaired by the presence of the salts. Such a mixture would, however, contain little arsenic, though minute traces must have been present. In sea-water, however, arsenic and phosphorus are, in winter, present in amounts which are roughly equal or of the same order of magnitude. Arsenite present in sea-water would certainly have been converted almost entirely into arsenate by the prolonged evaporation with nitric acid which forms a part of Raben's method, and the ammonium arsenomolybdate produced would have been precipitated and weighed with the phosphomolybdate.

Nevertheless according to Kuhn (1923) it is impossible to base a method for quantitative estimation of arsenic upon the separation of ammonium arsenomolybdate. Under the usual conditions for the precipitation of phosphate, Kuhn states that only a small fraction of the arsenic will be precipitated at 75°, and even at 90° precipitation is incomplete, while at the higher temperatures varying amounts of molybdic acid are precipitated according to the period of heating. Kuhn, however, has overlooked Maderna's (1910) method for the quantitative precipitation of ammonium arsenomolybdate. Raben's analyses appear accordingly to have been vitiated by the weighing of a certain proportion of arsenomolybdate with the phosphomolybdate. This explains why he never obtained results indicating the complete removal of phosphate from the

surface waters, since arsenite remained in the sea-water and was recorded as phosphate.

Pending a study of the arsenic content of sea-water throughout the year it is of interest to note that Gautier and Clausmann (1904) record the presence of 11 mg. per m.³ of arsenic—given as element, not oxide—for surface water 40 kilometres from the coast of Brittany. Near the Azores they found 25 mg. per m.³ at 10 m. depth, and note that the arsenic showed much increase at greater depths. The season is not recorded. The results were obtained by precipitation with a ferric salt and estimation with Marsh's apparatus—and it may be pointed out that Gautier and Clausmann's results afford direct evidence that the phosphate precipitated by Raben also contained arsenic. The values obtained for arsenic are quite in keeping with that found by the Government Chemist, London, 25 mg. per m.³ of arsenic, recorded as As_2O_3 , for water near the bottom, 70 m. depth, in the English Channel in November. Since Orton (1924) records a considerable amount of arsenic in oysters, more, in fact, than the amount allowed by law to be sold in foodstuffs, and since oysters feed largely upon diatoms, it is clearly indicated that diatoms must contain a certain amount of arsenic. The increase of arsenic with depth also suggests that in the upper layers its amount has been diminished through absorption by plants. The analyses of Jones (1922) are direct evidence on this point, for he found that the arsenic content of eleven species of algæ varied from seven parts per million of As_2O_3 in *Chondrus crispus* to 125 p.p.m. in *Laminaria digitata*; most of the arsenic is soluble in cold water, and the arsenic content seems to run roughly parallel to that of iodine. Comère (1909), too, has shown that potassium arsenate can be substituted, though apparently not entirely, for phosphate as a nutrient salt for the cultivation of *Stichococcus flaccidus* and *Spirogyra crassa*; of these the former resists the action of various solutions better than the latter, and can take up much more arsenate. Similar experiments showed that *Edogonium capillare* could not thrive on arsenate.

SUMMARY.

1. Much of what was formerly considered to be phosphorus in organic combination, in sea-water, is in reality arsenic.
2. Certain analyses giving high values for phosphate in sea-water and a June minimum very far from complete exhaustion of phosphate are vitiated by the inclusion of arsenate, as arsenomolybdate, in the phosphomolybdate precipitate.
3. Arsenic in sea-water exists mainly in the form of arsenite. The arsenate present, if any, has hitherto been included in the results obtained for phosphate.

4. Since arsenic is found in algæ and has been recorded as increasing in quantity with increase of depth it seems that the arsenic present in sea-water must undergo seasonal changes.

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**Summary of a Report on a Survey of the Fal Estuary
Oyster Beds**

(November, 1924),

With Notes on the Biology of the Oyster (*O. edulis*).

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INTRODUCTION

THE Summary given in the following pages is a condensed account of a report* on a Survey of the Fal Estuary Oyster Beds carried out by the surveyor, for the Fisheries Branch of the Ministry of Agriculture and Fisheries, with the permission of the Director and Council of the Marine Biological Association, Plymouth. Thanks are due to Mr. W. H. Lupton and Mr. F. Parkin, the respective Town Clerks of Falmouth and Truro, and their Oyster Committees, and especially also to the bailiffs, Mr. E. Searle and Mr. C. May, and also to many fishermen; all of whom materially assisted the surveyor in his work. The survey could not have been carried out in the detailed method adopted without the willing and valuable assistance of Mr. Stevenson, who was courteously spared for the work by Mr. H. E. Tresidder, the Falmouth Borough Surveyor.

* J. H. Orton. Report on a Survey of the Fal Estuary Oyster Beds (November, 1924), with Notes on the Biology of the Oyster (*O. edulis*). Published by subscription at Falmouth in 1926. (Copies can now be purchased from the Marine Biological Association, Plymouth, at the price of 2s. 6d. per copy.)

SECTION A.

SUMMARY.

The spatfall in 1924, as in 1923, was very slight and from the point of view of the oyster-producer was a failure, and was little better in 1922.

The growth of oysters in the summer of 1924 was unusually great; this has had the effect of bringing a large proportion of small oysters to a legally takeable size.

The dredging results have, therefore, been much better than they were expected to be in the season of 1924-25, but the effect has been to deplete the beds still more of reserve stocks of small.

Practically all the present stocks of small oysters are of a size between 2 and $2\frac{1}{2}$ inches.

With only average growth in 1925 and 1926 a large majority of these small oysters will have attained a size which will not pass through a $2\frac{1}{2}$ -inch ring; hence the beds are in a dangerous state.

If, therefore, dredging continues under the present conditions, almost the whole of the *present* stock of small will have grown to large oysters and be cleared off the beds in the season of 1926-27.

It is shown that although oysters may grow to a size of $2\frac{1}{2}$ inches at Falmouth in small numbers in three summers, yet four summers are required before a fair proportion of spat can be expected to attain a size of $2\frac{1}{2}$ inches.

Thus, even if a great fall of oyster spat occurs in 1925, this fall will not affect legal dredging in appreciable numbers until the season 1928-29.

As the beds will be almost cleared of *existing* stocks in 1926-27 if the present conditions of oyster dredging continue, there must be, in any case, a lean year for oyster dredging in 1927-28.

The proportion of large to small oysters on the average in dredge-hauls was, in October, 1924, on the Vilt grounds about 1 to 1; on the North Bank, 1 to 2; on Carclase Point, 1 to 1.3. In November the same proportion on the Truro banks generally was 1 to 1.6, but higher off Pill Creek and on the South part of the East Bank, and as high as 1 to 5 on the average on Turnaware Bar.

Hence the total stock of oysters remaining on the grounds at the end of the season cannot be very much greater than the total amount of large oysters present on the grounds at the beginning of the season 1924-25. Estimates of the total stock of oysters on the grounds were made from records of catches of sailing and rowing-boats by dredge hauls and grabbing. It is estimated that the total stock present on the Truro beds in April, 1925, will be about five million small and about half a million large; and on the Falmouth beds about one

and a quarter million small and *at least* one-eighth of a million large. To these totals can safely be added a quarter million oysters in those parts of the channels rarely dredged, giving a total of rather more than seven millions. The total stock on the Fal Estuary *main* dredging grounds in April, 1925, is estimated at six and a quarter million small and about five-eighths of a million large.

The rate of growth of the small oysters of different sizes and ages in 1924 was worked out in detail, and the average growth calculated. From this average growth of small in 1924 the average growth in 1925 is estimated, and on these assumptions it is calculated that the following totals may be dredged in the 1925-26 season at the given sizes of ring :—

	Ring 2½.	Ring 2¾.	Ring 3.
Truro . .	2½ millions.	1¼ millions.	$\frac{6}{10}$ million.
Falmouth . .	$\frac{3}{4}$ million.	$\frac{4}{10}$ million.	$\frac{1}{4}$,,
	—	—	—
	3¼ millions.	1 $\frac{3}{10}$ millions.	$\frac{7}{10}$ million.

Suggestions are made for obtaining estimates of the total stock in the future, and for obtaining returns of oysters taken from the grounds.

It is considered that the beds should be closed to reserve a minimum stock for spawning one month after it is found that not more than 13 oysters per man per hour can be dredged under good dredging conditions.

Of the present stock of oysters about 45% are dumps, which are thick shelled, somewhat Brazil-nut shaped oysters, apparently very slow in growing and almost certainly very useful for spawning purposes owing to their very good fish. These should be preserved if stocks do finally become very low.

Various matters are also discussed, namely, the distribution of cultch over the grounds, the mortality in 1924, pests, the improvement in "whiteness" of "fish" in Mylor Bank oysters, weight of fish in fast-grown oysters, and the beds of Falmouth Inner Harbour.

A relation between catching power of the grab, rowing-boat dredge, and sailing-boat dredge on Truro grounds is calculated as 13.75 is to 2.5 is to 1. The grab was usefully employed on parts of the ground where oysters were relatively abundant.

Biological recommendations and suggestions for the future administration of the beds are made.

Efforts are being made to obtain figures of the total number of large oysters dredged in 1924-25 to check the estimates made, and to obtain information of dredging results near the end of the season for the purpose of estimating the amount of large left on the beds at the close of the season.

CONCLUSIONS.

The depleted stocks of small, which are mostly near the present legally takeable size, should be eked out so that a maximum number may remain on the beds to provide spawn for re-stocking the beds. Of the total estimated stock of seven million oysters on the grounds, it is recommended that two million a year for the next two years be allowed to be taken from the beds, and the position be reconsidered at the end of those two years.

For the 1925-26 season it is estimated that, *with average growth* in the summer of 1925, about two million oysters will be dredgeable with a "ring" of $2\frac{5}{8}$ inches, and it is recommended that this ring should be adopted for the season 1925-26. The restriction in the output in the season 1926-27 should be regulated in accordance with the experience gained in the season 1925-26.

Other alternative methods of securing an output of two million oysters per year are suggested, but it is recommended that any alterations in the hours or days of work should be so made as to favour the regular dredgerman. The restriction in the output of oysters makes reasonable a restriction of licences to those dredgermen who have habitually worked on the beds in the past, but owing to the probable difficulty in effecting such a restriction, all possible means to help the regular dredgermen should be taken.

Power should be in the hands of the Truro and Falmouth authorities to shorten the dredging season by one month at each end as and when partially or wholly necessary until the beds are restocked with abundant young oysters.

Efforts should be made to provide a spawning stock of oysters as indicated, and to improve the beds, with a jury of dredgermen and a foreman.

Cultch laying of the kind indicated should be instituted at once, so that at least tilling, as well as harvesting, is done on the beds. There is every reason to believe that with care the beds will sooner or later recover their former prosperity, for the present shortage is certainly due to over-fishing, that is, taking more individuals from the beds than nature has replaced, during the last three years, and the beds and the oysters are in a healthy condition.

SECTION B.

I. BIOLOGICAL RECOMMENDATIONS.

(a) *Necessity of limiting the number of oysters to be taken from the beds in the next few years to one-fourth to one-third of the present stock per annum.* Owing to the facts that on all grounds the great majority of the small

oysters are of a size between 2 and $2\frac{1}{2}$ inches, and that the total number of oysters on the beds is relatively small, it is essential that the output of oysters by dredging be limited during the next three years, so that no more than one-fourth to one-third of the present stock is taken per year at least during the next two dredging seasons. Ways and means of effecting this result are discussed in the next section.

(b) *On the minimum stock of oysters which may be expected to restock the beds with spat, and the epoch when the beds should be declared closed.* The conclusion is reached that a practical definition of the minimum stock which must, under the present conditions, be retained on the beds for the purpose of re-stocking the beds with spat, may be given as follows: the beds should be closed one month after it is found impossible to dredge on the average more than 13 large oysters (whether with a $2\frac{1}{2}$ -inch or $2\frac{2}{3}$ -inch ring) per hour, in good dredging weather, or 90 per day of seven hours as is worked on the Truro beds, or 104 per day of eight hours on the Falmouth beds. This recommendation would be modifiable if a large number of big oysters could be retained on the beds by relaying them in a central position for the purpose of providing spawn.

(c) *Large oysters dredged from the Fal beds should be relaid on a central site on the beds for spawning purposes.* It is strongly recommended that in the immediate future efforts should be made to relay on a portion of the Fal beds the large oysters dredged from the main beds. These oysters might be relaid at the southward end of the East Bank, or some other suitable place to be decided, and retained for one or more years for the purpose of producing spawn. Suggestions for accomplishing the desired end are made in the following section.

(d) *Thinning out accumulations of small oysters.* The Truro authorities are recommended to thin out the small oysters, which are thick on Turnaware Bar, and also to some extent at Pill Creek, and at the southern portion of the East Bank. This thinning out can be accomplished to some extent in the same excellent way as was done last year, namely, by working at low spring tides and shovelling up the oysters. But another economical way would be to authorise the bailiff to load up cargoes of small from dredgermen working at these places during the present 1924-25 season, and spread them along with cultch at the same time over the poorer parts of the grounds. In the same way the Falmouth authority might thin out the accumulation of small at the north end of the Carclase Point grounds; and in both areas, if small have accumulated at any other points towards the end of the season, the bailiffs should be given authority to spread the excess on the poorer parts of the grounds.

(e) *Preparation for spat-catching by laying clean cultch.* A very serious matter on the Fal Estuary oyster beds is the fact that no preparation

and no attempt is made to catch oyster spat. So far as I know, at no other place in Europe where oyster-production is the chief source of income on the beds, is the sole reliance placed on nature. It may be argued that in the past this method has, except for certain periods, kept the beds stocked. The reply to that is that the stock has been maintained by chance, and might easily have been improved in the times of scarcity by a judicious laying of clean cultch. Indeed, if cultch-laying had been the practice on the Fal in the years 1920 and 1921 it is quite certain that the fishing in recent years would have been carried on with better results and the prospects for the future would be brighter. It is true that there are years when spat will settle on anything, at which times cultch-laying may be—but is not necessarily even then—superfluous. But these years of prolific fall are rare, and at other times the stock may be increased by preparing suitable material for the baby oysters to settle upon. The cultch in the water is, on the whole, either too dirty or overgrown too much with living organisms of all kinds, which compete for places on the cultch at the time the baby oysters are ready to settle.

Suggestions for the Supply of Cultch.

Any kind of clean shell, if placed on the beds *at about the time the oysters are settling*, will serve:—

- (1) The handiest supply of shell is the oyster-shell cultch on the grounds; but this must be taken out of the water and cleaned—exposure on the foreshore is sufficient—and put back again in suitable places at suitable times. Ways of doing this are suggested for choice in the next section.
- (2) Mussels are present in quantity in certain parts of the river; if these could be dredged with profit, and laid on the foreshore to clean, they would form useful cultch.
- (3) Cockle shell or any other form of shell, such as limpet shell, if it could be obtained cheaply enough in quantity, would also serve. Local beaches might be found where limpet and other shell may be obtained cheaply in some quantity.
- (4) Slipper-limpet shell, clean and dry, is available on the east coast, but may be too dear.
- (5) Cheap supplies of oyster-shell may possibly be obtainable in the district, and local buyers might be able to supply a certain quantity. All sources of shell should be tapped and utilised.

(f) *Time for laying cultch.* The clean cultch should be laid when there is the maximum amount of oyster-young swimming freely in the water. This period will probably fall in July, but no actual date can be fixed,

because the spawning, and hence the setting free of the young oysters, is dependent on a moderate degree of warm weather. An approximate period when the shell should be laid would be the first to the third week in July, but if the weather continues warm throughout the summer cultch may be laid continuously with profit from that time until well into August. An early summer will necessitate an earlier laying of cultch, and the earlier in the year the spat can be caught the better for the fishery. If a lot of shell is to be laid by a few men, it is often necessary to make an early start in order to put it out in good time. In practice it is easier to fix the time to put out cultch from observations on dredged oysters. If oysters are left in the store overnight periodically from the middle of June it is possible to find out very nearly the percentage of female spawning individuals. When a small percentage of oysters—as low as 1 to 5%—are found *in this way* to be black-sick, it is time some of the cultch was in the water. The following figures for 1924 on an East Coast ground, where spawning is probably quite as early as on the Falmouth grounds, are instructive:—

1924.	Number of oysters left in store overnight.	Female spawning oysters.	
		White-sick.	Black-sick.
June 11	2900	24	0
„ 12	4400	17	0
„ 12	3200 (small)	30	0
„ 13	2400 (small)	5	1
„ 13	2000	4	1
„ 25	1300	54	15
„ 26	1200	51	16
„ 27	900	32	29
„ 30	2400	16	5
July 3	1300	15	31

These oysters were mostly small and are therefore comparable with the stock at present available on the Fal beds.

If it is found impossible to investigate a sufficient number of dredged oysters for spawning an additional rule for laying cultch can be given, namely, that cultch-laying may begin when the body of the water in the Estuary is approaching in temperature 64° Fahrenheit. It will probably be found that cultch-laying can be begun earlier up the river than on the Truro Banks, and earlier on these banks than on the Falmouth grounds.

(g) *Place to lay cultch.* The best place or places to lay cultch on any oyster grounds can best be determined satisfactorily by persons who have known and observed their own beds for a long period of years. In 1924 spat fell more abundantly off Pill and Cowlands Creeks than anywhere else, but it does not follow that these will be the best places in 1925.

It is quite possible that the mouths of these creeks were good for spatfall in 1924, because the fresh water from the creeks cleaned the shell there. As the shell in the water in the river above Turnaware Point is likely to be cleaner than shell lower down, I recommend that the cultch be laid in 1925 on Turnaware Bar and the banks below, after consultation with the bailiff. Certain parts of the banks may be found to have a more consistent record for spatfall than others, and these places should have a larger supply of the available cultch, but it is urged that an effort should be made to spread cultch all over the banks in as great a quantity as can be obtained. It is certain that the banks will take more shell than the finances of the authorities can supply.

(h) *Observations required on the reproductive capacity of dumpy oysters.* It is most important that observations should be made this summer on the reproductive capacity of dumpy oysters. It has been shown that there is a very high proportion of this kind of oyster all over the beds. Since dumpy oysters are well fished and relatively old, it is probable that they will give a much larger number of oyster-young per individual than the remaining oysters. Hence, if it is necessary later to preserve a stock for spawning, these dumpy oysters, besides being less pleasing in appearance than the others, will probably be found to be more valuable for spawning purposes. Definite information is, however, required and can easily be obtained this summer.

(i) *Rate of growth in 1925 required to be known.* Observations should be made this summer on the average rate of growth of oysters on the Fal beds. This information will not be obtainable until the end of September, when it may be too late to be applied to regulations for the opening of the dredging season, if this occurs at the normal time; but it would be available for estimation or regulation of the output later. It would be preferable to carry out actual experiments to determine the rate of growth, so that the experimental results can be compared with work on the beds. An important point to be noted in this work is the extent to which the spring shoot becomes infiltrated with a green colour—presumably an algal growth in the shell—towards the end of the growing season.

(j) *Experiments on spatfall in 1925.* There can be no doubt that the Fal Estuary is an ideal spot for oyster-production, and the lake formed by the Mylor-Parsons and the East Banks, along with the river reaches, together afford an excellent situation for studying the fall of spat. The hydrographical conditions are at present unknown, but the general conformation of the Estuary makes it plain that a continuous grading of conditions may be expected. Thus, if there are particular hydrographical conditions most suitable for the fall of oyster-spat—and there can be little doubt that there are—then suitable conditions have a good chance of

occurring here at some points every year. If, therefore, the places where the best conditions for the fall of spat are likely to occur could be found, the cultch could be spread mainly in these places to the benefit of all connected with the fishery. Thus, as is so often the case, there is in this problem the double interest of immediate economic application of the result sought for and the great general interest in finding out in some detail the underlying conditions which favour a fall of oyster-spat on a natural bed. It is recommended, therefore, that experiments be carried out on the conditions for and distribution of the fall of oyster-spat in the coming summer. In this branch of work it is important to realise that spat may fall on the shells and not survive in each year in the same proportion. Our information on spatfall at present is almost entirely limited to the amount which *survives* each year. An early report on the nature of the spatfall in 1925 would be useful to the bodies responsible for the care of the beds.

II. SUGGESTIONS FOR FUTURE ADMINISTRATION.

1. *Necessity for restriction of output.* The low condition of the stocks on the oyster beds, as well as the fact that most of the small oysters are already 2 to 2½ inches in size and the impossibility of these being replaced in any adequate degree until 1928 at the earliest, will necessitate some curtailment of the taking of oysters from the Fal beds, so that a sufficiency may be retained for spawning purposes.

2. *Mode of restriction a matter of arrangement to suit particularly the dredgermen.* As, however, the output of the beds can be controlled to the same extent in several different ways, that is to say, the matter is one of politics, it is not intended to do more here than to suggest alternative methods of attaining the same end, while at the same time indicating the alternative which seems best to the surveyor.

3. *Joint administration of the Fal and Truro beds suggested.* It is convenient first to consider whether it would not be better to combine both the Truro and Falmouth beds under one authority. There would be many advantages in this course, namely :—

- (a) The beds could be treated as a whole for administration.
- (b) Supervision of the beds could be improved.
- (c) Concerted action for improvement of the beds could more easily be taken.
- (d) The public body chosen to control the fishery might be elected upon a new basis which would give the dredgermen direct representation, while at the same time maintaining the public character of the beds.

Whether the disadvantages in administration by a body of this kind would be greater than the advantages it is probably not easy to foresee until the matter is probed. In any event both Truro and Falmouth authorities should adopt the same administrative methods so far as this is possible.

4. *Conference of Truro and Fal administrators and representatives of dredgermen suggested to consider this Report.* In order to arrive at a solution of the present difficulties in administering the beds, the surveyor suggests the following procedure. A conference of representatives of the Truro and Falmouth authorities and dredgermen should meet as soon as possible to consider this Report. At this meeting it should be decided whether restriction of output to about one-third of the stock per annum, namely, about two million at $2\frac{5}{8}$ inches for the next two years, should be adopted. If this restriction is not adopted some statement should be made giving the general view of the conference, which could be dealt with according to circumstances. If the restriction is adopted, then the simplest procedure afterwards is to find the views of the fishermen as to the best way of meeting their needs whilst, at the same time, ensuring restriction of output, and to apply them, whilst also paying some attention to the needs of buyers. The dredgermen should be made to realise that the restrictions to be put on dredging are entirely for their ultimate benefit.

The following alternatives of effecting a reduction in the output of oysters may be summarised :—

- (a) Adoption of a ring of $2\frac{5}{8}$ inches, with powers, to be used if necessary, to shorten the spring end of the season by one month, and to shorten the hours of work.
- (b) Adoption of a system of weekly returns of catches, and closing of beds by one month's notice with ring at $2\frac{1}{2}$ or $2\frac{5}{8}$ inches.
- (c) Drastic reduction of present hours of work on beds with ring at $2\frac{1}{2}$ inches.
- (d) As in (c), but less drastic, with reduction of licences.
- (e) In all the above cases it would probably be advisable to shorten the season at the opening period by a fortnight, and power should be asked for to shorten the season by as much as a month, if necessary, at each end of the season.
- (f) The ring could remain at $2\frac{1}{2}$ inches and unrestricted dredging allowed until the minimum stock as defined remains on the beds, but the dredgermen would suffer ultimately and the beds may take many more years to recover than if a reasonable course is adopted.

From the fishermen's point of view, and probably also that of the buyer, it is essential to keep the beds open for dredging as long as possible.

Since, however, the beds will be dredged out before a fresh stock arrives, unless the conditions of dredging are altered, something must be decided as to how the stock is to be allowed to be taken.

5. *The preservation of the beds.* From a biological point of view the larger the stock which can be retained on the beds until a big spatfall is obtained, the better for the beds. We have seen that there is a total stock of about $5\frac{1}{2}$ million oysters on the Truro beds and about $1\frac{1}{2}$ million on the Falmouth beds available for the future and that the stock cannot be replaced until 1928 or later. A reasonable plan, therefore, would be to allow of an output for two years of approximately one-third of the stock each year, and revise the situation at the end of the dredging season in 1926-27. The problem, therefore, arises as to how to regulate the beds to permit of one-third of the oysters being taken each year for the next two years.

6. *Raising the ring to $2\frac{5}{8}$ inches recommended.* We have seen that if the ring remains at $2\frac{1}{2}$ inches the dredgeable oysters in the season 1925-26 will number about $3\frac{1}{4}$ million, which is too many. If the ring is $2\frac{5}{8}$ inches the dredgeable oysters will amount to nearly two million, which is about the number it is desired to lose from the beds. This procedure, i.e. the adoption of a ring at $2\frac{5}{8}$ inches, would be the simplest way out of the present difficulties, but if growth is good in the present summer, 1925, the number of dredgeable oysters will be greater than two millions. The great advantage of this method would be that the beds could be kept open and hours of dredging arranged in consultation with the dredgermen, so that work might be carried on continuously throughout the next dredging season.

7. *Hours of work to be arranged to suit the interest of the regular dredgermen.* The hours of work should be so arranged that non-dredgermen, already in other employments, should not find it worth while to change their occupation. Every effort should be made to retain for the dredgerman the work he has, and is obliged, to do, in times when the pay is poor and does not attract outsiders. This desirable result will be best obtained after consultation with the dredgermen. It is probable that an output of about two million large oysters from the whole of the beds could be regulated solely by a reduction in the hours of work permitted on the beds, whether dredging be restricted to certain days or certain parts of each day.

8. *Shortening of the season.* It is clear that something more than shortening of the season is necessary to restrict the output, but a restricted season will help and may be taken into consideration when the shortening of the hours of work is discussed. Power to shorten the season at the

spring end ought to be given to the administrators in the event of failure to restrict the output to the desired amount.

9. *Reduction in the number of licences.* If the necessity for reduction in output is agreed upon by everyone, then it will follow that a restriction of licences to *bona fide* dredgers may be considered permissible. However, as has already been pointed out, this is a difficult matter to deal with and reach a quick decision upon, it would be advisable to consider the alternatives thoroughly before attacking it.

10. *The interest of the regular buyer should be considered.* Since no oysters would be dredged if they could not be sold, it is reasonable that the regular buyers from the Fal Estuary beds should be given an opportunity of stating their needs for retaining those establishments which have been built up to meet the requirements of the Fal Estuary in past years.

11. *Establishment of a spawning stock.* It has been already pointed out that it would be a great help to the beds if a large number of older oysters could be relaid in a central position on the beds for the purpose of providing spawn. Various ways of effecting this result may be mentioned :—

- (1) The southern part of the East Bank and a part of the St. Just Flats might be put out of bounds for dredging.
- (2) The Channels—to be defined—might be put out of bounds for dredging.
- (3) The dredgers could co-operate to relay parts of their catches on a portion of the ground which should be given to them temporarily by the authorities for this purpose, provided the oysters were retained on the allotted ground during one or more summers than would otherwise be the case.
- (4) A portion of ground could be rented out to a buyer on the same conditions as mentioned in (3), and the rent so obtained used for buying new cultch.

It is suggested that arrangements be made to put this plan into operation for the summer of 1926 and continued until the grounds have again recovered to the extent of giving at least 20 small oysters of a size about 2 inches in an *average* haul from a sailing-boat dredge.

12. *Care of the beds. Cultch laying.* On the Fal beds at present the oyster-farmer is continually harvesting without doing any tilling or sowing. Nature's harvest is at times bounteous, but at others meagre, and can always be improved simply by depositing clean shell on the beds at times young oysters are ready to settle. The harvest of young oysters is, however, *great* only in years when the water is maintained warm and other conditions are suitable; for this reason cultch should be laid and relaid in quantity each year until the desired fall of young oysters is obtained.

It is, therefore, desirable that those responsible for the care of the beds should be prepared to lay out as much clean shell as possible in the immediate future. But since one cannot predict when the suitable summer will come, the expenditure on cultch laying should be distributed over a number of years, so that some improvement in the stock is effected each year, and the cultch be in the water in the particular year when conditions are suitable for a good fall. There should at least be enough revenue raised from licences or catches to pay for the general administration of the beds.

13. *Co-operation among the dredgermen to improve the beds.* The dredgerman on the Fal Estuary beds at the present time is like a hunter who hunts continually the same animal on the same ground without taking or being allowed to take any steps to ensure the survival of the hunted animal. It is suggested that opportunity should be given to the dredgerman to take an active interest in the welfare of the beds in the following way.

14. *An elected foreman.* A foreman should be elected from among the dredgermen to undertake the general direction of the improvement of the beds in consultation with the bailiff and a member or members of the Oyster Committee. If the bailiff's duties were considered such that they did not clash, there is no reason why he should not take the place of the foreman, but the surveyor's view is that the bailiff needs all his time for his particular work.

In addition to electing a foreman,

15. *A jury of dredgermen to improve the beds.* The dredgermen should agree to give free, in rotation, a half a day's work on a jury. The jury would work under the foreman and do whatever was wanted to improve the beds. A roster could be arranged of three or more men for each half-day as required. The foreman should be paid a suitable wage to compensate for his continual loss of work.

In this way (1) cultch could be culled over, and the small oysters picked out and relaid on suitable parts of the beds, while the cultch could be continually deposited on the shore throughout the winter ready for the following summer; thus a regular supply of clean cultch would be ensured. In addition, accumulations of small on the beds could be distributed at no expense and for the general welfare. Mussels in certain parts of the beds could be dredged up and cleared away. Improvements in certain parts of the beds and efforts to form new beds could all be made. Further possibilities of forming beds for spat, for other young and for special kinds of oysters, would follow as the dredgermen realised the advantages of co-operation in this way. It would not be necessary to have a jury working all through the dredging season, and probably one

turn per man per season to give a jury for about a month would be as much as should be attempted at the beginning.

It would be necessary for the controlling oyster committees to be advised of all the work requiring to be done and approved.

16. *Returns of oysters taken from the beds.* It is essential that those administering the beds should have information of the numbers of oysters taken therefrom, especially when the stock of oysters is low. It is, therefore, recommended that the obligation should be placed on each licensee to report weekly the number of legal oysters taken from the beds. It is possible that the dredgermen may be able to suggest a more convenient way of making this return, but any alternative way may be adopted which will give the information required.

17. *Iron "rings" should not be permitted, and certified brass "rings" should be supplied with the licence.* It is strongly recommended that dredgermen should possess a brass ring for the purpose of measuring oysters. Most dredgermen are now using an iron ring which is rusted inside and "rings" doubtful legal oysters. In this way discussions and serious misunderstandings are bound to occur when the bailiff measures the same oysters with a brass ring. The brass rings should be issued with the licence, and stamped and certified as correct, so that the dredgerman using the ring cannot fail to recognise himself what is and what is not a legal oyster.

18. *Motor boat for Falmouth bailiff.* The Falmouth bailiff cannot be expected to do his work effectively in a rowing boat, and although the provision of a motor boat may not be possible out of the proceeds of the licences under the present arrangements, it would be worth while if the two authorities amalgamated as suggested above. Undersized legal oysters must be detected in the boat on the dredging ground, as the proportion of small oysters which just hang by shoots has been shown to be fairly large; it is, therefore, too late to identify small oysters after they have been shot from one bag to another ashore.

Notes on Nucula.

By

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With 5 Figures in the Text.

THESE notes record the result of work done at the Plymouth Laboratory during the summer of 1926. They deal chiefly with the feeding habits of *Nucula*, a Protobranch possessing the type of feeding mechanism characteristic of that order, and not found in any other Lamellibranch. During the course of my work I found Vlès' interesting paper on the sense organ of *Nucula*. After studying the organ, I arrived at a different interpretation of its function from that reached by Vlès.

I owe very much to the kindness of the Director and other members of the staff of the Laboratory, and am also indebted to Professor H. G. Cannon for friendly advice.

Three species of *Nucula*, common in the vicinity of Plymouth, were used, namely, *N. nucleus*, *N. radiata*, and *N. nitida*. Much important work has been done on *Nucula nucleus*, the most common European species, as well as on *Nucula proxima* and *Nucula delphinodonta*, which live on the American side of the Atlantic. Of course, many characters are common to these species, but not all.

The material used was dredged in 20 to 30 fathoms off Plymouth by the research steamer "*Salpa*," *N. nucleus* being the most abundant species. The *Nucula* were kept alive in a small glass dish with a little of the mud that was collected with them. A current of water from the general aquarium supply was provided, and the animals remained quite healthy during the two and a half months of my stay at the Laboratory. They were observed alive and dissected under a binocular microscope and some serial sections were cut after feeding with ferrous saccharate.

THE FEEDING APPARATUS.

In Lamellibranchs the labial palp is the most important feeding organ, its function being to select food material, to reject unnecessary substances, to make the food into suitable masses, and, finally, to conduct these to the mouth. The gill is an almost equally important feeding organ, being primarily a collector of food material, the collection being

carried out in different ways and with different degrees of exactness according to the structure of the gill.

In Protobranchs, however, there is almost no co-operation between gill and palp.

The chief characteristic of the group is the primitive character of the gill, which is simple in structure, imperfect both as a selecting organ and a sieve for food-material, and possesses a very small surface area. Hence the palp is the sole organ of feeding in Protobranchs, and neither the high degree of specialisation in its structure nor the differentiation in function is surprising.

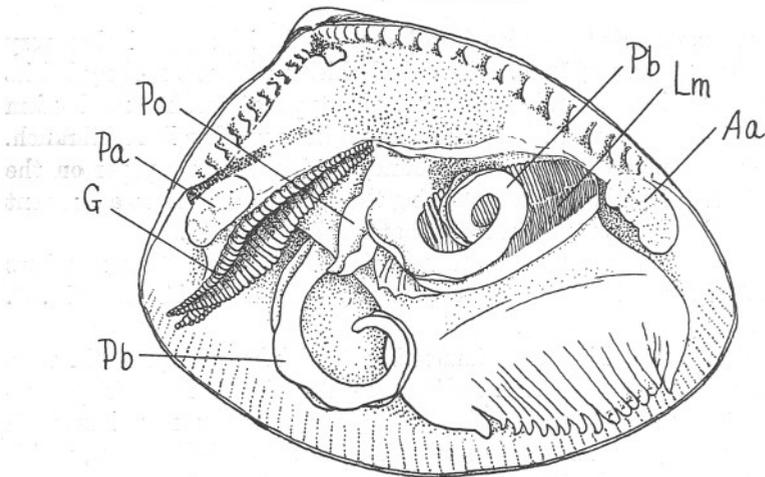


FIG. 1.—*Nucula nucleus*, alive; shell and mantle removed on right side. $\times 12$. Aa.: Anterior adductor muscle. G.: Gill. Lm.: Palp-lamella. Pa.: Posterior adductor muscle. Pb.: Palp-proboscis. Po.: Palp-pouch.

The palp of Protobranchs consists of three different parts, the most important being the palp-proboscis, as I propose to call it, which is the food-collecting organ in all Protobranchs, but not in any other Lamelli-branchs (Fig. 1, Pb.). Next comes the palp-lamella, corresponding to the labial palp of other bivalves, but a far larger organ resembling the gill (Fig. 1, Lm.). There is no palp-lamella in *Solenomya*. Finally, we have the palp-pouch, which is found only in *Nucula* (Fig. 1, Po.). These three structures form the complete feeding apparatus in Protobranchs, but the second and the third are sometimes lacking and only the proboscis is found in all species of the group.

I suggest this nomenclature, based on the form of the organ, to avoid confusion from the different names given by preceding authors. The *proboscis* has been called the "tentacular appendage of the labial palp"

(Mitsukuri, 1881), "appendice postérieur des palpes" (Pelseener, 1891), "ventral palp-appendage" (Drew, 1901), "palp-appendage" (Morse in Solenomya, 1913; Kellog in Yoldia, 1915). The *pouch* has been called "hood-like appendage" (Mitsukuri), "appendice dorsal des palpes" or "capuchon" (Pelseener), "dorsal palp-appendage" (Drew); and the *lamella*, "labial palp" (Mitsukuri), "palp" (Pelseener), "labial palp" (Drew), "anterior palp" (Kellog in Yoldia).

The proboscis and the pouch are not really appendages of the palp at all; they seem to me to be feeding organs of equal or even greater importance.

STRUCTURE OF THE FEEDING APPARATUS.

A. *Palp-proboscis.*

This is a strong, muscular and contractile organ, the true form of which is difficult to determine in preserved specimens, for it always shrinks into a spiral and looks like a broad thick band with corrugated ridges on both margins. This appearance is, however, quite unnatural, and is due to extreme contraction.

In the living animal, the proboscis is very sensitive and active, and its size is very variable. At times it becomes very long, slender, and translucent, with an especially active tip, which is strangely similar to the trunk of the Proboscidea. The proboscis searches around in all directions outside the shell, and even over the shell surface itself, creeping up nearly half-way to the umbo (Fig. 2, a). I have seen this natural movement in a few specimens of *Nucula nitida* only, which had been kept in the Laboratory in a small aquarium for some weeks in the way described above. Probably they were very hungry. The proboscis is very flexible, moving around freely in all directions and becoming narrower or broader as may be necessary (Fig. 2, b, c). Food material is picked up by the tip, and travels swiftly and smoothly along the floor of the groove towards the base of the proboscis.

Writing of *Nucula proxima* the late Professor E. S. Morse aptly said: "Without seeing the behaviour of these appendages (he refers to the proboscis) it is difficult to appreciate the remarkable action of these feeding organs. The graceful movements of these beautiful and translucent appendages, exceeding in diameter the length of the shell, sweeping rapidly the bottom of the dish in which they are confined, or even turned back and feeding on the surface of the shell, are a most curious and interesting sight." This description differs only in one point from what I have seen in *Nucula nitida*, namely, that the size of the proboscis is less in *N. nitida* than in *N. proxima* (Morse, 1919, p. 147, Fig. 3). The exact length or even the length relative to the size of the animal is very

difficult to ascertain, for the organ is only fully extended when the animal is alive. It is then extremely active, but the slightest shock causes it immediately to retract within the shell. I have several times tried to narcotise the animal, but it is very difficult to preserve it with the proboscis fully extended. From what I have seen it may be longer than the length of the shell by $\frac{1}{3}$ or $\frac{1}{4}$.

A proboscis lies under the mantle on each side, and almost in the centre of the body. The point of attachment is external to the postero-dorsal corner of the outer palp-lamella (Fig. 1, Lm., Pb.). In origin it must be only an outgrowth of the larval palp, as in *Nucula delphinodonta* (Drew,

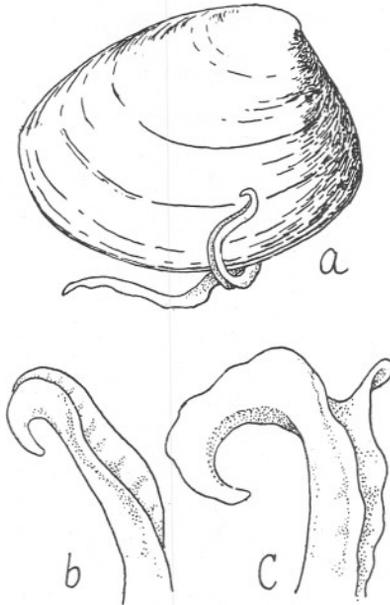


FIG. 2.—a, *Nucula nitida*, showing natural movement of palp-proboscis. b and c, ends of proboscis. All magnified.

Pl. 25, Figs. 54–57), but both in size and in function it is a very important organ in the adult.

In section the proboscis is V-shaped, as in *N. delphinodonta* (Drew, Pl. 25, Fig. 66), and the concave surface of its proximal part faces in a postero-dorsal direction. This surface and both its margins are covered by a single layer of high, columnar epithelial cells, with oblong nuclei and provided with long cilia, interspersed with secretory cells. The outer convex surface is also covered with a single layer of columnar cells, not as high as those of the inner surface, without cilia but accompanied by many secretory cells. Most of the space inside the epithelium is occupied

by muscle fibres and large blood-lacunæ. At the bottom of the concave surface a single large bundle of nerve fibres runs just beneath the epithelium. At the point of attachment the longitudinal muscle bundles are united to the posterior retractor of the foot.

B. *Palp-pouch.*

This is the special organ which is found only in species of *Nucula*, and not in other Protobranchs. The pouch is a safety-cover or bridge for the food material, whilst it is being transmitted from the proboscis to the groove of the lamellæ. It is attached to the body just behind the proboscis and hangs down from the postero-dorsal corner of the lamella. It is a spoon-shaped organ, with the tip downwards and the concave surface looking forwards. Its margin is irregular and pointed at the end. Sections show that its structure is very simple, being bell-shaped with a thin layer of homogeneous connective tissue with spherical nuclei lying under the epithelium. The latter consists of a single layer of cubical cells with spherical nuclei, which, on the concave surface, carry short cilia. The posterior or convex surface is without cilia and has fewer secretory cells than the ciliated anterior surface, though the epithelial cells are arranged more densely. At the margin the thickness increases slightly and the tissue is impregnated with a chitinous substance with scattered nuclei, which looks very similar to cartilaginous tissue of higher animals. At the extreme edge this substance is thick and dense, but it gradually fades away and merges into normal connective tissue. The edge is tinged with a slightly yellowish colour.

In its natural position the pouch bridges over and establishes continuity between the two neighbouring organs, the proboscis and the lamella. The concave surface covers over the inner half of the proximal part of the proboscis and the extreme postero-dorsal margin of the outer palp-lamella; in other words, the outer margin of the pouch is inserted into the groove of the proboscis, while its inner margin is inserted between the two lamellæ. The pouch moves very slightly, not actively except at its margin, which waves to and fro.

C. *Palp-lamellæ.*

This part of the palp corresponds to the labial palp of other bivalves, but is far more important and more differentiated than in them, because the gill is so primitive and so little developed as a primary selecting organ for food material. There are two lamellæ on each side covering the upper dorsal part of the foot which contains the stomach and many important visceral organs. These palp-lamellæ are much larger than in other Lamellibranchs, extending from the centre to the extreme anterior

part of the body, a very small slit remaining between them and the anterior adductor muscle. At its anterior end each lamella becomes continuous with the corresponding lamella of the opposite side, just above and below the mouth, the lamellæ thus forming as it were a roof above and a floor beneath the mouth. The width of the lamellæ decreases gradually towards the anterior end. On each side of the body the outer and the inner lamella become continuous dorsally, except in the region of the mouth, thus forming a longitudinal groove, the whole being suspended from the body wall by a common thin membrane, which consists of a single layer of epithelium on each surface with a small quantity of connective tissue between. The margins of the lamellæ in their postero-ventral parts contain chitinous substance, which gradually changes to normal connective tissue in the dorsal and anterior parts; a few ridges in the posterior regions also contain some chitinous substance.

In both lamellæ the outer surfaces are covered with a single layer of cubical or rather squamous epithelial cells, with inconspicuous short cilia on the outer lamella, and devoid of them on the inner lamella, except on its ventral portion; whilst on the inner surfaces, which face each other, the cells of the single layer of epithelium are high columnar cells with long cilia.

These inner surfaces of the lamellæ are not smooth, but are profusely covered with ridges, those on the upper half being broad and high, those on the lower half narrow, low, and insignificant, the two kinds of ridges uniting in the middle line and forming a knob at the end of the higher ridges (Fig. 4, p. 637). These structures are very conspicuous through the thin wall of the lamella, and make the lamella look striated on the outer surface, although this surface is really quite smooth. The ventral margins of all the lamellæ are smooth and without ridges.

Between the two epithelial surfaces the space is narrow and occupied by connective tissue. Beneath the dorsal groove formed where the two lamellæ meet there is a large nerve cord and a spacious blood-lacuna immediately under the epithelium.

As regards the finer structure of the lamellar ridges, I think there are three different parts on the surface of each. The distinction is clearest in the posterior ridges, since the ridges gradually diminish in size towards the anterior end of the lamella. The ridges bend naturally forwards or towards the oral side, and consequently the posterior surface is somewhat broader than the anterior. The upper portion of the ridge (Fig. 3, A) is covered with strongly ciliated high columnar cells with oblong nuclei. This portion is very strongly developed in the posterior and dorsal part of the lamella, being broad in section and containing a large mass of connective tissue. The posterior surface of the middle portion (Fig. 3, B) is covered by the highest columnar cells, with very slender oblong nuclei,

and there is a mass of finely granulated cytoplasm at the base of the long cilia. The lowest portion of the ridge (Fig. 3, C) forms a semicircular groove with the neighbouring ridge on each side. It is covered by a layer of epithelial cells, with bulky spherical nuclei and very long cilia. The cytoplasm of these cells is hyaline near the surface, having probably a very dense and homogeneous consistency. On the oral side of this part of the ridge there is one large knob formed by a mass of cells with spherical nuclei and many secretory cells.

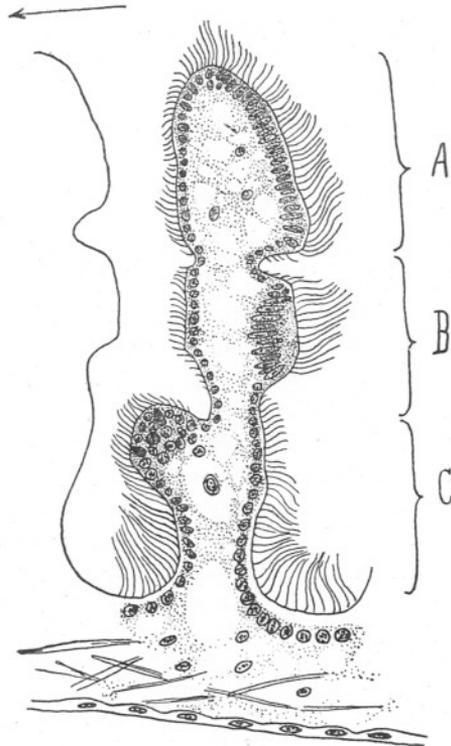


FIG. 3.—Diagrammatic sketch of lamellar ridge, in transverse section. Arrow shows oral or anterior direction.

The oral surface of the ridge is not provided with long cilia, except in its lowest portion which forms a groove with the next ridge. Many spaces were seen in the subepithelial connective tissue which seemed to be blood-lacunæ, the largest of them being in the basal portion.

There are no recognisable muscle fibres in the ridge, these being found only below the epithelium of the outer surface of the lamella.

I have already explained that the ridges on the dorsal side of the middle line of the lamella are much higher than those lying ventrally to that line

Considering these ridges in more detail, it may be noted that if one single ridge is followed from its dorsal to its ventral end, the three portions, which I have called parts A, B, and C, do not decrease in the same ratio, but, at the point where the ridges cut the middle line of the lamella, part C suddenly disappears and the ridges in the ventral portion of the lamella consist of the two other parts only. The ridges therefore become suddenly very low and narrow, with shallow grooves lacking long cilia between them. On the other hand, part C is well developed on the upper half of the lamella, and there is a deep furrow with long cilia between neighbouring ridges, the furrow gradually becoming shallower towards the ventral half. There is a conspicuous and sudden disappearance of part C in the middle of the lamella, forming a knob-like prominence followed ventrally by a lowering of the ridge.

THE FUNCTION OF THE FEEDING APPARATUS.

In order to study the function of this mechanism I have made use of starch grains stained with tincture of iodine, by means of which it is possible to follow the ciliary currents in the living *Nucula*. I have also cut sections of animals which had been fed with ferrous saccharate one hour or half an hour before fixation, for the purpose of determining the real orientation of food material in these organs.

I have already described the function of the proboscis in the living animals. From further observations with the binocular microscope on living specimens, the shell and mantle of which had been removed on one side, it has been possible to follow completely the system of ciliary currents (Fig. 4). When any particles are put on the inner concave surface they are carried very rapidly by the beating of the cilia to the bottom of the central furrow. Having collected there they travel still more rapidly to the proximal end of the organ, being moved along by the strong cilia which occupy the centre of the furrow. They then enter the pocket-like pouch, the cilia lining which change their direction and carry them to the posterior end of the lamellæ. Most of the particles which arrive at this point are swept into the central groove of the lamellæ by the strong ciliary current and carried along the groove to the mouth. But those particles which do not reach the groove fall by gravity or for some other reason on to the other part of the lamellæ and are moved along by the ciliary current of the ridges.

Speaking generally, the size of the ridges is large posteriorly and gradually diminishes towards the mouth. The action of the ciliated ridges is probably more powerful in the posterior half of the lamellæ, and the coarser particles may be rejected here where they first strike the ridges.

As already explained each of the ridges consists of three different parts on the dorsal half of the lamella, and it appears to me that the function of each part is different. The distal part A (Fig. 3), with strong cilia which normally beat towards the ventral margin of the palp, removes material which is too large or not wanted. The second part B, the posterior surface of which is covered with very high columnar epithelial cells with long cilia, that are perhaps sensory cells, is in my view the place where the material collected is selected and sorted, being in part filtered by the ciliary sieve. The proximal part C is the most important organ of transport, where the already selected food material is pushed rapidly towards the central furrow by the powerful cilia which beat in exactly the opposite direction to those of part A. On the anterior face

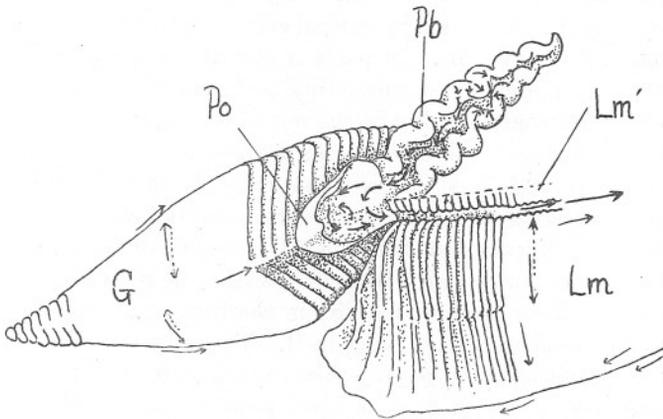


FIG. 4.—Diagrammatic sketch of palp-feeding mechanism of *Nucula nucleus*, ventral view, showing direction of ciliary current on right side; outer right lamella almost removed (*Lm'*). Broken arrows show ciliary currents in deeper zones. *G.*: Gill. *Lm.*: Palp-lamella. *Pb.*: Palp-proboscis. *Po.*: Palp-pouch.

of the ridges of part C are the large knob-like protuberances, which constitute the main secretory organs, the secretion from which consolidates the food material into masses of a size suitable for propulsion by the powerful ciliary movement.

There are thus on the whole two main currents running in opposite directions on the inner surface of each lamella, these currents being produced by ciliary action taking place at different levels on the ridges. First there is a superficial current due to the cilia of part A, by means of which unnecessary material is swept to the ventral margin of the lamella, while, secondly, in the deeper zone, the selected food substance travels to the dorsal side of the lamella, finally reaching the central lateral furrow between the two lamellæ, which is the main route to the mouth.

On the ventral edge of the lamella there are also ciliary currents which

convey all particles to the posterior end of the lamella, where they fall into the mantle cavity and are soon expelled outside the shell.

Before leaving this part of the subject it will be useful to compare the lamellar ridges of the palp of *Nucula* with those found in other Lamelli-branchs. In the common mussel (*Mytilus edulis*), which is provided with one of the most active and complicated labial palps, and has been the subject of many investigations (List, 1902; Wallengren, 1905, etc.), the ridges of the palp are differentiated as in *Nucula* into three parts. Part A is here also strongly ciliated, and covered by columnar epithelium interspersed with goblet cells. Part B is considerably larger than in *Nucula*, but is equally covered by very high columnar cells. Part C differs more from the corresponding part in *Nucula*, the furrow is very deep, especially anteriorly, the knob-like protrusion being high up on the ridge, and it is also very narrow. It is lined by cubical cells with short cilia, interspersed with many secretory cells. In parts A and B the sub-epithelial tissue contains many muscle fibres connecting both surfaces, which mostly run obliquely or horizontally. But in the rest of the organ only "vesicular" cells are found, muscle fibres being quite absent.

By a study of these structures, especially by cutting sections after feeding, I found that the functions of parts A and B were exactly the same in *Mytilus* as in *Nucula*, but that of part C was quite different. I conclude that there is no transmission of food towards the mouth by the latter part, because there are no long cilia in the furrow, nor could I find in sections any food substance lying in it. The main function of part C in *Mytilus* seems to me to be secretory and the part has no concern with food conveyance, except that it gives more room for the contractile activities of neighbouring parts.

According to Wallengren (1905, pp. 49-53) the work of sorting the food materials is completed by the co-operation of the different zones of ciliated epithelium, which beat in different directions with the changes of inclination of every individual ridge.

In many cases the ridges bend forward and their inclination becomes very oblique to the plane of the main surface of the labial palp, in which state the furrows between the ridges almost cease to function. But when the ridges are erect and perpendicular to the plane of the whole palp, almost all material falls into the furrows, and is conveyed to the margin of the palp, where it is rejected.

In *Mya* (Yonge, 1923, pp. 28-32) this furrow is very important for rejecting materials which are superfluous or rather heavy and unsuitable for food. These fall directly into the furrow and are removed by the same ciliary current that Wallengren described in *Mytilus*. The ridges in *Mya* are different in form from those in *Mytilus*, being short and broad, with part B not conspicuously developed. Changes in inclination and

alterations in shape of the ridges are therefore quite difficult; the ridges remain almost stationary, and all the furrows are open the whole time.

In *Mya*, therefore, the furrows are important and provide the only method of rejecting unsuitable material, whereas in *Mytilus*, according to Wallengren, the method is different, the greater part of the rejection taking place in the higher zone of the ridges, and not in the bottom of the furrows. My observations support Wallengren's view, and I consider that the function of part C in *Mytilus* is quite different from what it is in *Nucula*.

Parts A and B are exceedingly active and contractile; sometimes the ridges are very broad and short, and then by the contraction of the muscles they become tall and slender. Under the binocular microscope a peristaltic depression of the ridges can be seen running from one end of the lamella to the other and forming a temporary groove between neighbouring high ridges. This motion occurs normally on the palp surface, the food particles rolling into this temporary groove, which travels rhythmically forwards in the direction of the mouth by the contraction of each neighbouring ridge. The change of inclination of the ridges, as Wallengren (1905) described it, is not so conspicuous. The change of ridge form is the consequence of muscular activity, which is controlled by nerve centres connected with the sensory epithelium of the surface of the ridge.

The transmission of food material to the mouth is not performed by part C, as in *Nucula*, but by part B, which with the corresponding part of the next ridge makes a tubular channel lined with long cilia, which convey the food particles, cemented together into one mass by mucus secreted by part C, in a forward direction. This fact was established by sections made after feeding, which always showed the food material formed into a mass in part B, present as separate particles in part A, and entirely absent from part C.

There is therefore this essential difference in manner of functioning between the palp-lamellæ of *Nucula* and *Mytilus*, notwithstanding their general similarity of form.

I have already said that the *gill* of *Nucula* is very defective as an organ for the collection of food, but probably it is not entirely inoperative, for there is the capacity of making a slit-like opening between the pouch and the inner lamella, by the movement of these organs, and particles can then stream from the posterior part of the pouch into the space between the lamellæ.

But although there is no real connection between the gill and palp organs, the gill has its own system of ciliary currents on its surface. These are indicated in Fig. 4. There are two opposite ciliary currents in each gill surface, a superficial one sweeping towards the margins of the gill, and

a deeper interfilamentar current directed towards the central groove or depression. In this central groove and along both the gill margins particles travel rapidly in a forward direction.

But almost all particles on the gill fall into the mantle cavity, without getting on to the lamellæ of the palp, and by the action of the surface cilia of the foot and mantle they are collected at the mid-dorsal margin of the mantle, from which point they are expelled by an outgoing current produced by a movement of the foot, passing out from the shell just behind where the foot protrudes.

Several authors have suggested that the palp acts as a respiratory organ, for it seems to them to be too extensive for a feeding organ, and, on the other hand, the gill has such a small surface area. But this is not really so, as the lamella has quite a different histological structure to the gill, and one which is very similar to that of the alimentary canal. It seems to me more reasonable to regard the lamella as a pure feeding organ, its function being, like that of the intestine, the conveyance of food.

THE CEPHALIC SENSE ORGAN.

The sense organ of *Nucula nucleus*, which is innervated directly from the cephalic ganglion, was described by a French biologist in a preliminary note (Vlès, 1905), and no further account has, as far as I have seen, been published.

Walter Stempell (1899, Figs. 25 and 26) had already described the same organ in *Solemya togata*, and called it "adorale Sinnesorgan." He writes: "Ihre physiologische funktion dürfte in einer Prüfung des Wasserbestehen, welches mit der Nahrung zusammen der Mundöffnung zuströmt," and its function therefore according to his view resembles that of Thiele's (1887, 1889) "neues Sinnesorgan," or abdominal sense organ. Vlès' interpretation of the organ in *Nucula* is the same. It is strange that Stempell did not find this organ during the whole of his anatomical research on the Nuculidæ (Stempell, 1898).

Thea Clasing (1923) has described in *Mytilus* a tubular organ near the mouth and the cephalic ganglion, and almost in the same position as Vlès' organ in *Nucula*. He considered it to be a sensory organ for the perception of currents or of the pressure of the surrounding water. Its structure is, however, quite different from that of the cephalic sense organ of *Nucula*.

While I was investigating the feeding process in *Nucula*, I found this organ in *N. nucleus* and in two other species. It is situated very near to the mouth and to the point of attachment of the lamella, just below the cephalic ganglion. In section it appears as a remarkably differentiated part of the epithelium, consisting of two layers of cells in contrast to

the single layer of cells in the rest of the epithelium (Fig. 5). Owing to its thickness it protrudes beyond the neighbouring epithelium, but there are one or two concave depressions on its surface denoting slight invagination. Superficially it is covered by a thick and structureless layer without nuclei, which seems to be of a very dense and homogeneous character, closely resembling the cornea of the eyes of other

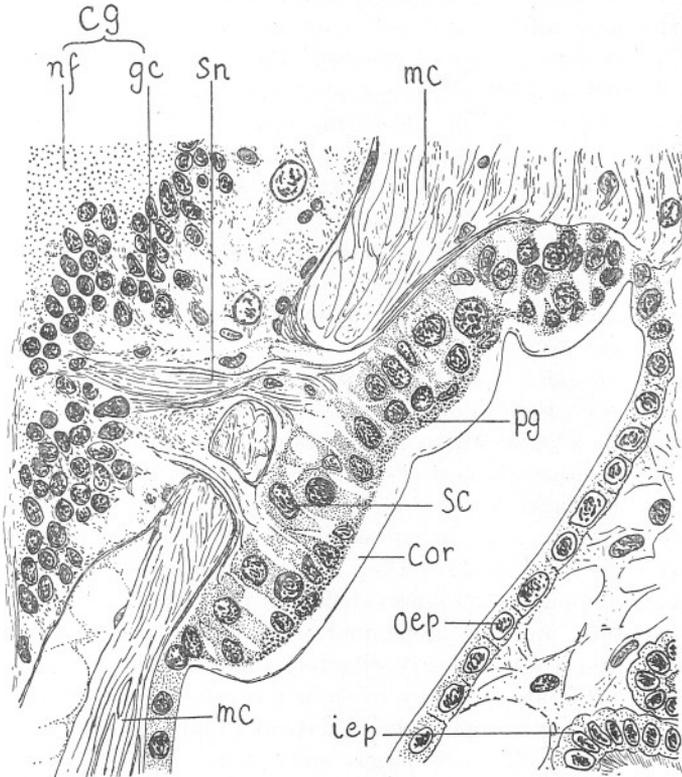


FIG. 5.—Cephalic sense organ in *Nucula nucleus*. *Cg.*: Cerebral ganglion. *Cor.*: Cornea. *Gc.*: Ganglion cells. *iep.*: Inner epithelium of lamella. *mc.*: Muscle. *nf.*: Nervous fibres. *oep.*: Outer epithelium of lamella. *pg.*: Pigment. *sc.*: Sensory cell. *sn.*: Sensory nerve.

invertebrates, and I propose to call it cornea (*Cor.* in Fig. 5). Its surface is clearly devoid of cilia.

Immediately below the cornea I found a single layer of cells with inconspicuous nuclei, which resembled normal epithelium, except that it contained pigment granules, but not in considerable amount (*Pg.* in Fig. 5).

The third or basal layer is the important sensory part of the organ, which is innervated on its proximal side. The cytoplasm has fine granules

of several different kinds, and a large spherical nucleus (Sc., Fig. 5), and it sometimes appears vacuolated. Probably its finer structure could be made out with higher magnification.

All the nerve fibres which come from these sensory cells collect into one large nerve bundle, sometimes with one or more minor bundles, all of which pass directly into the cephalic ganglion, breaking through the muscles of the retractor pedes (Fig. 5, Sn.). The cephalic ganglion (Fig. 5, Cg.) is the most anterior and most conspicuous ganglion in *Nucula*, and really consists of two ganglia connected by a short commissure just above the mouth and in front of the œsophagus. In section it is a spherical mass with a fibrous part in the centre, surrounded by ganglion cells and covered by a thin membrane, which also extends around the basal part of the sense organ (Fig. 5, Gc., nf.). The sense organ has an exactly similar structure in the other two species.

As regards its function, from its histological structure and anatomical relations Vlès considered it to be an olfactory organ analogous to Hancock's organ in Gastropods, especially in Cephalaspides (a group including *Bulla*, *Aplysia*, etc.).

Hancock's organ is a real olfactory organ, which is regarded as quite homologous with the rhinophores on the tentacles. The latter are found in Gastropods, whereas Hancock's organ only occurs in burrowing forms in which tentacles are almost or quite absent (Plate, 1924).

In Lamellibranchs the osphradium and also abdominal sense organs are very common, both being sometimes found in the same animal. They are both innervated from the visceral ganglion, whereas Hancock's organ and rhinophores are innervated from the cephalic ganglion. Both the osphradium and the abdominal sense organs are concerned with respiration and are not purely olfactory organs. They have therefore been called by Plate, "respiro-receptor" organs (or "atmungs-geruchsorgane"). Most of the opisthobranchiate and nudibranchiate gastropods possess both true olfactory organs and respiro-olfactory organs at the same time. It seems quite correct that these two classes of organs have different functions, the former (rhinophores, Hancock's organ) are more highly differentiated and are purely olfactory, the latter (osphradium, abdominal sense organs) are more primitive in structure, and are used to test the purity of the water before it is allowed to pass over the gill.

There is no Lamellibranch which possesses a real, independent olfactory organ. Probably the palp plays this rôle.

As already described by Pelseneer (1891, p. 167, Pl. VII, Fig. 11, III), *Nucula* possesses an osphradium in the neighbourhood of the gills, situated on the surface of the retractor muscle of the foot and directly innervated from the visceral ganglion. Its structure is quite different from that of the cephalic sense organ, for it consists of a single layer of

large, cubical epithelial cells with long cilia, but without the thick transparent covering layer found in that organ.

For these several reasons I do not regard the cephalic organ as an olfactory organ, but as a visual organ or the remnant of a larval eye. Its structure, as I have described it, is particularly characteristic of a visual organ, that is to say, its invaginate form, the existence of a transparent external layer, the presence of pigment and of sensory layers. As a visual organ it is, however, very incomplete in structure; for example, the pigment is so poorly developed that it shows only faintly. It is probably, therefore, only the remnant of a larval sense organ, for eyes would be very useful in the larva, before the palp-lamellæ are developed or whilst these lamellæ and the shell are all quite transparent. It is true that in the excellent description by Drew of the development of *Nucula delphinodonta* there is no mention of an eye, but the reason for this may well be that the larval stage of that species is spent almost entirely in the brood-sac. It is to be hoped that this point will be cleared up in the future by a study of the development of *Nucula nucleus*.

The visual organs of Lamellibranchs fall into two categories: (1) cephalic eyes and (2) pallial and siphonal eyes. The former are primitive in structure, but are the original eyes of the group mollusca; the latter are very highly differentiated, but have developed secondarily in the group.

These cephalic eyes are only found in the more primitive groups of Lamellibranchs, such as Mytilidæ, Arcidæ, Avicula, Anomia, all belonging to the order Filibranchia. They are well known, especially in *Mytilus* (Pelseñeer, 1900; List, 1902; Field, 1922; Clasing, 1923), being situated at the anterior ends of the animals, for example on the anterior margin of the inner gill lamella in *Mytilus*, and innervated directly from the cephalic ganglion. Their structure is of a very simple type, with a slight invagination, an imperfect lens or without a lens, and pigment cells interspersed amongst sensory cells or lying above them.

The cephalic sense organ is similar in *Nucula*, but it is very simple compared with the eye of *Mytilus*, and resembles somewhat the cephalic eye in *Patella*, which is the most primitive one amongst the Gastropods.

It seems to me to be most rational to regard this cephalic sense organ of *Nucula* as a visual organ, in the first place because of its structure, and, secondly, from phylogenetic considerations, for the Protobranchs are very closely related to the Filibranchs.

THE MOVEMENT OF THE FOOT.

I agree entirely with Drew, who described the foot of *N. delphinodonta* as being not a creeping, but only a burrowing organ.

All three species of *Nucula* with which I experimented burrowed immediately when mud was present, travelling very swiftly under it.

When, however, the animals were put in a glass dish without mud, they always remained quite helpless, notwithstanding full activity of the foot. The thrusting out and retraction of the foot accomplished only a slight shifting of the shell, turning it in different directions. The flat surface of the foot-sole never reached the smooth substratum at all.

But I once saw a small mollusc creeping very rapidly among some *Nucula* immediately after their collection, and at first I thought that it also was a young *Nucula*. It crept to the extreme edge of the glass dish and even hung down from the surface of the water by its foot. Afterwards I found that it was quite a different species, notwithstanding its great resemblance to a young *Nucula*. It was some species belonging to the genus *Mactra* or its relatives, and I am afraid that it was in this way that Forbes and Hanley were deceived when they described a swiftly creeping habit in *Nucula nucleus* (p. 217).

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The Eggs and Newly Hatched Young of the Common Blennies from the Plymouth Neighbourhood.

By

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With 1 Figure in the Text.

THE three common blennies of Plymouth are the Shanny, *Blennius pholis*, the Gattorugine Blenny, *Blennius gattorugine*, and the Butterfly Blenny, *Blennius ocellaris*. These have their habitat from just below high-water mark downwards. Thus, *B. pholis* inhabits the rocky pools from near high-water mark to the regions left dry by the tides; *B. gattorugine* is also to be found between tide-marks, but not so high up as *B. pholis*, and is more frequent in those parts uncovered by the spring tides; whereas *B. ocellaris* inhabits the deeper water and is always covered by the tide; it is frequently to be found on the dredging grounds in the region of the Mewstone and beyond the Breakwater.

In a paper by Ford (1922) the young of these three blennies are described from the earliest planktonic stage up to the time when the adult characters begin to show. The eggs of *B. pholis* and *B. ocellaris* have frequently been found and hatched out, but those of *B. gattorugine* have apparently up to the present time not been identified. In April, 1926, Mr. William Searle and Mr. Douglas Wilson, whilst collecting at Wembury, found two lots of eggs of this last species, and from one of these a few young were hatched out in the Laboratory. A brief account is given here, with figures of the eggs, of all three species, and a comparison of these with Ford's specimens from the plankton shows that they agree in every way.

BLENNIUS PHOLIS (L.).

Blennius pholis is to be found in rock pools, even those of the smallest size, from just below high-water mark to the upper regions between tide marks. Its eggs are deposited on the under surface of flat stones in deep crannies usually only accessible by some narrow crack through which the fish can squeeze and be safe from enemies. These crannies are covered at high water and exposed at low water, and a parent (presumably the male) guards the eggs until they are hatched. In order to see the eggs

it is always necessary to break the surrounding rocks. The eggs and newly hatched larvæ have already been described and figured by Hefford (1910), who found them on Plymouth Breakwater. The eggs are deposited in a single layer several inches in area, each egg attached to the stone and coloured purple and gold; gold mixed with black from the eyes and body chromatophores, and purple from the yolk sac, which gradually becomes brownish as the fish grows. Each egg measures about 1.4 mm. across (Fig. 1, b), and is spherical except at the attachment, where it is flattened so that the egg is usually really rather more than three parts of a sphere. Hefford's specimens are flatter and measure 1.6 mm. across. Eggs still attached to the stone were kept in a tank in the aquarium in running water until almost ready to hatch, and then transferred to a plunger jar, where the larvæ emerged from the egg. On the day of hatching, in a fish 5.4 mm. long, the yolk is already gone and teeth are present. The smallest figured by Ford is 5 mm., and is without teeth, but otherwise agrees very well with mine. A long pointed pectoral fin, deeply pigmented with black spots, is characteristic, one or two chromatophores on the front of the head, few or none on the top, and one or two near the operculum with pigment internally along the dorsal surface of the intestine, and a few very small chromatophores ventrally towards the end of the tail. These larvæ become members of the plankton immediately after hatching and remain until at least 18 mm. in length, the young of this size often occurring in the Plymouth plankton. Young fishes over 25 mm. are sometimes found in the small rock pools near high-water mark. The main breeding season is in the early spring, eggs having been found from March to July, and young stages in the plankton from April through the summer.

BLENNIUS GATTORUGINE (L.).

Blennius gattorugine lurks in the larger rock pools lower down than *B. pholis*, and also in those regions only uncovered at spring tides or never uncovered at all, but not far from the coast. It was among the rocks uncovered by spring tides at Wembury that the two lots of eggs were discovered on overhanging rocks, each batch guarded by the parent. The eggs in this case were not in such deep crevices as those of *B. pholis* and were more accessible. They were laid in a single layer like *B. pholis* and the colouring is also black and purple, but the diameter of the egg is slightly larger than any of those of *B. pholis* measured by myself, being 1.6 mm. across and the egg is flatter, being composed of slightly more than half a sphere closely adhering to the stone (Fig. 1, a). Thus the eggs of *B. gattorugine* were more like those which Hefford attributed to *B. pholis*. And the young he hatched from these seem to be *B. pholis*.

It would therefore appear that the eggs of the latter vary in shape and size, and may be extremely like those of *B. gattorugine*.

The eggs of *B. gattorugine* hatched with difficulty, and only a few larvæ lived long enough to draw. In the same way as *B. pholis* the eggs were kept in a tank in running water until nearly ready to hatch, and then transferred to a plunger jar. The reason for the failure was probably owing to the eggs being in an early stage of development when captured.

The newly hatched fish measures 4.9 mm. in length. Ford's smallest from the plankton was 6 mm. in length and rather older. They are, however, much alike, and very evidently belong to the same species. The larva from the plunger jar has a perfectly colourless tail and pectoral fin, a large brownish yolk sac, internal dark pigment in the dorsal region of the intestine from behind the eye to the anus, and a few chromatophores on the snout and on the top of the head. Ford's specimen has chromatophores ventrally along the hind end of the tail.

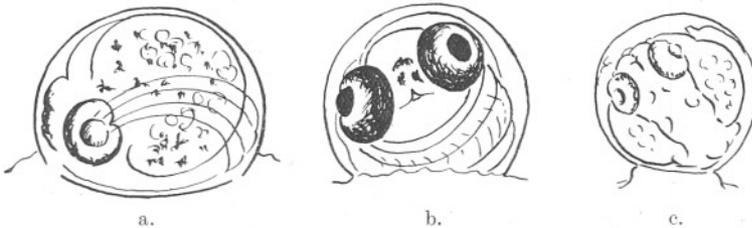


FIG. 1.—a. Egg of *Blennius gattorugine*: 1.6 mm. diameter. Wembury, April, 1926.
 b. Egg of *Blennius pholis*: 1.4 mm. diameter. Wembury, July, 1924.
 c. Egg of *Blennius ocellaris*: 1.12 mm. diameter. Trawled, July, 1926.

Older larvæ are found in the plankton up to about 20 mm. or more. The eggs were found only in April; young fishes are found in the plankton throughout the summer.

BLENNIUS OCELLARIS (L.).

Blennius ocellaris is well known from the rearing experiments of Garstang (1900), but the eggs and young are not figured by him. They are described from Devonshire by Cunningham (1889), who found the eggs in an old ox bone with the male parent inside, dredged by some fishermen. Ford figures a larva from Garstang's material measuring 4.6 mm. in length, which corresponds very well with those newly hatched from the egg. The eggs are usually laid in any old shell or bottle, an empty shell of *Buccinum undatum* is a favourite place, or a narrow-necked bottle, and in the shell or bottle the parent fish establishes itself to guard the eggs until hatched. It is a common sight to see the fish's head peeping out from a bottle or shell aperture. The eggs are a pinkish colour, owing

to the yolk, which changes to purple and then to brown. They are laid in a single layer inside the receptacle chosen. Each egg measures about 1.12 mm. to 1.2 mm. across, and is very nearly spherical, being fixed at one pole by a much smaller attachment than either of the other two (Fig. 1, c). Garstang succeeded in rearing these blennies from the egg up to quite a good size, but a very great deal of personal attention is required for such rearing. The young fish measures 4.4 mm. in length. It has a rounded pectoral fin with thick dark masses of pigment arranged in rays, two chromatophores on the snout, a thick mass of radiating chromatophores on the top of the back and dark internal pigment over the intestine. Ventrally on the tail are a few chromatophores reaching from the centre to nearly the end of the tail. The form and pigmentation are practically the same as in Ford's figure of a larva of 4.6 mm. in length.

Eggs are very commonly found through the late spring and summer. Young stages in the plankton throughout the summer.

It is thus seen that all the three blennies can be identified from the egg and first larval stages, all three agreeing with the early planktonic stages described by Ford.

LITERATURE.

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On a New Ciliate, *Ptyssostoma thalassemae* nov. gen.,
nov. sp., from the Intestine of the Echiuroid Worm,
Thalassema neptuni Gärtner.

By

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With 3 Figures in the Text.

THE intestine of the Echiuroid worm, *Thalassema neptuni* Gärtner, is occasionally found at Plymouth to be infected with a small parasitic ciliate. I have searched the literature on the anatomy of *Thalassema*, but have been unable to find any reference to this Protozoon. In fact, I have not as yet come across any record of ciliates infesting the Gephyrea,* though Mr. Dobell has informed me that, some years ago, the late Professor Ikeda mentioned to him the presence of ciliates from some of the Gephyrea he was then studying; but I have not been able to find any reference to ciliates in Ikeda's papers on Japanese Gephyrea. Lankester (1881), in a paper on *Thalassema*, merely records the occurrence of a gregarine which I also have observed in a number of specimens from the neighbourhood of Plymouth. I am, therefore, led to the conclusion that this ciliate must be new, and I have decided to name it *Ptyssostoma*† *thalassemae* nov. gen., nov. sp.

The occurrence of this parasite at Plymouth seems somewhat erratic. I first observed it at the Marine Biological Laboratory in April, 1922, when two or three worms were found to contain the parasite. I did not get another opportunity of examining it again until Easter, 1925, when four out of five specimens were found to be infected. Among these I was lucky in discovering one quite heavy infection, though, as a rule, not more than about half a dozen ciliates were to be found in a single worm.

Since that time, during the summer of 1925, I had specimens of *Thalassema* sent to me in London from Plymouth, but I found no ciliates in

* Since the above was written, Professor Tregouboff, of the Marine Biological Laboratory at Villefranche, has kindly brought to my notice a ciliate, *Cryptochilum Cuenoti*, described by Florentin (1898) from the œsophagus of *Phascolosoma vulgare* Blainville. This ciliate is, however, quite distinct from the species under consideration.

† πτυσσῶν, to fold; στόμα, a mouth.

the two dozen examined. At first I was uncertain as to whether this negative result was due to the ciliates not standing the journey (though the worms seemed to be quite active and in good condition on arrival), or whether the worms were only infected in the spring. However, in April, 1926, I examined at Plymouth thirty-four worms without success. It looks, therefore, as though the occurrence of this ciliate is erratic, and not due to any localised infection; in 1925 it was found in worms from the littoral region both of Rum Bay (Plymouth Sound) and Wembury Bay, whereas I obtained *Thalassema* this year (1926) from both these areas and also dredged from deeper water in the Sound, but all were uninfected.

DESCRIPTION.

Ptyssostoma thalassemae (Fig. 1) inhabits the intestine of *Thalassema neptuni*. It is of a somewhat ovoid form, though it can change its shape to a certain extent, having a short prominence at its anterior end, which can

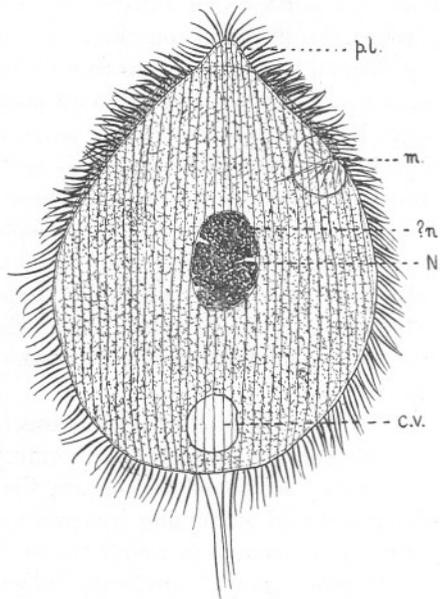


FIG. 1. A stained *Ptyssostoma thalassemae* (Mayer's acid hæmalum and Orange G.) $\times 700$ approx.

c.v., contractile vacuole; m., mouth; N., meganucleus; ? n., ? micronucleus; pl., anterior projecting lobe.

be slightly extended or contracted. This prominence seems to overhang the anterior part of the animal and probably acts as a sort of tactile organ for feeling its way through the debris in the intestine. As a result of this, fixed and stained specimens tend to vary somewhat in outline.

The body is not quite cylindrical, but is slightly flattened from side to side. The animal swims on one side, usually with the mouth, which is situated a little way posterior to the anterior prominence, on the right. As the ciliate turns over, one can see that the lower (i.e. left) side is slightly concave, whereas the upper (i.e. right) side is convex.

It is an active animal, burrowing its way in a determined manner through the debris in the intestine, like most intestinal ciliates. It will live for quite a considerable time on the slide, provided that there is no prolonged exposure to air; but if a cover-slip is not placed over it quickly, it will die in a very short time.

Apart from the effects of the slight contractility that the animals possess, there is not much variation in the size of the individuals, the measurements ranging from about 75–100 μ in length, and from 55–75 μ in breadth.

It is not of any marked colour, the cytoplasm being merely of a transparent greyishness, and without any very coarse granularity. Distinction into ectoplasm and endoplasm is not very noticeable. A few small food vacuoles are to be found in the cytoplasm.

The cilia are evenly distributed all over the body, except in the posterior region, where a few long cilia are to be found sticking out from a slight posterior prominence. These are about a quarter the length of the body of the ciliate. The ordinary cilia sweep with a very definite motion backwards over the surface of the body. They are arranged in longitudinal rows, giving the animal a striated appearance; there seem to be about thirty-five of these rows on each of the lateral surfaces of the body, a number that appears to be constant.

Towards the posterior end of the ciliate is a well-marked contractile vacuole. In position it lies somewhat nearer the oral border. It is not perfectly spherical, but is apparently compressed out of shape, so that it appears more as an irregular ellipse. Its expansion is so slow that it is not possible to observe its enlargement; but the systole is very rapid and sudden.

The mouth (Fig. 2), which is the most distinctive feature in this Protozoon, is a curiously shaped structure, situated about a quarter the way from the anterior end of the body. It lies on the edge formed by the two lateral borders. It consists of an invagination of the pellicle, which looks as if it were thrown into a number of folds, the whole being supported by a conspicuous horseshoe-shaped structure, which appears to be a continuation of the pellicle. In form, this apparatus is a little reminiscent of a section of a mammalian kidney, with a number of ducts opening into the pelvis. It gives the impression of being a kind of flattened sucker-like organ, which may be capable of evagination for the ingestion of food. No such movement has, however, been observed; and it is

not known in what way this apparatus works. From this "pelvis" there runs a gradually narrowing cone-shaped passage leading down into the endoplasm. This, which is presumably the gullet, lies on a different level from the sucker-like organ. In a specimen lying with the mouth on the right side, the gullet may be seen to be running obliquely upwards towards the mouth. No cilia have been observed in this or in any other part of the mouth apparatus.

The meganucleus is a subspherical body situated in the centre of the organism, and is about 13μ in diameter. It stains heavily, forming a dense opaque mass with a number of indentations at the surface. Its position in a living specimen can fairly readily be seen as a comparatively clear space.

The micronucleus can, as a rule, be seen only with difficulty even in stained specimens, as it appears to lie laterally to the meganucleus.

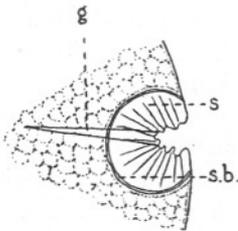


FIG. 2. Mouth apparatus of *P. thalassema*. $\times 1350$ approx. *g.*, gullet; *s.*, folded sucker-like organ; *s.b.*, supporting bar to sucker-like organ.

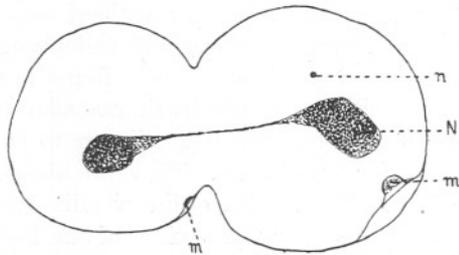


FIG. 3. *P. thalassema* in division. $\times 550$ approx. *m.*, mouth; *N.*, meganucleus; *n.*, micronucleus.

Consequently in most specimens it is obscured by the opacity of the meganucleus. In fact, I have only observed it with any certainty in an individual undergoing division, where in one of the daughter ciliates I have seen it as a small, rather faintly stained, round dot, lying a little distance from the meganucleus.

Division has only been observed in this one instance, which is shown in Fig. 3. It is a late stage, the micronucleus having divided, while the two daughter meganuclei are just completing their separation.

Conjugation has not been observed.

SYSTEMATIC POSITION.

This ciliate belongs to the Holotricha, and, owing to the structure of its mouth, should probably be included among the Gymnostomata. I have been unable to find any form to which it bears much resemblance. The nearest appears to be *Clathrostoma viminalis*, described by Penard (1922). This type also possesses a kind of sucker-like mouth, but it is

not supported by any bar. Moreover, the sucker which "peut s'épanouir comme une ventouse circulaire," is perforated by the gullet, which leads into the endoplasm, whereas in the ciliate under consideration the gullet passes down to one side at a different level.

It seems necessary, therefore, to create a new genus, *Ptyssostoma*, making *P. thalassemae* the type species, of which the following is a diagnosis.

Ptyssostoma thalassemae nov. gen., nov. sp.

Somewhat flattened holotrichous gymnostomatous ciliate, with one side more convex than the other; the mouth situated about a quarter the way from the anterior end, consisting of a kidney-shaped, folded apparatus, supported by a horseshoe-shaped skeletal loop, with the gullet running obliquely into the endoplasm at a different level; cilia arranged in about thirty-five longitudinal rows, with a group of a few long cilia at the posterior end; anterior end of the body modified into a mobile prominence; meganucleus in the centre of the body, irregularly spherical; micronucleus apparently lying laterally to the meganucleus and generally hidden; contractile vacuole conspicuous and at posterior end.

Dimensions: 75–100 μ by 55–75 μ .

Habitat: Intestine of *Thalassema neptuni* Gärtner, from Plymouth.

In conclusion, I wish to express my thanks to Dr. D. L. Mackinnon, of King's College, London, and to Mr. C. C. Dobell, F.R.S., for their kind help and criticism.

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The Hydrogen Ion Concentration of the Muscles of Marine Animals.

By

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AND

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IN view of work which was in progress on the hydrogen ion concentration of mammalian muscles (1 and 2), it was thought interesting to test the pH of the muscles of some marine animals. It was desired to find the pH of muscles immediately after, and 20–24 hours after, excision, and to make buffer curves of the change of hydrogen ion concentration with added acid and alkali. This paper is only a preliminary communication, as the buffer curves have not yet been completed. It was thought that the pH determinations in themselves might be of interest.

METHOD.

Samples of muscles (about 1 gram) were cut out of the animal with sharp scissors. The hydrogen ion concentration of the minced muscle was measured by the glass electrode method, using a portable set with a Lindemann electrometer (3). The minced tissue without dilution was placed in the electrode. All determinations were made at room temperature (12–14° C.). The results are tabulated below:—

	pH		
	immed.	after 20–24 hrs.	
Scyllium canicula . . .	6.98 (3)*	6.10 (5)	tail.
Homarus vulgaris . . .	7.03 (2)	6.49 (2)	abdomen.
		6.42 (1)	claw.
Eupagurus bernhardus . . .	7.11 (2)	6.22 (1)	abdomen.
Maia squinado . . .	7.08 (1)	6.19 (4)	abdomen.
		6.84 (1)	heart.
Pecten opercularis . . .	7.13 (1)	6.44 (1)	adductor muscle.
Conger vulgaris . . .		6.19 (1)	tail.
Lophius piscatorius . . .		6.31 (1)	abdomen.
Carcinus mænas . . .		6.52 (1)	abdomen.
Cancer pagurus . . .		6.33 (2)	claw.
Holothuria nigra . . .		6.38 (2)	longit. muscle of body wall.

* The number in brackets denotes the number of experiments made in each case.

All the specimens of crustacea used for the above experiments were hard-shelled. Experiments on soft-shelled specimens are recorded elsewhere (4).

The mean value for the normal pH is 7.06, and for the pH 20-24 hours later 6.33. The average deviation from the latter mean value is ± 11 , and the probable error of the mean ± 10 . The one experiment on the heart of *Maia* has not been included in the calculation of the mean, as it is much more alkaline than the determinations on other muscles. Similar differences between cardiac and skeletal muscles have been observed in mammalia.

The chief interest in this work lies in the close agreement between the above results and those obtained by us on mammalian muscle, and by Meyerhof and Lohmann (5) on frog's muscle. A comparison is made in the following table:—

	pH of muscles.	
	Resting.	In <i>Rigor</i> or 20 hrs. after death.
Various marine animals	7.06	6.33 \pm .10
Cat—skeletal muscle	7.04	6.02 \pm .07
Cat—cardiac muscle	7.07	6.39 \pm .11
<i>Rana esculenta</i> (Meyerhof and Lohmann)	7.11	6.33

The resting values are the same in all the above cases within the limits of individual variation. In each case these values are probably more acid than pertains in the body, as acid is unavoidably produced during the excision process. It is to be inferred that approximately the same amounts of acid were formed in each technique (which was slightly different in each case). In the case of the experiments of Meyerhof and Lohmann on the frog, the muscles were put into chloroform rigor before the measurement of the figures recorded in the second column. In the experiments on cats and the marine animals, the muscles were kept 20-24 hours at room temperature, so that the post-mortem formation of lactic acid might be complete.

The pH of the marine animal muscles under these conditions is approximately the same as that of frogs, and of the cardiac muscle of cats. It is interesting to note that the average deviation from the mean of the pH measurement of the various marine specimens is not greater than that found between different individual cats. It has been shown elsewhere (4) that the amounts of glycogen present in marine muscle are comparable with that found in mammalian. It therefore appears probable that the buffering powers of the muscles are also approximately the same.

In conclusion, we beg to offer our sincere thanks to Dr. E. J. Allen and the staff of the Marine Biological Laboratory for valuable help and hospitality.

SUMMARY.

Measurements have been made of the hydrogen ion concentration of the muscles of various marine animals immediately after death and 20-24 hours after. The results obtained are of the same order as those previously found for the muscles of the frog and the cat.

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Rays and Skates.

No. 2.—Description of Embryos.

By

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With 11 Figures in the Text.

THE MATERIAL.

IN the years 1921 and 1922 a series of experiments on the rearing and hatching of the species of Rays and Skates occurring on the English side of the western end of the English Channel was carried out at the Laboratory of the Marine Biological Association, Plymouth. The egg-capsules were collected from fish landed at the Barbican at Plymouth and from fish captured by the Research steamers, *Oithona* and *Salpa*. The egg-capsules were kept in the circulation of sea-water in the tanks at the Laboratory, and for six species the period of incubation under these artificial conditions was determined.

The experiment of introducing mature-spawning females into the large aquarium tanks was tried successfully. Two species—*Raia brachyura* and *Raia clavata*—thus provided a large number of eggs which, being extruded naturally, had a much better chance of developing than these taken from fish landed at the fish market, the capsules of which had probably been subjected to much handling before transference to the tanks could be effected.

The six species hatched out in the tanks were kept in captivity to describe the specific characters of each species at hatching, and to determine the extent of the changes before the adult characters are assumed.

In a previous publication ("Rays and Skates," No. 1, Clark, 1922) the experiment in rearing and hatching, and the characteristic features of the young forms immediately after hatching, were described in some detail.

The greater part of the large material, however, was set apart for a special study of the developmental stages, and capsules were opened periodically so as to provide a consecutive series illustrating the changes taking place within the capsule. This material was fixed and preserved according to standard methods, so that it might be available for future histological and embryological work.

The descriptions of these changes taking place within the capsules have been given, however, not only as a guide for future histological and embryological work, but to extend the specific descriptions to the embryonic stages.

The sequence of developmental changes appear to be similar for the species occurring at Plymouth, as has been ascertained by examination

GRAPH 1.

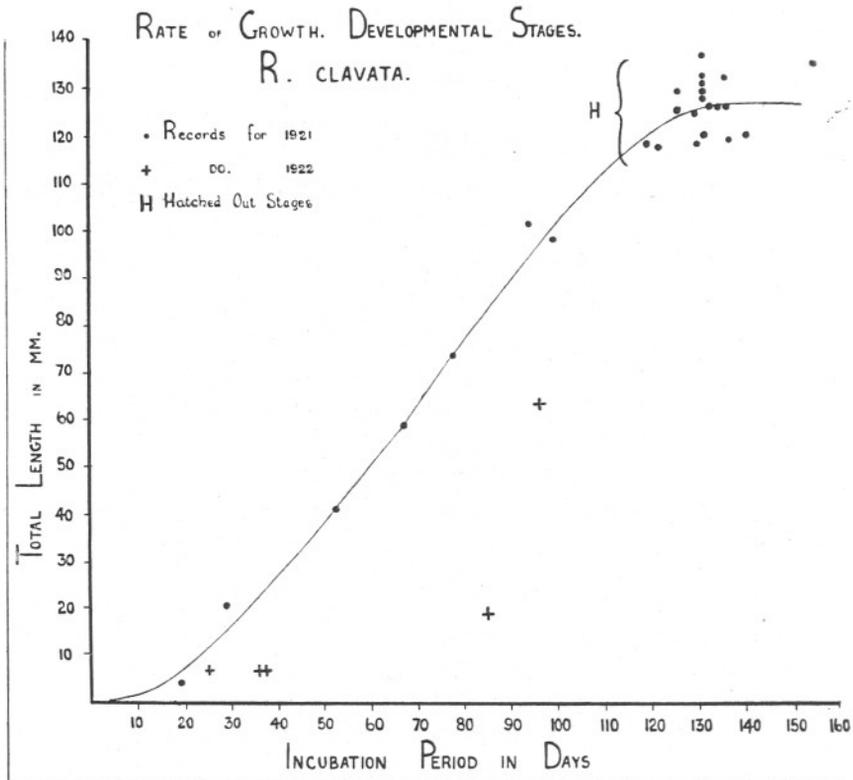


FIG. 1.—Rate of growth. Developmental stages. *R. clavata*.

made at different times during the incubation period. The material is most complete for *Raja brachyura*, and this species has therefore been described in detail. The descriptions of the embryos are given also in tabular form for easier reference.

In "Rays and Skates," No. 1, where the incubation periods for the different species have been given (Clark, 1922, p. 587), it will be seen that there are considerable differences. For example, *Raja clavata*, which

has a mean total length of 126 mm. on hatching, may take 121 to 154 days, while *Raia brachyura*, requiring 189 to 219 days to hatch out, may attain a mean size of 178 mm. The growth rates of these two species throughout the period of incubation are illustrated in the accompanying graphs (Figs. 1 and 2).

The two graphs show similar features after the tail has been straightened out and there is free rhythmical movement. Growth in length (tip of snout to end of tail) is progressive until the approach of hatching. The

GRAPH 2. RATE OF GROWTH. DEVELOPMENTAL STAGES.
R. BRACHYURA.

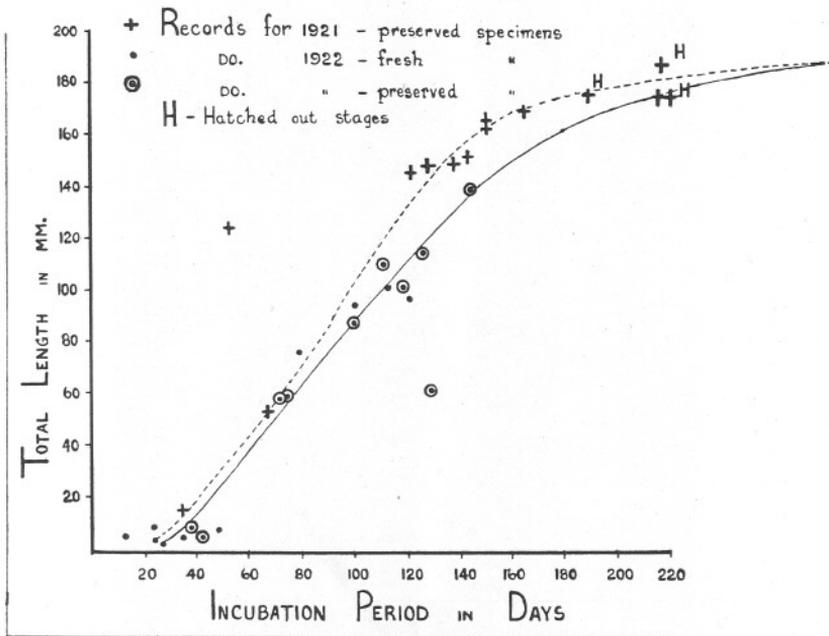


FIG. 2.—Rate of growth. Developmental stages. *R. brachyura*.

graphs in both cases appear to indicate that there is a slowing down at this stage. In "Rays and Skates," No. 1, Clark, 1922, p. 611, the absorption of the post-dorsal part of the tail after hatching has been described, and it is therefore probable that this process of absorption has already begun before the embryo emerges.

From a consideration of the measurements of total length and the distance from the tip of the snout to the origin of the 1st dorsal fin, it is evident that there is a definite differential rate of growth of the parts—pre-dorsal and post-dorsal. After a total length of 58 mm. the actual

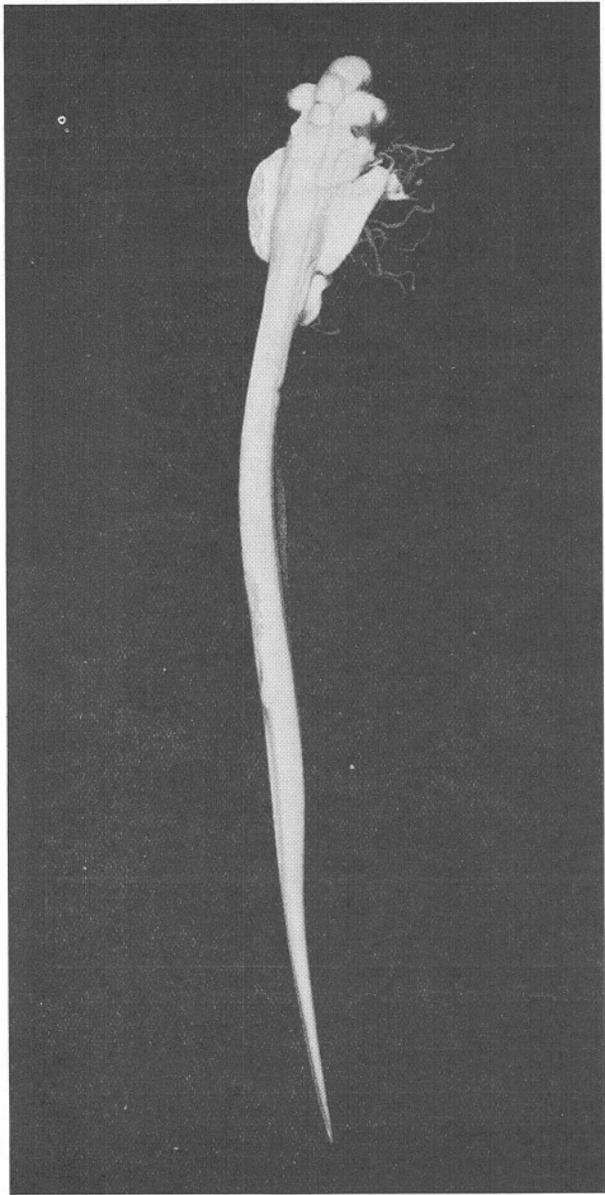


FIG. 3.—*Raia brachyura* embryo, No. 8. Dorsal view. $\times 2.47$.

length of the post-dorsal remains practically stationary. On the other hand, the pre-dorsal length shows a progressive growth. The relative position of the dorsal fins during development may be shown by the following percentages:—

<i>Embryo total length</i>	58.5	59	88	110	115	139	146	147	148	150	162	169 mm.
<i>% Length of predorsal</i>	47	47	54.5	60	61.7	64	68.1	65	69.5	70.6	70.3	73.9

DESCRIPTIONS OF EMBRYOS OF *RAIA BRACHYURA* Lafont.

Most of the egg-capsules from which the following stages were taken were spawned in the tanks of Plymouth Aquarium by a large Blonde (*R. brachyura*), which was secured alive for other experimental purposes (*vide* No. 1 of this Series, Clark, 1922, p. 582). Close and constant observation was kept on the appearance and deposition of the capsules, many of which were marked as they protruded from the fish, so that the period of incubation may be taken as fairly accurate.

The embryos were anaesthetised with drops of 90 per cent alcohol, fixed usually in saturated corrosive sublimate, or occasionally in osmic-corrosive, corrosive-acetic, picro-formol-acetic, and corrosive formol, and preserved in 80 per cent alcohol.

1. Segmentation stage. Duration, 4 days (28.5.22–1.6.22). The germinal disc was 5–6 mm. in diameter, and the blastoderm showed a single furrow, cf. Dean "On the Development of *Chimæra*," Fig. 20.
2. Segmentation stage. Duration, 1 day (19.5.22). The diameter of the germinal ring was 6 × 6.5 mm., and of the blastoderm 4 × 4.5 mm. The disc was nearly circular. This stage corresponds to Balfour's Plate 1, Figure 5. It is more advanced than No. 1, and the earlier cleavages must have taken place while the egg was hung up in the oviduct.
3. Early embryo. Duration, 6 days (1st–7th.6.22). The embryo appeared as a scar, and showed the beginning of the medullary groove. It is equivalent to Balfour's Stage B and Scammon's Figure 4.
4. Early embryo. Length, 3.5 mm. Duration, 24 days (21.4–17.5.22). There is a median constriction, and the medullary folds are closely set, but still separate. This stage is comparable with Scammon's Figures 11 and 12, and lies between Balfour's Stages E and F.
5. Embryo. Length, 4–4.5 mm. Duration, 43 days (30.3–11.5.22). This embryo showed no lateral movement. The head is bent at

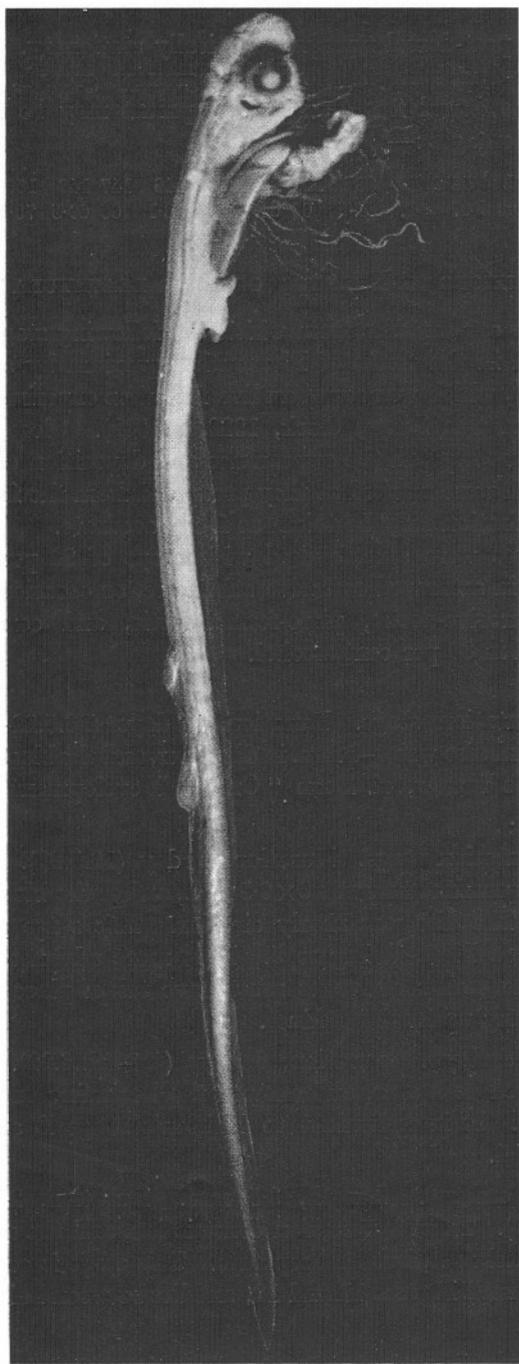


FIG. 4.—*Raia brachyura* embryo, No. 9. Lateral view. $\times 2.98$.

less than 90° from the body. The blastoderm shows a pitted structure. It is near to Dean's Figures 38, 41A, and 41B ("Development of *Chimæra*") and to Scammon's Figure 15.

6. Length, 8 mm. (fresh). Duration, 38 days (19.4-27.5.22). The tail was free for part of its length, and the embryo showed rhythmical lateral movement. The end of the tail is slightly knobbed. It appears to correspond to Scammon's Figures 21 and 22. There is a distinct advance in development from No. 5. The tail is longer and free for the greater part of its length, while the lateral movement is a distinct departure.
7. Length, 7.5 mm. (fresh). Duration, 48 days (24.3-11.5.22). The head of this embryo is at right angles to the body. The lateral movement was quite pronounced on extraction from the capsule. Three clefts were visible. It seems to be slightly less advanced than the previous embryo (No. 6) and corresponds to Scammon's Figure 19.
8. Length, 58.5 mm. (preserved). Duration, 72 days (17.6-28.8.22). There is a considerable gap between this stage (Fig. 3) and embryo No. 7, which was due to accident. The gap, however, can be partially bridged by similar material for another species, *R. clavata*, which will be treated in a future contribution. Both dorsal fins are present. The caudal, from the end of the 2nd dorsal fin to the tip of the tail, measured 23 mm. The distance from the beginning of the 1st dorsal to the tip of the tail was 31 mm. The anal fin membrane is continuous except for a concavity, 15-16 mm. from the tip of the tail, which gives it a double appearance. The anterior half is much deeper than the posterior. There is also a membrane extending from the 2nd dorsal to the caudal tip. The mid-brain projects considerably beyond the snout. The branchial filaments are long.
9. Length, 59 mm. (preserved). Duration, 74 days (15.6-28.8.22). This embryo (Fig. 4) is exactly similar to No. 8. The caudal from end of 2nd dorsal to tip of tail measured 23 mm., and the distance from the beginning of the 1st dorsal to the caudal tip 31 mm. There is a slight constriction in the anal membrane at 18 mm. from the tip of the tail. The pelvics are well developed, and the branchial filaments are long. The snout and pectoral are united.
- 9A. Embryo of *R. clavata*. Length, 63.5 mm. (preserved). Duration, 96 days (12.7-16.10.22). This embryo (Fig. 5) is included here to illustrate a further stage in development than the preceding No. 9. The division of the anal membrane is well shown, while

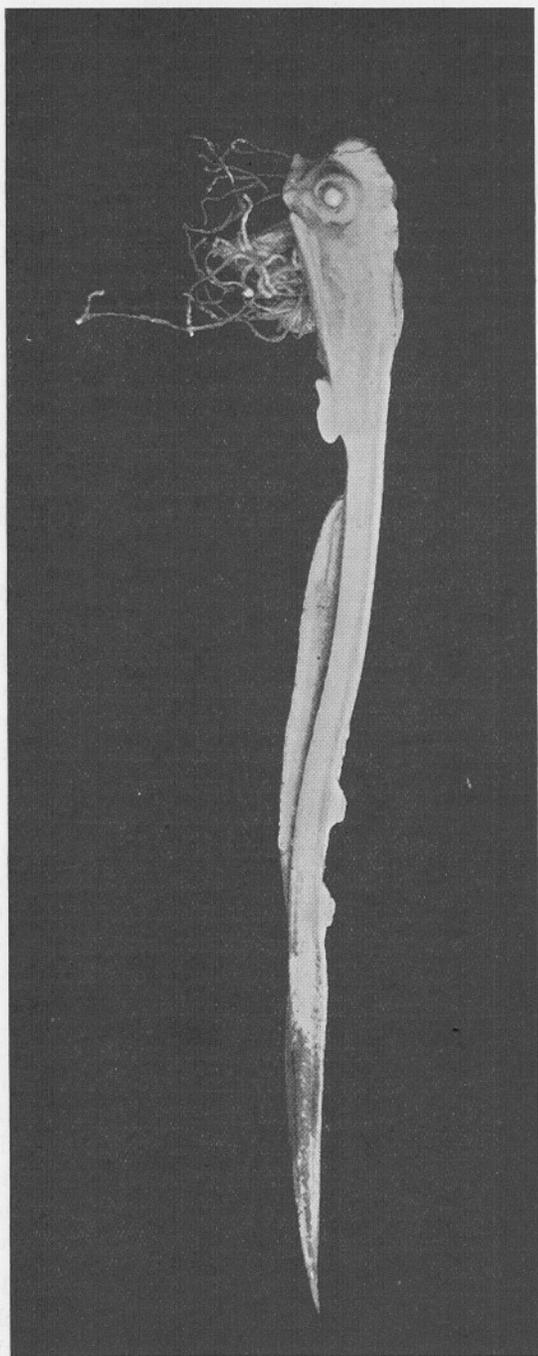


FIG. 5.—*Raia clavata* embryo, No. 9A. Lateral view. $\times 2.45$.

the snout has advanced considerably. The snout and disc are beginning to unite. The length of the caudal fin from the end of the 2nd dorsal is 20 mm., and the distance from the beginning of the 1st dorsal is 28.5 mm. The mid-brain still projects beyond the tip of the snout.

10. Length, 94 mm. (fresh), 88 mm. (preserved). Duration, 100 days (13.5-21.8.22). This embryo (Fig. 6) is much further advanced than No. 9. The disc and snout are united, but the union is not quite complete. There is still a notch anteriorly. The following are the more important measurements:—

Width of disc	20 mm.
Length of disc	19 mm.
End of 2nd dorsal to tip of tail	28 mm.
Beginning of 1st ,, ,, ,,	40 mm.

There is a concavity in the anal fin membrane below the dorsals and the depth of the membrane is greater anteriorly than posteriorly.

The mouth and nasal openings are as in the adult. The teeth have not broken through.

11. Length, 100 mm. Duration, 119 days (1.5-28.8.22). This embryo (Fig. 7) is slightly more advanced than No. 10. The snout and pectorals are completely united. The frontal angle of the mid-brain is not so pronounced as in the previous embryo.

Width of disc	19 mm.
Length of disc	18 mm.
End of 2nd dorsal to tip of tail	21 + x mm.
Beginning of 1st ,, ,, ,,	36 + x mm.

The tip of the caudal was very delicate, and was accidentally lost.

12. Length, 110 mm. Sex ♂. Duration, 111 days (9.5-28.8.22). The claspers are well defined. There is a well-defined skin flap along the sides of the tail longitudinally. The anal membrane is much reduced in depth (Fig. 8).

Width of disc	28.5 mm.
Length of disc	27 mm.
End of 2nd dorsal to tip of tail	22 mm.
Beginning of 1st ,, ,, ,,	44 mm.

The position of the spines along the median ridge of the body and tail and on the sides of the tail is indicated by small knobs. The branchial filaments are still long, and the teeth are not visible.

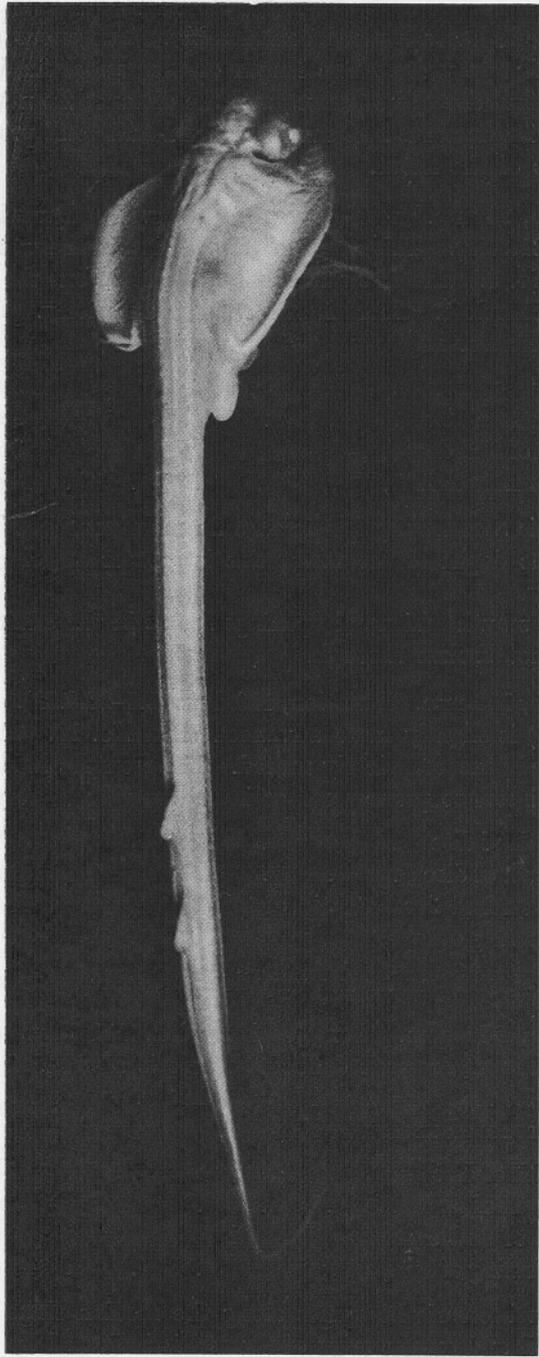


FIG. 6.—*Raia brachyura* embryo, No. 10. Dorso-lateral view. $\times 1.92$.

There is complete union of the snout and the pectorals. This embryo is further advanced than No. 11, and this is shown chiefly in the development of the spiny armature of the skin.

13. Length, 115 mm. Sex ♂. Duration, 128 days (12.6-16.10.22).

Width of disc	37 mm.
Length of disc	34 mm.
End of 2nd dorsal to tip of tail	27 mm.
Origin of 1st " " "	44 mm.

This embryo is exactly similar to No. 12. There is just a slight advance in development. The teeth are now defined. A pair of endolymphatics appear as open tubes on a level with the posterior margin of the spiracle.

14. Length, 115 mm. Sex ♀. Duration, 153 days (21.6-9.11.22).

This embryo (Fig. 9) was extracted on 15th October, 1922, for cinematograph purposes. It was kept alive for over 25 days in sea-water and isolated in one of the tanks. The period within the capsule amounted to 128 days. It is reproduced here to show the quick absorption of the elongated caudal and the reduction of the branchial filaments. The yolk sac is still large, and measures 32×22 mm.

Width of disc	49 mm.
Length of disc	42 mm.
End of 2nd dorsal to tip of tail	11 mm.
Origin of 1st " " "	31 mm.

Pigment is generally distributed over the upper surface, and the spines and spinulæ are well defined. The rapid advance in growth may be compared with embryos Nos. 12 and 13.

15. Length, 139 mm. Sex ♂. Duration, 144 days (11.5-2.10.22).

Width of disc	53 mm.
Length of disc	43.5 mm.
End of 2nd dorsal to tip of tail	30 mm.
Origin of 1st " " "	50 mm.

This embryo (Fig. 10) is more advanced than Nos. 12 and 13. The disc is much broader in proportion to the total length and the branchial filaments are shorter. The claspers and the teeth are well defined. Pigment is beginning to appear on the upper surface. The median spines and the spinulæ on the anterior margin are indicated as knobs. The anal membrane is disappearing. It has quite vanished on the area below the dorsal fins, but it is still present anteriorly and posteriorly to this blank space as a thin

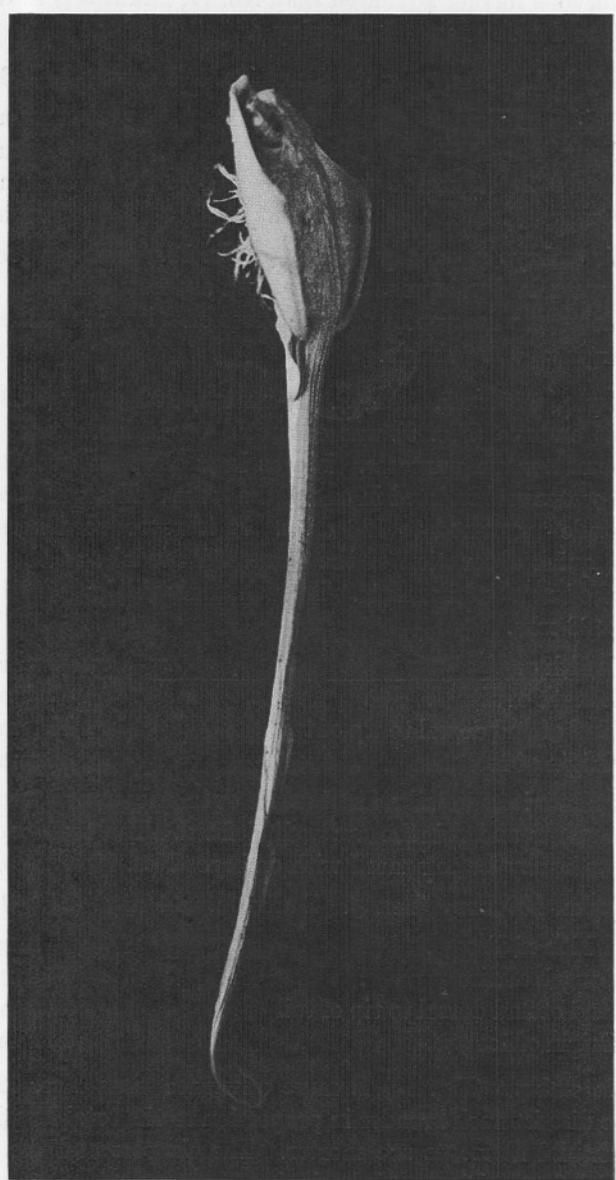


FIG. 7.—*Raia brachyura* embryo, No. 11. Dorso-lateral view. $\times 182$.

low ridge. The membrane behind the 2nd dorsal is continuous to the tip of the caudal.

16. Length, 146 mm. Sex ♀. Duration, 123 days (29.5-29.9.21). This embryo (Fig. 11) shows a big advance from No. 15. The disc is more circular in outline, and the snout is blunter. The branchial filaments are much reduced, and are seen to project only from the third and fifth gill clefts.

Width of disc	65 mm.
Length of disc	55 mm.
End of 2nd dorsal to tip of tail	25.5 mm.
Origin of 1st ,, ,, ,,	46.5 mm.

Pigment is well shown on the upper surface. The spines and spinulæ are strongly indicated. As yet, the points have not pierced the epiderm. A pair of open endolymphatic tubes and the ends of the mucous canals are well defined. There is a pronounced skin flap extending along each side of the tail. The membrane behind the 2nd dorsal fin is still continuous. The anal membrane which has vanished below the dorsal area persists anteriorly and posteriorly, but is not very pronounced.

17. Length, 147 mm. Sex ♀. Duration, 130 days (23.5-30.9.21). This embryo is identical with the preceding No. 16, but the branchial filaments are overgrown by the gill arches.

Width of disc	62 mm.
Length of disc	52 mm.
End of 2nd dorsal to tip of tail	29.5 mm.
Origin of 1st ,, ,, ,,	51.5 mm.

18. Length, 148 mm. Sex ♀. Duration, 138 days (1.7-16.11.21). This embryo is similar to No. 17, but the disc is broader and the caudal shorter.

Width of disc	70 mm.
Length of disc	53.5 mm.
End of 2nd dorsal to tip of tail	25 mm.
Origin of 1st ,, ,, ,,	45 mm.

The branchial filaments are absorbed. The tips of the median tail spines have pierced the epiderm. The yolk sac is still large and measures 32×26 mm.

19. Length, 150 mm. Sex ♀. Duration, 143 days (26.6-16.11.21).

Width of disc	71 mm.
Length of disc	56 mm.
End of 2nd dorsal to tip of tail	23 mm.
Origin of 1st ,, ,, ,,	44 mm.

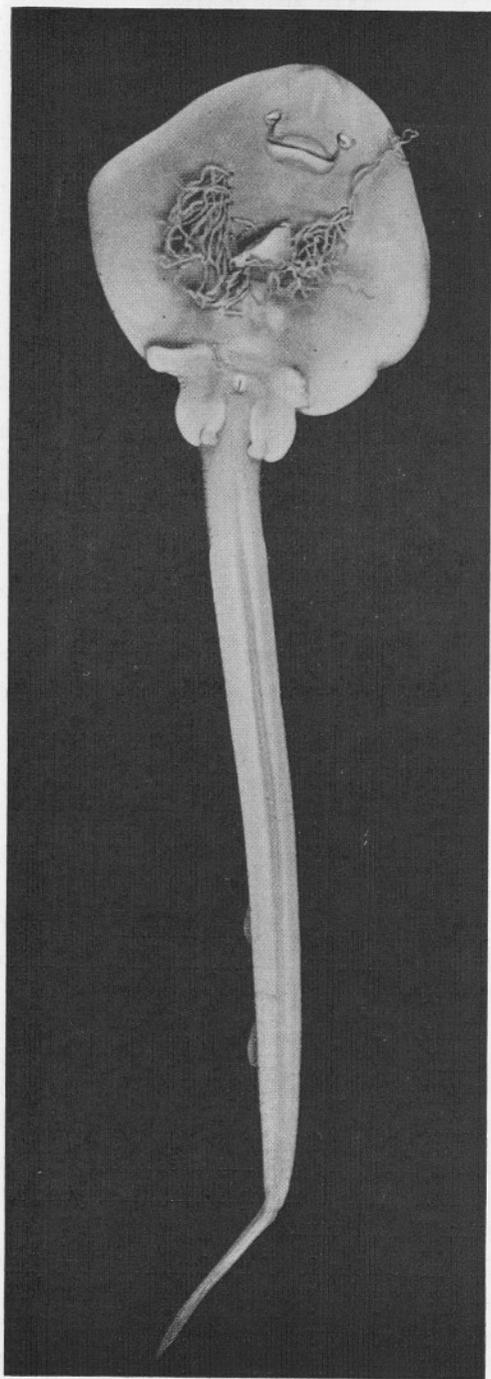


FIG. 8.—*Raia brachyura* embryo, No. 12. Ventral view. $\times 1.62$.

The tips of the median tail spines in front of the first dorsal are through the epiderm. The diameter of the yolk sac measures 29×26 mm. The anal membrane has practically vanished anterior to the position of the 1st dorsal, but is still present posteriorly behind the dorsal fin area, otherwise the embryo is similar to No. 18.

20. Length, 162 mm. Sex ♂. Duration, 150 days (4.6-1.11.21).

Width of disc	87 mm.
Length of disc	66 mm.
End of 2nd dorsal to tip of tail	27 mm.
Origin of 1st ,, ,, ,,	48 mm.

The teeth are more developed than in No. 19, and the anterior margin of the disc is broadly undulated. The tip of the snout does not project. Pigmentation is well developed on the upper surface. The spines on the median ridge have pierced the epiderm.

21. Length, 169 mm. Sex ♀. Duration, 165 days (4.6-16.11.21).

Width of disc	95 mm.
Length of disc	68 mm.
End of 2nd dorsal to tip of tail	22 mm.
Origin of 1st ,, ,, ,,	44 mm.

This embryo is much further advanced than No. 20. The tips of all the spines and spinulæ are clearly through the epiderm. The ends of the mucous canals are well marked. This stage is exactly similar to Fig. 9, Clark, 1922, p. 609. The tip of the snout is slightly recessed. The teeth are obtusely pointed. The anal membrane has vanished.

TABULAR DATA OF

DEVELOPMENTAL STAGES OF *R. BRACHYURA*. YEAR 1921-22.

Period of Incubation, 29th April, 1921, to 3rd February, 1922.

Incubation period.		Days' duration.	Total length of embryo.	Remarks.
Date begun.	Date ended.			
9/6/21	14/7	35	15	Capsule kept in shallow table trough exposed to direct sunlight.
23/5/21	14/7	52	123	

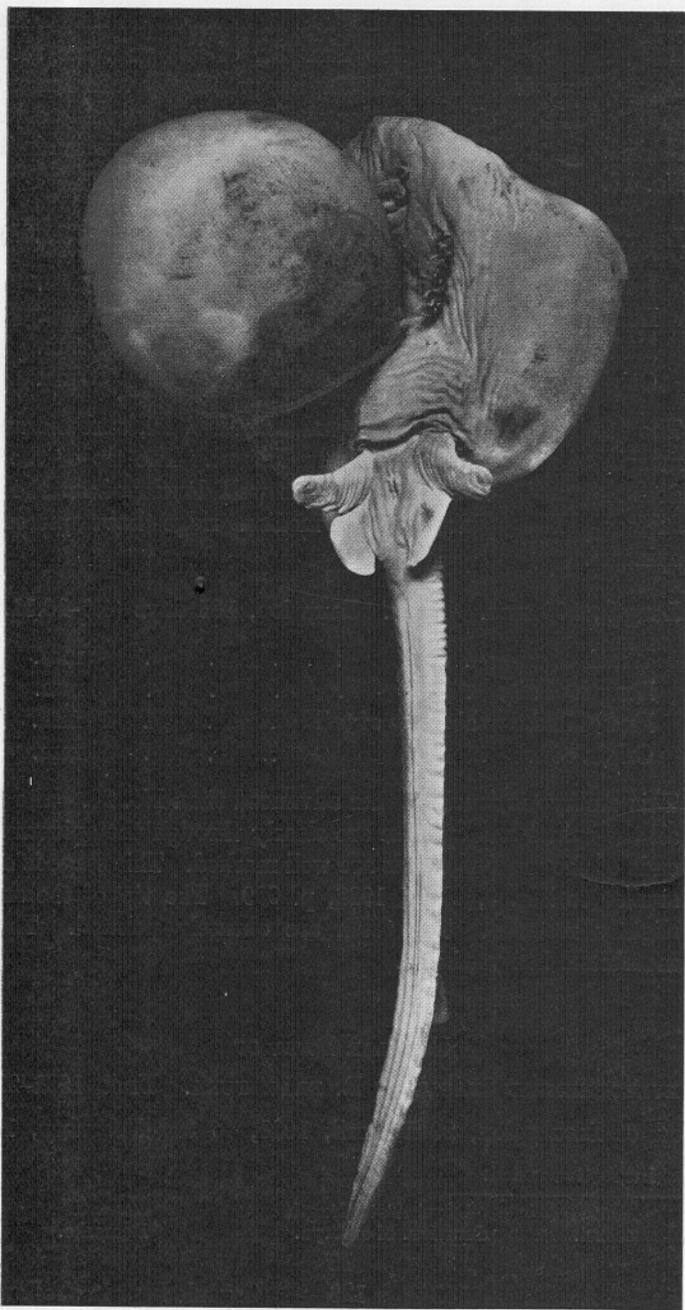


FIG. 9.—*Raia brachyura* embryo, No. 14. Ventral view. $\times 1.33$.

29/4/21	5/7	67	52	Albumen absorbed. Water drained off through slits in horns of capsule.
29/5/21	29/9	122	145	♀ Pigmented. Spines below epiderm. Branchial filaments visible in anterior gill clefts.
23/5/21	29/9	128	147	♀ Pigment. Spines not through epiderm. No branchial filaments visible.
1/7/21	16/11	138	148	♀ Yolk sac 32×26 mm. Median tail spines with tips through epiderm. Branchial filaments absorbed.
26/6/21	16/11	143	150	♀ Branchial filaments absorbed. Median tail spines through epiderm.
4/6/21	1/11	150	165	♂ Pigment spots. Median tail spines with tips through epiderm.
4/6/21	10/11	165	169	♀ ca. Hatching. All tail spines and most of interior spinulæ with tips through epiderm.
Mid-June-	21/12/21	ca. 189	175	♀ Hatched.
End June-	31/1/22	ca. 215	175	♂ Hatched.
1/7	3/2/22	217	187-5	♂ Hatched.
Mid-June-	20/1/22	ca. 220	174	♂ Hatched.

All the egg-capsules were secured from fish which were landed on the Barbican at Plymouth. They were first marked and then placed in the experimental tanks at the Laboratory of the Marine Biological Association. Reference to the average monthly temperatures of the sea-water in circulation in these tanks will be found in "Rays and Skates," No. 1, Clark, 1922.

TABULAR DATA OF
DEVELOPMENTAL STAGES OF R. BRACHYURA. YEAR 1922.

Incubation period.			Embryo.	Remarks.
Date begun.	Date ended.	Days' duration.	Total length in mm.	
19/5	19/5	0	—	Germinal ring 5-6 mm. in diameter. Initial cleavage. Single furrow. Barbican capsule.

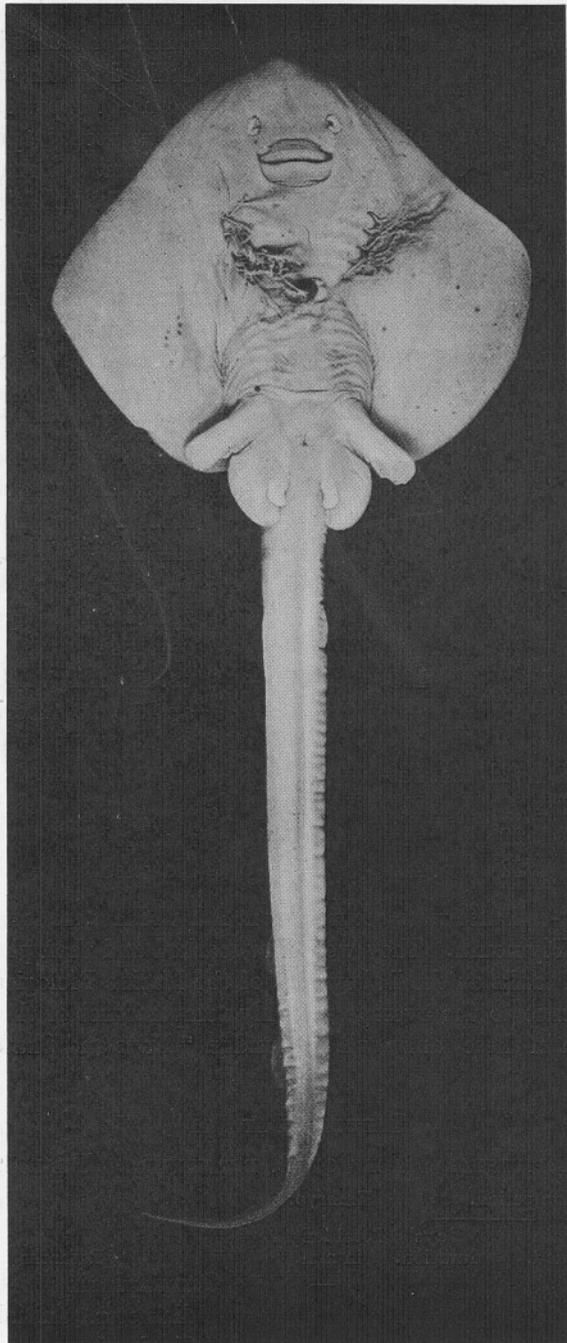


FIG. 10.—*Raia brachyura* embryo, No. 15. Ventral view. $\times 1.21$.

19/5	19/5	0	—	Capsule taken from living fish when first observed protruding. No visible sign of cleavage in blastoderm.
25/5	25/5	0	—	Capsule taken from living fish. Germinal ring 6×5 mm. Cleavage not observed.
31/5	1/6	1	—	Diameter of germinal ring 5-6 mm.
16/5	17/5	1	—	Tank spawned. Germinal disc showing. Segmentation stage, <i>vide</i> Balfour, Pl. I, Fig. 4.
29/5	1/6	2	—	Germinal disc 5-6 mm. in diameter with single furrow on the blastoderm.
23/5	25/5	2	—	Capsule first observed in living fish on 23/5. Also seen on 24/5. Deposited naturally. Germinal disc. Cleavage of blastoderm not observed.
28/5	1/6	3	—	Tank spawned. Germinal disc 5-6 mm. Blastoderm with single furrow.
13/5	17/5	4	—	Tank spawned. Germinal disc 7×5 mm. Segmentation stage, <i>vide</i> Balfour, Pl. I, Figs. 4-5.
1/6	7/6	6	—	Early embryo. Beginning of medullary groove. Balfour, Stage B.
5/5	17/5	12	—	Taken from living fish. Segmentation stage. Late cleavage, <i>vide</i> Balfour, Pl. I, Fig. 5.
21/4	17/5	24	3-5	Tank spawned. Embryo, <i>vide</i> Balfour, Stage F.
12/4	17/5	35	4-5	No lateral movement in embryo. Balfour, Stage G.

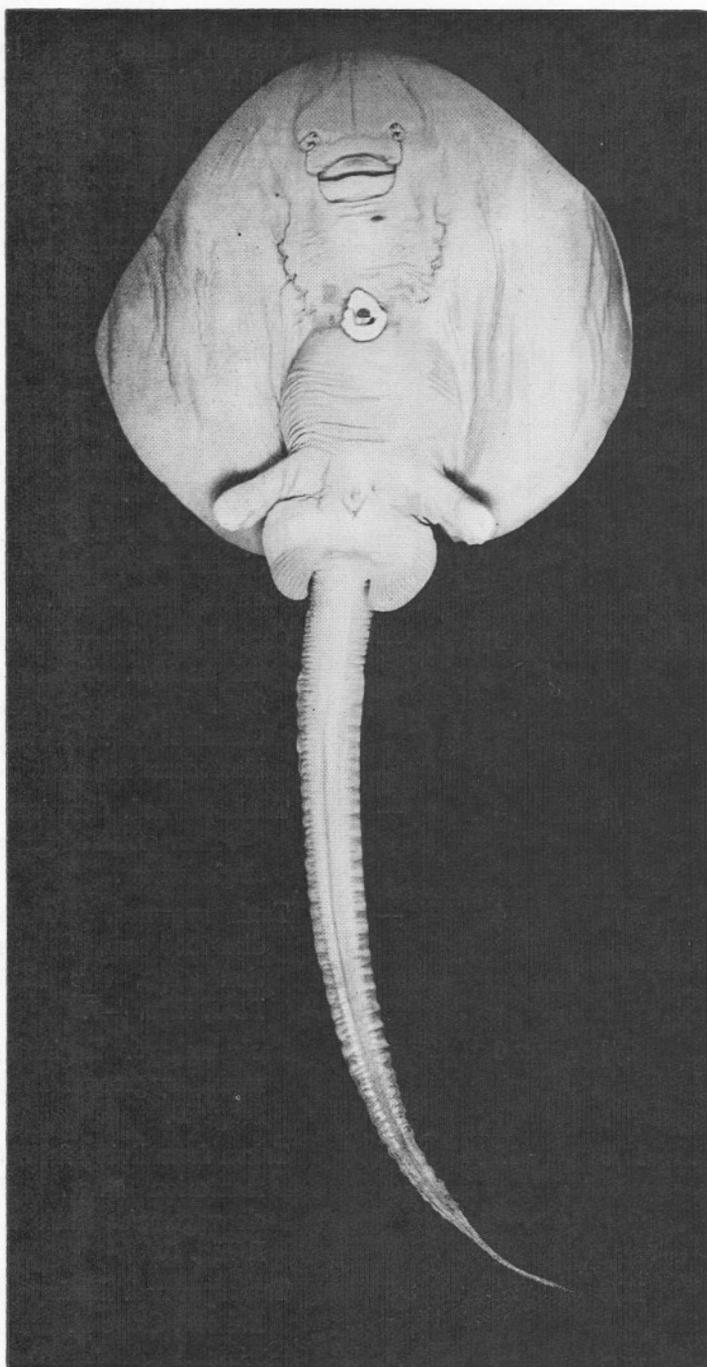


FIG. 11.—*Raia brachyura* embryo, No. 16. Ventral view. $\times 1.11$.

30/3	11/5	43	4-4.5	No lateral movement in embryo. Blastoderm much pitted, <i>vide</i> Dean, Fig. 38. "Chimæroid Fishes and their Development."
24/3	11/5	48	7.5 (fresh)	(5 mm. preserved measurement.) Deep furrow encircling yolk. Embryo showing lateral movement, <i>vide</i> Balfour, Stage I, 3 gill clefts.
17/6	28/8	72	58.5	Tank spawned capsule. (58.5 mm. = preserved length.) Snout and pectorals NOT united. Mouth subterminal. No filaments from spiracle.
15/6	28/8	74	59	Do.
3/6	21/8	79	76 (fresh)	Capsule tank spawned. Albumen absorbed. Snout and pectorals NOT united.
13/5	21/8	100	94 (fresh)	88 mm. preserved measurement. Capsule tank spawned. Albumen absorbed. Snout and pectorals UNITED, not completed. Vascular system well developed. Branchial filaments long. Width of disc 21 mm.
9/5	28/8	111	110	Preserved length. Capsule tank spawned. Sex ♂. Snout and disc united completely. Branchial filaments absorbed. Not visible externally. Width of disc, 28.5 mm.
1/5	21/8	112	100	Snout and disc united. Branchial filaments long. Vascular system well devel-

				oped. Water drained off through slits on horns on capsule being removed from tank. Width of disc 21 mm.
1/5	28/8	119	100	Preserved length. Snout and disc united. Branchial filaments long.
22/4	21/8	121	97	Measurement on fresh embryo. Albumen absorbed. Snout and disc united.
12/6	16/10	126	114	Preserved length. Sex ♂. Embryo inactive when extracted. Quick movement on transfer to outside seawater, and more so with initial stimulus of anaesthetic. Branchial filaments considerably reduced, but still visible. On removal of capsule from tank, internal water drained off readily through slits on horns.
9/6	15/10	128	?	Embryo extracted for cinematograph. Yolk large. Vascular system well developed. Disc and snout united. Branchial filaments reduced. This embryo was kept alive in a separate tank for a short period. The tail shortened very quickly, and the branchial filaments were similarly greatly reduced, <i>vide</i> Fig. 7.
11/5	2/10	144	139	Preserved length. Sex ♂. Pigment spots on upper surface. Branchial filaments still moderately long.

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Investigations Upon the Water Movements in the English Channel. Summer, 1924.

By

J. N. Carruthers,

Fisheries Laboratory, Lowestoft.

With 11 Charts.

REVIEW OF PREVIOUS INVESTIGATIONS AND THEIR RESULTS.

THE conspicuous success of Fulton's experiments with floating drift bottles in the northern North Sea (1)* gave a marked impetus to the study of marine currents by means of freely moving objects (both surface floating and bottom trailing). Finding that Fulton's results, "laissaient encore indécise la question des rapports de la Mer du Nord avec la Manche" (2, p. 55), Gilson, in 1899, carried out his well-known investigations with floating bottles in the south-west part of the Southern Bight (3). He used bottles of two kinds, simple and coupled, and put them out at different states of the tide. In 1897 the surface drift of the English Channel had been investigated by the Marine Biological Association, floating bottles being put out to the number of 430 during the year. The results of these investigations are to be found in a paper by Garstang (4). In 1911 the Board of Agriculture and Fisheries also made experiments with drift bottles; these threw light upon the water movements in the North Sea-English Channel junction area. The chief results of these latter experiments are embodied in Admiralty Chart 327. Further small bottle experiments have been made since by the Ministry of Agriculture and Fisheries, chiefly in definite connection with specific fishery research problems.

An account of these latter experiments has been given in reports devoted to researches on young herring (5).

As is well known, our knowledge of the water movements in the English Channel and its junction area with the North Sea is largely based upon researches into the distribution of waters of different salinity and temperature. Extensive data on salinity distribution have been amassed over a considerable period of years, and the consideration thereof has yielded valuable information as to the movements of the water in our area. It

* Bracketed numbers refer to the list of literature cited; this appears at the end of the paper.

is not our intention to refer in any detail to the numerous researches of this kind which have been carried out; the chief workers in this field have been Matthews, Jee, Lumby, and Harvey. The last-named writer has recently published a comprehensive review of the many researches which various workers have made upon the Hydrography of the English Channel (6). Harvey there gives a most valuable survey of the present state of knowledge, and the full bibliography provided by him in his paper renders unnecessary any exhaustive list of references here. We shall here merely indicate the broad features of the water movements in the English Channel, so that it may be possible to realise to what extent the investigations which are the subject of this paper have added to our knowledge.

In addition to the results gained from the experiments with drift bottles and the researches on salinity distribution, mention should be made of an attempt by Gehrke (7), using Knudsen's Hydrographical Theorem (*vide* 8, p. 692), to estimate the net flow of water through the Channel. Current measurements made at the Varne Lightvessel for fortnightly periods in the years 1911, 1912, and 1913, afforded useful information as to the water movements at different depths in the eastern end of the Channel. At the present time current measurements are being continuously carried out at the lightvessel just mentioned. The results of numerous log-ship observations made on the Sandettie Lightvessel and reported upon by Heldt (9) have served further to extend our insight into the current régime of the Dover Straits area, whilst Wollaston's investigations upon the distribution and drift of Plaice eggs have been useful in a similar connection.

The water movements of the southern North Sea have recently been extensively investigated by means of drift bottles by the Ministry of Agriculture and Fisheries; the experiments were reported on by the present writer (10). In this latter connection it might be stated that the movements of those bottles put out at the Sandettie Lightvessel were made the subject-matter of a separate short paper (11). Bidder's well-known experiments with bottom bottles (12) also served to indicate what were the movements of the bottom water in the southern part of the North Sea.

All the foregoing researches were fully considered by Harvey when his comprehensive survey was made (6), and occasional reference to his paper assists us to present a very brief and broad picture of the water movements in the English Channel.

There is evidence that bottom water passes up the Channel into the North Sea (at any rate at certain seasons), for bottom-trailing bottles liberated in the Channel have been recovered in the North Sea. Gehrke's calculations, already referred to, point to a similar

conclusion. It seems probable that this east-going bottom current rises to the surface in the eastern part of the Channel (13, p. 5) where the water is much shallower than it is farther westward. There is a pronounced surface drift from west to east along the length of the Channel. This surface "current" is supposed by some workers to be due entirely to the wind—which is predominantly south-westerly. It is well known, as a result of numerous current observations at the Varne Lightvessel, that the occurrence of winds blowing persistently from the east can hold up and reverse the direction of water movement so as to bring about a movement of the surface waters into the Channel from the southern North Sea. This state of affairs has been experienced fairly often in the course of the last two years, but the "North Sea to Channel" current is only of temporary persistence, and with the disappearance of the easterly winds the east-north-easterly current reasserts itself. It has been deemed a moot point whether the surface waters of the Channel would be devoid of an easterly movement in the absence of the wind effect.

Harvey (6, p. 66) calculates that the mean value of the speed of flow of the water in the Channel between the mouth and Dover Straits is 1.6 miles a day. During January, 1923 (see 5), bottom bottles moved from the longitude of the Isle of Wight towards the North Sea at the rate of $1\frac{1}{2}$ miles a day—whilst many records exist of surface bottles moving eastwards at a speed of as much as 6 miles a day.

It was felt to be desirable that experiments with bottles should be carried out in the *Summer*, to see how the results compared with those of certain experiments which had chanced to be made in *Winter* to assist in researches made upon the distribution of herring fry.

It was decided that bottles should be put out at the International Stations E2 and E3, and also that as good a distribution of bottles as possible should be made along the steamship route, Southampton to St. Malo. The Marine Biological Association at Plymouth and the Ministry of Agriculture and Fisheries were to be jointly concerned in the experiment. During the first half of July, 1924, the following liberations were made in the English Channel west of the Isle of Wight :—

1. Fifty surface and 50 bottom bottles at Station E2 ($49^{\circ} 27' N.$ — $4^{\circ} 42' W.$).

(These bottles were put out on 9.7.24 from the s.d. *Salpa* by the Marine Biological Association.)

2. Fifty surface and 50 bottom bottles at Station E3 ($48^{\circ} 34' N.$ — $5^{\circ} 13' W.$).

(These bottles also were put out from the s.d. *Salpa* by the Marine Biological Association on 10.7.24.)

3. Fifty surface and 50 bottom bottles at equal intervals between $50^{\circ} 20' N.$ and $50^{\circ} 5' N.$ on the night 10/11.7.24.
(These bottles were put out from the Southern Railway Company's s.s. *Lorina* on her passage between Southampton and St. Malo.)
4. Fifty surface and 50 bottom bottles at equal intervals between $49^{\circ} 35' N.$ and $49^{\circ} 20' N.$
(Put out from s.s. *Lorina* on passage between Southampton and St. Malo on night of 10/11.7.24.)
5. Fifty surface and 50 bottom bottles at equal intervals between $49^{\circ} 0' N.$ and $48^{\circ} 50' N.$ (per s.s. *Lorina* on 10/11.7.24)

When reporting upon the results obtained from a large-scale drift bottle experiment, it is desirable to condense the records in some manner which, whilst masking no features of real interest, shall render the records "manageable." In a former large experiment it was possible to present all the individual records in tabulated form on the basis of direction travelled; all bottles recovered were referred to direction sectors comprehending $\frac{1}{8}$ th part of the compass. These direction sectors were suitably superscribed on a chart, so that, for instance, the sector labelled "E.N.E." straddled $11\frac{1}{4}^{\circ}$ on each side of the actual direction E.N.E.

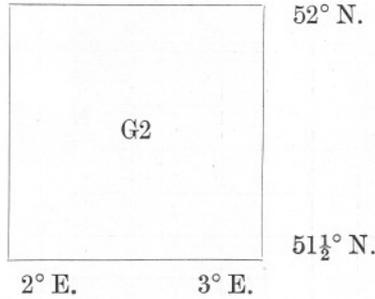
This procedure was well suited to the reporting upon experiments carried out in the North Sea, but in an area like the Channel it would, for many obvious reasons, be inconvenient. We do not, however, wish to present the details as to positions of recovery of the bottles in the form of a clumsy table of latitudes and longitudes—the method we adopt must be such that it will be an easy matter to refer the stated positions of recovery to a chart, so that a mental picture of the movements of a particular bottle may readily be formed. It is clear that we must set out the *individual* bottle histories in a report of the experiments under review since so few bottles are involved.

The following procedure has accordingly been adopted in reporting :—

A chart of sufficient geographical range was prepared embracing the whole of the English Channel, the North Sea as far north as the Shetlands, and the Cattegat—with the Belts. On this chart were superscribed the ordinary statistical rectangles, each rectangle being delimited by one degree of longitude and one-half a degree of latitude. The positions of recovery of the bottles were (as the records were received) referred to and tabulated in terms of these statistical rectangles. For greater precision in the statement of results, the rectangles were visually divided up

into sub-rectangles after the manner of Army cartography practice, thus :—

the rectangle



can be considered to be subdivided thus :—

a	b	c
d	e	f
g	h	j

so that the position of recovery of a bottle might be tabulated as :—

G2 g,

and the latter can be much more quickly referred to a chart than could the usual co-ordinates of latitude and longitude. Chart I shows the positions at which bottles were put out ; it is also divided up in the manner described to serve reference requirements for the recovery positions of the bottles.

For purposes of tabulation of results, a “shorthand method” of referring to the positions of liberation was also required. The International Stations at which the Marine Biological Association put out bottles are referred to in what follows by their ordinary names—E2 and E3.

The three liberation “stretches” on the Southampton to St. Malo route are thus referred to :—

Northernmost stretch	.	.	S.SM(a).
Mid-Channel	„	.	S.SM(b).
Southernmost	„	.	S.SM(c).

and these symbols appear on the chart.

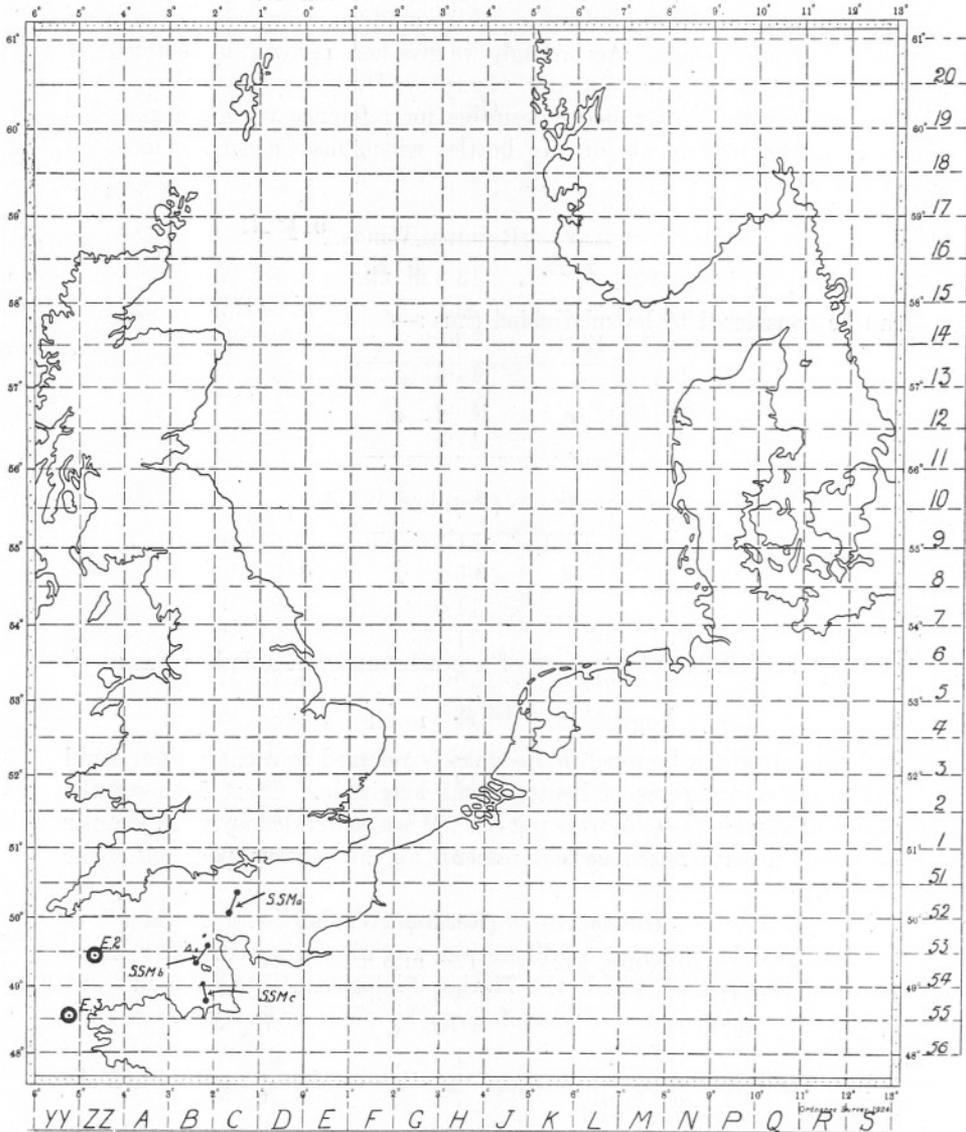


CHART 1.

Key Chart to which tabulated recovery positions of bottles may be referred.

Enough is known as to the effect of wind on the movements of the surface water to realise the necessity for an adequate study of prevailing wind conditions. Such a study was made, and it is convenient to give the results here, so that reference can be made to them when discussing the bottle movements. Accordingly we give here relevant meteorological details for the stations:—Scilly, Guernsey, Dungeness, and Great Yarmouth—the two latter being desirable for reference when we are considering the movements of any bottles which may penetrate into the North Sea.

SCILLY. (Residual Winds.)

July, 1924	.	.	13·8 m.p.h.	S. 76° W.
August „	.	.	19·4 „	S. 84° W.
September, 1924	.	.	15·5 „	S. 61° W.
October „	.	.	14·6 „	S. 38° W.
November „	.	.	15·5 „	S. 40° E.
December „	.	.	17·5 „	S. 42° W.

GUERNSEY. (Residual Winds.)

(4–10) July, 1924	.	.	11·7 m.p.h.	S. 67° W.
(11–17) „ „	.	.	6·2 „	S. 53° W.
(18–24) „ „	.	.	11·9 „	S. 83° W.
(25–31) „ „	.	.	11·4 „	S. 81° W.
<i>Month of July</i>	.	.	10·1 „	S. 73° W.
(1–7) August, 1924	.	.	11·5 m.p.h.	S. 88° W.
(8–14) „ „	.	.	2·1 „	N. 75° W.
(15–21) „ „	.	.	18·5 „	S. 77° W.
(22–28) „ „	.	.	15·6 „	S. 87° W.
<i>Month of August</i>	.	.	12·0 „	S. 84° W.

DUNGENESS. (Residual Winds.)

(4–10) July, 1924	.	.	12·8 m.p.h.	S. 62° W.
(11–17) „ „	.	.	4·3 „	S. 67° W.
(18–24) „ „	.	.	6·8 „	N. 79° W.
(25–31) „ „	.	.	7·5 „	S. 61° W.
<i>Month of July</i>	.	.	7·5 „	S. 70° W.
(1–7) August, 1924	.	.	10·4 m.p.h.	S. 77° W.
(8–14) „ „	.	.	3·3 „	S. 42° W.
(15–21) „ „	.	.	17·9 „	S. 71° W.
(22–28) „ „	.	.	9·5 „	N. 88° W.
<i>Month of August</i>	.	.	10·0 „	S. 77° W.

Dungeness (continued in a different form).

September, 1924	. 17.5 m.p.h.	S. 63° W.
October	„ . 14.6 „	S. 40° W.
November	„ . 15.9 „	S. 24° E.
December	„ . 19.6 „	S. 53° W.

GREAT YARMOUTH. (Residual Winds.)

July, 1924	. . 11.8 m.p.h.	S. 55° W.
August „	. . 9.6 „	S. 53° W.
September, 1924	. 15.5 „	S. 44° W.
October	„ . 11.3 „	S. 14° W.
November	„ . 13.8 „	S. 13° W.
December	„ . 13.5 „	S. 33° W.

THE RESULTS.

We shall here tabulate the relevant details as to the movements exhibited by the returned bottles; the positions of recovery are to be referred to the key-chart already given above (Chart 1). It may be noted in this connection that degrees of longitude east of Greenwich are lettered from "E" to "Z," omitting the letters "I" and "O"; degrees of longitude west of the prime meridian are lettered "D" to "A," then "ZZ" to "AA," omitting "II" and "OO."

Thus (0-1)° East is lettered "E," and (0-1)° West is lettered "D."

With regard to the lettering of degrees of latitude, the following is the conventional practice:—

(51-51½)° N. is numbered "1."

(51-50½)° N. is numbered "51."

The reference numbers increase by unity as one moves away from the datum latitude 51° N. in either direction. It is not necessary here to discuss the origin of this conventional procedure; suffice it to say that it is adopted for reference purposes in the compilation of statistical charts, and we use the method for purposes of convenience.

In the tables which follow, when arriving at the "week from liberation," a fraction of a week counts as one week, e.g. a bottle which was out for 65 days would be entered as recovered in the tenth week.

In the case of bottom bottles only, a double asterisk will be used to indicate all bottles which fulfil *all three* of the following conditions:—

1. Bottle has wire tail of 20 inches or over.
2. Bottle has been out for 4 weeks or over.
3. Bottle has been taken in a trawl.

RECOVERIES FROM THE E3 LIBERATION UP TO 31.5.26.

Fifty surface-floating and 50 bottom-trailing bottles were put out at this position ($48^{\circ} 34' N.$ - $5^{\circ} 13' W.$) on 10th July, 1924. Up to date, the following returns have been realised :—

Surface bottles—22, i.e. 44%.

Bottom bottles—nil.

The recoveries were as here set out.

TABLE I.
E3. SURFACE RETURNS.

Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).	
7	14	C 54 e	44	146	
		C 54 a	"	145	
		"	"	143	
		"	"	"	
		"	"	"	
		"	"	144	
		C 53 g	45	143	
		C 54 a	"	144	
		"	"	"	
		"	"	146	
		"	"	144	
		"	"	49	"
		8	4	"	50
C 53 g	"			147	
C 54 e	"			"	
C 54 a	"			144	
10	1	B 54 b	69	121	
24	1	R 16 d	165	860	
25	1	R 14 b	170	840	
26	1	R 14 c	181	"	

RECOVERIES FROM THE E2 LIBERATION UP TO 31.5.26.

The returns from Station E2 are given below. Fifty of each type of bottle were put out, and up to date the following numbers have been recovered :—

Surface bottles—25, i.e. 50%.

Bottom bottles—nil.

TABLE II.
E2. SURFACE RETURNS.

Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).
4	2	C 53 g	26	111
		C 54 a	24	112
11	2	J 4 c	76	425
		J 5 f	"	428
18	2	N 9 j	120	590
		N 12 g	"	630
23	2	R 16 a	158	830
		N 11 d	"	640
24	6	Q 18 h	168	852
		R 17 g	"	840
25	4	"	163	"
		R 16 a	162	830
		R 17 g	167	825
		R 16 a	166	820
		Q 18 e	172	860
		Q 18 h	"	838
26	2	K 17 c	"	745
		Q 18 h	173	855
		Q 17 b	177	835
		R 17 g	180	825
27	1	K 19 c	189	815
28	1	K 16 b	194	755
30	2	N 10 g	206	595
		L 15 e	208	710
31	1	K 16 e	217	714

RECOVERIES FROM S.SM(C), S.SM(B), AND S.SM(A) LIBERATIONS UP TO 31.5.26.

The other three liberating points may be conveniently treated in the order S.SM(c), S.SM(b), and S.SM(a).

S.SM(c). Fifty of each type of bottle were put out on 10/11.7.24 at equal intervals between $49^{\circ} 0' N.$ and $48^{\circ} 50' N.$ on the route between Southampton and St. Malo. If a north-south line be drawn on a chart from Jersey to the French coast, this "liberating stretch" will be seen to lie slightly to the west of the mid-point thereof.

Returns to date (31.5.26) :—

Surface	31, i.e. 62%.
Bottom	15, i.e. 30%.

TABLE IIIA.

S.SM(c).—SURFACE RETURNS.

Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).
1	1	C 55 e	7	33
2	13	C 55 a	11	25
		"	"	"
		C 55 b	13	32
		C 54 e	"	36
		"	"	35
		C 54 a	14	36
		C 54 e	"	37
		C 55 b	13	33
		"	14	"
		"	"	"
		"	"	32
		C 54 e	"	35
		C 55 e	13	33
3	9	C 55 b	15	"
		C 54 e	16	37
		C 54 a	"	"
		"	19	36
		C 55 b	"	31
		"	16	33
		C 54 a	"	37
		C 54 b	19	"
		C 54 e	"	34
4	5	C 54 b	22	37
		"	23	31
		C 54 e	25	37
		C 55 b	23	31
		C 54 h	24	34
6	1	C 54 e	41	37
9	1	C 55 b	58	33
10	1	C 54 e	68	35

TABLE III.B.

		S.S.M(c). BOTTOM RETURNS.				
Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).	Trawled or Stranded or Afloat.	Length of wire tail on recovery (inches).
3	1	C 54 e	15	35	Ashore	8
7	1	C 54 a	44	39	"	13
9	1	C 54 h	61	33	"	15½
10	1	C 54 a	67	37	"	Not stated
12	1	C 54 e	79	"	"	"
13	2	C 54 a	90	"	"	10
		B 54 f	87	20	"	8½
17	1	C 54 e	115	37	"	None
21	1	C 54 a	141	"	"	19
22	1	D 51 c	151	150	Not stated	Not stated
25	1	D 51 a	171	139	Ashore	14½
31	1	C 54 h	214	37	"	12
37	1	B 54 f	256	32	"	Not stated
38	2	B 56 c	261	33	" *	26
		B 55 h	262	17	"	18

S.S.M(b). Fifty of each type of bottle were put out at equal intervals between 49° 35' N. and 49° 20' N. on the route between Southampton and St. Malo—this on 10/11.7.24. This "liberating stretch" is centred on a point about midway between Jersey and Alderney.

Returns to date (31.5.26) :—

Surface	24, i.e. 48%.
Bottom	11, i.e. 22%.

TABLE IV.A.

		S.S.M(B). SURFACE RETURNS.		
Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).
2	6	C 54 a	9	20
		"	"	"
		"	"	21
		C 54 e	10	23
		C 54 a	"	12
		"	14	11
3	5	C 53 g	16	17
		C 54 a	"	19
		C 53 g	"	15

* Found 12½ miles up river.

Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).
		C 54 a	17	12
		C 54 d	18	21
4	4	C 54 a	24	15
		C 53 g	26	17
		"	25	"
		C 54 a	22	18
6	1	C 54 e	40	30
11	3	J 4 c	71	340
		"	"	344
		K 5 c	75	375
14	2	J 5 j	92	355
		"	94	336
15	1	N 12 a	101	580
20	1	R 14 b	137	690
32	1	K 15 c	221	635

TABLE IVB.

S.SM(B). BOTTOM RETURNS.

Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).	Trawled or Stranded or Afloat.	Length of wire tail on recovery (inches).
6	1	C 54 a	42	18	Ashore	13½
8	1	"	51	"	"	12
9	1	C 53 g	62	16	"	14
11	1	"	76	17	"	8½
17	1	P 13 c	118	680	"	nil.
19	1	F 1 g	127	165	"	"
21	1	E 51 e	145	130	"	"
26	1	P 14 j	182	645	"	?
28	1	N 9 b	192	525	"	?
30	1	J 5 f	210	350	"	19½
72	1	G 2 j	498	230	Trawled	12

S.SM(a). Fifty of each type of bottle were put out at equal intervals between 50° 20' N. and 50° 5' N. on the route between Southampton and St. Malo—this on 10/11.7.24. This "liberating stretch" is centred on a point about midway between the Isle of Wight and Alderney.

Returns to date (31.5.26) :—

Surface	29, i.e. 58%.
Bottom	7, i.e. 14%.

TABLE VA.
S.SM(A). SURFACE RETURNS.

Weeks from liberation.	Number recovered.	Position of recovery.	No. of days "out."	Distance travelled (miles).
9	3	J 4 c	63	307
		J 4 f	"	293
		N 8 a	61	480
10	5	J 4 c	64	306
		"	65	"
		N 8 a	67	460
11	3	J 4 c	75	307
		"	"	"
		"	77	296
15	1	P 14 j	101	625
16	1	R 14 f	106	685
17	4	R 14 b	114	680
		Q 17 b	113	710
		N 15 e	114	625
		N 12 a	115	550
18	1	R 13 c	121	710
19	1	K 15 c	127	590
20	5	J 17 f	137	660
		K 17 a	135	"
		K 19 b	134	740
		L 24 g	137	890
		Q 17 e	136	715
24	1	P 28 g	165	1080
26	1	N 10 g	182	490
27	1	N 25 c	189	990
28	1	Y 39 j	190	1440
96	1	Z 39 g	672	1445

TABLE VB.

Weeks from liberation.	Number recovered.	S.SM(A). BOTTOM RETURNS.				
		Position of recovery.	No. of days "out."	Distance travelled (miles).	Trawled or Stranded or Afloat.	Length of wire tail on recovery (inches).
9	1	B 52 a	61	35	Trawled	ca. 12
11	1	J 4 c	75	307	Ashore	None
18	1	P 13 c	125	610	"	"
21	1	E 51 c	142	111	"	18
22	1	A 52 b	151	65	Trawled	18
28**	1	A 52 j	191	55	"	24
30	1	A 53 c	208	56	Afloat	12 $\frac{3}{4}$

THE RETURNS REALISED FROM ALL LIBERATIONS.

Before discussing the results which have just been tabulated, we will consider the returns from the experiment treated as a whole.

Compounding the returns which have been given above for the various places at which bottles were put out, we get:—

	Surface bottles.	Bottom bottles.
Put out	250	250
Retaken	131	33*
Per cent	52.4	13.2

From all the liberating stations the return of surface bottles has been about the same. In the case of the bottom bottles it has been a great disappointment to receive no return from the E3 and E2 liberations; it was due to the desire to await such that publication has been delayed. It is, of course, not yet too late for recaptures of these bottom bottles to be made, but the fact that no returns are yet to hand is a matter for keen regret, as the information which they would have afforded would have been of much more than ordinary interest.

As would be expected from consideration of the respective positions of the Stations S.SM(a), S.SM(b), and S.SM(c), the returns of bottom bottles were greatest in the case of the last and least in the first case—S.SM(b) affording an intermediate number.

DISCUSSION OF THE RESULTS.

It will be much the most convenient procedure for us to discuss the results from the various liberations separately; we can later devote attention to the wind records when we attempt to summarise the resulting information from all the stations.

* Includes one bottle about whose position of liberation doubt exists.

E3.

(See Table I and Chart 2).

Of the 22 surface bottles returned, those taken within the first 10 weeks (19 bottles) had stranded as follows :—

14	in	C 54 a.
2	,,	C 54 e.
2	,,	C 53 g.
1	,,	B 54 b.

The last mentioned refers to a single stranding in Guernsey. All the others (18 bottles) went ashore on the Manche coast; the fastest of them accomplishing its journey of some 145 miles in about 44 days, i.e. at a speed of about $3\frac{1}{3}$ miles a day. The interesting question is to decide which way the bottles went, whether they skirted the coasts of Brittany, as it were, and then "came up" the Manche coast, or whether they went off straight up Channel and experienced an "indraught" into the Bay of St. Malo, which resulted in the strandings in and around C 54 a. The other alternative is that they followed a path in a north-easterly direction from E3, which took them between Jersey and Guernsey. It seems almost certain that by far the most of the bottles passed to the south of Jersey. This latter path was probably followed by the two bottles which stranded in C 54 e. It seems somewhat strange that only one bottle went ashore on an island. This seems to point to the existence of strong currents washing the shores of Jersey and Guernsey.* The chief point about the E3 surface bottles is, we see, that they nearly all stranded on that part of the Manche coast due east of Guernsey and Sark. A few went ashore (or were found ashore) farther north on the Manche coast, very near to Cap de la Hague. We draw the distinction in the last sentence since it appears probable that the bottles concerned went ashore (or into the shallows) farther south, and were then drifted northwards. Judging from the results of this E3 liberation only, it would seem that there was a strong surface current from the Ushant neighbourhood setting up Channel and impinging on the Manche coast more or less at right angles. It is probable that there was also a strong flow of the surface water from west to east close in to the coast of Brittany; this current, on "coming up against" the Manche coast, can be considered to give rise to a piling-up tendency which is relieved by the escape of the water as a north-going, fringing surface current up the coast in question. The existence of such a current would go far to explain the distribution of the stranded E3 surface bottles, for they were found

* The tides in this area are notoriously strong.

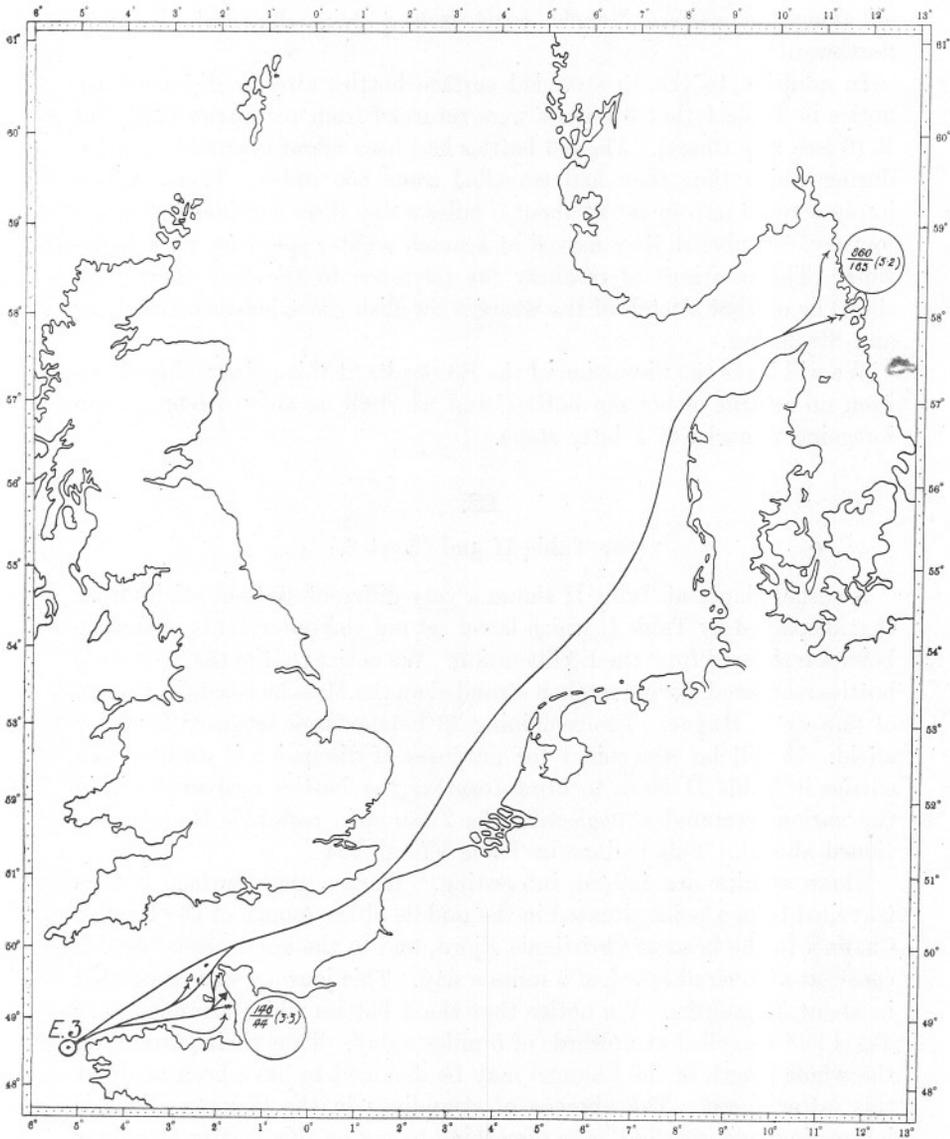


CHART 2.

Illustrating the actual movements of the surface bottles put out at Station E3 on 10 July, 1924. Where the arrows are multi-barbed, the number of bars denotes the number of bottles recovered at the place indicated—save that the solid triangular barb refers to 14 bottles. The figures in the circles refer to the stranding places near by, and have the following signification:—

- The numerator indicates chordal distance travelled in miles.
- The denominator gives the time "out" (in days) of the fastest bottle.
- The bracketed figures denote the corresponding speed in miles per day.

all along the western Manche coast from a point due east of Jersey northwards.

In addition to the 19 stranded surface bottles already discussed we notice in Table I that 3 bottles were returned from rectangles R 14 and R 16 (see Key Chart). These 3 bottles had been afloat about $5\frac{1}{2}$ months, during which time they had travelled some 850 miles. These travels imply a speed movement of about 5 miles a day if we consider the whole journey. Doubtless they moved at a much greater speed for part of the time. The positions of recovery (as reference to the Key Chart will show) lie on that stretch of the western Swedish coast between Goteborg and Stromstad.

We will leave the discussion of the E3 results at this point; there have been no returns of bottom bottles, and we shall be able to refer to the foregoing remarks at a later stage.

E2.

(See Table II and Chart 3.)

A casual glance at Table II shows a very different state of affairs from that displayed by Table I, which latter set out the movements of surface bottles recovered from the E3 liberation. We notice that of the 25 surface bottles recovered, 2 were retaken stranded on the Manche coast, just south of Cap de la Hague. The remaining 23 bottles were returned from far afield. It will be convenient for purposes of discussion if we treat the entries in Table II so as to bring together the bottles recovered within the various rectangles (neglecting the 2 found in rectangle C and mentioned above). This is done in Table VI—p. 704.

These results are indeed interesting. We see that surface bottles travelled from a point situated in the middle of the mouth of the English Channel to the head of Christiania Fjord, and to the north-west Swedish coast, at an overall speed of 5 miles a day. This journey was completed in about $5\frac{1}{2}$ months. We notice that the 2 bottles which stranded near Texel had travelled at upwards of 5 miles a day. Thus their journey up the whole length of the Channel may be assumed to have been made at this latter speed. The absence of strandings in the German Bight is interesting, and we shall have something to say on this matter at a later stage. The bottle which stranded in L 15 e is not very significant in point of speed, since it may have lain undiscovered for a considerable time. Again the "K" bottles were returned from the Dutch islands, and we notice that their time "out" is a variable quantity. There is a considerable likelihood of bottles being unnoticed in such places; their apparent defective speed, as compared with bottles which went ashore elsewhere, seems insignificant therefore. There were no bottom returns

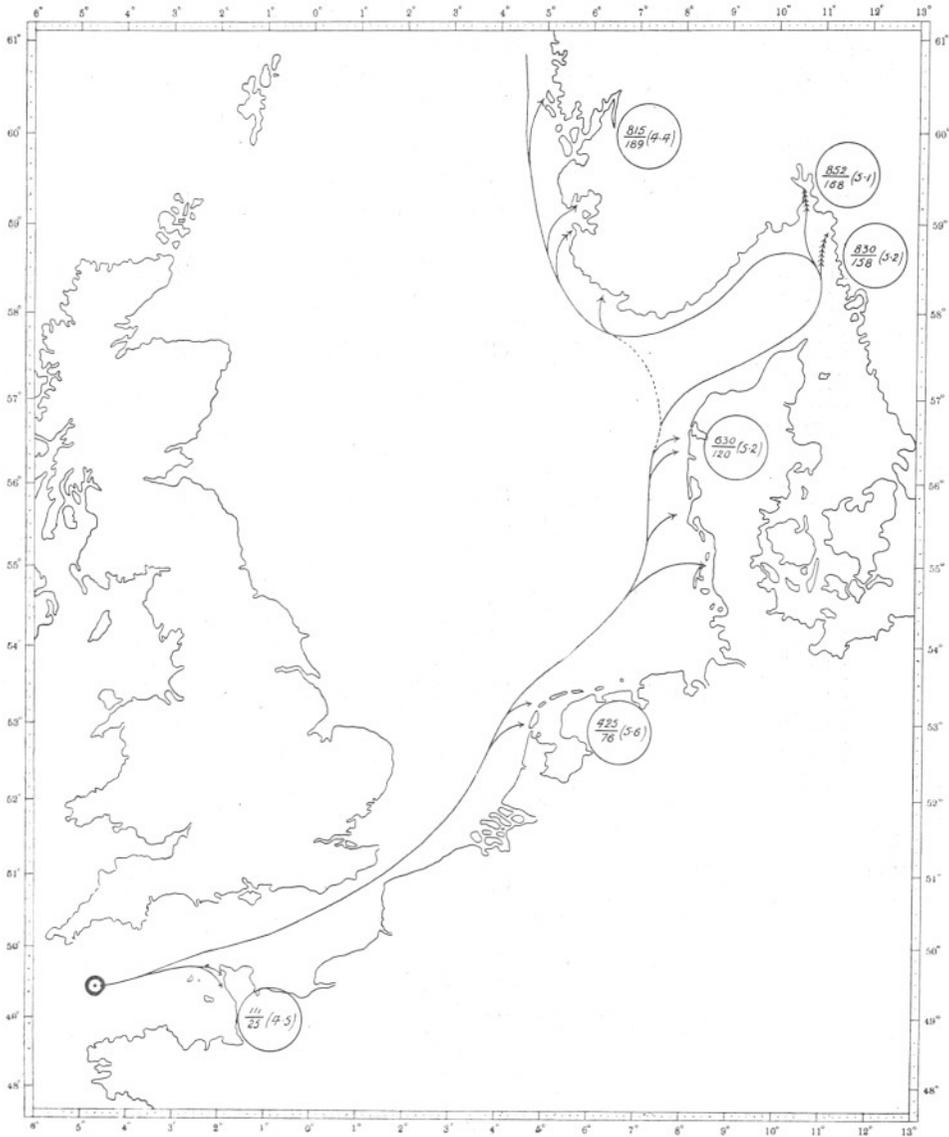


CHART 3.

Illustrating the actual movements of surface bottles put out at Station E2 on 10 July, 1924. Where the arrows are multi-barbed, the number of barbs denotes the number of bottles recovered at the place indicated. The figures in the circles refer to the stranding places near by, and have their previous signification.

TABLE VI.

Rectangle and sub-rectangle.	Number of bottles.	Distance travelled.* Miles.	Time* "Out." Days.	Speed.* Miles per day.
J 4 c } J 5 f }	2	425	76	$5\frac{3}{5}$
K 17 c } K 19 c } K 16 b } K 16 e }	4	745	172	$4\frac{1}{3}$
L 15 e	1	710	208	$3\frac{2}{5}$
N 9 j } N 12 g } N 11 d } N 10 g }	4	630	120	$5\frac{1}{4}$
Q 18 h } Q 18 e } Q 18 h } Q 18 h } Q 17 b }	5	852	168	5
R 16 a } R 17 g } R 17 g } R 16 a } R 17 g } R 17 g } R 16 a }	7	830	158	$5\frac{1}{4}$

in the case of this liberation, so that we may conclude our discussion of it at this point; we shall revert to it when we try to draw up a general picture to represent the results of the whole experiment.

S.SM (c.)

(See Tables IIIA and IIIB and Charts 4 and 5.)

Surface Bottles.

In this case there were returned 31 surface bottles and 15 bottom bottles; we shall first discuss the surface returns (see Chart 4).

The entries in Table IIIA are singularly monotonous in point of recovery position. Every returned surface bottle is seen to have stranded in one or other of the two rectangles, C 54 and C 55. The average distance covered by the bottles prior to stranding was some 34 miles; the speed

* The tabulated values refer to the fastest bottle of each group.

is not easy to estimate. We can, however, adopt as representative the speed of the fastest bottle—a procedure which is quite justified, and which has customarily been used in reporting on previous experiments. In this connection attention is to be devoted to the bottle which stranded in C 55 e, after moving 33 miles in not more (though possibly less) than 7 days. This, of course, points to a minimum "straight line" speed of just under $4\frac{3}{4}$ miles a day, as applicable to the surface currents in the area concerned. An observation worthy of notice is that the fastest



CHART 4.

Illustrating the actual movements of surface bottles put out at Station S.SM(c) on 10-11 July, 1924. The tips of the arrows indicate stranding places, the small figures near the coastline refer to the numbers of bottles recovered there, and the figures inside the circles have the usual signification.

C 55 bottle was retaken ashore before the fastest C 54 bottle. This fact seems to indicate that the currents flow almost due east, thereby creating a piling-up tendency on the western Manche shore, which tendency is relieved by a fringing coastal flow of surface water to the northward. In this connection attention may be drawn to the fact that the stranded surface bottles were distributed all the way up the western coast of the Manche department, though none rounded Cap de la Hague. Should any further returns come to hand in the future they will be particularly useful, if it be found that they had made their way out of

the bay. Certain features in the nature of negative evidence may be remarked upon; thus, there were no strandings in Jersey. This is very significant, since Jersey is only some 10 miles to the north of the liberating stretch, S.SM(c). Also no bottle was found ashore anywhere on the French coast to the southward and westward of the subrectangle, C 55 e. These facts, in conjunction with the results of the strandings of surface bottles from the E2 and E3 liberations, can fruitfully be compared with

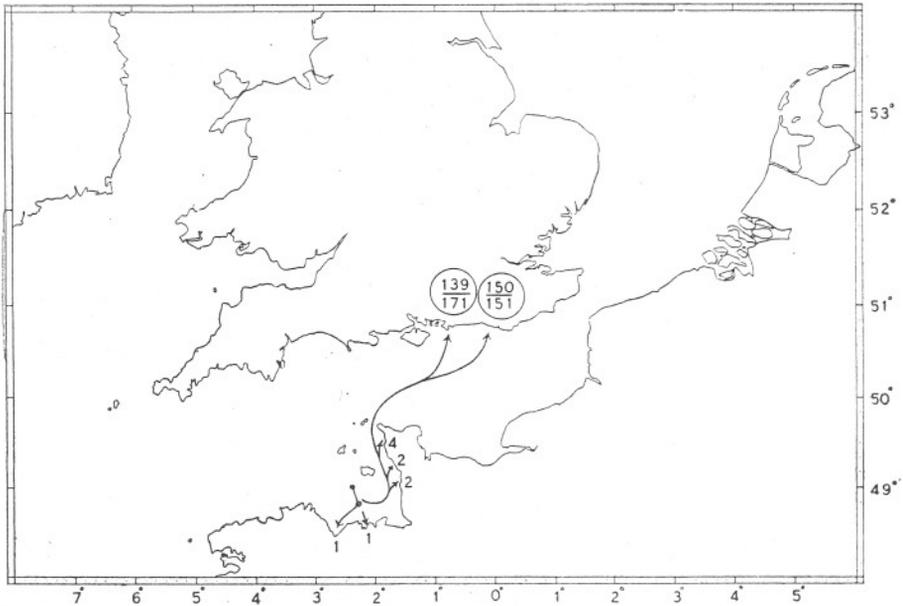


CHART 5.

Showing the actual movements of bottom bottles put out on 10-11 July, 1924, at S.SM(c). The arrows illustrate the deduced movements of the bottom water. Where figures appear near the coastline they denote the number of bottles which went ashore at the places indicated. The figures in circles refer to the bottles recovered near by, and have the following signification:—

Numerator denotes miles travelled.
Denominator denotes days out.

the information presented on Admiralty Chart 327 (q.v.). There it is seen that evidence has resulted, from past experiments, of a surface current coming up Channel from seawards of Ushant, and having a definite offset into the Bay of St. Malo. Arrows are noticed which indicate the occurrence of a definite set on the French coasts around Paimpol, St. Brieuç, and St. Malo. Our present experiments yield no evidence of this, and it will be necessary for us later to pay some

regard to the prevalent wind conditions which (there is *a priori* evidence to suppose) may afford some measure of explanation.

Bottom Bottles. (Chart 5.)

Fifteen of the 50 bottom bottles put out were returned in all. With one exception, it is safe to assume that they were all genuine bottom trailers. The exception referred to is the bottle which stranded at the position, C 54 e, after travelling 35 miles in 15 days; this speed (which is minimal by reason of the fact that the bottle may have lain undiscovered for some time) forces one to the conclusion that the bottle was a faulty one which floated—a not uncommon experience. We may consider first the bottles which were recovered at the least distance from the place of putting out. First, we notice that one bottle (recovered at B 56 c) had moved south by east and stranded on a river bank, after penetrating some way up the estuary. Another bottle (found at B 55 h) had moved towards south by west, and had stranded on the French coast in the neighbourhood of St. Brieuç. Two bottles moved in an east-north-easterly direction and went ashore on the eastern extremity of Jersey. Eight bottles stranded on the western Manche coast, and of these more were recovered at the most northerly position than at those farther south. This seems to point to a movement of the bottom water off the western Manche coast, towards north. There remain two very interesting bottles which were returned after having stranded on the Sussex coast—one on the western side of Selsey Bill and the other near Brighton. The faster of these had performed the journey of some 150 miles in about as many days. Such movements as were taken on by the bottom bottles put out at S.SM(c) could, therefore, be explained by assuming that within the area enclosed by a line drawn from Cap de la Hague to Paimpol, the bottom water moved at the time of the experiment as follows:—

There was a set towards south on to the coast between St. Brieuç and St. Malo; some little distance east of this there was a set towards north with an easterly element “in it.” The movements of the bottom bottles within this area could be explained if we assumed the existence of a bottom current coming from the west somewhat south of the forty-ninth parallel, which, on reaching about $2^{\circ} 30'$ west longitude, bifurcates, one branch trending north-north-easterly and the other southerly and south-easterly. This latter branch, on impinging on the coast around St. Brieuç, must be considered to flow towards east, and then to follow the Manche coast. Thus we should have a bottom “swirl” in the eastern part of the bay—the opposite thing to the “*buchtwirbeln*” of Böhnecke.

S.SM(b).

(See Tables IVA and IVB and Charts 6 and 7.)

From the liberations made at this position, 24 surface and 11 bottom bottles were recovered. We will discuss the surface ones first.

Surface Bottles. (See Chart 6.)

A casual glance at the table of returns (IVA) shows by no means the same monotony as did the corresponding table for S.SM(c). All bottles recovered within the first 6 weeks had stranded within the two rectangles, C 54 and C 53, but later recoveries were from far afield. Let us confine our attention, for the time being, to the 16 bottles which went ashore on the Manche coast. First, we may notice certain features of the liberating stretch, S.SM(b) :—

In part, it is open to the westward; part of it lies between Guernsey and the French Manche coast; and part of it lies opposite to the "strait" between Guernsey and Jersey. These facts (in view of our finding, from the movements of bottles put out elsewhere at the same time, that there was a current coming from the west) make it appear at least possible that bottles, put out at different points on the 15-mile stretch, might encounter different conditions of current. Of the 16 bottles in question, 9 went ashore in C 54 a, 1 in C 54 d, 2 in C 54 e, and 4 in C 53 g. Thus there was a marked surface set towards the east. The fastest bottles attained a minimal speed of some $2\frac{1}{4}$ miles a day. No bottle stranded anywhere on the Manche coast south of that part abreast of Jersey. The 2 bottles which stranded in C 54 e were put out at the southernmost part of the S.SM(b) liberating stretch, and the slight southerly element in their easterly movement is, no doubt, due to a southward bend in the surface current, coming from the westward, in rounding Jersey.

The fact that so many bottles stranded in C 54 a and C 53 g points again to the existence of a flow of the surface water up the Manche coast in a northerly direction. In fact, there seems to have been, at the time of the experiment, a pronounced flow against the whole of the western Manche coast, which necessitated a surface escape to the northward.

The far-travelled Surface Bottles.

Five bottles were recovered stranded on the Dutch islands, off the Zuider Zee, after covering a distance of from 340 to 375 miles. The speed attained was of the order of 5 miles a day. One had gone ashore near the entrance to the Lim Fjord, in Jutland, after accomplishing a journey of 580 miles in 101 days (possibly less). One went ashore north of Goteborg, in Sweden, after travelling some 690 miles in 137 days: the overall

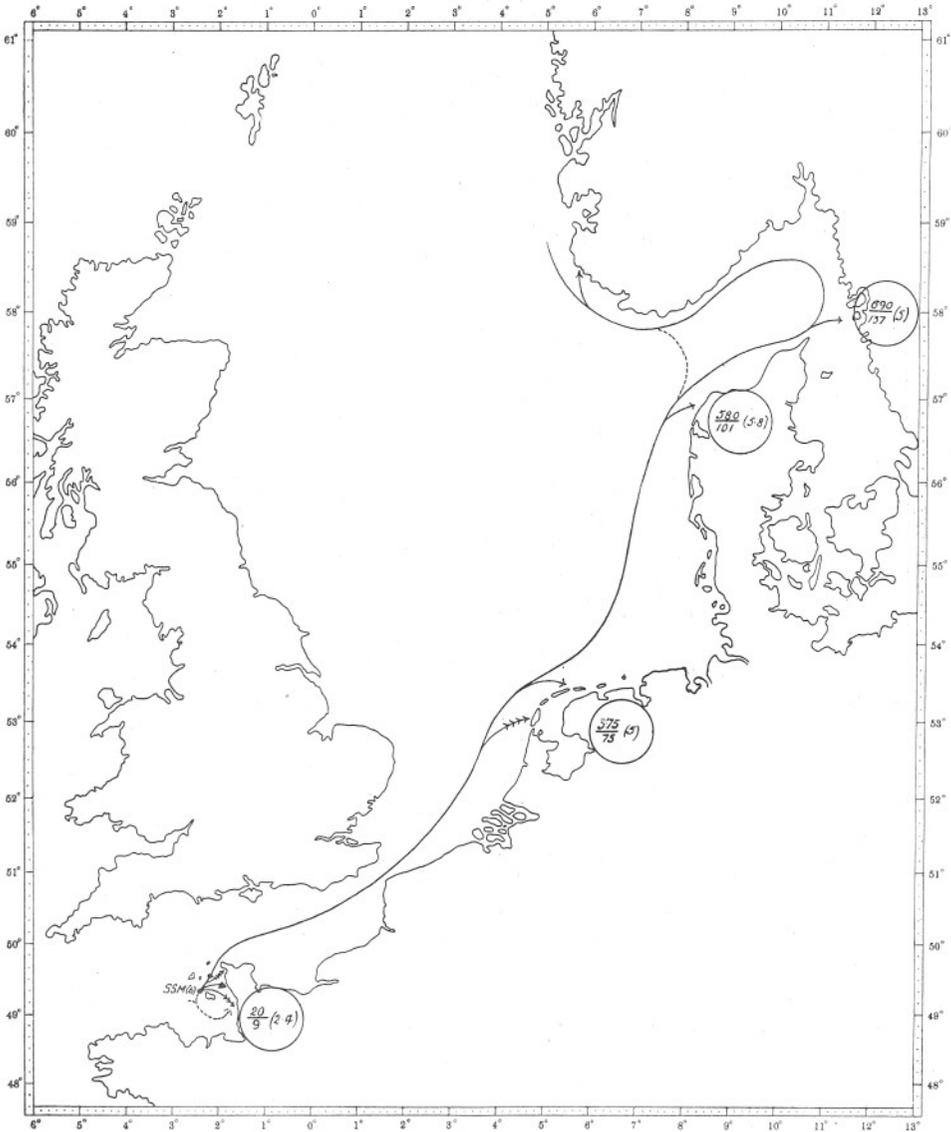


CHART 6.

Illustrating the actual movements of surface bottles put out at Station S.S.M.(b) on 10-11 July, 1924. The signification of the arrows and figures in circles is the same as on preceding charts, save that the solid triangular barb refers to 9 bottles.

speed for this long journey was approximately 5 miles a day. The remaining bottle was cast ashore in S.W. Norway, just north of Ekersund. It may have gone first (it probably did) into the Skager-Raek and Cattegat.

The Bottom Bottles. (See Chart 7.)

Of the 11 bottom bottles returned, only 1 had been retaken by trawl; the others were cast ashore. The direction of movement of the bottom

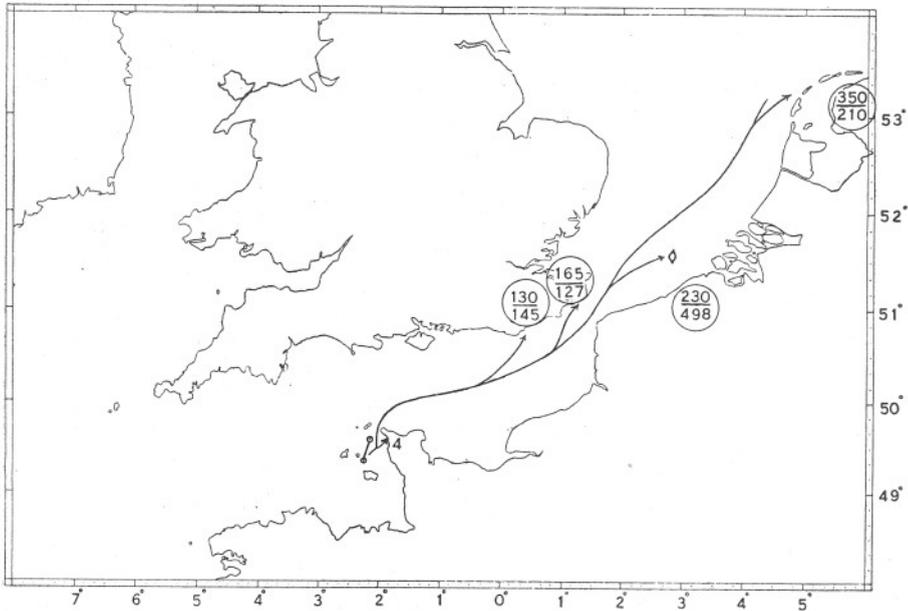


CHART 7.

Illustrating the actual movements of bottom bottles put out at S.SM(b) on 10-11 July, 1924. The arrows indicate the deduced direction of the bottom currents, and the various symbols have their usual signification, save that:—

4 refers to four bottles which stranded; the fastest of these had gone 18 miles in 42 days (at most), and

♠ denotes position at which one bottle was retaken by trawl.

water seems to have been in almost exact accord with that of the surface water. Four bottles went ashore on the western Manche coast; they moved due eastwards at a rate of slightly less than half a mile a day. The others, which were subsequently returned, had rounded Cap de la Hague and gone up Channel towards the North Sea. The bottle recovered in P 13 c was undoubtedly a faulty one which floated—as witness its high speed, which is the same as that attained by the surface bottles. The same can be said of those bottles which were returned from P 14 j

and N 9 b, respectively. This leaves us with 4 bottles calling for comment. One stranded near Beachy Head, after moving some 130 miles in 145 days; one went ashore on the Kent coast east of Dungeness, after having travelled 165 miles in 127 days; one was trawled in G 2 j (near Bligh Bank) in the Southern Bight, after a journey of some 230 miles in 498 days; whilst the other had stranded on an island off the Zuider Zee, after moving 350 miles in some 210 days. The journeys performed by the fastest bottles point to a bottom water movement up Channel, towards the North Sea, of about a mile a day.

S.SM (a.)

(See Tables V_A and V_B and Charts 8 and 9.)

From the liberations made here, 29 surface and 7 bottom bottles have been recovered. We will, as has been our custom above, first discuss the former.

Surface Bottles. (See Chart 8.)

Not one surface bottle was returned from any place on the Channel coasts. Those bottles, which had moved least far, were recovered stranded on Texel and neighbouring islands, and on the Dutch coast near Helder. In all, 8 bottles went ashore in rectangle J 4, and, of these, 7 were recovered in J 4 c—the other had stranded in J 4 f. These bottles had travelled some 300 miles in just over 60 days; their overall speed for the entire journey can be taken as 5 miles a day. Next, in point of distance travelled, are 3 bottles which stranded in Sylt (N 8 a), of which one completed a journey of some 480 miles in about 60 days. This corresponds to a representative straight line speed over the whole distance of about eight miles a day. Another bottle was cast ashore near Blavands Huk after a journey of 490 miles in 182 days. There were 2 more strandings in Jutland: 1 bottle just north of Lim Fjord and the other near Hirtshals; the latter had covered some 550 miles (at least) in 115 days. The remaining 15 surface returns were from even farther afield.

Three bottles went ashore on the Swedish coast, north of Goteborg, after performing a journey of some 680 miles in just over 100 days; 2 bottles stranded at the head of Christiania Fjord, after travelling some 700 miles in as little as 113 days (possibly less). There was one recovery from the Skager-Rack coast of Norway (near Christiansand Fjord): in this case the distance travelled was 625 miles, and the time occupied 114 days. The remaining returns from the Norwegian coast to the number of 9 are as follows: 1 from near Ekersund (590 miles in 127 days), 2 from the neighbourhood of Stavanger (660 miles in some 135 days), 1 from near Bergen (740 miles in 134 days), and 5 more from places farther north

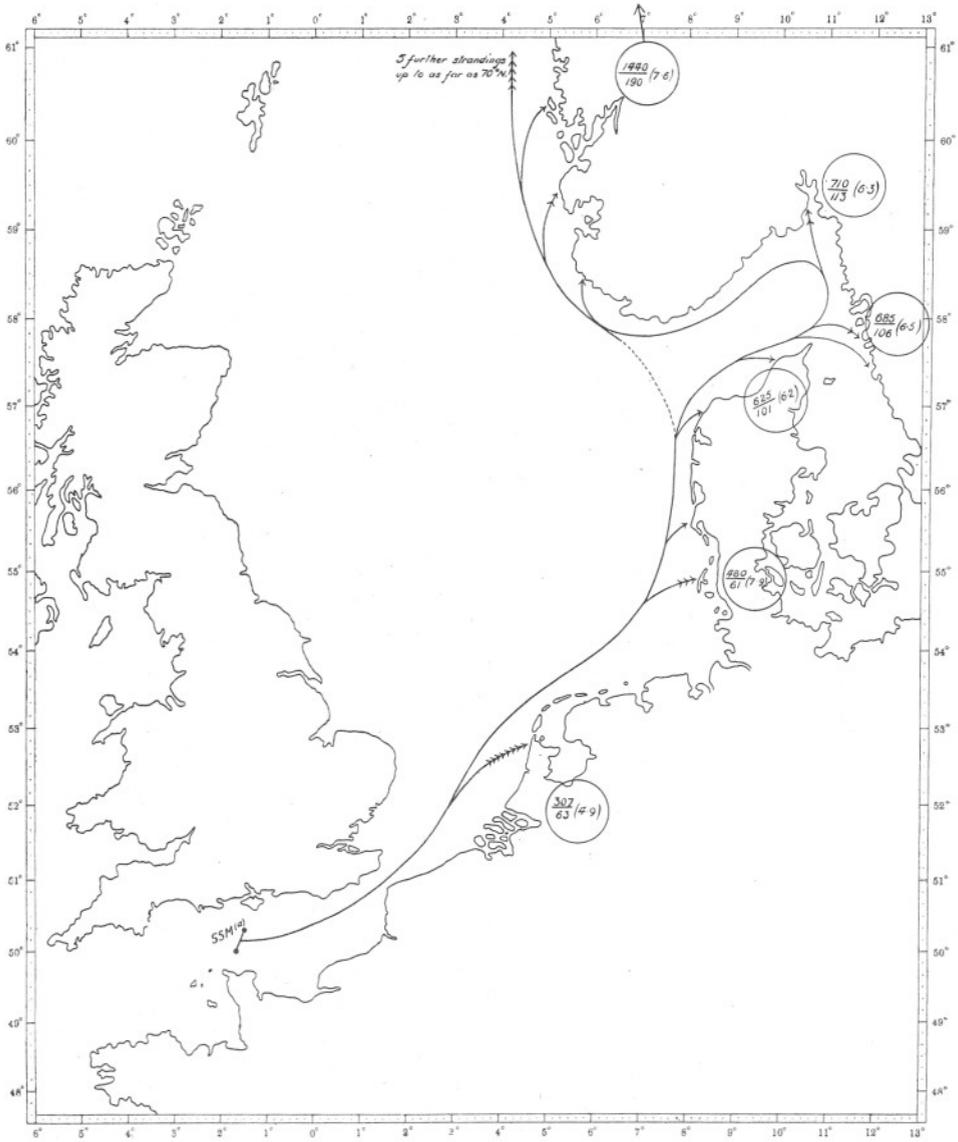


CHART 8.

Illustrating the actual movements of surface bottles put out at Station S.SM(a) on 10-11 July, 1924. The arrows and figures have their usual signification.

up to 70° N. The farthest travelled bottles of all had gone ashore north of Tromsø, 1 having been returned from the island of Senyen. One bottle had travelled 1440 miles, at least, since it was put out, and had performed this journey in some 190 days; this implies the amazing overall speed of some 7.6 miles a day.

The Bottom Bottles. (See Chart 9.)

Seven bottom bottles were returned as shown in Table VB above. Their movements are of great interest, and, as already remarked, it is

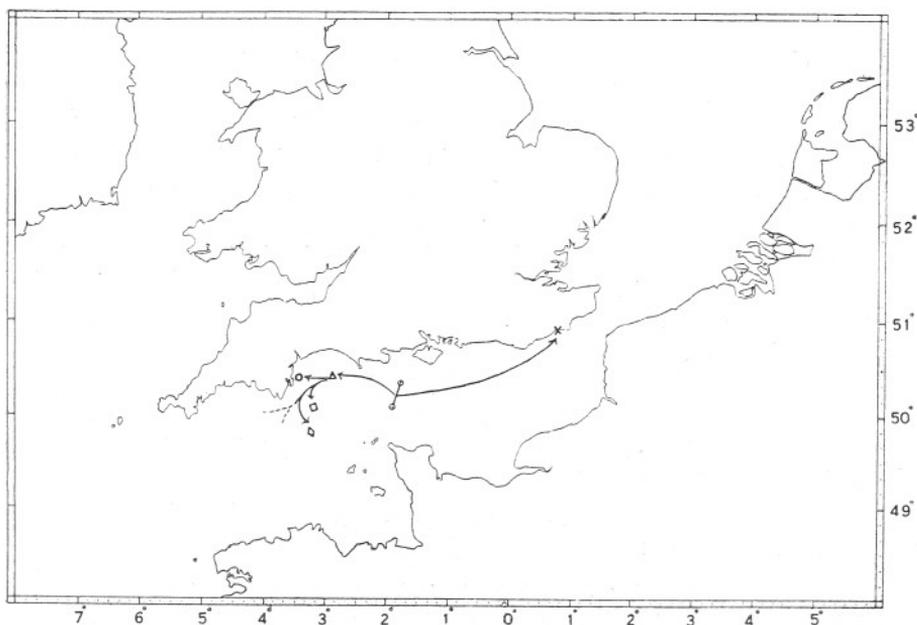


CHART 9.

Illustrating the actual movements of bottom bottles put out at Station S.SM(a) on 10-11 July, 1924. The arrows indicate the deduced direction of bottom-water movement, the various symbols denote positions of recovery, and represent the following journeys:—

X	.	.	111 miles in 142 days (at most).
Δ	.	.	35 " " 61 "
O	.	.	65 " " 151 "
□	.	.	55 " " 191 "
			(at least)
◇	.	.	56 " " 208 "
			(at least)

a matter for keen regret that as yet no returns have been realised from the E2 liberations for comparative purposes. If we omit the two bottles (J 4 c and P 13 c), which were without doubt faulty bottles which floated,

we find that of the 5 remaining bottles recovered, 4 were retaken to the westward of the position of liberation and the other near Dungeness. It is always extremely difficult to arrive at any useful idea as to the speed of the bottom currents from the movements of the bottom bottles, as these will certainly be carried along at a speed considerably in defect of that of the transporting current. We see from the table (V_B) that the bottle which stranded near Dungeness did so after a journey which points to an overall speed of movement of something less than 1 mile a day. The other 4 bottles, in having moved towards the west, present us with a problem of no little interest; in this connection, the fact that such S.SM(b) bottom bottles as rounded Cap de la Hague went towards east, would suggest that there may be, as it were, "a parting of the ways" in respect of the bottom-water movements in mid-Channel about longitude 2° W. Thus it may be that to the north of the fiftieth parallel there is a west-going bottom set, and to the south of it a set in the opposite direction. This matter is worthy of discussion, and it will be well to see if we can find any reference to it in earlier work. Harvey (6, p. 73) refers to the results obtained from a liberation of bottom-trailing drift bottles in May, 1921, at the routine Station E1, which is situated approximately 25 miles S.S.W. (true) from Plymouth (about 50° N.— $4^\circ 20'$ W.). It was found that a movement of bottom water to the westward takes place at times. The present writer has also shown reason to suppose that the bottom water as far east as the Isle of Wight (in latitude 50° N.) can, at times, exhibit a westerly movement (see 5, p. 37, Chart 16). The Charts drawn up by Lumby to illustrate the water circulation in the English Channel, during winter (February) and summer (August) of 1922, must be referred to here (13, Fig. V, opp. p. 12). Lumby's opinions may be summarised thus:—

Winter. Draw a line from Prawle Point to the mid-point of a line joining Lizard Head to Ushant, and produce it seawards. Then, on the north-west side of this line there exists a cyclonic circulation of the entire water column, whilst on the south-east side, there is a decided flow (comprehending the whole water column) from seawards up Channel.

Summer. Seawards of the Land's End-Ushant line is a pronounced northerly flow of surface water, flanked on the west by a cyclonic circulation involving the entire water column. This "cyclone" is elongated in a north by west to south by easterly direction. Now join Prawle Point to Ushant, and Land's End to Ushant, and a triangular area is defined, which "harbours" what may conveniently be described as resembling the eastern half of a cyclonic circulation involving both surface and bottom water. A rectangular area, of which the north Brittany and east Normandy coasts are two sides, "harbours" a large anticyclonic

surface swirl. There is a surface offset from this, east of the St. Alban's Head to Cap de la Hague line, which flows on up Channel towards the North Sea. Lumby further infers the existence of a continuous bottom flow up the entire length of the Channel, from west to east. These results of Lumby's are deductions from salinity distribution.

The results of our present experiments, considered together with the findings of Harvey and Carruthers just referred to, seem to point to the following conclusion a propos of the circulation of the bottom water in the areas discussed:—If we join the position of Station E2 to the mid-point between the Isle of Wight and Alderney, and consider the area defined by our line, so drawn, and the English coast, then we infer the existence therein of a cyclonic bottom water circulation—the “cyclone” being attenuated in an east-west direction.

What happens in and off the Bay of St. Malo is a vexed question indeed. Lumby would invest this area with a large anticyclonic surface circulation; the compilers of Admiralty Chart 327 infer a strong surface flow up Channel, with frequent pronounced surface insets into the bay. The views arrived at as a result of the present experiments can best (to avoid endless discussion) be presented in the form of a summary chart (see Charts 10a and 10b), which shall set forth the resulting information from the present experiments as a whole.

THE WATER MOVEMENTS CONSIDERED IN RELATION TO THE WIND.

(See Wind Tables, p. 691.)

The winds, as recorded at Scilly, were, during the whole of July, August, September, and October, overwhelmingly from the south-west quadrant. For the first three of these months the residuum of wind was from W.S.W. (true).

The winds of July and August, as recorded at Guernsey, were also overwhelmingly south-westerly, and so they were according to the Dungeness records.

Furthermore, the winds, as recorded at Yarmouth for the entire period of July to December inclusive, were from this same direction and that markedly.

The results of all past work would, in view of these wind conditions, lead us to expect what we have found, viz. that there existed a very pronounced surface set right up Channel towards the North Sea, and thereafter right across the southern North Sea towards the Skager-Rack. The frequent strandings of surface bottles on the Swedish and southern Norwegian coasts shows how marked was the Jutland current in autumn, for the bottles which so stranded would be “off” the Skager-Rack about

the end of October. This entry of surface water into the Skager-Rack in autumn has been remarked upon before (10, p. 46), and Pettersson has remarked that westerly winds favour the flow of the Jutland current. It seems to be hardly a fruitful matter to spend much time seeking any numerical correlation between wind speed and surface current speed; in the open ocean, where tidal streams do not call for much consideration, the search for such inter-relationship is more profitable perhaps. However, if we can obtain a useful representative value for wind force over a suitable period, we may be able to arrive at some idea of the numerical relationship between the two quantities in question.

Our present results do not provide us with really suitable material, for we should need to know the movements of bottles which were put out at different times, and which performed their travels during the prevalence of different wind conditions. Such material was forthcoming from Garstang's experiments, already referred to (4), and he was able to advance a formula connecting wind and drift. He established a connection between the two quantities:—

- (a) Number of miles drifted.
- (b) Resultant pressure of the wind.

A high degree of consistency between drifts deduced from his equivalent and the movements actually performed by his bottles was obtained by Garstang. This worker was of opinion that an expression of the formula,

$$V = MW,$$

where V = velocity of the water drift produced by a wind of velocity W , and M is a constant, could not be fitted to the results of actual experiment. Formulæ of this type had been advanced by H. Mohn and others; Garstang criticises Mohn's equation on the ground that it applies to currents *sustained* by a given wind and not to currents produced from rest. R. Witting,* like Garstang, decided that a formula of the type:

$$V = MW$$

was unsuitable, and he came to the conclusion that the formula,

$$V = MW^{\frac{1}{2}}$$

was better. The relationship arrived at by Witting (with modern velocity equivalents of Beaufort numbers) would stand thus:—

$$V = 0.44 W^{\frac{1}{2}}$$

V and W being in cm. per sec. Witting had arrived at this relationship as a result of investigating a large number of observations made at Finnish lightships.

* Quoted by Matthews, p. 680 (8).

It will be of some interest if we ascertain what constant results from fitting our present bottle travels to a formula of this latter type ($V = M W^{\frac{1}{2}}$). In our case the contemporaneity of the bottle liberations, together with the fact that the same wind conditions hold for all bottles, forbids us to attempt the *establishment* of a relationship. If we wish to evaluate the constant M we must have available :—

- (a) A reliable value for current speed.
- (b) A really representative value for wind speed.

Now in an area like the English Channel, where strong tidal streams occur, these two desiderata must be of a comprehensive nature, i.e. any accepted current speed must (in regard to drift bottles, at any rate) be estimated on the dual basis of a long journey accomplished and a considerable time out. Similarly our accepted wind speed must, of necessity, be the resultant for a considerable period. In the case of (a) we can get what we want from Chart 8, where we see that surface bottles had moved a very long way (over 600 miles in some cases) at a speed of $6\frac{1}{2}$ miles a day and over. The information as to (b) is not so easy to obtain even though we have, at an earlier point in this paper, made a full study of the winds at several observing places. We should welcome, in this connection, a continuous autographic wind record for some suitably placed station. We fortunately have access to such. The excellent meteorological reports of the Eastbourne County Borough Council provide just what is needed. The logged winds, estimated according to Beaufort's Scale, accord well with the records from the stations which we have already employed. In the Eastbourne report for 1924 there is a table of wind movements as recorded by the Indicating Cup Anemometer, and we find that the mean winds were as follows during those months of 1924 which interest us :—

July	.	.	.	204.21 miles per day.
August	.	.	.	219.87 " " "
September	.	.	.	216.06 " " "
October	.	.	.	200.41 " " "
November	.	.	.	202.82 " " "
Mean				208.66 " " "

These records are very consistent amongst themselves, though they differ very markedly from the winds for the preceding six months of the year. Let us now solve for M by using the V and W values already arrived at. We get

$$6.5 = M 208^{\frac{1}{2}}$$

whence $M = 0.45$.

We thus find that the relationship between wind speed and surface

current speed in respect of our far-travelled bottles (provided both quantities be expressed in miles per day*) is :—

$$V = 0.45 W^{\frac{1}{2}}$$

where V represents current and W wind. This equation is almost identical with that found by Witting, who found it convenient to estimate both wind speed and current speed in cm. per sec., and whose formula applies to this unit. If we convert our wind and current values from miles per day into cm. per sec., we find that the constant of the formula becomes 0.3 instead of 0.45.

ACKNOWLEDGMENTS.

Thanks are due and are here expressed to the following :—

To the writer's colleague, Mr. H. Stokes, for preparing the final printer's copies of the charts from drafts supplied.

To all the officers of the Southern Railway Company's Marine Department for the welcome co-operation which rendered possible the carrying out of part of the experiments.

SUMMARY OF RESULTS.

In July, 1924, 250 floating, and an equal number of bottom-trailing, bottles were put out at selected places in the western English Channel. Fifty of each type were put out at each of the two routine Stations E2 and E3, and the same number was "liberated" at each of three selected stretches along the steamship route from Southampton to St. Malo. Those surface bottles, which did not strand locally, travelled rapidly up Channel towards the North Sea and across it. Many bottles arrived in the Skager-Rack after performing their journey of some 700 miles at the rate of 6 miles a day and more. An adequate study of wind conditions, as recorded at several stations along the length of the Channel and at one station in the southern North Sea, revealed the fact that there was, for some $5\frac{1}{2}$ months (counting from the time of liberation of the bottles), an almost uninterrupted predominance of south-westerly winds—as recorded at all stations considered. The whole area of the Channel was swept by south-westerly winds of average speed of some 9 miles a day for at least $5\frac{1}{2}$ months subsequent to the time of putting out of the bottles. July, 1924, had (according to the Falmouth Observatory records) the largest proportion of westerly winds experienced for 54 years; 20 days of this month had winds with westerly components. The association of

* It will have been noticed that V is in sea miles per day, whilst W is in ordinary miles per day. No conversion was made, since the value of V depends upon an estimate of distance travelled which can at best be only approximate; the latter is probably considerably under-estimated, as it is substantially a straight line estimate.

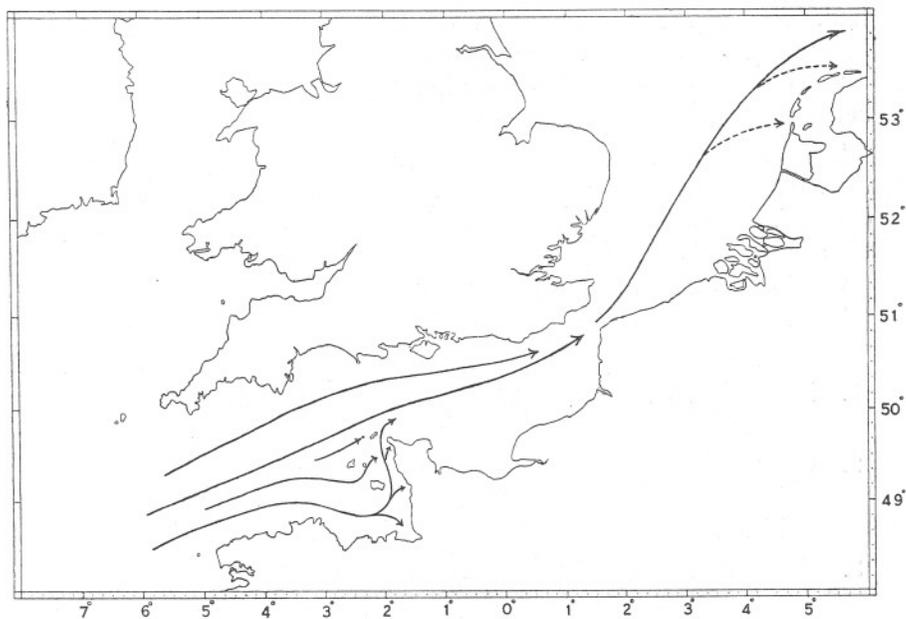


CHART 10a.

Showing the surface-water movements in the English Channel, as illustrated by bottles put out in July, 1924.



CHART 10b.

Showing the bottom-water movements in the English Channel as illustrated by bottles put out in July, 1924.

the unusually persistent westerly winds with the rapid travel of surface bottles towards and across the North Sea is interesting.

The chief feature of interest regarding the information yielded by the bottom bottles is the following:—

There seems to be in longitude 2° W. (approximately) a parting of the ways in respect of the movements of the bottom water. To the north of 50° N. latitude there appears to be a west-going bottom set, whereas to the south of this parallel there is a set in an easterly direction.

Charts 10a and 10b embody the results of the experiments.

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Temperature and Enzyme Activity.

By

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With 4 Figures in the Text.

I HAVE recently carried out an experiment upon the amylolytic enzyme of the crystalline style of the scallop (*Pecten opercularis*), which has given some unexpected results. The experiment was suggested to me by Mr. C. F. A. Pantin, and I wish to take this opportunity of thanking him very much for supervising the work, which was carried out at the Marine Biological Laboratory at Plymouth.

Crystalline styles were removed from sixty-four scallops, weighed, ground up with sand, and dissolved in distilled water to form a 1% solution, which was then filtered. Three experiments were started with this solution directly it had been prepared:—

The solutions were at about pH 6.

(1) *Optimum Temperature Experiment.*

10 c.c. of style solution and 10 c.c. of 1% starch solution were placed in each of six test tubes, which were kept for three hours at constant temperatures, varying from 0° C. to 65.5° C. At the end of this period enzyme action was checked by boiling, and the solutions titrated into Benedicts solution to find how much sugar had been formed. An ordinary optimum curve was thus obtained, which is shown in Fig. 1 (Yonge, 1923).

(2) *1½ Hours' Incubation Experiment.*

Test tubes containing 10 c.c. of the crystalline style solution were incubated for 1½ hours at constant temperatures varying from 0° C. to 66° C. All the test tubes were then placed at room temperature (16°), and 10 c.c. of starch solution was added to each. The tubes were left at room temperature for three hours and the amount of sugar in each estimated as before. The results of this experiment are shown by the graph in broken lines in Fig. 2.

(3) 3 Hours' Incubation Experiment.

Precisely the same experiment was performed, except that the test tubes were incubated at the various temperatures for 3 hours instead of $1\frac{1}{2}$. The unbroken line in Fig. 2 gives the result of this experiment.

A glance at these graphs shows at once that there is progressively increasing destruction of enzyme above a certain temperature (Bayliss, 1919). But another very remarkable and quite unexpected fact also

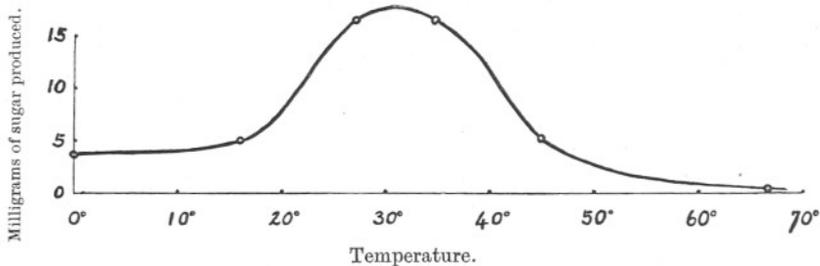


FIG. 1.

appears. This is that if one incubates the crystalline style solution filtrate at 0°C . or at room temperature before adding the starch solution, the amount of sugar subsequently produced is very much greater than if no such incubation had taken place. To put it in concrete terms, 10 c.c. of style solution produce 5.0 milligrams of sugar in 3 hours at room temperature; but if the style solution has been kept for 3 hours previously at room temperature, no less than 13.3 milligrams are produced! It was suggested to me that the reason for this may be that the protein base upon which the enzyme is absorbed is at first in

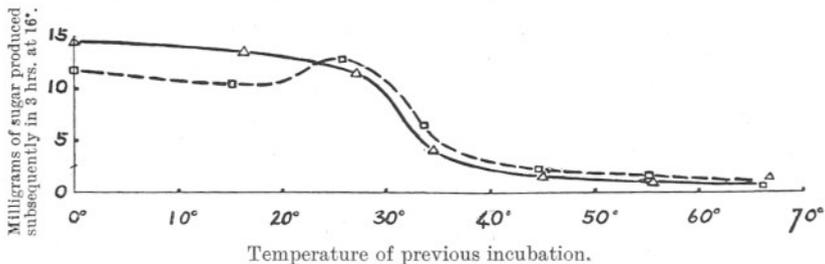


FIG. 2.

fairly large particles, which gradually become more dispersed. As they become more dispersed their surface area becomes greater and the efficacy of the enzyme is thus increased.

The action cannot be due to a co-enzyme; for this would have ample time to effect the activation of the style while in the body of the animal. It should be borne in mind that the style is a pure secre-

tion unmixed with digesting matter or tissue extracts and contains no proteases, lipases, etc.

These effects account for the form of the two curves in Fig. 2. The curves show the activity in producing sugar at room temperature (16°C). If the pure enzyme solution has previously been kept at a low temperature (0° — 10°C .) the activity is greater after three hours of such treatment than after $1\frac{1}{2}$ hours. This is because there is but little destruction of the enzyme at this temperature, but there is a considerable progressive increase in activity on standing. After previous treatment at high temperatures the destructive effect is overwhelming, and the greater the incubation period at the higher temperature the greater the destruction of the enzyme. Hence the activity after $1\frac{1}{2}$ hours' incubation is greater than that after three hours at high temperatures.

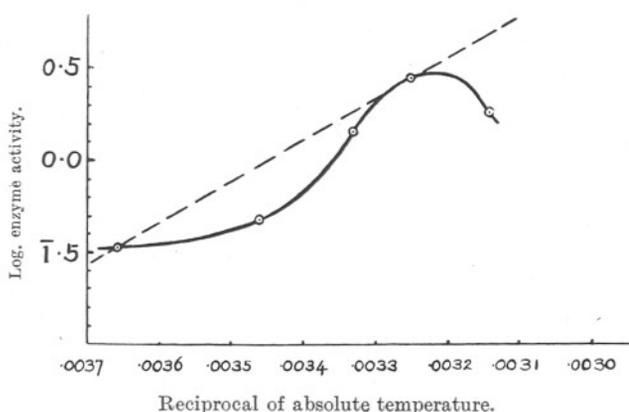


FIG. 3.

It appears, then, that two antagonistic processes are at work while the enzyme is mixed with the starch: (1) Destruction of the enzyme is taking place, particularly at high temperatures. (2) The enzyme is becoming more and more effective as time goes on, possibly as a result of dispersion of its protein base. An attempt has been made to calculate the true velocity of enzyme action, when these two processes are discounted, in a comparable way to that in which Pantin extrapolated a curve for the rate of movement of *Amoeba* above the temperature at which destructive processes are beginning to act (see *Brit. Journ. Exp. Biol.*, Vol. I, No. 4, pp. 519-38).

In Fig 3 the relative velocities of glucose formation are given for different temperatures. The sugar produced appears to be directly glucose: the style being without action on Maltose (Yonge, 1923.)

This is peculiar, inasmuch as in the normal course of digestion Maltose is an intermediate compound from which glucose is produced.

The log. of the velocity is plotted against the reciprocal of the absolute temperature. According to the Arrhenius formula these should be related linearly, the slope of the line depending on the value of μ (Critical thermal increment, cf. Crozier, 1925).

The unbroken line in Fig. 3 gives the results of my experiments. The curve is not taken above 45° C., because the amounts of sugar produced at higher temperatures are too small to give significant results.

The obvious departure from a straight line is probably not due to experimental error. There is no necessity to suppose that Arrhenius' law holds in a heterogeneous system where the effective enzyme surface may vary with temperature.

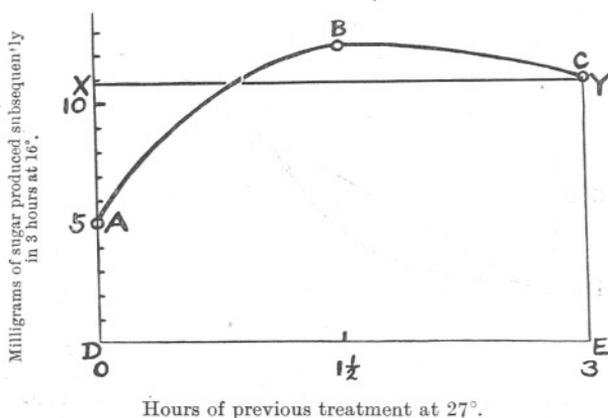


FIG. 4.

I will explain very shortly the method, suggested to me by Mr. Pantin, by which the figures were obtained on which the curve is based. I wish to thank my brother, Mr. S. J. Baker, for assistance in carrying out Mr. Pantin's suggestions.

Owing to the variation of enzyme activity with time, it is necessary to determine the *mean* enzyme activity.

Five graphs were drawn to find the *mean enzyme activity during 3 hours* at five different temperatures, namely, 0° , 16° , 27° , 35° , and 45° . In Fig. 4 I give the graph for 27° to serve as an example of these five graphs. The curve ABC shows the enzyme activity after various periods of incubation at 27° . The *mean* enzyme activity is found as follows: A line XY is drawn parallel to the abscissa DE at such a distance from it that the area of the rectangle XYED equals the area of the figure ABCED. The distance of the line XY from the abscissa DE gives the mean enzyme

activity for a period of 3 hours expressed in milligrams of sugar subsequently formed after another 3 hours at 16°.

The values thus obtained are given in the fifth column of the table below. They show the (combined) effect of destruction and (?) dispersion on the enzyme. As we are trying to obtain figures *discounting* destruction and (?) dispersion, we must *divide* the results obtained in experiment (1) by them. The results of this division are given in the sixth column. We now have figures proportional to enzyme activity when destruction and (?) dispersion are discounted. I have not attempted to calculate absolute values.

Centigrade Temperature.	Absolute Temperature.	Reciprocal of absolute Temperature.	Mg. of sugar produced in 3 hours with no previous incubation (Exp. 1.)	Mean Enzyme Activity.	Col. 4 divided by Col. 5.	Logarithms of numbers in Col. 6.
0	273	·00366	3·8	11·0	0·35	1·5441
16	289	·00346	5·0	10·0	0·5	1·6990
27	300	·00333	16·5	10·8	1·5	0·1761
35	308	·00325	16·6	5·8	2·9	0·4624
45	318	·00314	5·1	2·7	1·9	0·2788

SUMMARY.

The enzyme contained in the crystalline style of Pecten is destroyed more and more rapidly as temperature increases. On the other hand, it becomes more and more active if incubated at fairly low temperatures, possibly as a result of the progressive dispersion of the protein base on which it is absorbed. A graph has been calculated showing the effect of temperature on enzyme activity when both destruction and (?) dispersion are discounted.

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Preliminary Observations on the Relative Importance of the various Factors Responsible for the Death of Fishes in Polluted Waters.

By

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INTRODUCTION.

WITH the growth of modern industry the problem of the influence of polluted waters on the bionomics of fishes is becoming very important. Fortunately, biologists anticipated this and many works on the subject have appeared, especially during the last twenty-five years. The polluting substances can be divided into two main classes, namely, (i) those that are directly poisonous to organisms, e.g. gas liquor, sulphites, oils, etc., and (ii) those that give rise to poisonous substances or otherwise make the water undesirable after putrefying, e.g. organic matter in solution and the decomposing bodies of plants and animals. The substances in the first category act in a relatively straightforward manner, and numerous investigators have studied them from several aspects (Shelford, '17; Matthews, '04; Powers, Wells, '15, etc.); it is with regard to those in the second class that many questions are yet unsettled and the present communication deals. We roughly know that the effect of the putrefying substances is to increase the hydrogen ion concentration and decrease the oxygen content of water. It has also been suggested that the by-products of putrefaction themselves may be poisonous to animals. It is still an open question as to which of these factors is chiefly responsible for the death of fish; some investigators emphasize the influence of hydrogen ion concentration, others the importance of the deficiency of oxygen, and so on. One reason for this state of things seems to be that practically no systematic attempt has been made so far to isolate the various factors, and note their influence on the organisms separately. Therefore it was thought desirable to undertake a study on these lines, and some preliminary experiments have been performed, which are reported in the following pages.

A short bibliography of papers concerning factors affecting freshwater life is given at the end of this communication.

MATERIAL AND METHODS.

The freshwater fish, *Gasterosteus aculeatus*, the common "stickleback," found round about Plymouth, was chosen for the experiments. It is quite a hardy species. This selection is against the suggestion of Shelford ('18), who thinks that a sensitive individual should be taken for such investigations. But in the opinion of the writer, a hardy species affords a more definite and hence more reliable reaction. Moreover, if a certain factor is found to be toxic to a strong race, it should be all the more toxic to sensitive ones, and therefore have a wider application.

The average weight of the above fish was 0.8-1.2 gms. ; some specimens weighed as much as 1.8 gms. Fishes weighing 0.30-1.5 gms. behaved similarly, and all the experiments were performed on them ; those below 0.30 gms. or above 1.5 gms. died rather quickly.

To start with, three substances, all proteins, namely, peptone, albumen of eggs, and casein of milk, have been examined as putrefying substances.

The hydrogen ion concentration determinations were made by the colorimetric methods. The oxygen content was measured by Winkler's method. The "alkali reserve" was determined by titrating with 0.01N. H_2SO_4 , using methyl orange as indicator.

EXPERIMENTAL.

OPTIMUM HYDROGEN ION CONCENTRATION AND CO_2 PRESSURE.

On an average the pH of the waters in which sticklebacks were found in the field was 7.5-8.0 (not corrected for the salt error). The alkali reserve of these waters was 0.0045 N. In the Laboratory these fishes lived quite comfortably between pH 6.0-8.5. Outside this range, an increase on the acid side was more harmful than on the alkaline one. In water at pH 4.5 "stickles" died in about twelve hours, at pH 3.0 they did so within three quarters of an hour.

Jewell ('24) found several freshwater fishes flourishing in waters having pH 4.4.

As regards the pressure at which CO_2 becomes harmful it was noticed that as long as the concentration of this gas was not above 10.0-13.0 c.c. per litre the fish did not suffer any harm. Many freshwater fishes have been found to withstand even a higher concentration of CO_2 , up to 40-50 c.c. per litre (Reuss, '10 ; Wells, '13, etc.).

RESISTANCE TO LOW CONCENTRATION OF OXYGEN.

As elsewhere shown in detail by the present writer (p. 741 of this Journal), if pH and other conditions are suitable, sticklebacks can live without any harm till the oxygen content of water goes down as low as 0.25-0.50 c.c. per litre.

It appears that the power to withstand low pressures of oxygen is quite common amongst the freshwater fishes. Birge and Juday point out several cases in which a concentration of 1.0 c.c. per litre apparently did not prove dangerous to the individuals. Powers ('21) cites numerous authors to show that fishes do not suffer from oxygen want till its concentration reaches 1.7-0.4 c.c. per litre.

COURSE OF CHANGES IN THE PHYSICAL AND CHEMICAL CONDITION OF WATER ON THE ADDITION OF PUTREFYING SUBSTANCES.

Observations on this subject, as mentioned above, are based on the decomposition of peptone, albumen, and casein, under both aerobic and anaerobic conditions. These substances were dissolved in Plymouth tap water (pH about 7.0 and alkali reserve .0005N) in the proportion of 1 gram to a litre. The solutions subjected to aerobic conditions for the growth of bacteria were kept in wide shallow bowls of 6 litres capacity and were aerated at intervals of four hours in the daytime (9 am.-11 p.m.), no aeration being applied during the night. In the mornings, while traces of oxygen were often found in the solutions, the oxygen had sometimes been exhausted altogether. Winchester bottles were used for the solutions, which were kept out of contact with the atmosphere so that anaerobic putrefaction would proceed. All cultures were kept at room temperature, 65°-70° F.

Hydrogen Ion Concentration, etc.

The first noticeable result of decomposition is the production of CO₂ and organic acids which increases the hydrogen ion concentration. As above mentioned, the aerobic solutions were aerated frequently, which naturally interfered with the normal course of pH change. Therefore to ascertain accurately the changes in this factor, two separate solutions of peptone and casein were kept undisturbed in bowls, 6 litres and 500 c.c. capacity respectively. The data obtained from these solutions are given in Table I, an examination of which will show that during the first three or four days the pH fell, being 6.5 (casein) at the end of that period. Then it began to rise steadily and went up to 8.0. After reaching this point, the pH fell again and remained about 7.6 till the experiments were discontinued at the end of the forty-fifth day. The course of these changes resembles closely that observed in the solutions (Table II) which were aerated frequently.

In the anaerobic solutions, as in the above, the pH went down during the first few days, and did so much more, reaching the figure 6.0-6.1. Then it began to rise, but the rate of rise was much slower than that in the aerated solutions (Table II).

The interesting point that the above account brings out is that the pH after falling for a short time begins to rise, suggesting thereby that basic substances are being produced in the putrefying solutions. As will be discussed at a later stage, this has a very significant bearing on the

TABLE I.

COURSE OF CHANGES IN PH.

Solutions in wide shallow bowls. Undisturbed.
Room Temperature.

Age of solution in days.	Peptone pH.	Casein pH.	Remarks.
1	7.15		
2	6.8	6.5	
3	6.95	7.0	Oxygen totally exhausted in Casein solution.
4	7.2	7.6	Oxygen totally exhausted in Peptone solution.
5	7.3	7.65	
6	7.4	7.75	
7	7.45	7.8	
8	7.5	7.9	
9	7.55	8.0	
10	7.55	8.0	
11	7.65	7.7	
12	7.7	7.65	
13		7.7	
14		7.8	
18	7.7	7.65	
21	7.65	7.7	
28	7.75	7.7	
33	7.8		
45	7.7		

problem under investigation. The production of alkalinity during bacterial growth is a well-recognised phenomenon, Reddie ('23) having observed it in numerous cases.

The second point that may be emphasised in connection with the above-described variation in hydrogen ion concentration is that the pH does not go much below 6.0, both in the aerated and anaerobic solutions. As the

writer showed in the case of hay infusions ('26), the lowest pH that is reached in fermentations depends upon the alkali reserve of the water used, being minimum in the case of distilled water. The Plymouth tap water in having the low alkali reserve of 0.0005N is almost similar to distilled water. Hence it is fair to conclude that in natural waters,

TABLE II.
CHANGES IN pH IN AEROBIC AND ANAEROBIC SOLUTIONS.

Age of the solution in days.	Aerobic.				Anaerobic.		
	Peptone A.	Peptone B.	Albumen C.	Casein D.	Peptone E.	Albumen F.	Casein G.
3	6.6			6.7			6.5
4		6.6				6.4	
7			7.0	7.7			
8		7.3			6.45		6.2
9	7.4						
10				8.1	6.55	6.3	6.1
11			7.25	8.1			
12	7.65					6.15	6.3
13	7.75	7.8	7.3		6.65		
14		7.85	7.5	7.85			6.5
17		8.1	7.9			6.2	6.65
19					6.9	6.35	6.85
21					7.0	6.5	6.85
22		7.75	7.85			6.6	7.2
24					7.25	6.5	
26					7.45	6.5	7.2
30						6.5	7.8
34						6.6	7.7
38						6.6	

which invariably have some alkali reserve, the pH under similar conditions will not reach even 6.0.

Oxygen Content.

The changes in the oxygen content were also observed in the solutions kept undisturbed in wide bowls. The solutions when started had about 6.5 c.c. per litre of oxygen. There was a steady fall, and within three to four days the whole of the oxygen had been exhausted. When the supply

of oxygen was renewed, as in the case of the aerated solutions, it was noticed that the rate of oxygen decrease was not greatest in the first few days, but after the expiry of about a week. Moreover, this rate was not the same in the different solutions, being far higher in the fermenting casein than in the others.

Production of Toxic Substances.

The last important change to be observed in the nature of the water is the appearance of toxic substances, which are obviously produced as a by-product of putrefaction. To study this factor, the killing power of each solution at different stages in its growth was ascertained after it had been thoroughly aerated and its pH adjusted at 7.0-8.0, to exclude the harmful influence of hydrogen ion concentration, high carbon dioxide pressure, and the deficiency of oxygen. These experiments were performed in the 500 c.c. bowls, and generally each observation was based on the dying time of three specimens.

The data under this section are given in Table III. An examination of the same will show that the solutions become most poisonous when they are 7-15 days old, the anaerobic ones taking a few days longer; then they gradually lose their toxic power. Of the three kinds of solutions studied, namely, peptone, albumen, and casein, the last named is the first to acquire toxicity and becomes most poisonous, its shortest killing time being only half an hour, as compared with two and six hours for peptone and albumen respectively. It is interesting to add that the putrefying substance remaining the same, a solution becomes equally toxic whether aerated at intervals or kept under anaerobic condition, though under the latter, as mentioned above, it acquires toxicity more slowly.

As to the nature of the toxic substances, this is rather a complex problem and is left for further research, only a few remarks being made here. The fact that the solutions after becoming highly poisonous gradually lose their toxic power suggested that the toxic substances may be of a volatile nature. To verify this hypothesis the following experiments were performed: about 500 c.c. of the various solutions were boiled to half the volume, cooled, and water subsequently added to bring them to their original volume. Then they were aerated and their pH was adjusted at 7.0-8.0. The killing power of the solutions so treated was ascertained. It was very much reduced; for example, the peptone solution which killed the fish in two hours before the above treatment, did so in twenty-five hours after it. In this connection it was also thought desirable to ascertain the effect of the distillates from solutions which had putrefied and were distilled in both alkaline (pH 8.5) and acid (pH 4.0)

TABLE III.

APPEARANCE OF THE TOXIC SUBSTANCES IN THE 0.1% SOLUTIONS.

Age of the solution in days.	Killing time in hours after thorough aeration and adjustment of hydrogen ion concentration.						
	Aerobic.			Anaerobic.			
	Peptone A.	B.	Albumen C.	Casein D.	Peptone E.	Albumen F.	Casein G.
3	130			18			
4		72	60			18	
5							
6				2		18	
7			48	$\frac{1}{2}$			5
8		72		$\frac{3}{4}$	30	20	$\frac{1}{2}$
9	12				30		
10	3			6	30	20	$\frac{1}{2}$
11			48	7			
12	2						
13	$2\frac{1}{2}$	12	18		30		1
14		3					
15							3
16							
17			6		28		
18		6	9	10		20	
19		7					
20						7	
21							
22				15		3	
24		10			18		
25		11	10				
26		11			9		
27			10		4		
28							
29							
30					4		

conditions. In Table IV are given the killing times of the solutions (before distillation), of the residues and of the distillates. It will be observed that the residues in some cases are only very slightly toxic, while the distillates were decidedly toxic, although less so than the original putrefied solutions. They should have killed the fish almost instantly if all the toxic substances were volatile. This means that only some of the toxic substances are volatile, and that the residues lose the toxic power probably due to the mere action of heat. To examine this possibility some putrefied casein solution was heated at 70° C. for twelve hours; after this treatment the solution did not kill the fish in six days even (when the experiment was stopped), while originally its killing power was only one hour.

The other fact that the above experiments reveal, and which is likely

TABLE IV.

Putrefying substance.	Killing time in hours.			Remarks.
	Solution.	Distillate.	Residue.	
Peptone	15	48	79	Distilled in alkaline condition.
Peptone	3	5	60	Distilled in acid condition.
Casein	$\frac{1}{2}$	18	240	Do.
Casein	$\frac{3}{4}$	48	300	Distilled in alkaline condition.
Albumen	6	12	60	Do.

to have a bearing on the problem of the nature of the toxic substances, is that the stage of highest toxicity in the case of each putrefying solution was preceded by a period of rapid oxygen consumption.

RELATIVE INFLUENCE OF VARIOUS FACTORS.

After describing the optimum conditions and those that occur in water containing putrefying substances, some concluding remarks may be made as to the comparative significance of the various factors concerned.

The fact that pH does not go below 6.0 and that after falling for a short time begins to rise steadily, suggests strongly that hydrogen ion concentration as such has not got such a great importance in polluted waters as many investigators seem to think. On the other hand, carbon dioxide accumulates as has been described above. Sometimes, as in

the case of solutions putrefying under anaerobic conditions, a high pressure of CO_2 may occur sufficient to prove harmful to fish life, especially in still water. It is legitimate to emphasize its importance and urge the field worker to measure this gas even when the pH may be optimum.

All the infusions at some stage showed a high rate of oxygen consumption; therefore this gas, in spite of the fact that many freshwater fishes can withstand its low concentrations, is likely to be a factor of importance in polluted waters, especially in the bottom layers.

But the most important fact that the above experiments bring out is the great significance possessed by the toxic substances which appear as by-products of putrefaction, a factor hitherto almost ignored. Water containing any of the putrefying substance examined becomes highly toxic and kills the fish in $\frac{1}{2}$ -6 hours, even when it is saturated with oxygen has an optimum pH and a low pressure of CO_2 . But, as has already been pointed out, the toxicity varies in the case of different substances, and it will therefore be a fruitful problem to investigate, from a comparative point of view, the toxicity resulting from the decomposition of various proteins, carbohydrates, etc., which are likely to be thrown in waters inhabited by food fishes. On the other hand, the problem of the nature of the toxic substances is bound to be of great interest to bio-chemists.

In conclusion, I must thank Dr. E. J. Allen, the Director of the Plymouth Laboratory, and Dr. W. R. G. Atkins, the head of the Physiological Department, who arranged for all the facilities for performing the experiments. My indebtedness is also due to Mr. H. W. Harvey of the same Laboratory, who took a keen interest in this investigation and made some valuable suggestions. Mr. H. O. Bull rendered me assistance in various ways, for which I am grateful.

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The Ability of Fishes to Extract Oxygen at Different Hydrogen Ion Concentrations of the Medium.

By

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POWERS,* working on some marine fishes, arrived at the important conclusion that the ability of fishes to absorb oxygen at low pressures is more or less dependent upon the hydrogen ion concentration of the water. His method of research was briefly as follows : a fish was placed in a two-quart jar filled with water, which was closed airtight with a rubber stopper. The pH and the oxygen determinations were made immediately after all the movements of the fish had ceased. The amount of oxygen left at death represented, according to Powers, the pressure below which the fish at the particular pH could not extract any more oxygen from water. Powers did not control the amount of oxygen at the beginning of an experiment ; he says, "it was always sufficiently high so that the fish did not at first suffer from oxygen want."

While working recently on the influence of some physical and chemical conditions of water on May-fly larvæ, I observed that the amount of oxygen which was left at death at a particular pH depended on the amount of oxygen which was originally present in the water ; for instance, if at pH 4.0, starting with 6 c.c. per litre of oxygen, 3 c.c. per litre was left, only 1.0 c.c. was left if the original amount was 4.0 c.c. per litre. If in the first case the larvæ at the concentration of 3 c.c. per litre died for lack of ability to absorb any more oxygen, as Powers' conclusions will warrant us to assume, in the second case also the individuals should have died when that tension was reached. Moreover, it was noticed that the time for which the larvæ lived in two waters having the same pH but different amounts of oxygen was almost the same. This strongly suggested that the larvæ died, not on account of the fact that they could not at that pH extract any more oxygen at the particular pressure, but due to some other cause, presumably the direct influence of the hydrogen ions.

* *Journ. Gen. Phys.*, IV, p. 305.

As this point is of great physiological importance, to verify the above hypothesis a fish, *Gasterosteus aculeatus*, the common "stickleback," was chosen for detailed experiments, which are reported below:—

The most crucial test by which Powers could have tested his results and their interpretation was to observe on a fresh fish the effect of the water in which one had died previously, presumably on account of the fact that it could not absorb oxygen at that pressure, i.e. for instance, if the herring, *Clupea*, was observed to die at pH 7.1, leaving 2.5 c.c. per litre of oxygen, before concluding that *Clupea* at pH 7.1 cannot extract oxygen below 2.5 c.c. per litre concentration, Powers should have put another herring in the same water to see whether the fish died in a short time, which it should have done if his view was correct. Powers did not test his conclusion in this manner.

In the case of sticklebacks I have performed a long series of experiments on these lines, which are detailed in Tables 1–5 (p. 744). The pH of water was varied by adding small amounts of dilute HCl. Under Column I of the tables is given the time for which the first lot of stickles lived at a particular pH. Under Column II is given the time for which the second lot lived when put in the same waters in which the first lot had died. The mouth of the jar was opened, fresh specimens introduced, and the mouth was closed again as quickly as possible. As many as six lots were introduced in some jars in this way. An inspection of the tables will show that, contrary to what one would expect from the conclusions of Powers, the fish of the successive lots lived for almost the same time. If the first lot had died because it could no longer extract oxygen at that pressure, the second when introduced in the same waters should have died within a short time, and the third in any case should have done so at once.

It may be added that in all the above experiments the pH and oxygen content were checked before starting a fresh lot; the jars opened for this purpose were, of course, not used during the rest of the series. Moreover, on account of the fact that the fish as a product of respiration added some CO₂ to the water, the pH at the beginning of a fresh lot would be slightly lower than that at the start of a previous one, but the specimens being small (0.20–1.5 gm.) and the experimental jars quite big (200 c.c.), and because some CO₂ went out when the jars were opened and fresh fish introduced, no appreciable change in pH was noticed during the duration of the series detailed in the tables.

The problem was tackled by another method as well. As will be evident from Table 2, stickles when put in water at pH 3 and having 6.5 c.c. of O₂ per litre die within 40–45 minutes, leaving about 5.8 c.c. per litre of oxygen—a concentration below which, according to Powers' interpretations, stickles should not be able to absorb oxygen at this

pH. But when these fish were actually introduced in water of this pH and having as low a concentration of O_2 as 1.36 c.c. per litre, they lived almost as long as in the above water (Table 3). These experiments were repeated with even lower concentrations of oxygen, the fish lived about the same time unless the pH was lower (Table 4).

The ordinary suction pump was employed for reducing the amount of oxygen.

Thirdly, several pH ranges were prepared by adding HCl to waters having different amounts of dissolved oxygen. An examination of Table 5 will show that in each range the fish die leaving absolutely different amounts of oxygen. If the ability to extract oxygen at any pH depends upon the amount of O_2 present, then at a particular pH the individuals in the different ranges should leave almost the same amount of oxygen at their death.

It is interesting to add that in all the above-mentioned experiments the fish of the different ages behaved similarly, except very tiny ones (below 0.15 gm.), or those which were ready to breed (above 1.8 gm.)—see the weight columns in the different tables.

It may be pointed out, however, that the amount of oxygen which the fish absorb per hour per unit weight is not the same at different hydrogen ion concentrations. For instance, at a pH like 3 it is much less than at pH 7. This suggests that the hydrogen ions kill the fish by interfering with the respiratory system. But what the above-described experiments establish is that this interference is independent of the amount of oxygen present in the surrounding medium, unless its concentration goes down to 0.30–0.50 c.c. per litre, when the fish die of asphyxiation at any pH.

Incidentally, the above experiments suggest that in ponds and rivers where the oxygen content seldom goes down to such a low concentration as 0.30 c.c. per litre, fishes should not, as a rule, die of lack of oxygen, and that therefore other factors, e.g. pH, CO_2 pressure, poisons, etc., have more important ecological bearing than the amount of dissolved oxygen.

It is with great pleasure that I take this opportunity of thanking Dr. E. J. Allen, the Director of the Plymouth Laboratory, and Dr. W. R. G. Atkins, the head of the Physiological Department, who took a keen interest in this investigation, placed all facilities at my disposal and extended numerous courtesies during my stay at Plymouth.

TABLE 1.

pH 3.1, O₂ at start 6.5 c.c. per litre.

No. of Exp. jar.	I.		II.		III.		IV.		V.		VI.	
	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.
1	38	0.32	35	.27	42	0.21	35	0.23	40	0.20	34	0.25
2	32	0.35										
3	31	0.22	35	.21								
4	65	1.22	58	.25	60	0.23	60	0.20	65	0.20	67	1.00
5	47	0.28	48	.3								
6	60	0.20										
7	80	0.21	78	.2	70	0.2	75	0.2	65	0.18		
8	45	0.20	50	.29	51	0.23						
Average	50		51		56		57		57		51	

O₂ at the end of I lot 5.85 c.c. per litre (Nos. 2 and 6).

..	..	II	5.2	(Nos. 3 and 5).
..	..	III	4.8	(No. 8).
..	..	V	4.0	(No. 7).
..	..	VI	3.5	(Nos. 1 and 4).

TABLE 2.

pH 3.0, O₂ 6.5 c.c. per litre.

	I.		II.		III.		IV.		V.	
	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.
1	40	0.27	41	.18	50	.18	30	.15		
2	35	0.20	42	.20	40	.21	45	.22		
3	45	.17								
4	59	.18	55	.75	56	.15	26	.11	50	.18
5	39	.25	40	.15						
6	54	.18								
7	48	.19	60	.20	58	.16	46	.13	55	.8
8	43	.17	50	.21	48	.17				
9	48	.17	47	.8						
10	38	.30	32	.2	52	.16				
11	67	.2								
12	56	.4	51	.2						
13	35	.2	35	1.2						
14	43	.8	38	.32	39	.22				
15	32	.3	54	.28						
16	32	.25	45	1.2						
17	45	.35	50	.3						
18	38	.30	35	.25						
19	47	.27	49	.22						
20	37	.45	39	.3						
21	40	.4								
22	47	.3	40	.2	45	.25				
Average	43		44½		48		36½*		51	

* Individuals No. 1 and 4 in IV below .15 gms.

TABLE 3.

pH 3.0, oxygen at start 1.36 c.c. per litre.

Expt. jar No.	I.		II		III.	
	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams
1	35	.35	30	1.0	34	1.3
2	35	.40				
3	39	.45				
4	52	.45	39	1.1	38	1.2
5	33	.45				
6	37	.30				
7	37	.40	36	1.8	39	1.5
8	36	.32				
9	40	.35				
10	50	.35				
Average	39.5		35		37	

TABLE 4.

pH 2.9, oxygen at start 1.4 c.c.

Expt. jar No.	I.		II.	
	Dying time in minutes.	Weight in grams.	Dying time in minutes.	Weight in grams.
1	27	.4	31	.30
2	39	.35	43	.25
3	25	.35	45	.25
4	37	.30	33	.30
5	36	.25		
6	35	1.20	34	.22
7	30	.27	31	.25
8	30	.25	30	.17
9	30	.25	31	.18
10	29	.25	30	.20
11	30	.30	30	.20
12	29	.27	17	.20
13	31	.25	29	.20
Average	30		29	

TABLE 5.

Expt. No. and amount of oxygen at start.	Low Oxygen Concentration.				Control—Oxygen 6.5—7 cc. per litre.		
	pH.	Oxygen left at death.	Dying time in minutes.	Size-weight in grams.	Oxygen left at death.	Dying time in minutes.	Size-weight in grams.
I	3.3	1.6	45	0.50	5.5	45	0.50
Oxygen 3.0 c.c. per litre.	3.0	2.7	30	0.50	6.0	29	0.50
	2.9	2.8	30	0.50	6.24	30	0.50
II	3.1	2.20	37	0.20	6.4	40	0.20
Oxygen 2.50 c.c. per litre.	2.9	2.25	33	0.20	6.4	35	0.20
	2.7	2.32	20	0.20	6.4	30	0.20
	2.5	2.40	30	0.20	6.5	30	0.20
	2.4	2.42	25	0.20	6.6	32	0.25
III	5.2	1.20	480	0.30	3.28	500	0.40
Oxygen 2.0 c.c. per litre.	3.9	1.40	270	0.30	4.4	245	0.30
	3.6	1.52	360	0.25	4.8	150	0.20
IV	3.1	0.96	46	0.20	5.00	48	.25
Oxygen 1.50 c.c. per litre.	3.0	1.00	40	0.20	5.36	35	.20
	2.9	1.04	32	0.20	6.08	40	.20
V	3.7	1.04	82	0.25	4.24	150	0.22
Oxygen 1.75 c.c. per litre.	3.4	1.20	75	0.30	4.70	80	0.23
	3.15	1.56	55	0.22	5.04	55	2.5

A New Habitat for *Loxosoma phascolosomatum* Vogt.

By

D. Atkins.

With 4 Figures in the Text.

Loxosoma phascolosomatum was first described under that name by Vogt (6) in 1876 when he discovered it at Roscoff on the posterior extremity of *Phascolosoma elongatum* and *P. margaritaceum*, where it forms a small tuft. It had probably been observed previously by Norman (4), and described by him in 1861 (3) as tentacular appendages of "Strephenterus claviger"; he found it on gephyreans dredged in 1858 from Bantry Bay. Barrois (2, p. 8) mentions that he also saw this species in 1874-75, before the publication of Vogt's paper, at Roscoff, where it was abundant on sipunculids. Since then it has been recorded as occurring on Phascolion by Andersson (1) in East Greenland, and by Norman (5) in East Finmark.

While I was working on *Loxosoma* at Plymouth, in September, 1923, Dr. Orton brought to my notice some organisms attached to the outer surface of the shell of certain minute bivalves, *Lepton clarkia* and *Montacuta bidentata*. These proved on examination to include acinetarians, *Perigonimus* sp., and a species of *Loxosoma*, which is almost certainly *L. phascolosomatum*.

L. clarkia and *M. bidentata* occur associated with *Phascolosoma pellucidum*, being found in their burrows in the mud of the Salcombe Estuary; the former is the more common. These bivalves may occur either free in the burrows, partly embedded in the walls, or loosely attached to the gephyreans (Orton, J. H., "Nature," Vol. 112, Dec. 15, 1923, p. 861). It was found that if the *Lepton clarkia* were placed in a bowl of sea-water with a gephyrean for twelve hours or more some became attached; the attachment was of a slight kind, for when the water was changed the current from the syphon detached the shells. Of thirty-four specimens of *Lepton* and *Montacuta* all but five carried the *Loxosoma*. They were most frequently found round the edge of the shell, where they might be supposed to derive the greatest benefit from the current of water passing between the valves of the mollusc, but in some cases much of the surface of the shell was covered with the polyzoan (Fig. 1).

The large individuals are usually seen lying along the edge of the shell with the long stalk looped or curved (Fig. 2); it is generally the younger forms only in which the stalk is straight, standing out beyond the shell margin (Fig. 3). The chief movement of the *Loxosoma* is twisting or bending from side to side. The stalk is rarely seen extended to its full length; it is usually somewhat contracted when it may be very broad, in some cases nearly as broad as the calyx. Vogt says of his specimens that the lower extremity of the stalk was pointed like the nib of a pen, and there was no special organ of attachment; in his Fig. 1, Pl. I, it is

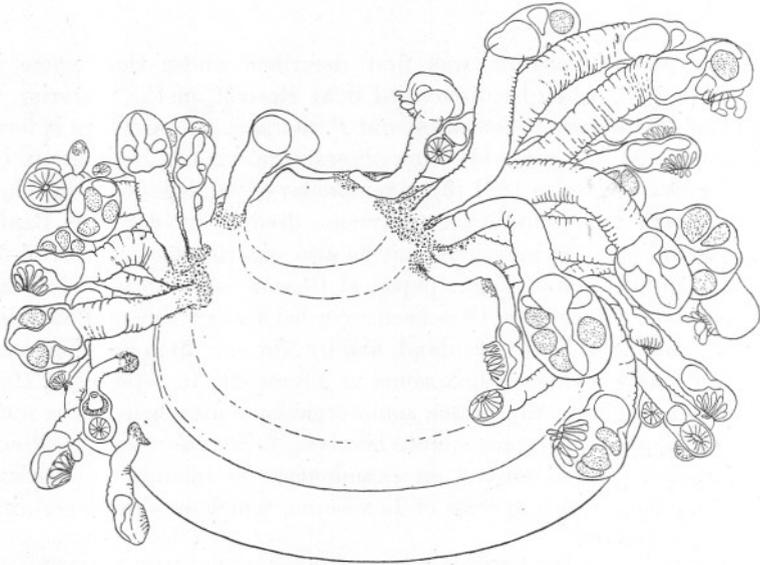


FIG. 1.—Sketch of *Loxosoma phascosomatum* on shell. The individuals are mostly female, some with embryos in the vestibule. They are somewhat contracted, the cuticle of the stalk is ringed. Small particles are seen adhering to the secretion by which the foot is attached to the shell. Alum carmine, oil of winter green. $\times ca. 41\frac{1}{2}$.

shown ending in a curious bisected extremity; in the specimens from Lepton and Montacuta the stalk ends in a small disc of attachment.

It is difficult to obtain measurements of large individuals owing to their generally curved condition; some measurements of rather small living specimens with straight stalk are as follows:—

Total length in mm.	Length of calyx in mm.	Length of stalk in mm.	Breadth of calyx in mm.
.5	.23	.27	.18
.69	.27	.42	.21
.78	.22	.56	
1.01	.29	.72	

The lophophore is large and very oblique. The tentacles are extremely difficult to count, as they are usually more or less retracted, and even when most fully extended are somewhat bent; this peculiarity was noted by Vogt. The number of tentacles in the adult appears to be twelve or more.

On either side of the calyx, slightly above the lower level of the lophophore, are the sense organs, one on either side, which are characteristic of *L. phascolosomatum*. These are often practically invisible, they contract and sink below the surface when their position is only marked by a slight elevation of the cuticle.

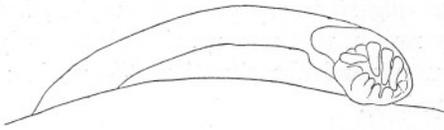


FIG. 2.—Sketch of a specimen lying along the edge of a shell. $\times 63$.

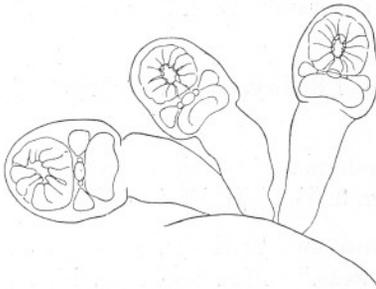


FIG. 3.—Three rather small male individuals attached near the edge of a shell, and standing out beyond the shell-edge. $\times 63$.

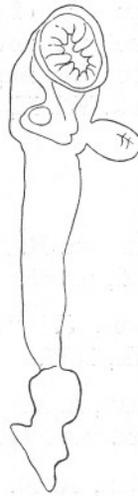


FIG. 4.—A specimen with a bud on either side. The cuticle of the lower part of the stalk is thickened, and was yellowish in colour. $\times 63$.

Ciliary movement was seen near the outer and lower border of the rather conspicuous dumb-bell shaped nerve ganglion, presumably indicating the position of nephridia.

Both male and female individuals were seen; the individuals of a colony are, as observed by Vogt, mostly of one sex (Fig. 1). In the living animal the testes and seminal vesicle of the functionally male individual are very conspicuous, the latter having the appearance of a tangled skein. Many of the females carried a varying number of embryos in the vestibule. The larva is like that figured by Vogt.

Many of the *Loxosomas*, both male and female, had buds (Fig. 4); the number of buds is apparently small, but not restricted to two, as Vogt supposed; the greatest number seen was five—three on one side,

one of which was very small, and two on the other. The buds have a large foot gland and duct or groove (pedal body and pedal gland respectively of Vogt). In the larger buds still attached to the parent that part which is traversed by the groove of the gland is sometimes strongly curved, the bud twisting backwards and forwards.

So far as I have been able to ascertain this is the first *Loxosoma* described as occurring on a mollusc; it is curious that though the gephyreans (*P. pellucidum*) were carefully searched, none were found on them; but Mr. Nunn told me he had sometimes found, when preserving *Phascolosoma pellucidum* at Plymouth, a few stray *Loxosoma* actually on the gephyreans. *L. phascolosomatum* is also, as is well known, found on the caudal extremity of *Phascolosoma vulgaris* in the Salcombe region, but this gephyrean is now apparently rare in the Estuary, though formerly it could be taken in good numbers in particular situations (Journ. Mar. Biol. Assoc., Vol. II, N.S., 1900, p. 164).

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Food and Habits of *Meganyctiphanes norvegica*.

By

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With 2 Figures in the Text.

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INTRODUCTION.

THE herring fisheries in the Clyde Sea Area, and in Loch Fyne in particular, have always been considered among the most important of the herring fisheries in Scotland. The factors which cause the herring to occur in this district in large numbers at certain times of the year have so far not been determined. Sir John Murray, who had considerable experience of the lochs in the West of Scotland, during summer and winter, over a period of many years, was of the opinion that not only are some lochs richer in different animal species, but also that others have species peculiar to themselves. For example, the Copepod *Euchaeta norvegica* is more abundant in Upper Loch Fyne than any other loch in the West of Scotland. It has never been found in Loch Aber, Loch Sunart, or Loch Carron. *Meganyctiphanes norvegica* and *Thysanoessa raschii* have never been found in Loch Etive or Loch Aber, whereas they

are plentiful in Upper Loch Fyne. The hauls I have made with the tow-net in Upper Loch Fyne confirm the presence in abundance in that locality of the above-mentioned Euphausiids and the Copepods *Euchaeta norvegica* and *Calanus finmarchicus*. *M. norvegica* and *T. raschii* attain their maximum in winter, November to February, and are seldom found during summer. *C. finmarchicus* reaches its maximum numbers in summer, although during winter it is present in large numbers in the deep waters (50-60 fms.). *E. norvegica* is very abundant for the greater part of the year, although scarce in the tow-nets during summer.

That *M. norvegica* forms an important item in the diet of some of our edible fish, more especially the herring, has been proved by many investigators. Hardy (1924) states that *Nyctiphanes* and *Meganyciphanes* form 5-65 per cent of the total food on the east coast. Brook and Calderwood (1885) and T. Scott (1887) have shown that towards the end of the feeding period on both the east and west coasts of Scotland the herring feed extensively on Euphausiids. Moore (1896) describes *M. norvegica* as the most important food of the herring on the Atlantic coast of America. Lissner (1919-23) finds that the chief food of the Skager-Rack herring consists of *M. norvegica* particularly during their "restitution" period. Continuing, he says: "It is doubtful that hydrographic conditions induce the herring to go into the Skager-Rack. Rather is one inclined to believe that this migration is at least in part a true food-seeking migration which leads the lean, exhausted and 'spent' herring to a well-spread table." Ehrenbaum (1919-23) remarks that it is noteworthy that the Skager-Rack herring feed chiefly on comparatively large animals, namely, for the most part, *M. norvegica*, 30-35 mm. long, whereas the herring of the west North Sea feed on Copepods and small Euphausiids, 10-12 mm. long. Further, he says that we cannot maintain with certainty that *M. norvegica* is present only in the deepest water layers, although it is found there during both day and night. It may well be that the herring is found in the deeper water layers, because of the fact that its food occurs there. Lebour (1924) and Holt and Tattersall (1902-3) have also found Euphausiids important in the diet of the herring.

The hake is apparently scarce in Upper Loch Fyne, but three specimens caught in January, 1925, and measuring 10 inches in length were all found to be feeding exclusively on *M. norvegica*. Hickling (1925) found that the small hake seem to select *M. norvegica* in preference to other crustacea or small fish, and suggests that when *M. norvegica* leaves the bottom the small hake follow it in its vertical migration towards the surface.

On many occasions I have found the stomachs of *Gadus virens* well filled with specimens of *M. norvegica* and *T. raschii*.

Owing to the importance of *M. norvegica* in the economy of the sea,

especially as food of edible fish (more particularly the herring), the following investigations with regard to food and feeding habits of *M. norvegica* were carried out from October, 1924, to May, 1926. Loch Fyne, for reasons indicated below, is very well suited for such investigation. Unfortunately, the station which we found most valuable, viz. Poll, is situated a day's journey from the Marine Station, Millport, and because of this and for other reasons the visits were not as frequent or prolonged as one would have desired. Visits were made at least once a month and sometimes more often.

DESCRIPTION OF *MEGANYCTIPHANES NORVEGICA* M. Sars.

Synonyms.—*Thysanopoda norvegica* M. Sars; *Thysanopoda nana* M. Sars; *Nyctiphanes norvegica* G. O. Sars; *Euphausia intermedio* Reggio; *Euphausia lanei* Holt and Tattersall; *Meganyctiphanes norvegica* Holt and Tattersall, 1905.

M. norvegica conforms in structure to that of a typical Euphausid (Sars). It is one of the largest known Euphausids in the waters of the Northern Hemisphere, attaining a length (from tip of rostrum to tip of telson) of 44 mm. The eyes are intensely black and very large, 2 mm. in diameter in the fully grown adult. The west-coast fishermen in Scotland call the animal "Súil dhu," i.e. black eye. The body is transparent, but for the region of the stomach which is translucent in the young adult and opaque later, the reason for this opacity being the elaboration of the hepatic cæca during development and the increased pigmentation of the outer surface of the stomach and alimentary tract. The hepatopancreas is well developed in *M. norvegica*, and forms in the larger specimens a conspicuous yellowish mass underneath the carapace.

The pigmentation in *M. norvegica* is characteristic. The mouth parts are vermilion to purple in colour. The thoracic appendages are closely set with scarlet chromatophores. So also is the outer surface of the stomach. Red chromatophores are scattered over the surface of the cephalothorax, abdomen and pleopods. A diffuse orange-coloured band may run down one or both sides of the basal segments of the pleopods. A similarly coloured band may sometimes be seen at the lower lateral edge of the abdominal segments and in the telson. The exuviae are pigmented, the pigmented parts being the mouth parts, which are remarkably densely coloured, and the regions where the diffuse pale orange colour occurred before ecdysis. The younger adults are not so richly pigmented as those fully grown.

The characteristic luminescent organs of Euphausids are prominent in *M. norvegica*. There are ten in all, as follows: two on the upper surface of the ocular peduncles; two pairs on the coxopodites of the

second and seventh thoracic appendages respectively; an unpaired series on the sternal surface of the abdomen between the bases of each of the first four pairs of pleopods.

GENERAL DISTRIBUTION.

This species has a very wide distribution, being found off the coast of N. Siberia, Spitzbergen, round Iceland, Jan Mayen, and at a few places in the east of Greenland as far north as Lat. 24° N., coast of Norway, Faroe Channel, Orkney, E. and W. Scotland, North of North Sea, Skager-Rack, Cattegat, W. Ireland. It also occurs along the Atlantic coasts of France, off the coast of Portugal, and is known throughout the Mediterranean. Specimens have been found in the Ægean and the Marmora. We meet with it again on the Atlantic coast of N. America, occurring at several places from the Gulf of St. Lawrence southwards, including the Gulf of Maine, being found as far south as Lat. 40° N. The species has not been found on the west coast of Greenland. Though going far to sea and penetrating to depths of hundreds of fathoms, it is not truly oceanic. It seems unable to exist below a depth of 500 fathoms, while it thrives at depths less than 100 fathoms (Holt and Tattersall, 1902-3). Holt and Beaumont (1900) found a number in the stomach of the ground-feeding dog-fish, *Pristiurus melanostoma*, at 154 fathoms. On May 10, 1925, Fleming (1925) examined the stomachs of over a hundred specimens of *Etmopterus spinax*, all of which had been caught in deep water S.W. of Ireland, and found the stomachs of several of the adult fish to contain remains of small squids and *M. norvegica*. Usually they were consumed along with mud. With regard to stomach contents of *E. spinax*, Fleming says: "Stomachs were crammed with mud which was of a greenish colour, and consisted of quartz sand grains and perfect skeletons of various Foraminifera. There were no remains such as setæ of worms, etc., to suggest that the mud had been obtained from the alimentary canals and the quantity of mud suggests that it had actually been eaten by the fish." This is interesting, as it is possible that *M. norvegica* was actually on the bottom when caught by the fish. Herdman (1898) obtained specimens at the surface by means of the pumps of an Atlantic liner, and it is noteworthy that the species was only met with off the coasts of the European and American continents, and not in the central part of the Atlantic. The only occurrence known from the central part of the North Atlantic is that in the Irminger Sea (Stephensen, 1912). Dr. A. G. Huntsman tells me in a letter that *M. norvegica* is a characteristic form of the slope waters, and is carried thence into coastal waters such as the Bay of Fundy. Usually it is found only in the depths, but in the Western Archipelago of the Bay of Fundy the strong tidal currents bring it to the surface, where frequently it may be dipped in large quantities.

LOCALISED DISTRIBUTION.

Patience (1909-10) records large numbers measuring 12-20 mm. taken at the surface with tow-net at midday between Fairlie and Keppel, Cumbrae. The strong tidal current which runs up this channel may account for this unusual occurrence. Throughout the Clyde Sea Area I have found adult *M. norvegica* at the surface, during the day, only at Keppel, and then very rarely and only one individual per haul. Bigelow (1912) found specimens at the surface at several stations in the Gulf of Maine. He says that the distribution of *M. norvegica* over the Gulf of Maine was practically uniform, except that it was found more regularly in the off-shore hauls, being taken in one off-shore station in considerable numbers at 80 fathoms. He also states that the oceanic data of captures indicates that out of six stations all but one show capture at the surface. Bigelow's observations were based only on the occurrence of large adults of unmistakable identity. On the other hand, Holt and Tattersall (1902-3) have only a single record from the surface tow-net worked during daylight. Dr. H. Broch further tells me that it is a well-known phenomenon (among fishermen in the Oslofjord near Dröbak) that *M. norvegica* suddenly appear at the surface and drift ashore in large numbers usually in autumn or early winter. He also says that on one occasion he put them out into the water again, and in a short time they turned and swam ashore. He mentions that the day was cold. He used some of the specimens as bait, and caught a large number of *Gadus virens*. After a few days the fish disappeared, and the beach was lined with a broad brim of dead and decaying Euphausiids. On another occasion in the month of October, while fishing for *G. virens*, he observed large shoals of these fish feeding on thousands of *M. norvegica* which suddenly appeared at the surface. We would suggest that the above observations indicate that the appearance of adult *M. norvegica* at the surface is caused partly by the presence of predatory fish and tidal currents.

Measurements of specimens caught are rarely detailed in records of occurrence, but some workers, e.g. Fowler (1903), state that large specimens are only found in deep water, an observation confirmed by Murray, and Vallentin and Cunningham. According to Kramp (1913), in the colder water of the Skager-Rack, *M. norvegica* continually lives from generation to generation having undoubtedly immigrated from the Norwegian Sea, and it may be found in the former water at every season of the year. In the Clyde Sea Area adult *M. norvegica* are most commonly found in the deeper waters (60-80 fms.). They are usually found about 10 fathoms from the bottom. Specimens measuring 35 mm. are very rarely fished less than 60 fathoms, unless during the night. The species is to be found in the deep enclosed waters of Upper Loch Fyne (60-75

fms.) practically throughout the year, although during the summer months they are only present in very small numbers.

With regard to depth as a factor controlling the distribution of *M. norvegica*, the following observation by Bigelow (1912) is interesting: "A phenomenon of some interest is the apparent absence of *M. norvegica* from Massachusetts Bay at all seasons. There seems to be nothing in temperature and salinity to bar it from the waters of the Bay, for in summer, at some depth, the Bay closely reproduces the combination of temperature and salinity in which we found it swarming in Eastport Bay in August (salinity about 37.4‰ to 32.6‰, temp. 52° F.), and in winter the Bay is very little colder than the northern part of the North Sea, where *M. norvegica* is common at that season. Its absence or rarity in the Bay is perhaps analogous to its absence in the southern part of the North Sea, where, as Kramp points out, both salinity and temperature would allow its existence. His explanation is that it is prevented from spreading southwards in the North Sea by the shallow water, *M. norvegica* being, according to his view, chiefly an inhabitant of the deeper water layers. But it can hardly be shallow water which bars it from Massachusetts Bay, because many of our records of the species were from hauls no deeper than the deeper parts of the Bay and because it was found in swarms on the surface at Eastport, in water of almost precisely the same temperature and salinity as the surface water off Cape Ann in November. Food supply, not hydrographic conditions, may be the factor which determines the local occurrence of *M. norvegica* in the Gulf." This last remark is interesting in relation to the present enquiry.

In the Clyde Sea Area specimens were caught in largest numbers in Upper Loch Fyne off Poll, at a depth of from 60–70 fathoms, and at "Cumbrae Deep," midway between the Little Cumbrae Light and Garroch Head Light, at a depth of 50–60 fathoms. In Upper Loch Fyne the numbers caught in each haul were fairly constant, averaging 20 per haul, throughout the months September to May, when *M. norvegica* is most abundant in the Clyde Sea Area. At Cumbrae Deep there was an indication of shoaling. Sometimes the number of specimens in one haul reached two or three hundred. Much more frequently the numbers were not more than 6 per haul, and sometimes no specimens were fished. Other stations visited where specimens were caught were Lower Loch Fyne, Kilbrennan Sound, Cock of Arran, Loch Striven, Loch Long, and Loch Goil. Shoaling was indicated at the Cock of Arran. Very few specimens were found at any time in Loch Long, Loch Goil, or Loch Striven, but of these three lochs most specimens were found at the last mentioned. *M. norvegica* disappeared entirely from these lochs towards the end of November. Young adults were caught in small numbers from October to May. They were found in greater numbers in the winter

months of 1924-25 than in the corresponding period, 1925-26. This suggests that spawning may take place at different times of the year, the spawning period varying from year to year. In 1925 eggs did not appear in the tow-nets till May, whereas in 1926 they were found in the first week in March. On both occasions the eggs appeared in fairly large numbers. In every case, except during the occurrence of large shoals already remarked upon, the specimens were caught only within 10 fathoms from the bottom between three hours after sunrise and two hours before sunset. Adults of all sizes tend to disappear from the Clyde Sea Area from May to September. Several hauls were made in May and June in Upper Loch Fyne, where the species is usually most abundant, but no specimens were found during the day, and only a few (not more than 6 in the 1-metre stramin net) during the night. On one occasion, May, 1926, about midday, the surface layers of mud were brought up from the bottom in the 1-metre stramin net, in which were found two specimens of *Meganyctiphanes* measuring 21 mm. and 27 mm. respectively and one specimen of *T. raschii* measuring 21 mm. Although hauls were made ranging from the bottom to the surface at 10 a.m., 1.30 p.m., and 4.30 p.m. on the same day, no specimens were found. The species, however, was present in tow-nets fishing at midnight at 30 fathoms. It was noted that fair numbers of *Meganyctiphanes* eggs were present in the tow-nets fishing at 20 fathoms during the day. No eggs were found in the tow-nets fishing at 10 fathoms and the surface.

Adults measuring 29-39 mm. were found in much greater numbers in Upper Loch Fyne than in any other part of the Clyde Sea Area visited, whereas those found in greatest numbers throughout the area measured 21-29 mm. (Fig. 1 and Table I).

Since Loch Fyne is the most important Loch in the Clyde Sea Area, with regard to the occurrence of *M. norvegica*, a description may not be out of place here. "In the Clyde Sea Area Loch Fyne is the largest of the sea lochs, being 41 miles in length from Ardlamont Point to the head and varying in width from 5 miles at Ardlamont Point to $\frac{1}{2}$ mile at Cuill. Loch Gilp terminates the extension of Loch Fyne, which then turns to the N.E. Loch Gair, a mere Bay, and Loch Shira, similar in all but size to Loch Gilp, branch off to the North. The largest streams run parallel to Loch Fyne on both sides with the exceptions of the Aray, the Shira, and the Fyne. Near its head only mountain burns flow into this fjord. Loch Fyne is roughly parallel to the upper part of the Firth of Clyde, and all the lochs branching off the latter run towards Loch Fyne. The upper 6 miles of Upper Loch Fyne are surrounded by hills both high and steep, and this portion is particularly subject to the influence of fresh water, as, in addition to the innumerable torrents that spring into being after every shower, it receives several rivers" (Mill, 1891). We suggest

that the inflow of fresh water will carry with it into the loch much vegetable debris which ultimately will be precipitated to the bottom. Upper Loch Fyne is singularly free from strong currents, and there is apparently comparative stillness in the deep trough running from a point midway between Inveraray and St. Catherines to Strachur. According to Gregory (1913) this fjord owes its origin to preglacial earth movements. Murray

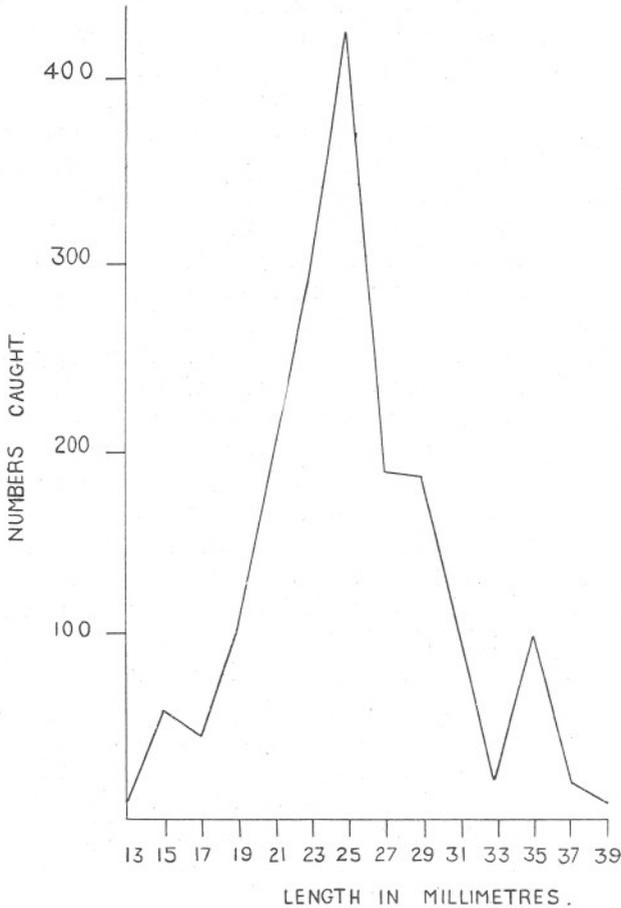


FIG. 1.

(Murray and Hjort, p. 13) has found evidence of an arctic fauna in Upper Loch Fyne. The bottom consists of fine mud, which is believed to be the result of deposition going on since the Glacial period.

A detailed description of the other stations where specimens were caught is unnecessary, as these stations in contradistinction to Upper Loch Fyne do not appear to provide suitable conditions as a permanent habitat for *M. norvegica*.

TABLE I.

TOTAL NUMBERS CAUGHT AT DIFFERENT STATIONS.

October, 1925, to May, 1926.

	Station.	13 mm.		15 mm.		17 mm.		19 mm.		21 mm.		23 mm.		25 mm.		27 mm.		29 mm.		31 mm.		33 mm.		35 mm.		37 mm.		39 mm.	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
October	Loch Fyne	-	-	-	-	-	-	-	-	15	14	14	14	-	-	-	-	2	-	1	1	-	-	-	-	-	-	-	-
	Loch Goil	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	Loch Striven	-	-	-	3	-	3	1	5	1	5	-	3	1	3	1	-	-	-	-	-	2	-	-	-	-	1	-	-
November	Cumbræ Deep	-	3	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	C. of Arran	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	Loch Striven	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	L. Loch Fyne	-	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	U. Loch Fyne	-	-	-	-	-	-	-	3	5	13	7	25	29	2	3	-	4	2	-	-	-	-	1	3	-	3	-	-
	Kilbrennan S.	-	-	1	-	-	-	-	1	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
December	C. of Arran	-	-	-	1	-	-	-	1	2	1	1	3	3	2	1	2	3	10	9	4	2	-	-	-	-	-	-	-
	U. Loch Fyne	-	-	-	-	-	-	-	5	1	-	2	3	-	-	1	2	1	4	-	-	-	-	-	-	-	-	-	1
January	Cumbræ	-	-	1	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	C. of Arran	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	-	-	1	-	-	-	-	-	-	-
	Keppel	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	U. Loch Fyne	-	-	-	-	-	-	1	2	4	7	16	30	93	52	10	7	4	1	6	7	1	-	21	8	1	-	4	-
February	Cumbræ	-	5	20	24	23	18	38	39	56	68	54	78	44	36	10	9	15	18	34	14	-	3	-	-	-	-	-	-
	C. of Arran	-	1	-	1	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	8	-	-	-	-	-	-	-	2
	U. Loch Fyne	-	-	-	-	-	-	3	-	10	4	15	16	59	37	18	14	1	1	1	-	1	-	5	1	2	1	2	-
March	U. Loch Fyne	-	-	-	-	-	-	-	1	-	4	-	8	1	9	-	4	-	1	-	7	1	33	6	7	-	1	-	
April	U. Loch Fyne	-	-	-	-	-	-	-	1	-	1	-	12	14	55	31	55	30	8	5	6	-	13	3	6	2	2	-	-
	Cumbræ	-	-	-	1	-	-	1	-	1	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
	Loch Long	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
May	U. Loch Fyne	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	17	9	-	-	-	-	6	-	-	-	-	-	-
	Cumbræ	-	-	-	-	-	-	-	1	-	-	-	-	2	-	3	1	4	2	-	-	-	-	-	-	-	-	-	-
	C. of Arran	-	-	-	-	-	-	-	-	4	1	3	2	-	-	-	-	-	-	6	-	2	-	-	-	-	-	-	-

METHODS.

From the end of September, 1924, till the end of May, 1926, as far as possible, weekly visits were made to "Cumbrae Deep," and also once a month to Upper Loch Fyne. Tow-nettings were taken fairly regularly at Keppel. The net found most useful for the work had 30 meshes to the inch. A larger net (1-metre stramin net) was tried from April, 1925, onwards. There was no evidence to show that it was relatively more efficient than the smaller net. The rope used was 2-inch tarred hemp. This was found most convenient for handling, as no mechanical power was available for hauling in the nets. The duration of the hauls was from $\frac{1}{2}$ hour to 1 hour. When the weather was calm and there was accordingly very little "drift" the engine was run very slowly. The specimens were as far as possible examined fresh, although the greater majority were examined in 5% formalin into which they were placed shortly after being caught.

Measurements of specimens were taken from tip of rostrum to base of telson.

The carapace was removed and the stomach and gut were then drawn out from the body. Microscopic powers ranging up to oil immersion lens $\frac{1}{2}$ n.a. 1.28 were used.

THE FOOD OF MEGANYCTIPHANES NORVEGICA.

Some workers have remarked on the occurrence of much debris in the stomachs of Euphausiids. Observations on the stomach contents of Nyctiphanes fished in the Channel have shown that they "nearly always contained some dark substance in their stomachs, but in those from the bottom there was much more debris than fresh organisms, which occurred in numbers in those from the surface." . . . In a sample of 25 examined "from near the bottom, 8 only contained diatoms (*Paralia*) and these singly, whilst the remainder contained sand and debris alone" (Lebour, 1924). With regard to Meganyctiphanes, Thysanoessa, and Nyctiphanes, Hickling (1925) says: "All three species had, in my samples, been feeding on detritus, and not only their leg-baskets, but their mouth-parts and stomachs were often full of it. . . . This detritus consists largely of very flocculent, dust fine, olive-green particles, with fragments of crustacean remains, diatoms, particularly *Paralia* and *Coscinodiscus* spp., and inorganic grit. The schizopods had been feeding extensively on it; but it is possible that an alternation of fresh diatom food may be of advantage to Nyctiphanes, at least."

During the first week in February, 1926, there was evidence of a congregation in large numbers on the part of *M. norvegica* and *Thysanoessa raschii* in the "Cumbrae Deep." Several hundreds of both species were

fished in one half-hour haul. Ten days later only two or three specimens were fished in a half-hour haul at the same place. It was noticed that during the time these Euphausiids were abundant much detritus was present in the nets fished at various depths from 10 fathoms above bottom to 20 fathoms from the surface (Cumbrae Deep is 60 fathoms deep). All the specimens examined of both species were found to be feeding extensively on the detritus which consisted chiefly of decayed vegetable tissues. It was noted later, when very small numbers of Euphausiids were fished, that the catches were remarkably free from detritus. The presence of such large quantities of detritus in the tow-nets may possibly be caused by the "dumping" of Clyde river dredgings, which takes place regularly two miles west of the "Cumbrae Deep." The reasons for the sudden appearance and disappearance of this detritus are not apparent, as the "dumpings" take place daily. Water movements have, no doubt, something to do with the distribution of such suspended material. No occurrence of such quantities of detritus in the catches have taken place in any other part of the Clyde Sea at which I have worked.

On another occasion (May, 1925) *M. norvegica* was found in large numbers in the "Cumbrae Deep." This time *C. finmarchicus* was found in great abundance in the tow-nets. On examination the great majority of *M. norvegica* were found to be feeding extensively on this Copepod. About a week later *M. norvegica* was absent from the hauls, *C. finmarchicus* and other Copepods being found in very small numbers.

It is interesting to note that Bigelow (1912) observed a somewhat similar occurrence of large numbers of *M. norvegica* in Eastport Bay, Gulf of Maine, U.S.A., and he suggested that this was probably due to the large amount of detritus and sardine factory refuse present in the water, on which *M. norvegica* was apparently feeding. With regard to the occurrence of large numbers in "Cumbrae Deep" just described, we would not suggest that either the vegetable detritus on the one hand or *C. finmarchicus* on the other attracted *M. norvegica* to this particular locality; but that, finding itself in the presence of an abundance of suitable food brought about by causes probably mechanical (tidal currents, etc.), it fed on vegetable detritus or *C. finmarchicus* voraciously.

It is evident from the above results that organic detritus forms an important item in the diet of *M. norvegica*. It is very difficult to estimate the actual amount of detritus in the gut, and in the meantime no attempt has been made to do so. Of the substantial pieces of vegetable tissues some pieces found in the stomach were as large as 1 sq. mm. Strands of vegetable tissue frequently attained a length of 5 mm. Among the coloured pieces of vegetable detritus of land origin which appeared in the stomach, pieces of leaves of *Blechnum spicant*, *Sphagnum*, and herbaceous bark, were most common; while the most common pieces of decayed vegetable

tissue which occurred in the gut were pieces of Gymnosperm and cellular parenchyma. From Tables 2 and 3, giving the food analysis, it is concluded that: (1) organic detritus is eaten most abundantly during the first months of the year; (2) Meganyctiphanes, ranging from 21–29 mm., feed more extensively on vegetable detritus than do larger or smaller specimens (it should be noted that this size was by far the most abundant in the Clyde Sea Area (see Fig. 1)); (3) Copepods are eaten most extensively by the larger specimens, viz. 31–39 mm., and (4) the smaller specimens, 13–19 mm., feed most extensively on diatoms and “wet dust.” The stomach contents in all cases show that, when substantial pieces of organic detritus are abundant, sand grains are present in comparatively small quantities, or altogether absent, whereas, when flocculent detritus is abundant and substantial pieces of organic detritus less abundant, sand grains are more numerous. Of the microplankton food organisms diatoms are the most important. *Paralia sulcata* and the naviculoid forms are typical of deep water. *P. sulcata* is most frequently found singly, and is present from May to October in the large majority of specimens indicated in column 1 of Tables II and III. *Thalassiosira nordenskioldi*, *T. gravida*, and *Coscinodiscus* spp., are eaten frequently, and occur in greater abundance than any other diatom in each individual stomach. *Fragillaria*, *Navicula* spp., *Pleurosigma*, and *Nitzschia*, are eaten occasionally. *Skeletonema* does not appear in the gut until February, and then not in such large quantities as *Thalassiosira*, although the latter is not so abundant in the tow-nettings as *Skeletonema*.

Among Dinoflagellates, *Peridinium pellucidum* and *P. depressum* are eaten most abundantly in November and March. *Phalocroma rotundata* is found in the gut in greatest abundance during December and January. *Dinophysis* and *Prorocentrum* appear occasionally from November to April. *Ceratium tripos* was found in small numbers in the stomach of a large specimen in October, 1924, and again in May, 1925; both specimens were caught in Upper Loch Fyne. *Heterocapsa triquetra* is eaten frequently and sometimes in large numbers in January and February.

Silicoflagellates are eaten in very small quantities. *Distephanus speculum* and *Dictyocha fibula* occur from October to March; the former is more common.

Crustacean remains are very frequently found in most guts throughout the “Period” (October to May). *Calanus finmarchicus* is the most abundantly eaten Copepod. *Pseudocalanus elongatus* is of second importance in the smaller adults, whereas *Euchata norvegica* occurs most frequently in the gut of the largest specimens. *Oithona helgolandica* and *Acartia clausi* are present most frequently in December and January, but appear to be of less importance as food than the other Copepods mentioned.

TABLE II.

Length, 13-19 mm. October, 1924, to May, 1925.

Date.	Number examined.	Percentage of Specimens in whose Alimentary Tract food as specified is present.								Analysis of food indicating percentage of specimens in whose gut specified food is most abundant.		
		Diatoms % Column 2	Dino-flagellates % Column 3	Silico-flagellates % Column 4	Crust. remains % Column 5	C.V.T. % Column 6	Detritus D.V.T. % Column 7		F.D. % Column 8	Silic. parts., etc. Column 9	Diat. & F.D. % Column 10	Crust. remains % Column 11
Sept. 23rd	149	100	74	6	100	8	12	100	83	48	36	10
November												
December	250	92	54	18	100	43	50	90	74	33	52	15
January												
February	94	74	23	—	92	44	68	82	82	46	44	10
March												
April	246	100	5	—	67	40	85	100	90	60	5	23
May												
UPPER LOCH FYNE. Length, 31-39 mm.												
January	24	25	—	8	100	66	42	50	12	—	50	25
February												
April	45	58	26	—	100	100	29	43	17	—	23	50
May												
Length, 21-29 mm.												
February	26	100	58	—	100	100	4	69	38	19	31	46
CUMBRAE DEEP. Size, 31-39 mm.												
May	5	100	100	—	100	—	—	50	—	—	100	—
Length, 21-29 mm.												
	234	87	—	—	100	18	27	37	10	—	74	—

C.V.T. (Coloured Vegetable Tissues), consist of Blechnum, Sphagnum, herbaceous bark, leaves of Phanerogams and Gramineæ, Filamentous Algæ, e.g. *Cladophora* and *Ectocarpus*, etc.; Thalloid Algæ, e.g. *Ulva*, *Laminaria*, etc. Thalloid Algæ occurred much less commonly than Filamentous Algæ.

D.V.T. (Decayed Vegetable Tissues). These were pieces of cellular parenchyma, Gymnosperms (woody tissue). Strands of algal tissues, possibly *Laminaria*, which occurred most abundantly.

F.D. (Flocculent Detritus). This has been termed "Wet Dust." It consists of a mass of greenish brown unidentifiable particles, amongst which may be found the shells of diatoms and peridinians, spores of algæ, and what would appear to be argillaceous particles. In the qualitative analysis of food (Column 10) we have combined Diatoms and Dinoflagellates with flocculent detritus, as, owing to the fine state of division of the latter, it was impossible to say how much of it could be attributed to disintegrated microplankton.

Some observations have been made on the food of the larvæ of *M. norvegica* with the following results. The nauplius has no mouth. Although an open mouth is present in the Metanauplius it was not found to feed. From the Calyptopis stage to the late Cyrtopia stage filamentous algæ and pieces of coloured vegetable debris seem to be increasingly substituted for diatoms. The remains of small Copepods also appeared in the stomachs of the late larvæ, e.g. Cyrtopia. It is interesting to note that the great majority of larvæ, like the adults, had recognisable food in the gut. There was no marked difference in character of food between those caught during the night and those caught during the day. In the adult specimens the "food basket" (formed by the endopodites of the thoracic appendages) was frequently filled with food. This food was, as a rule, entangled by viscid strands. At the General Meeting of the Linnean Society of London on 17th December, 1925, Dr. H. Graham Cannon gave an account of the Feeding Mechanism of the fresh-water Ostracod, *Pionocypris vidua*, and suggested that, like many other animals which feed on detritus, these Ostracods make use of a viscid secretion for capturing food particles. Holt and Tattersall (1902-3) and Lebour (1924) have remarked on the "food basket" in *Meganocythanes* and *Nyctiphanes* being well filled with food material. We have so far not been able to determine whether this viscid matter is secreted by *M. norvegica*. Viscid material was also found in the stomach. The "food basket" was found to be filled with food, chiefly organic detritus, most frequently in the first three months of the year. Those specimens caught nearest the bottom were generally found to have their food baskets well filled with food, chiefly organic detritus. It would appear then that when the adult *M. norvegica* seeks the bottom layers, in depths of 60-80 fathoms, it feeds on matter in suspension, the material eaten being microplankton, organic detritus, and to a lesser extent silicious particles. Accordingly, *M. norvegica* may be classed as a "Suspension feeder" (see Hunt, 1925). The larvæ are found near the surface, where they feed chiefly on diatoms, and to a certain extent on coastal filamentous algæ and coloured vegetable detritus.

As already pointed out (Holt and Tattersall, 1902-3), *M. norvegica* appears to be most commonly met with inside the 100-fathom line. This depth, according to Murray, is the average depth in the open ocean at which mud commences to be laid down, and may be taken with regard to our western seaboard to be the limit of wave action where the organic particles from the continents and shallow waters slowly come to rest on the bottom, and supply food to a wealth of Crustacean forms which are captured in such situations. Murray terms this region the "mud line," and believes it to be the great feeding ground of the ocean (Murray and Renard, 1891; Murray, 1895). The question now arises, how far is the

TABLE III.

Length, 13-19 mm. October, 1925, to May, 1926.

Date.	Number examined.	Number of Specimens in whose Alimentary Tract recognizable food is present.							Analysis of food indicating percentage of specimens in whose gut specified food was most abundant.						
		Diatoms %	Dino-flagellates %	Silico-flagellates %	Crust. remains %	C.V.T. %	Detritus D.V.T. %	F.D. %	Silic. parts., incl. Sponge spicules %	Diats. & Dinoflag. F.D. %	Crust. remains %	C.V.T. & D.V.T. %			
	Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9	Column 10	Column 11	Column 12			
October . . .	} 21	100	76	52	62	25	25	100	90	45	30	20			
November . . .		} 16	75	63	31	100	68	75	100	62	25	50	5		
December . . .			} 172	92	18	2	70	97	91	100	66	42	35	25	
January . . .				} 5	100	100	-	100	-	-	100	100	100	-	-
February . . .					} 162	81	86	14	98	86	46	100	78	5	60
March . . .	} 180					53	68	17	93	90	75	100	61	3	50
April . . .		} 150				69	33	1	90	93	71	100	56	20	25
May . . .			} 160			62	50	-	100	75	44	100	57	66	12
October . . .				} 16		-	-	-	100	25	26	25	12	-	25
November . . .					} 65	15	-	-	100	60	80	26	15	-	30
December . . .	} 130					7	-	-	100	98	92	12	35	-	45
January . . .		} 59				50	42	-	100	76	63	16	-	-	73
February . . .			} 59			50	42	-	100	76	63	16	-	-	73
March . . .				} 59		50	42	-	100	76	63	16	-	-	73
April . . .					} 59	50	42	-	100	76	63	16	-	-	73
May . . .	} 59					50	42	-	100	76	63	16	-	-	73

abundant life peculiar to boreal waters due to supplies of nutriment from the shore? To answer this important question satisfactorily would require much more intensive work on the Atlantic Slope waters, as at present we know little or nothing of the food and feeding habits of the deep living macroplankton, which, according to Jespersen (1924), is particularly abundant on the eastern Atlantic Slope. Although an intensive study has been made of the food of *C. finmarchicus* by Marshall (1925), the material being for the most part obtained in comparatively shallow waters off Keppel Pier, Millport, no systematic investigation of the food of Copepoda, including *C. finmarchicus*, which inhabit the deeper water layers, viz. 50–100 fathoms, has so far been carried out. This enquiry we believe is of particular importance with regard to deep sea fishing, and would be fruitful in producing valuable information. With regard to Upper Loch Fyne, where *M. norvegica* is apparently a permanent inhabitant, it may be useful to consider the conditions prevailing in this region which might account for its constant occurrence there. In the first place, if we consider the depth distribution of *M. norvegica* throughout the world, we find that the depth (60–80 fms.) in Upper Loch Fyne is favourable, it being necessary, apparently, for this species to seek these depths periodically. Two comparatively large streams enter the loch about one mile distant from the deep trough in which *M. norvegica* is found. It is a well-known fact that the detrital matter which is carried into the sea by rivers is rapidly deposited on meeting salt water. There will therefore be a fairly constant deposition in the deeps of detrital material carried in by the above-mentioned rivers. This will at least provide some suitable food in the form of land vegetable detritus. Again the entrance of cold fresh water to the lochs will reduce the temperature of the surface salt water of the latter; the warmer lower layers rising to the surface will bring about mixing. Accordingly, detrital matter will be kept longer in suspension, and therefore more will be available as food for *M. norvegica*, which is a "suspension feeder." Marshall and Orr, at present engaged on a biochemical survey of the Clyde Sea Area, believe that mixing of waters in lochs is an essential factor in causing the repeated sudden increase of diatoms which is characteristic of sea lochs. (See also Nathanson's work in Mediterranean, 1909.) Such diatom increases, which may occur several times in the year, especially in spring and autumn, again form a source of food supply for *M. norvegica*. It is also to be remembered that large supplies of *E. norvegica* and *C. finmarchicus*, which form another source of food, are always to be had in the deeps. It is interesting to note that not only in Upper Loch Fyne, but in other widely separated parts of the world, e.g. the shores of Norway, Gulf of Maine in North America, etc., *M. norvegica*, *E. norvegica*, and *C. finmarchicus* are found together abundantly in deep waters (60–80 fms.).

It may be that there are some conditions which are equally favourable to all three organisms.

An examination of the stomachs of *E. norvegica* and *C. finmarchicus* taken from 60 fathoms in Upper Loch Fyne revealed very little recognisable food. In common with Euphausiids, masses of brownish green flocculent detritus containing a few shells of diatoms and peridinians were found in the stomachs of both species. It was noted that during the winter months there was no appreciable difference in the percentage feeding during the day and night. This does not agree with Marshall (1924). It is to be noted, however, that the specimens examined by that author were for the most part taken from surface waters.

With regard to the feeding of *E. norvegica* (Sars, 1903) the mature males have so far never been found with any food remains in their digestive tracts, whereas the immature males and mature and immature females were commonly found to feed, and the body cavity to contain much yellow oil. The mature male is very slender, and the mandibles and other mouth parts are degenerate. The immature male resembles the female in structure much more closely than when mature, and was erroneously believed by Lubbock (Claus, 1863) to be a different species. Dana, also, was deceived by this striking resemblance, and described the immature male as a female with five pairs of legs. The mature males occur much less frequently than do the mature females. It is interesting to note that the functional males apparently do not feed, and possibly die off after mating.

Finally, we wish to draw attention to the importance, brought about by the above investigations, of the debris of plants of land and coastal origin as a source of food for Euphausiids. It is a surprising conclusion that the herring, which is essentially a planktonic feeding fish, should be dependent, even though indirectly, on the abundance of terrigenous vegetable detritus. How much the deeper living Copepods, which are, no doubt, eaten by the herring, utilise such detritus is left for future investigations. The importance of detritus as food of bottom animals has been shown by Petersen and others, and Murray suggested a correlation between the bottom deposits and the distribution of animal life. It may well be that the nature of the bottom deposits, together with the presence or absence of bottom-currents, are important factors in the distribution of *M. norvegica*.

VERTICAL DIURNAL MIGRATIONS OF MACROPLANKTON IN UPPER LOCH FYNE.

During the early part of the year, when the macroplankton is very rich in Upper Loch Fyne, an attempt was made to determine if there was any evidence of vertical diurnal migration on the part of *Meganyctiphanes norvegica*, *Thysanoessa raschii*, *Calanus finmarchicus*, and *Euchaeta*

norvegica, the members of the macroplankton which are present in greatest abundance in these waters.

The first series of hauls was made on 19th-20th January, 1926. The hauls were made every four hours in the deep trough that runs parallel to the shore off Poll. Each haul lasted half an hour. Fortunately, a hard up-loch wind blew continuously over the 24 hours, so that the boat drifted about one mile during each haul. At 4 a.m., however, the wind blew somewhat harder, and it was estimated that during this haul the boat travelled about $1\frac{1}{2}$ miles. Lights were placed at convenient vantage points on the shore so that bearings could be taken, the moon being in her first quarter and the sky cloudy. Rain and hail showers were common throughout the 24 hours. Two tarred hemp 2-inch ropes were used. On one a 1-metre stramin net was attached to fish at 65 fathoms, and ordinary coarse tow-nets, 30 meshes to the inch, were attached to fish at 50 fathoms and 40 fathoms respectively. On the other rope a 1-metre stramin net was attached to fish at 30 fathoms, and ordinary coarse tow-nets as above were attached to fish at 20 fathoms, 10 fathoms, and surface respectively. The nets were open-nets, therefore they were liable to catch anything in the water between the depths to which they were sunk and the surface. The length of time that the nets were fishing at the stated depths was, however, much longer than at the intermediate depths passed through while shooting and hauling. Accordingly, although the results are not as accurate as would be obtained with closing nets, they are not without relative value. According to Russell (1925) the variation in depth at which a net may be fishing is very great on account of currents, etc. In the enclosed waters of Upper Loch Fyne it is believed that any currents present are chiefly surface currents, accordingly one can judge approximately by the angle at which the rope enters the water how deep the nets are fishing. We suggest that in Upper Loch Fyne variation in depth at which nets may be fishing as a result of action of bottom currents is apparently at a minimum. In comparing the numbers in the catches at the various depths account has to be taken of the much greater fishing capacity of the nets used at 30 fathoms and 65 fathoms. To make the numbers comparable we have divided the numbers caught by the 1-metre stramin nets by four.

The second series of hauls was made on 24th-25th February. The hauls were made at longer intervals than the first series. The moon was almost full, but the sky was overcast. The wind was blowing from the south-west.

The results shown in Tables IV-VIII indicate that there is a vertical diurnal migration on the part of *M. norvegica*, *T. raschii*, *C. finmarchicus*, and to a lesser extent of *E. norvegica*. All sizes of *Meganyctiphanes* migrate towards the surface. Even the largest specimens (39 mm.) are found

TABLE IV.

MEGANICTIPHANES NORVEGICA.

January 19th-20th, 1926.

Depth in fms.	8-8.30 p.m.			12-12.30 a.m.			4-4.30 a.m.			8-8.30 a.m.			12-12.30 p.m.			4-4.30 p.m.				
	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.
10	25	-	1	1																
	21	1	1		25	1	1													
20	25	4	2		35	1	-	3												
	27	-	2																	
	35	-	3	13																
30*	21	1	-	1	23	14	6		21	-	3									
					27	7	6		23	3	7									
					31	4	2		25	17	12									
					35	3	1	11	27	1	-	13								
									31	-	1									
									35	3	1									
									39	2	1									
	21	1	-		21	1	-		25	2	1	3								
	23	1	1		23	1	-													
40	25	8	2	18	25	7	2	15												
	27	1	1		31	2	-													
	31	1	-		35	1	-													
	35	2	-		39	1	-													
	21	-	1		21	1	-		21	1	-		25	-	2					
	23	2	-		23	2	2		23	1	-		29	1	-	3				
	25	5	3		25	3	3		25	4	-									
50	27	4	-	22	27	1	-	15	27	1	-	10								
	29	1	1		31	1	-		29	-	1									
	31	1	1		35	2	-		31	-	1									
	35	3	-						39	-	1									
	21	-	4		23	1	-		19	-	1		23	-	1		21	-	1	
	23	4	15		25	2	1		21	1	-		25	2	2		23	1	3	
	25	21	11		31	1	-		23	2	-		39	1	-	2	25	3	2	3
65*	27	4	4	18	35	2	3	2	25	18	9	12					27	1	-	
	29	2	-						31	2	4									
	31	-	1						35	9	2									
	33	-	1																	
	39	-	4																	

* The hauls at 30 and 65 fms. were made with the metre net: the numbers in the "total" columns are, therefore, the total divided by four.

TABLE V.

THYSANOESSA RASCHIL.

January 19th-26th, 1926.

Depth in fms.	8-8.30 p.m.			12-12.30 a.m.			4-4.30 a.m.			8-8.30 a.m.			12-12.30 p.m.			4-4.30 p.m.						
	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.	Length in mm.	♂	♀	Total.		
10	15	2	-		15	4	5		17	3	1											
	17	3	-	7	17	7	5	24	21	2	2	8										
	21	1	1		21	1	2															
20	15	9	8		15	7	11		15	4	3											
	17	12	9	50	17	23	18	77	17	12	10	46										
	21	4	8		19	4	4		21	10	7											
					21	7	3															
30*	17	-	1	1	15	15	17		15	48	76		15	3	4							
					17	29	35	33	17	162	111	161	17	9	7	12						
					19	11	15		19	51	36		19	3	1							
					21	21	19		21	69	93		21	12	9							
					15	17	14		15	7	4		17	2	3	5						
40	17	4	4	17	17	15	18	108	17	6	12	44										
	19	1	3		19	5	8		19	4	7											
					21	12	19		21	2	3											
					15	3	2		17	18	5		17	2	2							
50	17	1	1	5	17	11	8	27	19	3	4	86	21	2	1	7						
	19	-	1		19	-	1		21	27	29											
					21	1	1															
					15	4	5		15	19	27		17	9	13							
65*	17	1	1	1	17	1	1	9	17	44	59	63	21	7	8	9			17	2	-	1
	19	-	1		19	13	6		19	23	27											
					21	2	4		21	35	20											

* The hauls at 30 and 65 fms. were made with the metre net: the numbers in the "total" columns, therefore, are the total divided by four.

at 30 fathoms below the surface. These organisms are to be found in the bottom layers at all times of the day and night. It appears that at midday the greatest numbers are to be had immediately above the sea bottom. At that time *M. norvegica* and *T. raschii* seem to be on the sea

TABLE VII.

VERTICAL DIURNAL MIGRATIONS OF CALANUS FINMARCHICUS AND EUCHÆTA NORVEGICA. January 19th-20th, 1926.

Depth in fms.	Numbers per 20 c.c.*											
	8-		12-		4-		8-		12-		4-	
	8.30 p.m.		12.30 a.m.		4.30 a.m.		8.30 a.m.		12.30 p.m.		4.30 p.m.	
	Euchæta.	Calanus.	E.	C.	E.	C.	E.	C.	E.	C.	E.	C.
Surface.	-	8	-	3	-	1	-	-	-	-	-	-
10	-	25	-	20	-	10	-	-	-	1	-	-
20	-	50	4	28	-	14	-	15	-	12	-	14
30	-	1	2	45	-	36	-	70	-	13	-	13
40	9	120	7	140	1	115	4	200	1	210	1	12
50	6	130	4	200	3	123	5	180	3	150	8	230
65	33	63	40	100	10	100	40	150	90	140	50	120

TABLE VIII.

VERTICAL DIURNAL MIGRATIONS OF CALANUS FINMARCHICUS AND EUCHÆTA NORVEGICA. February 24th-25th, 1926.

Depth in fms.	Numbers per 20 c.c.†							
	6.15-6.45 p.m.		1.30-2 a.m.		10-10.30 a.m.		1-1.30 p.m.	
	Euchæta.	Calanus.	E.	C.	E.	C.	E.	C.
Surface.	-	8	-	4	-	-	-	-
10	4	10	1	15	-	20	-	6
20	8	40	1	10	2	20	-	12
30	15	40	2	20	1	10	-	25
40	35	90	1	5	1	6	-	22
50	16	70	12	8	10	20	3	40
65	50	60	40	50	30	40	40	50

bottom since they only appear at 65 fathoms (i.e. 5 fathoms above the bottom), and then in very small numbers. At the surface the greatest numbers are to be found before and at midnight. All the species tend to leave the surface long before daylight. Esterly (1912), with reference to Copepods, says: "The animals appear to leave the surface before the

* The catches made at 30 fms. and 65 fms. respectively were placed in a wide mouth glass vessel, and the volume made up to 2800 c.c. The contents were now well mixed, and a dip was taken with a glass capsule capacity 20 c.c. The catches made at the other depths were in each case placed in a wide mouth glass vessel, and the volume made up to 700 c.c. A 20-c.c. sample was dipped, as indicated above.

† See previous table.

light increases at all in intensity. This suggests that decreasing light is not the cause of downward movement." Russell (1925) says, with regard to *C. finmarchicus*, "I have no observation between 12.20 and 4 a.m. at the surface, but at any rate the 12.30 haul in the 3rd series indicates

TABLE IX.

Date.	Hour.	Position.	Depth in fms.	Depth of Sample.	Temp. C°	Salinity.	Diff.	Average.
17.11.86	11.55	Strachur	76	Surface	7.1	25.32	6.66	8.04
				Bottom	7.4	31.98		
	8.35	Inveraray	56	S.	6.5	22.16	9.41	
				B.	7.7	31.57		
29.12.86	17.5	Strachur	71	S.	0.8	31.76	1.60	
				B.	0.3	33.36		
30.12.86	9.0	Inveraray	71	S.	3.3	29.57	3.69	2.65
				B.	3.8	33.26		
4.2.87	15.50	Strachur	72	S.	6.1	27.59	5.36	
				B.	6.6	32.95		
29.3.87	14.0	Strachur	75	S.	11.0	17.78	14.03	11.49
				B.	10.3	31.81		
	13.0	Inveraray	66	S.	10.7	22.82	8.95	
				B.	11.0	31.77		
10.5.87	15.30	Strachur	72	S.	10.7	31.83	1.18	
				B.	10.1	33.01		
	16.30	Inveraray	63	S.	10.1	31.44	1.63	1.16
				B.	9.2	33.07		
	19.20	Strachur	72	S.	14.2	32.66	.76	
				B.	15.5	33.42		
16.6.87	10.50	Inveraray	60	S.	18.4	19.26	14.06	
				B.	16.8	33.32		
8.7.87	12.15	Strachur	72	S.	17.5	32.97	.48	
				B.	17.2	33.45		
	11.20	Inveraray	60	S.	18.3	32.08	1.17	.83
				B.	13.8	33.25		
23.9.87	16.40	Strachur	74	S.	15.7	32.12	1.24	1.19
				B.	13.3	33.36		
	17.30	Inveraray	64	S.	14.0	31.33	1.14	
				B.	13.9	32.47		

that they had already started to leave the surface." Apparently there are a number of specimens of all the species investigated which do not migrate to the surface, but remain at or near 65 fathoms. This suggests that light is not the only factor, if it is a factor, affecting their diurnal

vertical movements. Hickling (1925) finds that *Meganyctiphanes* and *Thysanoessa* "tend to increase as the water deepens, while their presence on the Cockburn Bank is very marked." He remarks further that this is "a disturbing factor in any effort to show the behaviour of these crustacea with reference to light alone."

Dr. H. Broch has kindly sent me specimens of *Meganyctiphanes* measuring from 21–29 mm. which were caught at the surface in daylight in the Oslofjord in October. Elmhirst has records of all sizes of *M. norvegica* during the day from October to May in different years either in tow-nets off Keppel, Millport, or being eaten by gulls dipping at the surface. These may have been brought to the surface by mixing brought about by the strong current which runs up Fairlie Channel (Elmhirst, 1922).

An extract has been made of other factors, such as vertical distribution of temperature and salinity, from data brought together by Mill (1891), as follows:—

Poll, the position at which the hauls were made in Upper Loch Fyne, lies approximately midway between Inveraray and Strachur. From Table IX we see that the largest difference in surface and bottom salinity at Strachur is found from November to March. The same also applies to Inveraray, except for the June record. The reason for the low surface salinities recorded at Inveraray is, no doubt, due to the proximity of that position to the influence of river waters from the Shira and Aray (see Fig. 2). The low surface salinity recorded on 16–8–87 is possibly the result of very heavy rainfalls which generally occur intermittently throughout the summer in this district. Assuming that the average of the differences of surface and bottom salinities at the two positions indicate the condition at Poll we find that here again the largest differences occur from November to March. There is no marked variation in differences between surface and bottom temperatures throughout the year. The lower temperatures, however, are found from November to April. As stated earlier in this paper, Euphausiids are found most abundantly in Upper Loch Fyne from November to April. Thus we may correlate wide differences of surface and bottom salinity and low temperatures, i.e. averaging 7° C. with maximum abundance of Euphausiids in Upper Loch Fyne.

Salinity then, at least within comparatively wide limits, would not appear to be a controlling factor in the vertical diurnal migration of Euphausiids found in the Clyde Sea Area. Experiments now in progress in the Laboratory indicate that *T. raschii* can live happily for weeks at a very low salinity, ca. 15‰.

That light has a lethal effect on certain macroplanktonic organisms is suggested by our experiments on *Meganyctiphanes* in captivity and the experiments of Huntsman already cited. There may be an optimum

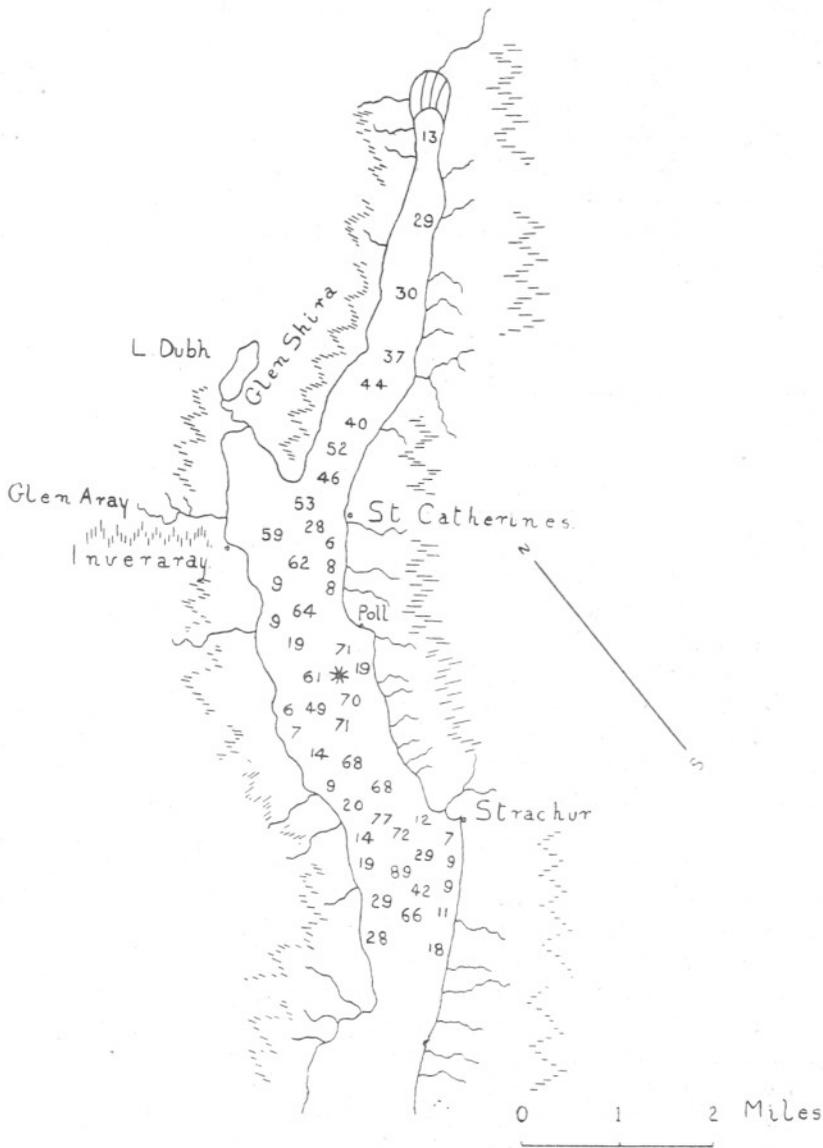


FIG. 2.—Upper Loch Fyne.

* Station at which hauls were made.

light intensity which is sought by each of the species under discussion, and to obtain this light intensity vertical migrations may be necessary. At the same time in any attempt to explain vertical diurnal migrations, on the part of Euphausiids at least, we must take into account factors such as tidal currents, temperatures, food requirements, proximity of ecdysis, sexual maturity, etc., if we are to arrive at trustworthy conclusions. It would appear then that the stimulus which has diurnal vertical migrations as its response is something less apparent than a mere presence or absence of light, but rather a summation of many factors. Further investigations are at present being carried out.

OBSERVATIONS ON MEGANYCTIPHANES NORVEGICA IN CAPTIVITY.

Adult specimens measuring 25-31 mm. have been kept in captivity for nine weeks, January to March, in outside sea-water in tanks fitted with plungers.

Three tanks measuring 12 inches by 18 inches by 12 inches were used. All light was completely shut off from two of the tanks. These tanks had their walls covered with black paper and the top covered in with thick cardboard, in the centre of which was a small hole to permit the entrance of a piece of cord to which the plunger was attached. Thus the contained specimens were practically in darkness. The other tank was freely exposed to diffuse daylight. The water was changed every day during the first week and every second day thereafter. There were from seven to nine specimens in each tank. Those specimens which lived longest, viz. nine weeks, were found in the darkened tanks. The shortest lived specimens in the darkened tanks lived for three weeks. In the undarkened tank none were found alive after fifteen days. It appeared, in some cases at least, that death took place just as the animal was about to moult. A few specimens, however, moulted successfully in all the tanks. Huntsman (1924) found that the unfavourable effect of light depends upon the condition of the individuals as well as upon the strength of light.

In our experiments it was noticed that in the undarkened tank the specimens always sought that part of the tank where the light was least intense. Light then would appear to have some effect on *Meganyctiphanes*, but as to the nature and extent of that effect we are unable to say without further experiments. One or two comments are made on this matter under Diurnal Migrations.

A $\frac{1}{2}$ -inch layer of mud, dredged from Cumbrae Deep at 60 fathoms, was put in the undarkened tank after all the specimens in that tank had died. Fresh specimens were put in, and their movements observed. They would frequently lie perfectly still on their sides on the surface of the mud. Suddenly they would work their pleopods actively, thus

stirring up the mud and organic particles from the bottom. Raising themselves slightly above the mud they would, by lateral movements of the thoracic appendages and movements of the pleopods, cause the cloudy water to pass from before backwards through the "food basket." Having caught a quantity of suspended detritus in the "food basket," they would once more settle on the bottom and proceed to devour their catch. Few Copepods were fed to any of the specimens, and at death the stomachs contained organic detritus.

The movements of the animals are sometimes very rapid. The normal position of the telson is slightly flexed downwards, but when a quick movement is necessary the abdomen is straightened, and the uropods quickly brought to the median position. The telson was never seen to be drawn under the abdomen, as is the case with Crangon, Pandalus, and allied Crustaceans. When rising to the surface the movement is frequently gyratory. The animals, as a rule, do not swim to the bottom, but with the pleopods held forward close to the abdomen they fall slowly to the bottom. They may at times swim quickly, occasionally breaking surface. Again they often make complete somersaults, as many as eight in succession, the telson and uropods together proving a very efficient and powerful steering apparatus.

No specimens have been seen to luminesce voluntarily in captivity after being twenty-four hours out of the sea. Immediately on being taken out of the sea the luminescent organs are very active, especially at night. On one occasion six specimens, averaging 27 mm. in length, were placed in a two-litre jar. By means of the light emitted voluntarily (i.e. without mechanical or other disturbance on my part) it was possible to read newspaper print. The light appeared suddenly like a flash, remained three or four seconds, and disappeared more slowly than it had come. The luminescent organs in the ocular peduncle seemed to be most powerful. Sometimes they alone would light up. The thoracic luminescent organs lit up together as also did the abdominal set.

When specimens were placed in 10% formalin immediately on being caught the luminescent organs would invariably light up momentarily. Murray (1912) believed that the luminescent organs are used as a kind of "bull's-eye lantern," and enable *Meganyctiphanes* to see and pick up the minute particles of organic matter which are settling on the bottom deposits. This seems probable as the amount of light penetrating to 60-80 fathoms is extremely small. That these organs may have other functions is possible, as is suggested by the fact that in *Stylocheiron carinatum* there are only three present, one between the bases of the first pair of pleopods and one on either of the penultimate legs. In the male the latter luminescent organs attain an extraordinary development (Sars).

Apart from the occasions when the luminescent organs are active, *Meganyctiphanes* must be practically invisible. The greater part of the body is transparent, and those parts which are opaque are thickly covered with red pigment bodies. Owing, however, to the fact that red rays are nearly all absorbed at the above-mentioned depths, the red colour would tend to be as invisible as would black. Accordingly, the invisibility of *Meganyctiphanes* is doubly secured. This invisibility would appear to decrease the probability of attack by enemies. *M. norvegica*, however, apparently lays itself open to attack when it luminesces. Certain fish may have learned to associate such luminescence with suitable food. For example, there are certain deep living angler-fish which have luminescent lures. Lissner (1919-23) suggests that the fact that the majority of the food organisms of the herring caught in the Skager-Rack and North Sea are luminescent is significant. This assisting and elaboration of the visual sense respectively by means of luminescent organs and relatively large eyes would appear to be a very efficient adaptation to the environment. Should, however, this specialisation tend to bring about the destruction of the species by attracting enemies one would expect to see a reduction of the luminescent organs. It may be that although the luminescent organs are essential in the life of *M. norvegica* they form under certain circumstances a considerable source of danger. The balance, however, would appear to be in the animal's favour. Owing to the limited nature of our knowledge of the environmental relations of *Meganyctiphanes* and other Euphausiids it is impossible at present to make any general conclusions of value.

PARASITES.

The following are some parasites found in *Meganyctiphanes norvegica* :—
Ectoparasites.

1. *Staphylocystis racemosus* (Coutière), a dinoflagellate found on the carapace of a specimen caught at "Cumbrae Deep" in March, 1925. The only record of this parasite is that of Kroyer on *Pasiphaea tarda* in N.E. Iceland.

2. A Suctorian often present on the pleopods. Not yet identified.

Endoparasites. A Gregarine appears in the gut from the second Calyp-topsis stage to the adult of 29 mm. length. This Gregarine appears in spring, and becomes more common during early summer.

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SUMMARY.

1. Vegetable detritus of land and coastal origin is of notable importance as a source of food, especially to those specimens measuring 21–29 mm., which is the most abundant size found in the Clyde Sea Area.

2. *Meganycytiphanes* in the Clyde Sea Area for the most part lives and feeds between 10 and 20 fathoms above a muddy bottom, usually in waters about 60–80 fathoms deep.

3. *Meganycytiphanes* feeds by selecting from the surrounding water the suspended micro-organisms and detritus, and would thus come under the category of a "suspension feeder."

4. The larger specimens measuring 29–31 mm. are found chiefly in Upper Loch Fyne. The largest specimens measuring 37 mm. are found exclusively in Upper Loch Fyne.

5. Adult specimens tend to decrease in numbers from May till September. During these months they appear to live during the day immediately above or on the muddy bottom.

6. The association of *Meganycytiphanes norvegica*, *Thysanoessa raschii*, *Euchæta norvegica*, and *Calanus finmarchicus*, in large numbers in Upper Loch Fyne would indicate that conditions there are specially favourable to all these species.

7. In Upper Loch Fyne *M. norvegica*, *T. raschii*, *E. norvegica*, and *C. finmarchicus*, make partial vertical diurnal migrations, specimens being found a few fathoms from the bottom during both day and night.

8. Under certain circumstances light appears to have a harmful effect on *M. norvegica*.

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Irregular Development in the Larval History of *Meganyctiphanes norvegica*.

By

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With 1 Figure in the Text and 1 Plate.

THE object of this paper is to draw attention to some irregularities in the larval development of *Meganyctiphanes norvegica*. Sars (1898) described a Euphausiid larval development which he said would seem to refer to two forms, viz. *Nyctiphanes norvegicus* and *Boreophausia raschii*, which both at times occur rather abundantly in the Christiania Fjord. These Euphausiids, now known as *Meganyctiphanes norvegica* and *Thysanoessa raschii* respectively, are also found occasionally associated in large numbers in certain parts of the Clyde Sea Area. In individual lochs, however, though contiguous, one species generally occurs much more abundantly than the other, e.g. *M. norvegica* is the predominating species in Upper Loch Fyne, whereas *T. raschii* is the more numerous in Loch Striven. Both species are found in Loch Goil and Loch Long, where *T. raschii* is again the more common. In all cases the largest numbers of adults are found from mid-September to mid-March. The doubt expressed above by Sars has been cleared, and I have been able to distinguish the life histories of these Euphausiids from the unsegmented egg to the mature adult.

The life history of *M. norvegica* fits in with that described by Sars (1898) and Lebour (1925), with, however, the following interesting differences. The eggs found in the Clyde Sea Area have not only a wider range in size (the diameter of the outer shell measuring .59–.85 mm.), but two different types of nauplii are produced. The smaller type of nauplius agrees with that described by Sars, and arises from eggs the diameter of whose outer shell measures .59–.70 mm. The larger type of nauplius which apparently is now described for the first time, comes from eggs whose outer shell diameter measures .65–.85 mm. In all the sizes of eggs the young embryo which measures ca. .40 mm. is tinged (towards the abapical pole) with a distinctive salmon pink colour. The colouring becomes more intense as segmentation proceeds. All the nauplii, whether before or after hatching, have their posterior ends tinged with this colour.

The larger nauplius arises as follows: Segmentation and gastrulation takes place, as described by Sars. The limbs of the developing nauplius are laid down (Plate I, Fig. 1), and ultimately the nauplius is formed (Plate I, Fig. 2). It is somewhat elongated, and measures .42 mm. in length and .30 mm. at its greatest breadth. The nauplius still within the outer shell becomes larger, .48 mm. in length and .32 mm. at its greatest breadth, and narrowed posteriorly (Plate I, Fig. 3). During the enlargement of the nauplius while still in the shell no sloughing of a naupliar skin was observed, although it will be seen that distinct alteration in form has taken place.

On emerging from the shell the nauplius takes the form seen in Plate I, Fig. 4, and measures .53 mm. long by .32 mm. at its greatest breadth. The anterior end is broad and somewhat truncated, whereas the posterior end is more or less pointed. As development proceeds the metanaupliar form is prefigured below the outer skin and we may have either of two forms produced, the second nauplius having either the form indicated in Plate I, Fig. 5 or, on the other hand, showing at its posterior end six spines, four short and two long, as depicted in Plate I, Fig. 6. The second nauplius measures .55 mm. in length and .33 at its greatest breadth. An ocellus is present, and there is also a foreshadowing of the ocular plate seen in the metanauplius, from which the compound eyes develop in the later larvæ. Traces of three pairs of limbs which become free buds in the metanauplius are indicated as are also the mouth and anus. The metanauplius differs only in size, measuring .62 mm., from that derived from the smaller nauplius, and described by Sars and Lebour. The telson of the metanauplius is shown (Plate I, Fig. 7). In the Clyde Sea Area

EXPLANATION OF PLATE I.

Meganyctiphanes norvegica.

1-3 (all drawn to same scale).

FIG. 1.—Egg with developing nauplius. Egg, .67 mm. in diameter.

FIG. 2.—Egg with nauplius further developed than in Fig. 1.
Egg, .72 mm. in diameter. Nauplius, .42 mm. long.

FIG. 3.—Egg with nauplius further developed than in Fig. 2.
Egg, .85 mm. in diameter. Nauplius, .48 mm. long.

4-7 (all drawn to same scale).

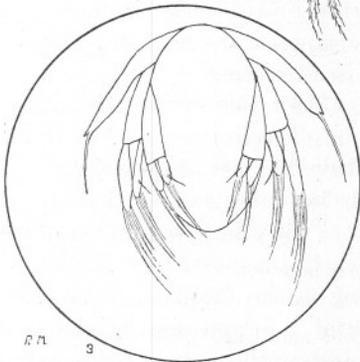
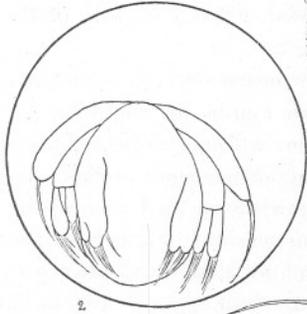
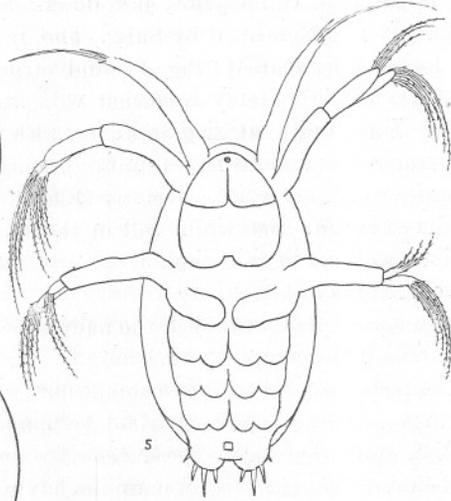
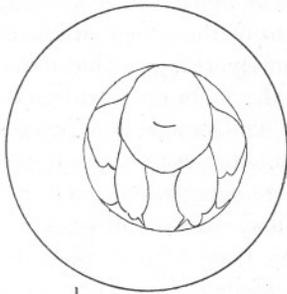
FIG. 4.—First nauplius from egg .53 mm. long, ventral view.

FIG. 5.—Second nauplius from first nauplius, .55 mm. long, ventral view.

FIG. 6.—Posterior end of body as it appears in the other form of second nauplius, which arises from first nauplius, ventral view.

FIG. 7.—Telson of metanauplius, dorsal view.

PLATE I.



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the larger type of nauplius, just described, is much the more common form. It is generally distributed, and is sometimes very abundant in the lochs. The smaller type of nauplius, corresponding to that described by Sars, has so far only been met with in the more open waters of the Area. I am quite satisfied from rearing experiments in the Laboratory and from observations made on the plankton that both types of nauplii give rise to *M. norvegica*. The reason for there being two types of nauplii produced by *M. norvegica* is not apparent, and constant observations at various stations in this district are necessary before the problem can be solved. It may be that here we have in- and off-shore forms, or that variation in size of nauplii may be correlated with density of yolk of the egg from which the nauplii were derived.

The metanauplius and first calyptopis, whether derived from the small or large nauplius, have each six terminal spines on the telson. The median spine does not appear until the second calyptopis. I also find six terminal spines in the first calyptopis of *Thysanoessa raschii*. Lebour (1924, p. 4) records the absence of a median spine in the telson of the first calyptopis of *Thysanoessa inermis*, and with regard to *Stylocheiron sukhi* states that the central spine is not present until the appearance of the single spine of the adolescent form. The median spine is also absent in the telson of the first calyptopis of *Nyctiphanes Couchii* (Lebour, 1924; Plate II, Fig. 1, p. 423). G. O. Sars (1873-76) figures the first calyptopis of *Nyctiphanes australis* as having seven spines on each side of the telson and no median spine present. The same arrangement of spines on the telson of the first calyptopis is shown by Claus (1876) for *Euphausia*.

In *Thysanoessa raschii* I find in the late cyrtopia larvæ that the median jointed spine becomes considerably reduced in size, though there is no stage where it is absent, before being ultimately replaced by the unjointed single spine of the adolescent form. In *Thysanoessa longicaudata* Fowler (1903, p. 130) draws attention to a cyrtopia form where the median spine is altogether absent. This tendency to suppress the median jointed spine in a late stage of larval development is interesting.

The number of spines on each side of the telson of the first calyptopis for the species mentioned above is seven. This number, as Fowler (1903) has pointed out, agrees with the primitive number of spines, viz. (7+7), which Meyer attributes to the primitive Macruran and Brachyuran. The presence of a median spine in addition to the primitive number of spines (7+7) on the larval telson is apparently diagnostic for Euphausiidae, the median spine being always lacking in the Caridean larvæ, Lebour (1926, b, p. 4.) The above evidence of a suppression of the median spine in the early larvæ of some Euphausiids would suggest a close relationship between the *Euphausiidae* and primitive Decapods.

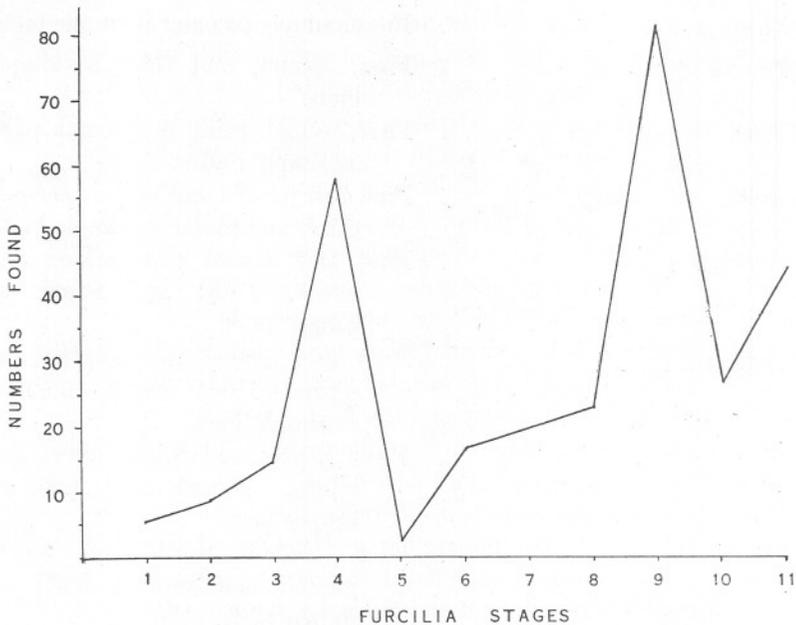
I have been unable to detect any anatomical difference in the meta-

nauplius and calyptopis stages from that described by Lebour (1925). While this is true I have found evidence of interesting modifications and variations in the development of the furcilia forms. The furcilia are distinguished as follows: (1) eyes are no longer covered by the carapace; (2) the appearance of the pleopods. The sequence of the appearance of the latter has been used to distinguish successive stages in the development as follows:—

First furcilia	. . .	Eyes free, no pleopods.
Second	„ . . .	First pair of pleopods as simple buds.
Third	„ . . .	First and second pairs as simple buds.
Fourth	„ . . .	First, second, and third as simple buds.
Fifth	„ . . .	First, second, third, and fourth pairs as simple buds.
Sixth	„ . . .	First pair jointed and setose; second, third, and fourth as simple buds.
Seventh	„ . . .	First and second pair jointed and setose. Third and fourth as simple buds.
Eighth	„ . . .	First and second pair jointed and setose. Third, fourth, and fifth as simple buds.
Ninth	„ . . .	First, second and third jointed and setose. Fourth and fifth as simple buds.
Tenth	„ . . .	First, second, third, and fourth jointed and setose. Fifth as simple buds.
Eleventh	„ . . .	All five pairs of pleopods jointed and setose.

In June, 1925, while examining a furcilia, corresponding to the fourth stage above, under the binocular the specimen moulted, and now obviously belonged to the sixth stage instead of the fifth. Later a typical fifth furcilia stage was found in the plankton, and accordingly it was decided to make a closer study of these so-called stages by rearing experiments in the Laboratory. During the summer of 1926 I had several opportunities of studying larvæ of *M. norvegica* in captivity, and although there was a large mortality, was successful in bringing some of them through one or two moults. The result of the work showed that in the development of the furcilia forms certain stages tend to be dominant and others to be suppressed. In other words, there is a tendency to reduce

the number of larval stages. I also found that those furcilia stages which were observed to be sometimes omitted during development in captivity were less frequent in the plankton than the other furcilia stages. On the other hand, there were certain stages which predominated in numbers in the plankton (see Text Fig. 1). Unfortunately the amount of material available was not as large as was desired, but from the examination of 302 furcilia specimens it is found that the stages with the best marked tendency to be suppressed are the first furcilia and the fifth furcilia, and those tending to be dominant are the fourth furcilia and the



TEXT FIG. 1.—Graph showing relative numbers of furcilia stages found in the plankton in the Clyde Sea Area during June, July, and August, 1926.

ninth furcilia. Specimens were taken from the plankton, and placed in glass vessels, each containing 500 c.c. of sea-water. The glass vessels were kept in diffuse daylight in running water whose average temperature was ca. 12.9° C. The results are indicated in the following table:—

No. of specimens which moulted successfully.	No. which moulted regularly.	No. which moulted irregularly.						
		3rd Calyptopis to 2nd Furcilia.	3rd Calyptopis to 3rd Furcilia.	2nd Furcilia to 4th Furcilia.	4th Furcilia to 6th Furcilia.	4th Furcilia to 7th Furcilia.	4th Furcilia to 7th Furcilia.	7th Furcilia to 9th Furcilia.
26	12	3	2	3	1	2	3	

Mr. Elmhirst has shown me records made by him of cases in which a furcilia jumped from stage four to stage nine, and from stage two to stage

four. Again Lebour (1925, p. 813) records a third calyptopis giving rise to a second furcilia. Among specimens of the fourth furcilia stage two forms can be distinguished, one having all three pairs of simple buds of the same size, another having the third pair of simple buds half as long as the first two pairs, neither of the latter being setose. On one occasion, however, a specimen was found in the plankton, having the first pair of pleopods setose and two pairs as simple buds. This particular stage is said to be characteristic of *Stylocheiron suhmii* (Lebour, 1926 (a), p. 205). This stage, however, appears to be of rare occurrence, as I have not been able to find another of the same. Two forms can also be distinguished in the ninth stage, one form having both pairs of simple pleopod buds the same size, the other having the second pair of simple buds smaller than the first pair. In this case the first form moulted in captivity to give the second form. One other irregularity was observed. On several occasions the following specimens occurred in the plankton: seventh furcilia with left member of second pair of pleopods non-setose; seventh with right member of second pair of pleopods non-setose; eighth furcilia with left member of second pair of pleopods non-setose; ninth furcilia with left member of second pair of pleopods non-setose; eleventh furcilia with left member of fifth pair of pleopods non-setose. Two interesting points may be noted: (1) the irregularity is practically consistent, since in almost every case it is the same member (viz. left) of the last pair of pleopods formed that is undeveloped. (2) There is an apparent metameric progression of an irregularity in accordance with the usual sequence of development, that is from before backwards.

With regard to morphological differences for particular stages as described by Lebour, it was noted that in the forms I have studied the thoracic appendages and abdominal luminescent organs develop earlier. Development agrees with that described by Lebour (1925, p. 823), in so far as the first thoracic appendage is well formed in all stages. With regard to the appearance of the other thoracic appendages, thoracic and abdominal luminescent organs, I find the following:—

Sixth furcilia	.	.	.	Second thoracic appendage is jointed.
Eighth*	„	.	.	Luminescent organ on first abdominal segment.
Ninth	„	.	.	Second thoracic appendage, five jointed with setose exopod and luminescent organ. Luminescent organ on second abdominal segment.

* The luminescent organ on first abdominal segment may not be present till the ninth furcilia, but so far as I have found it is never later in appearing.

Tenth furcilia	Third thoracic appendage jointed with non-setose exopod and one-lobed gill. Fourth and fifth appendages as buds.
Eleventh ,,	Third thoracic appendage, five jointed with setose exopod. Fourth appendage unjointed. Luminescent organ present on seventh appendage, which has a two-lobed gill.

The stage following this is the first cyrtopia where all the luminescent organs are present. According to Lebour there are twelve furcilia stages, and the appearance of luminescent organs and development of thoracic appendages are described as follows:—

Ninth furcilia	Second thoracic leg jointed, third and fourth unjointed with rudimentary gills. No luminous organ except on eyes.
Tenth ,,	About the same size as the ninth.
Eleventh ,,	Much like the twelfth, but smaller and not quite so far advanced with regard to appendages.
Twelfth ,,	Second thoracic leg five-jointed with setose exopod and two-lobed gill and with luminous organ; third leg five-jointed with non-setose exopod and no gill, fourth leg unjointed with two terminal setæ, exopod, and no gill, fifth limb rudimentary; three abdominal luminous organs.
First cyrtopia	All luminous organs present, those on the seventh thoracic being not quite perfect.

From the above observations it would appear that during the development of *M. norvegica* in the Clyde Sea Area the furcilia period is one of instability, and that we have here evidence of an incipient shortening of the larval existence by the numerical reduction of instars in addition to a hastening of development by the earlier appearance of the luminescent organs and growth of the thoracic appendages (Macdonald, 1926).

Recently evidence of curtailed larval history has been found with regard to other species of Euphausiids, where the omission of particular stages would appear to have gone farther than that found in *M. norvegica*. Concerning *Nematoscelis microps*, Lebour states (1926, p. 766): "The youngest stage found is presumably the second furcilia, measuring 2.4 mm. in length, and having one pair of simple bud-like pleopods. . . . The next seen has one pair of pleopods setose and three pairs simple, presumably the sixth furcilia . . . measuring 2.7 mm. in length. These two stages correspond with the second and sixth furcilia of Nyctiphanes and Meganyctiphanes, but it is conceivable that intermediate stages are skipped. It is striking that these stages, together with the tenth, seem to be dominant as no intermediate stages were found, whilst these were abundant. Moreover, the sixth and tenth are the stages described by Hansen and Sars."

Again (p. 770) with reference to *Euphausia krohnii*, "Sars describes the second and seventh furcilia having one pair of simple pleopods, and one pair setose with four pairs simple respectively. Curiously enough no stages between these two have been found in the Alexandria samples, although many specimens of both these stages occurred. Possibly this is again a case of jumping over several stages which was suggested above for *Nematoscelis*."

Among Crustacea continuous larval development is considered a primitive feature, whereas a marked metamorphosis is characteristic of more highly developed forms (Gurney, 1924, p. 48). For this reason the above observations are interesting, as they suggest tentative steps in an evolutionary progress in the order Euphausiaceæ towards reduction in number of larval stages. They also suggest that in those Arthropods in which the life history consists of a few pronounced stages these are to be regarded not as having evolved independently from a continuous life history, but rather as the survivors of a once greater number of successive yet distinct stages.

I am indebted to Professor Graham Kerr, F.R.S., for helpful advice, and to Mr. Elmhirst who so very kindly put his records and material at my disposal.

SUMMARY.

A new type of Nauplius belonging to *Meganyctiphanes norvegica* is described.

Attention is drawn to irregularities in the development of the furcilia forms in which particular stages are sometimes omitted.

It is suggested that in the larval history of *M. norvegica* in common with other Euphausiids there is an indication of evolutionary progress in the group Euphausiaceæ.

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Studies of the Plymouth Brachyura. I. The Rearing of Crabs in Captivity, with a Description of the Larval Stages of *Inachus Dorsettensis*, *Macropodia longirostris* and *Maia squinado*.

By

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With 4 Plates.

It is difficult to rear crabs from the egg, and few experiments of the kind have been successful. It is intended in these studies of the Plymouth Brachyura to rear as many species as possible from the berried crab, and thus to ascertain without doubt the larvæ of each species in all stages, so that they may be recognisable in the plankton.

The members of the Oxyrhyncha so far observed in the Plymouth district are the following :—

Inachus Dorsettensis (Pennant), *Inachus Dorynchus* Leach, *Macropodia longirostris* (Fabricius), *Macropodia Egyptia* A. Milne-Edwards, *Macropodia rostratus* (L.), *Achæus Cranchii* Leach, *Maia squinado* (Herbst), *Pisa biaculeata* (Montagu), *Hyas araneus* (L.), *Hyas coarcticus* Leach, *Eurynome aspera* (Pennant).

Unfortunately, Williamson (1915) calls all these *Inachus*, except *Maia* and *Eurynome*, which causes much confusion. Three sub-families of the Maiidæ are usually recognised (Borradaile, 1907 ; Rathbun, 1925) ; the *Inachinæ*, including *Inachus* and *Macropodia* ; the *Maiinæ*, to which *Maia* belongs ; and the *Pisinæ*, in which group are usually placed *Pisa* and *Hyas*. From the existing descriptions of the larval forms of these last it seems very unlikely that they ought to be placed so close together, for the larva of *Pisa*, according to Cano's (1893) description, is much more like the *Inachinæ*, and that of *Hyas*, according to Williamson's description (op. cit.), more like *Maia*, although quite distinct and easily separated. *Eurynome aspera* is usually placed in the *Parthenopidæ*. Its larval form, however, does not agree with those of other members of the family described by Cano.

Claus (1876) gives a good drawing of the first zoea of *Inachus Dorsettensis* (as *I. scorpio*), also Cano (op. cit.). Nothing further is known of the

larval forms of this species which are described in this paper. Williamson (1915), under the name of *Megalopa niga* nov. spec. describes and figures a megalopa, obviously an Inachus. Gourret (1884) figures the larva of *Inachus Dorynchus*, evidently the pre-zoea without its cuticle but not yet in the zoeal stage. *Macropodia longirostris* is so far not known in its larval stages, and is described here for the first time. The larval stages of *M. Egyptia* are not known, but *M. rostratus* (as *Stenorhynchus phalangium*) is figured and described by Cano (op. cit.) in the first zoea, megalopa, and first crab stage. He also gives drawings of the pre-zoeal telson and antenna, details of the carapace, and some of the appendages of the other stages. He does not, however, describe the second zoea, not having seen it either in *Macropodia* or *Inachus*. Lo Bianco (1904) figures the first crab stage of this species, as the megalopa, which is noted by Williamson. J. V. Thompson (1836) figured its early larva (as *Macropodia phalangium*) before it reached the zoea stage. His figure of the megalopa reproduced (1915, p. 533) and named by Williamson "*Inachus rostratus* (L.) (?) or either *Macropodia phalangium* or *dorsettensis*," is more likely to be *Hyas*, already noted by Cano, as it has setose fifth pleopods and more than six abdominal segments. *Achæus Cranchii* has not been described in the larval state, although the large eggs are known. Cano (op. cit.) describes and figures the zoea of Pisa. Gourret (op. cit.) also figures it, but his drawing is entirely different from Cano's and so much resembles the zoea of a *Pinnotheres* common in the plankton at Plymouth (probably *P. veterum*) that one cannot help wondering whether by any chance the larvæ have got mixed, especially as Gourret also figures the telson of *Pinnotheres veterum*. *Hyas araneus* has been well worked out by Williamson (1900, 1915), and a good deal is described of the larval stages of *H. coarcticus* by Stephensen (1912) and Williamson. They are easily recognisable by their prickly carapace spines and in the megalopa by the three-spined rostrum and conspicuous dorsal spine. *Maia squinado* was known in the pre-zoeal stage by Couch (1843), who is quoted by Bell (1853). Schlegel (1911) succeeded in rearing this species at Roscoff from egg to crab, but unfortunately gives no description of his methods nor any figures of the larvæ. Cano (op. cit.) describes the life history of its relative *Maia verrucosa* from the Mediterranean from egg to crab and gives good figures. Claus (op. cit.) gives a drawing of the first zoea of the same species which might equally well do for *Maia squinado*. In this, however, he omits the lateral spines of the carapace. *Eurynome aspera* is figured by Kinahan (1857) in the pre-zoea and by Cano (op. cit.) in the first zoeal stage. Gurney (1924) also gives an account of these stages. In the present paper all the larval stages from egg to crab are described for the first time in *Inachus Dorsettensis* (the first zoea only being previously described) and *Macropodia longirostris*,

and figured for the first time in *Maia squinado*. All of these were reared in the Laboratory from egg to megalopa, the crab stages being reared from late zoeæ and megalopæ from the plankton.

METHOD OF REARING.

A successful method has been found by which the larvæ of several crabs have been reared through different stages. So far the megalopa has not been successfully brought to the crab stage, but it is hoped soon to succeed in this also. The method adopted was to place the berried crab in an aquarium—plunger jar, aërated jar or in running water. In the first two cases the crabs were left until the eggs hatched; in the last case the water was turned off or the crab transferred to a plunger jar or aërated jar just before the eggs were hatched. The newly hatched larvæ were then transferred to various receptacles, plunger jars, aërated jars, or small glass dishes, filled with water from outside the Breakwater, in which had been placed special food. A selection of diatoms from the very fine tow-nets or a culture of *Nitzschia* were not satisfactory as food. Evidently something more substantial was necessary. Miscellaneous plankton containing chiefly small copepods was also not suitable, probably because much of it died and sank to the bottom of the jar without being eaten. Finally, oyster larvæ from the oyster itself were tried, and this proved very successful. I am indebted to Mr. O. D. Hunt for suggesting mollusc eggs as food, and to Dr. J. H. Orton for the regular supply of oyster larvæ. With a diet of oyster larvæ *Maia squinado* and *Inachus Dorsettensis* were brought to the megalopa stage. Sometimes the megalopæ were transferred to other vessels and fed on small crustacea or pieces of mussel, but in no case did one turn into a crab. That the crab larvæ really ate the oyster larvæ was apparent by examining the stomachs and intestines, which contained remains of the shells.

The oyster larvæ were washed out of the parent oysters and pipetted into the jar containing the crab larvæ. Here they swam about and could be seen scattered throughout the jar. For several days this might last and when the water was clear again a fresh supply was put in.

As the spawning season of the oyster finished in October it was necessary to find other food. At the suggestion of Dr. C. M. Yonge, who kindly gave the wood in which the molluscs were found, *Teredo* larvæ were tried. Artificial fertilisations were made and the one-day-old larvæ given to the crab larvæ as food. It is extremely easy to make fertilisations of *Teredo*, the eggs of one female and a small sample of sperm from a male serving for food for several days. The eggs, which are opaque and colourless, are washed out from a female and pipetted into glass bowls containing clean sea-water, and sperm added. In a few hours activity is shown, and

by the next day larvæ with shells are present and can be used for food. The wood with *Teredo* had been in a tank in the Laboratory for some months, but still contained the ripe molluscs. *Maia squinado* and *Inachus Dorsettensis* were again reared to the megalopa on this, and in addition *Macropodia longirostris*.

Another satisfactory food was found to be the larvæ of the tube-building annelid *Pomatoceros*. This is useful as it breeds all the year round, but more specimens must be used in order to obtain enough food. About six ripe females serve for two bowls of food. The purple eggs which are easy to see are washed out from the female, after having crushed the tube and extracted the worm, put into a bowl of clean sea-water and sperm added. The larvæ are moving in a few hours, and by the next morning are small trochospheres ready to be given as food.

These three larval forms are thus found to be excellent food for larval crabs. The aquarium is quite clean, as the food is eaten before it can die, and it is evident that larval crabs thrive on a diet of small moving living animals, which is apparently preferred to plants. The usual size of the food is the following:—

Oyster larvæ	0.17–0.18 mm. across.
Teredo larvæ	0.05–0.06 mm. across.
Pomatoceros larvæ	0.08 mm. across.

On *Teredo* and *Pomatoceros* *Macropodia longirostris* was reared as far as the megalopa, which, as well as the last zoea, also ate other crab larvæ. The zoea ate the first zoea of *Portunus depurator* and the megalopa ate this also, besides the first zoea of *Inachus Dorsettensis*. These were caught when perfectly lively, the megalopa swimming all the time and clinging to its prey with its legs (Plate III, Fig. 4). The first zoea of *Inachus Dorsettensis* also ate the eggs of *Carcinus mænas*.

Besides these three crabs, which have been reared as far as the megalopa, others have been brought as far as the last zoeæ, and many zoeæ from the plankton have been reared through crab stages. A description of these is deferred until more complete.

THE LARVAL STAGES OF THE BRACHYGNATHA.

It is easy to distinguish a typical zoea of a spider crab (*Oxyrhyncha*) from a typical zoea of an ordinary crab (*Brachyrhyncha*). Judging by the British species and any foreign species which have been described, the zoeæ differ in the following particulars (excepting a few forms which from their habit make special modifications necessary):—

Brachyrhyncha. More than two and frequently five stages, the first

and second, with only a slight or without any trace of pleopods, the antenna without, or with only a trace of, a flagellum.

Oxyrhyncha. Only two zoea stages, the pleopods showing in the first zoea and underneath the pre-zoeal skin, the antenna with a flagellum. Certain members of the Parthenopidæ are probably exceptional in having more zoeal stages and an early zoea like the Brachyrhyncha. In the following notes on the Oxyrhyncha the Parthenopidæ are excepted. As far as one can tell from any exact descriptions and individual observations the megalopæ of the two groups seem to be differentiated by the presence of long feelers on the last leg in the typical Brachyrhyncha (except the Pinnotheridæ, which are exceptional in their habit) and their absence in the Oxyrhyncha. *Ebalia* belonging to the Oxystomata is also without them.

Excepting the Dromiacea, which very possibly should not be included in the Brachyura at all, the brachyuran zoea is flattened from side to side and has two pair of maxillipedes developed as swimming organs, the third pair being quite rudimentary in all the zoeal stages. On the extremities of these swimming maxillipedes are long setæ, which are very regular, and we are able to recognise the different zoeal stages from the number of setæ on the maxillipedes. Thus the first zoea always has four setæ. This I believe is without exception, unless the zoea is abnormal. The second zoea has six, although five are sometimes present; never, I think, have more than six been observed. Here the ordinary Oxyrhynchan zoea stops, therefore a zoea with more than six spines on the maxillipedes almost certainly does not belong to the typical Oxyrhyncha. The zoeæ of the Brachyrhyncha and some at least of the Oxystomata (*Ebalia*) have eight setæ at the third stage, later stages, if present, having ten at the fourth, and usually twelve at the fifth. There may, however, be one less on one or both maxillipedes and it is possible that the fifth zoea may have only ten (Hyman, 1920, in *Gelasimus*). Thus all the species of *Portunus* seem to have five zoeal stages; *Carcinus*, *Pilumnus*, and *Gonoplax*, four. It is interesting, however, to find that in certain species of the Pinnotheridæ the second zoea with six setæ on the maxillipedes and conspicuous pleopods is the last, and changes into a crab-like megalopa. This is found to be the case at Plymouth with a zoea, which is probably *Pinnotheres veterum*, but Hyman (1924) thinks it probable that there are more than two zoeal stages in some species.

As far as British crabs go the above differentiating characters appear to hold good between the Oxyrhyncha and Brachyrhyncha except in Pinnotheres, which on account of its habit has an abbreviated life history.

From the egg of all Brachygnatha known issues a pre-zoea. That is to say, the zoea enclosed in an extremely thin embryonic cuticle, which

has no segmentation, and bears very long and broad setose spines on the antennules, antennæ, and telson. This embryonic cuticle is considered by Gurney (1926) to bear metanaupliar characters, the first zoea corresponding to the protozoa of the penaeids. It is difficult to discuss such a question with crabs, because the zoea has become so complicated by specialisation that it has characters of both early and late stages together. In the present notes the stage bearing the embryonic cuticle is called the pre-zoea, the stages following being the first zoea, second zoea, and so on until the last zoea changes to the megalopa. The chief character of the Brachygnathan zoea being its possession of two pairs of maxillipedes functioning as swimming organs, the remaining thoracic appendages being rudimentary, and its laterally compressed body. The telson tends to be forked and is truly forked in all typical forms. The megalopa is characterised by its free swimming pleopods, the body being flattened dorsoventrally and all the legs functional. The abdomen is usually held straight out, while the pleopods act as swimming organs. The megalopa changes to a crab with the abdomen tucked in under the body, and the pleopods, usually much reduced, no longer serving as swimming organs.

The pre-zoea may cast off its embryonic cuticle at once, or it may keep it for several hours. In the case of all the three crabs here described it is retained for several hours and the little larva swims actively. Its movement is, however, a peculiar one, for it is hampered by the cuticle, possesses no dorsal spine, and the maxillipedes are enclosed in simple sheaths without setæ although free from the body. The chief movement is a bending inwards to the body and out again of the abdomen. The large flat spines on the antennules, antennæ, and telson, by spreading out apparently help in keeping it up. The whole movement is a jerky one and lacks restraint, its object probably being entirely the casting of the cuticle. In all the pre-zoæ known there are seven spines on each side of the telson, six of them usually setose and very long, and one, the fourth from the side, being shorter and non-setose covering the spine which will form the point of the fork in the zoea. On the antennule there are usually two long setose spines, one larger than the other, and on the antenna three or four long setose spines.

The pre-zoea of *Maia squinado*, *Inachus Dorsettensis*, and *Macropodia longirostris*, differs little in each species except in size and colour, due to the zoea which it covers. In *Maia* it is an olive-green, in *Inachus* and *Macropodia* yellow and orange, thus making the general appearance totally different. The pre-zoæ of *Inachus* and *Macropodia* are very much alike both in colouring and structure.

The zoea of *Maia* and the zoæ of *Inachus* and *Macropodia* differ very much, representing as they do two very distinct sub-families of the Maïidæ. In the sub-family *Inachinæ* the zoea has no rostral spine nor

lateral spines on the carapace, only the dorsal being present, the second zoea has only six segments in the abdomen and only four pairs of pleopods, and the megalopa is also destitute of the last segment of the abdomen which is fused with the telson, and has only four pairs of setose pleopods, the fifth pair being represented by the tiniest of rudimentary buds. In the *Maiinæ*, however, there is a rostral as well as lateral spines to the carapace besides the dorsal, and there are the usual seven abdominal segments and five pairs of pleopods. The first zoea in all three has rudiments of pleopods, in *Inachus* and *Macropodia* on the second, third, fourth, and fifth abdominal segments, and in *Maia* on the second, third, fourth, fifth, and sixth, although the sixth is not yet cut off from the telson. In the second zoea the pleopods are well developed with two branches, one long and one very short, the sixth abdominal segment in *Maia* being now separated from the telson.

Here it may be noted that in the larval forms there are no pleopods on the first abdominal segment. If they are normally present in the crab they are developed in later stages. It thus comes about that the fifth pleopods of larval crabs borne on the sixth abdominal segment correspond with the uropods of Crustacea such as the shrimp, but they are not differentiated from the others to form a tail fin. It often happens, however, that the number of setæ on these differs from those on the other pleopods, and this may be used as a good distinguishing character in many species. In most of the adult crabs the first pair of pleopods borne on the first abdominal segment appears later, and only the first and second are usually present in the adult male. I have found that they appear in the second crab stage of *Corystes* reared from the zoea in the laboratory. In the female the first pleopods are usually absent as in the larva. The second to the fifth pleopods are used for holding the eggs until hatched. The uropods (sixth abdominal appendages) are absent in all typical crabs, therefore these present in the megalopa usually abort, having already aborted in those crabs in which the sixth segment is fused with the telson (e.g. *Inachinæ*).

In the first zoea of all the typical *Oxyrhyncha* the antenna has three branches, two long and more or less spiny representing the exopodite and the spinous process, and a short soft process without spines, which forms the flagellum (Plate IV, Fig. 12). This last is the endopodite. The *Oxyrhyncha* thus differ from the typical *Brachyryncha* where the flagellum is not present or only extremely indistinct, in the first and often in the second zoea, and only appears at any length in the later stages. In the second zoea of the *Oxyrhyncha* the flagellum is fairly long. In the megalopa and crab stages only the endopodite persists at any length, although a small process may represent the exopodite (Plate IV, Figs. 4, 8, 14). In the three crabs described *Maia* differs from the

other two in having the exopodite much shorter than the spinous process in both zoeal stages, whereas they are of nearly equal length in *Inachus* and *Macropodia*,—a fact noticed by Cano for *Maia verrucosa*.

The antennules, mandibles, maxillæ, and maxillipedes, do not differ much in the three species, and the remaining legs are all present although rudimentary. In the second zoea the appendages are remarkably backward in development, and the antennules and legs still unjointed whilst there is as yet no palp to the mandible. The megalopa and crab stages are easily distinguishable in all three species.

A description of the larval stages of these three crabs is given below. Specimens of all the zoea and megalopa stages were procured from the plankton and compared with the reared forms. These were kept until they cast their skins, and in all cases the numbers of larval stages and their structure were exactly like those which were reared. In all these there were found to be two zoeal stages and one megalopa, the megalopa changing into the young crab.

OXYRHYNCHA.

MAIDÆ.

INACHINÆ.

Genus *Inachus*.

Inachus Dorsettensis (Pennant) is perhaps the commonest of all the Spider Crabs in the Plymouth district, living on the sea bottom from beyond the Breakwater on almost all the dredging and trawling grounds. It is trawled abundantly by the *Salpa* in Plymouth waters, and breeds all the year round. Berried females are found from January to December, and so also are the larval stages in the plankton. In 1926 a maximum of these larval stages was noted in November, but large numbers may be seen in any other month. The eggs are reddish orange when first extruded and remain hidden in the pouch until they are nearly ready to hatch, when the colour changes to a dull pale yellowish brown and the pouch opens slightly as the eggs occupy more space. The orange-red colour is due to the yolk, which disappears when the larva is ready to hatch. The eggs certainly take some weeks to hatch, probably some months, and enlarge considerably, being nearly twice the original size when ready to hatch. Breadth of early stage, 0.48 mm. ; late stage, 0.72 mm. When one batch of eggs has been hatched another frequently takes its place, but these have not been hatched out in the Laboratory.

The berried female was placed in a plunger jar, and the eggs hatched out, when the larvæ were transferred to a fresh plunger jar, aerated aquarium and small glass dishes. All these were fed on fresh oyster larvæ and thrive well. The pre-zoea moved about for some hours but did not feed, soon cast its cuticle, and the first zoea appeared.

The following dates show the length of time taken for changing into the different stages. These are quite typical, other batches being much the same:—Pre-zoea to first zoea, 21/7/26; changed to second zoea, 26/7/26; changed to megalopa, 6/8/26. If the aquarium was not congenial it might take longer. Young crabs from the megalopa procured from the plankton took various times to change, from about a fortnight to more than a month. These were placed separately in small glass dishes and fed on small bits of mussel. If more than one were put into any dish the stronger specimen would invariably eat the weaker until only one was left.

The colour is the same from pre-zoea to last zoea. These have a yellowish appearance, the body being pale yellow almost all over, the colour, however, not reaching the greater part of the dorsal spine nor the spines and tips of the antennules, antennæ, maxillipedes, and telson. The eye is a deep blackish brown with a superficial splashing of yellow, and the yellow tends to become orange in the region of the stomach. Bright orange chromatophores occur at the base of the dorsal spine posteriorly, the side of the first abdominal segment between the eyes, on the mandible, above the maxillipedes and on the second maxillipede, and a diffuse pinkish tinge is to be found round the fore part of the body under the carapace. Blackish brown chromatophores are present with the red pigment at the base of the spine, between the eyes and, separately on the carapace and ventrally on the abdominal segments two to five and at the base of the telson. This general scheme of colour may be intensified or the reverse by changes in the chromatophores, some even tending to disappear, so that it is not possible to lay down any hard and fast rule. The main colour is pale yellowish with pink in parts with orange-red and black spots, the most conspicuous of the red spots being at the sides of the first abdominal segment.

The *pre-zoea* (Plate I, Fig. 1) first hatched in March, others hatched at intervals until November. About 1.9 mm.* in length. It is, however, difficult to measure accurately, as when alive it is rarely straight and when dead it contracts immediately. The cuticle encloses the first zoea; dorsal spine of the carapace folded down and retracted underneath; first and second maxillipedes free from the body but enclosed in sheaths

* All measurements of the body length are taken from the front of the head to the tip of the telson fork (in the pre-zoea exclusive of embryonic spines). Spines are measured from base to tip.

with the terminal setæ retracted. Antennule (Plate I, Fig. 4) provided with two long spiny setæ, very flat, one about a third longer than the other and altogether stouter. Antenna (Plate I, Fig. 5) with four long spines coming from the same base enclosing the exopodite; flagellum and spinous process enclosed in separate simple sheaths. Telson (Plate I, Fig. 6) provided with the usual seven spines each side, six long and setose, the fourth from the side non-setose and short enclosing the terminal spine of the fork of the zoea.

Having cast the embryonic cuticle after several hours the first zoea appears.

The first zoea (Plate I, Fig. 7), about 2.4 mm. in length. Dorsal spine, 0.72 mm., curved gently backwards, no rostral nor lateral spines on the carapace. Midway between the dorsal spine and the front of the head is a slight protuberance. Eyes large, and sessile; antennule uniramous with two aesthetes and two spines; antenna with spinous process and exopodite very long; spinous process 0.64 mm. in length; exopodite hardly so long; both spiny at the tips, exopodite with two large spines slightly behind the centre. Flagellum (endopodite) unjointed, between the two processes, about 0.16 mm. in length. Mandibles bilobed and heavy with thick teeth; first and second maxillæ of the usual type. First and second maxillipedes armed with four long setose spines, the first with a five-jointed endopodite, the second with one three-jointed. Third maxillipede bilobed, but quite rudimentary and bearing a gill. First leg chelate, but also rudimentary with a gill; remaining legs only long buds, the second and third with gills. Pleopods show as small buds on the second to the fifth abdominal segments. Carapace bordered postero-laterally with small spines. Abdominal segments each with a couple of hairs dorsally, the second with a hooked spine on each side, and the third to the fifth with a long spine posteriorly each side. There are six abdominal segments, including the telson which has long forks with one large spine laterally on the outer margin each side and six setose spines inside the fork. Very minute spicules round the points of the fork.

The second zoea (Plate II, Fig. 1), much like the first but easily recognisable by its long pleopods, six setæ on the maxillipedes, and stalked eyes. Only slightly larger than the first, about 2.9 mm. in length. Dorsal spine smaller, 0.64 mm. in length. Antennules and antennæ have progressed little. Antennule unsegmented; antennal flagellum longer, although still unsegmented. Mandibles (Plate II, Fig. 4) with no palp; maxillæ and maxillipedes have progressed in the usual way. Legs still unsegmented, but larger and pleopods long, otherwise the abdomen has altered little, there being still only six segments including the telson, the latter having hardly altered at all.

The megalopa (Plate III, Fig. 1), which comes from the second zoea, has a peculiar feature, characteristic of both the British species of *Inachus* and probably generic, in the bicornuate rostrum. Body, 1.6 mm. in length, yellowish with brownish splashes and some red and black chromatophores. In common with all the larval Oxyrhyncha known the second to the fifth walking legs have slender pointed tips. In common with Macropodia, *Inachus* has the sixth abdominal segment fused with the telson throughout its life, and thus the megalopa of *Inachus Dorsettensis* still has only six abdominal segments and it has only four pairs of pleopods, the second to the fifth, the sixth pair being represented by the faintest buds. It swims about vigorously by means of its setose pleopods, the maxillipedes now being entirely used for eating purposes. Carapace with rostrum sticking straight out composed of two lateral pointed horns and on the dorsal surface several more or less pointed spinous processes, notably two behind the eyes, one just behind them in the centre, and three posteriorly. Eyes with fairly long stalks, antennule with a two-jointed base and two simple branches, the longer bearing a bunch of aesthetes, antennæ consisting of a base and the jointed endopodite with a blunt short stump representing the exopodite; spinous process completely disappeared; mandible has a small palp. Maxillæ and maxillipedes now of the usual crab structure, the third maxillipedes being completely formed; first legs chelate, remaining four with long and pointed extremities with fine spicules at the tips and all these legs are crab-like. First abdominal segment with no trace of pleopods, the second to the fifth bearing pleopods consisting of a large outer setose and small inner simple branch, each setose branch with eight setæ. Telson squarish with rounded edges. At the posterior dorsal edges of the first abdominal segment are two hairs, on the second segment two hairs and a pair of long lateral spines, on the third two hairs and two long spines outside them, on the fourth and fifth two long spines laterally, two dorsal spines and two pairs of hairs, and on the second is a median spine dorsally (Plate II, Fig. 10).

The megalopa changes into the first crab stage, 0.96 mm. across the carapace, with a bicornuate rostrum 0.16 mm. in length. Directly the young crab emerges it tries to find something with which to dress up, and is wonderfully successful in making itself as inconspicuous as possible by means of pieces of weed and debris placed on the curved spines and hairs which are present all over its body and legs. Eyes with long stalks; carapace with several protuberances. Legs long. Altogether the crab has a characteristic appearance easily recognisable, and, after two more moults, 1.28 mm. and 2 mm. respectively across the carapace, the young crab has the usual distinctive character in the four knobs on the carapace behind the eyes. The tips of the fourth and fifth walking legs have two

blunt thorn-like teeth, which distinguish them from *Macropodia* which has more than two and not so large. Unfortunately the young crab nearly always devoured most of the cast skin, so that it was not possible to make a drawing of the whole of it.

The only other species of *Inachus* in the Plymouth district is *Inachus Dorynchus*. This has also been reared in the Laboratory from the egg to the second and last zoea, but not as yet to the megalopa, which has, however, been found in the plankton and kept until it changed into the young crab. The stages in *I. Dorynchus* are very like *I. Dorsettensis* with certain distinguishing marks, notably the larger size. The two species both have the outstanding features which they share with *Macropodia* in the absence of rostral and lateral spines in the carapace in the zoea, and the sixth segment fused with the telson in all late stages. The zoea of *Inachus* can be distinguished from *Macropodia* by the very large lateral spine on the telson which is much smaller in *Macropodia*, the megalopa and young stages being easily recognised by their rostra.

Genus *Macropodia*.

Macropodia longirostris (Fabricius) is very nearly as common as *Inachus Dorsettensis*, occurring in the same situation and also breeding all the year round. The eggs are borne in the same way and are of the same colour, changing from reddish orange to a dull pale yellow and also increasing in size. Early eggs 0.55 mm. across, later eggs 0.6 mm. They take some weeks, possibly some months, to hatch, and as in *Inachus* when one batch is hatched another may take its place at once.

The eggs were hatched in the same way as *Inachus*, and the newly hatched larvæ separated into various vessels. Most of them were fed on *Teredo* larvæ, some on *Pomatoceros*, and others on oyster larvæ, the latter food giving out before rearing was complete. Some first zoeæ of *Portunus depurator* were placed in some of these vessels, and were certainly eaten by the second zoea and megalopa if not by the first. The first zoea of *Inachus Dorsettensis* was also eaten by the megalopa.

The following dates show about the usual time taken for reaching the megalopa stage:—Pre-zoea and first zoea hatched 6/10/26, second zoea from first 14/10/26, megalopa from second 4/11/26. This is probably a longer time than is natural for the second zoea to change to megalopa, judging from *Inachus* and *Maia*.

The pre-zoea (Plate I, Fig. 2), about 2.4 mm. in length, when hatched from the egg moved actively for some hours in the same way as *Inachus*, finally getting rid of its embryonic cuticle and emerging as the first zoea. In colouring it is extremely like *Inachus*, diffuse yellow with red and black, the red being specially conspicuous on the sides of the first ab-

dominal segment. In shape it is also very similar to *Inachus Dorsettensis*, a difference being seen in the telson under the cuticle, the lateral spine being much smaller than in *Inachus*. The embryonic spines on the antennules and telson are shorter than in *Inachus*.

The first zoea (Plate I, Fig. 8) is also very like *Inachus* at a first glance, and they have many features in common. The difference in colour is slight, but *Macropodia* seems to be somewhat darker. The length of the first zoea is about 2.7 mm., dorsal spine is longer than in *Inachus*, measuring 0.96 mm. in length; telson also longer. The edge of the carapace has small spines ventro-laterally, and has two hairs dorsally behind the spine. Antennule with two *æsthetes* and a short spine; antenna with a long spiny exopodite, a spinous process of about the same length and a short flagellum. Mandibles, maxillæ, and first and second maxillipedes are of the usual type, the third maxillipedes and legs being present but rudimentary. Pleopods show as small buds from the second to the fifth segment. On each of the abdominal segments are a couple of small hairs dorsally. On the second segment is a lateral knob each side, and laterally on the third to the fifth segment are long pointed spines. Telson with one lateral spine, which is much smaller than in *Inachus*, and six setose spines inside the fork.

The second zoea (Plate II, Fig. 2), about 3 mm. in length. Six, rarely five, spines to the first and second maxillipedes; eyes stalked. Dorsal spine about the same length or rather shorter than in the first zoea. Antennule unjointed with five *æsthetes*, one very long and curved, and a spine; flagellum of antenna long and faintly jointed. Mandible with no palp, maxillæ and maxillipedes have progressed in the usual way, the third maxillipedes being quite rudimentary but bilobed, the first leg large and chelate and the remaining legs long and pointed. None of the legs are truly segmented. Abdominal segments still five plus the telson, and each bears dorsally a pair of hairs. Second segment with a curved knob on each side and postero-laterally a very small spine, third to the fifth each bearing laterally a short and a long spine. Second to the fifth segment with long pleopods, each composed of a long and short ramus, the long one bearing eight setæ. Telson almost exactly the same as in the first zoea.

The Megalopa (Plate III, Fig. 2), 2 mm. to 2.3 mm. in length, the width across with legs outstretched but slightly bent, about 4.8 mm. It has a habit, common in the group, of folding its legs tightly against the body while swimming with its abdomen outstretched. It is conspicuously speckled with chestnut brown, and has a brownish orange appearance when seen with the naked eye. It may be watched catching the zoea of *Inachus*, making a cage with its legs for it whilst it swims by means of its pleopods; finally tearing it to pieces and extracting the soft parts

(Plate III, Fig. 4). The megalopa of *Macropodia longirostris* (and the other known species of the genus) differs from that of *Inachus* in its smoothness and much less prominent armature of the abdomen; but, on the other hand, the prominences on the carapace are much more conspicuous and project as long blunt spines; particularly those behind the eyes and one in the centre. The rostrum is bent down so that the dorsal outline is nearly straight, the bend making the two sides somewhat thickened, so that on tilting the carapace slightly backward it may look three-lobed, a character emphasized in its near relative, *Macropodia rostrata*. Abdomen with two hairs at the posterior dorsal margin of each segment; telson rounded and the four pairs of pleopods each with eight setæ as in *Inachus*, there being a small inner non-setose lobe to each; fifth pair of pleopods represented by two minute protuberances behind at the base of the telson. Antennule jointed, bearing a bunch of æsthetes; antenna consists now of the usual endopodite with the remains of the exopodite as a blunt process. Small palp on the mandible and maxillæ and maxillipedes formed entirely for eating purposes. Legs fully formed, the first strongly chelate, the second to the fifth, ending in slender points with minute spicules. None of the reared megalopæ reached a crab stage, but specimens from the plankton were easily kept alive until they changed into young crabs.

The first young stage (Plate III, Fig. 5) is remarkably large to come from the megalopa, the legs having a stretch of several times the breadth of the body. The rostrum is bilobed, each lobe being squarish with three lateral prominences, and, as well as the body and legs, armed with long curled hairs. Like *Inachus* it immediately covers its body with any weed or debris that it can find and soon succeeds in hiding itself. First crab stage 1.28 mm. across the broadest part of the carapace; legs with a stretch of over a centimetre. The two hind legs are armed with seven or eight, usually seven, strong thorn-like teeth. Carapace with two prominent knobs behind the eyes and two behind in a straight line, one almost central, the other posterior. Abdomen tucked in under the body, and pleopods much reduced.

Of the other two species of *Macropodia* in the Plymouth district one, *Macropodia rostratus*, has been hatched from the egg and the pre-zoea and first zoea procured, the latter corresponding very well with Cano's figure (op. cit.). The second zoea was found in the plankton (differing from *M. longirostris* in the long dorsal spine and very long branches to the antennæ), and kept until it changed to the megalopa. This (the megalopa) again agrees well with Cano's figure (differing from *M. longirostris* in its rostrum, which is conspicuously three-lobed). A young crab which emerged from the megalopa out of the plankton also agreed with Cano's figure and that of Lo Bianco (op. cit.). This young crab differs

from *M. longirostris* in the shape of its rostrum and numbers of thorn-like teeth on the extremities of the two last legs, but above all by its much smaller size and stretch of legs. Another megalopa from the plankton gave rise to a third form of Macropodia, almost certainly *M. Egyptia*, intermediate in size between *M. longirostris* and *M. rostratus*, with a differently shaped rostrum and different terminal joints to the two last legs.

MAIINÆ.

Genus *Maia*.

Maia squinado (Herbst) has been already reared by Schlegel (1911) as far as the first young stage, but as he gives no figures it is certainly worth while figuring and re-describing the larvæ of this well-known species.

This large Spider Crab is extremely common in the Plymouth district and abundantly present in the trawl. Its chief breeding season appears to be from July to September, although berried crabs may be taken occasionally earlier or later. They are recorded from March to June in the Plymouth Invertebrate Fauna (1904). The first brought to me in 1926 was in July and the last was in September. From July to October the larvæ were present in the plankton, chiefly first and second zoea with an occasional megalopa. In November all the female crabs brought in had shed their eggs. Schlegel states that the extended eggs are carried for at least six months. They are at first bright orange-red and hidden by the large abdomen, but as they get older they become nearly black and much larger, forcing out the abdomen so that they can be seen projecting from the body. Early eggs, 0.64 mm.; late eggs, 0.72 mm. The berried female with eggs nearly ready to hatch was kept in a tank with running sea-water. When the pre-zoea was about to emerge the water was turned off and the larvæ swarmed upwards towards the light, and could be drawn off with a pipette and placed in various vessels. As with *Inachus* and *Macropodia* the larvæ were only reared as far as the megalopa, but the last zoea from the plankton was reared over three crab stages.

The larvæ of *Maia* as representing the Maiinæ differ much from *Inachus* and *Macropodia*, which represent Inachinæ. In common they have only two zoeal stages and consequently have advanced larvæ, the megalopa having pointed tips to the legs, two to five; but they differ in that the zoea of *Maia* has lateral and rostral spines on the carapace, as well as a dorsal, and the telson has three lateral spines, whereas *Inachus*

and Macropodia have only the dorsal spine on the carapace and one lateral spine on the telson.

The colour of the larvæ of *Maia* is very characteristic, being a dark greenish brown with chromatophores of yellow and black covering the body. The zoeæ were reared on Oyster, *Teredo*, and *Pomatoceros* larvæ, the megalopa and crabs on bits of mussel. It is somewhat remarkable that although the zoeal stages are fairly large the actual crab emerging from the megalopa is extremely small, very much smaller than some of the crabs which in the adult stage are of a much smaller size than *Maia*.

The following dates show typical times for the different larval stages:—

Pre-zoea and first zoea hatched 11/8/26; changed into second zoea, 16/8/26; changed into megalopa, 20/8/26.

The eggs hatch out as pre-zoeæ, which remain active for several hours and move in the usual way, finally getting rid of the embryonic cuticle and emerging as first zoeæ.

The pre-zoea (Plate I, Fig. 3), about 2.5 mm. in length. Very large eyes and long embryonic spines of the same number and character as those of *Inachus* and *Macropodia*, and resembles these forms closely.

The first zoea (Plate I, Fig. 9), about 2.9 mm. in length; backwardly curved dorsal spine, lateral spines and a rostral spine, all short. The form of this zoea is characteristic and unmistakable in the Plymouth plankton. Pleopods present as distinct buds on the abdominal segments 2 to 5, all of which as well as the first have small lateral spines increasing in size to the fifth. Sixth segment not yet separated from the telson. Postero-lateral edge of carapace with a few long hairs, but the margin not toothed. Colour a general olive-green, composed of a yellowish green ground with black chromatophores at the posterior base of the dorsal spine, in front of the head, in the mouth parts, on the basipodites of the maxillipedes, and on the lateral portion of the carapace extending along the intestine for about a quarter of its length, and black chromatophores ventrally on all the abdominal segments as far as the fifth. Telson and spines of the carapace colourless. The same colour is continued in the second zoea and megalopa. No trace of red in any stage.

Antennule with three æsthetes; antenna with a fairly long serrated spine, an exopodite about half its length bearing three spines terminally, and an unjointed flagellum (endopodite) not quite so long as the exopodite. Thus the antenna differs much from *Inachus* and *Macropodia* where the exopodite is almost the same length as the spinous process. Mandibles, maxillæ, and maxillipedes of the usual form, the first and second maxillipedes with four long setæ, the third rudimentary and small. Legs all present, but rudimentary. Each abdominal segment with a pair of small hairs dorsally and posteriorly. Telson peculiarly straight and not spread

out. Laterally it bears three spines, the most anterior being the largest. Six spines internally to the fork.

The second zoea (Plate II, Fig. 3) not much bigger than the first, about 3 mm. in length. It has now seven abdominal segments including the telson and five pairs of pleopods on the second to the sixth segments, all long except the fifth pair, which are still buds. Dorsal spine shorter; eyes stalked. Antennule unjointed; antennal flagellum longer but unjointed, and mandible without palp. First and second maxillipedes with six setæ (rarely five). Third maxillipede and legs, although larger, quite rudimentary and unjointed. Telson hardly altered. The second zoea is thus in a backward state compared with its relative *M. verrucosa*, described by Cano, although it is the last zoea, and changes into a megalopa.

The megalopa (Plate III, Fig. 3), rather long for its breadth with the same characteristic colouring as the zoea, 2.4 mm. in length, with a long carapace measuring 1.4 mm. The legs rather short. Carapace with no spines but many protuberances, rostrum bent down and indented laterally, giving the appearance of the three teeth described by Schlegel. Tips of second to fifth legs pointed and armed with short spines, not with only minute spicules as in *Inachus* and *Macropodia*. Seven abdominal segments including the telson, which is nearly square, the last pleopods (sixth abdominal appendages and fifth pleopods) bearing five setæ, the others eight. Antennule with a base of two joints and two short branches, one ending in a bunch of aesthetes. Antenna has lost both exopodite and spinous process; endopodite jointed in the usual way. A very faint prominence represents all that is left of the exopodite. Mandible with a small but distinct palp.

The megalopa obtained from the plankton turned into a crab, and this lived as far as three young stages.

The first crab stage is exceedingly small, only 1.28 mm. across the carapace (Plate III, Fig. 10), of a roundish shape, with compact rather short legs and a pale brownish colour. Five lateral marginal spines on the carapace and a pointed rostrum with a crenulated margin. This does not agree with Schlegel's description, who says it is in all respects like the adult, for even in the third young stage the rostrum is not bifurcate.

The second crab stage, 1.9 mm. across the carapace, *the third* 2.5 mm. across. From the first the small crab seeks to cover itself with extraneous matter and usually is completely hidden.

COMPARISON OF LARVAL STAGES OF *I. DORSETTENSIS*, *M. LONGIROSTRIS*, AND *M. SQUINADO*.

We can now compare the three crabs representing three distinct genera and two distinct sub-families.

All three agree in having far advanced larvæ, only two zoeal stages and one megalopa before the crab stage is reached, and because of this the first zoea already shows pleopods and antennal flagellum and far advanced rudiments of the legs. There are no feelers on the extremity of the last leg of the megalopa. The representatives of the two sub-families differ in the number of abdominal segments in the second zoea, megalopa, and crab, there being the usual seven in *Maia* and only six in *Inachus* and *Macropodia*, and in consequence there are five pair of pleopods in *Maia* and only four in *Inachus* and *Macropodia* (the fifth pair occurring in these as the tiniest buds). The carapace differs in there being dorsal, rostral, and lateral spines in the zoea of *Maia* and only a dorsal spine in *Inachus* and *Macropodia*, and the telson differs in having three lateral spines in *Maia* and only one in *Inachus* and *Macropodia*. The antenna differs in the exopodite of *Maia*, being hardly more than half the length of the spinous process, and ending in three spines, whilst in *Inachus* and *Macropodia* the exopodite is pointed, and almost equal in length to the spinous process. In the megalopa the differences are also large. In *Maia* there are no spines on the carapace, only rounded prominences, and the last joints of the second to the fifth walking legs bear short spines, whereas in *Inachus* and *Macropodia* there are distinct spines on the carapace, and the last joints of the legs are long and pointed and the tips only armed with minute spicules. The number of abdominal segments also separate them at once. The young crabs are easily distinguishable, as they bear unmistakable resemblances to the adult.

Inachus and *Macropodia* can be distinguished from one another with difficulty in the zoeal stages, but one character is quite distinct and reliable, and that is the form of the lateral spine in the telson which in *Inachus* is large and solid and in *Macropodia* is slender and small. The megalopæ are quite distinct, *Macropodia* having a bluntly pointed rostrum bent down so that dorsally the margin looks almost straight, *Inachus* having the rostrum composed of two distinct straight horns. The young crab stages are distinguishable by the shape of the rostrum and the terminal joints of the two last legs, the rostrum of *Macropodia* being bifurcate with squarish lobes, that of *Inachus* bicornuate, and the last two legs in *Macropodia* having several (never less than three) conspicuous thorns on their last joints, *Inachus* having only one or two.

The last zoea of all three crabs are backward in development when compared with *Maia verrucosa* described by Cano and with several other genera described by him from the Mediterranean. He found that the last zoea in these all had jointed antennules, a palp on the mandible and jointed, although rudimentary legs. To this type of zoea he gave the name *Metazoea*. Cano never saw the second zoea of *Macropodia* and *Inachus*, although he figures the first zoea. It is interesting to find that

these genera are much further back in the development of the second zoea than those others described by Cano, and it is of special interest to find that even in members of the same genus the development is so different, *Maia verrucosa* being much further advanced than *M. squinado* in the same stage.

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EXPLANATION OF PLATES.

The figures are drawn to three scales : the pre-zoea and zoea to Scale A, the megalopa and carapace of megalopa and crabs to Scale B, half the scale of A, and the appendages and details of telson abdomen and rostrum to Scale C, three times the scale of A.

PLATE I.

- FIG. 1.—Pre-zoea of *Inachus Dorsettensis*, about 1.9 mm. long (Scale A).
- FIG. 2.—Pre-zoea of *Macropodia longirostris*, about 2.4 mm. long (Scale A).
- FIG. 3.—Pre-zoea of *Maia squinado*, about 2.5 mm. long (Scale A).
- FIG. 4.—Antennule of pre-zoea of *Inachus Dorsettensis* (Scale C).
- FIG. 5.—Antenna of same (Scale C).
- FIG. 6.—Telson of same (Scale C).
- FIG. 7.—First zoea of *Inachus Dorsettensis*, about 2.4 mm. long (Scale A).
- FIG. 8.—First zoea of *Macropodia longirostris*, about 2.7 mm. long (Scale A).
- FIG. 9.—First zoea of *Maia squinado*, about 2.9 mm. long (Scale A).

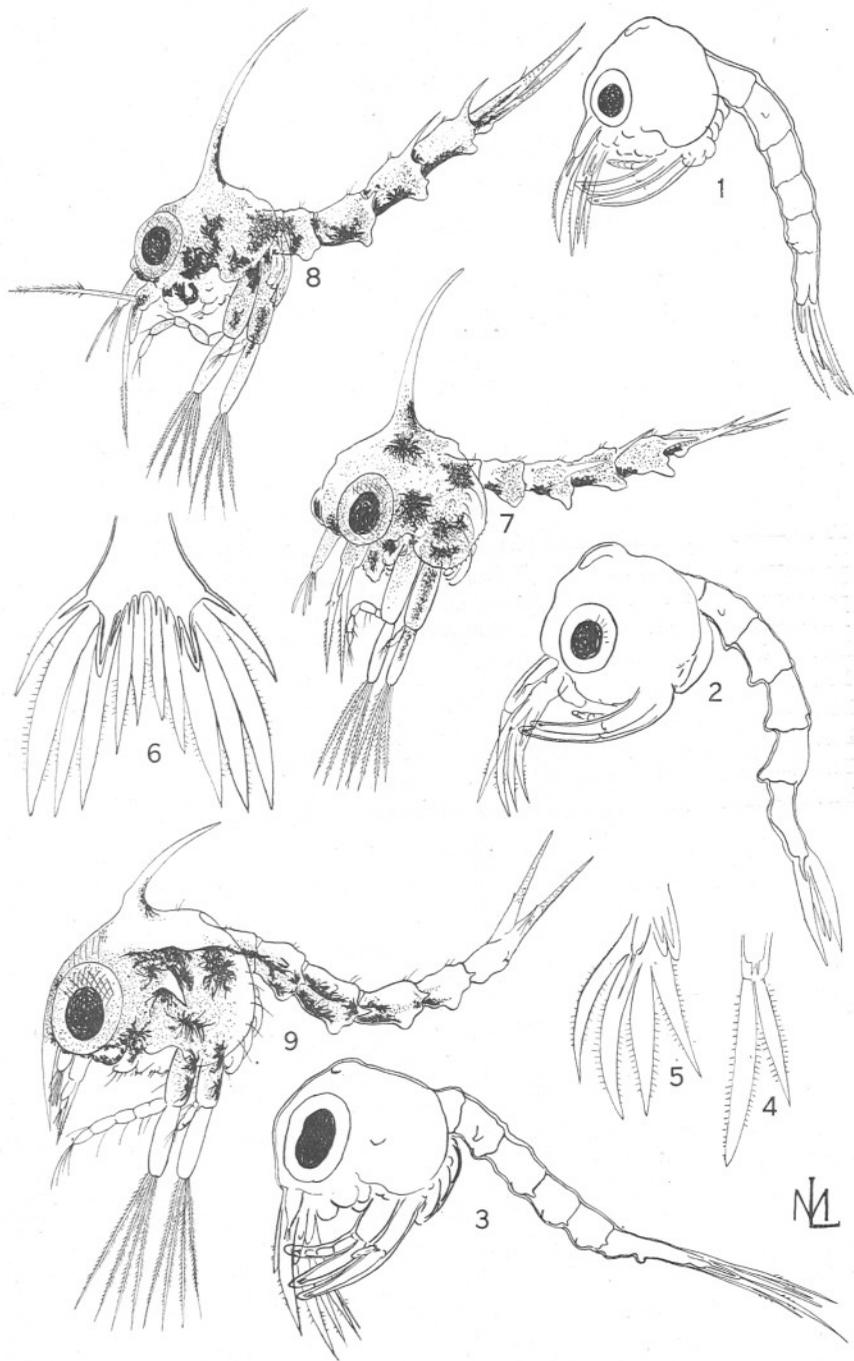


PLATE II.

- FIG. 1.—Second zoea of *Inachus Dorsettensis*, about 2.9 mm. long (Scale A).
FIG. 2.—Second zoea of *Macropodia longirostris*, about 3 mm. long (Scale A).
FIG. 3.—Second zoea of *Maia squinado*, about 3 mm. long (Scale A).
FIG. 4.—Mandible of second zoea of *Inachus Dorsettensis* (Scale C).
FIG. 5.—First Maxilla of same (Scale C).
FIG. 6.—Second Maxilla of same (Scale C).
FIG. 7.—Telson of same (Scale C).
FIG. 8.—Telson of *Macropodia longirostris* (second zoea), (Scale C).
FIG. 9.—Telson of *Maia squinado* (first zoea) (Scale C).
FIG. 10.—Abdomen of megalopa of *Inachus Dorsettensis* (Scale C).

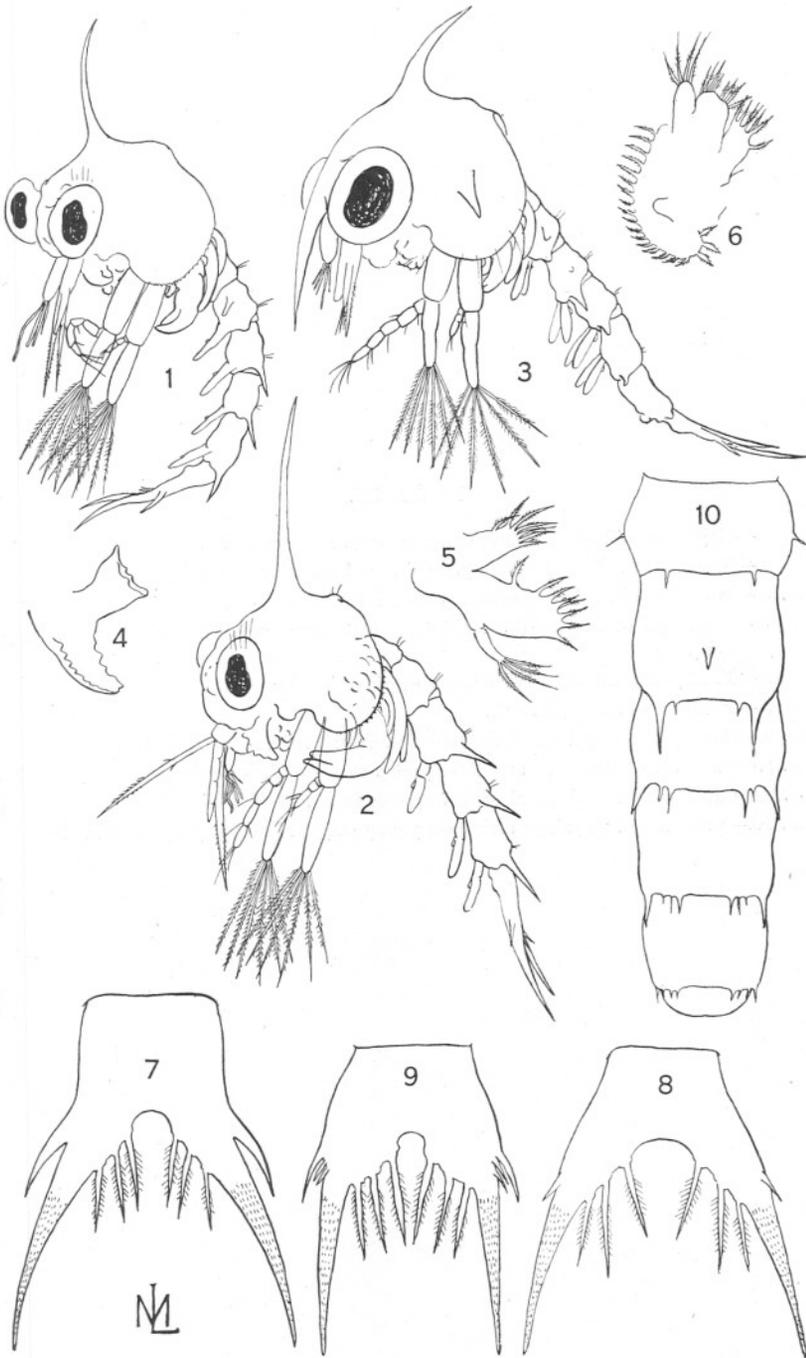


PLATE III.

- FIG. 1.—Megalopa of *Inachus Dorsettensis*, 1.6 mm. long (Scale B).
FIG. 2.—Megalopa of *Macropodia longirostris*, 2.3 mm. long (Scale B).
FIG. 3.—Megalopa of *Maia squinado*, 2.4 mm. long (Scale B).
FIG. 4.—Megalopa of *Macropodia longirostris* catching a zoea of *Inachus Dorsettensis* (Scale B).
FIG. 5.—First young stage of *Macropodia longirostris* (Scale B).
FIG. 6.—Rostrum of same (Scale C).
FIG. 7.—Carapace of megalopa of *Inachus Dorsettensis* from side (Scale B).
FIG. 8.—Carapace of megalopa and three young stages of *Inachus Dorsettensis* (Scale B).
FIG. 9.—Carapace of megalopa of *Maia squinado* from side (Scale B).
FIG. 10.—Carapace of megalopa and three young stages of *Maia squinado* (Scale B).

PLATE III.

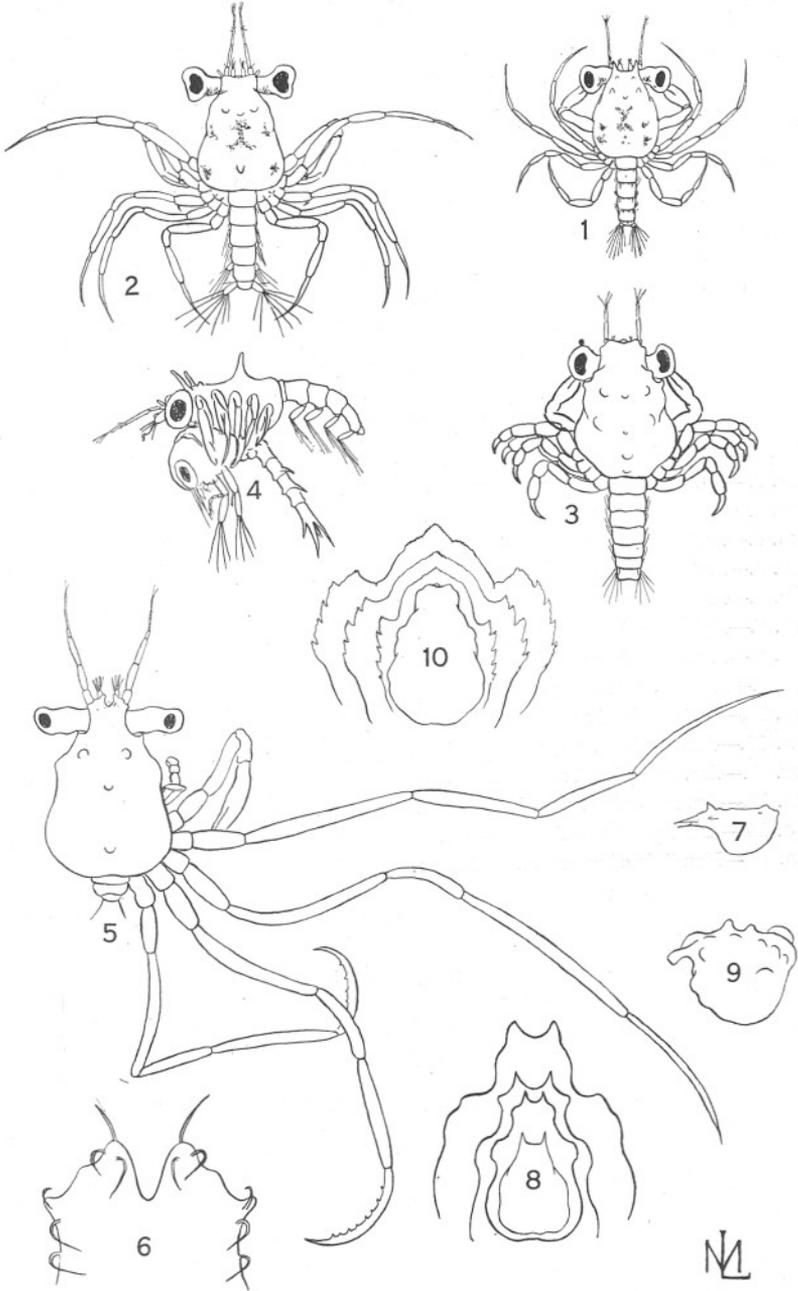
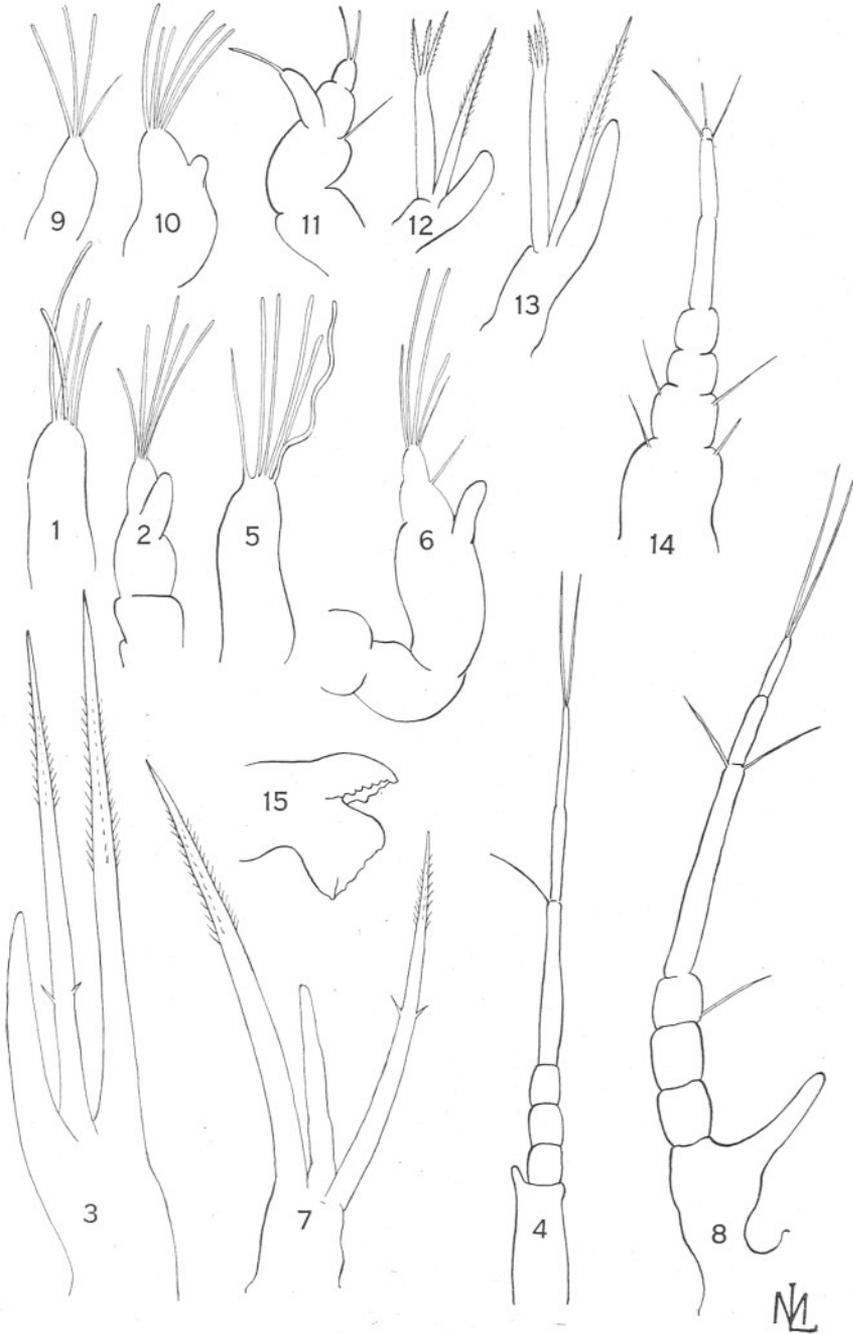


PLATE IV (all Scale C).

- FIG. 1.—Antennule of second zoea of *Inachus Dorsettensis*.
FIG. 2.—Antennule of megalopa of same.
FIG. 3.—Antenna of second zoea of same.
FIG. 4.—Antenna of megalopa of same.
FIG. 5.—Antennule of second zoea of *Macropodia longirostris*.
FIG. 6.—Antennule of megalopa of same.
FIG. 7.—Antenna of second zoea of same.
FIG. 8.—Antenna of megalopa of same.
FIG. 9.—Antennule of first zoea of *Maia squinado*.
FIG. 10.—Antennule of second zoea of same.
FIG. 11.—Antennule of megalopa of same.
FIG. 12.—Antenna of first zoea of same.
FIG. 13.—Antenna of second zoea of same.
FIG. 14.—Antenna of megalopa of same.
FIG. 15.—Mandible of second zoea of same.

PLATE IV.



Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

On Nocturnal Colour Change in the Pea-crab (*Pinnotheres veterum*).

By D. Atkins.

Nature, Vol. 117, 1926, pp. 415-416.

Two pea-crabs, from the branchial chamber of *Ascidia mentula*, were seen to hide during the day beneath fragments of sodden paper. At night they emerged, the female at dusk, the male an hour or more later, and were very active. Activity in the dark was accompanied in the male by loss of colour; the female, in this case having no definite colour, suffered no appreciable change. The male was golden brown, shaded with dark brown, the colour being due to orange and dark brown chromatophores, now fully expanded and their pigment diffuse. In the dark it became pallid and transparent, some faint yellow diffuse pigment only being visible; the gut contents showed black, the testes white. This loss of colour is due to the retraction of the pigment in the chromatophores induced by the onset of darkness. Of the two pigments the orange had the quicker rate of flow, and is probably lodged in a smaller cell.

The crabs when put in the dark during the day sometimes reacted as at night, taking forty to sixty minutes. When uncovered the male took the same time to regain its colour.

D. A.

A Quantitative Consideration of Some Factors Concerned in Plant Growth in Water. Part I. Some Physical Factors.

By W. R. G. Atkins.

Conseil Permanent Int. Explor. Mer. Journ. du Conseil, Vol. I, Pt. 2, pp. 99-126, 5 figs., 1926.

The paper is a review of work dealing with submarine illumination and algal distribution, experimental studies on algal distribution, measurements of submarine illumination, and of total submarine radiation. The importance of thermal stratification of the water has been discussed in relation to its importance as limiting the circulation of nutrient salts. A bibliography of forty-two titles is included.

W. R. G. A.

A Quantitative Consideration of Some Factors Concerned in Plant Growth in Water. Part II. Some Chemical Factors.

By W. R. G. Atkins.

Conseil Permanent Int. Explor. Mer. Journ. du Conseil, Vol. I, Pt. 3, pp. 197-226, 19 figs., 1926.

This paper is a review of work on the minor constituents of water, fresh and salt, in relation to plant growth. A bibliography of fifty-six titles is included. The subjects discussed include carbon dioxide assimilation and the alkalinity of sea-water, similar data for fresh water, and the seasonal changes in temperature, electrical conductivity, hydrogen ion, phosphate and silicate, concentrations. Analyses of the nitrate content of sea-water are also given, and it is shown that the deep waters of the ocean act as a reservoir for such nutrient salts, which are used up by the phytoplankton only in the well-illuminated surface layers. Though deficiency of phosphate apparently limits plant production in fresh water and in sea-water as a general rule, it appears that in the latter, nitrate is also, at times, completely used up. In its absence phosphate begins to accumulate. Estimates based on the phosphate depletion lead to the value of 1400 metric tons per sq. kilometre for the wet weight of the phytoplankton crop in the English Channel, depth, 70 metres.

W. R. G. A.

The Distribution of Red Algæ in Relation to Illumination.

By W. R. G. Atkins and H. H. Poole.

Nature (London), 118 (2961), pp. 155-156. 1926.

The reduction in the illumination in water may be considered as due to the selective absorption of the water, non-selective absorption due to gross particles in suspension, to the selective absorption or scattering due to very small particles and to the selective absorption due to tint in the water. Determinations of the coefficient of absorption were made by means of a photo-electric cell sensitive mainly to the blue, and a very great reduction in illumination due to particles in suspension became evident. Since fresh water is almost invariably more turbid than salt water it results that at the depth at which, in the sea, red algæ flourish, in fresh water the illumination is too low for plant life. There is therefore no general development of red algæ in fresh water.

W. R. G. A.

A Buffer Mixture for the Alkaline Range of Hydrogen ion Concentration.**By W. R. G. Atkins and C. F. A. Pantin.***Biochem. Journ.*, 1926, *Vol. XX* (1), pp. 102-104.

Clark's 0.2 M boric acid solution, made 0.2 M with respect to KCl also, was used with 0.2 M Na₂CO₃. The range for ninety-five of the former to five of the latter, and with the proportions reversed, is pH 7.44-10.85 at 16° C. Phenolphthalein may be used up to pH 10.5 and Sørensen's alizarine yellow R, sold as alizarine yellow G or *p*-nitrobenzene-azo-salicylic acid, from pH 10.1 to beyond the range of the mixtures given.

W. R. G. A.

Photo-Electric Measurements of Illumination in Relation to Plant Distribution. Part I.**By W. R. G. Atkins, Sc.D., F.R.S., and H. H. Poole, Sc.D.***Sci. Proc. Roy. Dublin Soc.*, *Vol. XVIII, N.S.*, pp. 277-298, 1 fig., 1926.

Almost simultaneous measurements were made of the illumination in a wood and in the open by means of two photo-electric photometers and apparatus previously described. The illumination in the shade may be correlated with its flora by expressing it as a percentage of the diffuse light in the open, the latter being measured with photometer horizontal or inclined to obtain the maximum reading. Data are presented concerning the distribution of various plants in terms of this daylight factor, which may be as low as 1-2 per cent on the floor of a wood of mixed deciduous trees in autumn and less than 0.06 per cent in heavy shade under rhododendron. The photo-electric cells were sensitive to the blue portion of the spectrum. Such values, 1-2 per cent, as are found in the wood are also found at depths of about 22 to 29 metres in clear water, some miles off the Cornish coast.

W. R. G. A.

The Colorimetric Estimation of Minute Amounts of Compounds of Silicon, of Phosphorus and of Arsenic.**By W. R. G. Atkins and Edith G. Wilson.***Biochem. Journ.*, 1926, *Vol. XX* (6), pp. 1223-1228.

The reagents of Diénert and Wandenbuleke for silicate give no colour with moderate amounts of phosphate, arsenate, or -ite; they may be used for the determination of silicate in natural waters. The method of Denigès for phosphate may be used for arsenate also, but not for -ite; the method is not vitiated by the presence of silicate in natural waters.

Bell and Doisy's method for phosphate is not as delicate as that of Denigès; it may be used for arsenate, but gives irregular results with arsenite. Pouget and Chouchak's reaction for phosphates is not given by arsenites, and only faintly by arsenates unless warmed. Save in so far as free phosphate is present the Denigès reaction is not given by glycerophosphate, triphenylphosphate, or tricresylphosphate. The reaction is not given by vanadates, by tungstates, or by phosphotungstates. With the last a purple tint is slowly produced, but this is not a sensitive reaction.

W. R. G. A.

Report on the Experimental Work of Drs. F. D. White and C. M. Yonge at Plymouth during July and August, 1924 (Dept. Sci. and Industrial Research.) The Deterioration of Structures in Sea Water.

By G. Barger, F.R.S.

Sixth (Interim) Rept. Comm. Inst. C.E., 1926, pp. 9-13.

The investigation was mainly concerned with the determination of the toxicity of some inorganic salts and a large number of organic substances to *Teredo* larvæ. The results for the most active inorganic salts previously found by Dr. Yonge, viz. mercuric chloride, 1 : 300,000; zinc sulphate, 1 : 30,000; potassium antimonyl tartrate, 1 : 16,000, were confirmed by Dr. White. The latter began and Dr. Yonge completed an examination of 13 chloro-, bromo-, and iodo-arsines and arsenious oxides, related to phenarsazine. D.M. (10 chloro, 5 : 10 dihydro phenarsazine) is lethal in a concentration of 1 : 750,000. A few derivatives were up to twice as active, others considerably less so. Diphenyl chloro stibine was sometimes less active (1 : 600,000), diphenyl chloro bismuthine much less so (1 : 50,000).

Of other organic compounds without arsenic some acridine derivatives were lethal at 1 : 100,000, but for the majority the limit of dilution was below 50,000.

The above figures refer to larvæ from 7 to 11 days old; Dr. Yonge found that young larvæ (3 days old) were much more sensitive, and older ones less so.

Dr. Yonge confirmed the chemotaxis of *Teredo* larvæ by an extract of wood, discovered by Harington, and showed that the simultaneous presence of a poison in the tubes does not repel the larvæ, but merely kills them.

Three rafts with impregnated test pieces were put out inside the Breakwater.

G. B.

Influence of Temperature on Biological Processes.**By J. Belehrádek.***Nature*, Vol. 118, July 24th, 1926, p. 117.

The temperature coefficient Q_{10} of Van't Hoff and the thermal increment μ of Arrhenius do not hold good in the majority of biological reactions, because they vary with temperature. The effect of temperature on biological processes may be expressed—in the most cases—by the following formula :—

$$y = \frac{a}{x^b}$$

in which x is temperature in centigrade Celsius, y time which is necessary to accomplish a given reaction, a and b constants. This formula may be used for temperatures up to the optimum. The constant a indicates time at $+1^\circ$, the constant b is a temperature coefficient which does not vary with temperature. In its logarithmic form, the equation gives a straight line :—

$$\log y = \log a - b \log x.$$

It may be supposed that the constant b has a biological significance, which shall be explained in a further paper.

J. B.

Rays and Skates : A Revision of the European Species.**By R. S. Clark, M.A., D.Sc.***Fisheries, Scotland, Sci. Invest*, 1926, 1.

The geographical range of the species treated herein extends from the Moroccan coast to Greenland and Spitsbergen. The work which was begun at Plymouth with the detailed investigations of the southern species was extended and completed by similar investigations on the northern forms at Aberdeen. Twenty-three species are described and figured, of which one Ray from the Mediterranean is new. As the nomenclature has previously given rise to considerable confusion, detailed discussions have been included, and an attempt has been made to bring some precision to bear on the synonymy of the species. For the most part, the descriptions and figures have been taken from material, the greater part of which has been obtained in a fresh condition, while due regard has been paid in the diagnoses to the differences exhibited by examples of the same species in its different growth stages from widely separated localities. The large amount of material landed at British markets from this extensive area has facilitated this study and has added greatly to our knowledge of the life-history and distribution of the species.

Within this large area there are typical northern and southern forms, but no species can be said to occupy an exclusively intermediate range. The problem of distribution, therefore, resolves itself into a determination of the factors which limit the range of these northern and southern forms. Eleven species are taken in the English Channel, and nine of these occur also in the Mediterranean. In this latter area, three species—*R. poly-stigma*, *radula*, and *melitensis*—have not been recorded elsewhere. Of the Channel species *R. microcellata* and *R. marginata* have, so far, not been recorded from the North Sea or north of the Irish coasts. Of the more northern forms, *R. radiata* alone seems to spread its range southwards, though other three species—*R. linteæ*, *fyllæ*, and *nidrosiensis*—may be found with fuller knowledge to be distributed along the edge of the Atlantic slope. The species of most commercial value are *R. clavata*, the Thornback or Roker, and *R. batis*, the Blue or Grey Skate.

The text and plates are in separate volumes, and there is a useful bibliography.

R. S. C.

**On the Correlation of the Life-History of the Acephaline Gregarine,
Gonospora, with the Sexual Cycle of the Host.**

By C. C. Hentschel, M.Sc.

Parasitology, Vol. XVIII, No. 2, pp. 137-143, 1926.

The life-history of the acephaline gregarine, *Gonospora varia*, is shown to be very closely bound up with the sexual cycle of its host, *Audouinia (Cirratulus) tentaculata*. The parasites live in the cœlom among the developing genital products of the worm, and complete their life-history contemporaneously with the growth and maturation of the gametes. Thus the gregarines are small in the autumn, when the reproductive cells are only slightly developed; but grow in winter, forming in the early summer spores which are presumably shed with the worm's genital products, when reinfection probably takes place and the cycle recommences.

Occasionally, gregarines are found in segments containing no reproductive organs. In these circumstances they cannot complete their proper life-history, but remain stunted and unable to form spores, often causing, apparently, some pathological effect on the host. It would appear, then, that the gregarines cannot develop properly except in the presence of the gonads. It seems as though some substance may be formed that is essential for their growth. This substance may be closely connected with the ovaries or testes, if not actually secreted by them; in fact, we are possibly dealing here with something analogous to a hormone.

C. C. H.

Studies in Colour Changes in Fish. Pt. II. An Analysis of the Colour of the Dab. Pt. III. The Action of Nicotin and Adrenalin in the Dab. Pt. IV. The Action of Caffeine in the Dab, and a Theory on the Control of Colour Changes in Fish.

By H. R. Hewer, D.I.C., B.Sc.

Phil. Trans. Roy. Soc. London, B. Vol. 215, pp. 177-200, 1926.

The markings constituting the colour pattern of the dab are analysed. The chromatophores found in these markings are mentioned together with their size and number per unit area. This leads to a discussion of the appearance of certain markings under various conditions of coloured background. It is shown that the distribution and size of the chromatophores forms a "morphological" basis for nearly all these markings, but that their appearances cannot be accounted for wholly on these grounds. Microscopical investigation shows that differential contraction and expansion occur. The origin of this reaction is then investigated. The actions of nicotin and adrenalin are examined, but the reactions evoked by the use of these drugs are characterised by complete uniformity. Caffeine is then used and it is found that differential reactions can be produced in a certain percentage of individuals. It is finally suggested that a centre for the control of colour exists in the brain, and that the fish is sensitive to certain features of the environment, and "adapts" itself to them as well as it can within the limits of its morphological pattern.

H. R. H.

The Viscous Elastic Properties of Smooth Muscle.

By A. V. Hill, F.R.S.

Proc. Roy. Soc. Ser. B. Vol. 100, 1926, pp. 108-115.

Gasser and Hill found that the sudden release, during an isometric tetanus, of the skeletal muscle of a frog is followed by an instantaneous drop of tension, and then by a gradual redevelopment along a curve identical with that of the original rise when stimulation began. This observation has been repeated, both for quick releases and for quick stretches, on the smooth muscles of *Holothuria nigra*, in which the speed of contraction is less than 1/100 of that of a frog's striated muscle. The return to the tension characteristic of the new length is precisely similar in its time relations to the initial rise of tension.

It is concluded that the development of a contraction during stimulation, and its redevelopment after release, are due to the same process, viz. the formation of an organised molecular pattern, arranged in space whether of two or three dimensions in the fibres of the muscles. Such a molecular rearrangement, either on stimulation or during actual shortening, is the basis of the "viscous-elastic" phenomena found in all contractile tissues.

A. V. H.

Observations on the Muscles of Normal and Moulting Crustacea.**By J. P. Hoet and P. M. T. Kerridge.***Proc. Roy. Soc. B.* 100, p. 116, 1926.

Glycogen was found in the muscles of normal, hard-shelled crustacea, but only small amounts in shelled specimens of the same species.

An early onset of rigor mortis, associated with alkaline reaction, was observed in crustacean muscles poor in glycogen. When glycogen was present in the muscles there was a post-mortem development of acid comparable with that in mammalian muscle.

P. M. T. K.

The Buffering Power of the Blood of *Maia squinado*.†**By P. M. T. Kerridge.***Journ. Phys. LXII*, 65, 1927.

The hydrogen ion concentration of the blood of *Maia squinado*, oxidised and reduced and exposed to various tensions of carbon dioxide was measured.

The buffering power of the blood, and its bicarbonate content under varying CO₂ tensions, was calculated.

It was found that oxyhæmocyanin is a stronger acid than reduced hæmocyanin.

P. M. T. K.

Cytological Observations on *Haplosporidium (Minchinia) Chitonis*.**By S. D. King, B.A., Sc.B., Ph.D.***Quart. Journ. Micros. Sci., Vcl. LXX*, 1926, pp. 147-158.

The golgi bodies of *H. chitonis* are juxtannuclear in the uninucleate stages formed by breaking up of the plasmodium, the sporoblast, spore, and probably also in the plasmodium. In the mature spore they scatter, and may give rise to fatty reserve material. In the sporoblast and young spore the portion of cytoplasm surrounded by the apparatus stains deeper than the surrounding cytoplasm. This is the "sphere" noted by previous workers. Mitochondria are difficult to demonstrate, but when visible are granular. The spore coat is formed within the cytoplasm of the sporoblast, the outer cytoplasmic envelope being apparently used up in thickening of the coat and formation of the spore tails.

S. D. K.

The Young of *Stylocheiron Suhmii* G. O. Sars and *Stylocheiron abbreviatum* G. O. Sars (Crustacea), from Mediterranean Plankton collected by Mr. F. S. Russell, in the neighbourhood of Alexandria, Egypt.

By Marie V. Lebour, D.Sc., F.Z.S.

Proc. Zool. Soc., London. Part I, 1926, pp. 203-211.

The larval stages of *Stylocheiron Suhmii* and *S. abbreviatum* are described. The life-history from early Furcilia is nearly complete for both species. These larvæ are very characteristic, and bear generic characters unlike any other euphausiid. Both are deep water forms, and probably come near the coast to breed.

M. V. L.

On Some Larval Euphausiids from the Mediterranean in the Neighbourhood of Alexandria, Egypt, collected by Mr. F. S. Russell.

By Marie V. Lebour, D.Sc., F.Z.S.

Proc. Zool. Soc., London, Part III, 1926, pp. 765-776.

This paper is supplementary to one on the larvæ of *Stylocheiron* published in the same publication. In it are described the larvæ of *Nematoscelis microps*, *Thysanopoda equalis*, *Euphausia Krohnii*, and some *Euphausia* species not identified, besides the calyptopis stages of *Stylocheiron Suhmii*. The numbers of larvæ taken close to the shore seem to indicate that these species come from the open sea to spawn. A list of all specimens taken is given with data.

M. V. L.

The Chromosome Complex of *Gammarus chevreuxi* Sexton.

I. Spermatogenesis.

By Richard Palmer, B.Sc.

Quart. Jour. Micr. Sci., Vol. LXX, Pt. III, 1926, pp. 541-551.

1. The chromosomes of *Gammarus chevreuxi*, as shown in spermatogenesis, are described. They are small, ovoid, and minutely heteromorphic, and have a diploid number in the male of twenty-six, including an X- and a Y-chromosome.
2. The spermatogonia fall into two distinct classes as regards chromosome size, the large plates being the later stages in the spermatogonial series.
3. While *Gammarus* does not provide favourable material for the detailed study of synapsis, the chromosomes appear to spin out in the typical way in the early synaptic stages.
4. Huxley's conclusions regarding cross-over values and chromosome configuration in *Gammarus* are discussed in the light of these facts.

R. P.

On the Physiology of Amœboid Movement. III. The Action of Calcium.**By C. F. A. Pantin.***Brit. Journ. Exper. Biol., Vol. III, No. 4, 1926, pp. 275-295.*

The action of certain ions on a marine amœba has been studied. Movement takes place between the limits pH 6 and pH 10: it is reversibly inhibited at the acid limit, but alkaline inhibition is reversible only after a brief immersion. Of the four chief cations of sea-water Ca alone is essential for movement. Movement takes place in balanced solutions of Ca with any alkali metal, with no other cation present. NH_4 is toxic. The optimum alkali-metal /Ca ratio for movement, and the velocity attained, increase with the atomic weight of the alkali metal. Viability in these solutions follows a different law: $\text{Na} > \text{K} > \text{Cs} > \text{Li}$ and Rb. Ca can be replaced by Sr, but not by Mg or Ba. For the optimum movement, $\text{Na}/\text{Sr} < \text{Na}/\text{Ca}$. Although movement occurs in either NaCl or KCl alone if Ca is present, yet it is maintained much longer when K is added to a $(\text{NaCl} + \text{CaCl}_2)$ solution. The effect is most marked where $\text{Na}/\text{K} \doteq 50$, as in sea-water. This specific action of K on viability is shared by Rb. In a solution of $(\text{NaCl} + \text{CaCl}_2)$ with excess Ca, movement is immediately inhibited, apparently owing to an increased ectoplasmic viscosity. The inhibition is reversible, and resembles that caused by acid. Inhibition from lack of Ca differs from that caused by excess. Movement is at first normal, but sooner or later falls to zero: the time required for this is less the lower the Ca concentration. This inhibition is not readily reversible. In the effect of Ca deficiency amœba resembles contractile tissues. In both cases the effect is counteracted by increased alkalinity. In amœba the action is complicated, because above pH 8 alkali tends to inhibit all movement if Mg is absent. There is a general similarity between the action of ions on amœba and on contractile tissues. The differences observed seem to be related to the long time required for effects to occur in amœba. This is probably connected with adaptation to the variable external environment, in-shore sea-water.

C. F. A. P.

On the Physiology of Amœboid Movement. IV. The Action of Magnesium.**By C. F. A. Pantin.***Brit. Journ. Exper. Biol., Vol. III, No. 4, 1926, pp. 297-312.*

Although movement only occurs if Ca or Sr is present in the medium, yet Mg and Ba as well are able to prevent the increased permeability and cytolysis seen in pure NaCl. Cerium also has a similar action at very low concentration, but it is very much less effective than Mg. Excess of Mg never causes the marked increase in viscosity seen in the ectoplasm

when Ca is in excess. For this and other reasons it seems that inhibition of movement in excess Ca is due to direct action on the contractile mechanism, and is not simply the result of decreased permeability. This is borne out by the fact that good movement occurs in mixtures of $(\text{MgCl}_2 + \text{CaCl}_2)$ alone, and over a far greater range of concentrations than occurs in mixtures of $(\text{NaCl} + \text{CaCl}_2)$. This can be readily explained by assuming that Mg reduces the permeability of the cell so far that Ca can neither penetrate nor leave the cell and thereby derange the contractile mechanism. Even in any mixture of $(\text{NaCl} + \text{CaCl}_2)$, or of $(\text{MgCl}_2 + \text{CaCl}_2)$, movement gradually falls off. Only when all four cations of sea-water are present is movement normal indefinitely: fully normal permeability is maintained only under these circumstances. Since the addition of Mg and K to a solution of $(\text{NaCl} + \text{CaCl}_2)$ not only establishes the normal degree of impermeability, but also enormously increases the absolute velocity of movement, it seems probable that the same mechanism which controls permeability is also a part of the whole mechanism of amœboid movement.

The relation of the action of ions to the chemical structure of protoplasm is discussed.

C. F. A. P.

Choreocolax Polysiphoniae, P. F. Reinsch.

By H. H. Sturch.

Annals of Botany, Vol. XL, No. 159, pp. 585-605.

This description of another of the small, sub-spherical, parasitic Florideæ, all formerly included by Reinsch in his genus *Choreocolax*, shows that the three species now examined, although very similar in size, external appearance and parasitic habit, belong to three distinct genera, differing markedly in the development of their carposporophytes. *Choreocolax* is shown to produce a sub-spherical cystocarp, bearing tufts of carposporangia in the enclosed cavity; a structure much resembling the cystocarp of *Galaxaura*.

The development of the sporophyte is described in minute detail. The distal portion of the peripheral filament upon which the carpogonium is laterally borne, becomes modified to a cœnocytic mass, forming a food store for the developing sporophyte.

It is suggested that the name *Holmsella pachyderma* should be substituted for the name *Harveyella pachyderma*, as this plant is not a *Harveyella*.

The three genera, *Choreocolax*, *Harveyella*, and *Holmsella*, of each of which only one species has yet been described, have now been shown to have an auxiliary cell development resembling that of the *Ceramiales*,

or of an allied group, while their mature cystocarps resemble very closely those of members of the Gelidiales. The three parasitic genera have therefore been placed in a provisional group, the Choreocolaceæ, whose position has, for the present, been left indefinite.

The situation of *Choreocolax* is interesting as a fully parasitic Floridean with very reduced soma, living on *Polysiphonia nigrescens*, which is hemiparasitic, but with a fully developed soma, on *Ascophyllum nodosum*. *Choreocolax* represents the limit, *Polysiphonia* the commencement, of parasitism in the Florideæ.

H. H. S.

Ciliary Feeding Mechanisms in the Thecosomatous Pteropods.

By C. M. Yonge, B.Sc., Ph.D.

Journ. Linn. Soc., Zool., Vol. XXXVI, 1926, pp. 417-429.

The Thecosomatous Pteropods obtain their food by means of ciliary currents on the middle and two side lobes of the foot. The ciliary mechanisms of the four species, *Cavolinia inflexa*, *Creseis acicula*, *Cymbulia peronii*, and *Gleba cordata* (all examined at the Station Zoologique Russe, Villefranche-sur-Mer), in the order named show a progressive reduction in area. Excess material is rejected by a ciliated tract anterior to the mouth. Correlated with the increased specialisation and efficiency of the ciliary mechanisms there is a reduction and final disappearance (in *Gleba*) of the buccal mass and its associated structures, which were probably handed down from carnivorous ancestors. There is both ciliary and peristaltic activity in the gut which possesses a triturating gizzard, a "digestive gland" into which food passes, and, at the junction of the two, a ciliated diverticulum which contains a hyaline secretion strongly reminiscent of the crystalline style of the Lamellibranchs. As in the latter, it may contain a starch-splitting ferment, and be correlated with the presence of ciliary feeding mechanisms which collect food largely of a vegetable nature.

C. M. Y.

Protandry in *Teredo Norvegica*.

By C. M. Yonge, B.Sc., Ph.D.

Quart. Journ. Micr. Sci., Vol. LXX, Pt. III, 1926, pp. 391-394.

Sections of the gonads of two specimens of *Teredo norvegica* undergoing change of sex are described. Histological evidence appears to point to a change of sex from male to female, and this agrees with the macroscopic examination of two to three hundred specimens of all sizes, the males being on the average only three-quarters the size of the females.

C. M. Y.

The Disappearance of the Crystalline Style.**By C. M. Yonge.***Nature, Vol. CXVII, 1926, pp. 691-692.*

The style dissolves not "as a direct response to the lack of oxygen" (Berkeley), but under adverse conditions which cause a lowering of metabolism, and so a reduction in the rate of secretion of the style. Since the head of the style is always being dissolved by the less acid fluid in the stomach, the style is only maintained as a result of a balance between the rate of secretion and the rate of dissolution. It is never completely dissolved in those animals in which it lies in a separate cæcum; and there is no correlation between the size of the style and the habitat of the animal as would be expected if it were concerned with anærobic respiration.

C. M. Y.

The Digestive Diverticula in the Lamellibranchs.**By C. M. Yonge, B.Sc., Ph.D.***Trans. Roy. Soc. Edin., Vol. LIV, Pt. III (No. 15), 1926, pp. 703-718.*

The structure of the digestive diverticula (so-called liver or hepatopancreas) was studied in 34 spp. of marine Lamellibranchs. They consist of blind tubules, which open into the stomach by ciliated ducts. There is only one type of cell in the tubules, but there are crypts of smaller, darkly staining cells whose nuclei divide mitotically; the older cells are very vacuolated, and contain many coloured granules. In the Teredinidæ there are also tubules specialised for the digestion of wood. A border cuticle was seen in sections of *Nucula* and the Filibranchs, but not in the Eulamellibranchs. In fresh material, long retractile cilia were seen in a number of species and probably occur in all. Iron saccharate was taken into large vacuoles in the cells of the tubules, being later passed on to amœbocytes. Blood corpuscles from dogfish are ingested by phagocytes before they reach the tubules, except in the case of *Teredo*, where they are ingested by the cells of the unspecialised tubules. The presence of intracellular digestion is indicated by the manner in which particles are ingested, and by the presence of digestive enzymes in extracts of the diverticula. There is no evidence, histological or physiological, that the cells of the tubules secrete. The diverticula provide the extensive surface characteristic of animals which possess intracellular digestion, while, as a result of the action of the various sorting mechanisms, only the very smallest particles are presented to the ingesting surface. The digestive diverticula possess none of the functions of a liver or pancreas, but are organs of absorption and intracellular digestion.

C. M. Y.

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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, and amongst the speakers in support of the project were the late Duke of ARGYLL, the late Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr. CARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY, the late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

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