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THE  
DINOFLAGELLATES  
OF  
NORTHERN SEAS

BY  
MARIE V. LEBOUR, D.Sc., F.Z.S.

NATURALIST AT THE LABORATORY OF THE MARINE BIOLOGICAL  
ASSOCIATION OF THE UNITED KINGDOM, PLYMOUTH

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# Experimental Legislation with Reference to the Crab and Lobster Fisheries of the East Coast of Britain.

By

Professor Alexander Meek, D.Sc.

*Dove Marine Laboratory, Cullercoats.*

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With Seven Figures in the Text.

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So large a demand has been made for copies of the recently published paper on the effects of legislation on the crab fisheries of the East Coast\* that a new paper is necessary. A summary is given of the previous paper and the figures have been reproduced. For convenience of reference they are arranged and numbered as before. The opportunity has been taken to give a review of the attempts to improve the lobster fisheries by legislation.

## 1. CRAB.

The Oyster, Crab and Lobster Act of 1877 gives a size limit of  $4\frac{1}{4}$  in., and protects the soft and berried crab. But, as will be seen from Figure 1 (p. 756), this apparently adequate protection was not sufficient to prevent a decline in the fishery on the East Coast in general. It has long been recognised that the winter fishing for crabs is a very destructive one, and two Committees attempted early to strengthen the Act by local legislation.

The Eastern Committee (Norfolk and Lincolnshire) passed in 1894 a by-law prohibiting the catching of soft or white-footed crabs from 1st November to 30th June each year. The by-law has had the effect of stopping the winter fishing, the crab-pots not being brought into use until February or even March as a rule. It may be regarded as conferring a close time during the season that soft crabs are prevalent along the coast.

The North-Eastern Committee (Humber to Tyne) passed a by-law which was in operation during the years 1896 to 1906 when it was repealed. This by-law gave a close time to the crab fishery between 1st September and 31st January each year.

Much later, after a great deal of enquiry and investigation, the Northumberland Committee (Berwick to Tyne) similarly passed a by-law

\* 1924. *Trans. Nat. Hist. Soc. of Northumberland, Durham and Newcastle-upon-Tyne*. New Ser., Vol. VI, Part 1, p. 63.



Fig 1.—The numbers of crabs, in thousands, landed on the east coast of Britain and on the east coasts of Scotland and England. The vertical lines at 1896 and 1906 indicate the duration of the North-Eastern close time, and the vertical line at 1914 the commencement of the Northumberland close time.

which gave a close time to the fishery from 1st October to 31st December in each year.

In each case the by-law is based on what every fisherman knows to be a fact that fishing during the season immediately succeeding the casting of the shell (ecdysis) is a destructive one. The aim of the legislation, in short, is to protect the fishery from the effects of destructive fishing.

The legislation in the Eastern district has been so long in force that it offers no figures for comparison. But, as will be seen from Figure 3 (p. 759), the catches have been maintained at a fairly constant level during the whole period.

Fortunately, in the case of the other two districts, the legislation has been in operation only for a limited period, and the effects may be readily ascertained. The North-Eastern Committee attempted a drastic remedy by closing the fishery for five months. The fishermen of the district from 1896 to 1906 were allowed to fish for seven months, and since 1906 have been permitted to fish all the year if they wished. The annual catches are displayed in Figure 2 (p. 758), and they indicate that despite the restricted period of fishing during the years in question—marked in the figure by vertical lines—the landings steadily improved, although the returns for the rest of the east coast of England exhibited a decrease. Since the by-law was withdrawn the fishery has followed the rest of the East Coast closely until the end of the period, when the figures sank below those of the rest of the East Coast.

Northumberland, as Figure 4 (p. 761) plainly shows, was undergoing a steady decrease during the greater part of the years under consideration. The decrease persisted during the years of the war—until 1918—when a rapid improvement took place, culminating in the year 1922. The delay in the improvement is much greater than that experienced by the North-Eastern Committee, and it does not appear to be due to the war. The fishery had declined so seriously that some years had to elapse before the protection began to take effect. The results of the two experiments in neighbouring districts at different periods become more clear when the two districts are compared, as is done in Figure 5 (p. 762). At the beginning of the period the two districts were landing about the same numbers each, and it is again at the end of the period that the catches in the two districts have become more equal.

The conclusion is warranted, therefore, that legislation designed to give protection during a period of destructive fishing produces good results.

Marking experiments have shown that the crab population as a whole is stationary, migrating seasonally into deep water in the winter and into shallow water in the summer. The larval stages are pelagic, and undergo a denatant, that is to say a down-current migration. The districts are related by current, and it follows that protection in one district will tend

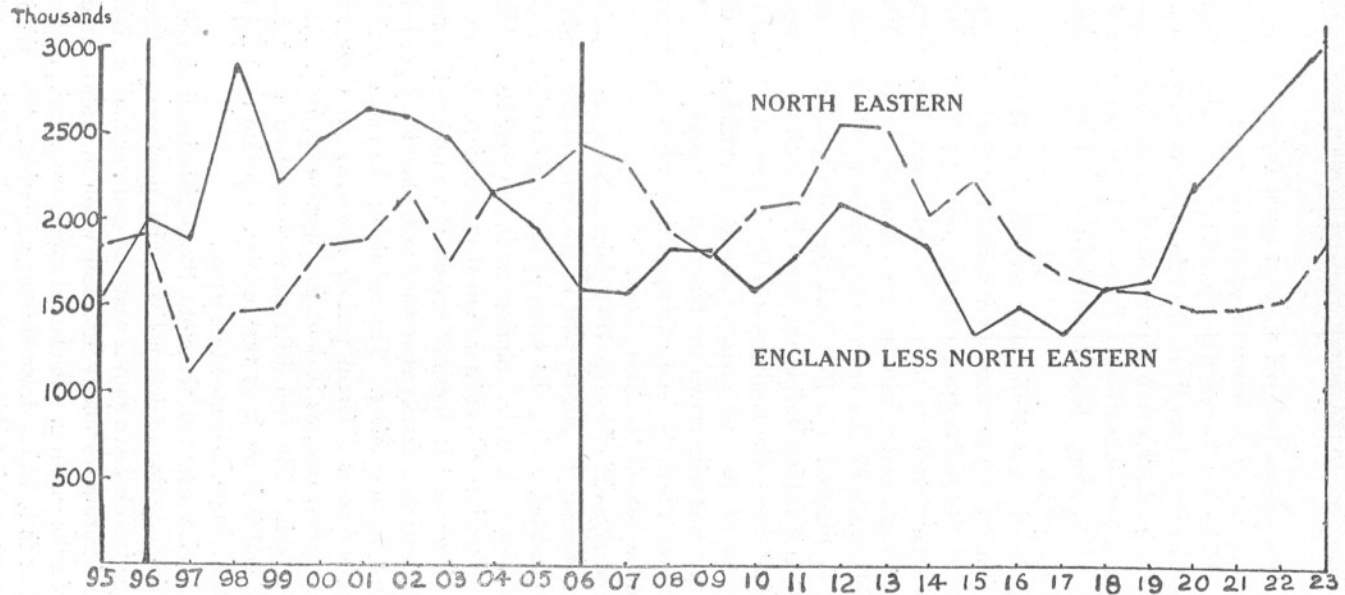


FIG 2.—The numbers of crabs, in thousands, landed on the east coast of England, less those landed in the district of the North-Eastern Committee, which latter are also shown.

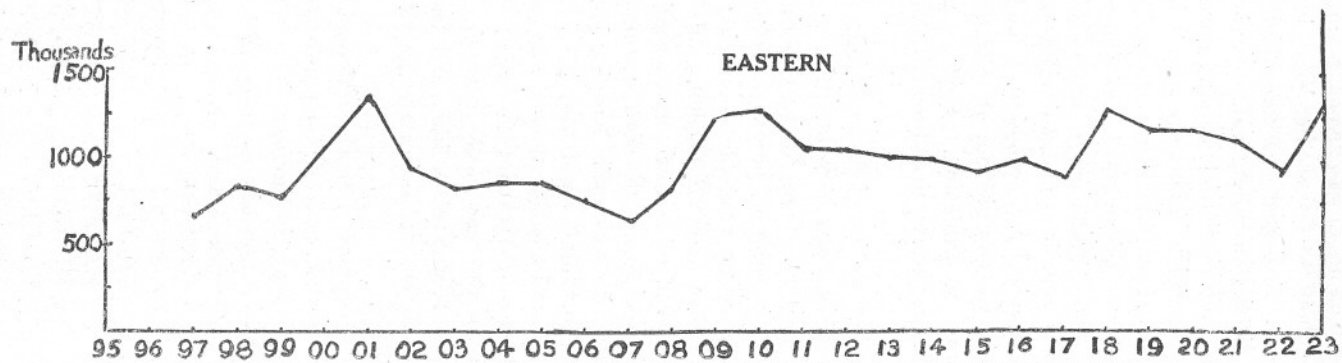


FIG. 3.—The numbers of crabs, in thousands, landed in the district of the Eastern Committee.



to benefit the district which lies down-current from it. Again, the female crabs, when they are about to become berried, migrate contranatanly, that is to say up-current. A district therefore which is protected may be expected to benefit a district on the contranatanant side.

This interrelationship of the districts around our shores makes it desirable that the legislation which has been proved to be productive should be made uniform. There does not seem to be much, if any, difference in the season of casting or ecdysis, nor as to the time required for converting the soft or white-footed crab into a marketable crab around our coasts. But the seasons vary in a manner which has not yet been explained as to the time required for hardening. Last year, for example, the east coast of Britain was occupied for an extraordinarily long period by crabs in the process of hardening. This year, 1925, the reports indicate that the crabs on the Northumberland coast are plentiful and in good condition.

The effects of the contranatanation of the berried females may be roughly estimated in the case of Northumberland. The average catch for the years 1895-1924 was 1,155,000. The marking experiments indicated that the fishermen were liable to catch 27 per cent of the population of adult crabs. If we assume, therefore, that the population is about 4,000,000, the females would number about 2,080,000. Of the females, about 14 per cent migrate each year to the north, most entering Scottish waters; most coming to rest in the Eyemouth district, but spreading generally along the coast from Berwick to Banff. Keeping in mind that many of the southern crabs of Northumberland would reach only the northern part of the county, it may be gathered that Scotland gains each year from Northumberland some 250,000 female crabs. The fact is, at any rate, that the catches on the east coast of Scotland since 1918 have undergone a notable rise (Figure 6, p. 763), and the improvement appears to be due to some extent to the improvement in Northumberland, with which it is coincident.

The inference receives support from the differences exhibited by the statistics in the districts to the south of Northumberland. The following table gives the landings of crabs in the four districts from 1918 to 1924; the districts are arranged in succession from north to south.

	Eyemouth.	Northumberland.	North Eastern.	Eastern.
1918	208,700	440,620	1,573,730	1,332,400
1919	223,700	626,859	1,560,612	1,200,200
1920	454,600	1,040,454	1,457,885	1,192,000
1921	678,800	1,211,930	1,457,777	1,126,000
1922	756,600	1,780,595	1,505,853	957,000
1923	760,900	1,594,437	1,840,793	1,324,400
1924	769,500	1,286,563	1,840,912	1,551,000

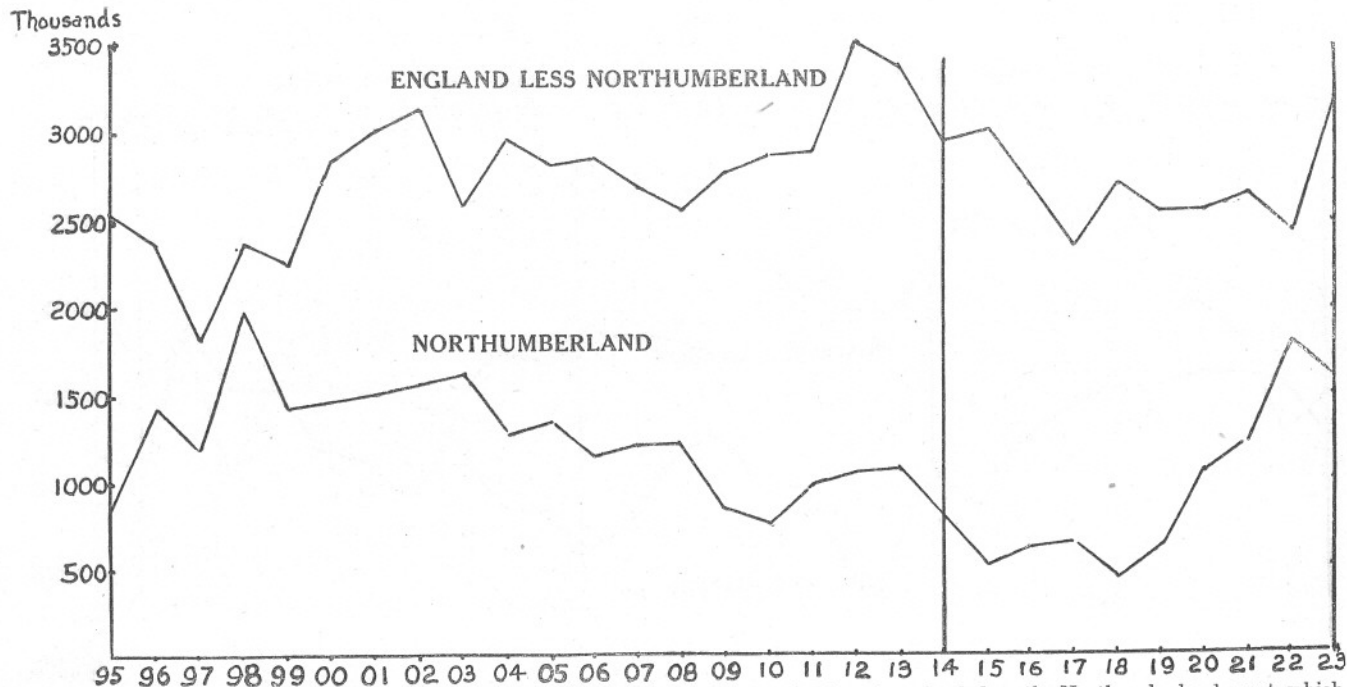


FIG. 4.—The numbers of crabs, in thousands, landed on the east coast of England, less those landed on the Northumberland coast, which latter are also shown.

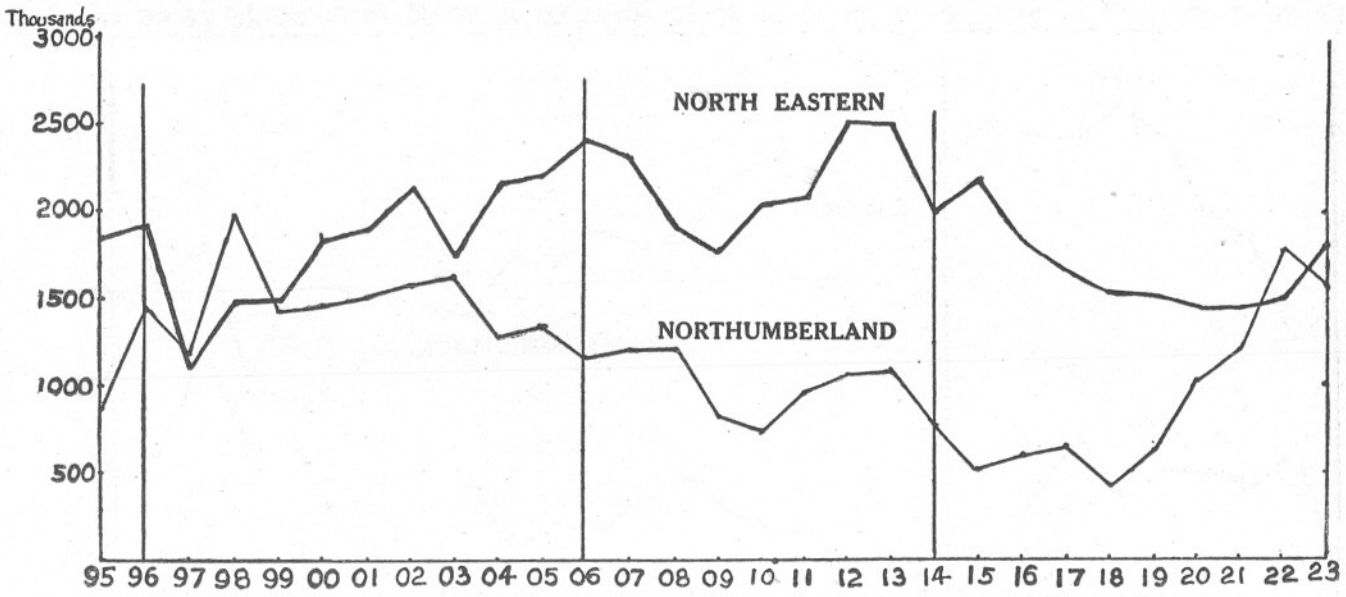


FIG. 5.—The numbers of crabs, in thousands, landed in the Northumberland and the North-Eastern districts.

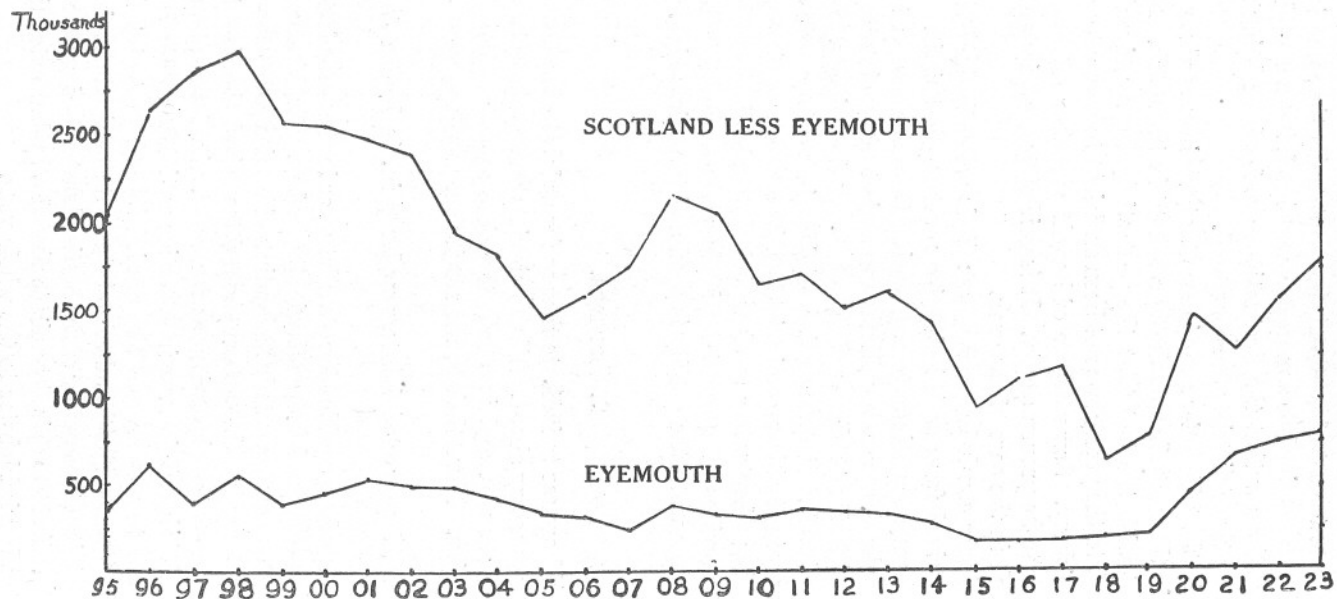


FIG. 6.—The numbers of crabs, in thousands, landed on the east coast of Scotland, less those landed in the Eyemouth district, which latter are also shown.

It will be observed that the first two agree. Both have trebled their catches, and the east coast of Scotland shows generally the same features. The last two have remained at a more constant level, but a consideration of the figures will show that the fluctuations are far from being regular when the two southern districts are compared.

The figures in the table offer no evidence that the increased number of berried crabs in the north has produced a benefit in the south. But this is in agreement with the fact that the protection already given to the berried crab and to the young has not been sufficient to prevent a general decline in the fishery. Some degree of benefit probably follows, but it does not appear to be proven as yet. It is evidently more important to protect the adult in the case of the crab.

The former paper concluded as follows: It is acknowledged that the benefit to be derived from such legislation must reach a limit. But so long as the fishermen continue to fish during the open season the rest enjoyed during the close season will have the effect of keeping the population up to a high, if not always the same, level of efficiency. Seasonal variation is inevitable. The protection as given in Northumberland and in a different way in the Eastern district has the advantage of preventing destructive fishing when prices are low and the crabs liable to be poor in quality. It provides a larger catch with less labour, and the crabs are marketed at a time when the quality is good and the prices high.

## 2. LOBSTER.

Figure 7 would appear to indicate that so far as lobsters are concerned there is nothing to worry about. All the districts on the East Coast have improved conspicuously, and it would therefore appear superfluous to speak of protection. Nevertheless, the results are worth some degree of consideration.

The Act of 1877 protected lobsters under 8 in. in length and that was all.

The Committees along the English coast have, as in the case of the crab, attempted to improve the lobster fisheries by by-law. The Eastern Committee since 1895 have prevented the landing of berried lobsters and soft lobsters. In 1896 the North-Eastern Committee raised the size limit to 9 in. and introduced the close time as for crabs, viz. 1st September to 31st January. This legislation was in operation until 1920, when the close time was brought to an end and the berried lobster protected for the whole year. In 1899 the Northumberland Committee raised the size limit to 9 in. and prohibited the landing of the berried lobster during the months of April to July. In 1915 this Committee passed a by-law extending the protection of the berried lobster to the whole year.

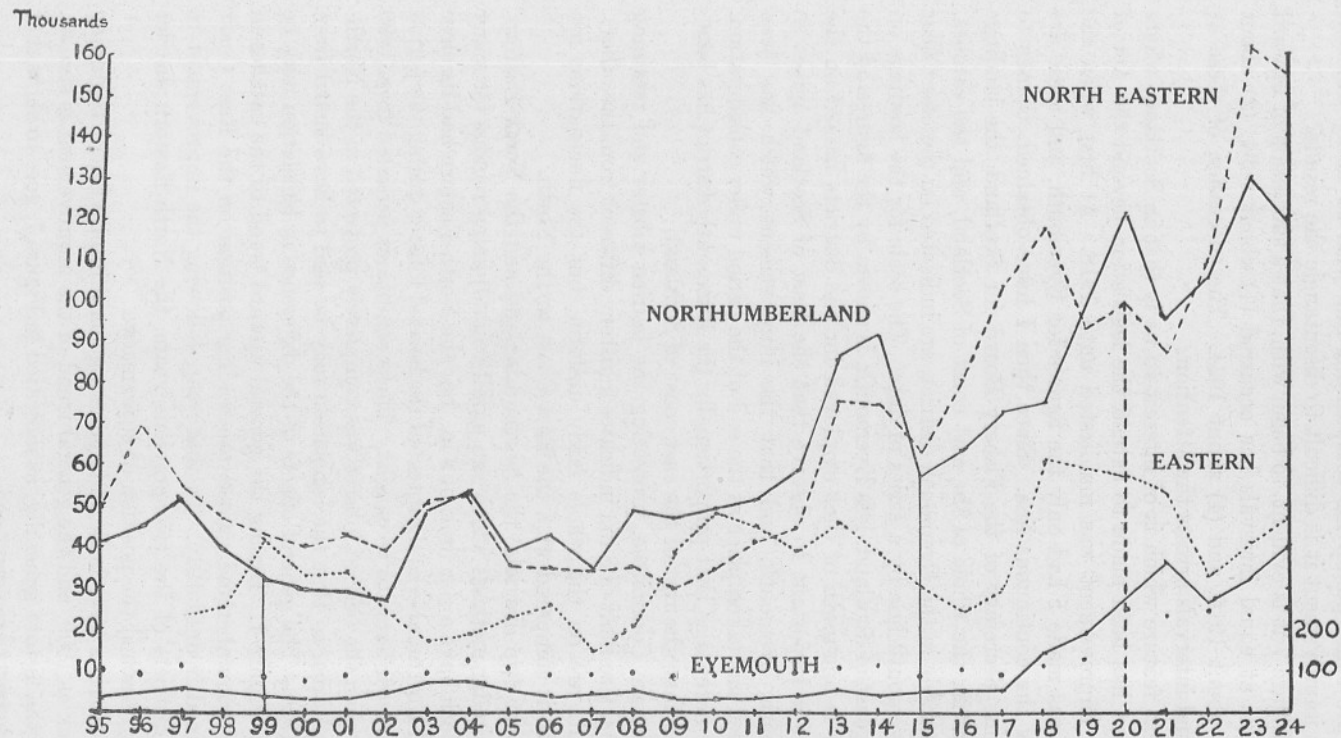


FIG. 7.—The numbers of lobsters, in thousands, landed in the Eyemouth, Northumberland, North-Eastern and Eastern districts. The dots in the lower part of the figure indicate on a tenth scale compared with the others the landings of lobsters on the east coast of Scotland, less those landed in the Eyemouth district.

There are some points for comparison, but with so many different efforts at improvement it is difficult to disentangle the results.

From Figure 7 it is evident, to begin with, that a succession of upward fluctuations at equal intervals has occurred (1) about 1894, (2) about 1904, (3) about 1914, and (4) about 1924. The succession of these at about equal intervals arrests the attention.

The next feature which is of interest to us is that in Scotland, where no attempt has been made to extend the legislation beyond the Act of 1877, no improvement was manifested until 1918. At first when the diagram was made I had only the figures for Eyemouth, and these are shown by the continuous line. Since then I have obtained, thanks to the obliging Secretary of the Fishery Board for Scotland, the landings of lobsters for the whole of the east coast of Scotland, and the catches, less those made in the Eyemouth district, are indicated on the chart near to the Eyemouth line by a series of dots. The scale for the landings on the east coast of Scotland, less Eyemouth, is shown by the figures on the right: it is one-tenth of that employed for the districts named on the chart. It is important to observe that the East of Scotland agrees so closely with Eyemouth, and that the improvement which has been experienced has taken place at the end of the period under consideration. It will be noted also that proportionally the Eyemouth district has benefited more than the rest of the east coast of Scotland.

The Eastern Committee, protecting the berried lobster and retaining the original size limit of 8 in., indicates a history different from the others. The results are on the whole fairly uniform, but the fluctuations are peculiar to it compared with the East Coast to the North.

The other two districts, the Northumberland and the North-Eastern, tried dissimilar methods which ran parallel in adjoining regions for many years. Both have a size limit of 9 in., but the North-Eastern had its close time, and Northumberland protected the berried lobster during the period when it is most liable to be caught. These conditions persisted from 1899 to 1915, when the berried lobster was completely protected in the Northumberland area, so that the legislation may be said to have lasted from 1899 to 1920. The general effects of the difference in legislation may be seen from Figure 7. During the general upward trend of the catches in 1903-4 Northumberland gained the leading position on the East Coast and retained it until 1915. In that year, following the improvement in the two districts of the two previous years, the North-Eastern district once more reached the position of supremacy.

These districts have both undergone a general improvement beginning as far back as 1909, and the general trend of the improvement is similar. This and the history generally, as indicated in Figure 7, goes to show that the two districts are correlated.

Marking experiments have been tried on the Northumberland coast on several occasions and the results have been presented in the reports of the Cullercoats Laboratory. The results did not show any definite sign of migration such as were obtained in the case of the crab. One female certainly was returned from a position ten miles north of the place of liberation. The want of evidence is probably due to two facts: (1) the experiments were made on too small a scale, (2) the marked lobsters were for the most part berried and had therefore no occasion to migrate.

We have not any definite knowledge of a benefit on the contranant side. But from the fact of the correlation of the two districts, and it is a correlation which is manifestly shared in by the east coast of Scotland, we feel that it is highly probable that the females about to be berried actually make a contranant migration. The rise, notably in the Eye-mouth district, following the marked increase of the population of lobsters in Northumberland, is interesting in this respect.

The experiments and the observations of the fishermen indicate that the lobster keeps more inshore, even in winter, and, probably, if it be shown that the females are contranant, the migration of the mature lobster is not to so great a distance as the mature crab. The rest enjoyed then during the period when the close time of the North-Eastern Committee was in operation may have had some result. But the rest is already given generally by the habits of the fishermen who, in the colder months place their crab-pots in deep water to catch crabs.

The marking experiments showed incidentally that the catching power of the fishermen is great, a return of as many as 36 per cent being recorded in one experiment. The average catch during the last ten years in Northumberland was 93,414 lobsters, and of this number some 13 per cent would be berried, that is 12,000. So that if a number near the borders of the district cross the boundary from the one to the other, and it is highly probable, the gain is a substantial one.

The larvæ are pelagic for about three weeks and are therefore liable to a considerable denant migration. But it has been a matter of surprise to us that so few have been captured in our plankton nets. In spite of the large amount of netting which has been done for nearly thirty years on the Northumberland coast, both inshore and offshore, a very small number only has been recorded. They must be present in the shore waters in plenty, for if the population of lobsters on the coast includes some 40,000 berried lobsters and each furnishes, say, 40,000 larvæ, to say nothing of the larvæ borne by current into the area, large numbers of larvæ must prevail during the hatching season.

Wondering if we had fallen into some mistake as to the habits of the larvæ, I asked Mrs. Cowan to obtain one or two berried lobsters and to watch the larvæ carefully. She found, as we had observed before, that



they were definitely pelagic and speedily died if they reached the bottom prematurely. The only conclusion we can arrive at, then, is that the larvæ are strong enough to evade or to swim out of the nets.

In spite of their swimming powers they are denatant, but because of the swimming powers probably not so much so as the crab larvæ. With this in mind I obtained the figures and attempted to show in 1914\* that the near part of the district to the south of Northumberland was gaining from the improvement in Northumberland.

This discussion leads to the conclusion that the lobster larvæ are better able to avoid capture than those of the crab, and that the increased population on the East Coast has been due to a survival above the normal to adult size. But it is an increase which from its incidence is clearly associated with the protection which is given on the north-east coast of England to the berried lobster.

The general result in each case, that of the crab and lobster, is interesting and important ; the demonstration that the coastal region is capable of supporting a very much larger population than in the past. And I think it will be conceded that the efforts at improvement in the one case by protecting the fishery from a season of destructive fishing and in the other by protecting the berried female have been justified.

\* *Report Dove Mar. Lab.* New Ser., III, p. 77.

## The Vertical Distribution of Marine Macroplankton. An Observation on Diurnal Changes.

By

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

*Assistant Naturalist at the Plymouth Laboratory.*

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With 1 Plate and 6 Figures in the Text.

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### INTRODUCTION.

WHILE many collections have been made on oceanographical expeditions to study the vertical distribution of organisms in deep waters, few observations have been made on the vertical distribution of the larger marine plankton animals in coastal waters. This is possibly in part due to their comparatively small numbers in a given volume of water as compared with the immense numbers of the more minute organisms, such as diatoms or even the smaller copepods, and hence the necessity for the filtration of a very large body of water in order to obtain significant figures; in part also to the fact that owing to the large size of the net required to filter so great a body of water, the fishing depth has always been unknown.

The first difficulty has been overcome of late years by the introduction of the material known as "stramin," which on account of its cheapness and durability compared with silk makes large nets for everyday use a possibility. Its large mesh (ca. 16 strands to 1") causes the retention of only the more bulky of the plankton organisms.

The Admiralty authorities have very kindly lent us an instrument which records graphically the depths at which a net has fished during the whole of its period under water: with this assistance the second hindrance is removed, and we can say with certainty the depths from which the plankton has been taken.

Researches were carried out primarily to study the vertical distribution of the larval and post-larval stages of our food fishes; the necessity of an understanding, not only of the vertical distribution of these stages but of their occurrence in relation to other living organisms of their environment, including both their food and their enemies, has naturally led to a more intensive study of the distribution of zooplankton as a whole.

The majority of observations up to date have been made in the daytime; but it is necessary to know also the distribution at night and the

successive changes that take place to bring about the well-known diurnal variations in vertical distribution. For this purpose a series of hauls was taken on July 15-16, 1924, and it is with these alone that this paper deals.

#### METHOD OF COLLECTING.

The net used was a ring trawl with an opening of 2 metres diameter ; it was made of stramin, and was 6 metres in length. A short account of the method of working this net has been given elsewhere (Russell, 14).

The locality chosen was the hydrographical Station L4, midway between the Plymouth Breakwater and the Eddystone Lighthouse. Here there is a depth of 28 fathoms (51 metres), and the bottom for some distance round is level. This position is sufficiently far from the coast line to avoid the local swirls and upward currents, which are the constant normal events of waters close inshore, and which might be strong enough to prevent the larger plankton animals from assuming their typical vertical distribution of more open waters : that vertical mixing does occur however in this region, especially during rough weather, is shown by temperature (Harvey, 6) and phosphate determinations (Atkins, 1). Results of day collecting also have shown that the inshore distribution is markedly different from that at L4, in that the upper layers are as rich in plankton as the deeper. For instance, on June 27th, 1924, about two miles from the coast over a depth of 45 metres the following quantities of plankton were caught in a metre closing net towed horizontally :—

Surface . . . . .	2 c.c.
4.3 m. (average depth) . . . . .	2 „
12.7 „ „ „ . . . . .	80 „
18.1 „ „ „ . . . . .	130 „
36.2 „ „ „ . . . . .	140 „

Whereas on the same day with the same gear, close inshore over a depth of 15 metres, the following results were obtained :—

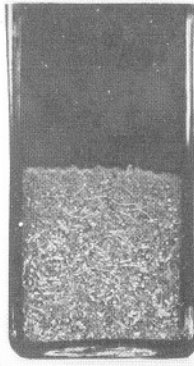
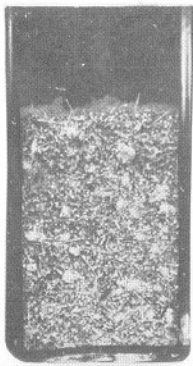
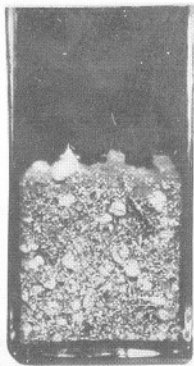
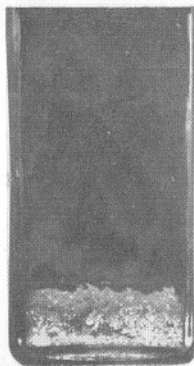
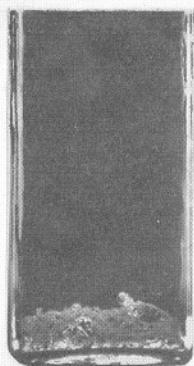
Surface . . . . .	65 c.c.
4.3 m. . . . .	100 „
9.6 „ . . . . .	75 „

This is probably to be accounted for by increased turbidity as well as by mixing.

Herdman and Scott (8) also remark that “ the surface plankton is often more abundant in the bay than at the offshore stations.”

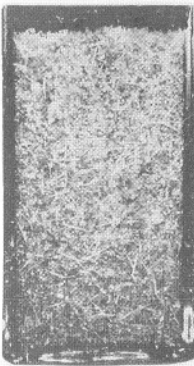
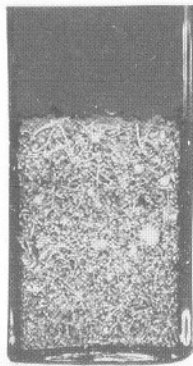
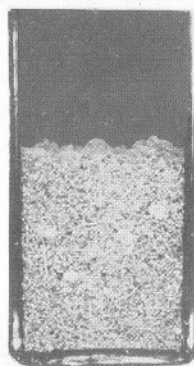
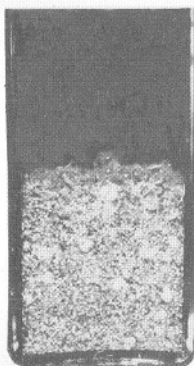
It was decided to collect samples from five different depths. To obtain ideal results five nets would be required to fish simultaneously at the five given depths, a depth-recorder would have to be attached to each net, and each net would have to possess an efficient opening and closing

3:25  
TO  
4:45  
P.M.



DAYLIGHT

7:55  
TO  
9:17  
P.M.



DUSK

Surface

7 m.

14 m.

18 m.

33 m.

PLATE I.

To face page 70.

Photo F. S. R.

Photograph of the actual catches of plankton made by the ring-trawl at five depths in daylight and at dusk, showing how the upper layers had little plankton in daylight and at dusk they had become thickly populated.

TABLE 1.

Date: July 15-16th, 1924.

Position: L 4.

Ship: S.S. "Salpa."

Gear: 2 metre ring-trawl.

	Depth.	Time net entered water.	Fishing time.	Time net left water.	Length of warp out.	Notes.
1st Series : Sun shining : sea calm : no wind	V	3.23 $\frac{1}{2}$ p.m.	3.25-3.35 p.m.	3.37 p.m.	50 fathoms	—
	IV	3.42 $\frac{1}{2}$ "	3.44-3.55 "	3.55 $\frac{1}{2}$ "	30 "	—
	III	4 "	4.1-4.11 "	4.12 "	20 "	—
	II	4.18 "	4.18 $\frac{1}{4}$ -4.28 $\frac{1}{4}$ "	4.28 $\frac{1}{2}$ "	10 "	—
	Surface	—	4.34-4.44 $\frac{1}{2}$ "	—	—	—
2nd Series : Sunset, 8.3 p.m. Clouding over : sea calm : no wind	V	7.54 p.m.	7.55 $\frac{3}{4}$ -8.6 p.m.	8.8 p.m.	50 fathoms	—
	IV	8.14 "	8.15-8.25 "	8.26 "	30 "	—
	III	8.31 $\frac{1}{2}$ "	8.32 $\frac{1}{2}$ -8.42 $\frac{1}{2}$ "	8.43 $\frac{1}{4}$ "	20 "	—
	II	8.49 "	8.49 $\frac{1}{2}$ -8.59 $\frac{1}{2}$ "	9 "	10 "	Getting difficult to see.
	Surface	—	9.7 $\frac{1}{2}$ -9.17 $\frac{1}{2}$ "	—	—	Lights necessary for reading.
3rd Series : Full moon rose at 9.40 p.m. : coming up from bank of clouds into clear sky with occasional flaky clouds	V	10.50 p.m.	10.52-11.31 $\frac{1}{2}$ * p.m.	11.6 p.m.	50 fathoms	Moon behind thin cloud.
	IV	11.15 "	11.16-11.26 "	11.27 $\frac{1}{2}$ "	30 "	Moon quite hidden by clouds.
	III	11.33 $\frac{1}{2}$ "	11.34-11.44 $\frac{1}{2}$ "	11.45 $\frac{1}{2}$ "	20 "	Small clouds passing over moon
	II	11.51 $\frac{1}{2}$ "	11.52 p.m.-12.2 $\frac{1}{2}$ a.m.	12.3 a.m.	10 "	Small clouds passing over moon
	Surface	—	12.9 $\frac{1}{2}$ -12.19 $\frac{1}{2}$ "	—	—	Moon hidden : raining at 12.18 a.m.
4th Series : Wind freshening : Sea lippy :  Raining	V	2.50 $\frac{1}{2}$ a.m.	2.52-3.2 a.m.	3.4 $\frac{1}{2}$ a.m.	50 fathoms	Clouded : grey-dark.
	IV	3.13 $\frac{1}{4}$ "	3.14 $\frac{1}{4}$ -3.25 "	3.26 $\frac{1}{2}$ "	30 "	Getting light.
	III	3.33 $\frac{1}{4}$ "	3.34-3.44 $\frac{1}{2}$ "	3.45 $\frac{1}{4}$ "	20 "	Deck light out : could just see to read.
	II	3.51 "	3.51 $\frac{1}{4}$ -4.11 $\frac{1}{4}$ "	4.1 $\frac{3}{4}$ "	10 "	—
	Surface	—	4.6 $\frac{1}{4}$ -4.16 $\frac{1}{4}$ "	—	—	—
5th Series : Sun shining : Sea slightly "loppy"	V	8.45 a.m.	8.46 $\frac{1}{2}$ -8.56 $\frac{1}{2}$ a.m.	8.59 a.m.	50 fathoms	—
	IV	9.6 $\frac{3}{4}$ "	9.7 $\frac{3}{4}$ -9.17 $\frac{3}{4}$ "	9.19 "	30 "	—
	III	9.25 $\frac{1}{2}$ "	9.26-9.36 "	9.36 $\frac{3}{4}$ "	20 "	—
	II	9.42 $\frac{1}{2}$ "	9.43-9.53 "	9.53 $\frac{3}{4}$ "	10 "	—
	Surface	—	10-10.11 "	—	—	Sun clouded.

\* The numbers of all organisms caught in this haul, which was 11 $\frac{1}{2}$  min., have been corrected for ten minutes.

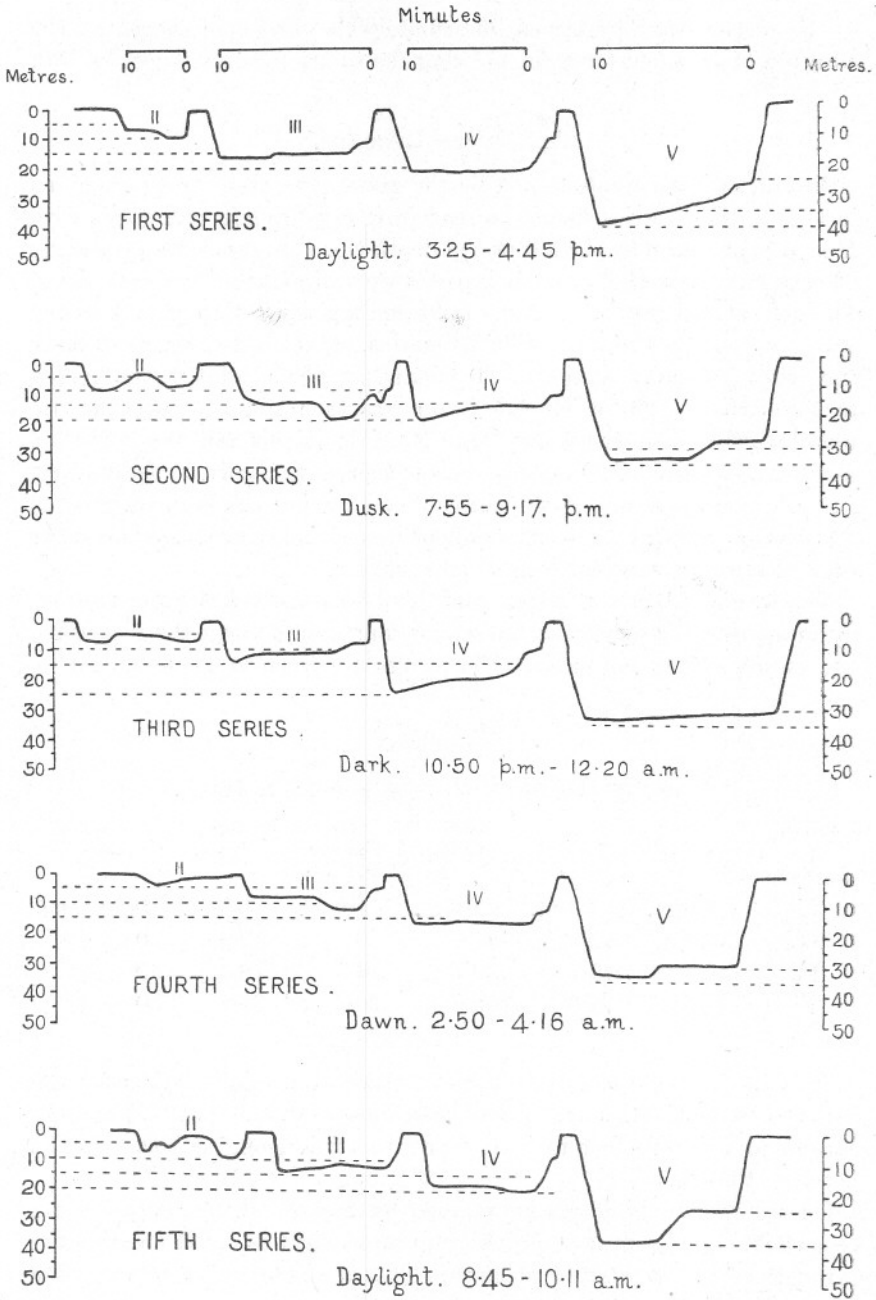


FIGURE 1. The five series of curves given by the depth-recorder indicating the path of the net through the water at the four depths II, III, IV, and V. (The surface haul is not included.) The net enters the water on the right-hand side of each curve. (The differences in the lengths of the curves are due to irregularities in the speed of the recorder clock and not to errors in timing.)

The catches were preserved immediately the net came aboard by the addition of sufficient formalin to bring the solution to a strength of 5%.

#### THE DEPTH RECORDS.

Tracings of the results shown by the graphic depth-recorder are given in Fig. 1. Each series should be read from right to left, and starts with the curve produced by the net at the depth No. V, that is with 50 fathoms of wire out. For the sake of clearness we will describe the first series. The net entered the water at the right end and immediately sank as the warp was paid out to a depth of 26 metres, at which it fished for a short time then gradually sinking to 40 metres, at which point it was hauled to the surface. The clockwork drum was then stopped until the net was ready for the next haul at depth No. IV; in this haul the net fished steadily at a depth of 20 metres, until it was again hauled to the surface. In each series a record of the surface haul tracing has been omitted as this was unnecessary; the net was kept in such a position that the upper edge of the ring was just beneath the surface.

The average depth at which each haul was made has been deduced by measuring the depths at ten equidistant points along the respective curves and taking the mean. The results are given in Table 2.

TABLE 2.

Depth.	AVERAGE DEPTH IN METRES FOR EACH HAUL.					Length of warp.
	1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.	
Surface	—	—	—	—	—	—
II	6.6 m.	7 m.	5.8 m.	1.9 m.	5.3 m.	10 fathoms
III	13.6 „	15.1 „	11.2 „	9 „	12.5 „	20 „
IV	19.5 „	17.1 „	20.7 „	16 „	18.3 „	30 „
V	34.5 „	32.3 „	32.2 „	30.1 „	31.1 „	50 „

It is interesting to note in Table 2 that the average depths for the hauls in the 4th series are all less than in any other. This is probably correlated with the fact that the wind was freshening at this time, as noted in the log.

On the whole, the levels maintained by the net on this occasion are remarkably good; in fact, probably quite as good as could be expected through such a large series of hauls. This is fortunate, as it brings the depths II, III, IV, and V very nearly the same in each series, and so helps comparison in distribution of the organisms caught.

TABLE 3.

SHOWING COMPLETE COUNT OF THE ORGANISMS IN THE SURFACE HAUL OF NO. II SERIES, OBTAINED BY MAKING UP TO 5 LITRES AND TAKING 10 SAMPLES EACH OF 500 C.C.

Sample No.	Phialidium sp.	Obelia sp.	Saphenia gracilis.	Cosmetira pilosella.	Beroë sp.	Sagitta bipunctata.	Tomopteris helgolandica.	Tornaria larvæ.	Porcellana Zoa.	Crab Zoa.	Crab Megalopa.	Pandalus or Processa larvæ.	Upogebia sp. larvæ.	Galathea sp. larvæ.	Callinassa larvæ.	Palinurus phyllosoma.	Calanus finmarchicus.	Candacia armata.	Anomalocera Patersoni.
1.	214	17	5	1	6	203	56	107	337	277	1	2	47	19	4	1	422	58	4
2.	246	15	0	1	6	189	54	119	313	267	0	0	72	20	8	0	339	47	1
3.	203	15	1	4	11	194	57	101	314	290	6	0	70	19	6	1	421	56	2
4.	255	20	3	2	8	208	63	105	327	375	4	2	61	22	16	4	446	61	4
5.	234	28	2	2	2	189	57	127	387	323	3	1	61	22	11	3	457	48	3
6.	241	19	4	0	11	223	53	99	415	380	2	1	97	25	16	2	643	70	1
7.	254	14	2	3	4	254	83	147	435	413	5	3	86	28	17	2	708	68	4
8.	231	20	2	4	7	204	52	129	371	315	5	1	58	21	16	1	451	64	2
9.	247	11	3	0	8	204	55	101	275	265	3	1	52	17	7	2	438	48	2
10.	205	11	4	2	6	192	51	118	324	303	5	2	59	18	11	2	489	52	2
Total	2330	170	26	19	69	2060	581	1153	3498	3208	34	13	663	211	112	18	4814	572	25
Mean	233	17	2.6	1.9	6.9	206	58.1	115.3	349.8	320.8	3.4	1.3	66.3	21.1	11.2	1.8	481.4	57.2	2.5
Standard* deviation	±18.4	±4.8	—	—	—	±18.8	±8.9	±14.8	±47.9	±49.2	—	—	±14.6	±3.5	—	—	±103.2	±8	—
Probable Error	±12.4 or ±5.3%	±3.2 or ±19%	—	—	—	±12.7 or ±6.2%	±6 or ±10.4%	±10 or ±8.7%	±32.3 or ±9.2%	±33.2 or ±10.4%	—	—	±9.9 or ±15%	±2.4 or ±11.4%	—	—	±69.5 or ±14.5%	±5.4 or ±9.5%	—

\* The standard deviation was obtained from the formula S.D. or  $\sigma = \sqrt{\frac{\sum (d^2)}{n}}$  where  $\sigma$  = standard deviation.  $d$  = the deviation from the arithmetic average,  $n$  = the number of samples. The Probable Error is  $0.6745\sigma$ .



## EXAMINATION OF MATERIAL.

At first an attempt was made to analyse the catches by making a complete count of each: when the first large catch was encountered, however, it took 10 days to exhaust, and it was therefore necessary to find some method of sampling.

The method adopted was to place the catch in a large open-mouthed bell-jar with a diameter of 12 inches: this was then made up to 5 litres. A 500 c.c. sample,  $\frac{1}{10}$ th of the whole catch, was extracted by using a finger-bowl as a dipper. The organisms were thoroughly mixed until their distribution appeared as even as possible and a rapid dip made, care being taken to scoop right to the bottom in order to sample any organisms that sank quickly. One dip would take up about 100 c.c.;

TABLE 4.

VOLUMES OF EACH CATCH IN CUBIC CENTIMETRES AFTER SETTLING FOR 24 HOURS.

Depth.	1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.
Surface	25 c.c.	225 c.c.	340 c.c.	205 c.c.	75 c.c.
II	50 "	220 "	145 "	200 "	150 "
III	220 "	250 "	150 "	230 "	335 "
IV	315 "	300 "	150 "	205 "	440 "
V	195 "	420 "	340 "	250 "	260 "

the operation was repeated 5 or 6 times until the complete 500 c.c. had been extracted, the whole being well stirred up between each dip. Taking 5 or 6 dips for each sample probably tended to increase the accuracy of the method, by smoothing over errors caused by organisms clinging together in clumps, although great care was taken to see that the various animals were separated from one another as much as possible.

For one bottle, the surface haul of the 2nd series, 10 such samples were taken, and thus a complete count was made. The results are set out in Table 3, and in view of the various sizes and shapes of the organisms in question the method is probably as good as can be found. On no occasion in which the average number of any one species in a sample was over 20 was the probable error greater than 15%. If there were less than 20 individuals of a species in a sample no importance could be attached to the actual figure, but at any rate it is a proof that the organism was not very abundant.

Before each catch was made up to 5000 c.c. a complete count was made of certain organisms that were easy to pick out on account of their

size or their colour, such as various mysids; *Turris pileata*, *Anomalocera patersoni*, *Themisto gracilipes*.

Those with any distinctive colour could be very quickly observed by placing the plankton in a shallow tray over a white ground for coloured animals and a black ground for white forms.

Also each catch was placed in a large measuring cylinder, and allowed to settle for 24 hours. The settled volume was then read off in cubic centimetres. The results are set out in Table 4. The actual catches in the first two series were photographed, and Plate I gives a very graphic impression of how the two upper layers were filled up at dusk.

For the identification of the various species my thanks are especially due to Dr. M. V. Lebour for the great assistance she has given me, to Mr. E. T. Browne for confirmation of the various Medusæ, and to Mr. R. Gurney for his assistance with the Decapod larvæ. My thanks are also due to Dr. E. J. Allen, F.R.S., and other members of the staff for their kind advice on many points.

#### RESULTS.

In considering the results shown by the numbers obtained, three points must be borne in mind that tend to obscure the true picture of events.

1. The net was not fitted with a closing apparatus: in Table 1 we can see the time required to shoot and haul the net at each successive depth. This time naturally increases for the deeper hauls. The time of shooting for the deepest hauls is from  $1\frac{1}{2}$  to 2 minutes, the time of hauling 2 to  $2\frac{1}{2}$  minutes. While shooting the net will be fishing to a certain extent, though the catch would probably be very small as the net is moving only a very slight distance through the water or is almost stationary, the ship leaving it behind as the warp runs off the winch; when hauling, however, the net is fishing efficiently for 2 to  $2\frac{1}{2}$  minutes over and above the scheduled 10 minutes. Whereas in the daytime this will not cause a very great error, because for half this time the net will be passing through the upper layers where there is little plankton; at night the error will be greater when the layers from top to bottom become filled with plankton.

No attempt has been made to correct for this; it would be too complicated on account of the different numbers met with at different levels.

2. As mentioned before each haul is taken in succession, and the net in one series, therefore, takes samples from five different bodies of water. This may cause misleading results if at any time during the series the ship passes into a region either more or less populated. There do not, however, appear to be many signs of this; when forms were encountered in large numbers in any one haul they were present in correspondingly

large numbers in the remaining samples of the series, and similarly they might be proportionately scarce right through the layers.

For instance, the two series of day hauls for the zoea of *Porcellana* sp. (p. 803), although showing very different totals when the five catches of each series are added together, nevertheless show remarkably similar proportionate distribution.

It is highly probable that when animals of the size taken in the ring-trawl are present in swarms that they are distributed over a very large area, in a manner very different from the possible compact little swarms of the smaller copepods.

TABLE 5.

	TOTAL NUMBERS OF ORGANISMS IN EACH CATCH.				
	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	958 <i>1.1%</i>	19,851 <i>15.2%</i>	28,487 <i>27.4%</i>	1709 <i>2.9%</i>	3291 <i>2.6%</i>
II	3408	20,774	13,043	5380	8403
2-7 m.	<i>3.8%</i>	<i>15.9%</i>	<i>12.5%</i>	9%	<i>6.6%</i>
III	17,458	21,968	11,754	18,401	35,659
9-15 m.	<i>19.5%</i>	<i>16.9%</i>	<i>11.4%</i>	<i>30.9%</i>	<i>28.3%</i>
IV	27,828	25,223	14,546	15,859	51,535
16-20 m.	<i>31.1%</i>	<i>19.4%</i>	<i>14.1%</i>	<i>26.6%</i>	<i>40.7%</i>
V	39,818	42,399	36,384	18,218	27,454
30-34 m.	<i>44.5%</i>	<i>32.6%</i>	<i>35%</i>	<i>30.6%</i>	<i>21.8%</i>
Total	89,470 <i>100%</i>	130,215 <i>100%</i>	104,214 <i>100%</i>	59,567 <i>100%</i>	126,342 <i>100%</i>

3. There are errors due to the method of sampling, but these are considered to be insufficient to affect the significance of the figures obtained.

Further, this is only *one* observation in *one* region on a *single* night in the year, and there is, therefore, no justification in attempting to draw conclusions as to the normal behaviour of any organism from the results obtained.

This is only a contribution to the many similar observations that must be made before we can understand the regular habits of the animals in question. There are so many factors making up the environment that it is necessary to have observations taken under all conditions. In this case collecting took place during a period of full moon, and it is highly possible that on dark moonless nights the animals' behaviour might be different. Also there is the time of year to be considered, the summer

distribution probably being very dissimilar from that in winter. Herdman and Scott (7), in their fifteen years' study of the plankton at Port Erin, are repeatedly remarking on the occurrence of large numbers of forms on the surface up to mid April that have their position of maximum abundance in the daytime at a depth of a few fathoms in summer, and my collections are showing the same results.

Table 5 gives the total numbers of organisms taken in each haul, and shows how the two upper layers have been filled up between 9 p.m. and midnight. Also it corrects the idea given by the settled volumes showing that by 4 a.m. most of the organisms have left the surface, the high volume being caused by large numbers of *Turris*.

Altogether some fifty different organisms occurred in this collection, and it is, of course, the sum of the various movements of each kind of animal that gives rise to the figures quoted in Table 5.

On this occasion the various distributions of the different species throughout the five series show that all the animals in question did not behave in the same manner. The reactions to the various environmental changes that occur in the passage from daylight to daylight shown by the animals captured on this occasion can be grouped under four headings.

1. Those that definitely migrated to the surface at night from the deeper layers in which they dwelt by day, showing a very large increase in numbers on the surface with a corresponding decrease in the deeper layers (Figure 2).

Some forms that exhibited this reaction were :—

*Calanus finmarchicus*, *Turris pileata*, *Tornaria* larvae, *Upogebia* larvae, *Callianassa subterranea* larvae, *Themisto gracilipes*, possibly *Tomopteris*, *Urothoë* sp.

2. Those that did not show a definite migration to the surface at night, but merely extended their distribution into the surface layers, which they avoided by day. In this case a diminution in numbers was shown at the region of maximum intensity in daytime, so that the distribution from surface to deeper layers was more or less uniform.

Such a reaction was exhibited by :—

Porcellana zoea, Crab zoea, and *Sagitta bipunctata* (Figure 3).

3. Those forms whose daytime distribution altered little or not at all at night (Figure 4). These were :—

*Pandalus* larvae, *Galatheid* larvae, *Pagurid* larvae, *Phialidium* sp., *Obelia* sp., *Apherusa* sp., Larval molluscs.

4. Those that showed a movement upwards from the bottom, appearing in large numbers at night at a level about 10 fathoms from the bottom.

These were mostly benthic forms, which probably live normally in the daytime, actually crawling on the bottom, e.g. Amphipods, burrowing e.g. Cumacea, or free swimming in the water layers immediately adjacent to the bottom, e.g. Mysids and also the later stages of the young of various decapods that are living near the bottom preparatory to taking up their permanent habitat there by day when they have reached their adult stages (Figure 5).

These were :—

*Leptomysis gracilis*, *Haplostylus Normani*, *Schistomysis* sp., *Dasymysis* sp., Crangonid post-larvæ, Galatheid post-larvæ, *Upogebia* sp. post-larvæ, *Eupagurus* sp. *Glaucothoë*, *Diastylis* sp., Cumacea (indet).

In the following list all the animals present in the collections are grouped under their respective types of behaviour. An asterisk (\*) denotes that the species in question was present only in small numbers, which were regarded as insufficient to be conclusive, though showing a tendency towards a definite behaviour. (c) signifies that a complete count was made of the animal in question; figures for the remaining species were obtained by sampling.

#### DEFINITE MIGRATION TO SURFACE.

<i>Stomotoca dinema</i> *. (c.)	<i>Anchialus agilis</i> . (c.)
<i>Turris pileata</i> . (c.)	<i>Themisto gracilipes</i> . (c.)
<i>Cosmetira pilosella</i> *. (c.)	Urothoë sp. (c.)
<i>Tomopteris helgolandica</i> . (?)	Callianassa larvæ.
<i>Calanus finmarchicus</i> .	Upogebia „
<i>Candacia armata</i> .	Tornaria „

#### EXTENSION OF DISTRIBUTION INTO UPPER LAYERS.

<i>Saphenia gracilis</i> *. (c.)	Palinurus Phyllosoma. (c.)
<i>Sagitta bipunctata</i> .	Crab zoea.
Porcellana zoea.	Crab Megalopa.

#### LITTLE OR NO MOVEMENT.

<i>Steenstrupia rubra</i> .	Apherusa sp.
Obelia sp.	Leander sp. larvæ.
Phialidium sp.	Pandalus „
<i>Aglantha rosea</i> .	Processa „
Peachia sp.	Galatheid „
Pœcilochètus larvæ.	Pagurid „
<i>Anomalocera Patersoni</i> . (c.)	<i>Limacina retroversa</i> .
Caligus sp. (c.)	Larval gastropods.

## MOVEMENT UPWARDS FROM BOTTOM OR DEEP LAYERS.

<i>Leptomysis gracilis</i> . (c.)	Cumacea (indet.). (c.)
<i>Dasymysis longicornis</i> . (c.)	Amphipoda ,, (c.)
<i>Schistomysis</i> sp. (c.)	Crangonid post-larvæ.
<i>Erythrops</i> sp. (c.)	Galatheid ,,
<i>Haplostylus Normani</i> . (c.)	Upogebia ,,
<i>Diastylis</i> sp. (c.)	Eupagurus Glaucotohö.

In the remaining pages the results for each organism are dealt with in detail.

## COELENTERATA.

## ANTHOMEDUSÆ.

## STEENSTRUPIA RUBRA FORBES.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	—	—	—
II 2-7 m.	—	—	—	—	—
III 9-15 m.	—	—	—	—	—
IV 16-20 m.	2	—	40	10	2
V 30-34 m.	12	—	23	40	29

This, the medusa of *Corymorpha*, was only taken in the deeper water layers in small numbers, and exhibited no marked vertical movements at night.

## STOMOTOCA DINEMA L. AGASSIZ.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	22	1	—
II 2-7 m.	2	—	2	10	4
III 9-15 m.	29	—	1	9	3
IV 16-20 m.	11	3	3	28	5
V 30-34 m.	—	3	6	39	3

This medusa was only taken in small numbers, but nevertheless there appears to be quite a marked assemblage at the surface at midnight; in all the other surface hauls it was absent save at 4 a.m., when one individual only was taken.

## TURRIS\* PILEATA (Forsk.) (Figure 2).

	1st Series, 3.25 p.m. to 4.45 p.m.	2nd Series, 7.55 p.m. to 9.17 p.m.	3rd Series, 10.50 p.m. to 12.20 a.m.	4th Series, 2.50 a.m. to 4.16 a.m.	5th Series, 8.45 p.m. to 10.11 a.m.
Surface	7 1.2%	217 44.5%	700 71.3%	517 31.6%	5 1.5%
II	36	103	46	484	44
2-7 m.	5.9%	22.1%	4.7%	29.6%	13%
III	285	61	18	151	134
9-15 m.	46.9%	12.5%	1.8%	9.2%	39.8%
IV	261	71	44	184	105
16-20 m.	42.9%	14.5%	4.5%	11.2%	31.2%
V	19	31	174	301	49
30-34 m.	3.1%	6.4%	17.7%	18.4%	14.5%

[In this and all succeeding tables in which percentages occur, each catch is expressed as a percentage of the total number of individuals of that species caught at the five depths of the series in which it occurs.]

A definite migration to the surface at midnight was shown. In the daylight the region of greatest intensity was somewhere between 10 and 25 metres (Fig. 2).

By 9 p.m. the majority were caught above a depth of 10 metres, and at midnight they were taken in greatest numbers right at the surface. At dawn they were beginning to leave the surface, and at 10 the next morning their distribution was much as that of the previous afternoon.

There are no previous records of the vertical distribution of this species.

## LEPTOMEDUSÆ.

## OBELIA SP.

	1st Series, 3.25 p.m. to 4.45 p.m.	2nd Series, 7.55 p.m. to 9.17 p.m.	3rd Series, 10.50 p.m. to 12.20 a.m.	4th Series, 2.50 a.m. to 4.16 a.m.	5th Series, 8.45 a.m. to 10.11 a.m.
Surface	—	170	40	9	—
II 2-7 m.	—	50	10	1	50
III 9-15 m.	—	270	—	—	2160
IV 16-20 m.	540	1880	130	—	2690
V 30-34 m.	30,600	18,670	14,852	830	6780

At all hours *Obelia* had its maximum occurrence at 30-34 m., and probably deeper. In the first three series of hauls it was encountered in very dense swarms at this depth. It cannot be said that there was any marked movement towards the surface at night: there were certainly larger numbers present in the upper layers during the hours of darkness,

\* The generic name *Turris* has been used here, although Mayer (12) remarks that the name is preoccupied and should be *Clavula*, as it will be more familiar to readers.

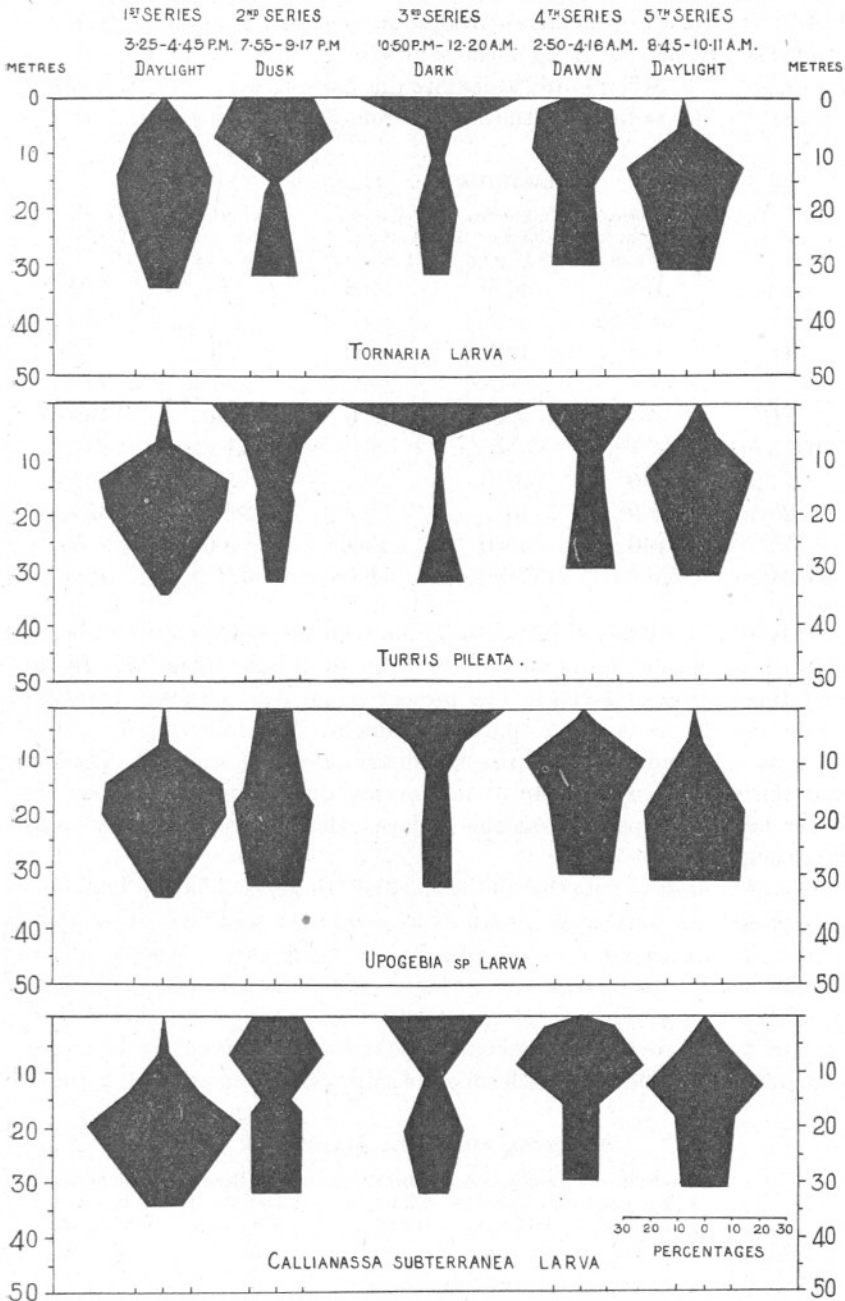


FIGURE 2. The vertical distribution of the above species between daylight, July 15th, and daylight, July 16th, 1924. The catch at each level has been expressed as a percentage of the total number caught in the five hauls of the series to which it belongs. These forms showed a definite migration to the surface in the dark hours.



but in view of the very dense swarms present in the deeper layers it is doubtful whether much significance should be attached to it.

Gough (4, p. 345) records a definite diurnal migration in this medusa, noting that it was taken at the surface from 8 p.m. until 1 a.m.

PHIALIDIUM SP. (Figure 4).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 28.45 a.m. to 10.11 a.m.
Surface	153	2330	460	4	720
	10.6%	18.3%	16.1%	0.2%	4.1%
II	154	1940	290	240	3430
2-7 m.	10.6%	15.3%	10.2%	12.7%	19.4%
III	165	1380	170	640	4980
9-15 m.	11.4%	10.9%	6%	33.8%	28.2%
IV	130	2040	380	410	5660
16-20 m.	9.1%	16%	13.3%	21.6%	32%
V	840	5030	1550	600	2890
30-34 m.	58.3%	39.5%	54.4%	31.7%	16.3%

This form, probably chiefly *Phialidium hemisphericum*, on this occasion showed no signs of being affected by changes in light intensity. In the first three series of hauls it was present in greatest numbers at about 30 metres, that is from 3.25 p.m. to midnight. The following day, however, at dawn and after sunrise the distribution is somewhat different, and the medusæ were more or less evenly distributed throughout the water layers except right at the surface, where there were only small numbers (Fig. 4).

It is of interest to note that in the 2nd and 5th series of hauls *Phialidium* was present in very large numbers as compared with the other three series. It is reasonable to suppose that on these two occasions the net was fishing in a dense area, and seeing that the large numbers are present in all layers some idea of the size of these areas may be gathered from the fact that it took about  $1\frac{1}{2}$  hours to take the full series of hauls in each case during the whole of which time the ship was towing at about 2 knots.

COSMETIRA PILOSELLA HARTLAUB.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 p.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	19	24	—	—
II 2-7 m.	—	26	1	—	1
III 9-15 m.	—	22	—	13	59
IV 16-20 m.	1	45	1	11	13
V 30-34 m.	3	25	6	28	9

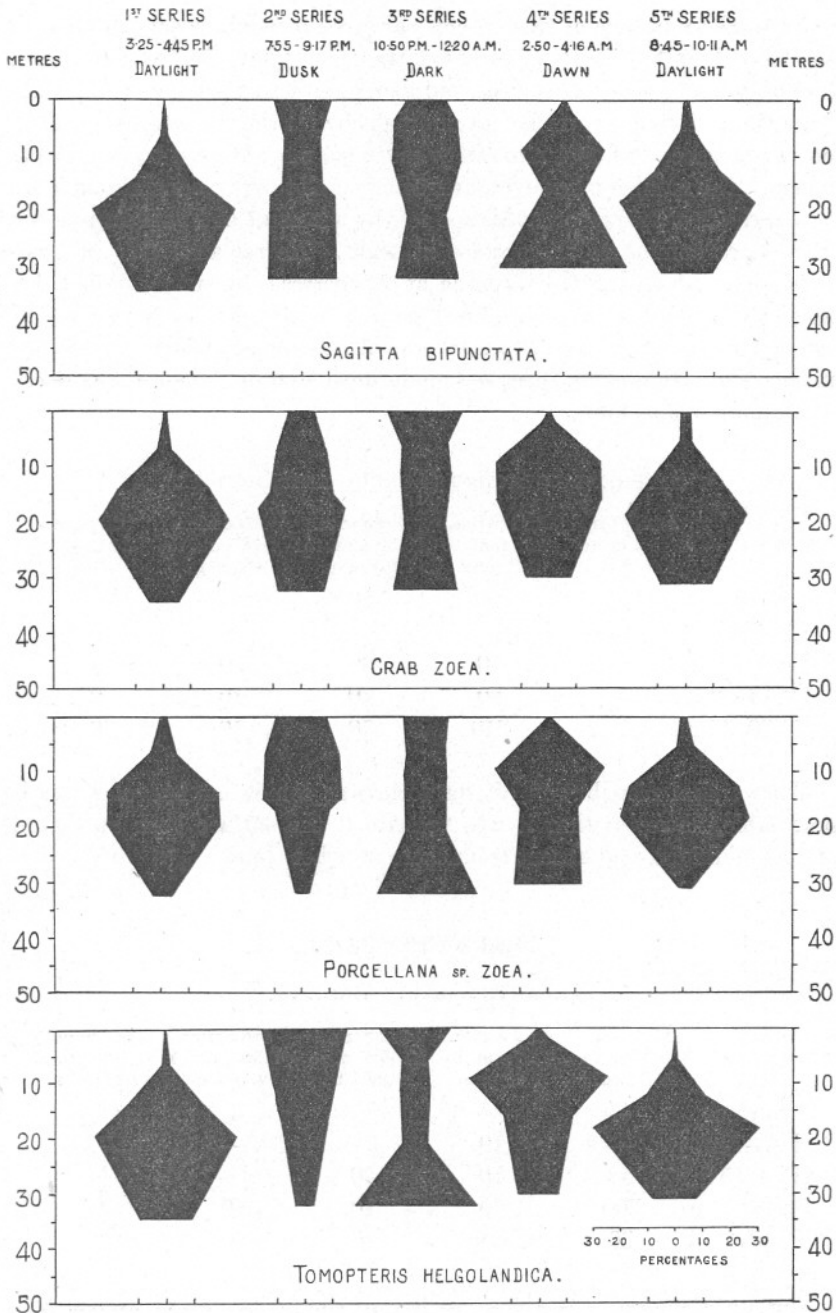


FIGURE 3. The vertical distribution of the above species between daylight, July 15th, and daylight, July 16th, 1924. The catch at each level has been expressed as a percentage of the total number caught in the five hauls of the series to which it belongs. The three upper forms showed an expansion of their day distribution into the surface layers,

From the numbers of this species captured it would seem that here is shown a definite migration to the surface at night. In the daytime it was only taken below 12 metres, but at 9 p.m. it was present in all layers from the surface downwards: at midnight by far the majority were taken on the surface, and at 4 a.m. they had once more retired to the deeper layers. The numbers, however, are rather small to draw conclusions from.

Gough (4, p. 345) records this species (by the name of *Euchilota pilosella* Forbes) as coming to the surface at night. He remarks that it "was only observed during the daytime at 30 metres; at sunset it had disappeared from the 30-metre level, and had not yet appeared at the 10- or 1-metre level. By 10 p.m. it was at the surface, where it remained until 1 a.m. It was not observed again until 10 a.m., when it was taken at 30 metres once more."

#### SAPPHENIA GRACILIS (FORBES AND GOODSIR).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	26	20	—	—
II 2-7 m.	—	—	—	2	—
III 9-15 m.	—	50	30	20	—
IV 16-20 m.	—	90	10	10	30
V 30-34 m.	—	210	50	10	70

The vertical distribution of this form was somewhat irregular; it is noticeable, however, that it was present at the surface both at 9 p.m. and at midnight, and absent from there at other times.

#### TRACHYMEDUSÆ.

##### AGLANTHA ROSEA BROWNE.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 a.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	—	1	—
II 2-7 m.	—	10	—	—	—
III 9-15 m.	58	10	20	—	—
IV 16-20 m.	200	50	10	40	10
V 30-34 m.	30	110	30	20	10

This form showed a tendency to live in the deeper water layers, and from the numbers captured it would appear that there was little vertical movement at night.

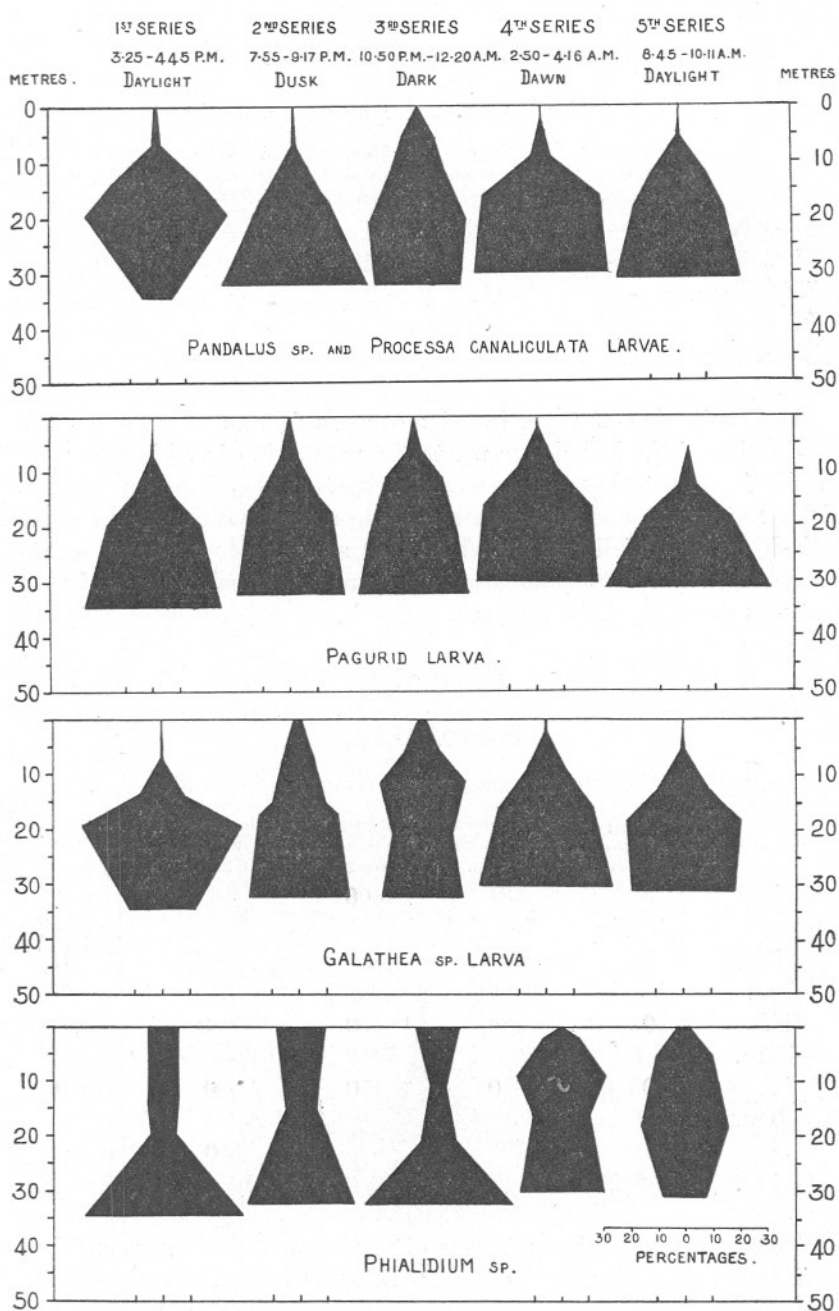


FIGURE 4. The vertical distribution of the above species between daylight, July 15th, and daylight, July 16th, 1924. The catch at each level has been expressed as a percentage of the total number caught in the five hauls of the series to which it belongs. These forms showed little or no movement at night.

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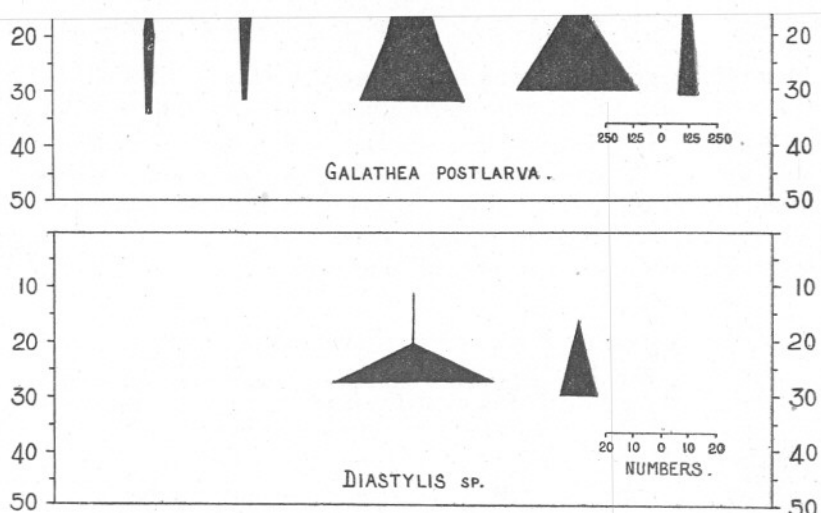


FIGURE 5. The vertical distribution of the above species between daylight, July 15th, and daylight, July 16th, 1924, showing actual numbers caught at each depth. These are bottom living forms, or deep living by day, which moved upwards at night,

## ANTHOZOA-ZOANTHARIA.

## PEACHIA SP. YOUNG STAGES.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	11	1	—	1
II 2-7 m.	—	7	1	—	20
III 9-15 m.	—	14	1	4	23
IV 16-20 m.	5	14	4	3	24
V 30-34 m.	2	21	14	1	19

The distribution of these larval anemones follows very closely the distribution of the *Phialidium* sp. to the manubria of which they were usually found attached. It is doubtful whether they have any powers of free movement, and they are dependent on their position in the water entirely on the *Phialidium* by which they are carried, and must consequently display the same apparent disregard to diurnal changes of light that was shown by these medusæ.

## ANNELIDA.

## POLYCHAETA.

## TOMOPTERIS HELGOLANDICA GREEF (Figure 3).

	1st Series. 3.25 p.m. 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	3 0.7%	581 31.7%	400 25.4%	46 1.3%	2 0.1%
II	13	460	150	312	20
2-7 m.	3.2%	25.1%	9.5%	8.5%	1.4%
III	108	360	180	1880	300
9-15 m.	26.4%	19.7%	11.4%	50.9%	21.6%
IV	205	310	150	920	840
16-20 m.	50.1%	16.9%	9.5%	24.9%	60.4%
V	80	120	695	530	230
30-34 m.	19.6%	6.6%	44.1%	14.4%	16.5%

Whereas in the daytime the zone of maximum abundance was below 10 metres, at 9 p.m. and at midnight this species was present in large numbers right on the surface, the numbers diminishing with the depth. At midnight there were still large numbers on the surface and fewer deeper down; in the bottom haul, however, a large catch of 695 was

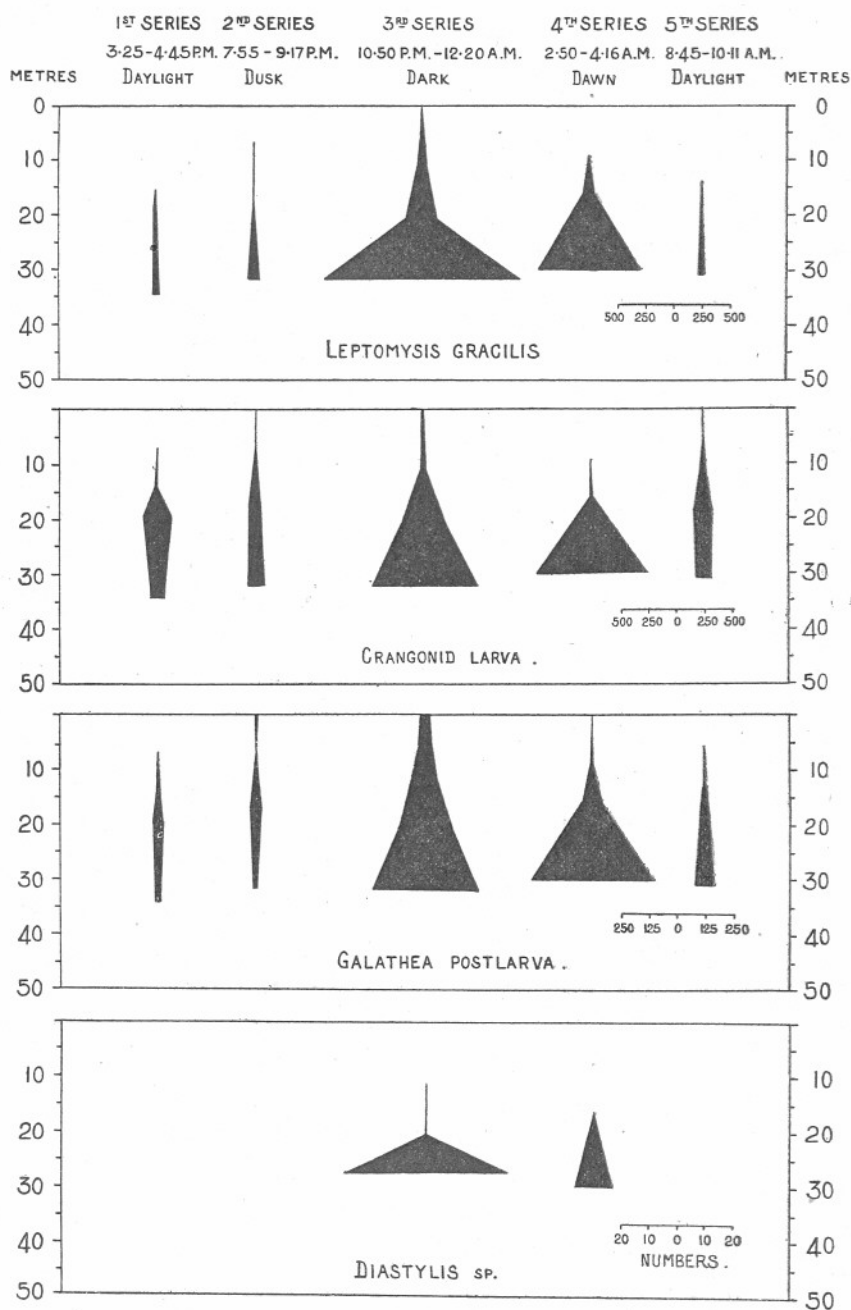


FIGURE 5. The vertical distribution of the above species between daylight, July 15th, and daylight, July 16th, 1924, showing actual numbers caught at each depth. These are bottom living forms, or deep living by day, which moved upwards at night,

taken; but it is noteworthy that these were nearly all very small individuals, and there were few of the large adults which were so marked a feature of the upper layers.

It is probable that there is exhibited here a definite migration to the surface layers; the diagram (Fig. 3), however, does not show the typical migration figure on account of the large number of small individuals encountered in the bottom haul. There is a possibility that the behaviour of the smaller forms differs somewhat from that of the full-grown adults: their swimming powers would not be so great, and in the upward migration they would tend to be left behind: this appears also in Series IV and V at dawn and daylight in which at 4 a.m. the catches of 46 at the surface and 312 at 2 metres both consisted chiefly of small worms, as did that of 300 individuals at 12.5 metres at 9.30 a.m., showing again that the large forms were able to return quicker to the deep water.

Gough (4), on July 1st to 2nd, 1903, observed the vertical movements of *Tomopteris*, using the Garstang closing net at four depths: 1 m., 10 m., 30 m., and 70 m. He says: "During the hottest part of the day the bulk of the *Tomopteris* was found near the bottom at 70 metres, only very few being at 30 metres. Shortly before sunset single specimens were found at 10 metres and 35 metres, the majority being still at the bottom. At 10 p.m. they had reached the surface, being in all layers from the bottom upwards. They remained at the surface till 12.55 a.m. At 3.50 a.m. they had left the top layers and retired to 10 metres and lower; by 7 a.m. they had sunk still deeper, not being found above 30 metres. By midday on July 2nd, most of them were again at 70 metres."

These results agree closely with mine, especially in the distributions from 9 p.m. to 4 a.m.: the daylight distributions, however, differ somewhat but Gough's observations were made in much deeper and probably clearer water. My daytime catches showed a maximum abundance between 15 and 30 metres: at 9 p.m. and midnight they were present in all layers from surface to bottom, and at 4 a.m. the majority had retired from the surface to a depth of 10 metres.

LARVÆ OF *PÆCULOCHÆTUS SERPENS* ALLEN.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	—	—	—
II 2-7 m.	1	10	—	1	—
II 9-15 m.	8	—	—	—	80
IV 16-20 m.	50	110	—	10	100
V 30-34 m.	90	300	40	20	50

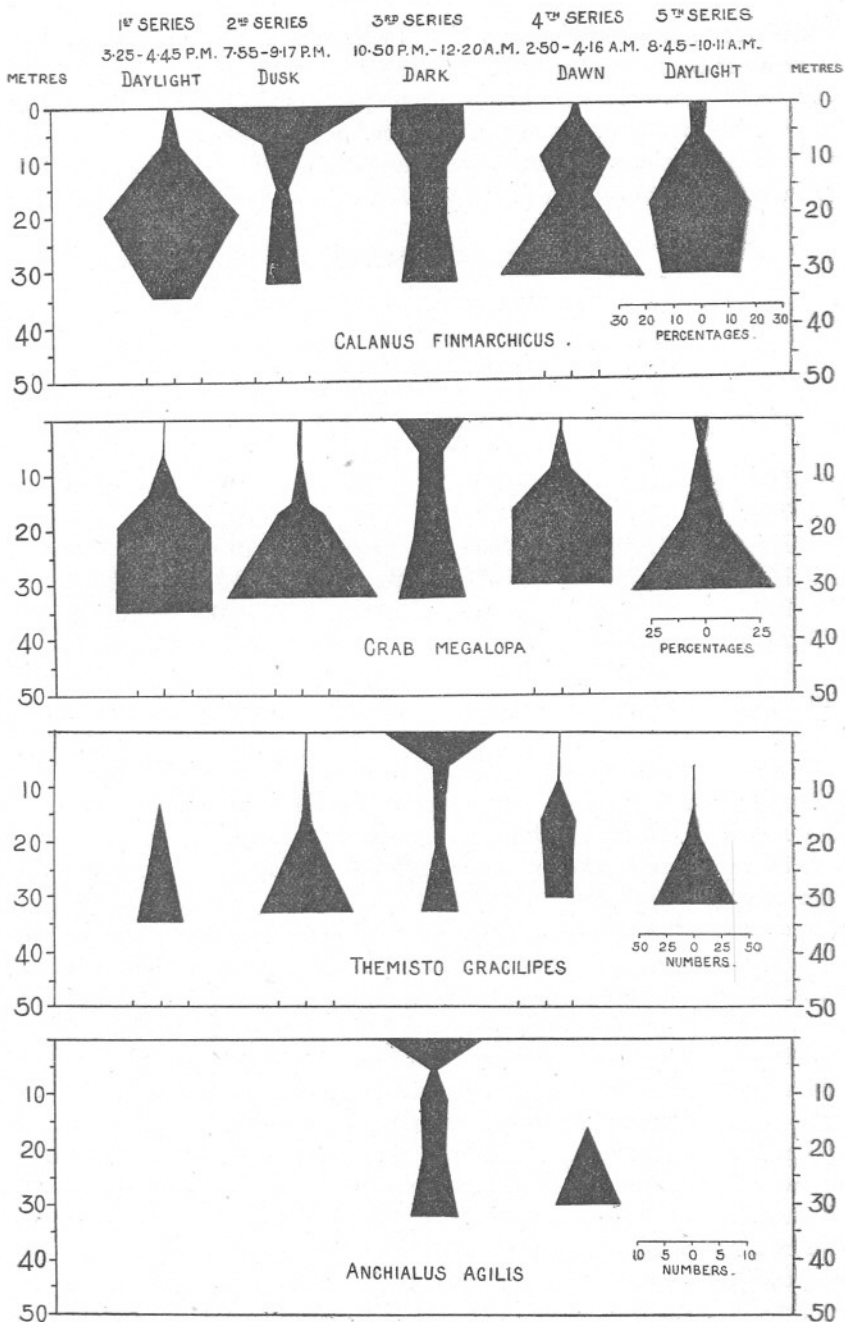


FIGURE 6. The vertical distribution of the above species between daylight, July 15th, and daylight, July 16th, 1924. Calanus, Themisto and Anchialus shows definite migrations to the surface.



The very characteristic larva of this seldom seen polychaete was taken in greatest abundance only in the deeper layers by night as well as by day, and there was no marked movement unless the large number taken at 30 metres at 8 p.m. has any significance. If this was so we would gather that at other times the larva was most abundant in the layers below 30 metres, and that at dusk it had risen slightly higher in the water.

### CHÆTOGNATHA.

#### SAGITTA BIPUNCTATA QUOY AND GAIMARD (Figure 3).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	98	2060	1040	66	355
	1.8%	21.8%	14.9%	2.1%	2.5%
II	196	1230	1600	203	760
2-7 m.	3.5%	13%	23%	6.2%	5.3%
III	1195	1460	1760	1010	3400
9-15 m.	21.3%	15.5%	25.3%	30.8%	23.7%
IV	2925	2290	990	490	7130
16-20 m.	52.2%	24.3%	14.2%	14.9%	49.7%
V	1190	2400	1573	1510	2710
30-34 m.	21.2%	25.4%	22.6%	46%	18.8%

In the daylight *Sagitta bipunctata* occurred in greatest abundance below a depth of 6 metres. By 9 p.m. it was taken in more or less equal numbers from the surface down to 31 metres; a similar distribution was maintained at midnight. At dawn the following day the upper 10 metres were again comparatively empty (Fig. 3).

The vertical distribution of this species has been worked up at length by Michael in the San Diego region (13). He concludes that between 6 a.m. and 6 p.m. the species is most abundant between 15 and 20 fathoms (ca. 27-36 m.), and between 6 p.m. and 6 a.m. it is most abundant above 15 fathoms. Further, that it has a maximum abundance at the surface within an hour after sunset, and then deserts the surface returning to cause a second maximum within an hour after sunrise.

Herdman, Scott (9) say: "A haul of the shear-net five miles off land at about 10 fathoms, on April 14th, gave 301 large specimens of *Sagitta*, although the surface nets worked at the same time caught none. . . . This result suggests that at that time, although not present at the surface, *Sagitta* was abundant a few fathoms below." And in later papers similar remarks on the distribution in the daytime point to the most populous zone being a few fathoms below the surface.

## CRUSTACEA.

## COPEPODA.

## CALANUS FINMARCHICUS (GUNNER) (Figure 6).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	27	4814	2410	63	150
	1.1%	60.1%	26.3%	2.4%	6.4%
II	171	1200	2450	168	110
2-7 m.	6.6%	15%	26.7%	6.4%	4.7%
III	747	420	1190	700	560
9-15 m.	28.9%	5.1%	13.1%	26.5%	24.1%
IV	1265	590	1280	320	840
16-20 m.	49%	7.4%	13.9%	12.1%	36%
V	370	990	1826	1390	670
30-34 m.	14.4%	12.4%	20.0%	52.6%	28.8%

This species was taken in the greatest numbers in the daytime at a depth of about 20 metres. It was present in small numbers above 6 metres, but below this at 12 metres there was a sudden large increase in abundance. By 9 p.m. large numbers had collected between 0 and 7 metres, and by far the majority were captured in the surface haul. At midnight the distribution was more or less even from surface to 30 metres with a tendency to larger numbers in the upper layers. By 4 a.m. Calanus was again seeking the deeper layers (Fig. 6). Whether there is any significance in the fact that at this time (4th series) the greatest number were caught in the deepest haul at 30 metres it is impossible to say from a single record, but it is curious that this dawn distribution is exactly similar to that shown by *Sagitta bipunctata* (Fig. 3).

Esterley has shown a similar diurnal migration of Calanus in the San Diego region, California (2). He found the region of maximum abundance in the daytime to be at 200 fathoms, in the evening at 100 fathoms, and at midnight at 5 to 10 fathoms, while from 4 to 6 a.m. it is at 100 fathoms.

He says: "The animals appear to leave the surface before the light increases at all in intensity. This suggests that decreasing light is not the cause of the downward movement" (p. 337).

I have no observation between 12.20 and 4 a.m. at the surface, but at any rate the 12.20 haul in the 3rd series indicates that they had already started to leave the surface.

Although naturally my depths of the various maxima do not agree with Esterley's results on account of the shallowness of the water and the

greater turbidity of coastal waters and probably the lesser strength of the light due to the differences in latitude, the general type of movement shown is in very close agreement.

Farran (3) says: ". . . while eggs and larvæ are to be found chiefly at the surface the main body of adult spawners occurs deeper, as Damas shows for the larger northern forms . . . adults occurring at 20-100 m."

CANDAÇIA ARMATA BOECK.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	1 0.2%	572 30.9%	220 24.5%	2 0.5%	— 0.0%
II	11	160	180	20	30
2-7 m.	2.4%	8.7%	20%	5%	5.2%
III	83	270	150	130	20
9-15 m.	17.6%	14.6%	16.7%	31.5%	3.5%
IV	235	330	90	130	90
16-20 m.	50%	17.7%	10%	31.5%	15.5%
V	140	520	300	130	440
30-34 m.	29.8%	28.1%	28.8%	31.5%	75.8%

In daylight this copepod was present in greatest numbers below 13 m. : by 9 p.m. it was taken in the surface hauls in large numbers, and was still present there at midnight. By 4 a.m. it had again left the surface layers. This behaviour would appear to have been very similar to that of *Calanus finmarchicus*, except that at 8 p.m. it was taken in large numbers at a depth of 30 m. as well as at the surface.

Scott remarks (16): "Though it may not be described as a deep-water species, it is frequently obtained at moderate depths. Its vertical range, however, does not appear to greatly exceed 200 m."

Gough (4, p. 336) says that it "occurs in all depths in the Channel from 150 metres to the surface, and is usually commoner in the lower layers."

ANOMALOCERA PATERSONI TEMPLETON.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	27	25	204	7	26
II 2-7 m.	16	16	16	5	13
III 9-15 m.	6	5	20	171	23
IV 16-20 m.	8	9	29	172	50
V 30-34 m.	2	11	36	30	26

This copepod would appear to be undisturbed by changes in light. On this occasion it was taken in greatest numbers on the surface at 4.30 p.m., at 9 p.m., and at midnight; but at dawn the next day it appeared in much larger quantities at 9 and 16 m. than elsewhere, and by daylight it was present in all layers from the surface to 30 m.

Scott (16, p. 142) says: "Its usual habit is to swim at or near the surface. . . . Although its vertical range is said to extend from the surface to about 700 m. it appears to be rarely met with in such deep water."

Gough (4, p. 336) says: "*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."

Seeing that this form is evidently capable of enduring the strongest light often living at the surface in the daytime it seems unlikely that it would show diurnal rhythm due to changes in light. It is possible, though, that on account of its carnivorous and predatory habits, as shown by Lebour (11), it might exhibit feeding migrations and that its presence in deeper layers at dawn, on this occasion, could be accounted for by its having followed its food down from the surface where it was abundant at night.

## CALIGUS SP.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	1	—	—	1
II 2-7 m.	1	3	3	2	—
III 9-15 m.	2	3	2	2	6
IV 16-20 m.	5	1	2	4	4
V 30-34 m.	1	2	2	2	4

Free-swimming forms were not abundant, and the numbers taken were insufficient to show vertical distribution; but they show the possibility that this form is evenly distributed through all layers by night, tending to be more abundant below 6 metres in the daytime.

## MYSIDACEA.

## LEPTOMYSIS GRACILIS (G. O. SARS) (Figure 5).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	2	—	—
II 2-7 m.	—	1	8	—	—
III 9-15 m.	—	6	78	7	—
IV 16-20 m.	30	16	289	99	1
V 30-34 m.	86	113	1793	942	25

In the daytime this Mysid was taken in small numbers at 20 and 30 metres only; at dusk the number in the lower layers had increased slightly, and one individual was taken at a depth of 7 metres. At midnight the number taken at 30 metres had increased tremendously, and two individuals were taken on the surface; at dawn they were still present in fair numbers at 30 metres, but by 9 a.m. they had resumed their daytime distribution (Fig. 5). On this occasion then *Leptomysis*, which normally lives in the water layer contiguous with the bottom by day, did not rise in large numbers much above 20 metres from the bottom.

DASYMYSIS LONGICORNIS (MILNE EDWARDS).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	—	—	—
II 2-7 m.	—	—	—	—	—
III 9-15 m.	—	—	5	—	—
IV 16-20 m.	1	—	22	—	—
V 30-34 m.	2	1	93	59	1

Although taken in smaller numbers than *Leptomysis* this species shows essentially the same behaviour.

SCHISTOMYSIS SP.

This species shows the same behaviour as *Leptomysis*; that is, if the numbers taken are indicative of its rarity compared with *Leptomysis gracilis*. It may, of course, mean that this species as also *Erythrops* and *Haplostylus* did not ascend so high in the water as *Leptomysis*, and that if a deeper haul had been taken much larger numbers would have been caught.

It was not captured at any of the levels in the 1st, 2nd, and 5th series. At 11 p.m. 3 were taken at 20 metres and 27 at 32 metres. At 3 a.m. only 6 were caught at 30 metres and none at the other levels.

ERYTHROPS SP.

Only 3 individuals of this species were taken, 1 at 20 metres at 11.15 p.m. and 2 at 32 metres at 11 p.m. They were absent in all the day hauls, at dusk and at dawn.

HAPLOSTYLUS NORMANI G. O. SARS.

This Mysid was only taken in very small numbers: it was absent in all hauls except those at 11, 20, and 32 metres at 11 p.m., when the numbers caught were 1, 2, and 6 respectively, and at 30 metres at 3 a.m., when 9 individuals were caught. It would appear that their behaviour was very similar to that of *Leptomysis gracilis*.

## ANCHIALUS AGILIS G. O. SARS (Figure 6).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	17	—	—
II 2-7 m.	—	—	1	—	—
III 9-15 m.	—	—	5	—	—
IV 16-20 m.	—	—	5	—	—
V 30-34 m.	—	—	9	14	—

Unlike the other Mysids, which never rose much above 20 metres from the bottom, this form exhibited a very sudden migration towards midnight right to the surface; by 3 a.m. it was only taken at 30 metres (Fig. 6).

## CUMACEA.

## DIASTYLIS SP. (Figure 5).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	—	—	—
II 2-7 m.	—	—	—	—	—
III 9-15 m.	—	—	1	—	—
IV 16-20 m.	—	—	1	1	—
V 30-34 m.	—	—	58	14	—

This species was absent in all hauls in the 1st, 2nd, and 5th series: at 11 p.m. it was fairly abundant at 30 m., and in smaller numbers at 3 a.m.; but only 3 specimens were captured above this level (Fig. 5).

Sars (15) remarks that "the Cumacea are . . . on the whole, true bottom forms, though the more agile males of some species may be found at times swarming near the surface, especially at night." It is interesting to note that on this occasion the majority of this species taken 20 metres above the bottom were females.

## CUMACEANS (sp. indetermined).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	1	—	—	—
II 2-7 m.	—	—	2	—	—
III 9-15 m.	—	—	1	1	—
IV 16-20 m.	—	—	—	4	—
V 30-34 m.	—	—	9	25	—

Time would not admit of the identification of these Cumaceans, which probably consist of *Bodotrius* sp. and *Pseudocuma* sp. These appeared at 30 metres, and above, only in the dark hours.

## AMPHIPODA.

		THEMISTO GRACILIPES NORMAN (Figure 6).				
		1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.
		3.25 p.m. to 4.45 p.m.	7.55 p.m. to 9.17 p.m.	10.50 p.m. to 12.20 a.m.	2.50 a.m. to 4.16 a.m.	8.45 a.m. to 10.11 a.m.
Surface	—	1	99	3	—	—
II	2-7 m.	—	2	13	—	1
III	9-15 m.	1	7	11	3	1
IV	16-20 m.	13	13	8	31	11
V	30-34 m.	40	82	26	25	76

There are several observations on the occurrence of this species at the surface at night, which appears to be a common characteristic of the genus.

This series shows a region of greatest abundance in the daytime below a depth of 20 m. and a marked migration to the surface at midnight (Fig. 6).

This agrees with Stephensen's findings from the material collected in the Atlantic on the Danish Expedition, 1908-10 (17). He says: "During the night the species was only taken close to the surface (at most 25 m. w.), during the day almost exclusively with 65-100 m. w."

## APHERUSA SP.

		1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.
		3.25 p.m. to 4.45 p.m.	7.55 p.m. to 9.17 p.m.	10.50 p.m. to 12.20 a.m.	2.50 a.m. to 4.16 a.m.	8.45 a.m. to 10.11 a.m.
Surface		7	4	—	4	20
		1.2%	0.8%	0.0%	1.1%	3.2%
II		5	11	70	2	10
2-7 m.		0.9%	2.1%	7.8%	0.6%	1.6%
III		74	40	70	70	80
9-15 m.		12.8%	7.8%	7.8%	19.7%	12.6%
IV		290	200	260	140	210
16-20 m.		50.4%	38.8%	29.1%	39.3%	33.3%
V		200	260	494	140	310
30-34 m.		34.7%	50.5%	55.3%	39.3%	49.3%

These amphipods, consisting probably chiefly of *Apherusa clevii* G. O. Sars, exhibited no marked movement at night, being present in greatest abundance below 15 metres in all the five series of hauls. If anything there is a slight tendency to rise at midnight, but the numbers are not conclusive.

## UROTHOË SP.

This amphipod, which in the daytime adopts a benthic habit, showed a remarkably sudden migration to the surface at 9 p.m. when 40 were captured; at midnight there were still 2 at the surface and 2 at 30 metres, but they were absent in all the remaining hauls. None were taken in the daytime or at dawn.

## MIXED AMPHIPODS (sp. undetermined).

At midnight and dawn a number of bottom living amphipods were taken in the lower layers. At 11 p.m. 11 were taken at 20 metres, and 27 at 32 metres; but at 3 a.m., while 19 were caught at 30 metres, only a single individual occurred at 18 metres.

Time would not allow of the identification of these forms, but there were present probably at least 7 or 8 species, amongst which were recognised *Monoculodes* sp., *Bathyporeia* sp., and *Ampeliscus* sp., all true bottom-living forms in the daytime.

## DECAPODA.

## LEANDER SP. LARVÆ.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 p.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	8†	9†	10	9†	11†
II 2-7 m.	6†	10	10	10†	2
III 9-15 m.	3†	40	—	10	—
IV 16-20 m.	—	—	10	10	10
V 30-34 m.	—	—	—	—	—

† Denotes that a complete count was made, the remaining figures were obtained by sampling only.

These larvæ, which probably consist of both *Leander serratus* and *L. squilla*, were mostly of Stage V in development, that is the last larval stage before the first post-larvæ. They were noteworthy for being present in greater abundance on the surface layers than in the deeper water both in the daytime and at night: in this type of distribution they differed from all other decapod larvæ present in the collection.

## PANDALID SP. AND PROCESSA CANALICULATA LARVÆ (Figure 4).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	11 0.4%	4 0.2%	2 0.1%	1 0.1%	1 0.1%
II	87	20	180	1	20
2-7 m.	3.2%	1%	12.7%	0.1%	1.3%
III	922	390	280	110	300
9-15 m.	33.5%	20%	19.7%	7.5%	20.3%
IV	1440	490	510	630	490
16-20 m.	52.4%	25.1%	35.8%	43.1%	33.1%
V	290	1050	451	720	670
30-34 m.	10.5%	53.7%	31.7%	49.2%	45.2%



There are the larvæ of at least four species present in these samples. The majority are larvæ of *Pandalina brevirostris*; the other species are *Pandalus borealis*, *Processa canaliculata*, and *Spirontocaris* sp.

While *Processa canaliculata* is not classified at present as being a Pandalid, the larva as pointed out by Gurney (5) is almost indistinguishable from that of *Pandalus*. I have examined carefully twelve of the samples with the following results:—

1st Series.					
III.	Pandalid sp.	883,	<i>Processa canaliculata</i>	27,	<i>Spirontocaris</i> sp. 12
V	" "	240	" "	40	" " 10
2nd Series.					
Surface	" "	2	" "	2	" " —
III	" "	310	" "	80	" " —
IV	" "	400	" "	90	" " —
V	" "	870	" "	160	" " 20
3rd Series.					
Surface	" "	2	" "	—	sp. —
III	" "	250	" "	30	" " —
V	" "	391	" "	60	" " —
4th Series.					
Surface	" "	1	" "	—	" " —
III	" "	110	" "	—	" " —
V	" "	640	" "	80	" " —

It would seem from these results that the distribution of *Processa* is probably not unlike that of *Pandalus* sp. *Spirontocaris* larvæ are present in too small numbers to be significant.

Fig. 4 illustrates that these forms did not on this occasion show any marked change in their distribution through the period from daylight to daylight. There is perhaps a slight tendency to rise at midnight, but the larvæ never appeared in numbers in the surface layers. They were present always in largest numbers below 7 metres.

#### CRANGONID POST-LARVÆ (Figure 5).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	1	20	—	—
II 2-7 m.	—	20	20	—	10
III 9-15 m.	10	70	50	—	70
IV 16-20 m.	285	100	440	20	150
V 30-34 m.	120	140	973	1020	130

There are a few larval stages among these, but by far the majority were post-larvæ. This accounts probably for their vertical distribution, which was typical of many benthic forms, seeing that at this stage they must be seeking the bottom.

Their behaviour was exactly similar to that of the Mysids; in the daytime they were taken only in small numbers in the lower layers, but at 11 p.m. and 3 a.m. they were caught at 30 metres in large numbers (Fig. 5).

## PALINURUS PHYLLOSOMA.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	18	—	4	—
II 2-7 m.	1	30	—	5	—
III 9-15 m.	—	20	—	30	—
IV 16-20 m.	15	10	—	20	30
V 30-34 m.	—	10	—	20	30

The phyllosoma larva of the Rock Lobster was present in the daytime in greatest numbers below 12 metres: at 8-9 p.m. it was taken in all layers from 30 metres to the surface, but was most abundant in the upper layers: at midnight none were captured, so that we have no evidence as to the midnight vertical distribution. At 4 a.m. the majority had returned to below 2 metres.

## GALATHEID LARVÆ (Figure 4).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 p.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	15 0.3%	191 2.7%	240 3.6%	4 0.1%	10 0.1%
II	24	800	870	42	130
2-7 m.	0.4%	11.5%	13.1%	0.9%	1.5%
III	961	1390	2060	630	1570
9-15 m.	16.4%	19.9%	30.9%	14.7%	18.7%
IV	3430	2000	1470	1520	3490
16-20 m.	58.5%	28.7%	22.1%	35.4%	41.5%
V	1430	2600	2020	2100	3210
30-34 m.	24.4%	37.2%	30.3%	48.9%	38.2%

These larvæ were present in greatest numbers below 12 metres in the daytime: at dusk and at midnight they tended to become more evenly distributed from the upper layers downwards, but were at no time very abundant on the surface; although the actual numbers captured give one the idea that they come to the surface in quantities at night, if we

examine the percentages we see that this is quite an insignificant movement.

In fact, these larvæ appeared to behave in a very similar manner to both *Pandalus* larvæ and *Enpagurus* larvæ, exhibiting no very marked changes in vertical distribution through the dark hours (Fig. 4).

With this form an attempt was made to determine whether there was any difference in distribution with age. The larvæ were accordingly separated into those stages without uropods, Group A, and those in which uropods were present, Group B. The results are set out in the two accompanying tables, and show that there was on this occasion a marked tendency for the earlier larval stages to have their region of maximum abundance slightly higher than that of the later stages.

*Group A : without uropods.*

	1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.
Surface	—	70	110	—	10
	0%	3.8%	15.2%	0%	0.4%
II	4	320	60	4	60
	0.3%	17.8%	8.3%	0.5%	2%
III	290	380	310	150	1070
	24.8%	21.2%	42.9%	21%	36.7%
IV	670	750	130	250	1450
	57.6%	41.6%	18%	35%	49.6%
V	200	280	114	310	330
	17.2%	15.6%	15.6%	43.5%	11.3%

*Group B : with uropods.*

	1st Series.	2nd Series.	3rd Series.	4th Series.	5th Series.
Surface	15	121	230	4	—
	0.3%	2.3%	3.8%	0.1%	0%
II	20	480	810	38	70
	0.4%	9.3%	13.4%	1.1%	1.3%
III	673	1010	1750	480	550
	14.3%	19.5%	29%	13.4%	9.9%
IV	2760	1250	1340	1270	2040
	58.8%	24.1%	22.2%	35.5%	36.8%
V	1230	2320	1910	1790	2880
	26.2%	44.8%	31.6%	49.9%	52%

For instance, in the three lower levels the daytime abundance of Group A, early stages, went 24.8%, 57.6%, and 17.2%, and 36.7%, 49.6%, and 11.3%, while that of Group B was 14.3%, 58.8%, and 26.2%, and 9.9%, 36.8%, and 52% respectively. In each case the early larval stages show a bias on the side above the level of maximum abundance,

whereas the later stages show the opposite distribution. Further at midnight the early larval stages show quite a marked tendency to move into the surface layers.

## GALATHEID POST-LARVÆ (Figure 5).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	20	40	—	—
II 2-7 m.	—	—	60	—	—
III 9-15 m.	6	30	110	10	10
IV 16-20 m.	45	50	240	90	40
V 30-34 m.	10	10	470	550	80

From the figures obtained it would seem very probable that in the daytime and at dusk these late stages of the young Galathea had their region of maximum abundance somewhere below the greatest depth sampled, 34 metres; at 11 p.m., however, they appeared in large numbers at 30 metres, and were present in diminishing numbers right to the surface at midnight: at 4 a.m. they had retired from the surface, but were still very abundant at 30 metres. In this distribution the Galathea showed exactly similar diurnal vertical movements to those shown by the benthic forms like Mysids and Cumacea (Fig. 5).

It appears from these observations on the various stages in the development of Galathea that there is a gradual sinking of the region of maximum abundance as we pass from the earliest stages to the latest and finally the adult bottom living form. It is most probable that this holds good for many other forms of decapod larvæ at this time of year.

## PORCELLANA SP. ZOEÆ (Figure 3).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	251 2.6%	3498 18.2%	740 16.5%	163 3.4%	650 1.9%
II	881	5340	660	556	2000
2-7 m.	9.1%	27.7%	14.7%	11.7%	6.4%
III	3906	5560	730	1860	13,300
9-15 m.	40.4%	28.9%	16.3%	38.9%	40.5%
IV	3955	3850	670	970	15,410
16-20 m.	40.9%	19.9%	14.8%	21%	47%
V	680	1020	1695	1180	1380
30-34 m.	7%	5.3%	37.7%	25%	4.2%

From a region of maximum abundance between 10 and 30 metres in the daytime these larvæ had spread out by 9.30 p.m. into all layers, and

were still distributed in this manner at midnight. By 3.30 a.m. they had deserted the upper 5 metres, and by 9 a.m. the region of greatest abundance was again below 10 metres (Fig. 3).

LARVÆ OF *CALLIANASSA SUBTERRANEA* LEACH (Figure 2).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	1	110	510	10	—
	0.3%	18%	37.8%	0.5%	0.0%
II	17	210	290	467	110
2-7 m.	4.3%	34.5%	21.5%	26.3%	17.5%
III	105	70	100	830	270
9-15 m.	26.7%	11.5%	7.4%	46.7%	42.8%
IV	220	110	300	240	140
16-20 m.	56%	18%	22.2%	13.5%	22.2%
V	50	110	130	230	110
30-34 m.	12.7%	18%	11.1%	13%	17.5%

In their behaviour these larvæ were very similar to those of *Upogebia*, showing a definite migration to the surface, and being taken there in greatest quantities at midnight. At 4 a.m. they had left the surface, and their maximum abundance was at a depth of 9 metres (Fig. 2).

UPOGEBIA LARVÆ (Figure 2).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	14	659	2010	8	27
	0.7%	12.1%	50.5%	0.5%	0.9%
II	78	880	830	131	170
2-7 m.	3.7%	16.1%	20.9%	7.7%	5.6%
III	897	1270	320	750	690
9-15 m.	42.9%	23.2%	8%	44.1%	22.6%
IV	950	1610	410	470	1150
16-20 m.	45.5%	29.4%	10.3%	27.7%	37.6%
V	150	1050	408	340	1020
30-34 m.	7.2%	19.2%	10.3%	20%	33.3%

In the daytime these larvæ were present in greatest numbers in the hauls from 13 metres down. By 9 p.m. they were present in all layers from the surface to 30 metres. At midnight by far the majority were taken on the surface indicating that a definite migration had taken place into this region from the lower layers. At 4 a.m. they had left the surface, and were caught chiefly at 9 metres and below, and by 10 a.m. the region of maximum abundance was again below 13 metres (Fig. 2).

## UPOGEBIA POST-LARVÆ.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	3	20	—	—
II 2-7 m.	—	—	20	1	—
III 9-15 m.	—	—	10	—	—
IV 16-20 m.	—	—	30	20	—
V 30-34 m.	—	10	60	90	—

The post-larvæ of *Gebia* exhibit the typical behaviour shown by most of the organisms living on or very near the bottom in the daytime. They were absent in all the day hauls. At 9 p.m. three were taken right at the surface: by midnight they were present at all depths, but the majority were captured at 30 metres. At dawn they had again left the upper layers, but were still present in large numbers at 30 metres.

## PAGURID LARVÆ (Figure 4).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	1 0.2%	18 1.2%	4 0.4%	1 0.1%	— 0.0%
II	4	100	50	10	—
2-7 m.	0.7%	6.5%	5.6%	0.9%	0.0%
III	84	340	190	150	40
9-15 m.	14.5%	22.3%	21.3%	14.3%	6.6%
IV	200	470	290	420	200
16-20 m.	34.5%	30.7%	32.4%	40%	32.8%
V	290	600	314	470	370
30-34 m.	50.1%	39.3%	40.3%	44.7%	60.6%

These larvæ showed very little change in their vertical distribution during the dark hours. There is a very slight rise at midnight, but no increase in numbers at the surface. Whereas in the daytime the greatest numbers were taken at 18 metres, and below, at midnight the upper limit is slightly higher at about 12 metres, as shown by Fig. 4, but it seems hardly sufficient to be significant.

## EUPAGURUS GLAUCOTHÖE.

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	—	20	—	—
II 2-7 m.	—	—	—	—	—
III 9-15 m.	1	—	—	—	—
IV 16-20 m.	—	—	60	—	—
V 30-34 m.	—	—	90	150	—

These late larval stages of *Eupagurus* occurred in the daytime and at dusk, probably below the deepest haul at 34 metres : at midnight they were taken on the surface, but in greatest numbers at 20 and 30 metres : at 3 a.m. they were only taken at 30 metres.

Jackson (10) remarks : " Like the fresh-water *Mysis*, they spend the day at the bottom of the sea and rise to the surface at night. It is during this stage that the animal first seeks a moveable residence, and the larvæ spend their time in alternately prowling on the bottom and swimming about."

CRAB ZOEAE (Figure 3).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	311 1.6%	3208 9.4%	4080 27.2%	218 1.2%	1250 4.6%
II	1100	6350	2510	1008	1400
2-7 m.	5.6%	18.6%	16.7%	5.4%	5.2%
III	6694	8120	2720	7170	7280
9-15 m.	34.1%	23.7%	18.1%	38.5%	26.8%
IV	9260	10,760	2270	7210	12,120
16-20 m.	47.2%	31.6%	15.1%	38.7%	44.6%
V	2260	5690	3452	3030	5110
30-34 m.	11.5%	16.7%	22.9%	16.2%	18.8%

Fig. 3 shows that these crab zoeas (species unknown) showed a very similar behaviour to the zoeas of *Porcellana*, living in greatest numbers between 10 and 30 metres by day and extending into the upper layers and surface at dusk and midnight.

CRAB MEGALOPA (Figure 6).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	12 1.2%	12 0.7%	290 30.5%	4 0.6%	62 5%
II	4	30	110	2	30
2-7 m.	0.4	1.7%	11.6%	0.3%	2.4%
III	135	150	110	70	130
9-15 m.	13.4%	8.8%	11.6%	10.1%	10.6%
IV	425	370	150	310	230
16-20 m.	42.2%	21.6%	15.8%	44.5%	18.7%
V	430	1150	290	310	780
30-34 m.	42.8%	67.2%	30.5%	44.5%	63.3%

At midnight these forms appeared on the surface in large numbers, being distributed from top to bottom. At all other times they were present in greatest numbers below 15 metres. This upward spreading must have occurred rapidly, as at 9 p.m. there was no indication of any change in vertical distribution; by dawn the daylight distribution was being resumed (Fig. 6).

## MOLLUSCA.

## LARVAL GASTROPODS AND LIMACINA RETROVERSA (FLEMM.).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	—	2	—	1	—
II 2-7 m.	19	10	—	12	20
III 9-15 m.	84	10	20	20	30
IV 16-20 m.	180	20	20	50	90
V 30-34 m.	80	260	70	80	30

These molluscs which consisted of *Limacina* and larval gastropods occurred mostly in the deeper layers, and exhibited no marked diurnal movements.

## CHORDATA.

## HEMICHORDATA.

## TORNARIA LARVÆ (Figure 2).

	1st Series. 3.25 p.m. to 4.45 p.m.	2nd Series. 7.55 p.m. to 9.17 p.m.	3rd Series. 10.50 p.m. to 12.20 a.m.	4th Series. 2.50 a.m. to 4.16 a.m.	5th Series. 8.45 a.m. to 10.11 a.m.
Surface	11 0.4%	1153 29.1%	14,840 59.1%	563 9.3%	— 0.0%
II	581	1740	2580	1682	20
2-7 m.	22.7%	43.9%	10.3%	27.6%	5.4%
III	887	120	1320	1920	160
9-15 m.	34.6%	3%	5.3%	31.6%	43.2%
IV	820	280	3890	840	120
16-20 m.	32.1%	7.1%	15.5%	13.8%	32.4%
V	260	670	2469	1080	70
30-34 m.	10.2%	16.9%	9.8%	17.7%	19%

It would appear that these larvæ show a definite migration to the surface at midnight.

In the daytime the majority were taken between 7 and 20 metres: by 9 p.m. most individuals were above 7 metres, and at midnight they were concentrated right on the surface. By 4 a.m. they were leaving the



actual surface, but were still caught in large numbers below a depth of 2 metres (Fig. 2).

The occurrence of this larva in such large numbers is worthy of mention. On this occasion we were evidently passing through a large shoal probably reaching the centre at midnight, when the numbers caught on the surface were as great as 14,000.

## VERTEBRATA.

### PISCES.

All the young stages of Teleostean Fishes have been picked out, and will be dealt with in another paper on the vertical distribution of young fishes.

### SUMMARY.

1. A series of hauls with the ring-trawl were made at five depths in water 50 metres deep, so that samples were obtained approximately in daylight, at dusk, at midnight, at dawn, and again in daylight.

A depth-recorder was used with the net giving a graphic record of its path through the water.

2. Examination of the catches demonstrated the diurnal changes in vertical distribution of the species caught by the ring-trawl.

3. Four types of behaviour were shown :—

(a) A definite migration to the surface in the dark hours of certain forms living in the deeper layers in the daytime.

(b) An expanding of the distribution of other organisms, that in the daytime had a zone of maximum abundance in the deeper layers, so that they were evenly scattered from the surface downwards.

(c) Certain animals showed no or very little change in their vertical distribution during the dark hours.

(d) A movement up to the midwater region by those forms that during the daytime adopt either a truly benthic existence or are congregated in the water layers immediately adjacent to the sea floor.

(Lists of species grouped under their respective types of behaviour are to be found on page 780.)

4. Many such observations are required before conclusions can be drawn as to the normal diurnal behaviour of plankton animals : this is a definite record of what occurred in this locality in mid-July at a period of full moon in fair weather.

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The Euphausiidæ in the Neighbourhood of Plymouth.  
 II. *Nyctiphanes Couchii* and *Meganyctiphanes norvegica*.

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With Plates I-IX.

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THE present paper is a continuation of last year's work on the Euphausiidæ in the neighbourhood of Plymouth (Lebour, 1924), in which the early larval stages were described of *Nyctiphanes Couchii*, *Meganyctiphanes norvegica* and, less fully, those of *Thysanoessa inermis* and *T. neglecta*. These two last-named forms are reserved for a detailed description in another paper, only *Nyctiphanes* and *Meganyctiphanes* being dealt with here. The first paper described these as far as the last Calyptopis stages, and it was shown that they were much alike although perfectly distinct, especially as regards colour. The nauplii and meta-nauplii were easily distinguishable. The whole of the remaining life-history of *Nyctiphanes Couchii* has now been elucidated and also that of *Meganyctiphanes norvegica*, with the exception of a few late larval stages. The absence of these, however, does not materially affect our knowledge of its life-history.

Much help has been obtained from Mr. C. F. Hickling, to whom my best thanks are due, who has kindly put at my disposal his collections from the Atlantic Slope from which I have been able to fill in gaps in the larval stages of both species.

*Nyctiphanes Couchii* being our only truly neritic species is obviously the easiest to study, and, as it is present on the Plymouth area more or less throughout the year, material of its various stages is easier to obtain than those of the other species which live commonly in the Atlantic and only come into the Channel occasionally and apparently at the breeding season. From two years' observations there is a distinct indication of both *Meganyctiphanes* and *Thysanoessa* entering the Channel to breed, and from Mr. Hickling's observations a tendency to come nearer inshore to breed is distinctly shown in both these genera. In his paper (1925) the notes on vertical migration of these euphausiids are extremely interesting, and the habit of living just above the bottom by

day, and presumably coming to the surface at night is borne out by our own observations in the Channel. His collections show clearly that *Nyctiphanes Couchii* is neritic and *Meganyctiphanes norvegica* and *Thysanoessa* oceanic. In his October collections *Nyctiphanes Couchii* only was breeding, several specimens carrying eggs and larvæ at various stages, whereas all the *Meganyctiphanes* and *Thysanoessa* were adolescent or, in the case of *Meganyctiphanes*, adult but not mature. In the writer's previous paper (1924) these were shown to be breeding in the Channel early in the year, together with *Nyctiphanes*. It is possible that the two oceanic species spawn usually at this time, but *Nyctiphanes* appears to spawn nearly all the year round, although chiefly in the spring. From Mr. Hickling's March collections, adult *Meganyctiphanes* and *Thysanoessa* were obtained, both of which were spawning.

It must be noted that the limb called here the first thoracic is regarded by Hansen in all his works as the maxillipede, and in this he is followed by many other workers. He thus admits only seven thoracic legs instead of eight. In this paper, which follows Calman (1909), the thoracic limbs are regarded as beginning after the second maxilla, and are therefore eight in number.

As Hansen (1908) has pointed out, the various larval stages in different genera do not always correspond (indeed they possibly do not always do so even in the various species), but the names used by Sars (1885) for the different stages have a certain significance. Thus the Calyptopis stages are characterised by having the carapace covering the eyes as the name implies. The Furcilia stages are characterised by having the carapace drawn away from the eyes so that they are exposed, and the antennæ are still retained as swimming organs, having two simple setose rami. The Cyrtopia stages are characterised by having the antennæ differentiated into a jointed and unjointed ramus, the flagellum and the scale, although the earliest Cyrtopia (*e.g.* in *Meganyctiphanes*) may show very little of this differentiation beyond having the flagellum three-jointed. Sars regards the post-larval stage as having all the limbs fully formed, and only differing from the adult in the absence or presence of certain setæ. The present observations show, however, that the Cyrtopia merges imperceptibly into the adult, and that both male and female may be mature before the appendages are fully formed as far as the exopodite of the male seventh thoracic limb is concerned, and also the number of gill lobes in both sexes. It has, therefore, been thought advisable to omit the term post-larva altogether, and regard the late Cyrtopia to be the direct predecessor of the adult.

Of the few workers who have attempted the life-histories of British euphausiids, Brook and Hoyle (1888) have given the most accurate and detailed information, although unfortunately *Meganyctiphanes norvegica*

and *Thysanoessa (Raschii and inermis)* are not separated. These they call *Nyctiphanes* and *Boreophausia* respectively. They recognise eleven Furcilia stages, twelve now being found, two late Furcilia stages being here shown to occur in both *Nyctiphanes* and *Meganyctiphanes* having all the pleopods biramous and setose.

The following notes on the Furcilia stages are given by these authors :

1. No rudiments of pleopods.
2. First pair of pleopods as simple rudiments.
3. Second ,, ,, ,, ,,
4. Third ,, ,, ,, ,,
5. Fourth ,, ,, ,, ,,
6. Fifth ,, ,, ,, ,,
7. First pair of pleopods biramous and setose.
8. Second ,, ,, ,, ,,
9. Third ,, ,, ,, ,,
10. Fourth ,, ,, ,, ,,
11. Fifth ,, ,, ,, ,,

And it is stated that in another form the anterior pair of pleopods become biramous and setose before the last are developed in rudiment. Now in the following account of *Nyctiphanes* and *Meganyctiphanes* it is shown that the pleopods in both are formed in this second way, the first to the fifth stage being formed as in the first form described, the sixth differing in having the first pair of the four present both biramous and setose. From observations on *Thysanoessa* from the Channel, we find that the sixth stage here has five simple rudiments. It, therefore, almost certainly follows that in *Thysanoessa inermis* (and probably *T. Raschii*) the Furcilia stages are as in the first form of Brook and Hoyle, and *Nyctiphanes Couchii* and *Meganyctiphanes norvegica* as in the second. They give four Calyptopis stages, whereas we find only three in all forms observed.

Elmhirst (1924) says of *M. norvegica* : "This species seems to pass through 2 Nauplius, 1 Metanauplius, 3 Calyptopis, 6 Furcilia and 5 Cyrtopia stages, *i.e.* 17 moults before the adult form is attained." A much underestimated statement, for we find 12 Furcilia and many Cyrtopia stages, although agreeing with him as to the nauplii, metanauplius and Calyptopis.

#### GENERAL REMARKS ON EUPHAUSIID LARVÆ.

The eggs of euphausiids are either shed directly into the sea or are carried for a longer or shorter period in an egg-sac, which may be double or single. In *Nyctiphanes Couchii* and in the other species of this genus the sac is double. The nauplii in *N. Couchii* are hatched in the sac and

retained therein for a considerable period, emerging into the water as pseudometanauplii, which almost immediately cast the skin and become true metanauplii. *Meganyctiphanes norvegica* apparently sheds its eggs into the sea in the one-celled stage. So far these have not been obtained direct from the parent, but eggs have been hatched out which produce *Meganyctiphanes* nauplii. Two naupliar stages and a metanauplius occur in this species. There are three Calyptopis stages in both *Nyctiphanes* and *Meganyctiphanes*, twelve Furcilia stages, and at least twelve Cyrtopia stages before maturity is reached.

The free-swimming nauplius, as in *Meganyctiphanes*, is a typical three-limbed nauplius with all limbs biramous. There is no mouth. The first nauplius has no spines behind, the second has two spines, and in the older specimens the metanauplius carapace and limbs can be seen through the skin. In *Nyctiphanes*, which carries its eggs, there is only one naupliar stage which has the mandible (third naupliar limb) only a uniramous stump, and, as stated above, emerges from the egg-sac of the female as a pseudometanauplius almost at once sloughing the skin which enwraps the metanauplius.

The metanauplius has a carapace covering most of the body, and a small abdominal piece protruding behind armed with spines at the end. There are buds present representing the two pairs of maxillæ and the first thoracic limbs. The median naupliar eye is present and the antennules project in front. The antennæ are the chief swimming organs, the mandibles being only stumps.

The three Calyptopis stages have the region of the compound eyes covered by the carapace, and a projecting abdomen which is unsegmented in the first stage and not separate from the telson. In the second stage it has five segments and in the third stage six segments besides the telson, which is armed with spines. The antennæ are still swimming organs, and persist as such all through the Furcilia stages. The two pairs of maxillæ and the first thoracic limb are well developed, but there are no other appendages although thoracic segments appear as narrow rings and the number of abdominal segments is complete in the third Calyptopis. Also the rudiments of the compound eyes appear as the ocular organs, and the eyes themselves are pigmented, with traces of the luminous organs. These characters are in all probability general, as they appear to exist in all the Calyptopis so far described.

The third Calyptopis changes into the first Furcilia, which has no pleopods in all those that are known. In my former paper the first Furcilia of both *Nyctiphanes* and *Meganyctiphanes* were described as having one rudimentary pair of pleopods, but later it was found that there was an earlier stage without pleopods, and although the Furcilia therein described (Lebour, 1924) was obtained from the sloughing of

a last Calyptopis it was probably abnormal, owing to captivity, and in reality represents the second Furcilia. After the first the Furcilia stages are to be distinguished from one another by the development of the pleopods which at first appear as simple buds, these giving place to setose biramous limbs. During the growth of the Furcilia the pleopods develop from one simple pair of buds to the five pairs all biramous and setose, slight differences in procedure occurring in the various genera, but from observations on many different forms it seems probable that they are the same in all species of a genus, and it is found here that in the closely related genera *Nyctiphanes* and *Meganyctiphanes* the order of development is the same. The thoracic limbs are developed progressively in the Furcilia, usually about as far as the rudiment of the fifth and sixth limb, the first, second and third being well developed. The antennæ are always still swimming organs and not differentiated into scale and flagellum, both rami being unjointed (with the exception of indications of joints at the tip of the scale ramus) and bearing long setæ. The antennules have a long spine (as in the Calyptopis) on the outside of the first peduncular joint, and the flagella are short and unjointed or only with very few inconspicuous indications of joints in the last stages. The luminous organs always occur on the eyes in all stages, those on the second thoracic limbs appearing in the later stages and on the first or also on the following abdominal segments. The telson undergoes characteristic changes during the later Furcilia and early Cyrtopia stages, during which from being of a square many-spined larval type it becomes the elongated pointed telson with two large and broad spines of the adult. These changes will be here briefly described as similar changes occur in all euphausiid larvæ, and the slight differences in these changes serve as important guides in distinguishing species. The typical early larval euphausiid telson is oblong, and armed laterally near the centre of its outer margins with a pair of short spines, one on each side. As these are universally present throughout all the stages they will not be referred to again. The terminal portion of the telson has in the Calyptopis (Lebour, 1924) one pair of short lateral spines on the outside (1), one pair of long, thin lateral spines inside these (2), one pair of long, usually thicker, lateral spines internal to 2 (3) and, typically, seven short terminal spines (Plate II, Fig. 1). As the larva grows the telson elongates and narrows, and most of these spines are gradually lost. The first change is the reduction of the seven terminal spines to five (Plate II, Fig. 4). This may occur in a late Furcilia stage or in an early Cyrtopia stage, the hind edge of the telson being gradually pulled out. In the next stage the terminal spines are reduced to three (Plate II, Fig. 5) and then to one (Plate II, Fig. 6), the lateral spines remaining as before but differing as to being ciliated or not, and finally the outer long, lateral pair (2) disappears (Plate II, Fig. 8). The

telson has now the ordinary adult number of spines, although the small pair disappear altogether in some adults. Instead of the outside long, lateral pair disappearing when there is only one terminal spine they may disappear when there are still three. This last form is apparently the usual one in *Meganyctiphanes norvegica*. This sequence described above, or a somewhat similar one, seems to occur in all euphausiids, but whereas the late Furcilia of one species may have reached the stage of Fig. 8, on the other hand the first Cyrtopia of another species may be still at stage one.

An interesting exception to the occurrence of seven terminal spines in the early larva of an euphausiid has recently been observed by the writer in *Stylocheiron Suhmi*, from plankton collected by Mr. F. S. Russell from near Alexandria, Egypt. A paper on these larvæ will, it is hoped, be ready shortly for publication. These had six terminal spines on the telson instead of seven, and this was a constant feature, occurring in all specimens which were quite frequent. In a later Furcilia these were reduced to four. This is apparently the only known exception.

The Furcilia now changes into the Cyrtopia with antennæ differentiated into scale and flagellum (Plate III, Figs. 3-5). The flagellum is always at least three-jointed, but may at first retain the shape of the unjointed ramus of the Furcilia, and still bear setæ both terminally and laterally. The scale may at first also closely resemble the Furcilia ramus, but is, however, always apparent as a scale in the second or third Cyrtopia if not in the first. The telson gradually changes to the adult shape. It may in the first Cyrtopia have seven, five or three terminal spines, which alter as described above. The thoracic limbs all appear and the remaining luminous organs. The antennules gradually assume the adult shape, and the male pleopods become modified. In fact, so gradually does the Cyrtopia change into the adult that it is almost impossible to fix a so-called post-larval stage (which is defined by Sars as having all the adult limbs, these only differing in setæ) for specimens may be mature before the limbs are perfect (*e.g.* before the exopodite is fully jointed in the seventh thoracic limb or the gills fully developed). Whilst the Cyrtopia changes the carapace alters considerably, the rostrum becoming more and more short and pointed, and in some cases the lateral denticle, present in most species in the early larvæ, disappearing (Plate II, Figs. 11-16). Sex may be discernible at an early age, sometimes as early as the third or fourth Cyrtopia, either by means of the modification of the male pleopods or in the modification of the penultimate thoracic limbs, when these are different in male and female. In some cases, however, the sex cannot be told until much later.

As stated above both males and females may be mature before being fully developed. For instance, *Nyctiphanes Couchii*, which may reach



a length of 17 mm., can breed at 9 mm., females carrying eggs and males with fully formed spermatophores being found at that size, in these cases the gills only having 8-10 lobes and the seventh thoracic male limb having the exopodite not fully jointed.

The male modified pleopods may be very different in the young stages from their form in the mature individual, and great care must be exercised in identifying such young males, especially as they may be very variable in size, and one may find a mature male in one locality which is hardly more than half the size of an adult from another locality, the young of the latter being quite different in regard to the pleopods when the same size as the former.

From these notes we may draw the following conclusions :

All euphausiids undergo similar or closely related changes in the larval telson, the number of spines being reduced in a certain order, but parallel stages are not always equally developed. Thus a late Furcilia of one species may have the telson more advanced than the Cyrtopia stage of another species. It is, therefore, unsafe to go by the telson in the identification of any stage unless the full life-history of the species is known.

The best way to distinguish a late Furcilia from an early Cyrtopia is by the flagellum of the antenna, which is unjointed in the Furcilia and jointed in the Cyrtopia.

Pleopods are not developed in the same order in all genera, although it is probable that all the species of a genus are similar in this respect, and also of closely related genera, such as *Nyctiphanes* and *Meganyciphanes*.

Irregular development may occur, and it is possible that temperature may hurry on growth. Furcilia and Cyrtopia stages have occasionally been found with the telson further developed than usual, such as a last Furcilia of *Nyctiphanes* with only one terminal spine to the telson, and one was found in Mediterranean plankton having three instead of five. Changes of skin under laboratory conditions may also be irregular, but on the whole the series described below for *Nyctiphanes* and *Meganyciphanes* appear to be fairly constant, and represent the normal method of development.

#### NYCTIPHANES COUCHII (Bell).

As stated above twelve Furcilia stages may clearly be made out. Some of these were obtained by the changing of skin in the Laboratory, but most of them were picked out from the plankton, either from material brought in by the *Salpa* from outside the Sound, chiefly from Station L4, half-way between Rame Head and the Eddystone, or they were obtained from Mr. Hickling's collections from the Atlantic.

All the Furcilia stages (Plate I) are clear and hyaline with orange-red

chromatophores above the telson, at the side of the thorax and round about the mouth region; otherwise they are colourless. The eyes are completely uncovered by the carapace, which now projects between them as an almost square rostrum, only very slightly emarginate in the earlier stages, reaching to about the level of half the eye or slightly further. The carapace is very slightly carinate dorsally near the middle where there is a small projection, not always perceptible and disappearing in the older stages. A distinct lateral tooth is present near the posterior end in all the Furcilia stages, and the posterior margin beginning as a simple convex curve gradually becomes indented and sinuate. The telson at first almost square at the end like the Calyptopis gradually tapers, and becomes triangular at the end with a truncated base. It is armed with seven terminal spines as described above. These are very nearly equal in length, and the three pairs of lateral spines all possess one large spine and two long laterals besides, the terminal spines are ciliated, the latter on both sides, the laterals on the inside only. The armature of the spines gradually disappears. The uropods are present in all the Furcilia stages, having first appeared in the last Calyptopis, and gradually elongate and become more setose. The antennæ are swimming organs, have two unjointed rami with long setæ and alter little in the various stages. The antennules have a long, thick spine at the outer side of the terminal portion of the first joint of the peduncle. (This is present in all euphausiid larvæ, but in *Nyctiphanes* and *Meganyctiphanes* persists in the adult, although much reduced, and is connected with the leaflet arming this joint which is typical of these two genera). The flagella at first very short with long setæ gradually elongate, lose their terminal setæ, and tend to be jointed. The mandibles in all the Furcilia stages have only the rudiment of a palp hardly more developed than in the last Calyptopis (Plate III, Fig. 6). The first and second maxillæ are also much like the Calyptopis. The first thoracic limb is well formed in all the Furcilia stages, the other thoracic limbs, beginning with a bud in the early stages, in the last reach four jointed legs with gills and the rudiment of a fifth. The pleopods beginning at the second Furcilia as a pair of simple non-setose protrusions are biramous with both rami setose in the penultimate and in the last. Luminous organs are present on the eyes in all the stages, and a pair on the second are present in the ninth Furcilia. All those on the abdominal segments present in the twelfth and last. The spine below the telson occurs in the third, the spine above the telson in the eleventh Furcilia.

*First Furcilia* (Plate I, 1, and Plate II, 1), 2.5 mm. long.\* Carapace

\* All measurements of the whole animal are from the tip of the rostrum to the end of the median spine of the telson. Those here given are for typical examples and may be slightly larger or smaller.

rounded posteriorly. Rostrum broader than long. Outer uropods reaching about half-way down the telson, inner shorter. No pleopods. Second thoracic limbs occur as small buds.

*Second Furcilia* (Plate I, 2 and 13), 2.5–2.6 mm. long. Differs from first only in having the first pair of pleopods developed, each divided into a basal and terminal non-setose portion.

*Third Furcilia* (Plate I, 3, and Plate II, 11), 2.8–3 mm. long. Two pairs of pleopods similar to the second stage. Carapace still rounded posteriorly. Telson narrower with terminal angles more cut off. Spine below telson present. Inner uropods longer. Second thoracic leg jointed. Rudiment of third.

*Fourth Furcilia* (Plate I, 4, and Plate II, 2), 2.8–3.3 mm. long. May be the same size as the third or smaller or larger. Three pairs of simple pleopods. Second thoracic limb setose.

*Fifth Furcilia* (Plate I, 5), 3.2–3.5 mm. long. Four pairs of simple pleopods.

*Sixth Furcilia* (Plate I, 6), 3.2–3.5 mm. long. Four pairs of pleopods, the first biramous and setose, the inner ramus very short with one seta. The other three pairs of pleopods simple as before.

*Seventh Furcilia* (Plate I, 7 and 14), 3.5–3.6 mm. long. Four pairs of pleopods: the first two biramous and setose, the third and fourth simple, uropods longer.

*Eighth Furcilia* (Plate I, 8), 3.2–3.6 mm. long. Five pairs of pleopods, the first two biramous and setose, the last three simple.

*Ninth Furcilia* (Plate I, 9), 3.8 mm. long. Three pairs of pleopods biramous and setose, two pairs simple. Second thoracic leg five-jointed, short, with two-lobed gill. Third and fourth unjointed. Luminous organs on second thoracic legs and between first pleopods.

*Tenth Furcilia* (Plate I, 10, and Plate II, 3), 3.8–4 mm. long. Four pairs of setose biramous pleopods, one pair simple. Gills beginning on second and third thoracic legs.

*Eleventh Furcilia* (Plate I, 11), 4–4.3 mm. long. All pleopods setose and biramous. Second thoracic leg long, third jointed, fourth rudimentary. Still with seven terminal spines to telson.

*Twelfth and last Furcilia* (Plate I, 12 and 15; Plate II, 4; Plate III, 1, 3, 6, 11–16), 4.3 mm. long. Five terminal spines to telson. Flagella of antennules slightly jointed. Second and third thoracic leg with all joints, the second bent. Two-lobed gills, tending to be three-lobed to second and third leg. Fourth and fifth unjointed with rudimentary gill. Luminous organs on four abdominal segments, or sometimes on only three. This last *Furcilia* now changes into the first *Cyrtopia*. As several times the change has taken place in a finger-bowl in the laboratory, the normal form seems to be a *Cyrtopia* with three terminal spines to the

telson coming from a five-spined Furcilia, these corresponding with numerous specimens of both from the plankton. A few variations have occurred, however, the Furcilia occasionally only having three or one terminal spine. The Cyrtopia of *Nyctiphanes Couchii* has not been found with more than three terminal spines.

The Cyrtopia stages all have one antennal ramus jointed, the flagellum, the other ramus remaining unjointed as the setose scale. They gradually change into the adults, as described above, and the term Cyrtopia is here used to cover the early stages after the Furcilia as well as those hitherto referred to as post-larval.

At first the carapace (Plate II, 12-16) is still notched laterally, but this soon disappears; the rostrum gradually diminishes and becomes more pointed and the carapace has the adult appearance. The antennules at first still have the large larval spine on the first peduncular joint, but soon this becomes smaller and the reflexed leaflet begins to be formed. The flagella, at first about the same length as the peduncle, elongate fast, the thoracic legs quickly develop from six to eight, at first with biramous gills which soon reach eight or ten. The mandibles have a palp, at first unjointed, soon reaching the adult jointed setose state. The telson at first with three terminal spines changes to one in the second Cyrtopia stage, then loses the outer long lateral spines, and soon has the adult appearance. In the first Cyrtopia all the luminous organs are present except those in the seventh thoracic limb, but this appears in the second stage. The last parts to develop are the exopodite of the last functional legs and the final gill lobes, but the animal may reach maturity before these are fully formed (Plate IV).

*First Cyrtopia* (Plate II, 5, 12; Plate III, 2, 4, 7, 9, 10, 17, 18, 19), 4.5 mm. long. Three terminal spines to telson. Rostrum long and broad, slightly more pointed than in the last Furcilia. Antennules with jointed setose flagella equal in length to the peduncles. Antennæ with a three-jointed non-setose flagellum, only very slightly longer than the scale which is armed with setæ terminally and on its inner edge for the last third of its length. Second thoracic leg long and bent with setose unjointed exopodite and two-lobed gill, third also bent with exopodite with one seta, fourth leg not bent but with full number of joints in the endopodite, and two-lobed gill, but no exopodite, fifth, sixth and seventh limb rudimentary, seventh only a small protruberance.

*Second Cyrtopia* (Plate II, 6; Plate IV, 1), 4.5-4.75 mm. long. Telson with one terminal spine and both lateral pairs of long spines, the large inner laterals having lost the cilia with which they were armed on their inner edges. All luminous organs present. Carapace still with lateral tooth, rostrum narrower. Antennules with long flagella and process standing up on the first peduncular joint. Antennæ with three-

jointed base to the flagellum, the flagellum itself reaching beyond the scale for more than half of its own length. Scale with setæ all along its inner margin and a spine at its base on the outside. Thoracic limbs two to five bent and with the endopodites fully jointed, the sixth four-jointed with rudimentary exopodite in male and bi-lobed gill, the seventh with luminous organs, unjointed endopodite and bilobed gill. The gill lobes of the eighth appendage beginning. Mandible with three-jointed palp armed with two terminal setæ.

*Third Cyrtopia* (Plate II, 7, 13; Plate III, 8), 4.75-5.5 mm. long. The telson is almost the same as in the second, but rather more elongated and with the outer long lateral spine without cilia. The seventh thoracic limb still unjointed, but slightly longer than in the second. There is very little difference between this and the second *Cyrtopia*, and they would have been regarded as identical if it had not been that several times the third was procured from the second by sloughing of the skin in the laboratory.

*Fourth Cyrtopia* (Plate II, 14; Plate IV, 2), 5.5-5.75 mm. long. The telson has lost the outer long lateral spine, the terminal portion being much elongated. The carapace has a much shorter rostrum, and the lateral denticle is smaller. The seventh thoracic limb has a one-jointed endopodite and a three-lobed gill.

*Fifth Cyrtopia* (Plate II, 8, 15; Plate V, 5, 6, 9), 6-6.2 mm. long. Telson as in the fourth stage. Lateral denticle of the carapace gone, but the margin still angular where it has been. Endopodite of seventh thoracic leg two-jointed with a terminal seta. Rudimentary eighth with eight-lobed gill. In the male the first two pairs of pleopods begin to be modified so that the sex can now be recognised, and the sixth thoracic leg has an exopodite and three-lobed gill. Exopodite also on the seventh thoracic leg, which is still two-jointed, but longer. Thoracic legs three and four setose with three-lobed gills.

*Sixth Cyrtopia* (Plate IV, 3), 6.5 mm. long. Seventh thoracic leg longer, endopodite two-jointed with one terminal seta; three-lobed gill.

*Seventh Cyrtopia* (Plate IV, 4), 7 mm. long. Seventh thoracic leg longer with exopodite in male still a simple lobe and a five-lobed gill. Rudimentary eighth leg fully formed.

*Eighth Cyrtopia* (Plate IV, 5), 7.5 mm. long. Much the same as seven with seventh thoracic leg longer.

*Ninth Cyrtopia* (Plate IV, 6; Plate V, 7, 10), 8 mm. long. Much the same as seven with seventh thoracic leg still longer.

*Tenth Cyrtopia* (Plate IV, 7), 8.5 mm. long. Gill to seventh thoracic leg six-lobed, with exopodite in male having two terminal setæ.

*Eleventh Cyrtopia* (Plate IV, 8), 9 mm. long. Exopodite of male seventh thoracic leg with two joints and two terminal setæ. At this stage both

male and female may breed, although the gills and exopodites have not attained their full development.

*Twelfth Cyrtopia* (Plate IV, 9), 9.5 mm. long. Exopodite of male seventh thoracic limb two-jointed with four terminal setæ and seven to ten lobes to gill.

*Thirteenth Cyrtopia* (Plate IV, 10), 10 mm. long. Exopodite of male seventh thoracic leg with five segments and seven to ten lobes to gill.

The *Nyctiphanes* may now be regarded as adult, although still continuing to develop, the male seventh thoracic leg having eventually six segments to the exopodite, with twelve setæ and the gill having thirteen lobes in a specimen 13 mm. long (Plate IV, 11). Certainly it may breed at 9 mm., at that size the male and female organs being ripe, the male copulatory organs fully developed, and only slight differences, such as the number of gill lobes and segments in the male exopodites of the seventh thoracic leg showing there is any difference from the fully formed adult. We may, therefore, take the form at 10 mm. to be the last *Cyrtopia*, although it can breed at 9 mm. and still go on developing up to 12 or 13 mm., the adult sometimes reaching 17 mm. in length. We thus have thirteen *Cyrtopia* stages leading up gradually to the adult form.

Hansen (1911) describes a few larval stages of *Nyctiphanes Couchii* from the Atlantic Monaco material which correspond well with those described above. The first specimen of 4.5 mm. is evidently the first *Cyrtopia*. In the second specimen he describes the disappearance of the lateral denticle of the carapace at the same stage as our own specimens, and one of his at 6 mm. corresponds almost exactly with ours. The only difference appears to be the rostrum, which in the early stages Hansen describes as emarginate, whilst in ours, except in the very early *Furcilia*, it is usually straight. Hansen believes Illig's *Nyctiphanes obtusifrons* (1909) to be the young of *N. Couchii*, which seems to be extremely likely.

A comparison with the larval stages of *N. simplex* Hansen, from the "Albatross" material (1912), shows that his "Intermediate *Furcilia* Stage" (p. 288, Plate 12, Figs. 3a-3f) corresponds with the eighth *Furcilia* of *Nyctiphanes Couchii*, having two biramous pleopods and three simple and uniramous, a difference being that in *N. Couchii* the inner ramus of the two first have each one seta and in *N. simplex* these are absent, and in *N. simplex* the rostrum is slightly emarginate, whilst in *N. Couchii* it is rounded. The length is the same and the other features are much alike. It, therefore, seems that in species of the same genus we may expect equivalent larval stages. The last *Furcilia* of *N. simplex*, as described by Hansen, corresponds with the penultimate *Furcilia* of *N. Couchii*, as it still has seven terminal spines to the telson, the last *Furcilia* of *N. Couchii* having five.

The life-history of *Meganyctiphanes norvegica* may now be compared with that of *Nyctiphanes Couchii*, and it is found to be very similar.

#### MEGANYCTIPHANES NORVEGICA (M. Sars).

The larvæ of *Meganyctiphanes norvegica* have been secured from the Channel from the egg through two naupliar stages, one metanauplius and three Calyptopis stages, which are described and figured in an earlier paper (Lebour, 1924), and later, also from the Channel, the Furcilia stages and many of the earlier Cyrtopia stages were identified. It is probable that this species goes into deeper and more open water when older and approaches the coast again to breed. Mr. Hickling has collected many adolescent and adult stages from the Atlantic, and in March these were breeding in the shallower water, eggs and early larvæ being abundant.

We thus have the life-history almost complete, for there is only a gap after the Cyrtopia of 9.5 mm. long and one of 13 mm., and these stages are so much alike and already show characters which identify them that the absence of these few intermediate stages is of no importance.

We have a series of larvæ closely resembling in the early stages those of *Nyctiphanes*, but always distinguishable. The first difference is the colour. This is only useful when we have fresh specimens, but then is very distinct, *Meganyctiphanes* being pinkish with very distinct red pigment round the mouth and on the back, and later on the legs, *Nyctiphanes* in its early stages being clear and colourless except for distinct red chromatophores at the base of the telson and in the mouth region. The early larvæ of *Meganyctiphanes* may have a trace of red chromatophores at the base of the telson, so that in preserved specimens it is not always easy to separate them by this character, although when alive this can always be done as *Meganyctiphanes* is always a diffuse pinkish colour all over.

The second difference is size, and this is very apparent in the later larvæ. Even, however, in the first Furcilia *Meganyctiphanes* is usually larger and of a somewhat heavier build. We may, however, have a large specimen of *Nyctiphanes* and a small specimen of *Meganyctiphanes* which are about the same size in the very early Furcilia stages only.

The third difference is the size of the eyes, which are always larger and very pronounced in *Meganyctiphanes*.

The fourth difference is the broader carapace of *Meganyctiphanes* which retains its larval characters much longer than *Nyctiphanes*. Dissecting off the carapace of any of the Furcilia stages and laying it out flat will distinguish it at once as being *Nyctiphanes* or *Meganyctiphanes*.

The Furcilia stages (Plate VI) correspond exactly with those of *Nyctiphanes*, twelve stages in all, the first without pleopods, the last two with

all the pleopods setose and biramous. There is, however, the difference in the last that it still has seven terminal spines on the telson instead of the five in *Nyctiphanes*. In size they range from 2.6 mm. in the first *Furcilia* to 5 mm. in length in the last, which is slightly larger than those of *Nyctiphanes*. As the *Furcilia* grows its proportional size grows, compared with *Nyctiphanes*, and after the last *Furcilia* the large size is so marked that it is impossible to mistake them, even if they did not differ in other ways.

The eyes are completely uncovered by the carapace, which is very square and only slightly emarginate in the younger stages, and still square in the last *Furcilia*. There is a distinct carination dorsally in the younger forms which tends to disappear, and often is not easily seen in preserved specimens. The very distinct lateral denticle occurs near the hind end, and the posterior margin, at first rounded, is only slightly and smoothly indented in the last *Furcilia*, and much further back in development than in the last *Furcilia* of *Nyctiphanes* (Plate IX, 12-14). The lateral spines on the telson are armed with one spine each in the early stages, and are ciliated on their inner margins, both spines and cilia disappearing later. The uropods gradually lengthen, and the antennæ are much the same in all the *Furcilia* stages with two unjointed rami with setæ. The antennules gradually growing longer do not alter much from the first to the last *Furcilia*, the flagella not being jointed at all and the general appearance being much like *Nyctiphanes*. In the last *Furcilia* there are no terminal setæ on the flagella. The mandibles are very backward and only show a small pointed rudiment of a palp in the last stage, the two pairs of maxillæ altering little. The first thoracic limb is well formed in all the stages, the other thoracic limbs gradually developing until in the last *Furcilia* the third is jointed, the fourth very short, and the fifth merely a small protuberance. The pleopods are developed exactly as in *Nyctiphanes*.

*First Furcilia* (Plate VI, 1; Plate IX, 3), 2.8 mm. long. Carapace very broad and rounded posteriorly. Eyes dark and very conspicuous, which is the case in all stages. Rostrum very broad. No pleopods.

*Second Furcilia* (Plate VI, 2), 3 mm. long. One pair of simple pleopods as in *Nyctiphanes*.

*Third Furcilia* (Plate VI, 3, 12; Plate IX, 12), 3 mm. long. Two pairs of simple pleopods.

*Fourth Furcilia* (Plate VI, 4; Plate IX, 4), 3.3-3.5 mm. long. Three pairs of simple pleopods. Spine below telson developed.

*Fifth Furcilia* (Plate VI, 5), 3.3-3.5 mm. long. Four pairs of simple pleopods.

*Sixth Furcilia* (Plate VI, 6), 3.8 mm. long. Four pairs of pleopods, the first biramous and setose, the three others simple.



*Seventh Furcilia* (Plate VI, 7), 3.8 mm. long. Two pairs of biramous setose pleopods, two pairs simple.

*Eighth Furcilia* (Plate VI, 8), 3.8–4 mm. long. Two pairs of biramous setose pleopods, three pairs simple.

*Ninth Furcilia* (Plate VI, 9), 4.4–4.5 mm. long. Three pairs of biramous setose pleopods, two pairs simple. Second thoracic leg jointed, third and fourth unjointed with rudimentary gills. No luminous organs except on eyes.

*Tenth Furcilia* (Plate VI, 10, 13), 4.6 mm. long. About the same size as the ninth. Four biramous setose pleopods, one pair simple.

*Eleventh Furcilia*, 4.8 mm. long. Much like the twelfth, but smaller and not quite so far advanced with regard to appendages. All pleopods biramous and setose.

*Twelfth Furcilia* (Plate VI, 11; Plate VII, 1, 4, 5, 6, 7, 8, 9, 10, 11; Plate IX, 5, 13), 5 mm. long. Still with seven terminal spines to telson. Rostrum narrower but still very square. Antennule with longer flagella but still unjointed. Antennæ as before. Mandible with a very short-pointed rudiment of a palp. 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 one-lobed gill, fourth leg unjointed with two terminal setæ, exopod and no gill, fifth limb rudimentary. Telson still broad, but rather more elongated. Three luminous organs on abdomen. The last *Furcilia* is thus very like that of *Nyctiphanes Couchii*, but is larger in every way and nearly 1 mm. longer. It is, however, further back in development as regards its rostrum, which is still very square, its having only three abdominal luminous organs and the telson with seven terminal spines.

The *Cyrtopia* stages, as in *Nyctiphanes*, lead gradually to the adult, and although very similar in many ways to those of *Nyctiphanes* still differ materially, so that they cannot easily be confused. They are all much bigger than the corresponding stages of *Nyctiphanes*; the telson differs in all, but most conspicuously in the younger stages, and the absence of the spine above the telson is a noteworthy feature. The eyes are still a good deal larger and more conspicuous than in *Nyctiphanes*.

The first *Cyrtopia* measures 5.5–5.6 mm. in length and has a jointed flagellum to the antennule. This is, however, still provided with setæ, and the scale is still very like the first *Furcilia*, in fact it apparently has not ceased to be a swimming organ. In the next stage it is very little different, and only in the third *Cyrtopia* do the two branches tend to be like the adult. The telson beginning with seven spines in the first *Cyrtopia* changes to five in the second, and there are three stages with five spines, then three and, finally, one. There is a difference, however, from *Nyctiphanes* for the outer long lateral spines disappear when there

are still three terminal spines, whilst in *Nyctiphanes* they disappear after the change to one terminal spine. The carapace is at first still very broad and only slightly indented behind, taking on the adult form very late. The antennules have the large lateral spine of the first peduncular segment hardly reduced at all for several *Cyrtopia* stages, at about the ninth *Cyrtopia* having the leaflet sticking up, the flagella elongating. The thoracic legs are very slightly more advanced in the first *Cyrtopia* than in *Nyctiphanes*, having the seventh leg with the rudiment of the luminous organ and gill, although only one-jointed. In the following *Cyrtopia* stages this seventh limb develops more quickly than in *Nyctiphanes* with a well-grown exopodite. Both sexes being alike as to the presence of exopodites it is not possible to tell the sex so soon as in *Nyctiphanes*, and it is only at about 13 mm. that the male pleopods begin to be modified, so that they can be distinguished from those of the female. The mandibles are slow in developing, being three-jointed at the fifth *Cyrtopia*. The gills many-lobed in the adult do not take on the final appearance for some time. At about 20 mm. the animal appears to have all the adult characters and the male pleopods are fully formed. *Meganyctiphanes norvegica* can, however, reach 40 mm. or more in length. It has not been possible to ascertain absolutely certainly the size at which it breeds, but circumstances point to any size from 20 mm., 20-35 mm. being the size of those found together with free eggs in the coastal Atlantic.

*First Cyrtopia* (Plate VII, 2, 12; Plate VIII, 1-15; Plate IX, 1, 6, 14), 5.5-5.6 mm. in length. Seven terminal spines to telson. All luminous organs present, those on the seventh thoracic being not quite perfect. Antennules still having the appearance of swimming organs, both rami being setose, the flagellum, however, being three-jointed, but about equal in length to the scale and armed with long terminal setæ.

*Second Cyrtopia*, 6-6.5 mm. long. Five terminal spines to telson. Antennules more distinctly differentiated into flagellum and scale. Rostrum more pointed, but still broad.

*Third Cyrtopia*, 7 mm. long. Five terminal spines to telson. Seventh thoracic leg unjointed with fully formed luminous organ, two-lobed gill and exopodite nearly half as long as the endopodite.

*Fourth Cyrtopia* (Plate VII, 3, 13; Plate IX, 7), 7.5-8 mm. long. Five terminal spines to telson. Flagella of antennule and antenna longer. Seventh thoracic leg with two-jointed setose endopodite, four-lobed gill and exopodite equal in length to the first joint of the endopodite. Here the size varies, and the fourth, fifth, sixth and seventh *Cyrtopia* may vary from about 7.5 to 8 mm. in length, the development of the seventh thoracic limb being the best point to show in which stage the *Cyrtopia* is. We may have the fourth *Cyrtopia* measuring 7.5 to 8 mm., having five

terminal spines, or the fifth *Cyrtopia* measuring 7.5 to 8 mm., having three terminal spines, or the sixth *Cyrtopia* measuring 7.5–8.5 mm., having three terminal spines, but the outer laterals gone, or the seventh *Cyrtopia* measuring 7.5 mm., with one terminal spine and no laterals. All of these stages showing a gradual lengthening of flagella and seventh thoracic limbs.

*Fifth Cyrtopia* (Plate IX, 8), 7.5–8 mm. long. Three terminal spines to telson, with outer laterals present. Flagella rather longer than in fourth stage. Seventh thoracic leg longer.

*Sixth Cyrtopia* (Plate IX, 9), 7.5–8.5 mm. long. Three terminal spines to telson, outer laterals gone. Flagella and seventh thoracic legs rather more advanced.

*Seventh Cyrtopia*, 7.5–8.5 mm. long. One terminal spine to telson, no outer laterals. Flagella and seventh thoracic leg rather more advanced.

*Eighth Cyrtopia*, 9 mm. long. Telson the same as in the seventh stage, but rather longer. Leaflet sticking up on first peduncular segment of antennule. Flagella and seventh thoracic legs still more advanced.

The *Cyrtopia* can now be easily recognised as *Meganyctiphanes*, and there is a gap in the material from 9 mm. (Plate IX, 10) until about 13 mm. (Plate IX, 15), when various sizes occur up to the adult. There is little difference in those of 9.5 and 13 mm., but in the males the pleopods are very slightly modified at 13 mm., just showing the rudiments of the specialised pleopods. It is interesting to follow up the development of the male organs and see how very different are the modifications in the adolescent and the adult (Plate IX, 15 to 18). It is then at 13 mm. that the sexes may be differentiated in *Meganyctiphanes*, and from that size onwards there is only a very gradual change until the adult is reached at about 20 mm.

It is thus seen that *Nyctiphanes Couchii* and *Meganyctiphanes norvegica* develop in essentially the same way even to the exact sequence in appearance of the pleopods, but in certain minor details they differ, so that they can be distinguished at any stage.

A tabular comparison may now be made with advantage:—

Larval Stage.	<i>Nyctiphanes Couchii</i> .	<i>Meganyctiphanes norvegica</i> .
Egg	Carried by ♀ in sacs.	Shed into water.
1st Nauplius.	} Only one nauplius without biramous mandibles and with 2 terminal setæ. Carried by ♀ in sacs.	Oval with biramous mandibles, no terminal setæ.
2nd Nauplius.		With 2 terminal setæ.
Pseudometanauplius.	Like metanauplius, only with skin covering true metanauplius. Hatched from sac at this stage.	Not present.
Metanauplius.	With simple margin to carapace.	With spiny margin to carapace.

Larval Stage.	<i>Nyctiphanes.</i>	<i>Meganyciphanes norvegica.</i>
1st Calyptopis.	Colourless, with red spot at base of telson, abdomen unsegmented. (Colour applies to all larval stages.)	Pinkish with diffuse red, especially in thoracic region, abdomen unsegmented. (Colour applies to all larval stages.)
2nd Calyptopis.	5 segments to abdomen.	5 segments to abdomen, slightly stouter than <i>Nyctiphanes</i> .
3rd Calyptopis.	6 segments to abdomen.	6 segments to abdomen, slightly larger than <i>Nyctiphanes</i> .
1st Furcilia.	No pleopods.	No pleopods, eyes larger than <i>Nyctiphanes</i> and carapace broader, whole animal stouter and longer (this applies to all following stages).
2nd Furcilia.	1 pair of simple pleopods.	1 pair of simple pleopods.
3rd Furcilia.	2 pairs of simple pleopods.	2 pairs of simple pleopods.
4th Furcilia.	3 pairs of simple pleopods.	3 pairs of simple pleopods.
5th Furcilia.	4 pairs of simple pleopods.	4 pairs of simple pleopods.
6th Furcilia.	1 pair setose, 3 pairs simple pleopods.	1 pair setose, 3 pairs simple pleopods.
7th Furcilia.	2 pairs setose, 2 pairs simple pleopods.	2 pairs setose, 2 pairs simple pleopods.
8th Furcilia.	2 pairs setose, 3 pairs simple pleopods.	2 pairs setose, 3 pairs simple pleopods.
9th Furcilia.	3 pairs setose, 2 pairs simple pleopods.	3 pairs setose, 2 pairs simple pleopods.
10th Furcilia.	4 pairs setose, 1 pair simple pleopods.	4 pairs setose, 1 pair simple pleopods.
11th Furcilia.	All pleopods setose and biramous.	All pleopods setose and biramous.
12th Furcilia.	5 terminal spines to telson.	7 terminal spines to telson.
1st Cyrtopia.	3 terminal spines to telson.	7 terminal spines to telson.
2nd Cyrtopia.	1 terminal spine to telson. Both pair of long laterals present.	5 terminal spines to telson.
3rd Cyrtopia.	1 terminal spine to telson, outer long lateral gone.	5 terminal spines to telson.
4th Cyrtopia.	Tip of telson elongates until adult stage is reached, 7th thoracic legs become longer, gills and exopodites develop further until at about 13 mm. adult stage is reached. May reach 17 mm.	5 terminal spines to telson.
5th Cyrtopia.		3 terminal spines to telson, outer laterals present.
6th Cyrtopia.		3 terminal spines to telson, outer laterals gone.
7th Cyrtopia.		1 terminal spine to telson, outer laterals gone. Tip of telson elongates until adult stage is reached, 7th thoracic legs become longer, gills and exopodite develop further until at about 20 mm. adult stage is reached. May reach 40 mm.

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### EXPLANATION OF PLATES.

ALL figures of the whole animal are drawn to one scale and those of the appendages to another scale, so that the sizes are proportional.

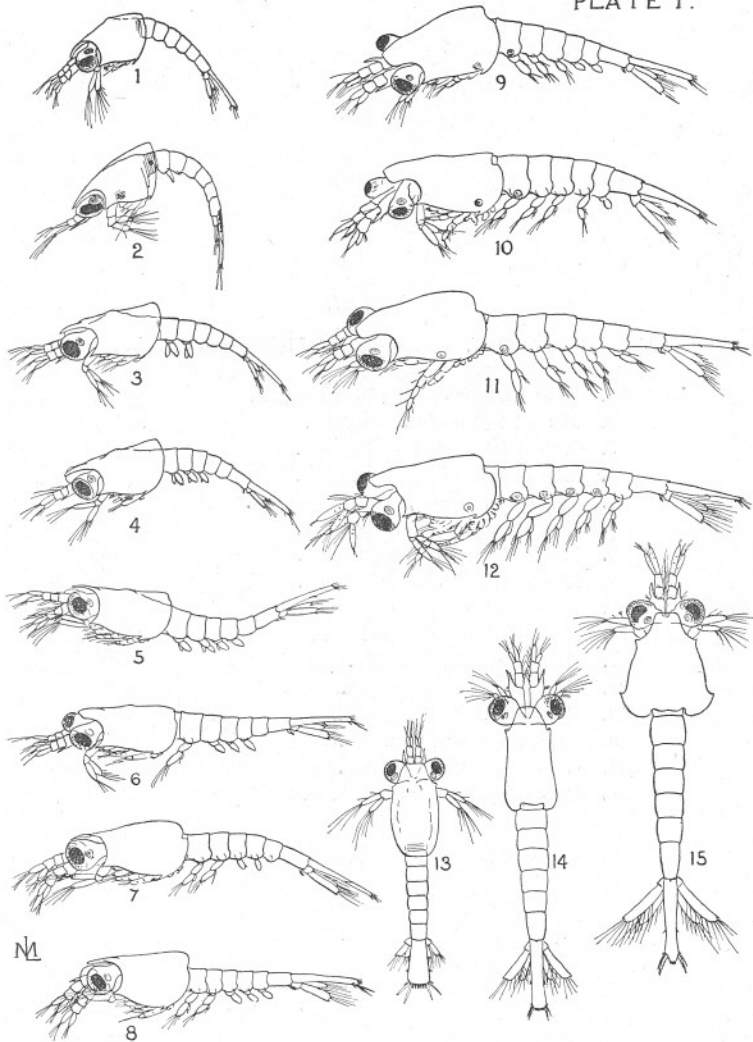
## PLATE I.

*Nyctiphanes Couchii*. Furcilia stages.

FIG.

1. First Furcilia, 2.5 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
2. Second Furcilia, 2.5 mm. long. Station L4, off Plymouth, March, 1924.
3. Third Furcilia, 2.8 mm. long. Station L4, off Plymouth, March, 1924.
4. Fourth Furcilia, 2.8 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
5. Fifth Furcilia, 3.2-3.5 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
6. Sixth Furcilia, 3.2-3.5 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
7. Seventh Furcilia, 3.5-3.6 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
8. Eighth Furcilia, 3.2-3.6 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
9. Ninth Furcilia, 3.8 mm. long. Mr. Hickling's Atlantic material, near coast, Oct., 1924.
10. Tenth Furcilia, 4 mm. long. Station L4, off Plymouth, June, 1924.
11. Eleventh Furcilia, 4.3 mm. long. Station L4, off Plymouth, June, 1924.
12. Twelfth and last Furcilia, 4.3 mm. long. Station L4, off Plymouth, June, 1924.
13. Dorsal view of 2.
14. Dorsal view of 7.
15. Dorsal view of 12.

PLATE 1.



*Nyctiphanes Couchii.*



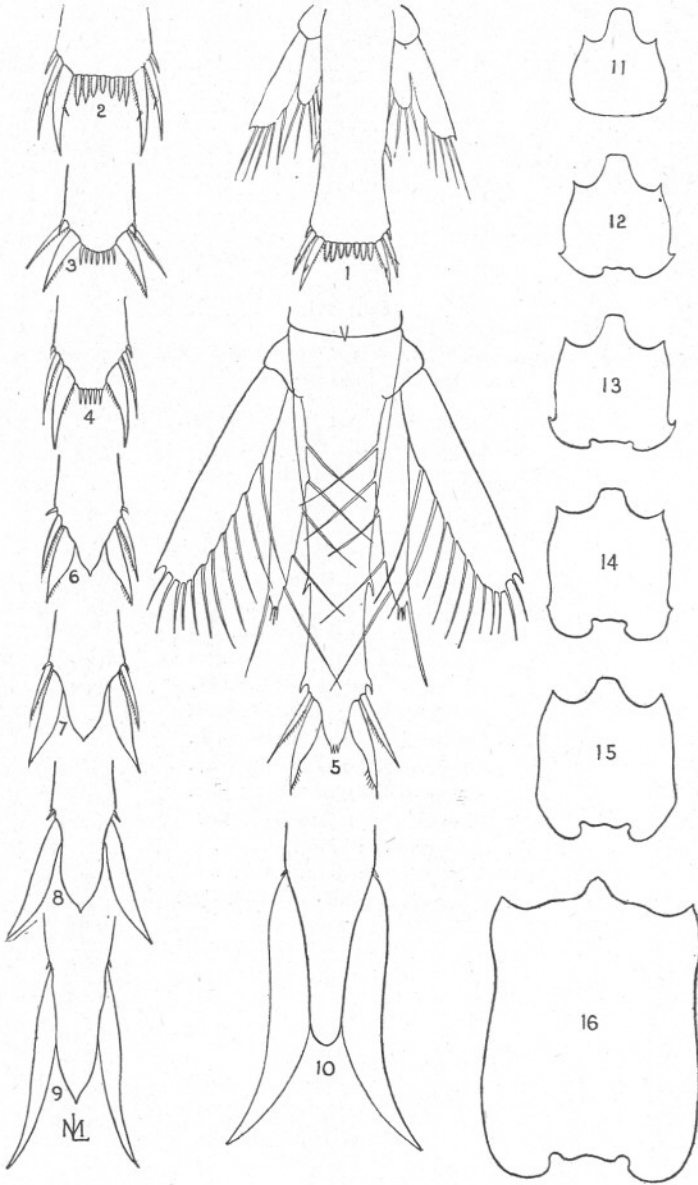
## PLATE II.

*Nyctiphanes Couchii*. Development of telson and carapace.

FIG.

1. Telson and uropods of 1st Furcilia.
2. End of telson of 4th Furcilia.
3. End of telson of 10th Furcilia.
4. End of telson of 12th Furcilia.
5. Telson and uropods of 1st Cyrtopia.
6. End of telson of 2nd Cyrtopia.
7. End of telson of 3rd Cyrtopia.
8. End of telson of 5th Cyrtopia.
9. End of telson of 9th Cyrtopia.
10. End of telson of a specimen 12 mm. long.
11. Carapace of 3rd Furcilia.
12. Carapace of 1st Cyrtopia.
13. Carapace of 3rd Cyrtopia.
14. Carapace of 4th Cyrtopia.
15. Carapace of 5th Cyrtopia.
16. Carapace of specimen 15 mm. long.

PLATE II



*Nyctiphanes Couchii.*

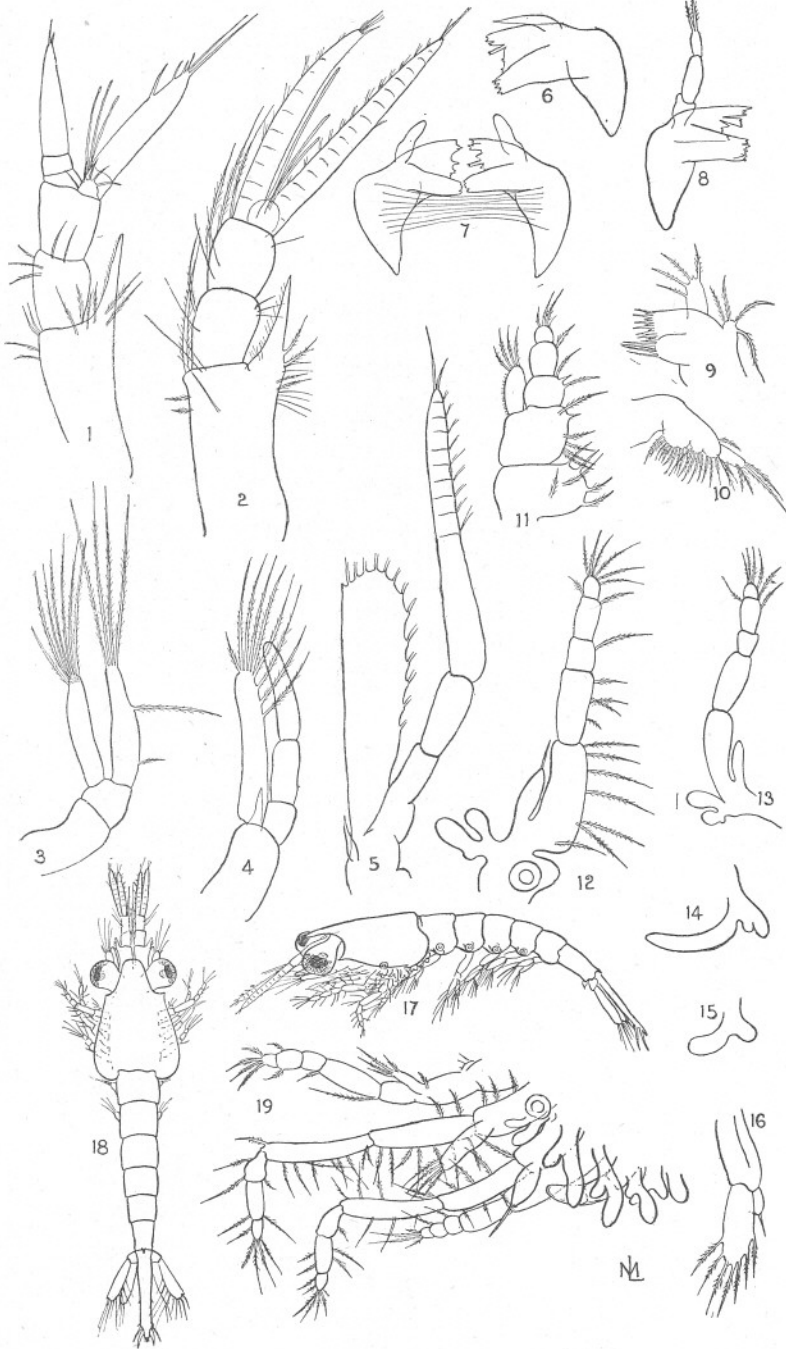
## PLATE III.

*Nyctiphanes Couchii*. 1st Cyrtopia and appendages of last Furcilia and 1st and 3rd Cyrtopia.

## FIG.

1. Antennule of last (12th) Furcilia.
2. Antennule of 1st Cyrtopia.
3. Antenna of last Furcilia.
4. Antenna of 1st Cyrtopia.
5. Antenna of 3rd Cyrtopia.
6. Mandible of last Furcilia.
7. Mandible of 1st Cyrtopia.
8. Mandible of 3rd Cyrtopia.
9. 1st maxilla of 1st Cyrtopia.
10. 2nd maxilla of 1st Cyrtopia.
11. 1st thoracic leg of last Furcilia.
12. 2nd thoracic leg of last Furcilia.
13. 3rd thoracic leg of last Furcilia.
14. 4th thoracic leg of last Furcilia.
15. 5th thoracic leg of last Furcilia.
16. Pleopod of last Furcilia.
17. 1st Cyrtopia: side view.
18. 1st Cyrtopia: dorsal view.
19. Thoracic appendages of 1st Cyrtopia.

PLATE III.



*Nyctiphanes Couchii.*

## PLATE IV.

*Nyctiphanes Couchii*. Development of 7th thoracic leg in ♂

FIG.

1. 2nd Cyrtopia.
2. 3rd Cyrtopia.
3. 6th Cyrtopia.
4. 7th Cyrtopia.
5. 8th Cyrtopia.
6. 9th Cyrtopia.
7. 10th Cyrtopia.
8. 11th Cyrtopia.
9. 12th Cyrtopia.
10. 13th Cyrtopia.
11. Adult, 13 mm.

PLATE IV



*Nyctiphanes Couchii*

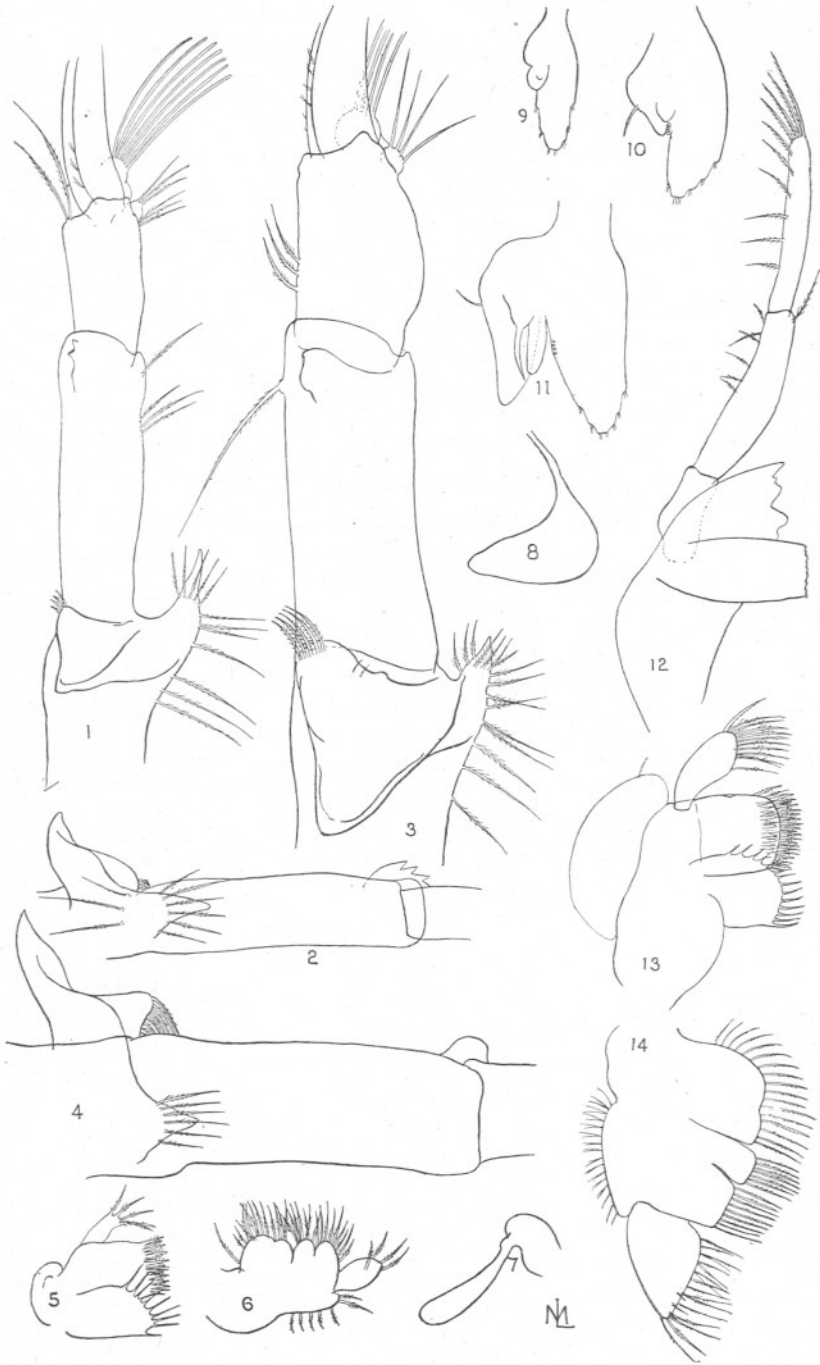
## PLATE V.

*Nyctiphanes Couchii*. Appendages of later Cyrtopia and adult.

FIG.

1. Antennule of adult ♀, 14 mm. long, dorsal view.
2. Part of the same, side view, showing processes of first and second joints.
3. Antennule of adult ♂, 14 mm. long, dorsal view.
4. Part of the same, side view, showing processes on first and second joints.
5. 1st maxilla of 5th Cyrtopia, 6 mm. long.
6. 2nd maxilla of 5th Cyrtopia, 6 mm. long.
7. 8th thoracic leg of 9th Cyrtopia, 8 mm. long.
8. Spermatophore of ♂ of 9 mm.
9. Inner ramus of 1st pleopod of ♂ 5th Cyrtopia, 6 mm. long.
10. Inner ramus of 1st pleopod of ♂ 9th Cyrtopia, 8 mm. long.
11. Inner ramus of 1st pleopod of adult ♂, 14 mm. long.
12. Mandible of adult, 14 mm.
13. 1st maxilla of adult, 14 mm.
14. 2nd maxilla of adult, 14 mm.

PLATE V



*Nyctiphanes Couchii*



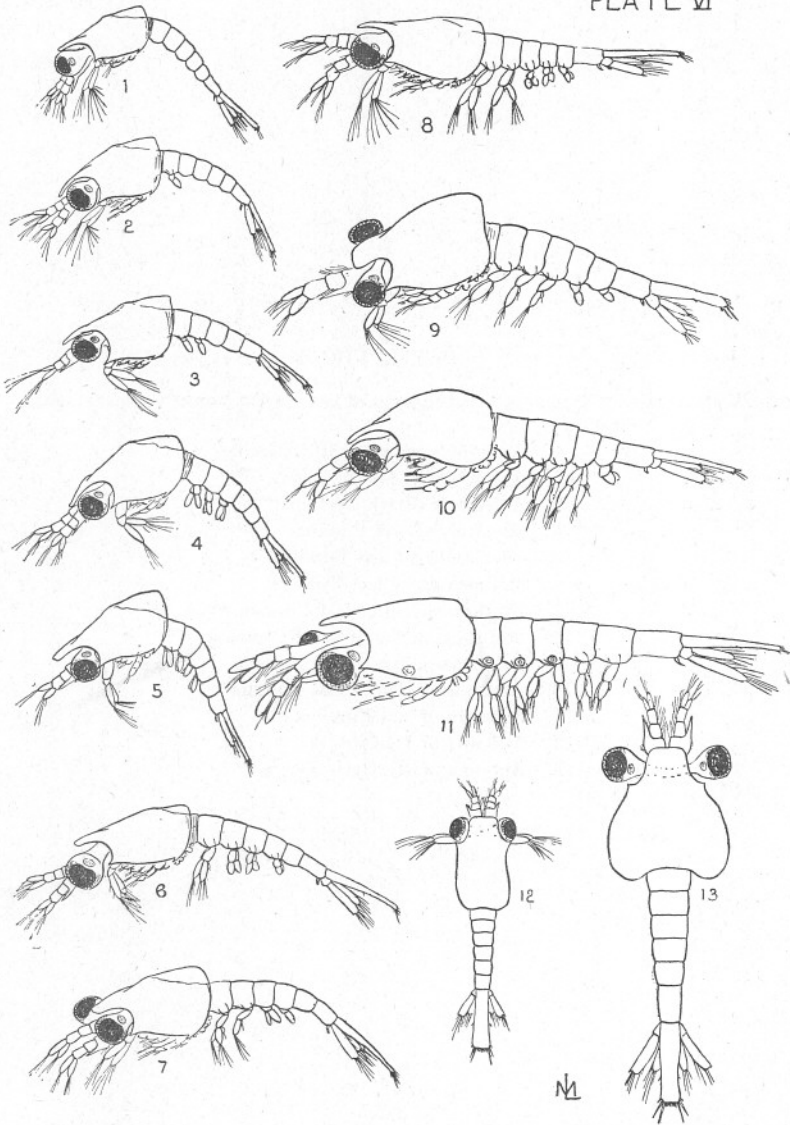
## PLATE VI.

*Meganyctiphanes norvegica*. Furcilia stages.

FIG.

1. 1st Furcilia, 2.8 mm. long, beyond Eddystone, May, 1925.
2. 2nd Furcilia, 3 mm. long, beyond Eddystone, May, 1925.
3. 3rd Furcilia, 3 mm. long, Station E1, April, 1924.
4. 4th Furcilia, 3.5 mm. long, Station E1, April, 1924.
5. 5th Furcilia, 3.5 mm. long, beyond Eddystone, May, 1925.
6. 6th Furcilia, 3.8 mm. long, beyond Eddystone, May, 1925.
7. 7th Furcilia, 3.8 mm. long, beyond Eddystone, May, 1925.
8. 8th Furcilia, 4 mm. long, Station E1, April, 1924.
9. 9th Furcilia, 4.4 mm. long, Station E1, April, 1924.
10. 10th Furcilia, 4.6 mm. long, Station E1, April, 1924.
11. 12th Furcilia, 5 mm. long, Station L4, May, 1924.
12. Dorsal view of 3.
13. Dorsal view of 10.

PLATE VI



*Meganyctiphanes norvegica.*

## PLATE VII.

*Meganyctiphanes norvegica*. Appendages of last Furcilia and Cyrtopia stages.

## FIG.

1. Antennule of last (12th) Furcilia.
2. Antennule of 1st Cyrtopia.
3. Antennule of 4th Cyrtopia.
4. Mandible of last Furcilia.
5. 1st maxilla of last Furcilia.
6. 2nd maxilla of last Furcilia.
7. 1st thoracic leg of last Furcilia.
8. 2nd thoracic leg of last Furcilia.
9. 3rd thoracic leg of last Furcilia.
10. 4th thoracic leg of last Furcilia.
11. Antenna of last Furcilia.
12. Antenna of 1st Cyrtopia.
13. Antenna of 4th Cyrtopia.



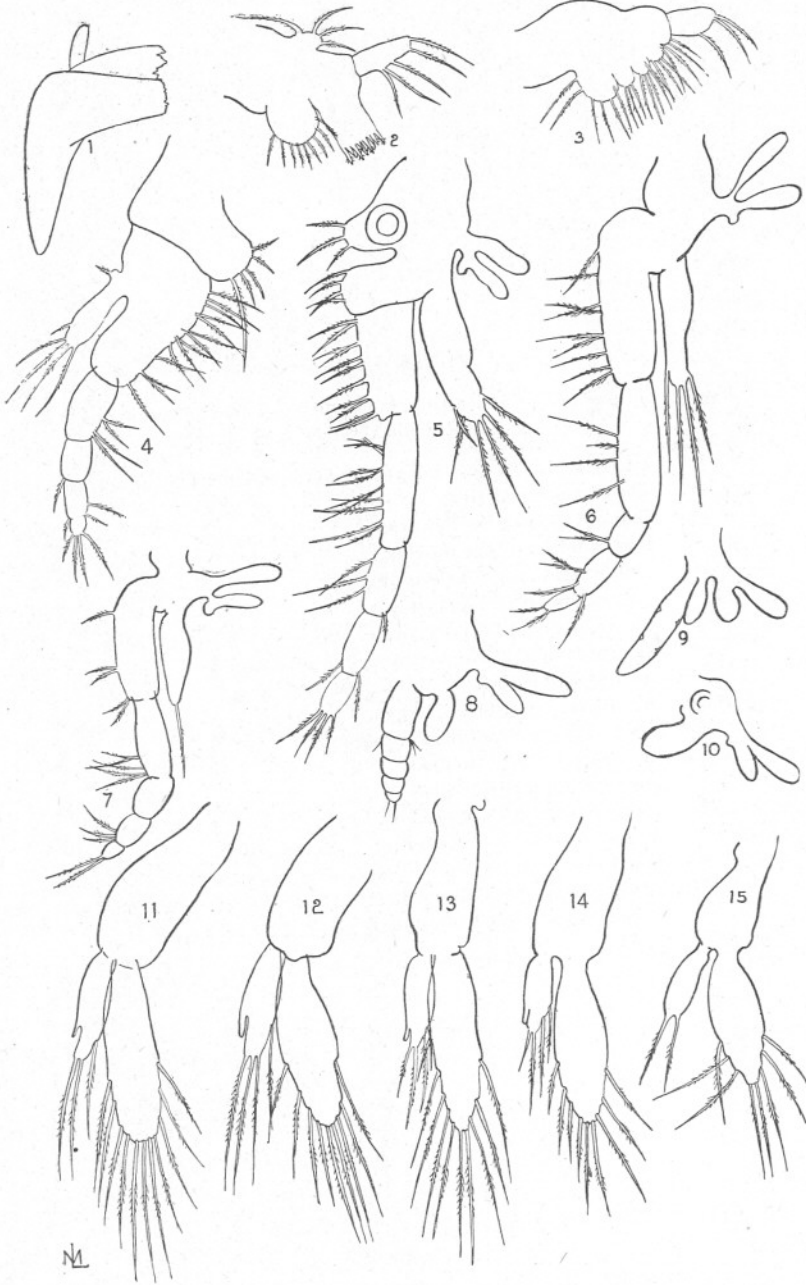
*Meganyctiphanes norvegica.*

## PLATE VIII.

*Meganyctiphanes norvegica*. Appendages of 1st Cyrtopia

## FIG.

1. Mandible.
2. 1st maxilla.
3. 2nd maxilla.
4. 1st thoracic leg.
5. 2nd thoracic leg.
6. 3rd thoracic leg.
7. 4th thoracic leg of 1st Cyrtopia.
8. 5th thoracic leg of 1st Cyrtopia.
9. 6th thoracic leg of 1st Cyrtopia.
10. 7th thoracic leg of 1st Cyrtopia.
11. 1st pleopod of 1st Cyrtopia.
12. 2nd pleopod of 1st Cyrtopia.
13. 3rd pleopod of 1st Cyrtopia.
14. 4th pleopod of 1st Cyrtopia.
15. 5th pleopod of 1st Cyrtopia.



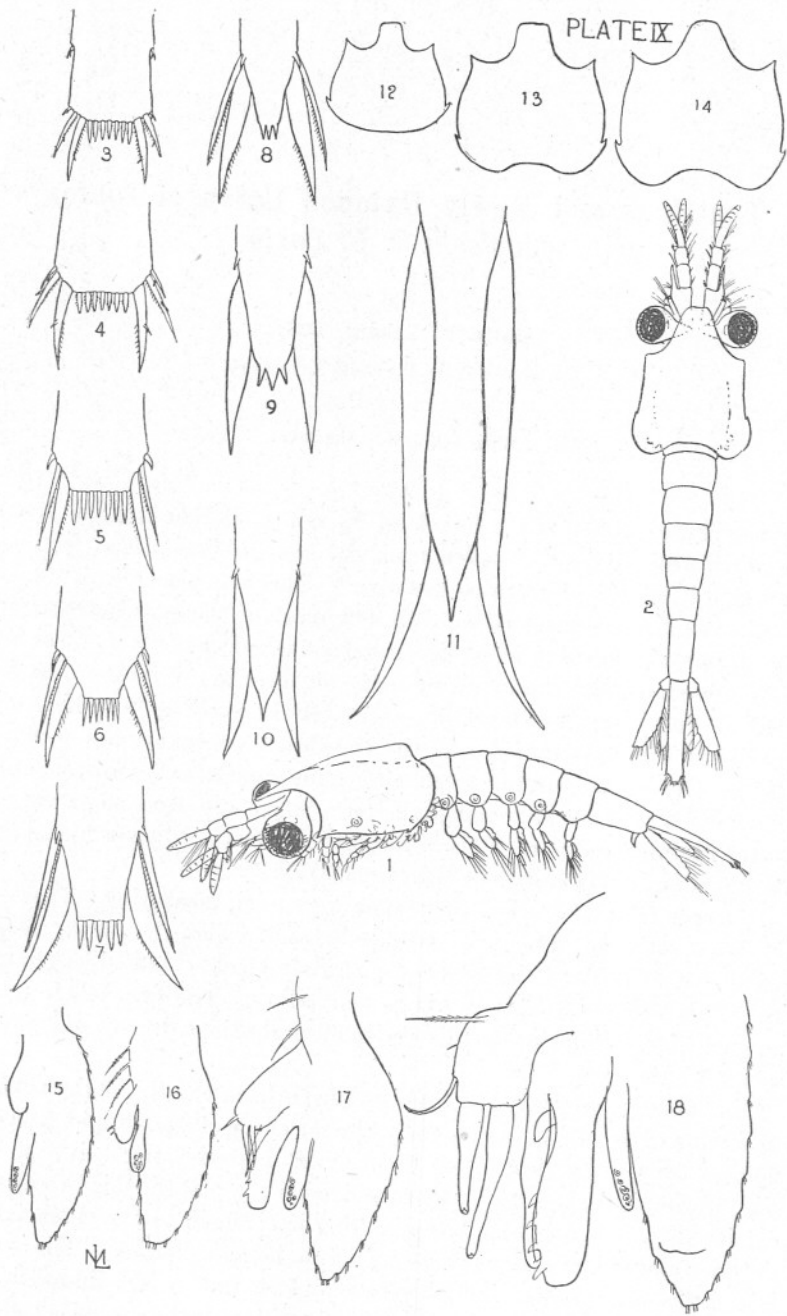
*Meganyctiphanes norvegica*.

## PLATE IX.

*Meganyctiphanes norvegica*. 1st Cyrtopia; development of telson and carapace in Furcilia and Cyrtopia.

## FIG.

1. 1st Cyrtopia, 5.6 mm. long, side view, Station L4, June, 1924.
2. The same, dorsal view.
3. End of telson of 1st Furcilia.
4. End of telson of 4th Furcilia.
5. End of telson of 12th Furcilia.
6. End of telson of 1st Cyrtopia.
7. End of telson of 4th Cyrtopia.
8. End of telson of 5th Cyrtopia, 7.5 mm. long.
9. End of telson of 6th Cyrtopia, 8.5 mm. long.
10. End of telson of 8th Cyrtopia, 9 mm. long.
11. End of telson of adult, 20 mm. long.
12. Carapace of 3rd Furcilia.
13. Carapace of last Furcilia.
14. Carapace of 1st Cyrtopia.
15. Inner ramus of 1st pleopod of ♂, 13 mm. long.
16. Inner ramus of 1st pleopod of ♂, 15 mm. long.
17. Inner ramus of 1st pleopod of ♂, 17 mm. long.
18. Inner ramus of 1st pleopod of ♂ adult, 25 mm. long.



*Meganyctiphanes norvegica.*



**The Eggs and Newly Hatched Larva of *Typton spongicola* O. G. Costa.**

By

**Marie V. Lebour, D.Sc.,**

*Naturalist at the Plymouth Laboratory.*

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With 3 figures in the text.

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At the end of June, 1924, a female of *Typton spongicola*, dredged by the *Salpa*, bearing eggs, was taken from the sponge *Desmacidon fruticosus* in which it lives, and given to me alive.\* This was placed in a Plunger Jar in the Laboratory, and on July 8th most of the eggs hatched out. The larvæ did not live long, and never sloughed the skin; but several were preserved, and the following notes on these are of interest, as very little is known of the development in the Pontoniinæ to which sub-family of the Palaemonidæ in the Caridea, *Typton* belongs (Gurney, 1925). The female continued to live for some months at the bottom of the Plunger Jar without any sponge shelter. It ate any dead plankton, and was a useful scavenger. This is interesting, as its ordinary food is the *Desmacidon* in which it lives (Hunt, 1923).

The eggs (Fig. 1, c) when first taken were oval, measuring 0.8 mm. by 0.5 mm., with an outer thin capsule through which the larva, already brightly coloured and the eyes conspicuously black, could be seen curled up. The colour was a deep orange and yellow. The eggs fell from the parent before hatching, but this was in all probability due to confinement and not natural.

The larva, measuring 2.08 mm. in length from the tip of the rostrum to the end of the telson, is extremely like the figure of a pontoniid, Stage II, figured by Gurney from the *Terra Nova* material (loc. cit., p. 127, Fig. 51, Species 1, a), with a very conspicuous hump at the third abdominal somite (Fig. 1, a and b). The colouring is confined to the thoracic and anterior abdominal regions, the long telson being colourless. The thorax is a diffuse dull yellow, inclining to a pinkish tint on the limbs, with a large pair of scarlet chromatophores in the middle of the carapace between and behind the eyes. The first four segments of the abdomen are yellowish

\* I am indebted to Mrs. H. Thompson for this specimen.

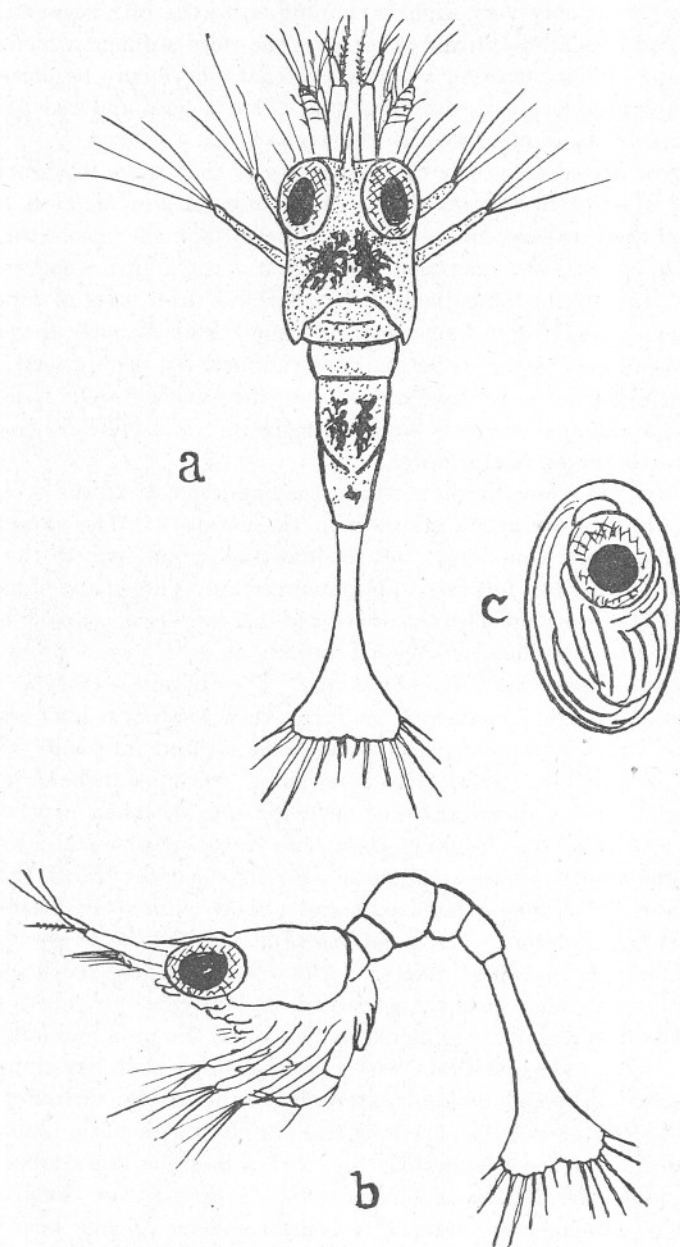


FIG. 1. Newly hatched larva and egg of *Typton spongicola*.  
(a) Dorsal view, length 2.08 mm.  
(b) Side view of same specimen.  
(c) Egg, 0.8 × 0.5 mm.

also, the colour only very slightly running on to the fifth segment, with a large pair of scarlet chromatophores on the third segment which forms the hump. A faint trace of a scarlet chromatophore may be present on the fifth segment, but is not constant. This yellow and red pigment together give the orange effect to the whole larva.

This first larval stage has the characters of that stage in the typical Caridea, as given by Gurney (*loc. cit.*). It possesses sessile eyes, has no spines on the carapace, has seven pairs of spines on the telson (the larva within the egg was not examined, therefore it is not known whether there are only six pairs in the embryonic cuticle), has three pairs of biramous maxillipedes, and the thoracic limbs are not simultaneously developed, for in this case there are two pairs of rudimentary legs present. The second maxilla has only three inner lobes, the antennal scale is jointed, the third abdominal somite is larger than the rest, and there are no dorsal spines to the abdominal somites.

The larva has a long simple rostrum reaching well beyond the eyes, with a slight indentation at its origin from the carapace. The carapace is simple and short, eyes large. Of the five abdominal somites the third is distinctly enlarged, forming a prominent hump. Three pairs of maxillipedes are well developed, two pairs of rudimentary legs occurring behind them, the first biramous, the second uniramous, with a small prominence at its base representing the other ramus. The antennule (Fig. 2, b) has a long unjointed peduncle with an inner knob bearing a long plumose seta and an outer branch with three aesthetes, and internally a short ciliated seta. The antenna (Fig. 2, c) has a short peduncle about half the length of the antennular peduncle bearing an inner very slender branch, the flagellum, reaching about two-thirds up the scale, with an inner spine and an outer long plumose seta: in the outer branch the scale is six-jointed with nine ciliated setae and a short outer spine, besides one seta on its outer margin. The mandibles (Fig. 2, d, and Fig. 3) are strongly toothed, each side slightly different, with a long feathery tooth situated just within the main crunching portion and internal to this a setose lobe. The first maxilla (Fig. 2, e) has two lobes, the proximal lobe short with short setae, the distal lobe with two large thick hook-like spines and two fine setae, also a short knob externally at the base of the outer thick spine. The endopodite has one long and one short seta and a blunt knob externally. The second maxilla (Fig. 2, f) has three inner lobes only, bearing four, two and two setae respectively, counting from the proximal end. The unsegmented endopodite bears one seta, or may bear three. The exopodite is large with five ciliated setae, two in front, two lateral, and one large seta directed backwards. The three maxillipedes are all of the same pattern, each with a long exopodite bearing four long terminal setae. The endopodite of the first (Fig. 2, g) is unjointed,

with three terminal setæ, one lateral and four at the base, those of the second and third (Fig. 2, h and j) have three joints, the second with a thick hook and two setæ on the terminal joint, the third with three thick hooks on the terminal joint, two of which come from its base and one terminal. There are also four setæ on the terminal joint, one at the base

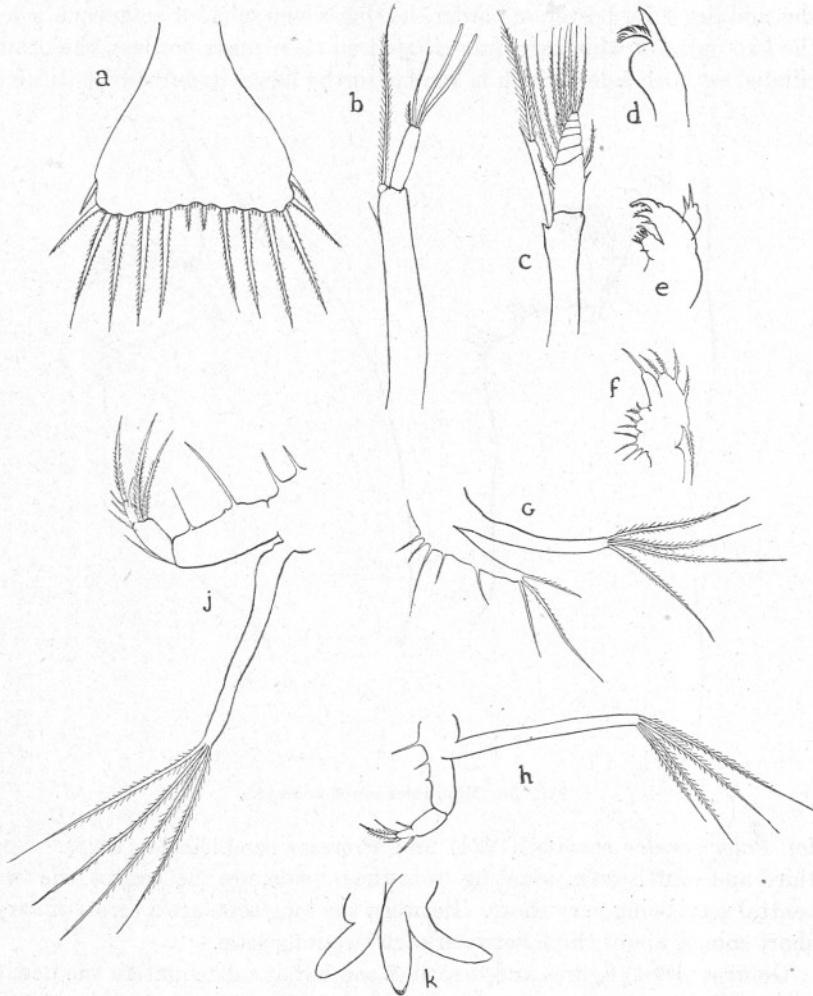


FIG. 2. Telson and appendages of the newly hatched larva of *Typton spongicola* (all drawn to same scale).

- |                    |                         |
|--------------------|-------------------------|
| (a) Telson.        | (f) Second maxilla.     |
| (b) Antennule.     | (g) First maxillipede.  |
| (c) Antenna.       | (h) Second maxillipede. |
| (d) Mandible.      | (i) Third maxillipede.  |
| (e) First maxilla. | (j) Third maxillipede.  |
|                    | (k) Rudimentary legs.   |

of the penultimate joint and two on the inside of the first joint, the base having two internal setæ. The three exopodites are unjointed, but there are indications of three segments which will probably appear in the next moult. The hook-like spines on the second and third maxillipedes (one terminal on each and two at the base of the last joint) are provided with three rows of short spines. The telson is only slightly indented at the middle of its posterior border, having seven ciliated setæ each side, the two outer of which are only ciliated on their inner borders, the other ciliated on both sides, which is similar to the larvæ described by Gurney

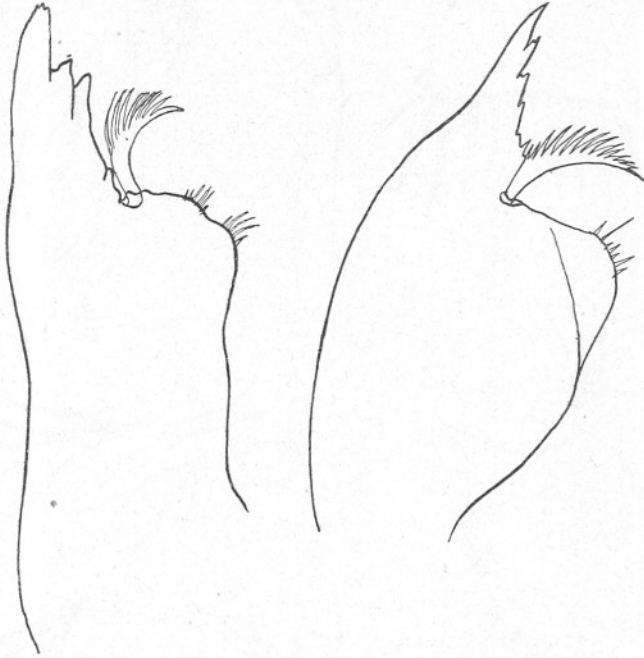


FIG. 3. Mandibles much enlarged.

for *Palaemonetes varians* (1924) and *Processa canaliculata* (1923). The third and fourth setæ, counting from the outside, are the longest, the two central setæ being very short. Between the long setæ are a series of very short spines, about three between each two long setæ.

Gourret (1884) figures and describes somewhat inadequately the newly hatched larva of a *Pontonia* parasitic in *Ascidia* from Marseilles. In its segmented antennal scales, the form of its antennules and general build, it resembles the larva of *Typton*. He describes them as being colourless with a few rare spots of yellow pigment, therefore differing from *Typton* widely in this. At present this appears to be the only information we have on the pontoniid larvæ.

A comparison of the newly hatched Typton larva with that of *Palaemonetes varians* described by Gurney (loc. cit.), shows much resemblance between the two, in particular the form of the telson with the arrangement of its setæ, the segmented antennæ and the form of these and the antennules. When we have only the first larval stage for comparison, however, there is not much to go upon, and further stages are much wanted to complete the life-history.

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1925. HUNT, O. D. The Food of the Bottom Fauna of the Plymouth Fishing Grounds. Journ. Mar. Biol. Assoc., Vol. XIII, No. 3.

## On the Amphipod Genus *Talitrus*, with a description of a new species from the Scilly Isles, *T. dorrieni* n. sp.

By

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*Assistant Naturalist at the Plymouth Laboratory.*

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With Plates I-III and 5 Figures in the Text.

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### INTRODUCTION.

DURING the winter of 1924-25 some living specimens of a terrestrial sand-hopper were sent by Major A. A. Dorrien-Smith, D.S.O., Governor of the Isles of Scilly, to Mrs. E. W. Sexton of the Plymouth Laboratory. The specimens, which were handed over to the writer by Mrs. Sexton, have proved on examination to belong to a new species, which is described below and given the name *Talitrus dorrieni*.

According to information received with the specimens the species has a truly terrestrial habitat: it is found living among the moist humus and under dead leaves in the gardens of Tresco Abbey.

In the course of examining the literature of the already described species of the genus *Talitrus* Latreille and the genus *Talitriator* Methuen, evidence has been accumulated which warrants the abandonment of the latter genus. Discussion of this and other supporting evidence, a reconstitution of the genus *Talitrus* and a key to the identification of the species form the first part of this paper, description of the new species being reserved till last.

### DISCUSSION.

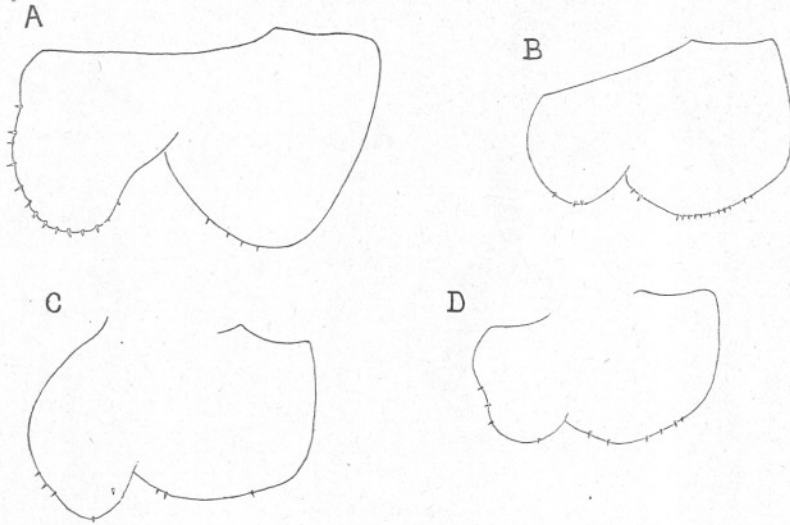
The genus *Talitrus* was instituted by Latreille in 1802 to receive, along with forms since removed from the genus, the European littoral species now known as *Talitrus saltator* (Montagu). Subsequently described species are *T. gulliveri* Miers, 1876 (8), from the Island of Rodriguez, presumably littoral; *T. sylvaticus* Haswell, 1879 (6), from New South Wales, terrestrial; *T. alluaudi* Chevreux, 1896 (3), from the Seychelles Is. and from European hot-houses, terrestrial; *T. kershawi* Sayce, 1909 (10), from Victoria, terrestrial; *T. hortulanus* Calman, 1912 (2), from Kew Gardens, terrestrial.

In 1913 Methuen (7) described a new genus and species, *Talitriator*

*eastwoodae*, for specimens of a terrestrial sand-hopper from Natal. Barnard, 1916 (1), accepted the new genus and transferred to it the two Australian species, *Talitrus sylvaticus* and *T. kershawi*. Finally, Stebbing in 1917 (12), while accepting Methuen's genus, shewed that the species was identical with the *Talorchestia africana* of Spence Bate, and renamed it accordingly *Talitriator africanus* (Bate).

The definition of the genus given by Barnard is as follows:—

“Like *Talitrus*, but with anterior lobe of 5th side-plate much larger than the posterior lobe, 1st antenna only slightly shorter than peduncle



TEXT FIGURE 1.—5th side-plates of A, *Talitrus saltator*; B, *T. dorrieni*; C, *T. africanus*; D, *T. alluaudi*.

of 2nd antenna, palp of maxilliped 4-jointed, 1st gnathopod not so long as 2nd gnathopod and not stronger, 5th joint of 1st gnathopod distally expanded, 2nd joint of 3rd peræopod moderately or scarcely at all expanded, telson longer than broad.”

This definition will, however, include also *Talitrus alluaudi* Chev., *Talitrus hortulanus* Calman and *Talitrus dorrieni* n. sp. The characters given by Barnard, in fact, with the addition of one other, namely, *degradation of the pleopods*, are common to all the terrestrial species, and if these characters be of generic value the terrestrial species should be united under the genus *Talitriator*, leaving the genus *Talitrus* for the 2 littoral species.

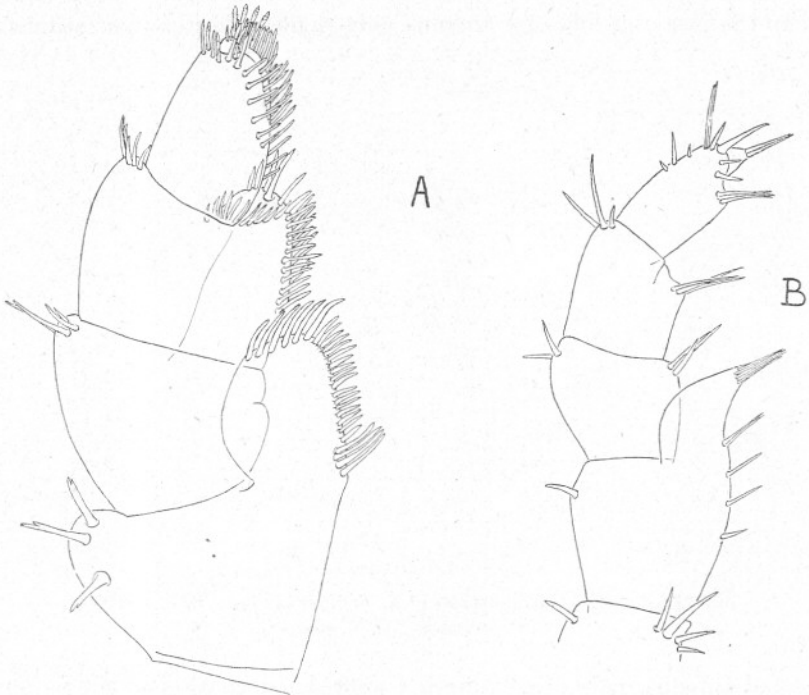
As generic characters, however, they are not satisfactory. In the following examination they may be treated in the order given by Barnard.

Sar's figure of the 5th side-plate of *Talitrus saltator* (*T. locusta* Sars, 9),



on which Barnard relies for his comparison with the first character in his diagnosis, is, as Stebbing (12) points out, misleading. The accompanying figures of the 5th side-plates of *T. saltator* and other species shew the invalidity of this character (Text Fig. 1).

The second character given, the comparative length of the 1st antenna, provides a constant distinction, though varying in degree. In *T. sylvaticus*, *T. kershawi* and *T. dorrieni* the 1st antenna reaches the middle of the

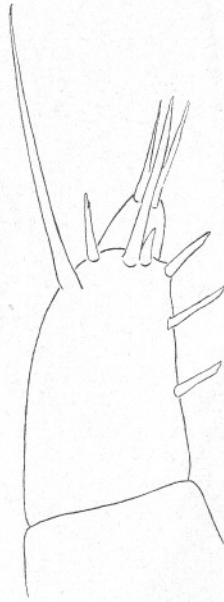


TEXT FIGURE 2.—Maxilliped-palp and outer-plate of A, *Talitrus saltator* ;  
B, *T. dorrieni*.

last joint of the peduncle of the 2nd antenna. In *T. alluaudi* and *T. hortulanus* it reaches beyond the middle of, and in *T. africanus* to the end of the last joint of the peduncle of the 2nd antenna.

The third character is not distinctive and varies considerably in degree. Careful examination of the maxilliped palp of *T. saltator* has revealed the presence of a minute, terminal, seta-bearing tubercle, representing the 4th joint, almost hidden by the dense rows of spines on the end of the 3rd joint (Text Fig. 2, A). The maxilliped palp of *T. alluaudi* is so minute that, up to the present, it had escaped unnoticed. The writer has examined and dissected specimens of *T. alluaudi* from the Seychelles,

kindly supplied by Dr. Louis Fage of the Paris Museum. Text Fig. 3 shews the minute but quite distinct 4th joint of the maxilliped palp in this species. In *T. kershawi* and *T. hortulanus* the minute 4th joint of the maxilliped palp is obscurely marked off from the 3rd joint. The number of joints in the maxilliped palp does not, therefore, provide a distinctive character. The maxillipeds of *T. saltator*, however, present a distinctive character not previously emphasized, in the much greater proportionate breadth of the palp segments and in the very different nature of their spination (Text Fig. 2.)



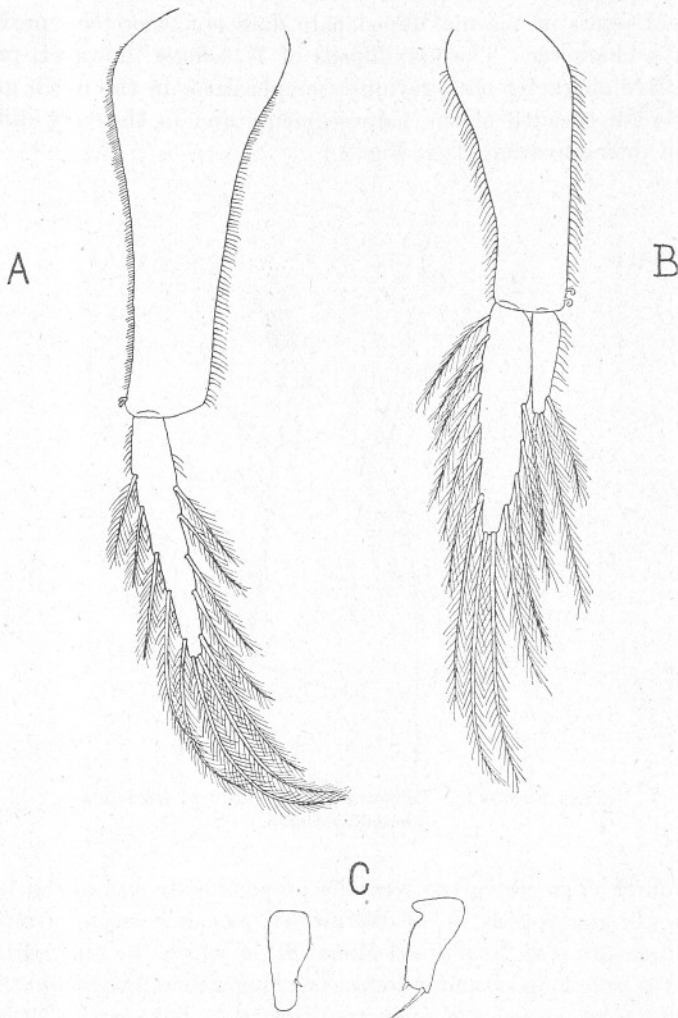
TEXT FIGURE 3.—*Talitrus alluaudi*: 3rd and 4th joints of maxilliped palp.

The fourth character given, viz. the proportionate size of the 1st and 2nd pairs of gnathopods, is not distinctive, as can be seen on reference to the description of *T. gulliveri* Miers (8), in which the 2nd gnathopod is stated to be as long as, and in some cases longer than, the 1st gnathopod.

The last three characters given are distinctive, but scarcely of generic rank.

All the terrestrial species shew a reduction in the size and development of the pleopods. This is most marked in *T. kershawi*, in which those of the 1st pair are very small and uniramous, those of the 2nd vestigial, without rami, while the 3rd pair is absent. The degradation is least marked in *T. hortulanus* and *T. africanus*, in which all three pairs are present and biramous, though—especially the 3rd pair—reduced in size.

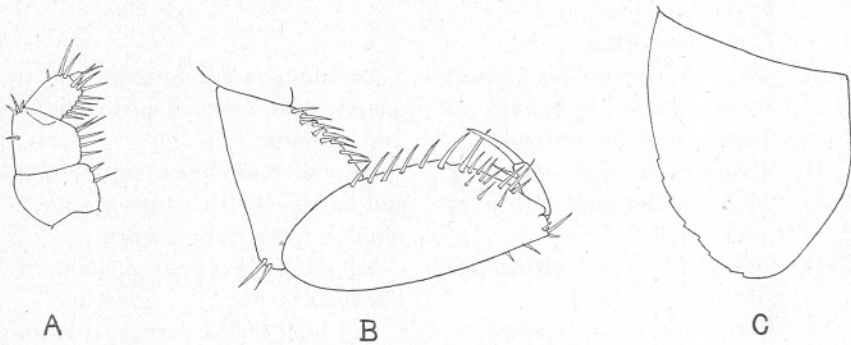
In *T. dorrieni*, *T. sylvaticus* and *T. alluandi* the 3rd pair is reduced to vestigial stumps, without rami, while the three species respectively shew successive stages in the degradation of the 1st and 2nd pairs.



TEXT FIGURE 4.—*Tabitrus sylvaticus*: A, 1st pleopod (outer ramus missing); B, 2nd pleopod; C, 3rd pair of pleopods.

There is a discrepancy in the published accounts of the pleopods of *T. sylvaticus* to which reference must be made as it concerns the specific significance which in this paper is attached to the characters of the pleopods. Calman (2) first drew attention to this discrepancy, and

Chilton (5) has further referred to it in a note on the species. Sayce's description states that the 3rd pair of pleopods is absent, whilst Chevreux (4), who examined Tasmanian specimens sent to him by Chilton, states that the pleopods of the 3rd pair resemble those of the 1st two pairs in being biramous, though of smaller size. Chevreux, moreover, figures the 1st pair, and his figure is quite different from that of Sayce (10). Calman examined specimens from the Australian Museum and did not, as Chilton wrongly states, confirm Chevreux's description. On the contrary, he states that the 3rd pair consists of minute vestigial stumps, without rami and small enough to have been possibly overlooked by Sayce. By courtesy of Dr. Calman I have been able to examine his preparations of the pleopods of this species and these are figured above (Text Fig. 4.) The 1st and 2nd pairs are as described by Sayce, the 3rd pair as described



TEXT FIGURE 5.—Specimen (not *Talitrus sylvaticus*) labelled *Talitrus sylvaticus*, Tasmania, in collection of M. Chevreux. A, maxilliped-palp; B, 1st gnathopod; C, epimeral plate of 2nd pleon segment.

by Calman. Further, through the kindness of Dr. Louis Fage of the Paris Museum, I have been able to examine a specimen, labelled *Talitrus sylvaticus* from Tasmania, ex collection M. Chevreux. Although unable to dissect this specimen, I can state definitely that it does not belong to the species in question, if indeed to the genus *Talitrus* (Text Fig. 5.) The 1st gnathopod is subcheliform with an oblique palm, the shape of the 2nd pleon segment is very different from that of any *Talitrus*, all 3 pairs of pleopods are present and biramous and apparently well developed, though too small to describe properly without dissection. The palp of the maxilliped is distinctly 4-jointed, but the form of the palp differs considerably from that in *T. sylvaticus* as regards shape, proportion and spination. The specimen is a female and may possibly belong to the genus *Parorchestia*. It seems probable, therefore, that the specimen described by Chevreux was not *T. sylvaticus*, which would explain the discrepancy in question.

It remains to restate, in the light of the foregoing, the characters which distinguish the terrestrial forms (*Talitrus* and *Talitriator*) from the littoral forms (*Talitrus*).

The writer has not examined specimens of *Talitrus gulliveri* Miers. Miers' description is very incomplete, and there is no figure. The sex of the specimens is not stated, which leaves even the genus uncertain. It has been thought best, therefore, to exclude this species from the following table:—

TERRESTRIAL HABIT.	LITTORAL HABIT.
<i>Talitrus alluaudi</i> Chev.	<i>Talitrus saltator</i> (Mont.).
<i>T. hortulanus</i> Calman.	
<i>T. dorrieni</i> n. sp.	
<i>Talitriator sylvaticus</i> (Hasw).	
<i>T. kershawi</i> (Sayce).	
<i>T. africanus</i> (Bate).	
I. 1st antenna reaching at least to middle of last joint of peduncle of 2nd antenna.	1st antenna reaching to end of penultimate joint of peduncle of 2nd antenna.
II. Palp of maxilliped not very broad or flattened, 4th joint very small.	Palp of maxilliped very broad and flattened, 4th joint extremely minute, quite rudimentary.
III. 5th joint of 1st gnathopod distally expanded.	5th joint of 1st gnathopod stout but linear.
IV. 2nd joint of 3rd peræopod narrowing distally.	2nd joint of 3rd peræopod regularly expanded.
V. Telson longer than broad.	Telson broader than long.
VI. Pleopods either small or degraded.	Pleopods neither small nor degraded.

The last of these characters is the only one that might warrant generic separation, but seeing that the range of difference in the condition of the pleopods within the terrestrial group itself is so great, the writer ventures to suggest that the genus *Talitriator* be abandoned and the genus *Talitrus* be reconstituted to receive all the forms of both genera.

#### Genus TALITRUS Latreille.

In accordance with the above view a fresh diagnosis of the genus *Talitrus*, with a key to the identification of the species, is here given. The diagnosis is altered as little as possible from that given by Stebbing (11).

*Diagnosis.* Peræon dorsally broad, pleon compressed. Side-plate 1 narrow, 5th broad and deep. Antenna 1 not longer than peduncle of antenna 2. Antenna 2, basal joint or joints soldered to head, with no gland-cone, ultimate joint of peduncle the longest. Epistome forming

an obtuse angle with the upper lip. Upper lip distally rounded. Lower lip with tuft of setules at inner corner of principal lobes. Maxilla 1, palp minute, 1 or 2-jointed. Maxillipeds, palp 3-jointed or with minute, rudimentary 4th joint. Gnathopod 1 simple, 5th joint strong. Gnathopod 2 similar in both sexes, 5th joint expanded, 6th produced beyond a minute, chela-forming finger. Peræopods 4 and 5 with expansion of 2nd joint only. Branchial vesicles twisted or bent. Brood plates small, lanceolate. Pleopods sometimes more or less degraded. Telson simple.

KEY TO SPECIES.

- |    |   |  |                       |
|----|---|--|-----------------------|
| 1. | { | 1st antenna scarcely reaching beyond end of penultimate joint of peduncle of 2nd antenna. Pleopods not small or degraded . . . . .               | 2                     |
|    | { | 1st antenna reaching at least to middle of last joint of peduncle of 2nd antenna. Pleopods small or degraded . . . . .                           | 3                     |
| 2. | { | 2nd antenna, peduncle stout . . . . .  | <i>T. saltator.</i>   |
|    | { | 2nd antenna, peduncle slender . . . . .  | <i>T. gulliveri.</i>  |
| 3. | { | All 3 pairs of pleopods present and biramous, though small . . . . .   | 4                     |
|    | { | 3rd pleopod vestigial or absent . . . . .  | 5                     |
| 4. | { | 2nd gnathopod not slender, shagreened expansion on under side of 4th joint . . . . .   | <i>T. africanus.</i>  |
|    | { | 2nd gnathopod slender, no shagreened expansion on under side of 4th joint . . . . .  | <i>T. hortulanus.</i> |
| 5. | { | 3rd pleon segment, antero-lateral border produced into acute triangular projection . . . . .   | <i>T. kershawi.</i>   |
|    | { | 3rd pleon segment, antero-lateral border evenly rounded . . . . .  | 6                     |
| 6. | { | 1st and 2nd pleopods, inner ramus reduced to a mere vestige . . . . .  | <i>T. alluaudi.</i>   |
|    | { | 1st and 2nd pleopods, inner ramus at least more than $\frac{1}{2}$ as long as outer . . . . .  | 7                     |
| 7. | { | 1st and 2nd pleopods, rami distinctly segmented, inner ramus the longer, outer border of peduncle clothed with long feathered setæ. . . . .      | <i>T. dorrieni.</i>   |
|    | { | 1st and 2nd pleopods, rami not distinctly segmented, outer ramus the longer, outer border of peduncle clothed with short, simple hairs . . . . . | <i>T. sylvaticus.</i> |

TALITRUS DORRIENI n. sp.

Plates I, II and III.

The number of specimens examined was 7, consisting of 2 males, 4 females and 1 immature.

*Adult male* : length 13 mm., colour dark reddish brown.

*Head* about  $1\frac{1}{2}$  times as long as 1st peræon segment.

*2nd, 3rd and 4th side-plates* : posterior border with marked sub-acute projection.

*1st pleon segment*: posterior corner obtuse, hind margin rounded, serrulate.

*2nd and 3rd pleon segments*: posterior corner square, hind margin serrulate.

*Eyes*: round, black, rather large.

*1st antenna* reaching almost to middle of last joint of peduncle of 2nd antenna: ultimate and penultimate joints of peduncle subequal: flagellum about equal in length to peduncle, 7-jointed.

*2nd antenna* almost as long as head and peræon combined; peduncle, ultimate joint more than  $1\frac{1}{2}$  times as long as penultimate; flagellum 31-jointed.

*Maxilla*: palp very minute, 1-jointed.

*Maxillipeds*: outer plate bluntly pointed, with tapering terminal bunch of long setæ; palp with minute 4th joint.

*1st Gnathopods*: 2nd joint as long as 3rd, 4th and 5th together; 5th as long as 3rd and 4th together, expanded distally to a breadth of more than  $\frac{1}{2}$  its length, hinder distal border forming a conspicuous shagreened lobe; 6th joint tapering distally; finger, with claw,  $\frac{1}{2}$  as long as 6th joint.

*2nd Gnathopods*: 2nd joint about as long as 4th and 5th together; 3rd and 4th joints subequal in length, shorter than 5th; hinder border of 4th, 5th and 6th joints produced as prominent, shagreened expansions, projecting distally in the 6th joint well beyond the small finger.

*Peræopods*: 1st peræopod longer than second; third peræopod about as long as 1st, 2nd joint narrowing distally, with hind margin straight, slightly crenulate; 4th peræopod much longer than 3rd, with 2nd joint evenly expanded, ovate, hind margin crenulate; 5th peræopod longer than 4th, with 2nd joint almost as broad as long, hind margin serrulate.

*Pleopods*: 1st and 2nd pleopods biramous, peduncles each with one pair of minute coupling-spines; 2nd pleopod slightly the longer and stouter, rami of both pairs distinctly segmented, with outer ramus 8-jointed, about as long as peduncle and slightly shorter than 9-jointed inner ramus, the rami and the outer margins of the peduncles fringed with long plumose setæ; 3rd pleopod reduced to vestigial stump, without rami.

*Uropods*: 3rd uropod more than  $\frac{1}{2}$  as long as telson, peduncle and ramus each bearing one spine.

*Telson* longer than broad, dorsal surface arched anteriorly, hollowed laterally and posteriorly, 5 or 6 spines on each margin and 1 on each side of the truncate or faintly emarginate tip.

*Adult female*: length 15 mm., scarcely differing from male; 2nd antenna with peduncle less setose than that of male, flagellum 24-jointed;

3rd and 4th side-plates considerably larger in proportion to length of attached limb than in the male.

*Immature*: rami of pleopods 1 and 2 with fewer joints, pleopods otherwise not differing in type from those of adult.

#### REMARKS.

*Talitrus dorrieni* comes very close to *T. sylvaticus*, from which it would be hard to separate it but for the quite different form of the 1st and 2nd pleopods. Minor distinctions are present in the telson, which is more spinous; in the outer-plates of the maxillipeds, the tip of which bears a long, tapering tuft of setæ and not a transverse row of short bristles as in *T. sylvaticus*; in the 5th joint of the 1st gnathopod, which is prominently rather than minutely lobed; and in the palp of the maxilla, which is smaller and without trace of a second joint.

Barnard (1) cites a feature of *T. africanus*, which he regards as characteristic of the species, namely, the sub-acute projection of the hind margin of the 2nd side-plate. The writer has found this projection well marked in side-plates 2, 3 and 4 of *T. dorrieni* and *T. alluaudi*. It is clear but less well marked in *T. saltator*, and is well shewn in Calman's preparations of the 2nd gnathopod of *T. sylvaticus*. It occurs in *Orchestia littorea* and is probably a widespread feature in the Talitridæ.

In conclusion I would like to express my indebtedness to the kind interest of Mrs. E. W. Sexton, who has given much helpful advice and criticism.

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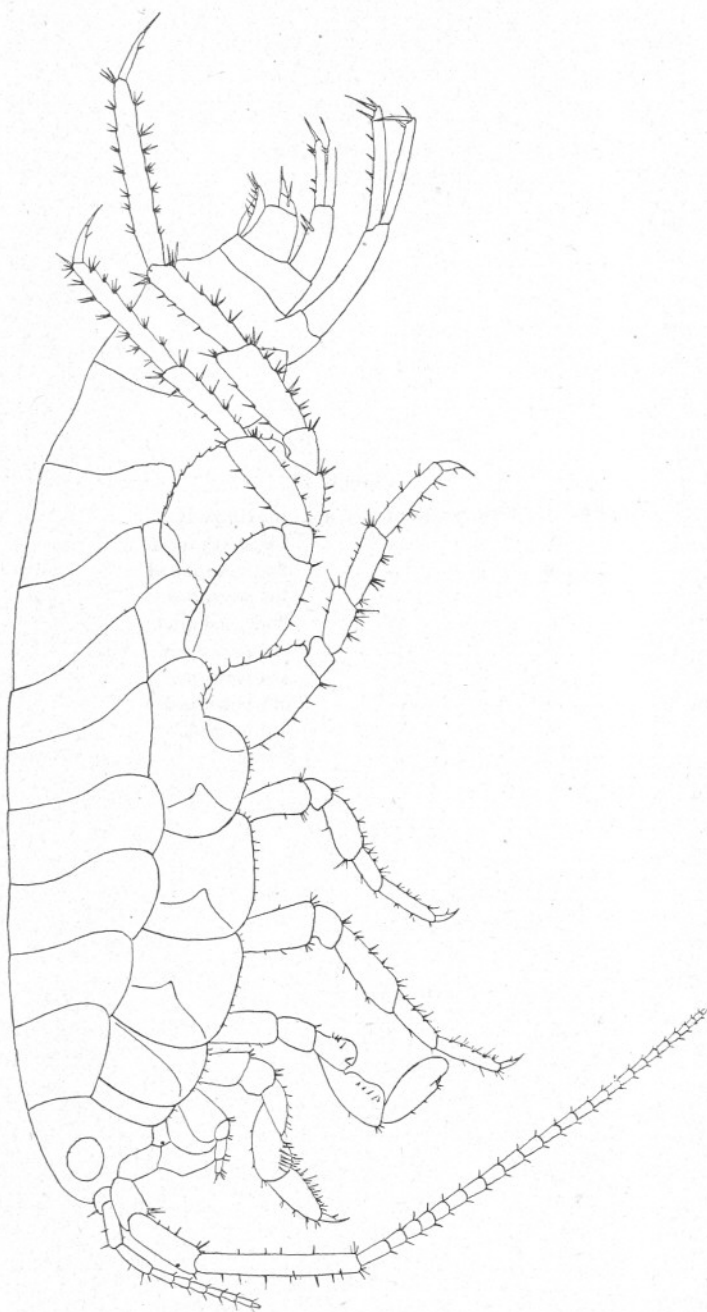


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#### EXPLANATION OF PLATES.

##### PLATE I.

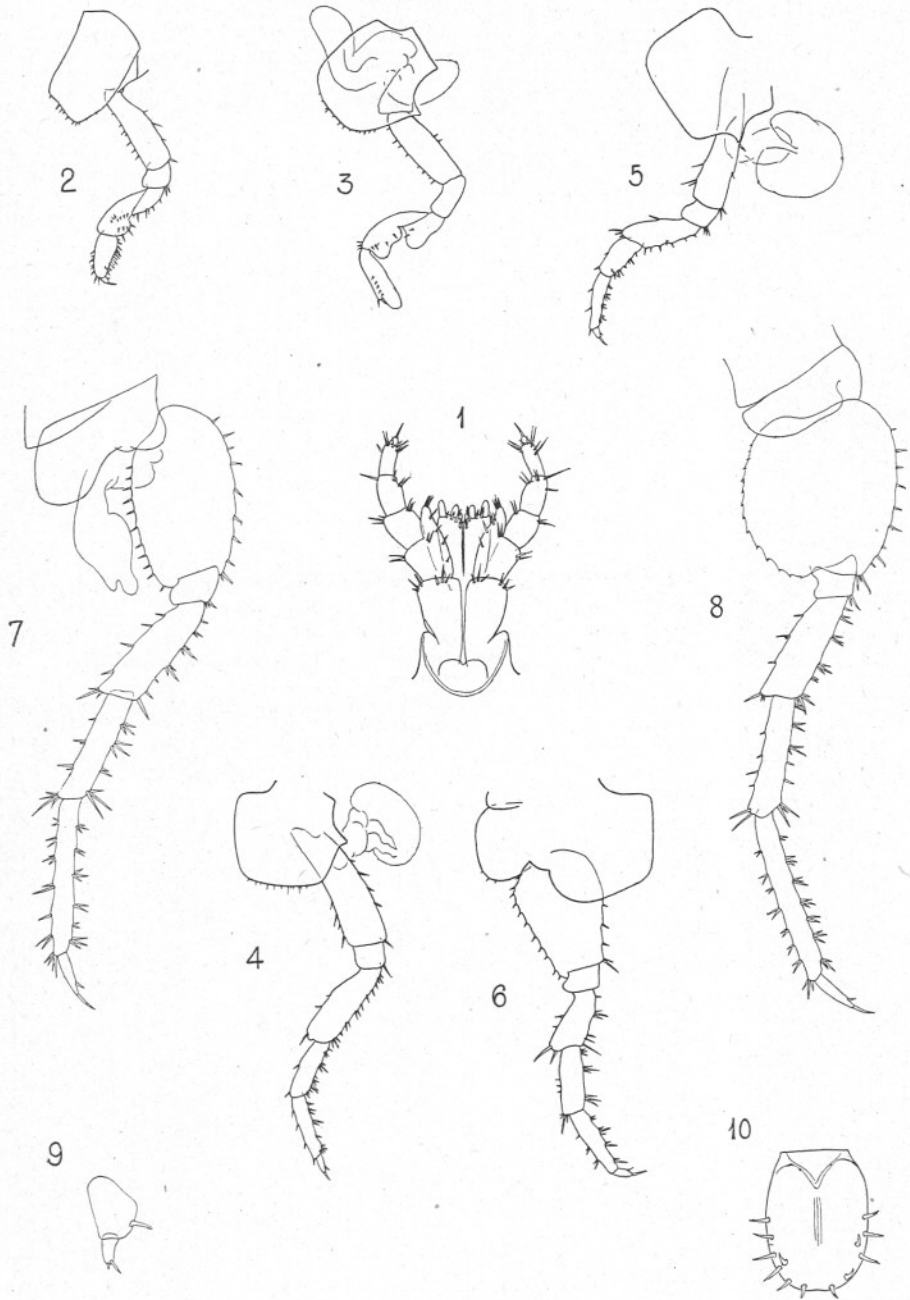
*Talitrus dorrieni*, n. sp. Adult female.



DEL. O. D. H.

## PLATE II.

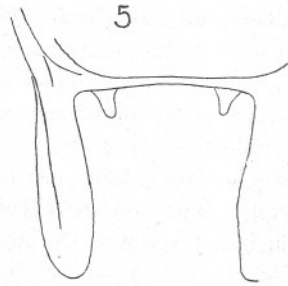
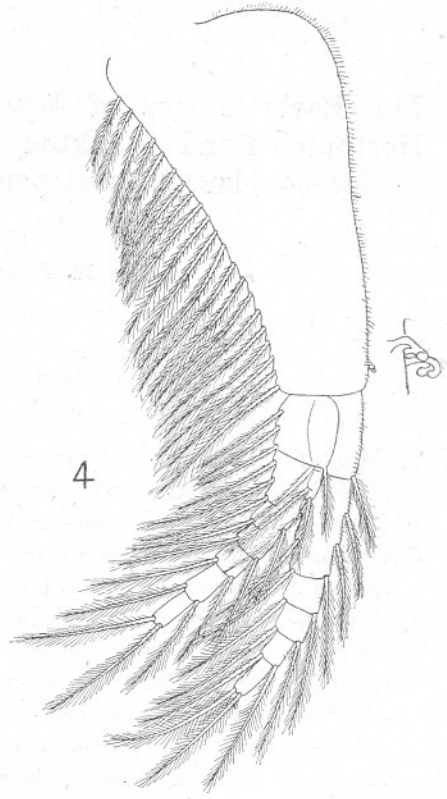
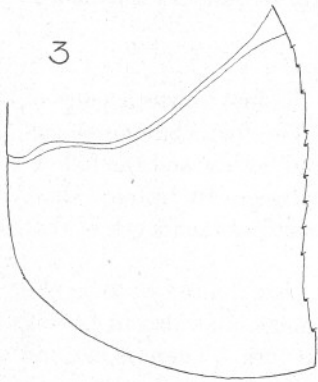
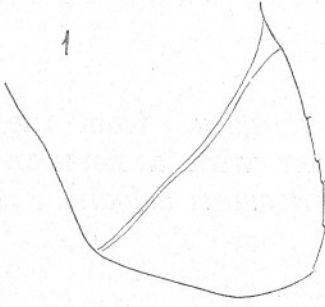
FIG. 1.	—	<i>Talitrus dorrieni</i>	n. sp.	maxillipeds.
”	2.	”	”	1st gnathopod.
”	3.	”	”	2nd gnathopod.
”	4.	”	”	1st peræopod.
”	5.	”	”	2nd peræopod.
”	6.	”	”	3rd peræopod.
”	7.	”	”	4th peræopod.
”	8.	”	”	5th peræopod.
”	9.	”	”	3rd uropod.
”	10.	”	”	telson.



DEL. O. D. H.

## PLATE III.

- |         |                                 |  |
|---------|---------------------------------|--|
| FIG. 1. | <i>Talitrus dorrieni</i> n. sp. | epimeral-plate of 1st pleon segment.                         |
| ” 2.    | ” ”                             | ” ” 2nd ” ”  |
| ” 3.    | ” ”                             | ” ” 3rd ” ”  |
| ” 4.    | ” ”                             | 2nd pleopod (coupling spines shewn separately, enlarged).    |
| ” 5.    | ” ”                             | 3rd pleon segment shewing 3rd pair pleopods (anterior view). |



DEL. O. D. H.

**The Early Stages of *Nephrops norvegicus*, from the Northumberland Plankton, together with a note on the post-larval development of *Homarus vulgaris*.**

By

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With Plates I to II and 1 Chart in the Text.

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ALTHOUGH adult Norway lobsters are extremely common on the southern part of the Northumberland coast, there were no records of the taking of larvæ of the species in this part of the North Sea until the Plankton Investigation now being carried out at Cullercoats (1) was commenced.

During the period 1921-23 a few specimens were taken from time to time in the ordinary plankton hauls, but the best catches of *Nephrops* larvæ were obtained from the young fish trawl used at a number of stations in 1922 and 1923. It is, therefore, chiefly on the material from the last two years' samples that the following observations are based.

All three of the larval stages have been obtained, together with a single post-larva, but the majority of our specimens are second and third stage larvæ.

FIRST STAGE LARVÆ.

The newly hatched larva is a zoea (2), with the first thirteen pairs of appendages fully developed (Plate I, Fig. 1). The first abdominal segment is entirely hidden beneath the carapace, and both it and the following one are devoid of dorsal spines. The third segment bears a short but distinct dorsal spine, measuring about one-sixth of the length of that on the following segment.

In all the three stages our larvæ differ from that figured by Sars (3), in having a spine on the third abdominal segment, and also in having a much larger spine in the angle of the caudal fork. There is a small protuberance on the third abdominal segment in one of Sars' figures, which makes it probable that his specimen was damaged.

The rostrum, in the first larval stage, is entirely devoid of armature, and the supra-ocular spines, present in the next stage, have not, as yet, made their appearance. The great claws and the two following pairs

of appendages are already chelate, and all five pairs of pereopods bear exopodites. Towards the end of the first instar the appendages of the second to the fifth abdominal segments can be seen as small buds beneath the cuticle of the next stage.

The length of this stage, measured from the tip of the rostrum to the angle of the caudal fork, is about 6.5 mm.

#### SECOND STAGE LARVÆ.

The appendages of the second to the fifth abdominal segments are now present as small biramous structures, but there is no sign of the appendages of the first segment. The segments of the antennæ are more fully differentiated than they were in the previous stage, and the large supra-ocular spines have appeared (Plate I, Fig. 2). As the second ecdysis approaches the developing uropods can be seen beneath the new cuticle in front of the caudal fork, which is still not differentiated from the last abdominal segment.

This stage is accurately figured by Sars, except as regards the spines mentioned in the description of Stage I, above.

The average length of Stage II larvæ is 8 mm.

#### THIRD STAGE LARVÆ.

When the third and last larval stage is reached the pleopods of the second to the fifth abdominal segments are fully developed, as are also the uropods, but the first abdominal segment is still devoid of appendages (Plate I, Fig. 3). The rostrum now bears three pairs of teeth dorso-laterally and the caudal fork is segmented off from the last abdominal segment. This stage is accurately figured by Sars, again with the exception of the dorsal abdominal spines. His figure shows the long spines on segments 3 and 5 instead of on 4 and 5.

This stage measures 10 mm. in length.

#### FIRST POST-LARVAL STAGE.

On reaching the first post-larval stage the creature no longer possesses the long spines, the caudal fork, nor the exopodites of the pereopods, and assumes, in general, the characters of the adult (Plate II, Fig. 1).

The rostrum has now four pairs of dorso-lateral teeth and a single ventral tooth near the tip. Groups of setæ are present on various parts of the carapace, and small protuberances, the precursors of teeth present on the cardiac region in later stages, are now visible.

The endopodite of the second antenna has now elongated to become the flagellum, and the whole appendage has the characteristic form of the adult structure. The telson also approximates to the adult form



(Plate II, Fig. 2), and the sculpturing on the terga of the abdominal segments is beginning to make its appearance.

The uropods differ from those of the adult in that the exopodite is not yet divided; but remains, as in the previous stage, a simple, oval plate.

It is interesting to note that the first abdominal segment is still devoid of appendages, and it would appear that the development of the first pair of pleopods, which are modified in connection with the reproductive function, is correlated with that of the gonads. It will be necessary, however, to examine later stages, not at present available, before it is possible to say at which stage the appendages appear and how far this supposition holds good.

At the ecdysis which changes the larva into the young adult the creature seems to direct all its energies towards the production of the new form, and to concern itself little, if at all, with growth. A first post-larval stage measured from the tip of the rostrum to the distal end of the telson had a length of 11 mm., or only 1 mm. longer than the average length of the Stage III larva.

#### DISTRIBUTION OF THE NORTHUMBERLAND LARVÆ.

Maps showing the stations worked and tables giving the date and other particulars concerning the plankton samples are given in the Dove Marine Laboratory Reports for 1923 (4) and 1924 (5), as are also tables giving similar information with regard to catches of the species under consideration (6). It is from these data that the chart showing the distribution of *Nephrops* larvæ in our district has been drawn up.

It would appear that the larvæ can be divided into three distinct groups: (1) those which are hatched on our local "prawn" ground; (2) those which come from the ground to the north of us, in the region of the Firth of Forth; and (3) some few which must have been freed still farther north.

Taking into consideration the three years' catches, the following facts are outstanding. Early in the season (May and June), Stage I larvæ were present in the southern region (marked A on chart). In August young larvæ, chiefly Stage I, were taken at the extreme north, in the Burnmouth-Berwick region, and a little further south samples contained a preponderance of Stage II. Hauls made about the same time in the southern area included only Stage III, and a first post-larval stage (B). The catches from the northern stations included also at this time a few old larvæ (C).

It will be seen from the chart that no samples were taken in the Burnmouth district in May and June, at the time when the first larvæ were obtained further south, so that we do not know when the Firth of Forth

larvæ first reach the Northumberland coast, but from the fact that in Group B we have Stage I off Burnmouth and the first post-larval stage off Newbiggin at the same time, the larvæ must have been drifting along the coast for some weeks. It is evident that they continue to arrive from May or early June until about the end of August.

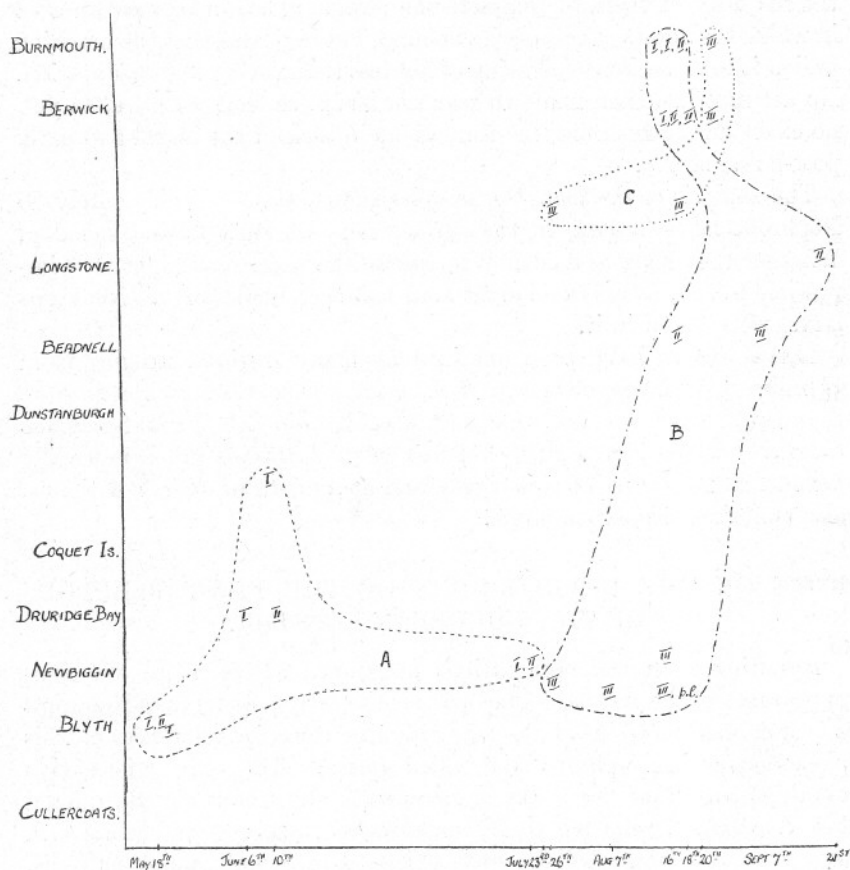


CHART showing the three groups of *Nephrops* larvæ obtained off the Northumberland coast during 1921-23.

Of the three groups of larvæ, only the second, B, is of importance to us from the point of view of the re-stocking of our local "prawn" ground, as those in A leave the district in Stages I or II, and those in C evidently do not really belong to our district at all, but appear to be stragglers from the stock of larvæ which, hatched still farther north than those of Group B, normally arrive at the end of the larval period in the Firth of Forth region. Whether these larvæ appear annually in the Berwick

district, or stray so far south only occasionally remains to be seen when further samples are examined.

Although we want more data before a complete account of the development of *Nephrops* can be given, the examination of our material shows not only the drift of the larvæ from north to south, and a tendency for the majority of them to complete the pelagic phase in or near an area in which the adults of the species abound, but indicates that the hatching period is to be reckoned as being of not less than three months' duration. No attempt has been made to rear the larvæ, so that we have, as yet, no exact data concerning the time spent in each of the larval and early post-larval stages.

The analysis of the plankton samples shows, also, that only rarely do *Nephrops* larvæ appear in the surface nets, at least during the day. Whether they show a tendency to rise to the surface at night it is impossible to say, as only one night haul has been made and no *Nephrops* larvæ were taken in it.

Larval stages have been obtained at many stations, ranging from  $1\frac{1}{2}$  miles to 10 miles offshore, but none have been taken nearer inshore than this. That is to say, that with one exception all our material was taken in water of from 20 to  $37\frac{1}{2}$  fathoms. A sample taken unusually far out, 12 miles east of Newbiggin, and at a depth of over 50 fathoms, also contained *Nephrops* larvæ.

#### NOTE ON THE DEVELOPMENT OF THE FIRST PLEOPODS OF THE EUROPEAN LOBSTER.

Resulting from the observations mentioned above as to the non-appearance of the first pair of pleopods in the early post-larva of *Nephrops* a search was made in all the available literature for references to this phenomenon in *Nephrops* and allied forms. The only information obtained was from the works of Barnes (7) and Chadwick (8), quoted below. Barnes, referring to *H. americanus*, states: "At the seventh stage the appendages of the first abdominal segment appear as buds, and by the eighth stage they have developed sufficiently to enable the sex to be told." Chadwick says of *H. vulgaris* that: "After further ecdyses (no size or stage given) . . . the appendages of the first abdominal segment develop. They are at first of similar form in the two sexes, but acquire sexual characters at a later stage."

With a view to gaining some more definite information on this point, a number of preserved specimens of young lobsters were examined, and even from this rather scanty material (all the specimens are females), it is possible to make out one or two features of interest.

The smallest specimen which bore any indication of the first pair of

pleopods was one which measured 3.5 cm. in length. A careful examination of the sternite of the first abdominal segment of this specimen revealed a pair of very small, blunt processes lying towards the posterior border, closely pressed against the sternite and with their distal ends towards the mid-ventral line (Plate II, Fig. 3). Specimens, measuring from 4.0 cm. to 5.3 cm., had the appendages present as a pair of straight, undivided rods about 2.5 mm. in length, and with a few small setæ near the tip (Plate II, Fig. 4), whilst those in the next stage, 6.0 cm. to 7.3 cm. long, bore pleopods on the first abdominal segment about 5 mm. in length, and having a definite resemblance to the adult female appendage. They still remained undivided into protopodite and endopodite, but were flattened and bore about twelve long plumose setæ on either border, along the distal half of its length (Plate II, Fig. 5). In a specimen 9.0 cm. long the development of the first pleopods was practically complete, the short, broad protopodite being distinct from the long, thin endopodite which now bore about twenty setæ on each side (Plate II, Fig. 6). Only the addition of more setæ as the organ increases in size is required for the attainment of the adult female form.

From a consideration of the statistics relating to size and age given by Meek (9, 10), it would appear that the initial stage in the development of the first pleopods of the European lobster occurs when the creature is from three to six months old, or in about the tenth stage; that the half-grown condition of the same appendages is attained at the age of six to twelve months; and that the fully grown but unsegmented organ is produced in the second year, and the perfect appendages, in the female at least, after that time—in about the thirteenth stage.

It is of interest to note also that the figures given for the Northumberland lobsters bear a very close relation to those of Waddington (11), particularly if it be borne in mind that his "tame" lobster was reared under conditions which tended to retard the normal rate of growth.

So far then as we are able to judge from the limited material available, the development of the first pair of pleopods in *H. vulgaris* is completed in four stages, beginning when the animal is about six months old and extending over four instars (probably the tenth to the thirteenth), and being completed only when the creature has attained the age of, at least, two years.

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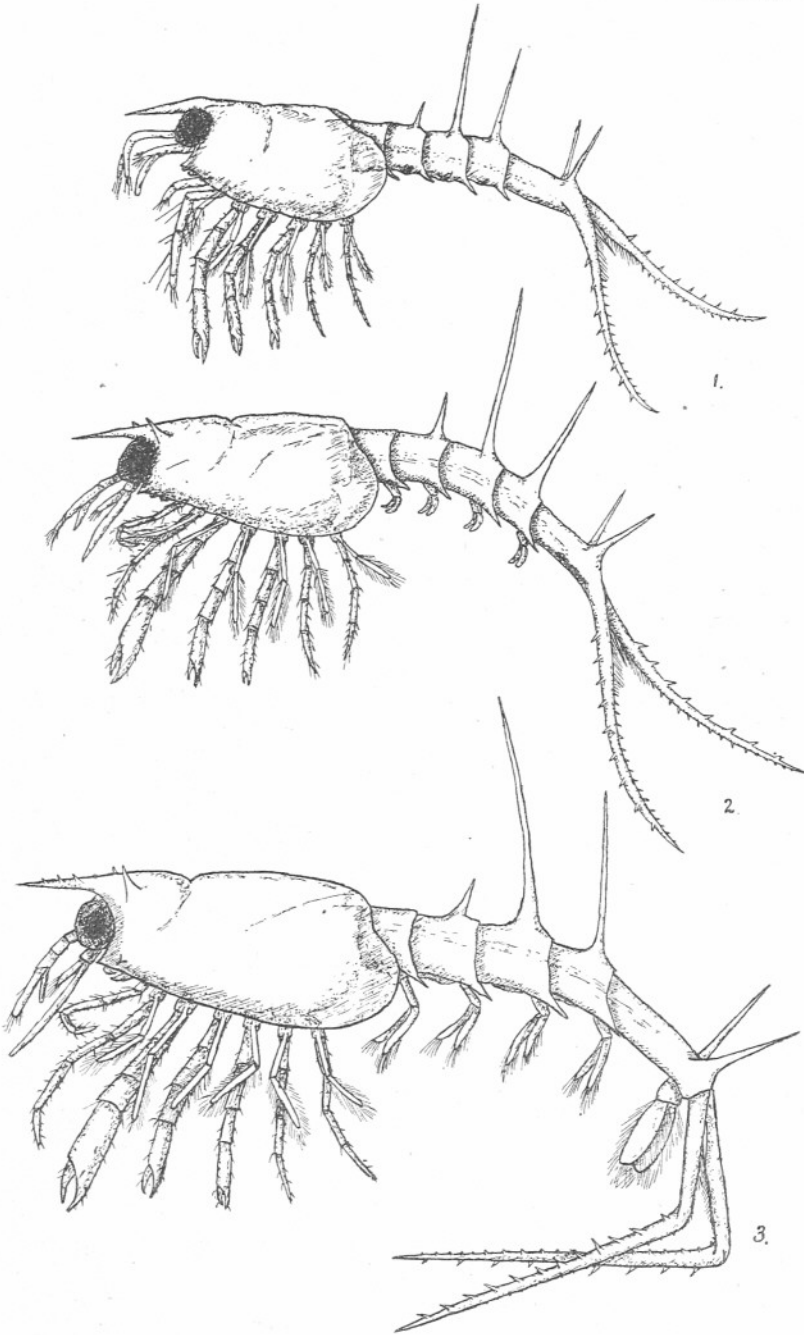
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### EXPLANATION OF PLATES.

#### PLATE I.

- FIG. 1. Stage I, larva of *Nephrops*, from the left side.  
,, 2. Stage II, larva of *Nephrops*, from the left side.  
,, 3. Stage III, larva of *Nephrops*, from the left side.

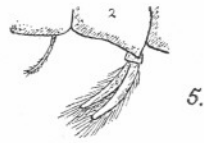
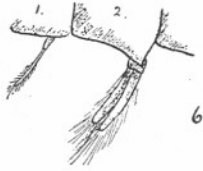
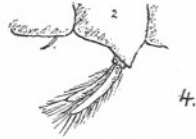
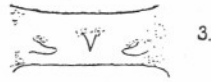
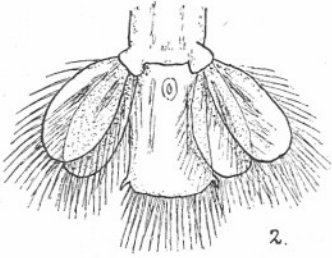
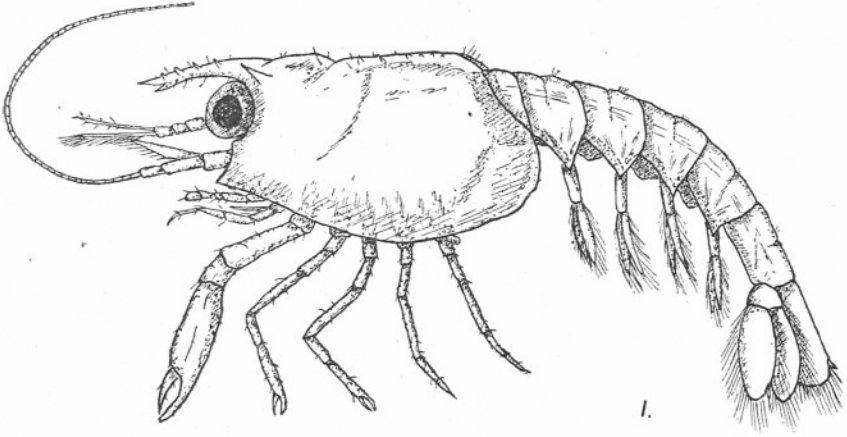
PLATE I.



## PLATE II.

- FIG. 1. First post-larval stage of *Nephrops*, from the left side.  
,, 2. First post-larval stage of *Nephrops*, telson and uropods, from the ventral aspect.  
,, 3. Sternite of first abdominal segment of *Homarus vulgaris*, showing first stage in development of the first pair of pleopods.  
,, 4-6. Anterior end of abdomen of *H. vulgaris*, from the left side, showing the later stages in the development of the same appendages.

PLATE II





## On a New British Sea Anemone.

By

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With 1 Figure in the Text.

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It is a curious fact that the majority of the British anemones had been discovered by 1860, and that half of them, as listed at that date, had been established during a burst of energy on the part of Gosse and his collecting friends. Gosse added 28 species to the British Fauna himself. It is still more surprising that since Gosse ceased work, no authentic new ones have been added, other than more or less offshore forms, with the exception of *Sagartia lucia*; and this species appears to have been imported from abroad. There is, however, an anemone which occurs on the Breakwater and Pier at Plymouth, which has not yet been described. Dr. Allen tells me it has been on the Breakwater as long as he can remember, and to him I am indebted for the details of its habitat given further on. Whether it occurs elsewhere than in the Plymouth district and has been seen but mistaken for the young of *Metridium dianthus*, is as yet unknown.

The anemone in question, which is the subject of this paper, is a small creature, bright orange or fawn in colour, and presenting at first sight some resemblance to young specimens of certain colour-varieties of *Metridium*. When the two forms are observed carefully, however, and under healthy conditions, it becomes evident that they are perfectly distinct from each other; and a study of their anatomy bears out this fact.

The following is a description of a typical individual of the new anemone.

*Body.* Base adherent, wider than column. Column variable in shape, typically cylindrical, capable of great elongation, becoming narrow and vermiform in full extension (e.g. length of animal 3.2 cm., width of body at same time .35 cm.). In partial extension it forms a fairly tall pillar with a long lower part (*scapus*) ending above in a slightly-marked bulge or collar, above which is a rather narrower part, this being the beginning of the more delicate upper region of the body (*capitulum*). Collar variable in distinctness according to state of expansion, smoothing completely away in full extension, but being nevertheless a definite structure, marking the point at which the thicker body-wall of the scapus passes into the

thinner wall of the capitulum, and forming a definite parapet and fosse when the column is not stretched out. Body translucent in expansion, allowing mesenterial insertions to show through the skin; skin smooth in extension, delicate, wrinkling up in contraction; no suckers. Capitulum extensive, its margin tentaculate, and without cinclides. Scapus with conspicuous cinclides, which are numerous and scattered, and which extend from collar right down to edge of base, but are more prominent above. They show up in certain states of expansion as minute mounds, a shade darker in colour than rest of skin, with a central perforation or thin spot. Column bright soft orange; scapus, in partial contraction, a richer colour than capitulum. Animal shrinks very readily when alarmed. Acontia present, and able to be protruded via cinclides.

*Tentacles.* Long, slender, graceful, and tapering, but rather more gradually tapering than in many forms. Disc and tentacles entirely retractile. Tentacles not quite regularly arranged, in some sectors, running 6, 6, 14, etc., in five cycles. Their colour is that of the body, of a rather lighter tone than the scapus, in partial extension; they are unmarked.

*Disc.* Small (though able to exceed column), circular, with not much free space within the tentacle-bases; translucent, with little colour; unmarked; mesenteries show clearly through it. Mouth and throat red-orange, this colour showing through the capitulum by transparency, in extension. Throat ribbed. Probably only one siphonoglyph.

*Variation.* The species seems to be subject to little variation. One specimen is much like another but for size, and but for the fact that there are two colour-forms. The specimens from the Breakwater are of the orange kind described; those from the Pier are fawn-coloured. In the specimens of the orange variety which I have seen the mouth is brighter orange than the rest of the flower, the lip is well ribbed, the tentacles are usually in five cycles, with six in the inner cycle. The inner tentacles are not necessarily evenly spaced out, and their arrangement is liable to irregularities. The directive tentacles and some or all of the other primary tentacles, may be stouter and more orange than the rest, or all the tentacles may be of one tone.\* There are pores in their tips. The free space on the disc is rather small, the tentacles being long in proportion to it and tapering slowly, but the disc can exceed the

\* Since the above was written, Mr. Evans tells me he has seen the Breakwater anemone stretch out a few tentacles to a great length, far beyond the others, and search about its environment with them; these tentacles, after they were contracted again, were thick, short, blunt and opaque. This doubtless accounts for the thick orange tentacles seen in some of my specimens. A similar phenomenon is well known in certain other anemones. Mr. Evans adds that when the Breakwater anemone contracts in alarm, the body often jerks down in a very characteristic way, one side generally contracting more than the other, so that the animal collapses corkscrew-wise and ends up lop-sided. I have noticed the same sort of thing.

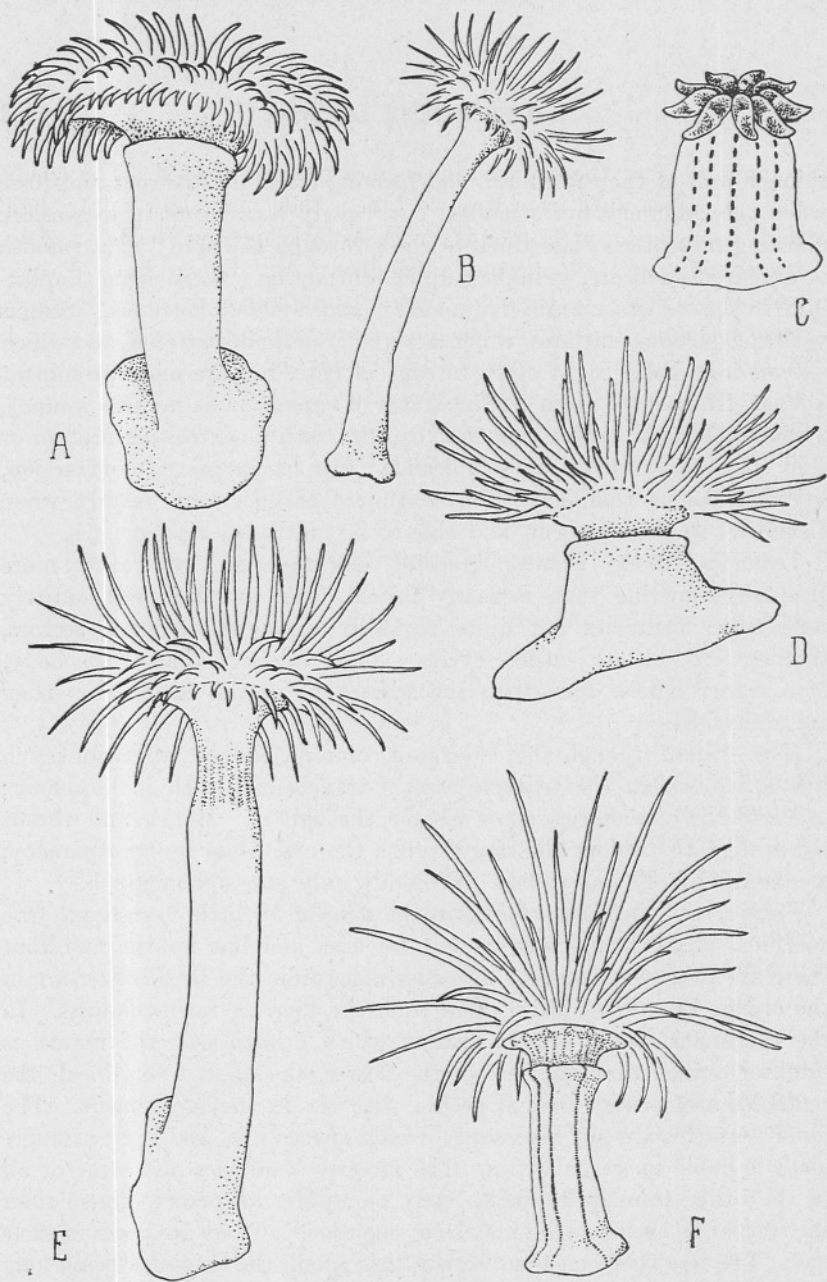


FIG. 1. Sketches, from living specimens, of the anemones dealt with in this paper.

A. Young specimen of *Metridium dianthus*, for contrast with *Diadumene cincta*. Nearly twice natural size.

B. *Diadumene cincta*. Well expanded. About natural size.

C. Tracing from Gosse's copy of a drawing, sent to him by Cocks, of *Sagartia chryso-splenium*. Natural size. The dotted lines on the body are rows of yellow spots in the actual anemone.

D. *Diadumene cincta*, with the column shortened, showing the collar as a parapet. Nearly twice natural size.

E. *Diadumene cincta*, partly extended, with the collar still visible and not smoothed out as at B. Nearly twice natural size.

F. *Diadumene (?) luciae*, well expanded, showing scapus and capitulum; the orange stripes on the scapus are shown as dotted lines, in reality they are continuous. About three and a half times natural size.

column, so that the capitulum becomes trumpet-shaped. The cinclides vary in appearance from time to time; they may show up as slightly dark spots or as little mounds with a dark spot on them, or may be transparent and somewhat bubble-like. Mr. Evans has seen them assume a curious appearance, those of the lower part of the body being inconspicuous, those up above much more marked, forming a sort of belt round the animal. I have not seen this myself, all my specimens having the cinclides (which are actually spread over the whole scapus, and are, wherever one can see them clearly, mostly endocœlic) more conspicuous above, but not presenting the appearance of a belt. The substance of the body is soft, but the base quite strongly adherent when well fixed. The size is not large, the best specimen I have seen not exceeding about 3 cm. in diameter of disc and tentacles, and 2 cm. in diameter of base; the length of its body could, however, much exceed these measurements. It had six cycles of tentacles, with a few odd additional ones, but the cycles not all fully represented.

The fawn variety, which Mr. Smith tells me turns up not infrequently on the Pier, has all the essential features of the orange form, but is otherwise coloured. The following is the colour of typical examples: Scapus buff, capitulum more translucent with the pink-buff throat showing through it by transparency; disc transparent, almost colourless, tentacles translucent, light buff, paler than body, a little opaque cream bar running across the bases of the outer ones. At the back of the base of each directive tentacle is a little cream patch, and there is cream on the directive radii. On the column a little cream stripe runs part-way down each directive endocœl. The throat has the most positive colour in the animal, and the lip is ribbed as usual, but not orange. The cinclides are easily seen as grey dots, often on little mounds. The largest specimen I have seen had three of its inner tentacles more solid and brighter buff than the others, and when it was preserved these three were longer than all the others. Two of them were adjacent, and they were both directive tentacles.

The species occurs near low-water mark on stones on the inner (north) side of the Breakwater. The stones are limestone, and the anemones appear to live both on the upper side of them and on the lower, when the latter hangs free. On some of the stones they occur in large numbers. They probably do not occur in profusion elsewhere in the neighbourhood, except on the Pier; but a few specimens may exist which have not been noted. They were found in numbers on the Breakwater by Garstang in the early nineties, since when they have been brought in very often by the Plymouth collectors. Other Zoantharia abundant on the Breakwater are *Caryophyllia Smithii* and *Corynactis viridis*.

The only form with which this species can be confused is the young of *Metridium dianthus*, as mentioned above. The young of *Metridium* has given a good deal of trouble at one time and another, by reason of its complete difference in appearance from the adult. It is a small rather pellucid anemone like a *Sagartia* in general build, and white, orange, or brown in colour; its tentacular crown is quite circular, and gives no sign of the lobed and frilled condition which it will gradually assume as it grows up. This has led to its being identified, incorrectly, as *Sagartia pallida* Holdsworth, and even as a new species. If it is carefully compared with the Breakwater anemone, it is found to be perfectly distinct from it. The more obvious external differences may be tabulated as follows:—

*Young Metridium.*

*Body.* Capable of stretching out a good deal, but not to the same extent as in the Breakwater form.

*Collar.* Sharply marked and definite, cannot smooth away in expansion.

*Capitulum.* Short in proportion to whole body.

*Tentacles.* Begin to be rather numerous at a fairly early age, and give a characteristically fluffy appearance, as a whole, to the tentacular crown.

*Disc.* Soon begins to expand more extensively beyond the column than ever does the disc of the Breakwater anemone.

*Colour.* The orange of the orange variety less vivid than in the Breakwater anemone.

*Animal.* Less irritable and less rapidly contractile than the Breakwater anemone.

*Breakwater Anemone.*

*Body.* Decidedly worm-like when well extended, forming a tall thin pillar, very much longer than wide.

*Collar.* Forms a distinct parapet or rim containing a fosse, in a rather short state of the column, but in better expansion it is a somewhat vague structure, not sharply marked, and smoothing away completely in full expansion.

*Capitulum.* Decidedly longer in proportion to whole body.

*Tentacles.* Probably never exceeding 200, and often rather few and of fairly large size, giving a different total effect.

*Cinclides.* Tend to be more conspicuous than in *Metridium*, being rather easily visible, with a lens.

These differences may not be absolute, but as far as my experience goes of the two forms, they are constant. I have examined a considerable number of both. The differences look very slight when reduced to black and white, but actually they constitute a marked difference of facies. My friend, Mr. W. Edgar Evans, has now kept the Breakwater anemone for over a year in his aquarium at Edinburgh, in a state of good health. He is quite convinced of its distinctness, and informs me that it does not change or show any tendency to "grow up," that it is shy and difficult to feed. It reproduces, moreover, by fragmentation, and not by longitudinal fission.

The anatomy of the Breakwater anemone has been studied in comparison with that of young *Metridium*, by Miss E. M. Stephenson (see p. 897 of the present issue of this journal), so that I need not go into it here. I will only remark that its lack of sphincter distinguishes it from young *Metridium*, which has a mesogloceal one; so does the arrangement of its cinclides, which are predominantly endocœlic in the former, exocœlic in the latter; and the rest of the anatomy bears out the distinction. I can add to Miss Stephenson's account that in the largest of the fawn specimens which I have seen from the Pier gonads were present and very strongly developed. In the middle of the body there are three cycles of mesenteries present; two pairs of these are directives, and are adjacent, not at the opposite poles of the throat; each has its own siphonoglyph. Six pairs of mesenteries are perfect. Gonads occur on all mesenteries of cycles 1 and 2, and on some at least of those of cycle 3. Basilar muscles are present in the species.

It remains to discuss the systematic position of the form in question, and this is not very straightforward. There are only two existing genera in which it can find lodgment, and they are *Diadumene* and *Aiptasiomorpha*. Neither of these genera is well known, unfortunately, so that in dealing with them one is on rather uncertain ground.

*Diadumene* has as its type the Indian brackish-water anemone *D. schilleriana*. The account of this, given by Annandale (*Records of the Indian Museum*, Vol. 1, Part 1, p. 47, Calcutta, 1907; and *Cœlenterata in Fauna of the Chilka Lake*, *Mem. Indian Museum*, Vol. 5, 1915, p. 65), is extensive and good, but it permits of more than one interpretation in some of the essential points. In my paper on classification (*Quart. Journ. Micros. Sci.*, 1920-22, Part 1, 1920, p. 425; see pp. 457, 499, 508, 521), I interpreted *D. schilleriana* from Annandale's account as a form with a division of the mesenteries into macro- and microcnemes, in which this division is not fully carried out; and this was, I still think, a permissible view. But at best, it is an intermediate form; and since my paper was written, Carlgren (*Actiniaria, The Danish Ingolf-Expedition*, Vol. 5, No. 9, Copenhagen, 1921, p. 1, see p. 21, and *Vidensk. Medd. fra Dansk.*

*naturh. Foren.*, Bd. 77, p. 179, 1924, see pp. 224 and 234), has taken the view that *Diadumene* has really no division of the mesenteries into macro- and microcnemes, and has consequently defined the family *Diadumenidæ* afresh on his basis, removing from it the genera *Pelocœtes*, *Phytocœtes*, and *Mena*, which I took to be relatives of *Diadumene*. This matter cannot yet be settled finally, as there are not enough data for a decision. Meanwhile, I have sections of about one-third of a good-sized specimen of *D. schilleriana*, and in this there are apparently (the specimen is not in first-class condition) three cycles of mesenteries represented; there are more or less diffuse to more or less circumscribed well-developed retractors on mesenteries of all the cycles, also gonads; though only some of the mesenteries of the third cycle are well developed. This rather supports Carlgren's contention about the mesenteries of *Diadumene*, and I have no wish to press my former view if another is better. But I do not think the question of the possible relatives of *Diadumene* can be settled summarily by the placing of *Pelocœtes* and *Phytocœtes* in the *Halcampactidæ*, as Carlgren has done. I can quite believe that it may prove best in the end to keep *Diadumenidæ* for *Diadumene*, and to put *Pelocœtes*, etc., apart from that family, but it has yet to be proved that *Pelocœtes* has no relationship to *Diadumene*. On the contrary, there is quite a possibility that the two may be connected, and in this event, even if they go into different families, those families should stand in juxtaposition. Further than that, I do not think we can go at present.\*

*Aiptasiomorpha* contains two genuine species, *A. minima* and *A. neozealanica*, both New Zealand forms. These have many of the characters of the Breakwater anemone, and it is a question also whether they differ essentially from *Diadumene*; in fact, Carlgren has recently united the two genera.

The Breakwater anemone is a fully retractile form, and *Diadumene schilleriana* appears to be the same; this is not a family character, but may be an indication of relationship. In considering *Aiptasiomorpha* one must remember that it may be related to *Aiptasia*; whereas the Breakwater anemone is certainly not directly related to *Aiptasia* as represented by *A. Couchii*, as a comparative study of the two forms, alive, clearly shows; if anything it is nearer to *Metridium*. *Aiptasia Couchii* is very distinct from any other anemone I know alive; it has the greater part of its skin covered by minute adhesive papillæ, like those of *Peachia* (these are absent from the submarginal region of the column), and its large curious tentacles have a very distinct arrangement of pigment on them as a microscopic network-pattern. For this reason I should not

\* *Mena* has been shown by Carlgren to lack acontia, and is thus a *Halcampid*. *Arkiv for Zoologi*, Bd. 17A, No. 21, Stockholm, 1925, p. 1; see p. 8.

be averse to Carlgren's family Aiptasiidæ, provided it fits in with other things later on.

We are faced then with two genera, neither of them well known, and which may be identical; and into either of which the Breakwater anemone may fit. For the time being I follow Carlgren in uniting the two genera and I place the Breakwater anemone in it, giving it the specific name *cincta*, because of its collar. If *Diadumene*=*Aiptasiomorpha*, the name *Diadumene* has priority, so that the Breakwater anemone will be *Diadumene cincta* unless further knowledge makes a change necessary. If it has to go by itself later on I propose the generic name *Farsonia* for it.

This settles the genus, but does not give us a clue to the family relationships of the new form. Since I subdivided the old family Sagartiidæ (1920), Carlgren has objected to my method of doing it, because he does not think we know enough yet about the anemones with acontia and basilar muscles to make a final arrangement. With this latter remark I agree, but one must begin somewhere, and the families which I proposed will do for a starting-point and can be modified as new facts come to light. They are not meant to be rigid or final, and I shall not be the last to make modifications where needed. We have at any rate, as Carlgren admits, groups within the "Sagartiidæ"; and of these groups there are undoubtedly four recognisable—the Chondractiniid series, the Phellias, the Metridiids (as represented by *Metridium*, *Calliactis*, and *Adamsia*), and the genus *Sagartia*. These groups stand out quite well, and even if there are intermediates, something will have to be done about them. But after these four sets there are the Aiptasias to be placed, and here we get on to more difficult ground. If these are to stand apart from the Metridiidæ, there is the difficulty that there are forms like the Breakwater anemone and its probable relatives, which appear to link up the two sets. The family *Diadumenidæ* may be the present representatives of the ancestral link, as I thought previously (1920). Carlgren himself admits subdivision of the old Sagartiidæ into Phelliidæ, *Diadumenidæ*, *Aiptasiidæ*, and *Sagartiidæ* (restr.), and as the subdivision is likely to have to go further in the end, my own method of doing it may well serve as a basis for further work—indeed, it has done so already, since Phelliidæ is one item in my scheme, and *Diadumenidæ* another (though how this family is to be ultimately limited is as yet uncertain); and I am not averse to *Aiptasiidæ*. Then again Carlgren does not think that presence or absence of cinclides is a family character, and doubts whether distribution of gonads will always be one. I cannot enter into this question here in detail, but hope to do so later. Summation of those available characters which are the least variable seems to me to be the only final criterion, since few characters are perfectly satisfactory. The above is the only



indication which can be given at present as to the position of the Breakwater form.

Before closing it seems advisable to consider another British anemone which may belong to the same genus as the Breakwater anemone. This is *Sagartia lucia*. It has been the subject of a recent paper by McMurrich (*Proc. Zool. Soc.*, 1921, pp. 729-739), who describes its anatomy and discusses its systematic position and past history. This study is very valuable, and has been long needed, because although *S. lucia* has excited considerable interest from points of view of distribution, experiment, etc.; its anatomy has been neglected. McMurrich shows that it possesses no sphincter, that it has a division of the body into scapus and capitulum, that its mesenterial formula, although actually irregular, because of its fissiparous habit, is clearly derived from a plan with six pairs of perfect mesenteries only, these being sterile; and, therefore, shows that it is not a member of the genus *Sagartia*, but belongs to the *Metridium* group, and to no actually recognised genus.

It would seem, however, that *S. lucia* is likely to be eligible for the genus *Diadumene*, or at least for the same genus as the Breakwater anemone. It has the same essential combination of characters, but for the sterility of the older mesenteries, on the basis of the facts as stated by McMurrich. I have not as yet a full enough series of preparations of *lucia* to be able to confirm McMurrich's account, but I am inclined to think it will be found that the older mesenteries can be fertile. At any rate in two specimens from Plymouth I have seen what I take to be young gonads on some of the largest mesenteries in the animal. The acontia of both *lucia* and *cincta* have large nematocysts, some which I measured in the former were nearly as large as those of the latter. Curiously enough both have a tendency to produce endocœlic stripes of colour, cream in *cincta* and orange in *lucia*. Both have scapal cinclides and not capitular ones, and what I have seen of those of *lucia* suggests that when studied fully they will prove to be arranged as in *cincta*.

Unfortunately, McMurrich has contended that *S. lucia* is probably identical with *Sagartia chryso splenium* Cocks, and that since *lucia* (= *chryso splenium*) needs a genus of its own, this genus should be called *Chrysoela*, a name put forward by Gosse (1860, p. 123) for *chryso splenium* in the event of its needing separation. This would be perfectly legitimate if *lucia* and *chryso splenium* were, indeed, identical, but I cannot see that there is any actual evidence in favour of their identity. *S. chryso splenium* has never been seen, either alive or preserved, by any competent observer, and Cocks, who described it (*19th Annual Report of the Royal Cornwall Polytechnic Society, for 1851*, p. 5, Pl. I, Fig. 17) has left such a poor description and figure that it is difficult to build upon it. But the following points may be noted.

*S. chryso splenium*, calculating from Cocks' figure, which is  $\frac{2}{3}$  nat. size, was just over  $\frac{3}{4}$ " wide (diameter of column without tentacles) and nearly an inch high (again not counting the tentacles), the measurements given by Gosse being very near this also; in fact, quite a solid creature; cf. Gosse's coloured figure (Pl. VI, Fig. 8, 1860), copied from a drawing by Cocks, which shows an animal about the size of a medium specimen of *Actinia equina*; as both figures seem to be of a somewhat contracted anemone it could probably be larger than this when healthy. This is too large for *S. lucia* altogether, as it occurs in England. *S. chryso splenium* has rather short tentacles, *S. lucia* very long ones. *S. chryso splenium* has yellow labial tubercles and a yellow line round edge of base (remarkable points, if true), *S. lucia* has neither of these things. In Cocks' figure his animal has small oval areas scattered over it, which, if they are suckers are absent in *S. lucia*, if they are cinclides are probably not arranged in the same way as in *S. lucia*, in which, as far as I have seen, they are mostly in rows on the orange stripes. McMurrich's remark that the tentacles in Cocks' figure are "quite as they are in *S. lucia*" is difficult to understand, unless it depends on his only having seen sick specimens of *lucia*; in a really healthy and expanded specimen the tentacles are very long and fine, longer in proportion perhaps than in any other British species, and not at all like Cocks' picture. Moreover, Cocks says the tentacles of *chryso splenium* are stouter than in *Actinia*; those of *lucia* are much longer than in *Actinia*, and slender although fairly wide at the base. Other remarks of McMurrich suggest too, that he does not know *lucia* in health—he remarks that the capitulum remains introverted when the animal is expanded (quite the opposite is true), and refers to the "somewhat pustulous" appearance frequently presented by *S. lucia*—an appearance absent in healthy expansion. In *chryso splenium* the yellow stripes seem to have been discontinuous, in *lucia* they are typically continuous. Cocks considered *chryso splenium* "allied to *crassicornis*," i.e. *Tealia*—he could never have thought this of *lucia*.\*

It is true that some of the discrepancies may be due to (a) sick specimens having been seen by Cocks, and (b) the imperfection of observation at the time when Cocks wrote; one cannot say it is impossible that *chryso splenium*=*lucia*, but it does seem to stretch things too much to assume identity where, even if there is not absolute proof *against* there is no evidence *for*. I have given this point more attention than its intrinsic interest warrants, because I feel that on the basis of Cocks' and Gosse's descriptions (and we have no other basis on which to go), it cannot be maintained that *S. lucia* is the same as *S. chryso splenium*, and it seems

\* Fig. 1 C is a tracing of Gosse's copy of a coloured drawing sent to him by Cocks, natural size.

a pity to dig up old and imperfectly described species such as the latter. They are better off decently buried, unless something really answering to their description turns up in the original locality. Unless this happens we shall never know what *S. chryosplenium* was. In this particular case, too, an assumption of identity would lead to a new interpretation of the geographical distribution of an interesting form, without any actual basis for it.

The following is a diagnosis of *Diadumene cincta* n. sp. :—

Base well developed, basilar muscles present. Column long and narrow in extension, divided into scapus (ending above in a collar varying in appearance according to state of expansion) and capitulum. Skin smooth, without suckers. Scapus with numerous cinclides, extending from collar to base, which are mostly endocœlic, and are typically partial ectodermal invaginations. Capitulum without cinclides, rather extensive, its margin tentaculate. No sphincter. Disc and tentacles fully retractile. Free space on disc rather small. Tentacles long, up to nearly 200 in number, often fewer than this, in 5–6 cycles. Lip ribbed. Siphonoglyphs and directives variable. Perfect mesenteries, six pairs. Retractors well developed, diffuse, on more than the first cycle of mesenteries. Labial and parietal stomata present. Mesenteries more numerous above than below. Acontia well developed, with large nematocysts. Gonads, filaments, and acontia on all stronger cycles of mesenteries. Ciliated tracts present. Longitudinal musculature of tentacles ectodermal. Animal irritable. General colour orange or fawn.

## On the Anatomy and Relationships of New or Little known British Actiniaria.

By

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With 24 Figures in the Text.

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### INTRODUCTION.

THIS paper contains anatomical descriptions of some British species whose systematic position has hitherto been uncertain because of the absence of detailed knowledge of their structure. To these descriptions are added notes on anatomical points of interest connected with other species.

Some of the facts gained have a general systematic bearing which will be pointed out as they occur in connection with the descriptions, or in the discussion at the end of the paper. I am indebted to Dr. Allen, Mr. W. Edgar Evans, Mr. R. Elmhirst, Miss M. Delap, and Dr. T. A. Stephenson for material, and to Dr. Esdaile for valuable guidance.

1. SAGARTIA COCCINEA Gosse, 1858, p. 416.

(NOT *Actinia coccinia* Müller, 1776, p. 231.)

*Sagartia coccinia* has usually been accepted as a species of small size, not reaching the dimensions of such forms as *S. miniata*, *S. viduata*, etc. During 1924, however, some specimens were taken at Millport which considerably exceed the size supposed to be characteristic of the species, showing that it may be as large as the more common forms under suitable conditions.

I have been able to examine 3 specimens, 1 from Millport and 2 from Valentia Island, co. Kerry.

The coloration and external characters have been described elsewhere (Gosse, 1860, p. 84, Pl. V, Fig. 4, and Walton, 1908, p. 208); it need only be remarked here that externally the species is a perfectly typical *Sagartia*, being one of the species without suckers, and being characterised, among other things, by its lacerate basal outline and constant habit of asexual reproduction by basal fragmentation.

The number of tentacles in this species is variable, in correlation with its habit of fragmentation; the formula may run 6, 6, 12, etc., 8, 8, 16, etc., 10, 10, 20, etc., and so on.

The following is a description of one of the *Valentia* specimens.

Expanse of disc and tentacles, during life, 3 cm.; total height of expanded animal, 2.2 cm. or more. Tentacles 6, 6, 12, 24, and a few additional ones (incomplete fifth cycle). Mesenteries in 3 cycles, with a few small additional mesenteries developing. Perfect mesenteries, 12 pairs,

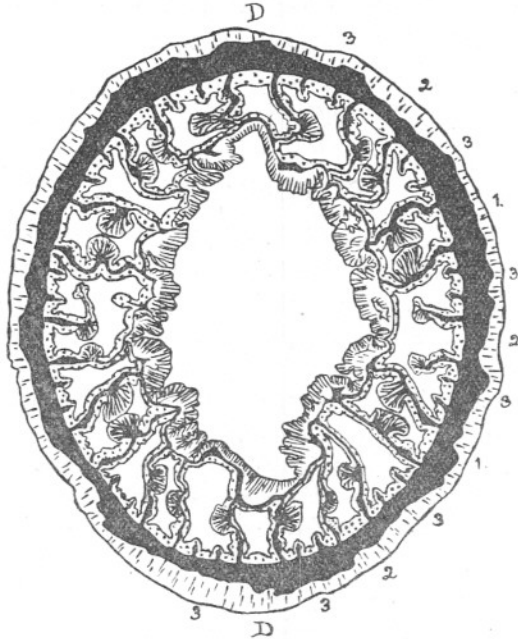


FIG. 1. T.S. of *Sagartia coccinea*, near lower end of throat.  
D. Directives: numbers 1, 2 and 3 indicate mesentery cycles.

including 2 pairs of directives connected with 2 siphonoglyphs. Imperfect mesenteries, 12 pairs, and a few additional young pairs. The cycles of mesenteries grade into each other, and are not distinguished into macrocnemes and microcnemes. Perfect mesenteries with strong circumscribed-diffuse retractors, older imperfect mesenteries with slightly developed ones. Retractors strongest on the 6 pairs of primary mesenteries; their individual muscle-processes stout, slightly branched, high. Perfect mesenteries with large parietal and small labial stomata, occurring within a narrow zone immediately below the top of the throat. Filaments occur on the mesenteries of cycles 1-3 inclusive, being well developed on the first two cycles. The reticulate area of the typical trefoil region is well marked, and ciliated streaks are present. Acontia well developed,

occurring on all mesenteries of cycles 1 and 2, and on most of those of cycle 3. Longitudinal musculature of tentacles ectodermal, its processes well branched. Gonads not developed. Large cinclides present, occurring in a zone about .6 mm. deep (in the preserved specimen), which starts at about the lower edge of the sphincter. Only 8 cinclides are present, 1 in each secondary endocoel, and 2 additional ones in primary endocoels. I cannot detect any cinclides near the edge of the base, such as occur in some *Sagartias*. The cinclides are all principally endodermal evaginations. A section of one is shown in Fig. 3 (this being a longitudinal section through part of the body wall of the other *Valentia* specimen). It will be seen that the thick part of the mesogloea (black) is completely interrupted, allowing the ectoderm and endoderm to come practically into contact with each other, only an attenuated diaphragm lying between them. None of the cinclides have an actual canal perforating the epithelium itself, all the way through; but such a canal is by no means a universal feature of cinclides, which are often, instead of being actual pores, simply organised soft spots where the mesogloea is interrupted or reduced to very little, and which may be burst open if pressure within the coelenteron becomes too great. From Fig. 3 it may be seen that there is a partial canal running out from the endodermal side and ending blindly; and that the greater part of the epithelium of the cinclis is endoderm, this being the layer initiating the cinclis in this case. Fig. 1 shows a complete transverse section of the specimen described above, at the level of the throat.

The other *Valentia* specimen was sectionised vertically to show the structure of the sphincter. This is strong, diffuse, mesogloea, lying towards the inner side of the mesogloea, but separated from the sheet of endodermal circular muscle by a narrow band of muscle-free mesogloea. The average depth of the sphincter (preserved) is .6 mm., this being about 8 per cent of the whole height of the column. A typical section of the sphincter is shown in Fig. 2. The cinclides seen in this specimen have the same structure as in the other.

The large Millport specimen has the mesenteries arranged as in the one described; but there are more of them, the fourth cycle being fully present, and part of a fifth also. This individual, moreover, is fertile, gonads occurring on cycles 1-3 inclusive, and also on the directives.

It is clear from the above data that *S. coccinea* possesses all the qualifications necessary for a typical member of the genus *Sagartia*, and its systematic position can now be established. It has a definite adherent base, soft smooth body, tentaculate margin, a submarginal zone of cinclides, a limited number of tentacles with ectodermal longitudinal muscle, gonads on all the older mesenteries, numerous mesenteries perfect, strong

retractors, acontia, no division of mesenteries into macro- and micro-enemes, and a strong mesogloal sphincter.

Carlgren has suggested (1894, p. 96) that possibly his variety *undata*  $\beta$  of *Sagartia undata* Müller is identical with Gosse's (not Müller's) *S. coccinea*. It is difficult, without seeing living specimens, to be quite sure about the identity or otherwise of the British and non-British forms. Carlgren's description of the colouring of his v. *undata*  $\beta$  certainly seems more like the British *S. coccinea* than that of his other varieties (v. *undata*  $\alpha$  and v. *troglydites*), and his var. *troglydites* may be our British *S. troglydites*. Whatever the truth of this may be, however, the situation is clear with

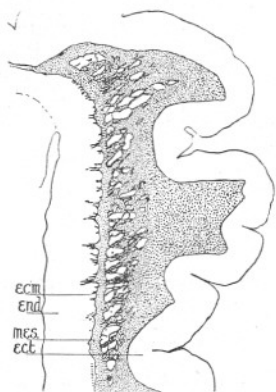


FIG. 2.—Sphincter of *Sagartia coccinea*.  
e.c.m. endodermal circular muscle :  
ect. ectoderm : end. endoderm : mes.  
mesogloea.

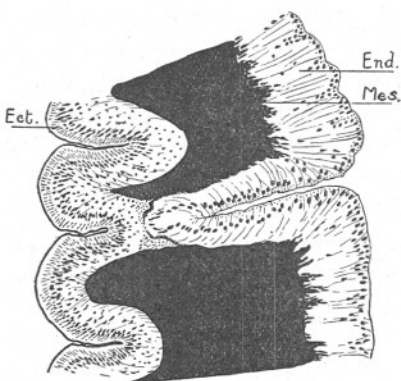


FIG. 3.—Cinclis of *Sagartia coccinea*,  
shown in L.S.  
Ect. ectoderm : End. endoderm : Mes.  
mesogloea.

regard to British species ; here we have *S. coccinea* Gosse, which is one thing, and *S. troglydites*, which is another ; they are not varieties of the same form. Anatomically *S. coccinea* seems to agree with Carlgren's description of *undata*  $\beta$  in some directions, but not as regards the cinclides ; and the sphincter also seems rather different.

## 2. METRIDIUM PALLIDUM (Holdsworth, 1855, p. 236, Pl. V, 4).

The external features of this species (usually called *Sagartia pallida*) have been described by Gosse (1860, p. 78, Pl. III, Figs. 4 and 5) and by W. Edgar Evans (1924, p. 185 *et seq.*), as well as by Holdsworth. I am indebted to Mr. Evans for 2 specimens, 1 from Torquay (var. *cana* Gosse), the other from Church Island, Valentia (var. *rufa* Gosse), collected by Miss Delap.

The following is a description of the Torquay specimen. Diameter of base, during life, 1.2 cm., the expanse of disc and tentacles the same

or more. Mesenteries in 4 cycles, with a few small additional mesenteries near the base. Sixteen perfect mesenteries are present, forming 7 pairs and 2 half-pairs; but these do not all belong to the first cycle, being irregularly distributed, as is often the case in forms which, like *M. pallidum*, reproduce asexually. The first cycle contains 7 pairs of mesenteries, 6 of these being perfect, and 1 partner of the seventh pair being perfect also. One pair of directives only, connected with the single siphonoglyph. Second cycle consists of 8 pairs, of which only 1 pair is perfect. Third cycle has 14 pairs, only a single mesentery here being perfect. Fourth cycle has 29 small pairs, and a few odd mesenteries belonging to a fifth cycle are present. This scheme of arrangement agrees exactly with the tentacular formula, which runs 7, 8, 14, 29, etc. Retractors occur on cycles 1-3, not very strongly developed, and diffuse in type (Fig. 4), the muscle processes moderately branched. Fairly large labial and parietal stomata present in the perfect mesenteries, smaller parietal ones in the second and third cycles of mesenteries. Filaments and acontia occur on mesenteries of all cycles, being best developed on the larger ones. Trifoliate region of filament present (Fig. 21), its shape characteristic and compact. Gonads not developed. Longitudinal musculature of tentacles ectodermal, the processes very small and short. Sphincter weak, mesogloal. Cinclides present, 20 in number, almost all endocoelic, irregularly arranged. One lies in a first-cycle endocoel, 1 in a second-cycle endocoel, 3 in third-cycle endocoels, 13 in fourth-cycle endocoels, 2 in exocoels. In each of 4 fourth-cycle endocoels there are 2 cinclides. No cinclides occur in the part of the body between the sphincter and the margin, i.e. the capitulum; they are scattered. In this specimen the structure of the cinclides is uniform, and in its typical condition is the same as that normally shown by cinclides of the other specimen. The structure may be understood from Fig. 6. The animal is small and has a thin bodywall, and the cinclides are rather reduced in structure. They are usually neither marked evaginations from the endodermal side nor strong invaginations from the ectodermal, but they tend to be the latter rather than the former, and are sometimes definitely so. There is no actual channel through the epithelium. The typical cinclis, in fact, consists of a definitely organised "soft spot"—a place where the mesogloea is reduced to little or nothing, and the ectoderm and endoderm covering the thin place both have their cells recognisably differentiated. On the endodermal side there are certain fibres which make a fringe to the mesogloea in the region of the cinclis; these may be fibres belonging to the endodermal-circular-muscle sheet of the bodywall, somewhat modified in direction by the presence of the cinclis.

The specimen from Valentia was sectionised vertically to show the



sphincter-structure. The sphincter is very small (Fig. 5), but is definitely mesogloal, of similar type to that of young *M. dianthus*. It does not occur at the actual margin, because the body is divided into a scapus (lower part), ending in a rim up above, and a capitulum (upper part), the wall of which is thinner than that of the scapus and has a modified ectoderm. The sphincter is in the uppermost part of the scapus, and



FIG. 4.—Retractor of *Metridium pallidum*.

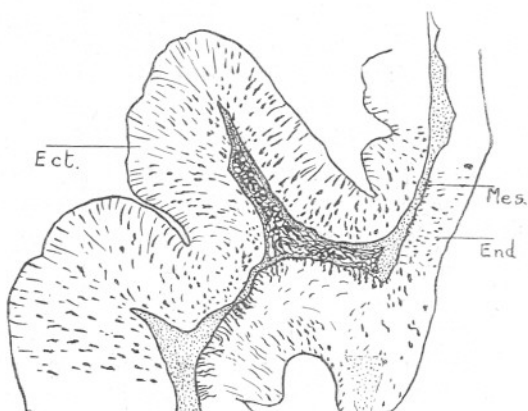


FIG. 5.—Sphincter of *Metridium pallidum*.  
Ect. ectoderm : End. endoderm : Mes. mesogloea.

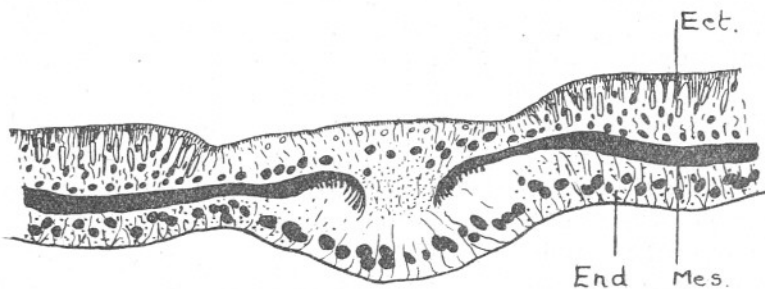


FIG. 6.—Cinclis of *Metridium pallidum*, shown in T.S.  
Ect. ectoderm : End. endoderm : Mes. mesogloea.

occupies only about 3 per cent of the total height of the bodywall (in the preserved condition).

From the details here set out, as also from the observations of Mr. W. Edgar Evans (1924, p. 185 *et seq.*), it is evident that this species can no longer be included in the genus *Sagartia*. The small number of perfect mesenteries, the weak sphincter, the division of the body into a scapus ending in a parapet, above which is a capitulum, are characters foreign to that genus. Its affinities are evidently with *Metridium*, and it should henceforth be known as *Metridium pallidum* Holdsworth. It may be

noted that when alive, *M. pallidum* and the young of *M. dianthus* are extremely similar. Its cinclides, moreover, of a peculiar type, are not like those characteristic of *Sagartias*, and their general distribution over the scapal part of the bodywall is not like the condition in typical *Sagartias*. The specimen sectioned vertically is fertile, but, unfortunately, the distribution of gonads is not clear in vertical sections.

### 3. DIADUMENE CINCTA T. A. Stephenson.

This species is instituted by T. A. Stephenson on p. 880 of the present issue of this Journal, where its external characters, habitat, and systematic position are dealt with. I am here concerned only with its anatomy, for the study of which I have used 4 specimens from the Plymouth Breakwater.

The following is a description of the individual selected for a series of transverse sections.

Mesenteries in 3 cycles, with additional small mesenteries in upper part of body; only cycle 1 (6 pairs) is perfect. One pair of directives and 1 siphonoglyph only. Retractors present on cycles 1 and 2, best developed on cycle 1; they are diffuse, the muscle-processes being fairly well branched (Fig. 7). Perfect mesenteries with large labial and parietal stomata; second cycle mesenteries with parietal stomata. The stomata occupy a fairly broad zone. Filaments occur on all older cycles, and are well developed. The trefoil region has a characteristic shape (Fig. 19) and is well developed. Acontia are present on all older cycles, best marked on the larger mesenteries. Longitudinal musculature of tentacles ectodermal, the processes short, thick, and unbranched. No gonads developed. The column is divided into 2 regions, a lower and more extensive scapus, and an upper shorter part or capitulum, which has a thinner wall than the scapus and different ectoderm. Capitulum devoid of cinclides. Scapus plentifully provided with them; they extend throughout its length and are irregularly arranged. They are 126 in number, and of these all are endocoelic except 19; the greatest number occur in third-cycle endocoels, where there may be as many as 10 in 1 endocoel. In structure the cinclides resemble to some extent those of *Metridium pallidum*, but are rather better developed, perhaps because they belong to a rather larger animal. They differ in appearance in sections, according to whether they are pierced by an actual channel or not. Very few are actually perforated (these having probably been recently used), and these are definitely ectodermal invaginations, with lips of ectoderm, strengthened by mesogloea, projecting inwards into the coelenteron (Fig. 8). The majority, however, have at their best the structure shown in Fig. 9. Here the mesogloea is either actually or virtually interrupted, and the epithelium is intact; but the endoderm

inside the cinclis is thickened, and the ectoderm sends inwards a little plug of tissue which forces itself through the mesogloea or forces the thin part of the latter inwards when it is not fully perforated. So that here the cinclis in its average state is a partial ectodermal invagination. Fibres such as those mentioned in *M. pallidum* occur here also, on the endodermal side of the mesogloea on either side of the point where it



FIG. 7.—Retractor of *Diadumene cincta*.

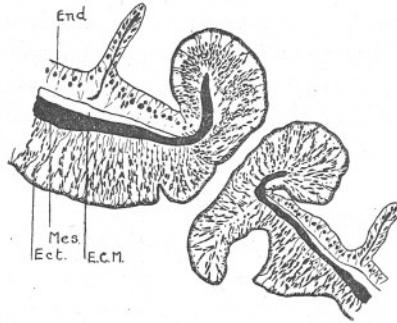


FIG. 8.—Cinclis of *Diadumene cincta*, shown in T.S.  
E.C.M. endodermal circular muscle: Ect. ectoderm: End. endoderm: Mes. mesogloea.

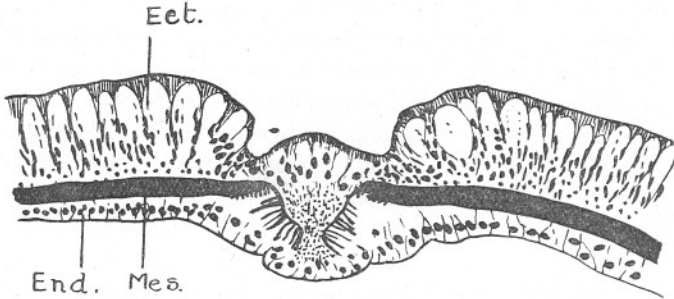


FIG. 9.—Cinclis of *Diadumene cincta*, shown in T.S.  
Ect. ectoderm: End. endoderm: Mes. mesogloea.

is interrupted; these are shown in Fig. 9, and seem likely to be a modified part of the endodermal circular muscle.

Three other specimens were sectioned vertically with a view to finding the sphincter. There is no trace of a sphincter in any of them. The cinclides seen have typically the same structure in these specimens as in the one described. The specimen described above was not measured during life, but was a moderate-sized one. The largest specimen of the species yet observed had a diameter (disc and tentacles together) of about

3 cm., diameter of base 1.8 or 2 cm. Another specimen, not so large, had a total length of 3.2 cm., width of body at the same time only .35 cm. The large one mentioned would be able to reach a good deal more than 3 cm. in height when well expanded.

#### 4. METRIDIDIUM DIANTHUS (Ellis, 1768, p. 436, Pl. 19, Fig. 8).

The external features of this species are well known. The anatomy of the adult has been described by O. Carlgren, 1894, and has been dealt with by others also. I have made a study of the young form, which is very different in appearance from the adult, for comparison with *Diadumene cincta*, to which it presents some external resemblance. I have used 4 specimens, 2 from Plymouth and 2 from Millport, all of them as nearly as possible of the same size as an average example of *Diadumene*; some of them were also of the orange colour variety, which most nearly resembles that species in appearance. The following is a description of an individual which was cut into a series of transverse sections.

Six pairs of perfect mesenteries. One pair of directives and 1 siphonoglyph only. Four complete cycles of imperfect mesenteries, with other small additional pairs developing in upper part of body. Mesenterial formula, therefore, according to the plan 6p., 6p., 12p., 24p., 48p., 96p.; but the sixth cycle is not fully represented, and the scheme is interfered with by an irregularity in 2 sectors opposite the directives, where the number is reduced. Cycles 1-3 inclusive bear well-developed retractors, and the larger mesenteries of the fourth cycle bear feebly developed ones. Retractors concentrated-diffuse in type (Fig. 13), the processes very high and fairly well branched. Mesenteries of cycles 1-4 have parietal stomata, very large ones in cycles 1 and 2. Perfect mesenteries with oral stomata also. Filaments occur on all cycles, and the typical trefoil region is compact and rather like that of *M. pallidum* (Fig. 20). Acontia are borne by cycles 1-4 inclusive. Longitudinal musculature of tentacles ectodermal, the processes short and unbranched. Sphincter occupying about  $4\frac{1}{2}$  per cent of total height of body (preserved). Cinclides occur scattered fairly evenly throughout the scapus; there are about 30 of them, 5 in endocoels and 25 in exocoels. Carlgren (1894, pp. 103 and 105) notes that in the adult form the cinclides are formed chiefly by endodermal evagination, and occur mostly in exocoels. In this specimen some of the cinclides are endodermal evaginations, but more of them are formed mainly by ectodermal invagination, so that we have 2 types in the same individual, the 2 types not separated into zones, but occurring erratically.

In other specimens the cinclides show the same kind of structure. In all specimens which I have examined, both ectodermal invaginations

and endodermal evaginations occur in the same individual. Few of them have a definite canal going all the way through the bodywall, but such a canal may occur. Fig. 10 shows a cinclis, an endodermal evagination which has broken through the mesogloea, and has in it a canal running out from the endodermal side (inner opening of this canal is in another

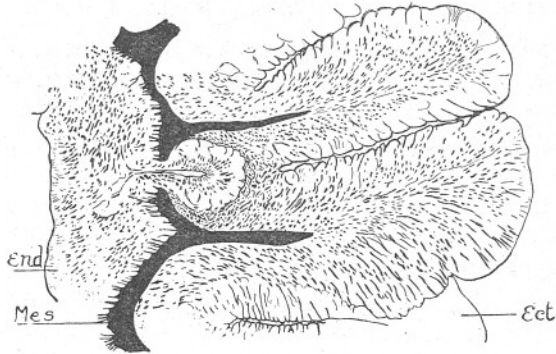


FIG. 10.—Cinclis of *Metridium dianthus*, shown in L.S.  
Ect. ectoderm : End. endoderm : Mes. mesogloea.

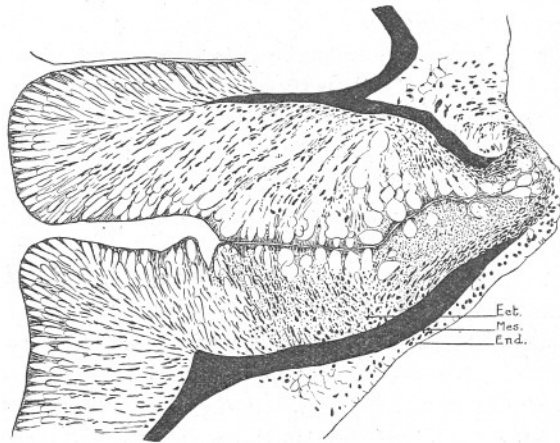


FIG. 11.—Cinclis of *Metridium dianthus*, shown in L.S.  
Ect. ectoderm : End. endoderm : Mes. mesogloea.

section) and ending blindly externally. Fig. 11 is another cinclis from the same individual, and this one is an ectodermal ingrowth penetrated by a canal all the way through, though the canal is not wholly shown in any one section.

The sphincter was observed in all 4 specimens. It is mesogloecal in all of them, and in the 2 from Plymouth it is well developed and lies in a

well-marked thickening of the bodywall, whereas in the Millport ones it is very insignificant (Fig. 12) and the thickening is slight.

The above examination establishes the fact that *Metridium* has a mesogloal sphincter when at the same size as *Diadumene cincta*, whereas the latter has none at all; that the cinclides in *Diadumene* are predominantly endocoelic, in young *Metridium* the opposite; the cinclides are, besides, different in detailed structure in the 2 forms. In the 2 specimens cut transversely, the number of tentacles and mesenteries in the *Diadumene* was less than that in the *Metridium* of, roughly, the same



FIG. 12.—Sphincter of *Metridium dianthus*.  
Ect. ectoderm: End. endoderm: Mes. mesoglea.



FIG. 13. Retractor of *Metridium dianthus*.

size; *Diadumene* can have more tentacles than the one sectionised, the largest specimen yet observed had 6 cycles of them and a few odd ones, though the numbers in the various cycles were not at their full complement; but *Metridium* as it grows up can far exceed this.

##### 5. GEPHYROPSIS DOHRNII (von Koch, 1878, p. 78).

This species has been described by von Koch (1878), by Andres (1883, p. 381), and by Haddon (1889, p. 325), but these descriptions deal mainly with external features. The form is well known at Plymouth, where it occurs on *Gorgonia verrucosa*. I have a series of transverse sections of a medium-sized Plymouth specimen. The length of the animal's longest axis (along the Gorgonian) is .7 cm. Width of body at the same place .4 cm. (when preserved). The region of the ectoderm which, during life, is in contact with the Alcyonarian (i.e. the basal disc) is specialised, being thickened and densely charged with gland-cells. Arrangement of mesenteries irregular and not reducible to a definite formula. There are 3 pairs of directive mesenteries, corresponding to 3 siphonoglyphs. Perfect mesenteries  $10\frac{1}{2}$  pairs, running as follows with relation to the directives: D3 D1 $\frac{1}{2}$  D3. There are 2 cycles of imperfect mesenteries, and a

few extra pairs beyond these, mostly developed aborally. Perfect mesenteries with oral and parietal stomata; most of the second cycle mesenteries with parietal stomata. Retractors occur on the perfect mesenteries and the larger imperfect ones; they are quite diffuse, feebly developed, and with low processes (Fig. 15). Filaments are present on all older mesenteries; the trefoil region is shown in Fig. 23. Acontia also occur on the older mesenteries. The non-directive perfect mesenteries are fertile, so are the larger imperfect ones. Directives sterile. Longitudinal musculature of tentacles ectodermal, the processes short,

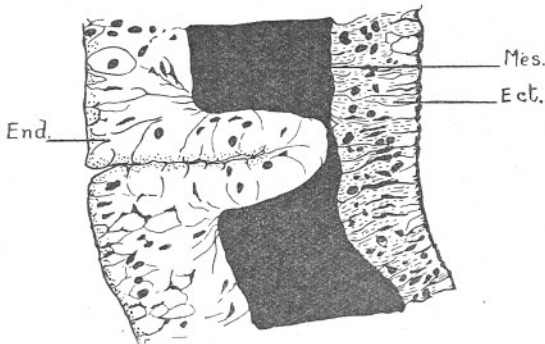


FIG. 14.—Cinclis of *Gephyropsis dohrnii*, shown in T.S.  
Ect. ectoderm: End. endoderm: Mes. mesogloea.

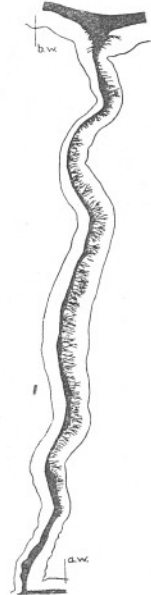


FIG. 15.—Retractor of  
*Gephyropsis dohrnii*.  
a.w. wall\* of throat: b.w.  
body wall.

thick, and branched. Sphincter mesogloea, strong, occupying about  $11\frac{1}{2}$  per cent of total height of bodywall (preserved). Cinclides present, 3 in number only. One occurs in each of 2 directive endocoels, and 1 in a non-directive endocoel. They are large, and are endodermal evaginations of a perfectly clear type, completely interrupting the mesogloea. The drawing in Fig. 14 is of a section passing slightly to one side of the actual point of interruption of the mesogloea, but showing the canal which runs outward from the endodermal side.

The name of this species, hitherto known as *Gephyra dohrnii*, has to be changed, according to Carlgren, because the name *Gephyra* is pre-occupied. It becomes *Gephyropsis dohrnii*.

It is difficult to decide the affinities of *Gephyropsis* exactly. Carlgren has just published a paper on this question (1925, p. 1), and concludes that there is no reason for erecting a separate family for *Gephyropsis* and its relative *Amphianthus*, at present; and that the group of anemones with acontia and basilar muscles, for which he still keeps the name *Sagartiidae*, is so far too little known to be accurately subdivided. Carlgren's account of the genus *Gephyropsis* agrees in the main with that given here, but he states that the genus has no cinclides. This is incorrect for British specimens at any rate. The one here described has perfectly clear and well-preserved cinclides about the presence of which there is not any doubt. Moreover, in living specimens of the species cinclides can be plainly seen, sometimes 2 on 1 directive endocoel.

Although not eligible for the family *Chondractiniidae* as at present defined, *Gephyropsis* presents certain definite affinities with that group and is probably more connected with them than with the *Sagartiidae* (sens. strict.), as represented by *Sagartia* and its immediate neighbours.

#### ADDITIONAL NOTES.

The following notes include a few facts connected with forms whose general anatomy is either already known, or which it has not been possible to study more fully.

##### HALCAMP A ARENARIA (Haddon, 1886, p. 616).

Haddon defined the genus *Halcampa* (1889, p. 333) as possessing "no sharply-defined circular muscle," i.e. no sphincter. It has since been shown by Carlgren (1900, p. 1171) and T. A. Stephenson (1918, p. 9, and 1920, p. 441) that there is a small mesogloal sphincter in *H. chrysanthellum*, and the genus has been redefined as possessing such.

I have been able to examine a specimen of *H. arenaria*, collected at Valentia by Miss Delap, and this also possesses a mesogloal sphincter (Fig. 16). This confirms a recent statement made by Carlgren (1921, p. 122) to the same effect.

##### SAGARTIA VIDUATA (Müller, 1776, p. 231).

I have examined some cinclides of this form, from a Plymouth specimen, for comparison with those of other species. The cinclides seen were all clearly and markedly endodermal evaginations, such as that shown in Fig. 17. This is the direct opposite of the cinclides observed by Carlgren (1894, p. 91, and Pl. VI, Fig. 7) in *S. viduata*, which were strongly ectodermal invaginations. There can be no doubt, however, of the nature of the cinclides in the Plymouth form. It is not impossible that the more northern one used by Carlgren is another species than the one



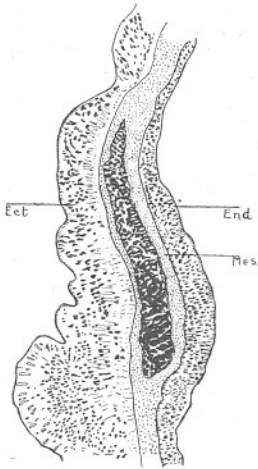


FIG. 16.—Sphincter of *Halcampa arenaria*.

*Ect.* ectoderm : *End.* endoderm :  
*Mes.* mesogloea.



FIG. 17.—Cinclis of *Sagartia viduata*, shown in T.S.

*Ect.* ectoderm : *End.* endoderm :  
*Mes.* mesogloea.

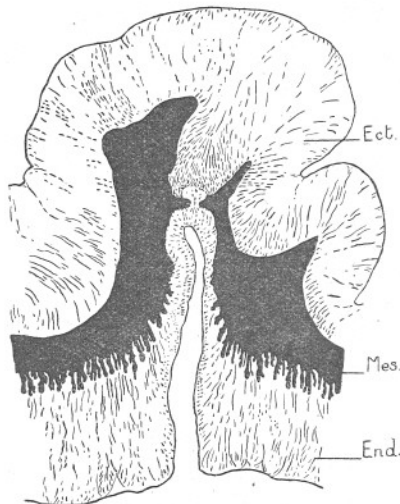


FIG. 18.—Cinclis of *Sagartia rosea*, shown in T.S.  
*Ect.* ectoderm : *End.* endoderm : *Mes.* mesogloea.

usually called by that name in this country—a suggestion which Carlgren himself has recently made (1924, p. 246).

SAGARTIA ROSEA (Gosse, 1853, p. 90, Pl. I, Figs. 5 and 6).

I can contribute a few facts towards the anatomy of this species, as the beginning of a study of its relationship to *S. miniata*, *S. nivea*, and *S. venusta*, which is not yet complete.

*S. rosea* has the same general characters as the other species mentioned. The longitudinal musculature of the tentacles is ectodermal. Numerous mesenteries are perfect, the retractors are strong-diffuse, acontia are present. The cinclides belonging to the upper part of the body are in all cases examined, endodermal evaginations in principle; one of them is illustrated in Fig. 18. In one specimen sectioned there were a considerable number of them, in endocoels, in a fairly broad zone a little below the sphincter. The specimens used were from Lydstep, Pembrokeshire.

## DISCUSSION.

### 1. *Mesenteric filaments.*

The form of these is very varied in different groups of Anthozoa, and is especially interesting in the case of the Ceriantharia. In the Actinaria the structural type is almost uniform, the great majority of forms having one general pattern of filament, and only a few more or less primitive forms having a less developed type. The majority of forms possess a three-fold region on their filaments, consisting of a median "cnidoglandular" epithelial cord and of two lateral cords of purely ciliated epithelium; this structure giving a trifoliate outline to a transverse section. In different Actinians the exact form of this trefoil varies very considerably; the shape of each portion varies, and so do the relative proportions of one part to another. There may be, too, on either side of the point where the trefoil joins the free edge of the mesentery a region presenting a network-like appearance—the "reticulate tract"; when these tracts are well developed the filament is rather five-fold than three-fold. In studying the anemones dealt with in this paper, I have been struck by the differences in pattern of the trefoil region of the filaments, and especially in the variation of the reticulate region. The pattern in any individual specimen appears to be constant, and so far as I have seen it holds good from one specimen to another. If it is constant throughout a series of individuals it would provide a rather useful character towards the determining of species from preserved material. But a much wider material than I have been able to use would be needed to confirm its specific constancy. The various filaments illustrated in this paper give

some of the variations in pattern to which I refer. Among those species which I have here examined the ones belonging to the Sagartiidæ (sens. strict.) have well-marked reticulate regions on their filaments; the Metridiid forms less marked ones or practically none.

## 2. Cinclides.

One of the objects of this paper has been to make out the structure and distribution of the cinclides in the species involved, with a view to finding out the value or otherwise of these structures as classificatory



FIG. 19.—Trefoil region of filament of *Diadumene cincta*.



FIG. 20.—Trefoil region of filament of *Metridium dianthus*.



FIG. 21.—Trefoil region of filament of *Metridium pallidum*.



FIG. 22.—Trefoil region of filament of *Sagartia rosea*.



FIG. 23.—Trefoil region of filament of *Gephyropsis dohrnii*.

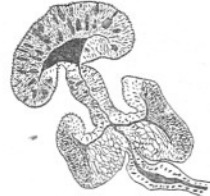


FIG. 24.—Trefoil region of filament of *Sagartia viduata*.

characters. The meaning of the cinclis-structure has also been given attention.

The genus *Sagartia* is a large one, and it is impossible to gain a final arrangement or understanding of it until more is known of it, and among other things the cinclides must be understood. The genus has been cleared up recently, to some extent, by the removal from it of *S. luciae* by McMurrich (1921, p. 729); and the present paper goes a step further by transferring *S. pallida* to *Metridium*. In the type species, *S. miniata*, the cinclides have been described by T. A. Stephenson (1920, pp. 446 *et seq.*). In this form there are 2 sets of them; 1 series occurs high up on the bodywall, just below the sphincter, the other set low down, immediately above the margin of the pedal disc; the 2 sets being separated by a cinclis-free zone. The upper-zone cinclides are frequently endodermal

evaginations in structure, those of the lower zone often being, on the contrary, ectodermal inpushings. In my own work on *S. coccinea*, *S. viduata*, and *S. rosea* I have been able to confirm this to some extent. In all of them there is an upper zone of cinclides which are typically endodermal evaginations. The lower-zone series requires further investigation than I have yet been able to give it, but I could detect no signs of it in *S. coccinea*, this being perhaps due to the small size of the specimens. Where it has been seen so far it has been in larger ones.

The work so far done on British Sagartias tends, therefore, to show that they all follow one kind of plan; but this conclusion is badly shaken by the conditions which Carlgren found in forms from further north, where, in *S. viduata* and *S. undata* from Gullmarfjord, etc., the upper zone cinclides were ectodermal invaginations. Whether this indicates simply that the cinclides are thoroughly variable, even within one and the same species, or whether a really extensive study will reveal a constant plan, it is as yet too early to say. The northern species are not necessarily the same as the British ones.

In *Diadumene cincta* and *Metridium pallidum* we find a plan contrasting with that of Sagartia. Here the cinclides are confined to the lower region of the body (the scapus), over which they are spread fairly evenly without being divided into zones, and they tend to follow a single type of structure only. This structure is rather curious, and not quite like that found in Sagartia.

In young *Metridium dianthus* the cinclides are either invaginations or evaginations, mingled haphazard.

At present it looks as if the structure and arrangement of cinclides will give a certain amount of guide to affinities, but that there is too much probability of variation to make it safe to build systematic characters upon them until more is known. In some cases they are useful, however, as in the instance of the contrast between *D. cincta* and *M. dianthus*, in the former of which the cinclides are predominantly endocoelic, in the latter the opposite. This is quite an arbitrary difference, and should prove diagnostic. It may also be found that in some forms the cinclides occur most extensively in endocoels of a given cycle of mesenteries, in other forms a different cycle or cycles being chosen, e.g. in *D. cincta* the greatest number occur in third-cycle endocoels, in *S. coccinea* all are in first- or second-cycle endocoels.

With regard to the function of cinclides, T. A. Stephenson has shown (1920, pp. 446 *et seq.*) that they appear in some cases to act as safety-valves, allowing fine jets of water to escape from the coelenteron of the anemone when the latter is obliged for any reason to contract very rapidly; they supplement the mouth as a means of exit and prevent rupture of the bodywall. In all cases they are probably connected in

some way with water-currents. My own work has extended some of the observations made in the paper mentioned, where it was noted that cinclides are not necessarily channels through the bodywall, as has usually been thought, but may be simply organised "soft spots" where the mesogloea is interrupted and the epithelium, etc., more or less modified; spots which can rupture neatly and without harm to the animal when needed as safety-valves. In my material I have found that cinclides of this kind are very common, and that in *D. cincta* and *M. pallidum* especially they are practically the normal condition. It may be that they are the typical variety for certain types of bodywall. After a cinclis has been used, it is not known whether it heals up again or regularises its channel. It may do the former in some cases and the latter in others.

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## Muscle-Tumours in the European Turbot.

By

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With a note by

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With 1 Figure in the Text.

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IN 1913 a successful attempt was made to introduce the European Turbot to New Zealand waters. On 12 January of that year 298 young fish, caught in the neighbourhood of Plymouth, and kept for some time at the Marine Biological Station, were put aboard the *Waimana*. Of these fish 195 were safely transported across the tropics, and were put into the tanks at the Portobello Marine Hatchery. The operation was a very successful one, thanks to the care of the late T. Anderton, who was then Curator of the hatchery.

The turbot were originally from one to two inches in length. It was intended to liberate most of them in the sea, but, on consideration, it was decided to keep them in captivity. Three years later (May, 1916) there were still 182 fish, 5 having died and 8 having been liberated in the sea. They grew very rapidly in the tanks, so much so that in May of 1916 many were about 18 inches in length. To keep these large fish healthy was difficult, and so, in 1916, 128 of them were liberated in Taukutu Bay.

The remaining fish did not appear to be getting ready to spawn. It was unlikely that they would do so in small tanks. So, in 1917, all but 14 of them were liberated in Taukutu Bay. Thus, in 1922, there were still left in the Portobello Tanks these 14 fish. They varied in length, from 18 to 24 inches. With the two exceptions about to be noted they have been, to all appearance, very healthy.

On 21 November, 1923, one fish, 18 inches long, died, and on 9 December, 1923, another one, 17½ inches long, died. There were no obvious indications as to the cause of death (bar, of course, the tumours to be

referred to presently). On making a post-mortem examination it was noticed that the stomach, in both cases, was swollen, and that there were broken sores on its peritoneal surface. This suggests some septic illness. In both cases there were tumours on the blind sides of the fishes, on the dorsal parts of the bodies. These tumours were oblong patches, about  $3\frac{1}{2}$  inches long and  $1\frac{1}{2}$  inches wide, and they were slightly raised above the general body surface. Internally they extended down towards the skeleton. They were sharply defined from the surrounding tissues in that the affected flesh was soft and yellow, while the normal tissues were firm and white. Throughout the substance of the tumour there were bright red streaks, appearances not to be observed in the healthy muscle substance.

Parts of each tumour were cut out, fixed in Mann's fluid for three hours, washed in alcohol, and preserved. These were sent to Dr. Drennan, of the Pathological Department of the University of Otago. The report furnished by Dr. Drennan is as follows:—

“The tumour consists of large, striped muscle fibres, with the usual perimysium and blood-vessels between the fibres. Many fibres are cedematous and partly disintegrated. At the skin surface there is necrosis of tissue and acute inflammatory change. It appears to be a simple tumour of striped muscle—a ‘Rhabdomyoma’—with degeneration and inflammatory changes.”

No further cases of the kind described above have occurred among the turbot kept in the tanks at the Portobello Hatchery. Scrupulous cleanliness and careful feeding at regular times have always been observed, and it appears that death, in the cases of these two fishes, was due to some acute affection. The beginning of the illness was held to be a certain date at which a slackening of appetite was observed: a fortnight later the fish died. It is not likely that the presence of the tumours was the direct cause of death.

[NOTE BY DR. J. JOHNSTONE.—Mr. Young kindly sent me the above report, and also some pieces of the fixed tumour. The structure of the latter is, as the pathologist reported, that of a rhabdomyoma: it is a mass of muscle fibres which tease out in very much the same way as do the ordinary muscles of a normal fish. Yet this muscular tumour is an abnormal structure, as shown by the gross appearance of the tissue and its difference from the surrounding parts. Also the disintegration of the fibres over large parts of the tumour is very striking, and indicates a loss of nutrition, the accumulation of excretory products, and so the beginning of necrotic changes.

In some marginal parts of the tumour there is a curious compression together of the individual fibres. Between the latter there ought normally to be a system of spaces (lymph channels) and a delicate tracery of con-



nective tissue. This is altogether absent, and the fibres are closely apposed: the appearance is quite a strange one to anybody who knows the normal structure. Text Fig. 1 represents such a microscopic field seen in a microtome section. The black lines separating the various fibres represents a structure staining blue with Mallory's combination: it is really a sheet of compact connective tissue. It was obvious in teased-out preparations that the cross-striation of the fibres was far less well marked than the longitudinal striation, so that the fibres easily broke up into the constituent sarcostyles, and hardly a trace of the very characteristic transverse striation might be evident. The figure shows this longitudinal striation well. The fibres are cut transversely, and the



TEXT FIGURE 1.—Transverse Section of a few fibres from the tumour.  
(Oil Immersion Lens.)

sarcostyles appear not as rounded fibrillæ, but as elongated, narrow plates, which tend to be arranged radially to the sarcolemma. This appearance rather suggests an embryonic character, which is, of course, what we should expect in the case of a malignant, rapidly growing tissue.

Rhabdomyomas are very uncommon among fishes. Adami (*Montreal Medical Journal*, 37, 1908, 163) has described such a tumour from a "lake trout," though this is not quite the same in structure as the tumour found by Mr. Young in the turbot. In a fairly large number of malignant growths in fishes I have never seen anything at all resembling a rhabdomyoma, and I think such a tumour must be of rare occurrence. It is interesting that those now noticed occurred in fishes kept in captivity, and in very exceptional conditions. The ordinary fish malignant tumour is a sarcoma. The connective tissue in the lower parts of the skin, or in the dissepiments between the muscle segments; or "flakes," or between

the individual muscle fibres begins to proliferate, grow and form an obvious swelling or tumour. As this increases in mass the muscle fibres gradually atrophy and disappear, pressed out of existence and starved by the huge accumulation of connective tissue. Here, however, the connective tissues have not grown at all, and the malignancy is exhibited by the muscle fibres themselves.

Rhabdomyomas are not uncommon among the mammals, and this case illustrates the essential similarity—not only in normal, but also in morbid histology—between the fishes and the higher mammals.]

## A New Type of Luminescence in Fishes.

By

C. F. Hickling, B.A.

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With Plates I-IV and 7 Figures in the Text.

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HARVEY, in his book, *Animal Light* (1919), divides luminous organisms into two sub-classes: (a) where the oxidisable material is burned within the cell where it is formed, to produce the light, and (b) where the material is secreted to the exterior and burned outside the cell. He gives a list of animals with extracellular luminescence, and mentions some of the medusæ, hydroids, pennatulids, Pholas and Phyllirhoë, some Cephalopods, decapod and Schizopod crustaceans, all myriapods, and the Balanoglossids. "The remaining organisms burn their material within the cell," a statement which includes the considerable number of fishes known to be luminous. The present paper attempts to describe a luminous organ of a new type found in a Macrurid fish, which falls into the second category of Harvey's classification in that the luminous material is secreted to the outside and not burnt within the cell. The organ seems to be unique in both structure and function.

*Malacocephalus laevis* (Lowe) is one of the fish which occurs along the outer edge of the continental shelf from Ireland south to Morocco. It is taken in considerable numbers in the trawls of the deep-sea hake trawlers, in depths of over 150 fathoms, though small specimens straggle over into water of 120 fathoms (off Galway, off the Fastnet).

Material was fixed, and experiments were made, during voyages to the deep water on the steam trawlers *Tenedos* and *Trawler Prince* in January, March, and May, and I here wish to express my thanks to Chief Skipper J. Yolland, D.S.C., R.N.R., and to Capt. Jones, and to the crews of these ships, for their hospitality, help, and interest in the work.

### THE FISH.

Farran (1924) mentions *M. laevis* as being "very abundant on the hake grounds to the south-west of Ireland," and he notices "a triangular, scale-less, black-coloured depression" between the base of the pelvic fins. He is apparently unaware of any luminous property in the fish,

and none of the authorities he quotes seems to have suspected it. Moreover, it is interesting to note that Gilbert and Hubbs (1916), whose classification of the group of Macrurids has been used for identifying the fish, remark a blackish colour on the belly of *M. nipponensis*, and it seems likely that this species also might be found to possess a luminous organ of the type to be described.

Text Fig. 1 represents a ventral view of the fish, which possesses the typical Macrurid figure, comprising a short and thick body, followed by a very long whip-like tail. The pectoral fin of one side is shown at PC, PL are the pelvic fins, and SD 1 and 2 are the black scale-less depressions lying between and behind the bases of these fins. OP is the operculum, and AP is the papilla in which the rectum terminates at the anus. Whether this papilla is the result of the forcing out of the rectum

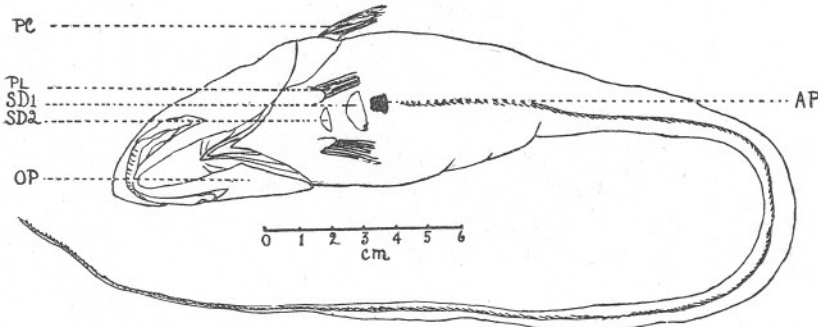


FIG. 1.—Ventral view of *M. laevis*, showing the position of the scale-less depressions SD 1 and 2.

by pressure, or whether it is natural to the fish, is impossible to say. It seems constant in all the specimens examined.

If the base of the anal papilla be examined with a seeker, a circular cleft will be found encircling the papilla, which is the opening of the duct of the luminous organ. The skin in this region is remarkably thickened and heavily loaded with black pigment. At the scale-less depressions the skin seems much thinner, especially at the anterior depression, where it is quite translucent except for small round melanophores scattered over it.

Dissection of the body wall at this point reveals the luminous organ, which is seen to lie among the muscles anterior to the rectum, and immediately behind the anterior and above the posterior scale-less depression. The relation of the gland to these other structures is indicated by Text Fig. 2, which is a very diagrammatic sagittal section through the middle of the gland and rectum.

The rectum is represented at R with very thick black walls and much-

pleated epithelium. It is seen protruding below as the papilla. The luminous gland is LG, and its duct is shown at D, passing downwards. The figure seeks to indicate that at this point the duct encircles the rectum—a point which will be again referred to. The scale-less depressions are indicated by SD 1 and SD 2, the latter being headward. L 1 and L 2 are two remarkable hyaline lens-like bodies, the one lying beneath the gland, the other anterior to it. Their relation to the gland and to the scale-less depressions is suggestive, and will be discussed below.

ML points to portions of the heavy sheaths of black pigment which partially or wholly enwrap all these organs.

Seen from above, the organ appears as a fluted swelling arising at the

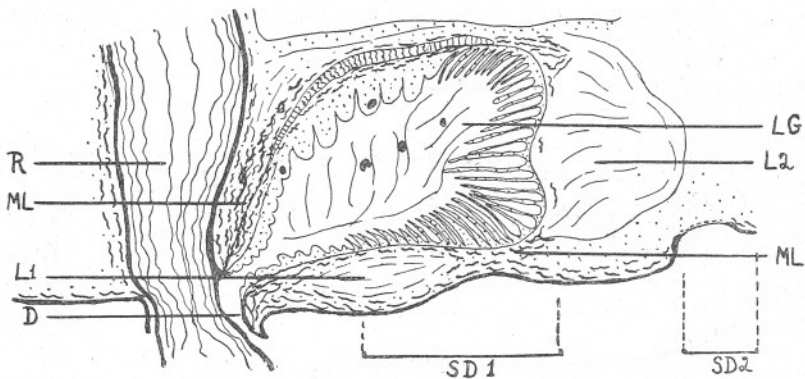


FIG. 2.—Diagrammatic sagittal section through luminous organ of *M. laevis*, showing the relation of the structures. SD 1 and 2, positions of depressions.

point where the rectum passes down from the coelome to the body-wall. So closely does the organ embrace the rectum that the latter appears to pass through the hinder part of it. The swelling is covered by the silvery peritoneum, but at the periphery abundant melanophores are present, with branched and ramifying processes.

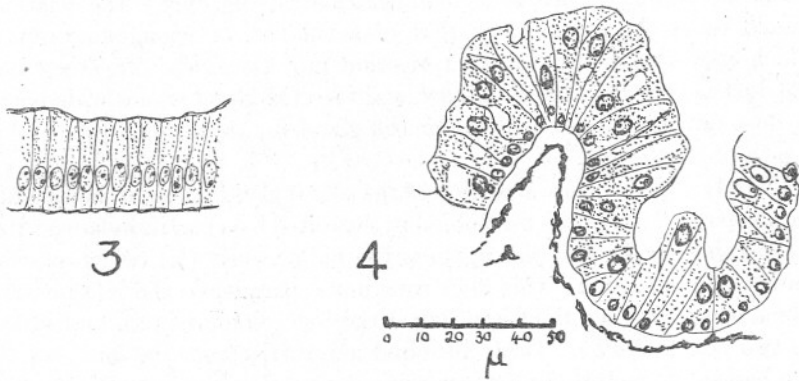
The gland is usually between 2 and 4 millimetres in length, but in large specimens it may be 7 or more millimetres.

#### THE DUCT.

Plate I, Figs. 1-3, represent three sections from a series cut transversely to the rectum. The rectal papilla is bent forwards, hence Fig. 1, which is a section very near the anus, includes a long tongue of tissue, which is the papilla cut obliquely. It consists chiefly of connective tissue, containing black pigment, and rich in blood sinuses (BV). The lumen of the rectum, very near the anus, is at R, and in this section is not

complete; a little faecal matter is present. Even at this point the luminous duct is seen at LD, with its characteristic epithelium.

Fig. 2 is at a slightly higher level, near the base of the papilla. The rectum is complete, represented as a much-pleated tube, with the lumen well defined and patent. The epithelium lining the rectum is seen to be very different from that lining the luminous duct. The difference is indicated in Text Figs. 3 and 4, which are both drawn to the same scale. The epithelium of the rectum is regular, columnar, and compact, with the nuclei regularly arranged, and the cytoplasm abutting on the lumen slightly denser than elsewhere. The epithelium of the duct is sharply distinct, being irregular in outline, its cells are indefinite, vacuolated, with their outlines difficult to determine; their nuclei are scattered



FIGS. 3 and 4.—Portions of the epithelium of the rectum and duct respectively, to the same magnification.

at all levels, and the cytoplasm is not more clearly defined at the surface of the epithelium. In Plate I, Fig. 2, the luminous duct is beginning to encircle the rectum. As before, abundant blood sinuses are present, and melanophores (ML) are very abundant in the connective tissue, both scattered, and as definite layers underlying the epithelium of the rectum, of the duct, and in the parts adjacent to the duct.

Fig. 3 is a third section, which shows the remarkable relation which the duct bears to the rectum. The latter is seen as a completely isolated body surrounded by the luminous duct, which entirely encircles the rectum for a short distance. At one side, the duct is seen slightly drawing away from the rectum; this indicates the headward direction, in which the duct will run forward to the gland. Some striped muscle appears in this section; it is doubtless part of the ordinary somatic muscles of this region. This section also shows particularly well the arrangement of the melanin sheaths (ML). A dense sheath surrounds the luminous

duct, a second lies beneath its epithelium, a third lies beneath the corresponding epithelium on the rectal side, a fourth beneath the epithelium of the rectum itself. Besides these, melanophores are everywhere scattered through the connective tissues.

Plate II, Fig. 4, represents a section at the level where the duct runs forward and upward to the gland. The rectum is no longer completely surrounded by the duct, which has drawn away from it at the hinder end. The duct is seen in oblique horizontal section. It is a flat cavity as broad as the rectum. Plate III shows the duct again in sagittal section. At this level the duct is very indefinite, apparently having a number of tubules and sacculi which communicate with the gland, and no doubt serve to collect the secretion. There is, therefore, no distinct orifice by which the gland communicates with the duct; the relation should rather be regarded as that of a tubular, or sponge-like organ which passes without a sharp transition into the duct. In any case, the duct is very broad and shallow, and taps the gland over a wide base. It does not extend forward under the gland for more than  $\frac{1}{4}$  to  $\frac{1}{3}$  the length of that organ.

Plate II, Fig. 5. Here a portion of the actual gland is seen in horizontal section (G). The rectum lies behind it, separated by a partition laden with melanophores. Behind this again is the kidney duct (K), which is well shown in this section; this duct runs down parallel to the rectum and opens behind it. To right and left of the line joining rectum and gland lie two pouches (PP). These are blind upgrowths from the duct, which run beside the rectum for a short distance and then die out.

In some of the sections the luminous duct is seen to contain fragments of the secretion.

#### THE GLAND.

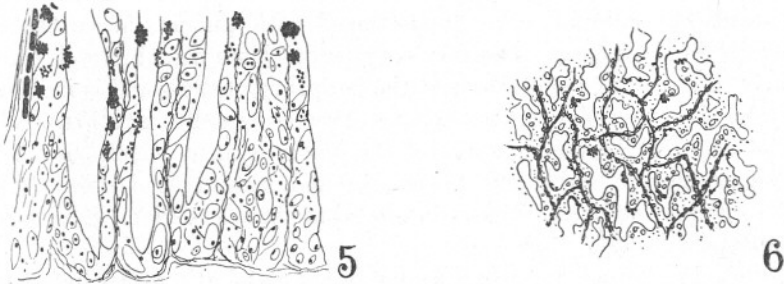
The luminous gland is oval in shape, flattened anteriorly, and tapering posteriorly. It is firmly bound in connective tissue, and is very definite in shape, being in no way a diffuse gland. It lies headward of the rectum, with its duct leading backwards and downwards to surround this organ. Plate III is a somewhat diagrammatic sagittal section of the gland, slightly to one side of the middle line. The rectum (R) is, therefore, obstructed by long tongues of tissue, which are the pleated walls of the rectum in longitudinal section.

There is an extraordinary amount of pigment about the gland. This is specially dense in the partition between the rectum and the duct and gland, where the connective tissue is loaded with melanophores (ML). This pigment also occurs in the connective tissue wrapping the organ, almost entirely surrounding it. The walls of the rectum are also heavily pigmented. In this drawing a portion of the coelome (C) is seen, and

below it a portion of the body-wall (CT) with connective tissue and some muscle, which will be referred to later.

Headward of the gland (L 1) is seen a section of one of the lens-like bodies referred to previously, and below the gland is the second (L 2). They are apparently hyaline connective tissue, with indications of a concentric striation. Further work will be done to make sure whether these lens-like bodies are part of an optical apparatus for casting light from the gland itself. At first sight it seems unlikely, as the organ is well surrounded with pigment, and the gland itself does not seem to give any light when cut out, apart from that of the luminous secretion which inevitably smears itself over the organ.

The headward part of the gland seems to be most active in secretion (S), and here the clumps of secretion, deeply stained, can be seen radiating in lines towards the centre of the gland, usually growing larger as one



FIGS. 5 and 6.—Longitudinal and transverse sections respectively of the secreting portion of gland.

follows them in. \* A high-power view of this region is given in Text Fig. 5. This represents the base of some of the long tongues of tissue which are seen to project into the gland. The granules of secretion arise in the cells lining these tongues of tissue, and appear as very deeply staining bodies in the cytoplasm; when set free into the lumina of the gland, they become much larger in size, rather hyaline and less deeply staining, and now measure from 1 to 1.5  $\mu$ . But more usually they appear as dense balls or aggregations of granules, which cling together to form lumps from 20–30  $\mu$  in diameter. These are the black objects shown in the drawings of the gland. Text Fig. 6 is drawn from Plate IV, and shows the appearance, in transverse section, of the secreting tissue of the gland. The granules of secretion are again seen in the walls lining the lumina.

Plates III and IV show the structure of the gland. It is seen to consist largely of long folds of tissue which arise at the periphery and extend towards the centre. Plate III shows the appearance of the folds in longitudinal section, and Text Fig. 5 shows the folds more highly magnified.



A strand of fibrous connective tissue is seen to run in the centre of the folds, no doubt acting as a support, and fine blood-vessels are also present in the folds, bearing the elongated and deeply staining corpuscles. A row of such corpuscles are shown in Text Fig. 5, to the left.

Towards the hinder end of the gland the structure becomes less definite, the spaces in the connective tissue which largely forms this portion functioning as collecting vessels (CV) or reservoirs, which mainly lead in a downward direction and contain abundant secretion. The folds, as indicated above, take here the form of stout walls, consisting chiefly of connective tissue, the epithelium lining the lumina containing no granules of secretion. They contrast with the folds at the anterior end of the gland, which are long, very slender, and consist largely of a vigorously secreting epithelium, with a small strand of connective tissue only. There is little doubt but that these structures are of essentially the same nature.

Plate II, Fig. 6, represents a transverse section of the gland rather towards the anterior end. It is stained with thionin, hence the cell details do not appear. The very complete melanin sheath is well shown (ML), the secreting epithelium at the periphery of the gland is indicated (S) by the very deeply stained masses of secretion radiating centripetally. The folds (F) appear in virtue of the black pigment which they bear, they are seen to lead chiefly downwards, and contain blood-vessels (BV); the lumina between them contain abundant secretion. The arrow indicates the middle line.

Plate IV shows a horizontal section of the gland at a rather high level. The rectum is seen in transverse section as a pleated tube (R), and between it and the gland is again seen the heavily pigmented partition (ML). Blood spaces (BV) are to be seen in section, while two masses of muscle (M) appear on either side of the rectum. These are typical striped muscles and seem to have no connection with the present organ. The secretory part of the gland is here seen (S) in transverse section, the folds of tissue are seen to be united at their bases to give a honeycombed or cerebrated appearance. Text Fig. 6 is an enlargement of a portion of this region; a strand of connective tissue, bearing a certain amount of pigment, is seen to run in the folds; this strand is also shown in longitudinal section in Text Fig. 5. At the anterior end of the gland is seen a strut of strong fibrous connective tissue (G) which projects into the gland. This is undoubtedly a skeletal structure, and at the top and at the sides of the gland there are other such struts which unite to form a meshwork. They are probably instrumental in enabling the gland to keep its shape or to return to it after compression.

In Plate III a muscle layer is seen lying immediately above the gland, running thence backward and downward in the partition between gland and rectum. It is an unstriped muscle, and apparently forms a sheath

at least around the hinder part of the gland, and possibly of the duct also. It is quite distinct from portions of the ordinary striped muscle of the body-wall, and is also visible in other views of the gland, though less well shown. It is seen in horizontal sections, such as Plate IV, as a layer lying between the gland and the melanin sheath, and occupies a similar position in Plate II, Fig. 6, where it is seen to form a sheath about the gland. It is probably closely connected with the function of compressing the gland to cause emission of the secretion, and probably originates from the splanchnic muscle of the rectum.

The nerve supply of the gland has offered great difficulty. There seems to be no conspicuous nervous organisation, and further work must be done with material specially prepared for neurological work.

Summing up, there is present in this fish a gland, lying in the body wall in front of the rectum, between and behind the pelvic fins; this gland is supported by connective tissue struts internally, a muscle layer, sheaths of connective binding tissue and of pigment, and a duct which opens backward and downward to the exterior as a tube completely surrounding the rectum. Though it is possible that there is an optical apparatus for casting light from the organ, it seems improbable, chiefly on account of the already well-marked secretory function of the gland, and also on account of the abundant pigment which seems to form a light proof sheath about all structures in connection with the gland.

As to the homology of the organ, it is probably to be regarded as a glandular area about the anus, which has become invaginated to form a pouch, and secondarily folded to give an enormous internal area of secretion, while becoming specialised for the secretion of luminous material.

Von Lendenfeld (1887) in his notes on the luminous fish collected by the *Challenger*, suggests (p. 288 and p. 384) that the original forms of phosphorescent organs in fishes arose from the small slime-glands of the skin, which by chance may have produced a slightly phosphorescent slime, as have those of some Batrachians. This would perhaps be of advantage to a fish living in great depths, and progressive evolution could have resulted in the production of a slime more and more luminous.

#### NOTES ON THE SECRETION.

When the fish are shot from the trawl at night, *M. laevis* is at once noticeable by the secretion, which smears the belly of the fish, and may spread over other fish. The secretion is mucous and viscid, adheres to the hand or to an oilskin, and glows quite perceptibly in lamplight. The glow of the pure secretion is distinctly blue, but the solution in sea-water glows bright green. In bright daylight, the secretion appears greenish

yellow, and when obtained by squeezing the abdomen of the fish, is usually mixed with fæces.

In some cases there is, no doubt, a spontaneous emission of the secretion by the dying fish, but it is difficult to say with certainty whether this is always the case, as the weight of overlying fish might cause the squeezing forth of the secretion. It suggests a comparison with *Pholas dactylus*, which Dubois (1892) shows to be permanently luminous when moribund.

Harvey (1922), in his work on Photoblepharon and Anomalops, shows that in these fish the luminous organs, while presenting the appearance of secreting glands, do not pass out any luminous material to the exterior. The pores which are present, and were noticed earlier by Steche and other workers, are to be regarded as exits for dead bacteria, the light of these fish shown by Harvey to be due to symbiotic bacteria multiplying within the organs.

It is quite certain that *M. laevis* actually pours forth a secretion, and I am satisfied that the light is not due to bacteria. Not only do the sections of the gland show no sign of bacteria, but smears of the fresh slime, made on board by Dobell's method (1911), show no sign of bacteria when stained with methylene blue. Instead, the granules of the secretion are seen in great numbers, very deeply stained, together with occasional cell fragments.

Moreover, the experiments made with the secretion, shortly to be described, indicate beyond much doubt that bacteria are not responsible for the luminescence in this case.

Each fish, when the abdomen is squeezed, yields a large viscid drop of greenish-yellow slime. The actual quantity obtained naturally varies slightly with the size of the fish, and the state of the organ, but in any case it seems to be enormously greater than that obtainable from other luminous organisms, and *M. laevis* seems to be a form exceptionally favourable for work on animal light.

It has been possible to carry out only a few crude experiments under the difficult conditions experienced at sea on a steam-trawler, but these are given below, and may be of use in future work on this type of luminescence.

#### (a) The Solution in Sea-Water.

When the slime in a dark room is allowed to pour down the side of a glass tube into sea-water, it forms drops which rapidly dissolve, giving a very bright, greenish-blue phosphorescence. The secretion squeezed from ten fish was dissolved in about 25 c.c. of sea-water. This solution did not long remain uniformly luminous, but the light became confined to a layer in contact with the air, at the surface of the solution. The optimum brightness

could only be maintained by constant shaking. The solution, viewed in the dark, has a turbid or granular appearance, the granules appearing to whirl about on agitating the fluid. "It is as if granules were dissolving with light emission" (Harvey, 1924). A strong solution, moreover, shows stratification, as if the granules tended to aggregate.

In total darkness the solution, described above, was photographed. This photograph is reproduced in Text Fig. 7. It was taken with an ordinary Ensign folding camera, using "Kodak" N-C films, at a distance of 5 feet with thirty seconds' exposure. The photo shows the solution lying at the bottom of the honey-jar which contained it, the lower and less distinct shape being the reflection of the light on the polished wood of the table.

A crude photometric experiment was performed with the same solution. A grease-spot photometer was set up, and the honey-jar containing

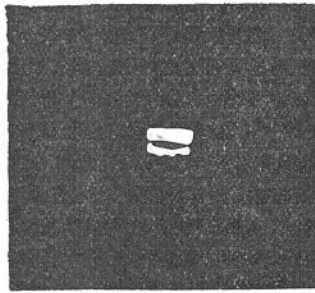


FIG. 7.—Photograph of luminous solution in honey-jar, 5 cms. in diameter, standing on a polished table. Exposure 30 seconds at 5 feet.

the secretion was placed at a distance of 8 cms. from the screen, measured from the centre of the honey-jar, which was 5 cms. in external diameter. Now an ordinary paraffin candle was lit, and advanced towards the opposite side of the screen until the bright green glow of the solution was no longer to be seen on the grease-spot, which now appeared bluish black. It was possible to find this point with some sharpness if the luminous solution was kept well agitated. The distances of candle and solution from the screen were now measured. They were as 8 cms. : 22 cms. This gives a candle-power of approximately .14.

The intensity of the glow also naturally depends on the quantity of solution used. Just sufficient of the same solution to cover the bottom of the honey-jar was used for a similar photometric experiment. The distances were now as 4 cms. : 24 cms. ; a candle-power of approximately .029.

Further experiments were made with the solution. It was found

possible to read the title of a daily paper at 70 cms., and the hands of a clock at 150 cms., both eye and solution being at this distance. The small print of a newspaper could be read easily when the solution was held against the paper, and it could also be used as a "torch" to find knives, matches, pencils, etc., on the floor. Held in the middle of the cabin, one could distinguish objects on the walls, such as clothing, papers, and fittings.

It is a strange thing that so much oxygen is apparently necessary for the steady glow of a strong solution that it must be kept in constant agitation. It suggests that the extraordinary brilliance of the glow is only obtained by a rate of oxidation far in excess of that found to obtain for such luminous forms as *Cypridina* (Harvey), which are luminous at extreme tenuity of oxygen. One of the facts that guided Harvey to the conclusion that the light of *Photoblepharon* and *Anomalops* is due to bacteria was their high oxygen consumption, as shown by the fact that the light only appeared where the material was in contact with the air, and that an emulsion of the glands of these fish becomes, as in the present subject, luminous only in the layers in contact with the air. He shows (*loc. cit.*) that the oxygen consumption of luminous bacteria is far in excess of that of forms which are self-luminous. As stated earlier, experiments and observations point to the fact that in *M. laevis*, in spite of this high rate of oxygen consumption, luminescence is not due to bacteria, and the phenomenon may be explained by the possibility of the luminous material being present in exceptionally high concentration.

As the sea-water becomes more dilute the colour changes, first to green, and then to a pale green or white colour. The light is still visible at extreme dilution—three drops of pure secretion were dissolved in sea-water and then poured into a gallon of sea-water in a canvas bucket, the bucket now appeared as though filled with milk, very distinctly luminous and pale white. Twenty-four hours later the bucket still appeared luminous, the solution having soaked into the walls.

The solution in sea-water remains luminous for a very long time. A jar was found to be still feebly phosphorescent after six days, but usually a strong solution begins to putrefy after forty-eight hours, and later becomes quite turbid with growths. This putrid solution may become perceptibly brighter on shaking up this turbid sediment, a fact which compares in an interesting way with Harvey's statement, in *Animal Light*, that bacteria can revive the light of a dead luminous solution by reducing the oxidisable substance, and thus again rendering it available for light production.

The more dilute solutions of the secretion are uniformly luminous throughout.

(b) **The Solution in Distilled Water.**

When allowed to trickle down into distilled water, the secretion forms very brightly luminous beads, which dissolve on shaking and fade out immediately. The glow cannot be revived by addition of sea-water, nor by treatment with a Luciferin solution (see below). But if the secretion be first dissolved in a small quantity of sea-water, and then diluted with distilled water to almost any extent, there is neither extinguishing nor brightening of the light, the new solution having the same appearance as a corresponding solution in sea-water. The glow soon fades out, however; the exact time is not certain, but it is usually between eight and twelve hours.

(c) **Other Observations.**

The secretion was allowed to stand over crystals of sugar for nine hours. The glow was not extinguished immediately, and after this interval the glow reappeared as before on dissolving in sea-water.

When poured on to crystals of  $MgSO_4$ , the glow of the solution was instantly put out, but was again revived on dissolving in a large bulk of sea-water after standing over these crystals for nine hours. These two experiments are especially suggestive in showing that bacteria can hardly be responsible for the light.

The temperature at which the glow was extinguished could not be determined, but it is worth noting that it was slowly extinguished by placing a tube of secretion in a mug of cocoa just cool enough to sip. It was also soon put out by being suspended over the cylinders in the engine-room, but here the ascending currents of air may be very hot.

LUCIFERIN AND LUCIFERASE.

Harvey suggests that all animal luminescence is due to the same fundamental principle, namely, the burning of luciferin to oxyluciferin in presence of the ferment luciferase. Attempts were made to demonstrate these bodies in the present fish, and I am satisfied that it is possible to show that here also the luminescence is of the above type.

Dubois (1887), in his work on *Pholas*, notes that the luminous tissue of this mollusc was extinguished by exposure to hot water, but that light was again renewed when over the darkened tissue was poured a solution containing the luminous secretion of *Pholas* which had exhausted its light. He suggested the names luciferin and luciferase, the last being a ferment which is destroyed by heat, but is still present in a solution of a luminous secretion which has burnt up all the available luminous material, luciferin.

A solution of luciferase was prepared from *M. laevis*, as mentioned

in a preceding paragraph, by allowing a solution of the secretion, much diluted with distilled water, to die out, a process which takes place between eight and twelve hours after solution. Oxidation seems more rapid when distilled water is added, as the sea-water solution remains luminous for days.

A luciferin solution was obtained by placing a strong solution of the secretion of the fish in a hot fluid, until the solution was completely dark.

When these two perfectly dark solutions are mixed, a distinct glow results, which lasts for some time.

As a control experiment, a similar tube of extinguished secretion was placed in an equal bulk of distilled water—there was no result.

To this dilute solution of luciferin was added a spot of pure secretion on the top of a pencil. The dark liquid at once "took fire" and glowed distinctly.

Finally, a similar spot of secretion added to distilled water behaved just as a previous experiment indicated. It formed a few bright spangles of light which soon faded out.

Hence the evidence points, in my opinion, to the luminescence of this fish being essentially of the same nature as that of *Cypridina*, *Odontosyllis*, *Pholas*, and fireflies, and it is not to be regarded as due to symbiotic bacteria.

*Malacocephalus laevis*, however, differs from all other such organisms in the remarkable size of the gland, and the quantity of luminous matter available for examination; in the unusually high oxygen consumption of a strong solution, in the length of duration of the luminescence, and in the fact that the luciferin-luciferase reaction cannot be demonstrated in distilled water, unless the secretion has been previously treated with sea-water.

#### CONCLUSION.

The function of the gland seems much more obvious than is the case with many other types of luminous organs. It has no sexual significance, since it is equally well developed in the smallest specimens seen. But it lies between the strong muscles of the body-wall behind the pelvic fins, and may have a special muscular sheath apart from these. Contraction of these muscles would cause the secretion to be shot out, and its use would seem to be exactly analogous to the ink-sac of Cephalopods, but whereas the latter emit a cloud of ink, this fish emits a cloud of light.

I have never seen a fully alive specimen of *M. laevis*, though I have often searched. When thrown back into the water my specimens float motionless, belly upward. But Capt. Jones tells me that off Cape Villano he threw a large specimen overboard alive, and that it emitted a cloud

of fire, which spread "like a dinner-plate," and apparently remained visible for some time. This leaves little doubt but that the function of the gland is as has been indicated in the previous paragraph.

There is no evidence of the gland being used as a flashing apparatus, in spite of the very suggestive relations of the hyaline bodies and the scale-less depressions with the gland.

We may imagine that a Macrurid possessing this organ would, on alarm, emit a puff of light and then make off in a different direction. Knowing the attractive power of light for many animals, especially fishes, we can understand that a pursuer might pause to investigate the nebula, and enable the prey to make good its escape. Dubois (1892) suggests that *Pholas dactylus* in a similar way envelops itself in a cloud of light, though here, apparently, the author considers that the effect would be to alarm a persecutor.

It is just possible that the secretion may be used in the same way for attracting the food of this fish. *M. laevis* feeds on crustacea mainly, such as *Cirolana borealis*, the crabs Geryon and Gonoplax, Nephrops, Pasiphaë, Crangonids, Pandalus and Amphipods, with other more occasional forms.

Three Macrurids are fairly common along the edge of the continental shelf within the reach of commercial trawlers, namely, *M. laevis*, *Coelorhynchus coelorhynchus*, and *Trachyrhynchus trachyrhynchus*. Farran (1924) states that *M. laevis* and *C. coelorhynchus* are common on the hake grounds S.W. of Ireland, but I have only seen five specimens of *C. coelorhynchus*, and these were taken in 300 f., in the greatest depth worked. *T. trachyrhynchus* is occasionally quite plentiful, and is one of the signs that the ship is fishing near coral.

Now *M. laevis* has small and thin scales, feebly armed with small spines, but it has a very well-developed luminous organ. *C. coelorhynchus* has well-armed spinous scales, and possesses, between the pelvic fins, a naked, pigmented patch recalling that of *M. laevis*; and dissection again reveals a flat pigmented sac lying in the body-wall adjacent to this pigmented patch. Material has been prepared for a further examination of this organ, but at present it gives one the appearance of being a rudimentary organ, yielding no secretion, but connected with the anus by a pigmented, functionless duct.

*T. trachyrhynchus* has very strongly armed scales, forming a thick and heavy coat of mail, and as far as present work has shown, there is no trace of a luminous organ. The scales of these three fish are photographed in Farran's paper (1924), but that of *T. trachyrhynchus* is probably from a young specimen, as my specimens have a very thick scale with three strong teeth, while Farran's scale shows but one strong central spine, and two small ones. He states, however, on p. 122, that in a



larger specimen the scale bears "one large, and usually, two smaller spines, short and robust, the whole scale being thickened and massive."

Pending further work on these fish, I would suggest that the increasing efficiency of external armour has rendered unnecessary the protective device of a luminous organ, and that these three forms show how the gland might have been reduced as the scale armour increases in importance. The scale of *M. laevis* is much nearer the gadoid type than any of the others, and Macrurids are regarded as derived from the Gadidæ.

As these three forms are not closely allied, according to the arrangement of Gilbert and Hubbs (1916), it suggests that the organ may be widely distributed among Macruridæ, and further work on other species might reveal its presence.

*M. laevis* occurs in the stomach contents of hake, but in a fresh condition, and it is probably to be placed among the adventitious contents which have been snatched up during the hake's struggles in the trawl. I have not so far seen a specimen which showed definite signs of digestion; hence, having in mind the extraordinary voracity and the catholic appetite of the hake, one must suppose that the protective device of a luminous gland fulfils its purpose efficiently.

I wish to acknowledge my thanks to Professor Newton Harvey for his help and correspondence, to Dr. E. J. Allen, F.R.S., Dr. Orton, Mr. Ford, and Mr. Russell for help and suggestions.

#### SUMMARY.

A luminous organ of a hitherto undescribed type has been found in a Macrurid fish. This organ is described in the present paper. It consists essentially of an epithelium for the secretion of luminous substance, which has been thrown into long folds and wholly invaginated to form a gland. This gland is bound in connective tissue and has a compact appearance, and is furnished with supporting tissue internally. The duct is a flat and wide passage, continuous with the gland, which opens to the exterior about the anus in such a way as to surround the lower part of the rectum. The gland lies in the thickness of the body-wall forward of the rectum and between and behind the pelvic fins.

The nature of the secretion is discussed and some experiments described. The luminescence appears to be due not to bacteria living as guests within the tissues of the fish, as has been shown for other species, but is essentially due to the well-known reaction wherein a substance *luciferin* is burnt to *oxyluciferin* in presence of the ferment *luciferase*, with emission of cold light.

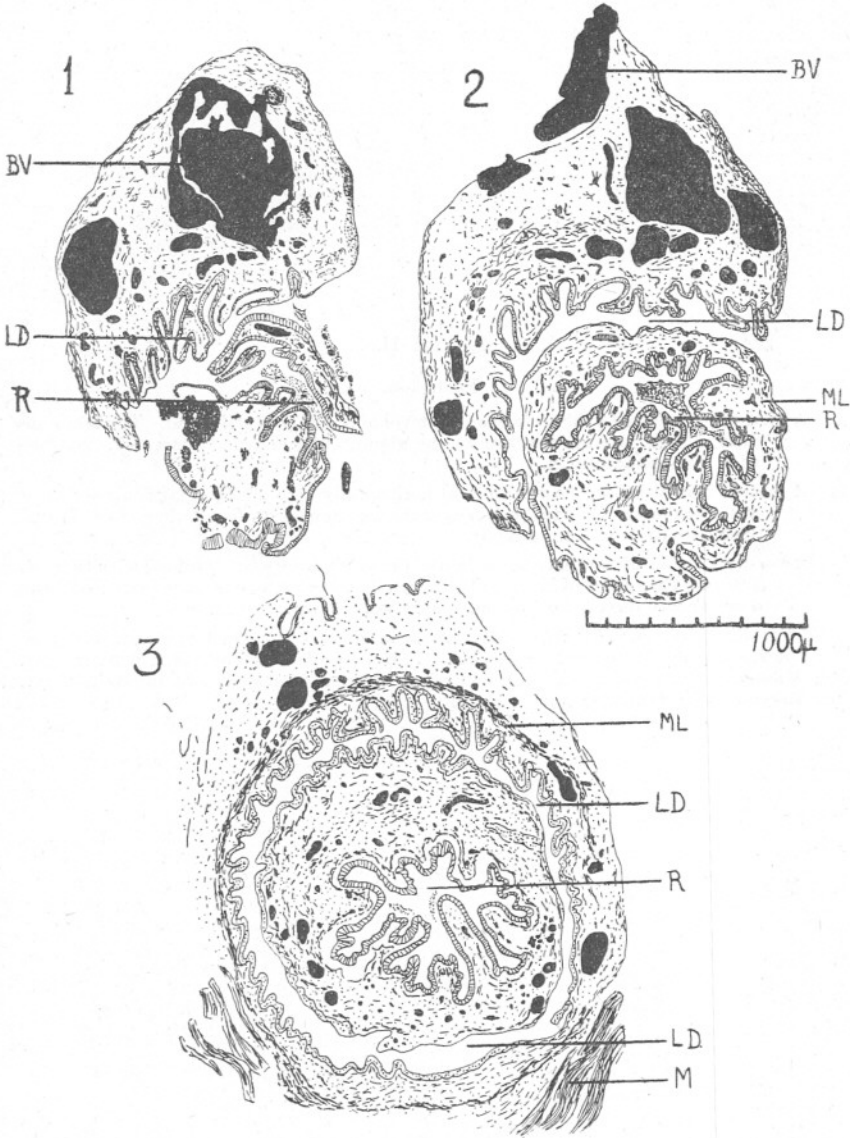
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## PLATE I.

## FIGS. 1-3.

1. A section through the papilla near the anus. The wall of the papilla cut obliquely, Luminous duct and rectum shown incomplete. Numerous blood sinuses.
  2. A section transverse to the rectum at a higher level in the papilla.
  3. A section transverse to the rectum at the level of the body-wall. The luminous duct completely surrounds the rectum.
- B.V. : Blood sinus. L.D. : Luminous duct. M.L. : Melanophore sheath. M. : Muscle.  
R. : Rectum. Stained with iron-hæmotoxylin.



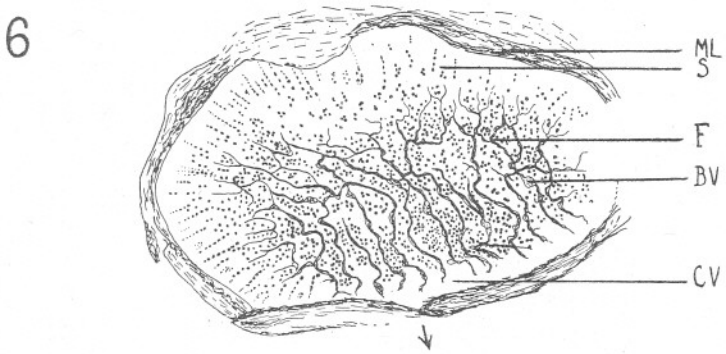
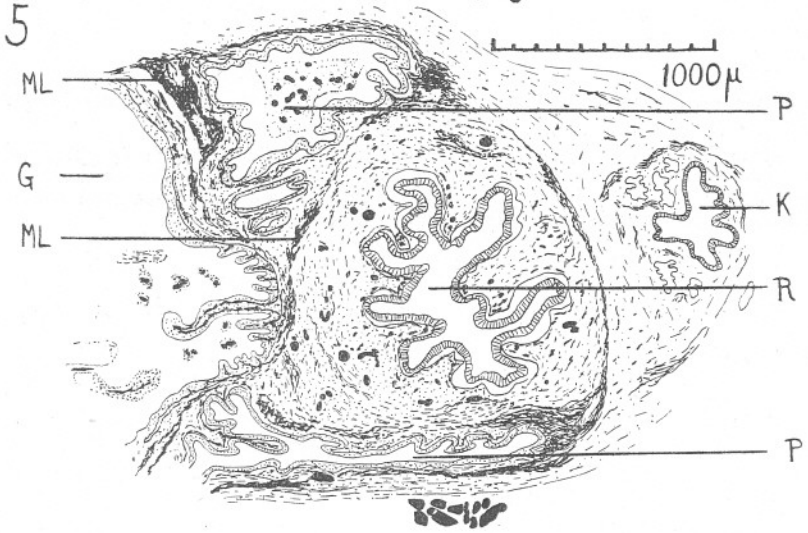
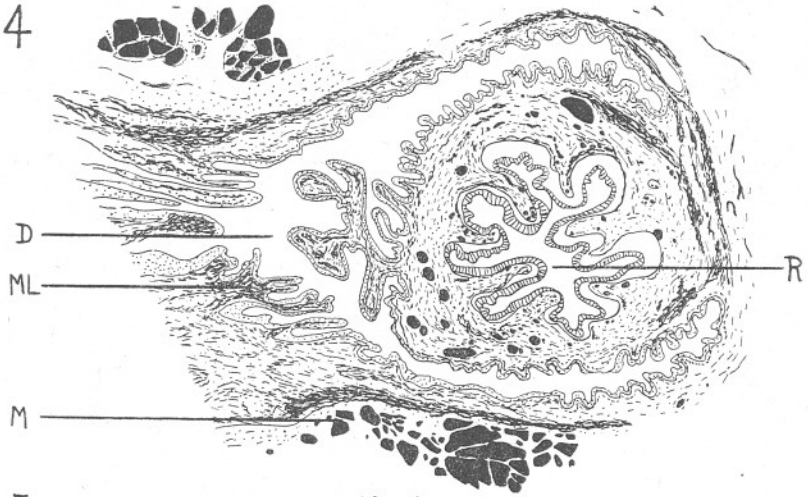
DEL. C. F. H.

## PLATE II.

FIGS. 4-6.

4. A section transverse to the rectum at the level of the base of the gland. The luminous duct is seen running forward to the gland, cut somewhat obliquely. Stained with iron-hæmotoxylin.
5. A section transverse to the rectum and horizontally through the gland, a portion of which is shown. The two pouches of the duct are seen. The kidney duct shown. Stained with iron-hæmotoxylin.
6. A low-power view of a transverse section of the luminous gland. Stained with thionin. The radiating lines of lumps of secretion are seen; the melanophore sheath and downwardly directed collecting spaces well shown.

B.V.: Blood vessel. C.V.: Collecting space in gland. D.: Duct of luminous organ.  
F.: Folds of tissue of gland cut longitudinally. G.: Luminous gland. K.: Kidney duct.  
M.: Muscle of body-wall. M.L.: Melanophore layers. P.: Pouch of luminous duct.  
R.: Rectum. S.: Secreting part of gland.



## PLATE III.

A somewhat diagrammatic sagittal longitudinal section of the gland and duct, slightly to one side of the middle line.

B.V.: Blood vessel. C.: Coelome. C.T.: Connective tissue. C.V.: Collecting space in gland. D.: Duct of luminous organ. L1 and L2.: Lens-like bodies associated with organ. M.: Muscle layer cut transversely. M.L.: Melanophore layers. R.: Rectum. S.: Secreting part of gland. Stained with iron-hæmatoxylin.



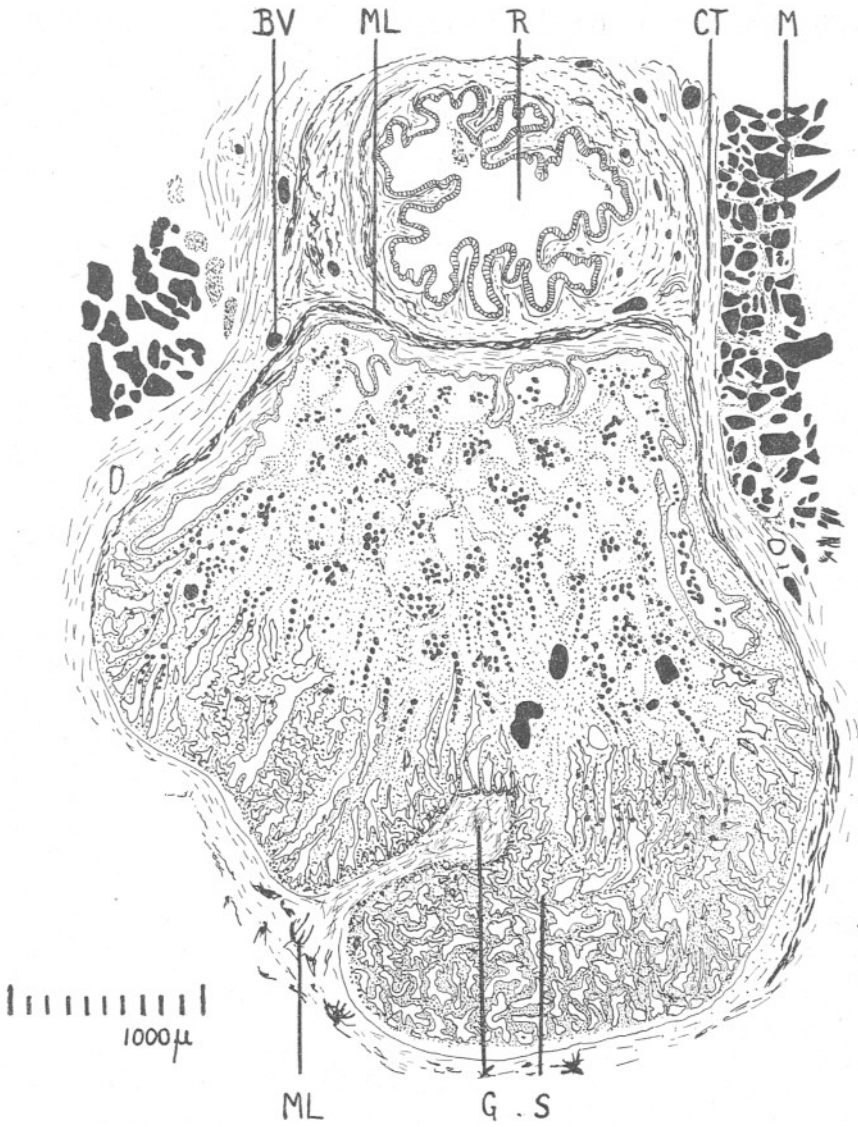
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## PLATE IV.

A horizontal section through the gland, cutting the rectum transversely

B.V. : Blood vessels. C.T. : Connective tissue. G. : Strut of connective tissue forming a skeletal support. M. : Muscle of body-wall. M.L. : Melanophores. R. : Rectum. S. : Secreting part of gland. Stained with iron-hæmatoxylin.



DEL. C. F. H.

## The Hydrogen Ion Concentration in the Gut of certain Lamellibranchs and Gastropods.

By

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So far as I am aware, no accurate estimations of the hydrogen ion concentration in the alimentary tract of the Mollusca have been made; we only know that the fluid in the gut usually gives an acid reaction to litmus and similar indicators. In this paper I have estimated the pH of the various regions of the gut in a number of typical Lamellibranchs and Gastropods. Clarke and Lubs' indicators were used, being mixed with the fluid or tissue to be tested on a white plate and the colours compared with those of the same indicators added to drops of standard solutions of known pH value; the usual corrections for salt error were made. I have also attempted to determine, as far as possible, the causes of the prevailing acidity of the gut, and also some of its effects, particularly on the permanence of the style and on the action of the cilia of the gut.

This research was carried out at the Plymouth Laboratory during the winter of 1924-25, while I was holding a Carnegie Research Scholarship of the University of Edinburgh. I wish to thank the British Association, the University of London, and the Royal Microscopical Society for granting me the use of their tables for various periods, and the Director and staff of the Laboratory for their kindness and help.

### LAMELLIBRANCHIA.

#### HYDROGEN ION CONCENTRATION IN THE GUT.

Three species were chosen for examination on account of their large size, namely, *Pecten maximus*, *Mya arenaria* and *Ensis siliqua*. Table I shows the pH value of the contents of the gut, of the crystalline style and of the tissue of the digestive gland in these animals.

The stomach is in all cases the most acid region of the gut (in *Ensis* the cesophagus gives the same value, but this is probably due to fluid from the stomach), after which the pH rises along the mid-gut and rectum. *The same results were obtained whether the animals examined were freshly fed or starved*, which shows that there is no outpouring of acid secretion in response to the entrance of food into the gut.

The most acid substance in the gut is the style, and this is responsible for the acid reaction throughout the alimentary tract. Hitherto the digestive gland has been regarded as the source of the acidity of the gut in the Lamellibranchs, an opinion which I held myself at the time of my earlier work on *Mya* (Yonge (12)); but, as a result of further work and investigation of literature, I have been led to the conclusion that

TABLE I.

Animal.	Eso- phagus.	Stomach.	Style.	Digestive gland.	Mid-gut.	Rectum.
range	6.0-6.8	5.4-5.8	5.4	5.5-5.8	5.8-6.2	6.4-6.8
<i>Pecten</i> —						
average	6.4	5.6	5.4	5.65	6.0	6.6
range	6.6	5.6-6.0	4.4-4.5	5.6-5.8	6.0-6.4	6.8-7.0
<i>Mya</i> —						
average	6.6	5.8	4.45	5.7	6.2	6.9
range	5.6-5.8	5.6-5.8	4.6	5.6-5.8	5.8-6.0	6.4-6.6
<i>Ensis</i> —						
average	5.7	5.7	4.6	5.7	5.9	6.5

the digestive gland in the Lamellibranchs (with the possible exception of the Septibranchiata, which I have not as yet been able to examine) is purely an absorptive, and *not* a secretory, organ.

If the digestive gland does not secrete, and since there are no salivary glands, the origin of the acidity of the gut must be the style. This is secreted in a special groove in the mid-gut in *Pecten*, and in a separate cæcum in *Mya* and *Ensis*. In order to determine whether the pH of the gut rose in their absence, the styles were removed from eight living *Mya* (by the method used by Edmondson (4)), which were then replaced in sea water. Four of the animals recovered from the operation, and, after five days, these were opened and the pH of their guts estimated, with the results shown in Table II.

TABLE II.

<i>Mya</i> number :—	1	2	3	4	Average.
Œsophagus . . .	6.8	6.4	6.6	6.9	6.67
Stomach . . .	6.4	6.4	6.6	6.9	6.625
Style Sac . . .	5.8	6.1	5.8	6.0	5.9
Digestive Gland . . .	5.6	5.8	5.7	5.7	5.7
Mid-Gut . . .	6.4	6.4	6.2	6.4	6.45
Rectum . . .	Too little fluid to estimate.				

Whereas the average values for the œsophagus and the digestive gland remained practically unchanged, the pH of the stomach showed a rise of 0.825, and that of the mid-gut a rise of 0.25. In no case was there any sign of a new style—which was hardly to be expected since Edmondson found that *Mya* takes seventy-four days completely to regenerate the style after it has been removed—but such fluid as was present in the empty style sac had a pH of 5.9, the result, presumably, of the acid secretion of the epithelium. The average pH of the sea water in the mantle cavities of the four animals was 7.1, and the reduction from this to the 6.625 of the stomach can be accounted for entirely by the entrance of the fluid from the style sac and by a certain excretion of CO<sub>2</sub> from the

TABLE III.

No.	Condition of Style.	pH in Stomach.	pH in Mantle Cavity.
1.	Absent	6.5	7.2
2.	„	6.8	7.2
3.	„	6.7	7.2
4.	„	6.4	7.2
5.	„	6.8	7.2
6.	„	6.6	7.2
7.	„	6.7	7.2
8.	Traces	6.2	7.1
9.	Absent	6.6	7.0
10.	„	6.4	7.1
11.	„	6.5	7.1
12.	Traces	6.3	7.3
		—	—
		Average=6.54	7.17

walls of the gut, which possibly possesses a slight respiratory function. The presence of CO<sub>2</sub> is frequently indicated by a rise in pH after exposure to the air for a few minutes. There is no need, therefore, to postulate the presence of an acid secretion from the digestive gland, although there is an excretion into the gut of the indigestible remnants of intracellular digestion which probably have an acid reaction, and may influence the pH of the gut to a slight extent.

It is well known that, under certain circumstances, the style is very readily dissolved and reformed in many Lamellibranchs in which it lies free in the mid-gut and is not enclosed in a separate cæcum. If the style is, indeed, the source of the acidity of the gut, it would naturally be expected that the pH of the stomach would be higher in animals of this type when the style is absent than when it is present. Accordingly,

experiments were performed on *Mytilus edulis*, *Tapes pullastra*, and *Pecten maximus* to discover whether this is the case.

Twenty-five healthy *Mytilus*, taken straight from the sea, were opened and the pH of the stomach contents determined. The average value for the twenty-five came to 6.08, and the average for the pH of the water in the mantle cavity to 7.4. A firm, fully developed style was present in every one of these animals. Since it has frequently been observed that in *Mytilus* the style dissolves when the animal is kept out of water, twelve specimens were placed in a cool dry place for four days, and were then opened and the condition of the style and the pH of the contents of the stomach and of the mantle cavity determined, with the results shown in Table III.

Although the twelve animals remained perfectly healthy, the style was absent in all but two cases, when slight traces were still present. The average value for the pH of the fluid in the mantle cavity was 7.17, a fall of 0.23, yet the average for the stomach had risen by 0.46 to 6.54.

Berkeley (2) found that the styles of *Saxidomus giganteus* and *Paphia staminea* disappeared when these animals were kept under anaerobic conditions, but reformed when they were returned to normal aerobic conditions. Accordingly, seven *Mytilus* were kept for six days in a sealed jar containing sea water from which the oxygen had largely been withdrawn in vacuo, and a similar number in boiled sea water. Both these jars were placed in the tanks of circulating water to keep them under normal conditions of temperature. Table IV gives the results of the two experiments.

TABLE IV.

Six days in Boiled Sea Water.			Six days in Deoxygenated Sea Water.		
No.	Style.	pH in Stomach.	No.	Style.	pH in Stomach.
1.	Absent	6.8	1.	Absent	6.6
2.	„	6.8	2.	„	6.4
3.	„	6.6	3.	„	6.5
4.	„	6.5	4.	„	6.2
5.	„	6.4	5.	„	6.3
6.	„	6.3	6.	Traces	6.0
7.	Traces	6.1	7.	„	6.1

The style was absent in eleven out of the fourteen animals, and the average value for the pH in the stomach in these animals was 6.49 as compared with 6.07 for the three cases in which the style was still present.

The most satisfactory method for ensuring the dissolution of the style was suggested to me by Dr. J. H. Orton, and consisted of clamping the

shell valves together and then replacing the animals in the tanks. Fifteen animals were treated in this way and left for seven days. Ten of these contained no style, and had an average value for the pH of the stomach of 6.49 and for the water in the mantle cavity of 7.2. Altogether, therefore, the average value for the pH of the fluid in the stomach in the thirty-one *Mytilus* which contained no style came to 6.53 and for the fluid in the mantle cavity to 7.2, compared with 6.08 and 7.4 respectively in the case of the fresh animals which all contained styles. Thus, in spite of the fact that the pH of the mantle cavity dropped by 0.2, the pH in the stomach rose by 0.45.

Similar experiments were carried out with *Tapes pullastra*, seven animals being clamped for seven days, and the results compared with those obtained from seven unclamped animals which had been lying side by side in the tanks with them. Table V shows the results obtained.

TABLE V.

Not Clamped.			Clamped for Seven Days.		
No.	Style.	pH in Stomach.	No.	Style.	pH in Stomach.
1.	Present	6.2	1.	Absent	6.9
2.	„	6.2	2.	„	6.9
3.	„	6.2	3.	„	6.6
4.	„	5.9	4.	„	6.7
5.	„	5.8	5.	„	6.7
6.	„	5.8	6.	„	6.7
7.	„	6.0	7.	„	6.6
Average = 6.01			Average = 6.73		

The results of this experiment are still more convincing. No trace of a style was present in any of the clamped animals, and the difference in the average values of the pH of the contents of the stomach in the two series amounted to no less than 0.72.

*Pecten maximus* was treated in the same way; but, though similar results—disappearance of the style and an increase in the pH of the contents of the stomach—were obtained in several cases, these animals are not at all suited to this treatment and many died.

From the results of the foregoing experiments, there can be little doubt that the acidity of the gut in the Lamellibranchs is due to the presence of the crystalline style since, when that is absent, there is a pronounced increase in the pH of the gut, even though the pH of the water in the mantle cavity has fallen.

## PERMANENCE OF THE STYLE.

The cause of the rapid dissolution of the style has always been a disputed point. Hazay (7) and Haseloff (6) based their theory that the style is a reserve of food upon the observed fact that it was absent in animals that had been starved, but was reformed when they were fed. Allen (1) and Dakin (3) state that the styles of Anodonta and Pecten are absent or present under the same conditions. Nelson (10) is also of the opinion that the "style is a structure intimately connected with the feeding activities of the mollusc." . . . "Absence of food or inactivity of the animal due to cold or adverse conditions bring about a gradual dissolution of the style." Orton (11) found by experiment that the style of *Ostrea* is dissolved when the animal is removed from water; but that the speed with which it dissolves, and also with which it is reformed when it is returned to water, depends upon the physical condition of the animal, of which the colour and condition of the "liver" are the best criterion. As long as the animals were in good condition starvation had *no* effect on the presence of the style. Berkeley (2) found that the presence of the style was quite independent of the food supply, but that it depended on the supply of oxygen, and, since he found an oxidase in the style substance, he advances the opinion that the style is a reserve of oxidase, which is used up when the animal experiences anaerobic conditions.

In my earlier paper, in order to account for the fact that the style is only dissolved in those species in which it lies free in the mid-gut, I suggested that it was dissolved by the proteolytic enzyme secreted by the digestive gland. In view of further, and contradictory, evidence, I have abandoned this theory; but, as I had also found that the style dissolves more easily in an alkaline than an acid medium, I thought it possible that valuable information might be obtained by extending these experiments. Accordingly, styles were extracted from *Ensis*, *Mya*, *Pecten* and *Mytilus* (i.e. two animals in which the style lies in a separate cæcum, and two in which it lies free in the mid-gut), and, after having been measured, they were placed in tubes containing about 10 c.c. of standard buffer solutions, a little toluol being added to prevent decomposition. The time which the styles took to dissolve was noted, the results being given in Table VI.

The results show that the styles are dissolved rapidly in alkaline media, but more and more slowly as the medium becomes more acid, until at a certain point they cease to be dissolved. The substance of the style is a protein of a globulin nature, and so an amphoteric substance with an isoelectric point, and, judging by the above results, it appears to be soluble above the isoelectric point, but insoluble below it. This, apparently, is not the same for all four styles, those of *Ensis* and *Mya*



having their isoelectric point at about 4.4 and 4.2 respectively, while in the case of *Pecten* and *Mytilus* it is decidedly lower, at about 3.6 in each. There is also, it will be noted, a difference in the pH of the style in the two types, those of *Ensis* and *Mya* being 4.45 and 4.6 respectively, and those of *Pecten* and *Mytilus* being both 5.4. Presumably these differences in physical properties are a result of the different conditions under which the two types of style are secreted.

The important point to be noted is that the style or, in the case of those which lie in a separate cæcum, the head of the style is normally surrounded by a fluid whose pH—at lowest 5.6—is always high enough to enable it to dissolve the style. The style, therefore, can only be maintained so long as new substance is secreted and added to the hinder end

TABLE VI.

pH	<i>Mya</i> .		<i>Ensis</i> .		<i>Pecten</i> .		<i>Mytilus</i> .	
	Length of Style.	Time to dissolve.	Length of Style.	Time to dissolve.	Length of Style.	Time to dissolve.	Length of Style.	Time to dissolve.
9.6	4.3 cm.	12 hrs.	2.6 cm.	1 hr.	4.6 cm.	$\frac{3}{4}$ hr.	3.6 cm.	$\frac{3}{4}$ hr.
8.0	4.4 cm.	21 hrs.	3.0 cm.	14 hrs.	4.6 cm.	$2\frac{1}{2}$ hrs.	3.0 cm.	$\frac{3}{4}$ hr.
7.2	3.8 cm.	2 days.	3.3 cm.	17 hrs.	3.6 cm.	$2\frac{3}{4}$ hrs.	3.1 cm.	$\frac{1}{2}$ hr.
6.0	4.6 cm.	2 days.	3.1 cm.	25 hrs.	4.8 cm.	23 hrs.	3.5 cm.	$7\frac{1}{4}$ hrs.
5.4	4.5 cm.	3 days.	2.8 cm.	4 days.	5.0 cm.	27 hrs.	3.3 cm.	22 hrs.
5.0	4.8 cm.	6 days.	2.6 cm.	4 days.	5.2 cm.	53 hrs.	3.6 cm.	26 hrs.
4.4	3.8 cm.	19 days.	2.3 cm.	Not dis.	4.7 cm.	70 hrs.	2.8 cm.	25 hrs.
4.2	6.0 cm.	Not dis.	2.5 cm.	"	5.3 cm.	74 hrs.	2.6 cm.	30 hrs.
4.0	4.5 cm.	"	1.8 cm.	"	5.1 cm.	75 hrs.	2.6 cm.	29 hrs.
3.6	4.4 cm.	"	2.5 cm.	"	5.1 cm.	Not dis.	3.5 cm.	Not dis.
3.0	4.3 cm.	"	2.2 cm.	"	5.0 cm.	"	2.9 cm.	"
2.2	5.1 cm.	"	2.3 cm.	"	3.6 cm.	"	3.0 cm.	"

at least as rapidly as the head is dissolved away by the fluid in the stomach. If, for any reason, the vital activities of the animal are reduced, then the style will be softened and finally dissolved.

This explanation will account for all the known facts. When animals are kept out of water, or under anaerobic conditions, or clamped, or for any other reason are in bad condition, their vital activities will be reduced, one result being that secretion of the style will either be greatly diminished or cease altogether. Wherever the style lies in a separate cæcum it will be protected from the action of the fluid in the stomach, so that at most only its head will be dissolved away. Edmondson (4) found that *Mya* can live for two weeks out of water, and that at the end of that period only the head of the style shows any sign of dissolution.

The style is dissolved when the animal experiences anaerobic conditions not, as Berkeley suggests, especially to set free the oxidase it

contains, but because of the diminution in the secretion of the style substance. (Incidentally, I may say that, by testing with tincture of guaiacum and pyrogallol, I have found an oxidase in the styles of all four species.) Moreover, if the oxidase was of the great importance which Berkeley suggests, surely the style would be larger and more readily dissolved in animals which are liable to experience anaerobic conditions, e.g. *Mytilus* or *Mya*, than in those, like *Pecten*, which are never exposed to these conditions. There is no such correlation; the setting free of the oxidase is one of the consequences, not the cause, of the dissolution of the style.

The style never disappears during starvation so long as the animals are kept healthy and the water well aerated. Orton (11) and Berkeley both found this, and I have myself kept twenty-four *Mytilus* for three weeks in filtered sea water, through which a stream of air was passed, and found styles in all of them at the end of that period. On the other hand, animals which have an ample supply of food, but are in poor condition, have either no style or else only slight traces. Orton states that ". . . oysters in a weak condition are either without a style or very soon lose it on being taken out of water and reform it with difficulty on being replaced in water." This is exactly what would be expected if the rate of secretion of the style is lower in unhealthy, than in healthy, animals.

Under normal conditions, the head of the style will be continually dissolving—which is essential in order that the contained enzymes may be set free—while at the same time the secretion of new substance behind will maintain the style at full size—which is also essential since it must press firmly against the gastric shield upon which it revolves. The style, therefore, is only maintained, and the digestive system can only function properly, as a result of a balance between the rate of its secretion by the style bearing epithelium and the rate of its dissolution by the less acid contents of the stomach.\*

#### RELATION BETWEEN THE PH OF THE GUT AND THE WORKING OF ITS CILIA.

Gray (5), working on the gill of *Mytilus*, found that the cilia quickly came to rest in solutions the pH of which was below about 6.0. Now, since the cilia of the stomach, style sac, and possibly of the mid-gut in all the Lamellibranchs here studied, must normally function in a pH

\* Martin (1923, Bot. Gaz., LXXV, p. 143) in a paper on the food of the oyster, states that "The development of a crystalline style is usually correlated with the taking of food, but this structure may appear in the complete absence of food, possibly as a response to the act of siphoning." Since only healthy animals siphon vigorously, this statement fits in perfectly with my findings.



below this, it follows that they must have a greater tolerance of the presence of hydrogen ions than those of the gills. In order to test this experimentally, small pieces (not more than a few mm. in diameter) of ciliated epithelium were removed from the gill, œsophagus, stomach, style sac, mid-gut and rectum of *Mya*, and placed altogether in outside sea water (normal pH 7.8), to which was added the requisite amounts of .1 N HCl or .1 N NaOH needed to make up a series of solutions of varying pH. In every case at least 80 c.c. of fluid was employed. The results of these experiments are given in Table VII.

It will be seen that where the cilia function for any length of time in any fluid they tend to bring the pH back to that of sea water. Thus water of pH 9.4 was reduced to 8.8 after twenty-two hours, and that of 4.8 raised to 5.8. It is impossible, therefore, to state at exactly what pH the cilia can function unless the pH at the end of the experiment, as well as at the beginning, is determined. In this case comparative results are more important than absolute results, and in Table VIII the six sets of cilia are arranged in order of their tolerance of the presence of hydrogen ions, and opposite each is shown the pH of the fluid which normally surrounds them.

TABLE VIII.

Cilia from :—	Minimum pH in which they can function.	Average pH of fluid normally round them.
1. Style Sac . . . . .	3.5-4.0	4.45
2. Stomach . . . . .	4.0	5.8
3. Mid-gut . . . . .	4.4-4.8	6.2
4. Œsophagus . . . . .	4.4-4.8	6.6
5. Rectum . . . . .	4.4-4.8	6.9
6. Gill . . . . .	5.2-5.8	7.2

The comparison between the two sets of figures is very striking, and demonstrates clearly that the more acid the medium in which the cilia normally function, the greater is their tolerance of the presence of hydrogen ions. On the other hand, no difference in their tolerance of hydroxyl ions can be discerned, all six working equally well at pH 9.4.

## GASTROPODA.

### HYDROGEN ION CONCENTRATION IN THE GUT.

Unlike the Lamellibranchs, the Gastropods are not a homogeneous group with essentially the same method of feeding, and hence the same type of digestive apparatus, throughout. On the contrary, they include species which feed in the most diverse ways, and the consequent modifica-

tion in the development of the various regions of the alimentary system and its associated glands is very great.

I have investigated the pH in the gut of five representative types of Gastropods, namely, *Crepidula fornicata* (Streptoneura : ciliary feeder), *Patella vulgata* (Streptoneura : herbivorous), *Buccinum undatum* (Streptoneura : carnivorous), *Doris tuberculata* (Euthyneura : carnivorous), *Aplysia punctata* (Euthyneura : herbivorous). The results are shown in Table IX.

TABLE IX.

Crepidula.									
pH	Sal. glands.	Oesoph.	Stomach.	Dig. gland.	Style.	Mid-gut.	Rectum.		
Range	5.7-5.9	6.6-7.0	5.8-6.2	6.1-6.3	5.8	6.7-7.0	8.0-8.6		
Average	5.8	6.8	6.0	6.2	5.8	6.85	8.3		
Patella									
pH	Crop.	Sal. glands.	Stomach.	Dig. gland.	Mid-gut.	Rectum.			
Range	5.4-6.0	6.0-6.2	5.4-5.7	5.6-6.0	7.8-8.0	7.8-8.4			
Average	5.7	6.1	5.55	5.8	7.9	8.1			
Buccinum.									
pH	Pharynx.	Sal. glands.	Oesoph.	Stomach.	Dig. gland.	Rectum.			
Range	6.6-7.0	5.8-6.4	6.2-6.8	5.4-5.8	5.6-6.0	6.4-8.2			
Average	6.8	6.1	6.5	5.6	5.8	7.3			
Doris.									
pH	Fore-gut.	Sal. glands.	Stomach.	Dig. gland.	Rectum.				
Range	5.6-6.4	5.8-6.4	5.6-5.8	5.6-6.0	5.9-6.4				
Average	6.0	6.1	5.7	5.8	6.15				
Aplysia.									
pH	Pharynx.	Sal. glands.	Crop.	Gizzard.		Dig. gland.	Mid-gut.	Rectum.	
Range	5.5-5.8	5.8-6.4	4.4-4.6	4.4-5.0	5.0-5.4	5.4-5.8	5.8-6.0	7.4-7.8	7.8-8.6
Average	5.65	6.1	4.5	4.7	5.2	5.6	5.9	7.6	8.2

There is a general resemblance between the pH of the various regions of the gut in the five animals. The pH of the salivary glands and of the digestive gland is much the same in all, the latter also closely approximating to the pH of the digestive gland in the Lamellibranchs. The fore-gut or crop and the stomach are invariably the most acid regions of the gut. There are three possible causes of this acidity : (1) The salivary glands. (2) The digestive gland. (3) The style. I will discuss them separately.

1. *The Salivary Glands.* These are present in all five animals ; but in the case of *Doris* and *Aplysia*, where the digestive gland possesses secretory cells, they are reduced in size and probably correspondingly reduced in function, while in *Crepidula*, where the style is well developed, they are also small. In *Patella* and *Buccinum* they are large and important glands (in the latter and in all the carnivorous Gastropods belonging to the Streptoneura they secrete a powerful proteolytic enzyme), and, apart from the very feebly developed style in *Patella*, are responsible for the entire secretion into the gut, and so must be responsible for its acid reaction.

2. *The Digestive Gland.* Of the animals studied, only Doris and Aplysia possess secretory cells in the digestive gland. The acid content of the fore-gut may, therefore, have its principal source in the digestive gland, being passed forward from there by an antiperistaltic movement (the fore-gut in these two animals is free and very muscular). The fluid in the crop of Aplysia, especially, is so markedly acid and so plentiful that it seems impossible that the small salivary glands can alone be responsible for it.

3. *The Style.* Only in Crepidula is there a well-developed style, although Patella possesses the vestige of one. Mackintosh (9) has shown that in its origin, structure and function this style bears the closest resemblance to that of the Lamellibranchs. It does not lie in a separate cæcum, but in a groove in the mid-gut—like the styles of Pecten or Mytilus. It disappears after the animals have been out of water for a day or two, but is reformed when they are returned to sea water, exactly as in Mytilus. As in the Lamellibranchs, it is the most acid substance in the gut (pH 5·8), and in order to determine to what degree it is responsible for the acid reaction of the stomach, twelve animals were kept out of water for two days and then examined for the condition of the style and the pH of the stomach; twelve fresh animals were examined at the same time. The two series of results are shown in Table X.

TABLE X.

Fresh Crepidula.			Crepidula out of water 2 days.		
No.	Style.	pH in Stomach.	Style.	pH in Stomach.	
1.	Present	6·2	Absent	6·8	
2.	„	6·0	„	7·4	
3.	„	5·8	„	6·6	
4.	„	6·0	„	7·2	
5.	„	6·0	„	6·7	
6.	„	5·8	„	7·4	
7.	„	5·9	„	6·9	
8.	„	6·0	„	7·4	
9.	„	6·1	„	6·8	
10.	„	6·2	„	7·2	
11.	„	6·1	Traces	7·0	
12.	„	5·9	„	6·9	
		Average = 6·0			Average = 7·025

As a result of their two days out of water, ten of the animals contained no style and the other two only traces, while the average pH in the stomach had risen by 1·025. There can be no doubt that, though the

salivary glands may have some slight effect (though here again a rise in pH after exposure to the air shows that the presence of  $\text{CO}_2$  has to be considered), the acid reaction of the gut in *Crepidula* is primarily due to the dissolution of the head of the style.

The mid-gut and rectum in *Crepidula*, *Patella*, *Buccinum* and *Aplysia* have all a pH on the alkaline side. In every case there is a copious secretion of mucus in these regions, and this appears to be responsible for the sudden rise in the pH. In *Doris*, however, where alone the mid-gut is free from surrounding tissue and has muscular walls so that peristaltic action can easily be observed, little mucus is secreted and, as a result, the pH is practically the same as that of the stomach and fore-gut.

I have not been able to find any very significant differences between the pH of the gut in starved animals and those which have been fed. In *Aplysia* which has been feeding on *Ulva*, the pH of the crop and anterior gizzard are raised from 4.5 and 4.7 respectively to 5.3 and 5.4, the result, doubtless, of the dilution of the crop fluid with sea water. A *Buccinum* whose stomach was full of pieces of squid showed a slight fall in the pH of the oesophagus, from 6.5 to 6.2. Since Hirsch (8) has shown that in *Murex* (a closely related species with similar feeding habits and alimentary system) the entrance of food into the gut stimulates the salivary glands to secrete, this fall in pH in the case of *Buccinum* may be due to a similar increase in salivary secretion.

#### PERMANENCE OF THE STYLE IN CREPIDULA.

A similar experiment to that performed on the styles of *Mya*, *Ensis*, *Pecten* and *Mytilus* was carried out on the styles of *Crepidula*, by exposing them to solutions of varying pH and noting the time taken in dissolving. Details of this experiment are given in Table XI.

TABLE XI.

pH	9.6	8.0	7.2	6.0	5.4	5.0	4.4	4.0	3.6	3.0	2.2
Length of Style . . .	1.5	1.5	1.4	1.3	1.5	1.5	1.3	1.3	1.5	1.4	1.3
	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
Time for dissolution . . .	13	14	13	28	31	39	43	46	(not dissolved)		
	min.	min.	min.	min.	min.	min.	min.	min.			

The style of *Crepidula* resembles those of *Pecten* and *Mytilus* in its mode of origin—in a groove off the mid-gut—in its high pH (5.8), as compared with those of *Mya* and *Ensis* (4.45 and 4.6), and in the lowness of its isoelectric point which is between 3.6 and 4.0. All that has been said about the permanence of the style in Lamellibranchs applies with equal force to the style in the Gastropods.

## RELATION BETWEEN THE CILIA AND THE pH OF THE GUT.

Experiments similar to those carried out on the ciliated epithelia of the gut of *Mya*, were performed on the ciliated epithelia of *Buccinum* and *Doris*. Although it was found that they will function in a pH of about 5.0, no very significant differences in their tolerance of hydrogen ions were discovered. Since the range of pH in the guts of these animals (1.7 for *Buccinum*; 0.45 for *Doris*) is much less than that in the mantle cavity and gut of *Mya* (3.0), this is not surprising.

## SUMMARY.

1. In the Lamellibranchs, as typified by *Pecten maximus*, *Mya arenaria* and *Ensis siliqua*, the entire gut has an acid reaction, the stomach being the most acid region and the pH rising along the mid-gut and rectum.

2. The origin of the acidity of the gut lies in the style. This has a low pH (5.4 in *Pecten* and *Mytilus*, 4.6 in *Ensis* and 4.45 in *Mya*), and, after it has been artificially extracted from *Mya* or induced to disappear, by keeping the animals under abnormal conditions, in *Mytilus*, *Tapes* and *Pecten*, the pH of the stomach invariably rises (by as much as 0.825 in *Mya* and 0.72 in *Tapes*), although the pH in the mantle cavity has fallen.

3. The style, which dissolves rapidly in alkaline or weakly acid media, is not dissolved in fluids below a certain pH—4.4 for *Ensis*, 4.2 for *Mya*, 3.6 for *Pecten* and *Mytilus*.

4. The style is never absent, even though animals are starved, so long as they are kept under otherwise healthy conditions. The disappearance of the style under abnormal conditions is probably due to a lowering of the vital activities, which include the secretion of the style substance, and the consequent dissolution of the style by the less acid contents of the stomach.

5. The style is only maintained as a result of a balance between the rate of its secretion and the rate of its dissolution.

6. There is a well-marked correlation between the tolerance of the presence of hydrogen ions possessed by the cilia from the various regions of the gut and the degree of acidity of the fluid with which they are normally surrounded.

7. The pH of the gut in five Gastropods has been investigated. The fore-gut and stomach have invariably the lowest pH.

8. This acidity may be caused by the salivary glands (*Patella* and *Buccinum*), the digestive gland (*Doris* and *Aplysia*), or the style (*Crepidula*).



9. The mid-gut and rectum have a high pH, except in *Doris*, where there is little secretion of mucus, the gut being free and muscular.

10. The style of *Crepidula* has similar properties to those of the Lamellibranchs. It has a pH of 5.8, and is not dissolved in fluid of pH 3.6 or lower.

11. The cilia from the gut of *Buccinum* and *Doris* can function in a pH of 5.0, but there is little difference in the toleration of the various cilia to the presence of hydrogen ions.

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## Oxidation in Sea Water.

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With 3 Figures in the Text.

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Positions of stations referred to in the tables and text.

- L1, in Plymouth Sound close to Mallard Buoy.
- L2, 200 yards off western end of Plymouth Breakwater.
- L3, 50° 18' N., 4° 11' W.
- L4, 50° 15' N., 4° 13' W.
- L5, off Eddystone Rocks, 50° 11' N., 4° 18' W.
- L6, 50° 06' N., 4° 20' W.
- E1, 10 miles south of Eddystone, 50° 02' N., 4° 22' W.
- E2, 49° 27' N., 4° 42' W.
- E3, off Ushant, 48° 34' N., 5° 13' W.

DURING the course of an investigation of the factors which affect the life of marine organisms *in vitro*, attention was directed to the oxidation of organic matter in sea-water. When a typical, open sea, free-swimming organism such as *Calanus finmarchicus* was kept in a limited quantity of water, its length of life was shortened if bacterial action (putrefaction) was apparent in the water. This is the experience of many others.

The very potent effect of the bacteria is due, in part at all events, to the soluble products of putrefaction set free. If the sea-water to which a trace of putrefiable organic matter has been added, is allowed to stand until putrefaction is complete and the bacteria begin to die down, and then filtered through a porcelain candle, the filtrate retains some of the toxicity of the bacteria laden water. Part at least of the toxic products remain some days in air-saturated water without being oxidised to non-toxic substances. Sea-water, to which a little sugar has been added and which shows a faint cloudiness due to bacteria, is very decidedly less toxic to *Calanus* than sea-water rendered very faintly cloudy by the development of bacteria on added traces of peptone or other nitrogenous organic matter. The specific toxic action of traces of peptone itself, if any, cannot readily be determined, owing to inevitable contamination with bacteria on the *Calanus*. This suggests that the toxicity is largely due to nitrogenous products of putrefaction, some of which with-

stand oxidation for a considerable time. The growth of green algæ in a toxic water appears to destroy most of the toxic substances.

Preliminary experiments showed that the length of life of *Calanus* in vitro was not markedly affected by variations in hydrogen ion concentration, by pH between 8.2 and 7.4 (due to carbon dioxide), nor by variations in salinity between 34.2 and 37.6 parts per mille.

It is of interest to note that the smaller the volume of water, the greater is the rate of multiplication of bacteria in it (Whipple, G. C., 1901, *Technology Quarterly*, XIV, 21; and Prescott and Winslow, 1908, *Elements of Water Bacteriology*, Wiley and Sons, New York).

At this stage it was considered of interest to investigate the power possessed by sea-water to oxidise organic substances in solution, and to investigate the oxidation of the organic matter in sea-water by added hydrogen peroxide. The addition of peroxide is a recognised method of "purifying" sea-water for small aquaria and for sterilising sea-water for culturing diatoms (E. J. Allen and E. W. Nelson, 1910, "On the Artificial Culture of Marine Plankton Organisms," *Quart. Journ. Micro. Science*, Vol. 55, Part 2, p. 378).

#### DECOMPOSITION OF HYDROGEN PEROXIDE IN SEA-WATER.

It was found that water from the aquarium tanks, and from a position close to the rocks in Plymouth Sound, allowed added Hydrogen peroxide to break down only very slowly for an initial period of several days, after which the reaction proceeded more rapidly (Fig. 1). Both these waters were polluted to some extent. The aquarium water was contaminated, owing to intense colonisation with fish and invertebrates. The Sound water, which was obtained at low tide, was contaminated with sewage and other decomposing organic matter.

With surface water from offshore stations across the mouth of the Channel, the reaction proceeds slowly, in the same manner as with aquarium tank water, but not so slowly. With water taken from a depth the reaction was more or less rapid. Where vertical mixing occurs, owing to tidal movement of the water over an uneven bottom, as at Station E3, off Ushant, the difference is less marked (see Table I), and the surface water more active, owing to admixture with deeper water.

Samples were taken throughout more than one year in the Channel, and, in every case except in April and May, a very marked difference was found between the surface and the "deep" water near the bottom.

At the various stations in the North Sea from which samples were examined (three weeks after being obtained), there was no very marked difference between surface and "deep" water.

## VELOCITY OF REACTION.

The rate at which hydrogen peroxide decomposes in the deeper and more active water was found to be approximately proportional to the amount of hydrogen peroxide present at any moment, that is

$$\frac{1}{t} \log \frac{a}{a-x} = K$$

Where  $t$  is the time the reaction has been proceeding,  $a$  the initial concentration of  $H_2O_2$ ,  $x$  the amount of  $H_2O_2$  decomposed in time  $t$  and  $K$  the velocity constant.

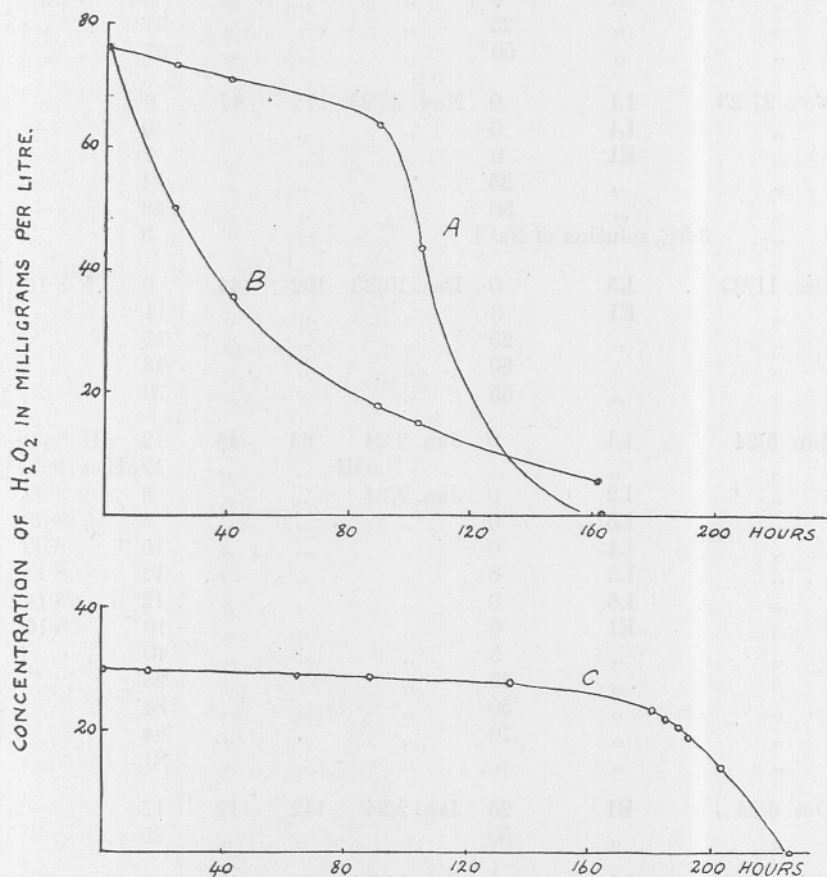


FIGURE I.

- Curve A. Decomposition of Hydrogen Peroxide in sea-water collected from Plymouth Sound close to Tinside Rocks at low water.  
 Curve B. Ditto in sea-water collected from Station E1, 22 miles S.W. of Plymouth, at a depth of 50 meters.  
 Curve C. Ditto in Aquarium tank water.  
 All at Room temperature.

TABLE I.

Date experiment commenced.	Position from which water sample was taken.	Depth in meters.	Date water sample was taken.	Approximate initial concentration of H <sub>2</sub> O <sub>2</sub> mg. per litre.	Reaction time in hours.	Percentage of H <sub>2</sub> O <sub>2</sub> broken down.	Hydrogen ion concentration when collected.
Nov. 5/23	L2	0	Oct. 15/23	19	90	29%	—
"	E1	50	"	"	"	76	—
	Aquarium tank			"	"	15	—
Nov. 14/23	L1	0	Nov. 7/23	27.5	42	9	8.11
"	E1	0	"	"	"	8	8.18
"	"	25	"	"	"	57	"
"	"	50	"	"	"	67	"
Nov. 27/23	L1	0	Nov. 23/23	175	47	6	—
"	L4	0	"	"	"	10	—
"	E1	0	"	"	"	7	—
"	"	25	"	"	"	14	—
"	"	50	"	"	"	48	—
"	3.5% solution of NaCl.		—	—	—	3	—
Dec. 11/23	L5	0	Dec. 10/23	192	44	6	8.16
"	E1	0	"	"	"	14	"
"	"	25	"	"	"	45	"
"	"	50	"	"	"	43	"
"	"	65	"	"	"	70	"
Jan. 5/24	L1	0	Jan. 2/24	63	46	12	pH 8.00
"	"	"	" + NaOH	"	"	12	pH ca. 8.3
"	L2	0	Jan. 2/24	"	"	6	8.02
"	L3	0	"	"	"	8	8.09
"	L4	0	"	"	"	15	8.09
"	L5	0	"	"	"	12	8.14
"	L6	0	"	"	"	12	8.14
"	E1	0	"	"	"	10	8.16
"	"	5	"	"	"	40	"
"	"	25	"	"	"	25	"
"	"	50	"	"	"	84	"
"	"	70	"	"	"	84	"
"	"	"	"	"	"	81	"
Oct. 6/24	E1	25	Jan. 2/24	142	19	17	—
"	"	50	"	"	"	25	—
Feb. 18/24	L1	0	Feb. 15/24	82	43	3	—
"	L4	0	"	"	"	7	—
"	E1	0	"	"	"	14	—
"	"	5	"	"	"	31	—
"	"	10	"	"	"	7	—
"	"	15	"	"	"	14	—
"	"	20	"	"	"	22	—

Date experiment commenced.	Position from which water sample was taken.	Depth in meters.	Date water sample was taken.	Approximate initial concentration of H <sub>2</sub> O <sub>2</sub> mg. per litre.	Reaction time in hours.	Percentage of H <sub>2</sub> O <sub>2</sub> broken down.	Hydrogen ion concentration when collected.
Feb. 18/24	E1	25	Feb. 15/24	82	43	22	—
"	"	50	"	"	"	28	—
"	"	70	"	"	"	41	—
"	E2	0	"	"	"	19	—
"	"	80	"	"	"	70	—
"	E3	0	"	"	"	20	—
"	"	50	"	"	"	26	—
"	"	105	"	"	"	31	—
Mar. 12/24	L4	0	Mar. 10/24	73	46	{ 20.5 17.8	—
"	"	45	"	"	"	{ 48 48	—
"	L6	0	"	"	"	{ 15 15	—
"	"	25	"	"	"	{ 35.6 37	—
"	"	60	"	"	"	{ 48 48	—
Mar. 18/24	L4	0	Mar. 17/24	96	22	{ 33 23	—
"	"	48	"	"	"	{ 40 44	—
April 11/24	E1	0	April 8/24	58	24	{ 14 17	—
"	E1	68	"	"	"	{ 10 17 14 17	—
May 22/24]	E1	0	May 20/24	110	24	{ 23 12	—
"	E1]	65	"	"	"	{ 14 12	—
Aug. 25/24	E1	0	"	88	22	4%*	—
"	E1	65	"	88	—	34%*	—
Aug. 9/24	E1	0	Aug. 7/24	86	19	{ 9 11 9	—
"	E1	67	"	"	"	{ 46 53 44	—

\* Note effect of keeping.

Date experiment commenced.	Position from which water sample was taken.	Depth in meters	Date water sample was taken.	Approximate initial concentration of $H_2O_2$ mg. per litre.	Reaction time in hours.	Percentage of $H_2O_2$ broken down.	Hydrogen ion concentration when collected.
Aug. 25/24	E1	0	Aug. 7/24	88	22	14	—
"	E1	67	"	"	"	0	—
"	E1	70	July 9/24	"	"	31	—
Aug. 26/24	L6	0	Aug. 25/24	88	17	13	—
"	L6	60	"	"	"	67	—
Sept. 4/24	E1	0	Sept. 3/24	80	14	18	—
"	E1	68	"	"	"	65	—
"	L1	0	"	"	"	6	—
Sept. 19/24	L1	0	Sept. 3/24	130	20	15	—
"	L4	50	"	"	"	72	—
"	{ Lat. 57° 51' N. Long. 6° 39' E.	0	Aug. 30/24	"	"	12	—
"	"	200	"	"	"	26	—
"	"	250	"	"	"	23	—
Sept. 22/24	{ Lat. 56° 28' N. Long. 2° 32' E.	0	Aug. 29/24	122	24	16½	—
"	"	60	"	"	"	23	—
"	{ Lat. 56° 05' N. Long. 1° 32' E.	0	"	"	"	18	—
"	"	70	"	"	"	18	—
"	{ Lat. 57° 10' N. Log. 4° 33' E.	0	"	"	"	18	—
"	"	50	"	"	"	18	—
"	{ Lat. 56° 49' N. Long. 3° 33' E.	0	"	"	"	16½	—
"	"	50	"	"	"	15	—
Oct. 3/24	L2	0	Oct. 1/24	139	22	1½ pH 8.24	—
"	L3	0	"	"	"	7	"
"	L4	0	"	"	"	8½	"
"	L4	40	"	"	"	26	"
"	L5	0	"	"	"	8½	"
"	E1	0	"	"	"	17½	"
"	"	5	"	"	"	13	"
"	"	15	"	"	"	11	"
"	"	25	"	"	"	14½	"
"	"	40	"	"	"	29	"
"	"	65	"	"	"	70	8.24
Oct. 10/24	E1	0	Oct. 1/24	139	20	1½	—
"	"	50	"	"	"	10	—
"	"	65	"	"	"	17	—

On the other hand, with aquarium tank water, with water close to the shore and with surface water, the velocity increases with the time the reaction has been proceeding. Hence, the greater the initial concentration of hydrogen peroxide, the greater is the proportion  $\frac{x}{a}$  decomposed after the lapse of a definite period of time. The experimental evidence is given later.

The rate increases with the temperature and with the alkalinity (OH concentration) of the water.

Changes take place in the water on storage. In no case has water from the aquarium tanks become similar to water from the surface offshore, and in no case has surface water from offshore become similar in activity to "deep" water. In all cases, except one, where a change has taken place during storage, "deep" water has lost activity. The one exception occurred in May, 1924, when water from close to the bottom at Station E1, initially only slightly active, became more active after a month's storage. This one instance might well have been an experimental error, since a minute trace of organic matter in the tube in which the experiment was carried out in May would have been sufficient to decrease the activity of the water. The influence of minute traces of organic substances on the reaction, which is discussed later, was not realised at the time, and no *extra* ordinary precautions were taken in the earlier experiments.

#### THE CATALYST ACTION UPON HYDROGEN PEROXIDE.

When a "deep" water is heated to 100° C., its activity in decomposing Hydrogen peroxide is not decreased, unless it is heated for long enough for a precipitate of magnesium hydroxide etc. to settle out. Then it completely loses its activity. If the precipitate is redissolved in the least quantity of dilute hydrochloric acid, its addition to a surface water increases the activity of that towards hydrogen peroxide, the hydroxide concentration having been adjusted to the original value.

The addition of a trace of ferric or ferrous salt (3 mg.  $\text{FeCl}_3$  per litre) causes a precipitate to be formed in sea-water, and when this occurs in the case of a deep water, the activity is lost, the catalyst being carried down with the precipitate.

The activity of a deep water is not affected by mercuric chloride (14 mg.  $\text{Hg Cl}_2$  per litre), but it is destroyed by the addition of a trace of soluble cyanide (6 mg. KCN per litre).

Although ferric ions do not occur in detectable quantity in sea-water, a minute trace of iron in solution can be detected after boiling with nitric acid. This ferric ion is more probably produced by the breakdown of organic iron compounds than by the oxidation of free ferrous ions, which



would not occur unoxidised in an alkaline air saturated solution. An analysis of water from the surface and from 68 meters at Station E1, collected in September, 1924, gave a value between 0.003 and 0.006 milligrams per litre of iron in solution.

Hæmatin can be added to sea-water without precipitation. It was

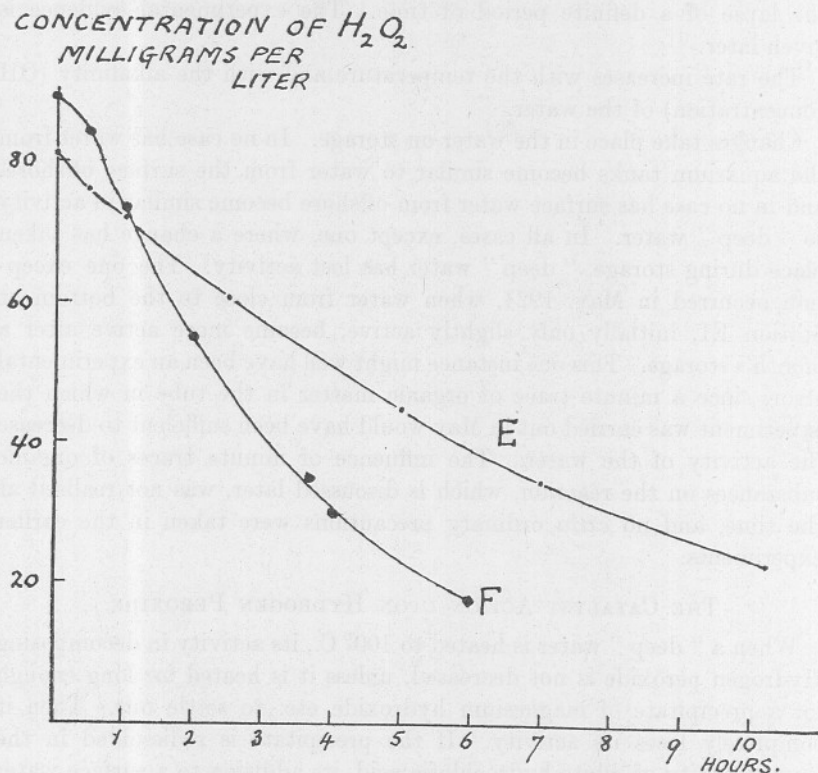


FIGURE 2.

Curve E. Decomposition of hydrogen peroxide in water collected from Station E1, 22 miles S.W. of Plymouth, at a depth of 70 meters, at a constant temperature of 20° C.

Curve F. Ditto in surface water collected at Station L4, 3½ miles off Rame Head, at a constant temperature of 30° C.

found that the addition of a trace of hæmatin increased the activity of a surface water towards hydrogen peroxide.

Cytochrome, occurring almost universally in animals and containing iron-pyrrol groups, behaves as a heat stable oxidase and catalase. (Keilin, *Proc. Roy. Soc.*, B. Vol. 98, p. 312, 1925.)

The inhibition by cyanide and the above considerations together point to the active catalytic agent being an organic compound of iron in solution in the sea-water.

It should be mentioned that no actual *proof* of the catalyst being an iron compound is afforded by its inhibition by cyanide. Among other heavy metals, copper salts catalyse the decomposition of hydrogen peroxide, and are known to be present in sea-water in very minute traces from the occurrence of copper in the hæmocyannin blood of many marine invertebrates; they form a complex cyanide which is not precipitated, like other copper salts, on the addition of a ferrocyanide. (Meyerhof, *Chemical Dynamics of Life Phenomena*. Philadelphia, 1925, p. 39.)

#### INHIBITION OF THE CATALYST IN SURFACE AND INSHORE WATERS.

Plymouth aquarium water, inshore and surface waters from the Channel contain iron in solution; there is no reason to suppose that such waters show little activity towards hydrogen peroxide on account of lack of iron.

This indicates that the activity of the catalyst is inhibited in such waters, assuming that the catalyst consists of a compound or compounds of iron in solution. In the case of aquarium water the inhibiting substances are in excess, since several days' action of dilute hydrogen peroxide at room temperature is necessary to decompose them, and to allow the catalyst to act upon the peroxide (Fig. 1). In the case of a surface offshore water the decomposition of added hydrogen peroxide proceeds from the start, the velocity of the reaction increasing as the inhibitor is oxidised and put out of action.

Fig. 2 (curve F) shows the rate of decomposition of hydrogen peroxide added to a surface water from Station L4,  $3\frac{1}{2}$  miles off Rame Head. The curve is not a logarithmic curve, as for a mono- or bimolecular reaction, but is "skewed." The initial concentration of Hydrogen peroxide was approximately 90 milligrams per litre, and the values of

$K_{30^{\circ}\text{C.}} = \frac{1}{t} \log \frac{a}{a-x}$  found after varying intervals were as follows:—

Reaction time (at 30° C.)	$\frac{a}{a-x}$	$K = \frac{1}{t} \log \frac{a}{a-x}$
0 h. 30 mins.	1.06	.051
1 h. 0 mins.	1.21	.083
2 h. 0 mins.	1.60	.102
3 h. 40 mins.	2.54	.109
4 h. 0 mins.	2.86	.114
6 h. 0 mins.	4.95	.116

The proportion of peroxide decomposed after a definite time by the same sample of water, was found to be greater, where the initial concentration of added peroxide was greater and more rapidly oxidised the inhibiting substances. Thus in an experiment made at room temperature

with the same water, after 47 hours the value  $\log \frac{a}{a-x}$  was found to be as follows :—

Approximate initial concentration of $H_2O_2$ in mg. per litre.	Value of $\log \frac{a}{a-x}$ after 48 hours.
134	·523
81	·389
54	·286

During the ensuing six hours the velocity of the reaction in all three cases was more nearly the same, the major portion of the inhibiting substances having been already oxidised.

Concentration of $H_2O_2$ after 47 hours ( $a-x$ )	After 53 hours ( $x_2$ )	Value $\log \frac{a-x}{x_2}$
41	31	·12
33	27	·09
29	24	·08

As previously stated, the velocity of the decomposition of peroxide in active deep water approximates to that of a unimolecular reaction. A sample collected at Station E1 on November 15, 1924, to which was added approximately 80 milligrams per litre of hydrogen peroxide, gave the following values for K at 20° C. :—

Reaction time T in hours.	$\frac{a}{a-x}$	$K = \frac{1}{T} \log \frac{a}{a-x}$
0·5	1·06	·051
1·0	1·13	·053
2·5	1·34	·051
5·0	1·80	·051
7·0	2·31	·052
10·23	3·45	·052

The proportion of peroxide decomposed after a definite time by this water was found to be practically the same irrespective of wide differences in the initial concentration of the peroxide. In an experiment conducted

at room temperature, the following values of  $\frac{a}{a-x}$  were found after the reaction had proceeded for 25 hours.

Approximate initial concentration of $H_2O_2$ .	$\log \frac{a}{a-x}$
133 mg. per litre	·24
66 " " "	·30
41 " " "	·25

When a slightly active, that is partially inhibited, surface water is mixed with an active deep water, the velocity of reaction with hydrogen peroxide was found to be rather less than the value proportional to the

relative amounts of the two waters in the mixture. The same quantity of peroxide (80 mg. per litre) was added to mixtures of surface water and water from 70 meters collected on January 2nd, 1924, at E1, and the concentration,  $a-x$ , determined after  $19\frac{1}{2}$  hours at room temperature.

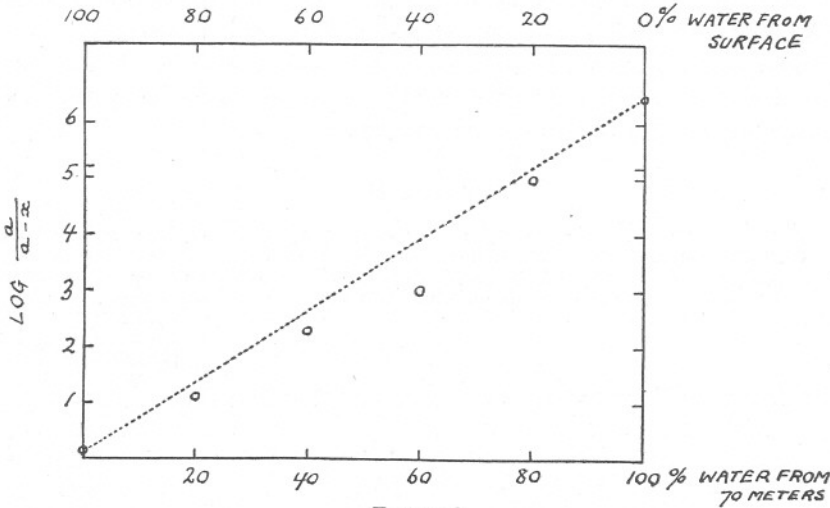


FIGURE 3.

Decomposition of hydrogen peroxide in mixtures of surface water and water from 70 meters at Station E1, after the same interval of time, starting with the same initial concentration of peroxide ( $a$ ).

Fig. 3 shows the relation of  $\log \frac{a}{a-x}$  to the relative amounts of the two waters in the mixture. The hydrogen ion concentration of the two waters was the same.

On the other hand, when aquarium tank water, containing an excess of inhibiting substances capable of practically stopping the reaction until oxidised by the peroxide, is mixed with an active deep water, the reaction velocity in the mixture is considerably less than the proportional value. The same quantity of peroxide was added to water from the surface at L3; to aquarium tank water brought to the same hydrogen ion concentration, to water from 65 meters at Station E1 collected on October 1st, 1924, and to mixtures. After 18 hours at room temperature the concentration  $a-x$  was determined.

$\log \frac{a}{a-x}$  (mean of duplicate determinations).

Surface water from L3	.054
Water from 68 meters at E1	.734
50% surface water L3 with 50% water from 68 meters at E1	.334
Aquarium tank water	.006
50% Aquarium tank water, 50% water from 68 meters at E1	.186

The addition of 50% surface water from L3 has reduced the velocity in deep water rather more than the proportional amount (.334 against .394), while the addition of 50% aquarium tank water has reduced the velocity considerably below the proportional amount (.186 against .370).

With regard to the nature of the inhibiting substances occurring in the sea-waters it is noteworthy that aquarium tank water and inshore waters contain a much larger amount of organic matter in solution than open sea-water, as shown by the quantity of alkaline potassium permanganate solution they are capable of reducing.

TABLE II.

Quantities of 100 c.c. of sea-water, filtered through a porcelain candle, were boiled for 10 minutes with 10 c.c. of a solution consisting of 0.395 gms. per litre of potassium permanganate in 10% sodium hydroxide solution, cooled, acidified, and backtitrated with sodium thio-sulphate solution after the addition of potassium iodide.

	Milligrams per litre of Oxygen consumed in oxidising contained organic matter.
Surface water from Station E1, 22 miles S.W. of Plymouth, collected 18.12.22	0.3 0.22 0.35
Surface water from 22 miles S.W. of Plymouth, collected 16.1.23	0.52
Surface water from close to Plymouth Breakwater, 1 hour before low water, collected 16.1.23	0.52.
Surface water from 150 yards offshore S. of Tinside in Plymouth Sound, collected 10.1.23, 1¼ hours before low water	0.83
Surface water collected at Saltash, 18.1.23, ½ hour before low water	0.97 0.98
Surface water collected close to rocks near Tinside in Ply- mouth Sound at low water, 4.1.23	1.09
Aquarium tank water, 4.1.23	1.77
Aquarium tank water, 16.1.23	1.96
Aquarium tank water, 16.1.23	2.09

Atkins (*Journal Marine Biol. Assoc.*, Vol. XII, p. 772, 1922) has shown that the upper layers of open sea-water turn more acid on standing, owing to bacterial action, thus proving that they contain more dissolved organic matter than the "deep" water.

Surface water from well offshore was allowed to stand in a sterilised test tube with the top covered by an inverted tube in order to keep out

dust. After five months there was a well-marked scum consisting of short rod-shaped bacteria in a gelatinous mass round the meniscus.

Two glass stoppered bottles were sterilised and 100 c.c. of surface water from Station E1 was filled into each, together with 1 milligram of hydrogen peroxide in solution. Paper was tied over the stoppers to keep out dust particles. After three months there was a considerable growth of bacteria in each bottle, quite obvious to the naked eye. Similar treatment of water from the aquarium tanks gave rise to a gelatinous mass of bacteria several cubic centimetres in volume.

Sea-water, even from well out to sea, contains sufficient dissolved organic matter to permit the growth of a bacterial fauna, and such develops when the water is kept in a small vessel.

It appears from the following experiment that water from the surface contains more putrefactive bacteria than water from a depth. A series of test tubes were partly filled with 10 c.c. of a 0.02 per cent solution of Wittes peptone in sea-water. To one of these was added 1 c.c. of aquarium tank water, and all were steam sterilised. To each tube, the control excepted, was added 1 c.c. of one of the following sea-waters:—

Aquarium tank water.  
 Surface water from L1.  
 Surface " " L3.  
 Surface " " E1.  
 Water at 25 meters from E1.  
 Water at 70 " " "

After 48 hours the control tube, to which the aquarium tank water had been added previous to sterilisation, showed no opalescence due to the growth of bacteria. The other tubes showed a growth of bacteria in the order given above, most marked in the tube with aquarium tank water added, and least in the one with water from 70 meters at E1. The three surface waters showed about equal growth. The water from 25 meters at E1 fell intermediate between surface waters and water from 70 meters.

Experiments have shown that the addition of traces of the following soluble organic substances very materially reduce the activity of "deep" water in decomposing  $H_2O_2$ .

Gelatin . . .	5 mg. per litre.
Asparagin . . .	1 " " "
Tartaric acid . . .	5 " " "
Ethylamine . . .	2-3 " " "
Glycin . . .	2 " " "
Tyrosin . . .	3 " " "

With regard to the oxidation of the inhibiting substances by hydrogen peroxide deduced from the increase in the velocity of decomposition of peroxide in surface or inshore water, Dakin found that amino and fatty acids were oxidised by hydrogen peroxide in the presence of iron salts. (*J. Biol. Chem.*, 1908, 4, pp. 63, 77, 227, also 1909, 5, p. 409). Later, Warburg (*Biochem. Zeitschr.*, 136, p. 266, 1923) found that amino acids were oxidised by peroxide without the presence of iron.

That aquarium tank water contains the catalyst is indicated by the fact that after boiling with NaOH and redissolving the precipitate, it becomes active towards hydrogen peroxide. The inhibiting substances have probably been hydrolysed. Further if the precipitate of magnesium hydroxide, etc., obtained by boiling aquarium water is collected and redissolved in the least quantity of dilute hydrochloric acid, the addition of this to an offshore surface water increases its activity, the hydroxyl concentration having been adjusted to the original value of the surface water.

#### EXPERIMENTAL.

It was found convenient to carry out the reaction in vessels coated with paraffin wax. These should be allowed to soak in distilled water for some time before use. To the sample of sea-water in the vessel 1 c.c. of a solution of hydrogen peroxide of suitable strength was added, and 5 or 10 c.c. portions of the mixture withdrawn for titration with 0.02% permanganate after addition of sulphuric acid. The hydrogen peroxide used should be a pure solution; some proprietary brands are reputed to contain traces of "preservative," such as salicylic acid, to improve their keeping qualities.

The experiments were carried out at room temperature, except those for the rate of reaction (Fig. 2). The values obtained in each experiment are comparable between themselves, but not with other experiments, owing to the varying room temperature.

#### OXIDATION OF ORGANIC COMPOUNDS IN SEA-WATER.

It was found that the rate at which a number of compounds oxidise when dissolved in sea-water varied considerably according to the position and depth from which the water was taken, and according to the season.

A solution of pyrogallol or of hydroquinone in sea-water turns brown. A solution of equimolecular parts of paraphenylene diamine hydrochloride and  $\alpha$  naphthol in potassium carbonate solution (Röhman-Spitzer reagent) when added to sea-water oxidises to a blue dye, indophenol. Tincture of guaiacum gradually takes on a green hue, more blue-green in the case of an "active" deep water. The most convenient reagent was

found to be either hydroquinone or Röhman-Spitzer reagent, the latter developing a strong colour within a few minutes.

The rate of oxidation increases with the alkalinity (OH concentration) of the sea-water. In order to show definitely that samples of water possessed different powers of oxidation when at the same hydrogen ion concentration, acid or alkali was added in some cases, so that the sample could be shown to possess both greater power of oxidation and lesser OH concentration, than the other sample with which it was being compared.

TABLE III.

Date of experiment.	Position from which water sample was collected.	Depth from which sample was collected in meters.	Acid or alkali added.	pH.	Relative amount of oxidation of reagent.	Reagent used.	Date water sample was collected.
—	E1	Surface	—	Same	+	Pyrogallol in distilled water	Nov. 23/23
Dec. 3/23	"	50	—	"	++	"	"
Dec. 3/23	E1	Surface	—	Greater	+	Hydroquinone in distilled water	Nov. 23/23
Dec. 5/23	"	50	Acid	Less	++	"	"
Dec. 5/23	Aquarium tank		Alk.	8.0*	+	Hydroquinone in distilled water	Nov. 23/23
	E1	Surface	Alk.	7.85*	++	"	"
	"	50	—	7.0*	+++	"	"
Dec. 12/23	L5	Surface	—		+	Hydroquinone in distilled water	Dec. 10/23
	E1	"	—	} Same	++	"	"
	"	50	—		++	"	"
	"	60	—		+++	"	"
Jan.—/24	E1	Surface	—	} Same	+	Hydroquinone in distilled water	Jan. 2/24
	"	70	—		+++	"	"
Feb. 19/24	E1	Surface	—	} Same	+	Hydroquinone in distilled water	Feb. 15/24
	"	70	—		++	"	"
April 9/24	E1	Surface	—	} Same	+†	Hydroquinone in distilled water	April 8/24
	"	68	—		++	"	"
Aug. 26/24	L6	Surface	—	8.25	+	Hydroquinone in distilled water	Aug. 25/24
	"	60	—	8.20	+	"	"
	L6	Surface	—	8.25	+	Röhman-Spitzer reagent	Aug. 25/24
	"	60	—	8.20	+	"	"
Sept. 4/24	E1	Surface	—	} Same	+	Hydroquinone in distilled water	Sept. 3/24
	"	68	—		+	"	"
Oct.—/24	E1	Surface	—	} Same	+‡	Hydroquinone in distilled water	Oct. 1/24
	"	65	—		+++	"	"
Oct.—/24	E1	Surface	—	} Same	+	Hydroquinone in distilled water	Oct. 1/24
	"	65	—		+++	"	"
Oct.—/24	E1	0	CO <sub>2</sub> §	} Same	+++	in distilled water	Oct. 1/24
	"	65	—		+++	"	"
Oct.—/24	E1	65	—	} Same	+	Röhman-Spitzer reagent	Oct. 1/24
	"	65	—		+++	"	"
Oct.—/24	E1	Surface	—		pale green	Tincture of guaiacum	Oct. 1/24
	L3	"			"	"	"
	L4	"			"	"	"
	E1	40			pale blue-green	"	"
	"	50			"	"	"
	"	65			"	"	"

\* After addition of the hydroquinone solution.  
 † Difference not well marked.  
 ‡ Dubosq colorimeter readings 100 and 125 respectively.  
 § Heated on water bath for 30 minutes and pH adjusted by passing CO<sub>2</sub>.



On reference to Table III it is seen that there is no marked difference between surface and deep water collected on August 25th and September 3rd, 1924, while the samples behaved very differently towards hydrogen peroxide. This points to the difference in behaviour towards peroxide and these reagents between surface and deep water being due to different causes.

A notable point of similarity is that a trace of cyanide slows the oxidation (of Röhman-Spitzer reagent) very considerably. The rate is reduced to the same order as the rate of oxidation in distilled water brought up to the hydrogen ion concentration of sea-water with sodium peroxide.

A trace of glycin very considerably slows the oxidation in sea-water.

By boiling surface water with sodium hydroxide, redissolving the precipitate in hydrochloric acid and adjusting the hydrogen ion concentration to the original value by adding sodium hydroxide, the oxidising power of the water is actually increased. It is suggested that this treatment hydrolyses part of the inhibiting substances present in the surface water.

These points of similarity suggest that sea-water contains in solution a compound or compounds of iron which act catalytically by increasing the rate of oxidation of a number of easily oxidisable organic substances. An iron compound in sea-water which is an active catalyst towards the decomposition of hydrogen peroxide is not necessarily active towards these other reagents (August and September, 1924) and vice versa (April, 1924). Surface water and inshore water contains inhibitory substances which are partly hydrolysed by boiling in sodium hydroxide solution.

Dr. Keilin suggested to the writer that the catalytically active iron compounds in sea-water may be enzymes—catalases and oxidases—excreted by, or dissolved out from dead organisms. He further pointed out that there are several known cases of oxidising enzymes withstanding a temperature of 100° C. or more for some hours.

#### GENERAL CONCLUSIONS.

The preliminary experiments showed that the products of putrefaction of organic matter occurring in the sea, if they accumulated and were not oxidised, would in time exert an influence upon the life of marine organisms.

The oxidation of such products may be expected to vary in velocity in sea-water from different depths and localities; this was found to be the case with a variety of easily oxidisable organic substances.

The reaction of sea-water with hydrogen peroxide, being readily measured, permits conclusions to be drawn regarding the mechanism of this oxidation in sea-water.

The conclusion that dissolved organic substances, which inhibit the

action of the catalyst, are present in the upper layers of water, is in agreement with Atkins' conclusion regarding the vertical distribution of dissolved organic matter occurring in the water of the open sea (Atkins, W. R. G., *Journ. Marine Biol. Assn.*, Vol. XII, p. 772). The minute trace of dissolved organic matter plays a part in reducing the oxidation potential of the water.

The action of cyanide in stopping oxidation, the presence of iron in solution in sea-water, the catalytic action of hæmatin which remains in solution in sea-water upon hydrogen peroxide, and also the analogy to the action of iron on the oxidation of cystein, all point to organic compounds of iron being the active catalyst in sea-water.

It is suggested that the greater amount of dissolved organic matter in estuarine and polluted water, and the greater concentration of physiologically active products of putrefaction and their lesser rate of oxidation to non-active products, may *in part* account for the difference in fauna between such waters and those of the open sea. The major physiological difference undoubtedly is, that such water, being relatively shallow, is subject to greater and more rapid changes of temperature.

#### SUMMARY.

1. Putrefaction in sea-water sets free compounds toxic to *Calanus*. A portion of these compounds withstands oxidation to non-toxic forms in air saturated water for considerable periods.
2. "Deep water" from the English Channel contains a catalyst, probably an iron compound, which increases the rate of oxidation of a number of easily oxidisable organic compounds. Its action is inhibited in surface and inshore waters by dissolved organic matter.
3. Hydrogen peroxide decomposes relatively quickly in "deep water" from the English Channel, at a velocity corresponding to that of a monomolecular reaction. A catalyst, probably an iron compound, active towards hydrogen peroxide, occurs in sea-water. The action of the catalyst is inhibited by dissolved organic substances in surface and inshore water, until such substances are oxidised by the hydrogen peroxide.

## A Colorimetric Method for Studying the Dissociation of Oxyhæmocyanin suitable for Class Work.

By

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And

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With 6 Figures in the Text.

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### INTRODUCTION

THAT hæmocyanin can act as a carrier of oxygen may now be regarded as established beyond doubt, though, as in the case of hæmoglobin, in some of the lower forms the significance of this property to the normal respiratory processes of the organism is not yet clear. The determinations of Winterstein (1908) on the oxygen capacity of the blood of invertebrates endowed with and devoid of hæmocyanin, and the more recent observations of Dhéré (1916–21), who has correlated the oxygen capacity of the blood of species which possess hæmocyanin with the blood copper content, leave no doubt regarding the former issue. Dhéré, Craifalneau and Quagliariello have respectively made observations on the chemical properties of the hæmocyanin of crustacea, pulmonates and cephalopods: Alsberg and Clark have studied the hæmocyanin of *Limulus*. But as yet there has been little detailed work on the physical chemistry of its respiratory property. Redfield and Hurd (1925) have plotted the dissociation curve of the oxyhæmocyanin of *Limulus* and *Loligo* by a colorimetric method; and in this laboratory the Stedmans (1925) have performed a great service by comparing the dissociation curve of several genera of decapod crustacea by direct measurement with van Slyke's technique. But so far as we are aware no data have yet been published with reference to the effect of hydrogen ion concentration, salinity, temperature and other factors, which are known to influence the dissociation curve of hæmoglobin, on the oxidation of hæmocyanin.

By the use of a very simple device, to be described, observations made

by the present authors shew that the dissociation of hæmocyanin under these conditions is influenced in a manner closely analogous to that of hæmoglobin; and as the physical chemistry of hæmoglobin necessitates the use of a considerable amount of elaborate and expensive apparatus, the method which we have explored, primarily with a view to class work, provides, we believe, an admirable means of illustrating some essentials of the general physiology of respiratory pigments with the minimum expenditure of time, equipment and technique. We have therefore thought it desirable to issue a detailed account of the procedure which may prove acceptable to others who are concerned with the teaching of zoology on experimental lines. For this reason we have ventured to set forth the details of the method rather fully, so that no difficulty should be experienced in carrying it out. At the same time the observations which we have recorded may, it is hoped, suggest fields of further enquiry by the more direct but laborious procedure for the study of oxygen transport by animal pigments.

#### METHOD.

As Redfield and Hurd have pointed out, the fact that reduced hæmocyanin is colourless renders it possible to estimate the degree of oxidation by a colorimetric method which is not applicable to the case of hæmoglobin. Subject to certain safeguards which will be mentioned later, the percentage saturation may be directly determined by comparison with known dilutions of blood in contact with air, without recourse to the more elaborate procedure adopted by these authors, i.e. the preparation of colour standards by mixture of the reduced and oxidised pigment.

Since the oxygen content of the atmosphere is constant, the oxygen pressure may be varied directly by exposing the blood to air at reduced pressure without the customary preparation of analysed mixtures of gases. Thus the only apparatus required besides a series of uniform tubes for the colour standards is a manometer and pump provided with a stop-cock. For the latter purpose a filter pump amply suffices to lower the gas pressure to a value not differing significantly from the pressure of water vapour at the given temperature, that is to say the partial pressure of oxygen can thereby be reduced to zero within the limits of experimental error. The apparatus is illustrated in Fig. 1. Large quantities of blood containing hæmocyanin can be obtained readily from the larger decapod crustacea, such as the crawfish, *Palinurus*; the lobster, *Homarus*; or the crab, *Cancer*. The method is also applicable for the study of molluscan blood, for which purpose the edible snail, *Helix*, is most convenient for laboratory work.

*Preparation of serum.* *Palinurus* was found to provide the most favourable material as a crustacean type. To prevent movement it is

convenient to secure the animal lengthwise to a stout rod applied to the ventral surface, with the head uppermost. The last abdominal tergum is removed so that the blood may drain into a vessel: it is well to cut the aorta, but if this is done care should be taken on no account to include the rectum, the contents of which will pollute the blood. The blood, as is well known, coagulates with phenomenal rapidity. The coagulum is ground with sand in a mortar, the exudate being filtered or cleared by centrifuging. The yield should be about 60 cc. for a medium-sized crawfish. After shaking with air the clear serum is of a dark blue tint by reflected light. Occasionally individuals are found which have little hæmocyannin in their blood: these cannot be used for experiment. The same serum should be used both for the preparation of the comparator and for whatever subsequent operations are to be performed. If a few drops of toluol are added the serum will keep for several days; but after twenty-four hours' standing a peculiar form of spontaneous reduction occurs. The colour disappears, but is rapidly restored to its original intensity on shaking in the presence of air. The precise nature of this change has not been determined. It will be mentioned later that the character of the dissociation curves obtained with stale serum was not precisely identical with those derived from fresh blood. This would appear to be due, partly at least, to the fact that, though well-buffered, the blood becomes more acid on standing.

To obtain blood from snails the animal is first anaesthetised or killed with chloroform, the shell is chipped off above the mantle cavity, into which an incision is made. The blood is allowed to drain off without coming into contact with the yellow slime. In the case of hibernating snails it is sufficient to make an incision in the foot. The yield is about 1 cc. per individual. On being shed the blood is of an opalescent blue tint. It should be shaken with sand and filtered or centrifuged.

*Preparation of colour standards.* For making the comparator a series of uniform test tubes of thick glass (preferably about 1.8 cm. bore) are mounted in a rack as for pH determination. As reduced crustacean blood displays a pale orange tint owing to the presence of an ether-soluble pigment, the serum cannot be simply diluted with water. A little serum is shaken up for at least ten minutes in a tube thoroughly exhausted, as described below. A very dilute solution of orange G with a trace of logwood and Indian ink gives a perfect match for the reduced serum by reflected light, and can be prepared in a few minutes. This solution is used for diluting the serum from 0-100 per cent in 10 per cent stages. A slight opalescence may appear after shaking the exhausted serum, and it is well therefore not to prepare the diluting solution till the serum has been shaken for the time stated, though two minutes' shaking of a small quantity such as 5 c.c. in a fairly large test tube should suffice

for equilibration. For the colour standards 5 c.c. of each solution are sufficient. The experimental serum is compared with the diluted solutions by reflected light: the same diluting solution will not serve for use with artificial light. In preparing colour standards for the snail's blood a very dilute solution of orange G with a faint trace of methylene blue is satisfactory.

## APPARATUS

The arrangement of the apparatus is illustrated in Fig. 1. A manometer is connected by a T-piece with a filter pump (*F*) and a rubber stopper fitting into a test tube (*E*) of the same bore as those used for the

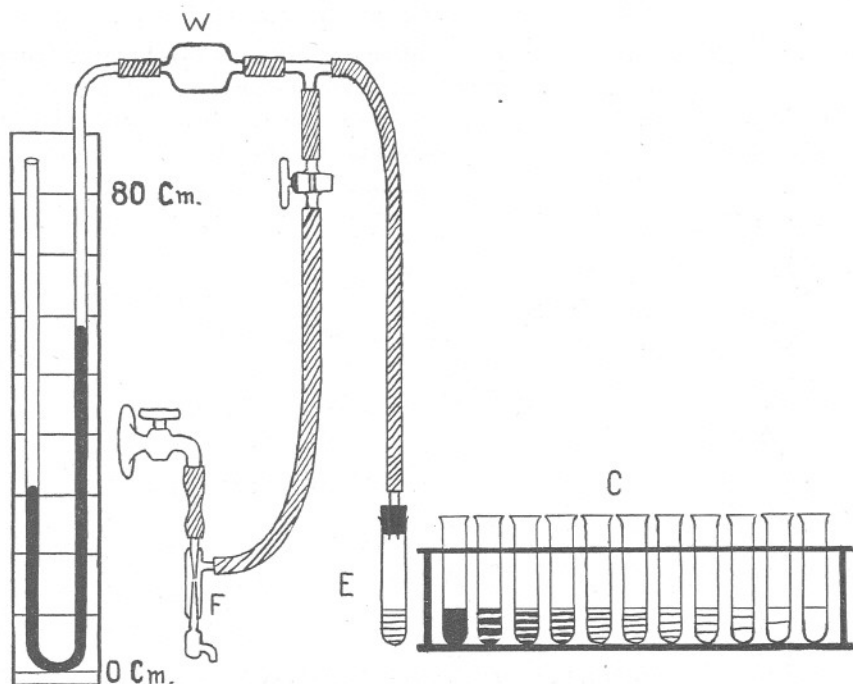


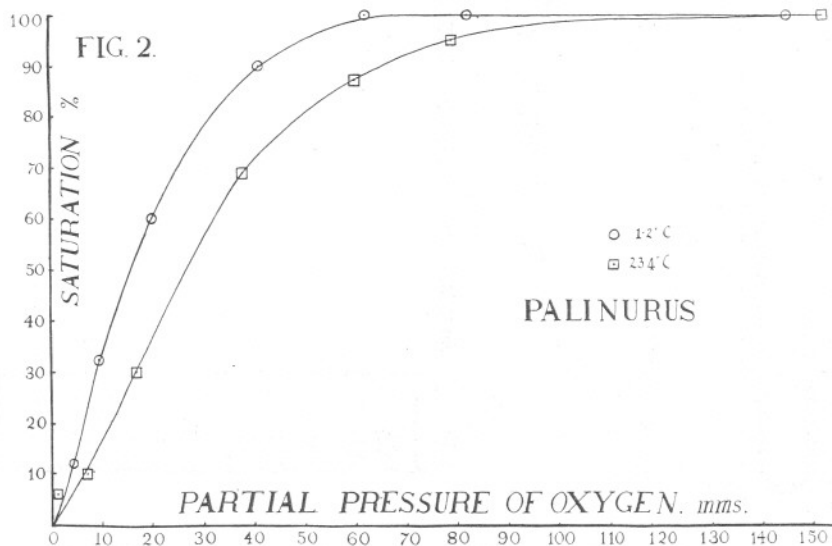
FIG. 1.—Apparatus for colorimetric determination of percentage of oxidised hæmocyannin. W. Water trap. E. Tube for experimental serum. F. Filter pump. C. Colour standards.

colour standards. A glass stopcock is interposed between the filter pump and the T-piece, and it is advisable to insert in the position indicated a water trap (*W*) which can be made conveniently from a large pipette. Five cubic centimetres of serum are placed in the test tube which is then exhausted. The stopcock is turned and the tube shaken till the serum is completely reduced. This need not occupy more than five minutes,

in the case of crustacean blood rather less. The stopcock is then loosened so that the system is refilled with normal air. If this is done there is no danger of error at low pressures in consequence of the oxygen evolved. Such error would in any case be very minute owing to the low oxygen capacity of the blood and the relatively large internal volume of the apparatus. In subsequent operations in which comparison is made on the same sample at different pressures, the oxygen tension is given by  $0.21(b-v-m)$ ,  $b$  being the observed barometric pressure,  $v$  the vapour pressure of water for the temperature at which the experiment is carried out,  $m$  the manometer reading, and 0.21 the proportion of oxygen in atmospheric air.

#### THE DISSOCIATION CURVE OF CRUSTACEAN BLOOD.

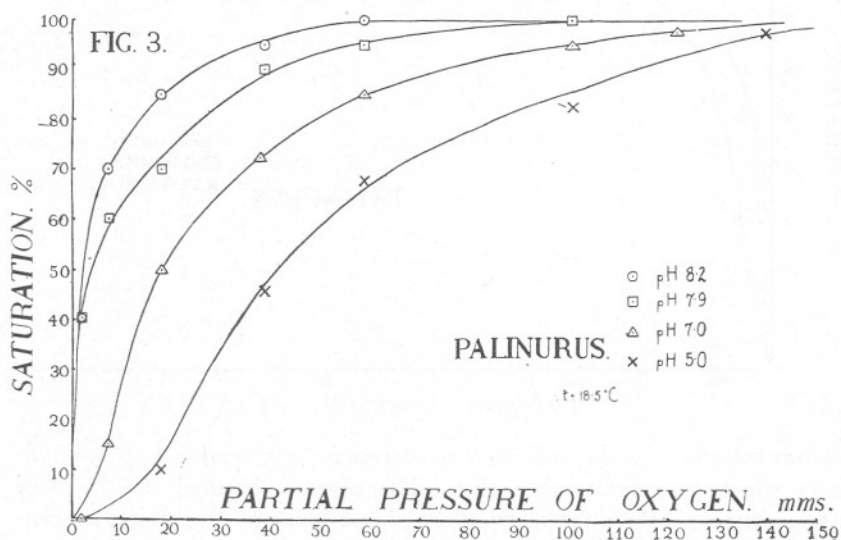
Since colorimetric methods are often regarded as involving a large personal error, we have not attempted to use the method outlined above until satisfied that our independent observations were consonant with one another and with those of other workers in the laboratory not conversant



with the object of the experiment. Furthermore, in all experiments one of us recorded observations (including tensions) of which the other, responsible for the colorimetry, was kept in ignorance. For *Palinurus* the limits of error were found to be well within 5 per cent: in the case of *Helix* the error was perhaps a little greater, possibly on account of the greater time required to complete equilibration. Having satisfied ourselves both as to the accuracy of the method and its serviceability for persons inexperienced in colorimetry, we have employed it to investigate

some aspects of the physical chemistry of hæmocyanin which are eminently suitable for class experiments. These include the effect of temperature, hydrogen ion concentration and salinity on the character of the dissociation curve of oxyhæmocyanin. Since a six or seven point curve can be completed on the same sample within half an hour, the method should not make undue demands upon the time of the student.

*Effect of temperature.* In Fig. 2 are given two curves, one representing the dissociation of the hæmocyanin of *Palinurus* equilibrated at room temperature, the other based on the same specimen equilibrated by shaking in a large vessel of ice-cold water. At the lower temperature the affinity of the hæmocyanin for oxygen at low tensions is considerably increased in a manner precisely analogous to the well-established effect of temperature on the dissociation curve of hæmoglobin. However, it is to be noted that, while the points on each curve are ideally consistent, both curves are flatter than might be expected, compared with those obtained

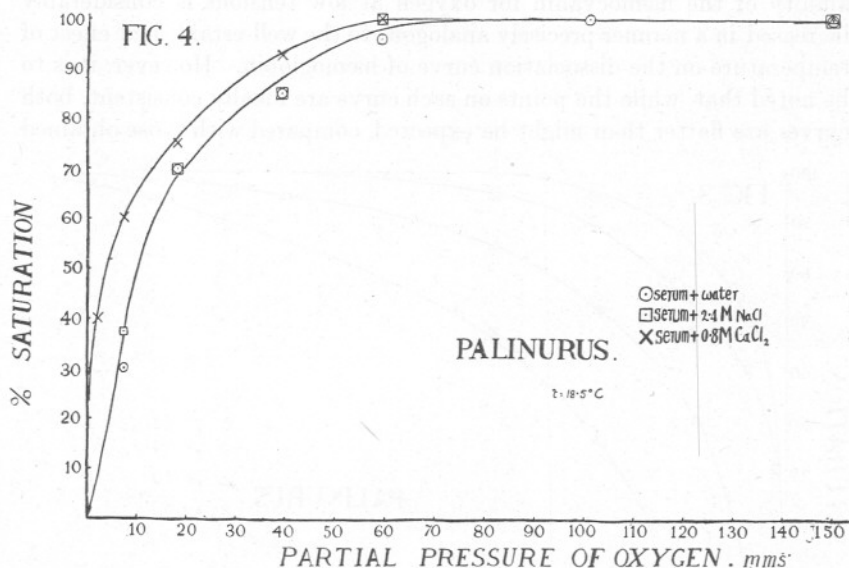


from fresh serum (Figs. 3 and 4). The serum used in the experiments on the influence of temperature had stood for twenty-four hours: as already remarked, blood of *Palinurus* becomes more acid on standing.

*Effect of hydrogen ion concentration.* No data are as yet available, to our knowledge, with reference to the isoelectric point of crustacean hæmocyanin; but the determinations of Quagliariello on the hæmocyanin of *Octopus* lead one to anticipate the possibility of varying the pH on the alkaline side of the isoelectric point over a much wider range than can be done in the case of hæmoglobin. The buffer action of *Palinurus* blood is fairly considerable, and as the blood requires little dilution to



eliminate the bluish tint by *transmitted* light, colorimetric determination of pH may be made without any serious error arising, subject to correction for protein content. In Fig. 3 are depicted four curves on the same specimen of fresh serum, one made more alkaline to pH 8.2 by addition of one drop per c.c. of a double strength of Palitzch's boric acid-borate mixture, two others being made more acid than normal serum (pH 7.9) by addition in one case of one drop of acidified saturated sodium phosphate to 5 c.c. (giving pH 7.0) and in the other case of a corresponding quantity of saturated sodium acetate acidified with acetic acid (giving a pH 5.0). In comparing each sample it is best to treat the



colour standards in the same way to correct for any tendency to coagulation which might alter the tint. The results obtained are in close agreement with the established effect of increasing hydrogen ion concentration on the dissociation of hæmoglobin at low tensions. The curve marked 7.0 is subject to a protein + salt error of about +0.4.\*

*Effect of salinity.* The effect of salinity may be investigated by diluting the serum half and half with water or saline solutions of various strengths, due regard being paid to hydrogen ion concentration. In comparing the action of salts on the dissociation of crustacean and mammalian blood

\* Protein error of diluted Palinurus blood was approximately determined as follows: 1 cc. of blood is added to each of two tubes; one of these is made up to 5 cc. with distilled water, the other to 5 cc. with a *strong* buffer of known pH. The pH is then determined by adding indicator in the usual manner, the first tube being placed behind the standard tube to allow for the colour of the serum. The apparent pH of the buffered solution is subtracted from the known pH of the strong buffer.

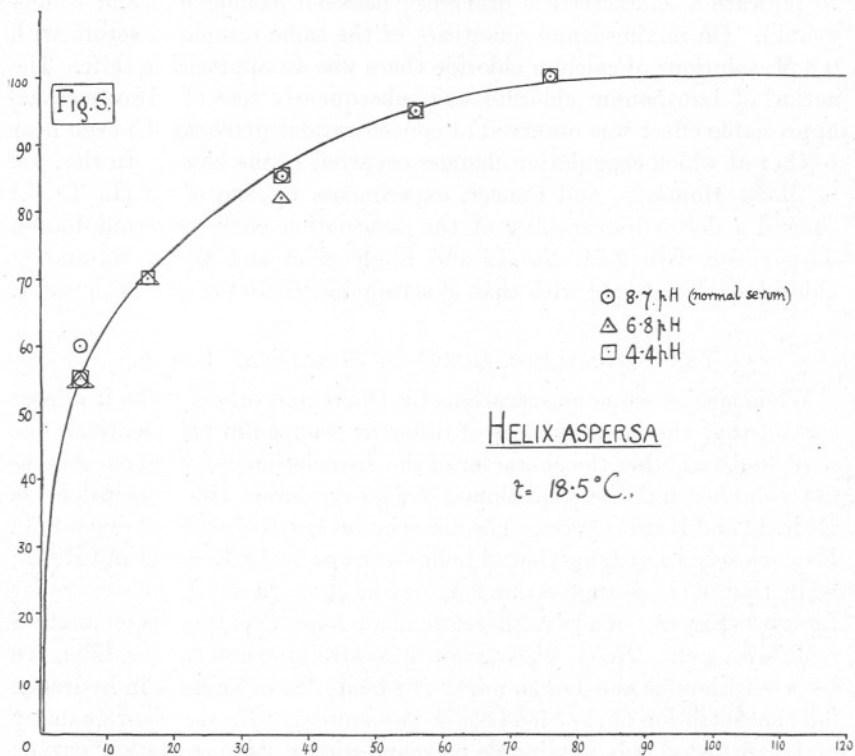
it is well to bear in mind that the absolute concentration of saline constituents in the former is at least three times as great as in the latter. A corresponding series of colour standards are made for these experiments. Fig. 4 shows the effect of certain salts at pH 7.9.

Dilution to half strength with a 2.4 M. solution of sodium chloride was not found to have a significant effect on the dissociation curve of *Palinurus*, as compared with the normal curve, and also with the curve of serum diluted with water. For the reason stated above this need not be taken to indicate a characteristic difference between hæmoglobin and hæmocyannin. On mixing equal quantities of the same sample of serum with 0.8 M. solutions of calcium chloride there was an appreciable shift. The action of Lanthanum chloride was subsequently tested. However, no appreciable effect was observed at concentrations (0.00025 M.) even near to that at which coagulative changes occurred in the blood. In the case of *Maia*, *Homarus*, and *Cancer*, experiments by one of us (L. T. H.) shewed a decided steepening of the dissociation curve of serum diluted 50 per cent with 2 M. Na, Li and K chlorides and M Ca, Mg and Sr chlorides as compared with that of serum diluted 50 per cent with water.

#### THE DISSOCIATION CURVE OF MOLLUSCAN BLOOD.

While spectroscopic observations by Dhéré and others make it almost certain that the hæmocyannins of different groups are not identical, one may doubt whether the character of the dissociation curves of the Arachnid *Limulus* and the Cephalopod *Loligo* reinforces this conclusion, as Redfield and Hurd suggest. The dissociation curve of acidified crustacean blood closely approaches that of *Loligo* as recorded by Redfield and Hurd; while that of the normal serum is more like Redfield and Hurd's curve for *Limulus* (Fig. 6). We have therefore made a few experiments on another molluscan genus, *Helix*, with a view to ascertaining how far the difference between *Limulus* and *Loligo* might not be due to differences in hydrogen ion concentration of the blood of the two animals. No sufficient quantity of *Loligo* blood was obtainable to reinvestigate its dissociation curve; but a single determination of the pH of the blood gave a value of about 5.4-5.6 as contrasted with 7.9-8.0 for the blood of *Palinurus*. The first curve which was plotted for the blood of *Helix aspersa* proved to be of the steep type characteristic of *Limulus* and *Palinurus*. The pH of snail's blood (*H. aspersa*) is about 8.7, and the curve is a little flatter than the correspondingly alkaline curve for *Palinurus*; and it at first seemed likely that by acidifying the blood a condition approximating to that of *Loligo* would be obtained. In this surmise we were, however, disappointed; but the experiments performed brought out two points of some general interest. The first is the extraordinary extent to which

the snail's blood is buffered, especially in view of the observations of Collip and of Parsons and Parsons on the alkali reserve of the blood of invertebrates. In one experiment five drops of a saturated sodium phosphate solution acidified with concentrated hydrochloric acid to pH 4 when added to 5 c.c. of normal blood (pH 8.7) only reduced it to pH 8.2. The second point is illustrated in Fig. 5. The dissociation curve of the snail's hæmocyantin was not found by this method to be affected appreciably by considerable variation in hydrogen ion concentration. Indeed the points



obtained from blood acidified to pH 4.4 were consistent with the curve for normal serum; and closely located points were obtained when the blood was made alkaline to approximately pH 10.5 with sodium carbonate. There seems to be a possible analogy between these facts and data given by Clark on the oxidation and reduction of certain simple organic compounds (e.g. hydroquinone and methylene blue). In these cases within a specified range of hydrogen ion concentration the oxidation-reduction potential of 50 per cent oxidation varies with the pH, but below a certain degree of acidity it is little affected.

It has been shown by Parsons and others that hæmoglobin has an im-

portant buffering action in relation to the transport of carbon dioxide, and more recent observations of Parsons and Parsons indicate that hæmocyanin may have an analogous function. The well-known action of the hydrogen ion upon the dissociation of hæmoglobin follows from Le Chatelier's principle, on the assumption that oxy-hæmoglobin is a stronger acid than the reduced form. The similar effect of acidity on the dissociation of crustacean hæmocyanin would therefore appear to reinforce the conclusions of Parsons and Parsons regarding the importance of hæmocyanin to carbon dioxide transport, and would lead one to anticipate that oxyhæmocyanin is a stronger acid than hæmocyanin itself. In

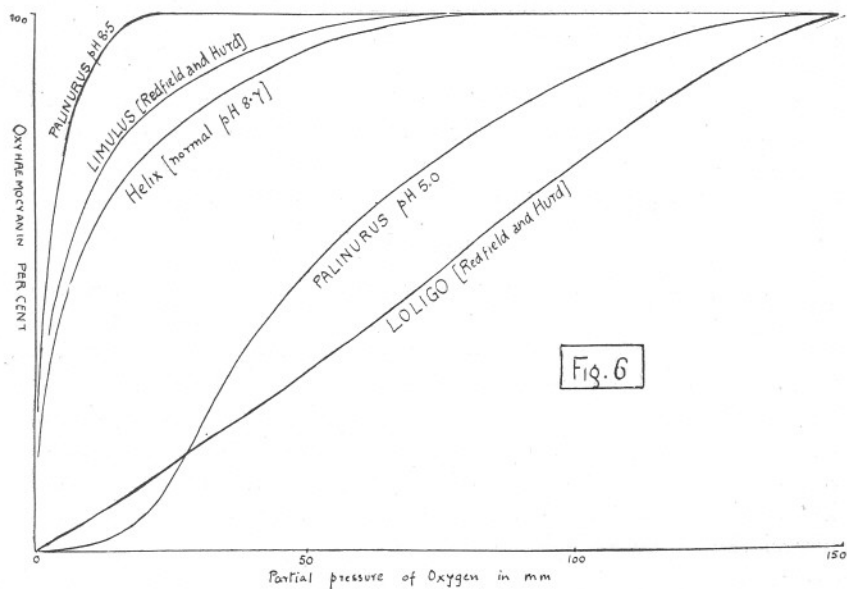


FIG. 6.—Dissociation of oxyhæmocyanins of *Limulus*, *Helix*, and *Loligo* compared with that of *Palinurus* at pH 8.5 and pH 5.0.

the case of the snail—within physiological limits—we should then conclude in the first place that the oxygen-combining power of its hæmocyanin does not facilitate the buffer action. The coincidence of the curves implies either that oxyhæmocyanin is not in this case significantly more acidic than its reduced form, or else that both are so little, or so completely, dissociated as to have no appreciable buffer action. In other words, the buffering action of the snail's hæmocyanin, if it has any such action, is not different in kind from that of other blood proteins. It may be well to note in this connexion that both in the case of crustacea and pulmonates, whatever may be true of *Limulus* and Cephalopods, hæmocyanin does not by any means represent the entire protein content of the blood.

The newly shed blood of the snail appears to be completely oxidised ; and it remains to be proved that it fulfils a respiratory function in relation to oxygen transport, though Dhéré's observations shew clearly that it is a reversibly oxidisable pigment. On the other hand in crustacea the hæmocyantin of freshly shed blood is often almost completely reduced. Until more attention has been paid to control of hydrogen ion concentration it is perhaps premature to conclude from the observations of Redfield and Hurd that the hæmocyantins of *Limulus* and *Loligo* are very different or to infer from those of Stedman and Stedman that the hæmocyantins of all the decapod crustacea are identical (cf. Fig. 6). But it would seem most probable that the hæmocyantin of the snail differs more profoundly from that of *Loligo* and of *Palinurus* than do the hæmocyantins of the last two from one another. It should, however, be remembered that it is quite possible that the effect of other kations may have to be taken into account. So that a satisfactory demonstration of the identity or otherwise of the hæmocyantins can only be obtained from pure solutions of the isolated pigments under properly controlled conditions.

#### SUMMARY.

1. A simple colorimetric method for plotting the dissociation curve of hæmocyantin is indicated. The limits of error are within 5 per cent. The simplicity of the method commends it for laboratory class work.

2. The effect of hydrogen ion concentration on the dissociation of the hæmocyantins of the crustacean *Palinurus* and the pulmonate *Helix* have been compared. In the snail change of hydrogen ion concentration over a wide range was not found to affect the dissociation of the hæmocyantin : in the crustacean there is a marked effect similar to that seen in the dissociation of hæmoglobin.

3. The similarity of crustacean hæmocyantin to hæmoglobin is also seen in that increasing temperature depresses the dissociation curve. The effects of certain salts upon hæmocyantin have also been recorded.

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## On the Occurrence of *Onchidella celtica* (Cuvier) on the Cornish Coast.

By

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

*Assistant Naturalist at the Plymouth Laboratory.*

*Onchidella*\* *celtica* (Cuvier) is the only representative of its genus found on our shores. Included in the Sub-order Stylommatophora of the Pulmonates, it is believed to be a land mollusc that has reverted to a marine habitat. It is quite devoid of a shell and closely allied to the land slugs.

On account of its apparent rarity I have thought it worth while to note the occurrence of this species at Newquay on the North Coast of Cornwall.

In 1882, Joyeux-Laffuie† gave a full account of the morphology and development of the animal under the name of *Oncidium celticum* Cuvier. He says that it was first found by Cuvier on the Coast of Brittany, but there was no record of the locality taken. Later, Andoin and M. H. Milne-Edwards found it at the mouth of the Ranche on the Brittany Coast, where it was again discovered in 1870 by M. Vaillant. From then until 1882 there were no more records of it until Joyeux-Laffuie started to search for new localities. He discovered it in abundance at Duon, les Sept-Iles, Le Conquêt, and Morgate. In addition to these five points on the Brittany Coast it has been reported on the shores of Cornwall at Westcomb, Lantivet Bay near Fowey, by Couch, and at Whitsand Bay near Plymouth by Spence Bate.

Joyeux-Laffuie states that in the regions in which it occurs *Onchidella* is very local in its distribution. As regards its actual habitat at three places the animals were found 2 or 3 metres above high-tide mark, but in the other two regions they were in a zone that would be completely covered at high water. They occur in rocks where there are crevices into which they can retreat; into these they creep at high water to shelter

\* This generic name has recently been readopted from Gray by H. Watson in a paper on The South African Species of the Molluscan Genus *Onchidella*. *Annals of the South African Museum*, Vol. XX, Pt. 4, No. 6, 1925. The genus has been known in most textbooks as *Oncidiella*.

† J. Joyeux-Laffuie. Organisation et Développement de l'oncidie *Oncidium celticum* Cuv. Archives de Zoologie Expérimentale et Générale, Tome X, 1882, pp. 225-383.

from the force of the breaking waves, which might dislodge them from the rocks on which they only have a feeble foothold. They leave their retreats an hour or an hour and a half after the tide begins to go down, and move about over the rock seeking the small algæ on which they feed. The length of time they stay out of the crevices is governed by conditions of humidity and temperature: on dull, damp days they may remain out for three or four hours, but on hot, dry days for two hours only. In the cold winter months they seldom leave their shelters: if the nooks are examined then the animals are found huddled together in small groups. I might add that this thigmotactic response is very evident; if the animals are kept together in a jar, they will crawl all over each other and congregate into a compact little clump.

I found this species on an island rock in the Fistral Bay at Newquay, in a position well provided with crevices and cracks for retreat: the animals were walking about in groups at a level about the half-tide mark, and would most certainly be covered at high tide, the whole island becoming submerged then. It agrees with Joyeux-Laffuie's remark that they are extremely local that I have never found them on any of the other rocks in the immediate neighbourhood, rocks which to all appearances would offer a similar habitat.

This mollusc is very difficult to see because of its dull greyish colour which harmonizes so well with its background, and it seems probable that careful search in summer months would considerably widen its known distribution. It is interesting to note that it has spread to the North Coast of Cornwall, Lantivet and Whitsand Bays both being on the South Coast almost exactly opposite the region on the Coast of Brittany, which would seem to be its main locus of distribution.

## Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

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### **The Rapid Determination of Available Phosphate in Soil by the Coeruleo-molybdate Reaction of Denigès.**

By **W. R. G. Atkins.**

*J. Agric. Science*, 1924, Vol. XIV, 192-197.

The method affords a rapid means of estimating phosphates in aqueous extracts, one soil to five water by weight, even when the extract is diluted twenty-fold. The majority of the soils studied gave to the extract phosphate corresponding to under two parts per million of phosphorus pentoxide. Dunged soil gave up to 20 p.p.m. or more. Extraction for 3-4 hours gives values as high as extraction for 4-7 days with soils of low phosphate content, but the phosphate of richer soils may undergo a reversion to an insoluble form during prolonged extraction.

W. R. G. A.

### **The Electrical Conductivity of Extracts from Soils of various types, and its use in Detecting Infertility.**

By **W. R. G. Atkins.**

*J. Agric. Science*, 1924, Vol. XIV, 198-203.

The electrical conductivity of aqueous extracts of soils varies according to the time of extraction. With one of soil to five of water extraction of the more fertile soils for 3-4 hours gives less than half as great a conductivity as is given in 4-11 days. In peat a high conductivity is reached quickly. Certain infertile soils also reach their maximum quickly, but the actual conductivity is low, closely similar to that of the purest upland streams. A rapid increase in conductivity as extraction proceeds may be considered an indication of fertility. A low conductivity, which remains low on continued extraction, denotes a soil so insoluble as to be unfertile.

W. R. G. A.



**Solubility of Phosphates in Relation to Hydrogen Ion Concentration.**

By W. R. G. Atkins.

*Nature*, 1924, Vol. CXIV, 275.

The method of Denigès was used to study the solubility of a sample of tricalcic phosphate (B.P.) between pH 7.0 and pH 5.1, hydrochloric acid being used to increase the acidity. Over this range the solubility increased from 114 to 786 parts per million. From the form of the solubility curve it results that a small change in pH value around pH 5 gives rise to a large increase in solubility. The phosphates of strontium and barium give curves which are qualitatively similar. Other "insoluble" phosphates were also studied and work is in progress.

W. R. G. A.

**Notes on the Filtration and other Errors in the Determination of the Hydrogen Ion Concentration of Soils.**

By W. R. G. Atkins, Sc.D.

*Sci. Proc. Roy. Dublin Soc.* 1924, Vol. XVII, 341-347.

Increase or decrease in the proportion of soil to water within limits does not alter the pH value by as much as pH 0.1 for soils between pH 6 and 8. For lightly buffered acid soils one part of soil to two of water is recommended; for other soils one of soil to five of water. The pH value of soil some extracts is markedly modified by filtration, even when a first filtrate is rejected. Both untreated and acid-extracted filter papers may reduce the acidity. Clearing by a centrifuge is the best practice. Unextracted filter papers are at about pH 7-7.6; they give up traces of alkali to distilled water. Acid-extracted papers are near pH 4.8, but washing is not found to render them less acid. The indicator brom cresol green is to be preferred to methyl red for about the same pH range.

W. R. G. A.

**The Preservation of Fishing-nets, Mosquito-nets and Tent Fabrics.**

By W. R. G. Atkins.

*Nature*, 1925, Vol. CXV, 761.

The work of Taylor and Wells regarding the use of copper oleate in petrol or benzol has been confirmed as regards stramin nets. The preservative has also been found specially useful for silk plankton nets which rapidly deteriorate.

A mixed copper soap prepared specially by Mr. W. A. Davis, of Lever Bros., was found preferable to copper oleate, for a five per cent solution gave considerably better protection than a ten per cent oleate solution.

Trials with tent fabrics are in progress. There is every indication that copper soaps should preserve mosquito netting also.

W. R. G. A.

**Report on Biological work and on the effect of Poisons on Teredo.**

By George Barger.

*Fourth (Interim) Report of the Committee of the Institution of Civil Engineers. H.M. Stationery Office, 1924, pp. 23-27.*

Control test blocks of wood, exposed inside the pier at Lowestoft, were only slightly attacked by Teredo, probably because the blocks became covered with sludge; they were, therefore, removed to a more exposed situation on the outside of the pier. Organic compounds of arsenic, such as diphenylchlorarsine and other substances used in chemical warfare, protect against Teredo at high dilution, but much less against Limnoria. The resistance of greenheart wood to Teredo attack is not due to the mechanical properties of the timber, but to the presence of a poison (probably the alkaloid bebeerine), because Baltic fir, impregnated with an alcoholic extract of greenheart sawdust, is protected in comparison with untreated Baltic fir controls.

Mr. C. M. Yonge grew Teredo larvæ for four weeks at Plymouth. In the end they all crowded on to strips of wood immersed in the cultures; but no boring, or even metamorphosis preliminary to it, could be detected. Mr. Yonge also measured 300-400 Teredos taken from a raft and carried out toxicity experiments with Teredo larvæ.

G. B.

**On a new Ciliate, *Cryptochilum boreale* nov. sp., from the Intestine of *Echinus esculentus* Linn., together with some notes on the Ciliates of Echinoids.**

By C. C. Hentschel, B.Sc.

*Parasitology, Vol. XVI, No. 3, July, 1924.*

This paper describes a new ciliate, *Cryptochilum boreale*, found in the intestine of *Echinus esculentus* from Scottish waters, being first observed at Fetlar, Shetland Islands, and afterwards from Millport and Aberdeen. Specimens of *Echinus* from Plymouth were examined with a negative result. It would thus appear to be a northern form. This ciliate appears

to differ in a number of points from a species, *C. echini*, described in 1883 by Maupas from *Strongylocentrotus* from the Mediterranean ; but there does not seem to be sufficient justification for the creation of a new genus for the inclusion of the Scottish form.

Finally, in view of the inaccessibility of some of the literature on the ciliates from Echinoids, it has been thought worth while to add brief descriptions of those ciliates that have been recorded as parasites or commensals of this group, with references to all the papers known up to date.

C. C. H.

### Studies on Internal Secretion III. The action of Adrenaline and Pituitary extract upon Invertebrate Muscle.

By Lancelot T. Hogben and A. D. Hobson.

*Brit. Journ. Exp. Biol.*, Vol. I, 1924, pp. 487-500.

The effect of adrenaline and of pituitary extract upon the isolated heart of *Maia*, crop of *Aplysia* and *Aphrodite*, and on the perfused heart of *Pecten* was investigated. Adrenaline and the allied sympathomimetic amine *epinine* have a powerful excitatory action on the musculature of all these structures : the crop of *Aplysia* responds to less than one in a million of the latter. Pituitary extract was in all cases without action, though histamine exerted its characteristic action on the plain muscle of vertebrates. The specificity of the oxytocic action of pituitary extract, and the physiological activity of adrenaline and allied substances in animals without a sympathetic nervous system is indicated.

L. T. H. AND A. D. H.

### On the Photo-electric Measurement of Submarine Illumination.

By H. H. Poole, Sc.D.

*Sci. Proc. Roy. Dublin Soc.*, 1925, Vol. XVIII, 99-115.

A method is described of using photo-electric cells for submarine photometry which may be employed in a comparatively small vessel at sea in fine weather. The photo-electric current is passed through a known high resistance, the P.D. between the ends of the latter being balanced against a potentiometer. A telephone is fitted as a detector instead of a

galvanometer as used by Shelford and Gail in calm water. The telephone circuit is interrupted many times per second by a special interrupter. A two-stage valve amplifier is interposed between this circuit and the telephone. A vacuum photo-electric cell is used as a standard, and also for recording fluctuations in the surface light, while the light below the surface is measured by a cell of the Kunz type enclosed in a brass case. Corrections are applied for the effect of obliquity in the incident light and for loss of light at the front surface of the photometer window. Preliminary tests at Cawsand Bay, Plymouth Sound, showed that the mean absorption coefficients per metre for shallow water varied from 0.7 on a day when the water was obviously sandy to 0.25 in calm weather a few days later.

H. H. P.

#### On the Life-History of *Harveyella pachyderma* and *H. mirabilis*.

By H. H. Sturch.

*Annals of Botany*, Vol. XXXVIII, 1924, pp. 27-42.

The two plants are true algal parasites, without photosynthetic structures, growing respectively only on *Rhodomela subfusca* and *Gracilaria confervoides*, and in habit, external morphology and somatic details are very similar. The external soma is hemispherical in shape, made up of radiating filaments enclosed in a gelatinous outer coat, occupying about the same space as the mass of parasitic filaments inside the host.

In both the Zygote nucleus is transferred to an auxiliary cell, from which the ooblastema springs. In *H. mirabilis* the auxiliary mother cell is the subtending cell of the carpogonial branch, and the very long ooblastema is connected with the gametophyte only at this auxiliary cell, while in *H. pachyderma* the auxiliary mother cell is situated on a neighbouring branch, and the ooblastema is also connected by secondary fusions with every somatic cell in its neighbourhood. The plants should be placed in, at least, different genera, but this has been postponed until further species have been examined. During the year both plants pass twice through the full Floridean life cycle in moderately deep water, accompanied by the same cycle once, from October to April, in very shallow water, in greater numbers. Both plants entirely disappear from this shallow water from May to October on British coasts.

H. H. S.

**Studies on the Physiology of Reproduction. I. The Flocculation of Sperm Suspensions in Relation to Surface Charge.**

**By Arthur Walton, B.Sc.**

*Brit. Journ. Exp. Biol., Vol. II, 1924, pp. 13-20.*

The surface charge on spermatozoa of *Echinus esculentus*, and *E. miliaris* was determined approximately by observation of the rate of migration in an electric field. With varying pH a maximal negative charge was observed between pH 7 and pH 8. On the acid side an isoelectric point occurred about pH 3, beyond this the charge was positive. On the alkaline side of the maximum the charge was also reduced but the increase of alkalinity was accompanied by inaccuracy of determination. Correlated with this decrease of charge, flocculation occurred with both acid and alkali, being greatest at the isoelectric point. Flocculation could be observed microscopically in about fifteen minutes, but the full macroscopic effects were not seen until 3-4 hours had elapsed. The stability of the suspension was greatest in a molar solution of cane sugar. It was reduced by the addition of sea-water (electrolytes), and still further reduced by sea-water in which ripe eggs had stood for twenty minutes. Flocculation with acid was accompanied by agglutination of the heads while with alkali the tails of the spermatozoa were involved, resulting in the formation of a network of threads. Acknowledgments for scientific hospitality are due to the Marine Biological Association, and to the British Association for the use of the Table.

A. W.

**The Growth of the Egg in the Dab (*Pleuronectes limanda*).**

**By J. F. G. Wheeler.**

*Quart. Journ. Micr. Sci., Vol. LXVIII, Pt. IV, 1924, pp. 641-660.*

The egg of the dab takes only one year to attain maturity.

At each spawning season a fresh crop of oocytes appears, and no division can be observed. It is probable that the eggs develop from some of the cells of the follicular layer of the previous crop.

With Da Fano's cobalt nitrate modification of Cajal's process the Golgi bodies can be demonstrated in different phases during the growth of the oocyte. A negative image of the same structure can be seen after fixing in fluids such as Bouin and staining in iron hæmatoxylin. This

apparently depends upon the absence of the Golgi bodies and the staining of the rest of the cytoplasm.

Osmic acid and osmic mixtures fix and blacken the whole cytoplasm. The negative image can be obtained by removal of the Golgi bodies with turpentine.

Yolk-formation is intimately connected with the Golgi bodies. This structure plays a leading part in the chemical changes resulting in yolk-formation, if, indeed, it is not itself converted into yolk. The mitochondria appear to play no particular part in the formation of yolk. The nucleus, nucleoli, and vitelline body also have no definite rôle in yolk-formation.

Growth-rings and plasmatic zoning in dab oocytes are artefacts.

J. F. G. W.

**Experimental Work carried out at Plymouth Marine Biological Laboratory during July–August, 1922.**

**By C. M. Yonge, Ph.D.**

*Dept. Scient. Indust. Research, 4th (Interim) Report of Com. Inst. C.E., 1924, pp. 9–22.*

The common species of *Teredo* at Plymouth was identified as *T. norvegica*. Attempts were made to rear *Teredo* from artificial fertilizations. The larvæ were kept alive for thirty-five days, during which time they increased in size from  $48 \times 48 \mu$  to  $90 \times 72 \mu$ , but their natural food was not found and no sign of change into the adult form was observed. The females are on the average larger than the males. Experiments on the relative toxicity of a number of substances to the larvæ were carried out.

C. M. Y.

## Marine Biological Association of the United Kingdom.

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### Report of the Council, 1924.

#### The Council and Officers.

Four ordinary meetings of the Council were held during the year at which the average attendance was eleven. The thanks of the Association are due to the President and Council of the Royal Society, in whose rooms the meetings have been held.

A committee consisting of five members of the Council visited and inspected the Plymouth Laboratory in March, and later a special meeting of the Building Committee, attended by six members of the Council, met at Plymouth.

The Council has to record with deep regret the deaths of three of its members, Sir William Herdman, Sir William Bayliss, and Mr. J. A. Robertson.

#### The Plymouth Laboratory.

The engines and pumps have been maintained in good working order and the aquarium tanks have been particularly well stocked with fish, of which consignments have been sent to the Aquarium of the Zoological Society in London at frequent intervals.

The three-inch water main from Hoe Road to the Laboratory, laid in 1887, has been replaced, the old pipe being choked and badly corroded.

The Council have had again to consider seriously the question of accommodation both for the permanent staff and for visiting naturalists. During the busy seasons of the year the working space available has been severely taxed, and it was only by making use of the students' classroom, which was recently erected by voluntary subscriptions from

former students and workers, that places were found for all. A Special Committee of the Council has examined the matter at Plymouth, and has drawn up plans for a new two-story building, estimated to cost £3500, which can be used entirely for laboratory purposes. In order to obtain the necessary funds an appeal has been issued which is meeting with a generous response. Up to the present a sum of £2,600 has been promised or subscribed. The Council hopes soon to be in a position to begin the new building.

A promising development was commenced during the summer by the establishment of a laboratory and camp at the old torpedo station at Pier Cellars in Cawsand Bay. Two useful sheds were rented from the War Office and permission to use the Pier for experimental work was obtained. A party of three students was established at the station, and some useful experiments were carried out from the Pier, where animals can be kept alive under much more natural conditions than is possible in a marine aquarium.

### The Boats.

The steam drifter-trawler *Salpa* has worked continuously throughout the year. The periodical boiler survey by Lloyd's was made in June, and the half-time survey of the hull in October. The hull was found to be in exceptionally good condition. At the same time the opportunity was taken of reconditioning part of the machinery and pumps, under the supervision of Lloyd's surveyor, preparatory to the half-time machinery survey which is due next year.

The motor boat *Gammarus* has been in almost daily use for inshore work. The motors have proved reliable.

The sailing boat *Anton Dohrn* is kept available at short notice for collecting in the Sound, and was used by the party working at Pier Cellars, Cawsand Bay, during the summer.

### The Staff.

Mr. F. S. Russell joined the staff in January as an Assistant Naturalist, and Mrs. E. W. Sexton, who has worked for many years at the laboratory upon the natural history of the Amphipoda, and more especially upon Mendelian inheritance in *Gammarus*, has been appointed Director's Research Assistant as from April 1st, 1924.

Miss E. G. Wilson, of Trinity College, Dublin, was employed temporarily during the summer to assist Dr. Atkins in the Physiological Department.

In other respects the scientific staff remains as last year.



## Occupation of Tables.

The following naturalists have occupied tables at the Plymouth Laboratory during the year :—

- G. BANKS, Oxford (General Zoology).  
 N. J. BERRILL, Bristol (Environmental Factors in Development).  
 Dr. G. P. BIDDER, Cambridge (Grantia).  
 Prof. J. BAYLEY BUTLER, Dublin (Biology of Cardium).  
 H. GRAHAM CANNON, London (Crustacean Larvæ).  
 A. J. CLOWES, London (Phosphate Determination in Sea-Water).  
 Captain G. C. C. DAMANT, R.N., Cowes (Buoyancy of Corethra Larvæ).  
 Miss E. M. DELF, London (Marine Algæ).  
 F. DICKENS, London (Islets of Langerhans in Fishes).  
 Mr. DINAN, Dublin (Biology of Cardium).  
 Dr. H. DITLEVSEN, Copenhagen (Nematode Parasites of Fishes and Polychaetes).  
 Dr. J. S. DUNKERLY, Glasgow (General Zoology).  
 Miss G. H. FAULKNER, Aberdeen (Filograna).  
 Dr. E. A. FRASER, London (Teleost eggs and young stages).  
 Miss S. GARSTANG, Leeds (Botryllus).  
 Prof. R. R. GATES, London (Algæ).  
 R. GREESON, Edinburgh (General Zoology).  
 Miss V. M. GRUBB, London (Marine Algæ).  
 L. A. HARVEY, London (General Zoology).  
 W. F. HERDMAN, London (Phosphate Determination in Sea-Water).  
 Miss M. L. HETT, London (Nemertine Development).  
 H. B. HEWER, London (Blennius).  
 C. F. HICKLING, Cambridge (Vertical movements of Schizopods).  
 A. D. HOBSON, Cambridge (Histology of Invertebrate Muscle).  
 Dr. L. HÖGBEN, Edinburgh, Ray Lankester Investigator (Action of Pituitary Extract and other Reagents on Invertebrate Muscle).  
 (Physiology of the heart in *Maia squinado*).  
 F. R. HORNE, Cambridge (General Zoology).  
 Miss M. JEPPE, Glasgow (Gromia).  
 Dr. P. JESPERSEN, Copenhagen (Plankton).  
 Miss S. D. KING, Dublin (Cytology of Protozoa).  
 Miss B. LLOYD, Aberystwyth (Peridinians).  
 Dr. A. D. MACDONALD, Edinburgh (Nature of the response to adrena-line by the fish heart).  
 Miss E. MALONE, Dublin (Spermatogenesis in Cœlenterata).  
 Miss O. S. MUNDY, Plymouth (Vertebrate Embryology).  
 H. G. NEWTH, Birmingham (Development of Starfishes).  
 F. T. PENTELOW, Cambridge (Myxosporidia).  
 M. G. L. PERKINS, Cambridge (Sacculina).  
 E. PONDER, Edinburgh (Hæmolysis and Phagocytosis of Fish Blood).  
 Dr. H. H. POOLE, Dublin (Penetration of light into sea-water).  
 F. A. POTTS, Cambridge (Pomatoceros).  
 The Rev. L. D. SAYERS, Cambridge (General Zoology).  
 W. SCHLAPP, Edinburgh (Lipolytic Enzymes of various Invertebrates).  
 Mrs. E. W. SEXTON, Plymouth (Gammarus).  
 C. C. STOCKMAN, Cambridge (Respiration of Marine Animals).  
 Sister MONICA TAYLOR, Glasgow (General Zoology).  
 H. THOMPSON, }  
 Mrs. H. THOMPSON, } Aberdeen (Classification of Tunicates).  
 D. L. THOMSON, Aberdeen (General Zoology).

- Miss M. TRIBE, London (Early Development of Pomatoceros).  
 Prof. SWALE VINCENT, London (Islets of Langerhans in Fishes).  
 A. WALTON, Edinburgh (Studies on Fertilisation).  
 Prof. D. M. S. WATSON, F.R.S., London (General Biology).  
 Dr. F. D. WHITE, Edinburgh (Toxicity experiments with *Teredo* Larvæ).  
 Miss E. G. WILSON, Belfast (Estimation of Phosphates).  
 R. L. WIMPENNY, Leeds (Parasitic Isopoda).  
 F. R. WINTON, London (Relation of Electrolytes to Fish Melanophores).  
 Miss M. S. WOODS, London (Shallow water ecology).  
 Dr. C. M. YONGE, Edinburgh (Physiology of Digestion in Mollusca).

The usual Easter Vacation Course in Marine Biology was conducted by Dr. J. H. Orton, and was attended by thirty-eight students from Oxford, Cambridge, London, Birmingham, Nottingham, Bristol, and Edinburgh. Another Course was held during the Summer Vacation, and was attended by thirteen students.

Mr. E. W. Shann brought a class of ten boys from Oundle School, Mr. A. G. Lowndes a class of thirteen from Marlborough College and Greshams School, Holt, and Mr. Gillespie three from Monkton Combe School during the Easter Vacation.

#### General Work at the Plymouth Laboratory.

Dr. J. H. Orton has continued his studies of Marine Bionomics, and has again spent a good deal of time in field work. A study has been made of the natural conditions of spatting and growth in young oysters, and the work on sex-change in both the oyster and *Crepidula* has been continued. It has been shown that, contrary to the general belief among oyster producers, oysters spat as late in the year as August may attain a size of three-quarters to more than one inch in length and depth by the following July. This result is an important one economically, inasmuch as it proves that cultch may be laid profitably over a much more extended period of the season than is at present in vogue, provided that the cultch laying is carried out under favourable conditions, of which knowledge of the proportion of black-sick oysters on the beds, and a temperature of the sea-water not less than 64° F., appear to be the most important.

Much time has been absorbed in fortnightly examinations of cages in the sea containing oysters; but it has now been established that oysters may experience *four* changes of sex, alternating from female to male, in less than thirteen months; while the normal sex-experiences in this mollusc on good beds in English waters comprise in all probability in a large proportion of cases a change in each year from male to female or from female to male. Dr. Orton has pointed out that the rapidity of the

change in sex, particularly from female to male, suggests strongly the existence in the oyster at this epoch of a sex-hormone.

Dr. Orton has made good progress in the preparation of a reference card catalogue for the use of students attending courses in Marine Biology, which were held during seven weeks in this year ; and also in the writing-up of researches for more extended publication.

He also attended in June on behalf of the Marine Biological Association a conference convened by the Cornwall Sea Fisheries Committee to discuss the conditions of the oyster beds in the Fal Estuary, and wrote a report on the discussion, which was published by the Cornwall Sea Fisheries Committee. At a later date he attended a Government enquiry meeting at Falmouth on the decline of the oyster fishery as scientific adviser to the Chief Inspector of Fisheries, Mr. Moss Blundell, and is now engaged in preparing a report on a survey he has made of the beds with a view to providing facts for the future administration and development of the oyster fisheries in the Falmouth and Truro areas.

Mr. E. Ford has continued his work on the material collected with the Petersen bottom-sampler, and a report on the value of the lamelibranch stocks represented in the hauls as food for fishes is now in the press. Since completing this report he has given special attention to a study of the Whiting, and a large number of fishes taken from the local Whiting grounds have been measured and examined. During the summer of 1924, motor trawlers working on inshore grounds regularly landed catches of Whiting, practically all small fishes born in the years 1922 and 1923. The financial yield of this fishery was poor, owing to the small size of the fish, and on several occasions whole catches were unsaleable. Such fish, if they had been allowed to live and grow at the normal rate, would have been economically valuable certainly in 1926, and in some cases in 1925.

The winter herring fishery which commenced in November is being closely followed, and samples from the catches have been taken twice weekly and examined for length, age, sex, state of maturity, and number of vertebrae. The data obtained, in conjunction with the results of Herring race investigations in 1913 and 1914, reported on by Dr. Orton, should yield useful information on the composition of the shoals visiting Plymouth each winter.

During the month of October, Mr. Ford, after attending the meeting of the Challenger Society in Aberdeen, visited the leading fishing ports on the East Coast, and gained an insight into the routine methods of landing and selling fish at the different markets, as well as the collection of the statistics of landings. He was also able to see something of the methods of curing and smoking fish, the preparation of fish meal, fertiliser, and glue.

Dr. Lebour has devoted most of her time to the study of the Euphausiidæ of the Plymouth district, these being specially interesting as fish food, since they are fed upon largely by the Herring during the winter fishery. The most important of these is *Nyctiphanes couchii*, but three others have been found breeding in the district. The life-histories of all four are being studied, one paper having been already published in the Journal on the early larval stages and a second one being in preparation in which it is hoped to complete the study of the later stages. Nearly all the stages in the life-history of *Nyctiphanes* have now been studied and drawn, and most of those of *Meganyctiphanes*, the larval stages of the two being recognisable at all ages in the plankton. Besides these the young of two species of *Thysanoessa* are being worked at, and it is hoped to differentiate *T. neglecta* and *T. inermis*, so that they also may be recognised in all stages.

A paper by Dr. Lebour on the food of young Herring has been published, showing that the larvæ feed more frequently at, or near, the surface than at greater depths. Samples of adult Herring have been regularly examined for food, when these fish are landed at Plymouth.

The experiment has been continued of keeping living plankton in the plunger jars. Some anglers (*Lophius piscatorius*) were hatched from the spawn and kept alive for eleven days, and a lobed Ctenophore, probably *Bolina*, was reared from the egg or very young larva and reached a length of 30 mm. These Ctenophores were seen to devour young fishes, including the Anglers, using their lobes to enclose the captured food. Other plankton organisms seen to capture living young fishes were the Phyllosoma larva of *Palinurus* and the Copepod *Anomalocera Pattersoni*. The larva of *Squilla* was kept alive for some weeks, and was seen to capture living food nearly as large as itself, using its predaceous claws for firmly holding its prey.

Mr. F. S. Russell has made a special study of the vertical distribution of pelagic stages of young fishes. To assist in this work the Admiralty were good enough to lend to the Association a depth recorder, which gives a graphic tracing of the course of the net through the water, from which the depth at which the net is fishing at any moment can be measured with accuracy. During May, June, and July a series of day hauls were taken from the shore to the 40-fathom line. The stations in deeper water were fished with the stramin ring trawl, and at each of them hauls of ten minutes duration were made at 4 or 5 different depths. At the inshore stations a one-metre bolting silk tow-net was used. For this net Mr. Russell devised a special releasing apparatus designed to close the net while being towed horizontally, stout enough to bear the attachment of the somewhat bulky depth recorder.

There are certain indications that some species of young fish are most abundant at one depth and others at another.

The volumes of macro-plankton taken at each haul show that in the deeper offshore waters during the middle of the day in these months, macro-plankton is very scarce in the upper 7 or 8 fathoms, then suddenly increases below this. On July 1st, when working where the depth of water was 26 fathoms, at 5 fathoms in a ten-minutes' haul there were only 50 cc. of plankton, while at 9 fathoms the plankton catch measured 300 cc. As shallower water is approached the depth at which the greatest abundance of plankton begins becomes less, and close inshore there is almost as much plankton at the surface as in deeper layers. This may be due to increasing turbidity of the water near the coast, causing less penetration of light. Very near the shore also a mixing of the water layers occurs. The young fish also show a tendency to shun the surface layers in the daytime, becoming more abundant there as the shore is reached.

Further, Mr. Russell carried out a series of hauls on July 15th-16th, showing the diurnal vertical migration of the macro-plankton. With the ring trawl, in a depth of 26 fathoms, he took sets of ten-minute hauls at five different depths at the following times: 4.30-5.30 p.m. (sunlight), 9-10 p.m. (dusk), 12-1 a.m. (dark), 4-5 a.m. (dawn), 10-11 a.m. (sunlight).

These samples showed that whereas at 4 p.m. the plankton exhibited its usual daylight distribution, by 10 p.m. the surface layers were as thickly populated as the deeper water; and also that by midnight many forms that haunt the bottom during the day were very abundant 10 fathoms above the bottom. At 10 a.m. the next day the usual daily distribution had been resumed.

An account of Mr. O. D. Hunt's study of the food of the bottom-living animals has been published in the Journal. In continuation of this work Mr. Hunt is investigating the micro-biology of the bottom deposits, and also carrying out feeding experiments with suspension-feeding animals (small bivalves), in order to get information on the comparative value of different food-materials in promoting growth.

An experiment to determine the rate of digestion and frequency of feeding of the starfish *Astropecten* was carried out at Pier Cellars. The starfishes and the small bivalves on which they were fed were kept successfully during fine weather in submerged boxes suspended from the pier.

Mr. H. W. Harvey has worked hydrographic stations in the *Salpa*, as during the previous two years. The data obtained are being sent to the International Council and to the French Fishery Department for co-ordination with the French and Irish results. Samples have also been collected for hydrogen ion and phosphate determination by Dr. W. R. G.

Atkins. A record of the seasonal changes in temperature of the water at Station E 1, 22 miles S.W. of Plymouth, which is visited monthly, shows marked variations from year to year, such as may have a considerable influence on the biological conditions. Besides movement of the water mass, which was not very marked during 1922 and 1923, judging by the hydrographic data collected, it appears that evaporation from the surface of the sea plays an important part in regulating the seasonal changes in temperature. Evaporation is determined rather by the difference in vapour pressure between surface water and the air, than by the amount of wind. Particular attention is being paid to the temperature changes in the sea and to the causes which govern them.

From observations made by Mr. Harvey it appears that putrefaction of organic matter in sea-water gives rise to poisonous substances which are oxidised in the sea. Wide differences have been found between inshore and surface water and water from a depth of 20 fathoms or more, in their behaviour towards a number of easily oxidisable substances. From a study of the reaction, sea-water appears to contain one or more catalytic substances, probably organic compounds of iron, which promote oxidation. Substances which inhibit this catalysis are also present in greater amount in inshore and surface waters than in deep water from a distance offshore.

Mrs. E. W. Sexton has continued her experiments on certain new mutations in the eye-colour of *Gammarus chevreuxi*, to which reference was made in the last report. The new red mutation has proved to be essentially different from the original red one, which had previously been studied in detail, whilst a new white mutation, though in some respects suggesting the albino formerly met with, has also proved entirely different. The experiments have been continued this year in a special chamber, which is artificially warmed and kept at a temperature of about 70° F. By this means the time taken to complete the life of a generation is much shortened, so that a larger number of generations are produced in the year and results are obtained much more rapidly. A paper dealing with the times required for development at different temperatures is in course of preparation. Mrs. Sexton has received valuable help in her work from Miss A. R. Clark.

Working under the direction of a Committee of the Institution of Civil Engineers, Dr. F. D. White and Dr. C. M. Yonge, both of the University of Edinburgh, have continued experiments on the effect of poisons in destroying the larvæ of the wood-boring mollusc *Teredo* (the Ship-worm), and trials are being made with wood impregnated with different poisons, with a view to discovering a method of preventing the ravages of these animals in marine structures built of wood.

Three students training for research, with grants from the Department

of Scientific and Industrial Research, are now working at the Laboratory. These are Mr. F. T. Pentelow, of Cambridge, who is studying *Myxosporidia* parasitic in fishes; Mr. N. J. Berrill, of Bristol University, whose subject is the influence of the environment on developing eggs; and Mr. C. F. Hickling, of Cambridge, who, by means of voyages on commercial steam trawlers, is investigating the effects of physical conditions on the distribution of marine animals.

### Department of General Physiology.

During the year Dr. Atkins extended his work on the phosphate content of fresh and salt waters, and the seasonal changes were traced through a second year. At Station E1 the total consumption of phosphate was closely similar to that which occurred during 1923, but on the whole the changes took place earlier in the year. This appears to be correlated with a high sunshine record for March. The deep water off Norway and to the west of Scotland, from which samples were obtained through the courtesy of the Fishery Board for Scotland, was found to be remarkably rich in phosphate, and it was shown that even during the winter the surface waters of the Eastern Mediterranean and Red Seas were denuded of phosphate. Determinations were also made upon the solubility of various phosphates at different hydrogen ion concentrations.

Dr. Atkins and Miss E. G. Wilson collaborated in a critical study of various analytical methods for the estimation of phosphate and their liability to error on account of the presence of other substances.

Dr. H. H. Poole carried out preliminary work upon the measurement of the penetration of light into water by means of a photo-electric apparatus devised by him. This was continued by Dr. Atkins, mainly at the pier in Cawsand Bay. The site proved remarkably convenient for all the work which it was possible to do in comparatively shallow water.

Experiments have also been carried out upon the preservation of nets by means of copper oleate dissolved in petrol, which had been found valuable in the United States. Silk tow-nets soaked in frequent changes of sea-water were found to be rotten in about a month, whereas those treated with copper oleate are still serviceable after almost four months' soaking.

Mr. C. F. A. Pantin is continuing his researches on amœboid movement. An unexpected similarity appears to subsist between amœboid and other forms of contractility. Amœboid activity only takes place over a definite range of hydrogen ion concentration. If the hydrogen ion concentration be raised, amœboid activity is reversibly inhibited as is the case also with muscular and ciliary activity. This effect is shown to be due to the hydrogen ions and not to the acid radicle or concentration

of carbon dioxide present. In the presence of citrate and tartrate radicles amœbæ can stand a higher concentration of hydrogen ions; this protective effect is as yet inexplicable.

By means of an accurate method of measuring amœboid activity quantitatively, the effect of changes of temperature has been determined in two kinds of limax marine amœbæ. In both cases it is shown that amœboid activity is reversibly inhibited near  $-3^{\circ}$  C., and rises to a maximum in the one case at  $20^{\circ}$  C., and in the other at  $22^{\circ}$ - $23^{\circ}$  C. Above the remarkably low optimum the activity rapidly falls to zero and ends in complete inhibition and death. The inhibition by heat is shown to be due to the destruction of some definite mechanism necessary for amœboid activity.

The curve relating amœboid activity to temperature is closely similar to those obtained for ciliary and heart activities.

A careful analysis of the mechanics of amœboid movement shows that the effect of temperature cannot be explained by supposing activity to be controlled directly by a chemical reaction. But there appears to be strong evidence that the activity is directly controlled by the rate at which the sol endoplasm changes into the gel ectoplasm and vice versa. This change may be effected by a chemical reaction which would thus control activity only indirectly.

Since knowledge of the effect of temperature on the viscosity of protoplasm was necessary in the foregoing work, a series of experiments were performed to determine this in the protoplasm of Nereis eggs by Heilbrunn's centrifuge method. The results showed that there is a progressive increase in viscosity as the temperature falls, the increase becoming very great near  $0^{\circ}$  C. Attention is redirected to the necessity of correcting the temperature coefficients of biological processes for changes in viscosity. It is shown that, if this correction is made, the temperature coefficient becomes sensibly constant over a wide range.

### Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association:—

ATKINS, W. R. G. *The Rapid Determination of available Phosphates in soil by the coeruleo-molybdate reaction of Denigès.* Journ. Agric. Sci., 1924, Vol. XIV, pp. 192-197.

ATKINS, W. R. G. *The Electrical Conductivity of Extracts from Soils of various types, and its use in detecting infertility.* Journ. Agric. Sci., Vol. XIV, 1924, pp. 198-203.

ATKINS, W. R. G. *Notes on the Filtration and other errors in the Determination of the Hydrogen Ion Concentration of Soils.* Sci. Proc. Roy. Dublin Soc., Vol. XVII, 1924, pp. 341-347.



- ATKINS, W. R. G. *Solubility of Phosphates in Relation to Hydrogen Ion Concentration*, "Nature," Vol. CXIV, 1924, p. 275.
- ATKINS, W. R. G., AND HARRIS, G. T. *Seasonal Changes in the Water and Heleo-plankton of Fresh-water Ponds*. Sci. Proc. Roy. Dublin Soc., Vol. XVIII, 1924, pp. 1-21.
- ATKINS, W. R. G., AND LEBOUR, M. V. *The Habitats of Limnaea truncatula and L. pereger in Relation to Hydrogen Ion Concentration*. Sci. Proc. Roy. Dublin Soc., Vol. XVII, 1924, pp. 327-331.
- BARCROFT, J., AND BARCROFT, H. *The Blood Pigment of Arenicola*. Proc. Roy. Soc. B., Vol. XCVI, 1924, pp. 28-42.
- BARGER, G. *Report on the Work of C. M. Yonge at Plymouth*. Dept. Scientific and Industrial Research. Deterioration of Structures in Sea-Water. Fourth (Interim) Report of Com. Inst. C.E., 1924, pp. 6-8.
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- DAKIN, W. J., AND FORDHAM, M. G. C. *The Chemotaxis of Spermatozoa and its Questioned Occurrence in the Animal Kingdom*. Brit. Journ. Exp. Biol., Vol. I, 1924, pp. 182-200.
- DE MORGAN, W. *Foettingeria actiniarum (parasitic in Anemones)*. Quart. Journ. Micr. Sci., Vol. LXVIII, 1924, pp. 343-360.
- HAAS, P., AND RUSSELL-WELLS, B. *On the Significance of the Ash Content of certain Marine Algæ*. Biochem. Journ., Vol. XVII, 1923, pp. 696-706.
- HENTSCHEL, C. C. *On a new Ciliate, Cryptochilum boreale nov. sp. from the intestine of Echinus esculentus Linn., together with some Notes on the Ciliates of Echinoids*. Parasitology, Vol. XVI, 1924, pp. 321-328.
- HOGBEN, L. T., AND HOBSON, A. D. *Studies on Internal Secretion. III. The Action of Pituitary Extract and Adrenaline on Contractile Tissues of certain Invertebrata*. Brit. Journ. Exp. Biol., Vol. I, 1924, pp. 487-500.
- KYLIN, H. *Studien über die Delesseriaceen*. Lunds Univ. Arsskr. N.F. Avd. 2, Bd. XX, 1924, pp. 1-111.
- LEBOUR, M. V. *Food Chains in the Sea*. Trans. and Proc., Torquay Nat. Hist. Soc., Vol. IV, 1922-23, pp. 18-22.
- ORTON, J. H. *An Account of Investigations into the Cause or Causes of the Unusual Mortality among Oysters in English Oyster Beds during 1920 and 1921*. Part I, Report. Part II, Appendices. Ministry of Agriculture and Fisheries, Fishery Invest., Ser. II, Vol. VI, 1923, No. 3; 1924, No. 4.
- ORTON, J. H. *Some new Commensals in the Plymouth District*. "Nature," Vol. CXII, 1923, p. 861.
- ORTON, J. H. *Sex-change and Breeding in the Native Oyster, O. edulis*. "Nature," Vol. CXIV, 1924, pp. 191-192.
- ORTON, J. H. *English Enemies of the American Slipper-limpet*. "Nature," Vol. CXIV, 1924, p. 312.

- ORTON, J. H. *An Experimental Effect of Light on the Sponge, Oscarella.* "Nature," Vol. CXIII, 1924, p. 924.
- ORTON, J. H., AND LEWIS, W. H. *A Plea for Continuous Fundamental Research on the Problems of River Pollution.* "Nature," Vol. CXIII, 1924, p. 236.
- PANTIN, C. F. A. *On the Physiology of Amœboid Movement. II. The Effect of Temperature.* Brit. Journ. Exp. Biol., Vol. I, 1924, pp. 519-538.
- STURCH, H. H. *On the Life-History of Harveyella pachyderma and H. mirabilis.* Ann. Bot., Vol. XXXVIII, 1924, pp. 27-42.
- WALTON, A. *Studies on the Physiology of Reproduction, I. The Flocculation of Sperm Suspensions in Relation to Surface Charge.* Brit. Journ. Exp. Biol., Vol. II, 1924, pp. 13-20.
- WHEELER, J. F. G. *The Growth of the Egg in the Dab (Pleuronectes limanda).* Quart. Journ. Micr. Sci., Vol. LXVIII, 1924, pp. 641-660.
- YONGE, C. M. *Experimental work carried out at the Plymouth Marine Biological Laboratory during July and August, 1922.* Dept. Scientific and Industrial Research. Deterioration of Structure, in Sea-Water. Fourth (Interim) Report of Com. Inst. C.E. 1924, pp. 9-22.

### The Library.

Both the general library and the special physiological library have continued to increase during the year, and the collection of books dealing with the science of the sea is now one of the most complete in the country.

The thanks of the Association are again due to numerous Government Departments, Universities, and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library. Thanks are due also to those authors who have sent reprints of their papers to the Library.

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## Vice-Presidents, Officers, and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1924-25 :—

*President.*

Sir E. RAY LANKESTER, K.C.B., LL.D., F.R.S.

*Vice-Presidents.*

The Duke of BEDFORD, K.G.	The Right Hon. AUSTEN CHAMBERLAIN, M.P.
The Earl of STRADBROKE, C.V.O., C.B.	G. A. BOULENGER, Esq., F.R.S.
Viscount ASTOR.	W. B. HARDY, Esq., Sec. R.S.
Lord MONTAGU OF BEAULIEU.	Sir ARTHUR STEEL-MAITLAND, Bart., M.P.
The Earl of BALFOUR, K.G., F.R.S.	Prof. W. C. McINTOSH, F.R.S.
The Right Hon. Sir ARTHUR GRIFFITH-BOSCAWEN.	

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Prof. E. S. GOODRICH, F.R.S.	Prof. D. M. S. WATSON, F.R.S.
LANCELOT T. HOGBEN, Esq., D.Sc.	

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*Hon. Secretary.*

E. J. ALLEN, Esq., D.Sc., F.R.S.,  
The Laboratory, Citadel Hill, Plymouth.

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G. P. BIDDER, Esq., sc.D.	LOTHIAN D. NICHOLSON, Esq. (Fishmongers' Company).
E. T. BROWNE, Esq.	Major NIGEL O. WALKER, O.B.E. (Fishmongers' Company).
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W. T. BRAND, Esq. (Fishmongers' Company).	Sir ARTHUR E. SHIPLEY, G.B.E., D.Sc., F.R.S. (Cambridge University).
GEORGE EVANS, Esq. (Fishmongers' Company).	F. CHALMERS MITCHELL, Esq., C.B.E., D.Sc., F.R.S. (British Association).
His Honour Judge CHAPMAN (Fishmongers' Company).	Prof. E. W. MACBRIDE, D.Sc., F.R.S. (Zoological Society).

## List of Annual Subscriptions

Paid during the Year, 1st April, 1924, to 31st March, 1925.

	£	s.	d.
Dr. W. M. Aders . . . . .	1	1	0
E. J. Allen, Esq., D.SC., F.R.S. . . . .	1	1	0
G. L. Alward, Esq. . . . .	1	1	0
William Arkwright, Esq. (the late) . . . . .	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S. . . . .	1	1	0
Prof. W. Bateson, F.R.S. . . . .	1	1	0
W. J. Bazeley, Esq. . . . .	1	1	0
Lieut.-Col. T. T. Behrens . . . . .	1	1	0
N. J. Berrill, Esq. . . . .	1	1	0
Colonel H. F. Bidder (1923 and 1924) . . . . .	2	2	0
Mrs. M. G. Bidder . . . . .	1	1	0
E. J. Bles, Esq., D.SC. . . . .	1	1	0
H. H. Bloomer, Esq. . . . .	1	1	0
H. Moss Blundell, Esq. . . . .	1	1	0
Mrs. H. Moss Blundell . . . . .	1	1	0
J. O. Borley, Esq. (1920—1923) . . . . .	4	4	0
L. A. Borradaile, Esq., SC.D. . . . .	1	1	0
E. G. Boulenger, Esq. . . . .	1	1	0
Prof. G. C. Bourne, D.SC., F.R.S. (1924 and 1925) . . . . .	2	2	0
Sir J. Rose Bradford, K.C.M.G., M.D., D.SC., F.R.S. . . . .	1	1	0
Brighton Public Library . . . . .	1	1	0
L. R. Brightwell, Esq. (1924—1926) . . . . .	3	3	0
H. H. Brindley, Esq. . . . .	1	1	0
R. H. Burne, Esq. . . . .	1	1	0
L. W. Byrne, Esq. . . . .	1	1	0
Dr. W. T. Calman, F.R.S. . . . .	1	1	0
H. Graham Cannon, Esq., D.SC. (1924 and 1925) . . . . .	2	2	0
G. S. Carter, Esq. . . . .	1	1	0
Prof. C. Chilton . . . . .	1	1	0
Dr. James Clark . . . . .	1	1	0
Carried forward . . . . .	39	18	0

	£	s.	d.
Brought forward	39	18	0
R. S. Clark, Esq., D.S.C.	1	1	0
Lieut.-Col. A. M. Cockshott, R.A.S.C.	1	1	0
J. F. Coonan, Esq. (1924 and 1925)	2	2	0
J. Omer Cooper, Esq. (1923 and 1924)	2	2	0
Miss E. J. Courthope	1	1	0
L. R. Crawshay, Esq.	1	1	0
Capt. G. C. C. Damant, R.N.	1	1	0
Prof. Otto V. Darbishire	1	1	0
Dr. W. Cameron Davidson	1	1	0
Mons. J. Delphy		12	6
W. C. De Morgan, Esq.	1	1	0
G. Despott, Esq. (1924 and 1925)	2	2	0
Director of Agriculture and Fisheries, Travancore, S. India	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
H. V. Dobson, Esq., J.P. (1924 and 1925)	2	2	0
Prof. J. C. Drummond	1	1	0
F. Martin Duncan, Esq.	1	1	0
J. S. Dunkerly, Esq., PH.D.	1	1	0
Howard Dunn, Esq., J.P.	1	1	0
George Evans, Esq.	1	1	0
G. P. Farran, Esq.	1	1	0
Rev. W. Fotheringham, F.R.M.S. (1924 and 1925)	2	2	0
G. Herbert Fowler, Esq., B.A., PH.D.	1	1	0
Dr. E. L. Fox	1	1	0
Thomas Fox, Esq.	1	1	0
Miss E. A. Fraser, D.S.C. (1924-1926)	3	3	0
Prof. F. W. Gamble, D.S.C., F.R.S.	1	1	0
John S. Gayner, Esq.	1	1	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
J. R. Groome, Esq.	1	1	0
Sir Eustace Gurney	1	1	0
Wilfred Hall, Esq.	1	1	0
A. C. Hardy, Esq.	1	1	0
Cecil B. Harmsworth, Esq.	1	1	0
A. E. Hefford, Esq. (1921-1923)	3	3	0
Carried forward	86	14	6

## LIST OF ANNUAL SUBSCRIPTIONS.

1005

	£	s.	d.
Brought forward	86	14	6
Sir W. A. Herdman, C.B.E., F.R.S. (the late), 1923 and 1924	2	2	0
Prof. J. P. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
T. V. Hodgson, Esq.	1	1	0
Dr. Lancelot T. Hogben	1	1	0
Capt. G. C. L. Howell	1	1	0
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Plymouth Corporation (Museum Committee)	1	1	0
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Mrs. H. Porter	1	1	0
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C. Tate Regan, Esq., F.R.S. (1922-1924)	3	3	0
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Chas. H. Rudge, Esq.	1	1	0
Carried forward	133	18	6

## LIST OF ANNUAL SUBSCRIPTIONS.

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Edgar Schuster, Esq., D.SC. . . . .	1	1	0
W. L. Selater, Esq. . . . .	1	1	0
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Harold Thompson, Esq. . . . .	1	1	0
Sir Herbert Thompson, Bart. . . . .	1	1	0
Sir John Thornycroft, F.R.S. . . . .	1	1	0
Torquay Natural History Society . . . . .	1	1	0
Lieut.-Col. H. J. Walton, I.M.S., M.D., F.R.C.S., C.M.Z.S. . . . .	1	1	0
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W. A. Willes, Esq. . . . .	1	1	0
R. Winckworth, Esq., M.A., F.R.G.S. . . . .	1	1	0
Total . . . . .	<u>157</u>	<u>0</u>	<u>6</u>

## List of Donations to the Building Extension Fund

For the Year 1st April, 1924, to 31st March, 1925.

	£	s.	d.
Zoological Society of London . . . . .	300	0	0
The Worshipful Company of Fishmongers . . . . .	250	0	0
The Mac Fisheries, Ltd. . . . .	100	0	0
Colonial Office, "Discovery" Committee . . . . .	52	10	0
Jesus College, Oxford . . . . .	50	0	0
E. T. Browne, Esq. . . . .	500	0	0
Herbert Pantin, Esq., and Mrs. H. Pantin . . . . .	52	10	0
Lady Murray . . . . .	50	0	0
Mrs. E. T. Browne . . . . .	25	0	0
Ambrose Harding, Esq. . . . .	25	0	0
Miss J. Lindley . . . . .	25	0	0
Arthur W. W. Brown, Esq. . . . .	20	0	0
Colonel W. Harding . . . . .	15	15	0
W. T. Brand, Esq. . . . .	10	10	0
W. Hargreaves Brown, Esq. . . . .	10	10	0
His Honour Judge Chapman . . . . .	10	10	0
P. Cox, Esq. . . . .	10	10	0
G. Herbert Fowler, Esq., PH.D. . . . .	10	10	0
J. J. Lister, Esq., F.R.S. . . . .	10	10	0
W. De Morgan, Esq. . . . .	10	10	0
C. F. A. Pantin, Esq., and Mrs. Pantin . . . . .	10	10	0
W. A. Pantin, Esq. . . . .	10	10	0
Sir William Plender, Bart., G.B.E. . . . .	10	10	0
Sir James Roberts, Bart. . . . .	10	10	0
The Telegraph Construction and Maintenance Company . . . . .	10	10	0
Mrs. F. J. Weldon . . . . .	10	10	0
Viscount Astor . . . . .	10	0	0
Miss Anna Bayly . . . . .	10	0	0
His Grace The Duke of Bedford, K.G. . . . .	10	0	0
Sir Horace Darwin, K.B.E., F.R.S. . . . .	10	0	0
Prof. J. Stanley Gardiner, F.R.S. . . . .	10	0	0
Cecil Harmsworth, Esq. . . . .	10	0	0
Miss M. V. Lebour, D.SC. . . . .	10	0	0
Carried forward . . . . .	1,672	5	0



## LIST OF ANNUAL SUBSCRIPTIONS.

	£	s.	d.
Brought forward . . . . .	1,672	5	0
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A. H. Blake, Esq. . . . .	5	5	0
W. Edgar Evans, Esq. . . . .	5	5	0
Sir Sidney Harmer, K.B.E., D.S.C., F.R.S. . . . .	5	5	0
H. W. Harvey, Esq. . . . .	5	5	0
C. W. Heath, Esq. . . . .	5	5	0
Mrs. H. Porter . . . . .	5	5	0
N. C. Burton Row, Esq. . . . .	5	5	0
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C. F. Vincent, Esq. . . . .	5	5	0
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Miss Friedli Abel . . . . .	3	0	0
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H. H. Brindley, Esq. . . . .	2	2	0
Coates & Co. . . . .	2	2	0
W. E. Coombes, Esq. . . . .	2	2	0
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Joseph Gundry & Co., Ltd. . . . .	2	2	0
Eden Phillpots, Esq. . . . .	2	2	0
John Ridgewell, Esq. . . . .	2	2	0
E. M. Wallis, Esq. . . . .	2	2	0
Howard Dunn, Esq. . . . .	2	0	0
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L. A. Borradaile, Esq., D.S.C. . . . .	1	1	0
F. Pelham Brown, Esq. . . . .	1	1	0
C. L. Fox, Esq. . . . .	1	1	0
R. Gurney, Esq. . . . .	1	1	0
A. C. Hardy, Esq. . . . .	1	1	0
Carried forward . . . . .	1,807	10	0

## LIST OF ANNUAL SUBSCRIPTIONS.

1009

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Stanley Kemp, Esq., D.Sc.	1	1	0
Prof. A. Liversidge	1	1	0
W. S. Millard, Esq.	1	1	0
George Ord, Esq.	1	1	0
E. S. Russell, Esq., D.Sc.	1	1	0
C. H. Sanders, Esq.	1	1	0
H. P. Sherwood, Esq.	1	1	0
Lieut.-Commdr. R. Spry, R.N.	1	1	0
H. H. Sturch, Esq.	1	1	0
Commander Charles Williams, R.N., M.P.	1	1	0
John R. Baker, Esq.	1	0	0
Julian S. Huxley, Esq.	1	0	0
Admiral Sir Edmond Slade, K.C.I.E., K.C.V.O.	1	0	0
J. J. Judge, Esq.		10	6
Total	£1,823	12	6

## For the Year commencing April 1st, 1925.

	£	s.	d.
The Worshipful Company of Fishmongers (Second donation)	250	0	0
The Institution of Civil Engineers	100	0	0
Magdalen College, Oxford	25	0	0
Dr. G. P. Bidder	500	0	0
E. J. Allen, Esq., D.Sc., F.R.S.	10	10	0
W. T. Brand, Esq. (Second donation)	10	0	0
Birmingham University Zoology Club	3	3	0
Prof. W. Bateson, F.R.S.	2	2	0
Stuarts and Jacks, Ltd.	2	2	0
Prof. J. Bayley Butler	1	1	0
J. T. Cunningham, Esq.	1	1	0
Total	904	19	0
Year 1924-25	1823	12	6
Year commencing 1st April, 1925	904	19	0
Total	£2,728	11	6

Dr. *Statement of Receipts and Payments for the*

		GENERAL					
		£	s.	d.	£	s.	d.
To Balance from 31st March, 1924 :—							
Cash in hand.....		12	12	9			
Cash at Bank .....		687	11	8	700	4	5
„ Grants :—							
„ Ministry of Agriculture and Fisheries Grant from Development Fund .....		9,500	0	0			
Fishmongers' Company .....		600	0	0			
Royal Society, Gore Fund (for two years, 1924 and 1925) .....		60	0	0			
British Association .....		25	0	0	10,185	0	0
„ Subscriptions .....					157	0	6
„ Donations .....					0	10	6
„ Sale of Specimens ( <i>less</i> Purchases) .....					885	7	5
„ „ Fish ( <i>less</i> Expenses) .....					22	15	6
„ „ Nets, Gear, and Hydrographical Apparatus .....					332	5	11
„ Table Rent (including Trustees of the Ray Lankester Fund, £20; Oxford University, £52 10s.; London University, £50; Bristol University, £25; Birming- ham University, £10 10s.; Leeds University, £10 10s.)					347	19	0
„ Tank Room Receipts .....					359	5	7
„ Interest on Investments :—							
4% War Stock .....		3	2	8			
4% New Zealand Stock .....		12	14	8			
Deposit Account .....		17	1	4	32	18	8
„ Royalties on Films.....					37	14	10

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£13,061 2 4

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The Association's Bankers hold on its behalf :—  
 £410 14s. 8d. 4% New Zealand Stock, 1943-63.  
 £78 9s. 4d. 4% War Loan, 1929-42.  
 £51 War Savings Certificates.

## BUILDING

		£	s.	d.
To Donations .....		1,823	12	6
„ Interest on Building Fund Deposit .....			2	2 1
		1,825	14	7

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## PUBLICATION OF DR.

		£	s.	d.
To Grant from Royal Society .....		£75	0	0

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OF THE UNITED KINGDOM.

1011

Year, 1st April, 1924, to 31st March, 1925.

£r.

FUND.

By Salaries :—	£	s.	d.	£	s.	d.
Director .....	962	10	0			
Physiologist .....	807	10	0			
Naturalists .....	2,890	5	6			
Hydrographer .....	498	6	8	5,158	12	2
„ Laboratory Wages (including National Insurance).....				1,506	14	4
„ Annual Upkeep of Library .....				375	14	5
„ Scientific Publications :—						
Journal, Vol. XIII, Nos. 2 and 3 .....	513	15	10			
Less Cost of Special Plates .....	52	15	0			
	461	0	10			
Less Sales .....	49	8	0	411	12	10
„ Annual Upkeep of Laboratories and Tank Rooms :—						
Buildings and Machinery .....	267	9	7			
Electricity, Gas, Coal, and Water .....	243	11	7			
Chemicals and Apparatus .....	497	19	8			
Rates, Taxes, and Insurance .....	74	8	3			
Travelling .....	95	19	3			
„ Challenger Society Meetings .....	56	4	0			
Stationery, Postages, Telephone, Carriage, and Sundries.....	352	7	9	1,588	0	1
„ Annual Maintenance and Hire of Boats :—						
Wages (including Diet Allowance, National Insurance, and Casual Labour) .....	1,552	19	3			
Coal and Water.....	619	10	9			
Maintenance and Repairs, with Nets, Gear, and Apparatus .....	989	4	11			
Boat Hire and Collecting Expeditions .....	22	4	1			
Insurance .....	308	14	11	3,492	13	11
„ Balance :—						
Cash in hand .....	37	5	2			
Cash at Bank.....	490	9	5	527	14	7
				<u>£13,061</u>	<u>2</u>	<u>4</u>

FUND.

By Balance, Cash at Bank .....	£	s.	d.
	1,825	14	7
	<u>£1,825</u>	<u>14</u>	<u>7</u>

M. V. LEBOUR'S BOOK.

By Balance, Cash at Bank .....	£	s.	d.
	75	0	0

Examined and found correct,

(Signed) N. E. WATERHOUSE.  
W. T. CALMAN.  
L. D. NICHOLSON.  
J. O. BORLEY.

3 Frederick's Place,  
Old Jewry, London, E.C. 2.  
28th April, 1925.

## Marine Biological Association of the United Kingdom.

## LIST

OF

## Governors, Founders, and Members.

1ST SEPTEMBER, 1925.

\* Member of Council. † Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea.

C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual Subscription.

## I.—Governors.

The British Association for the Advancement of Science, <i>Burlington House, W.</i> 1 .....	£750
The University of Oxford .....	£552 10s.
The University of Cambridge.....	£500
The Worshipful Company of Clothworkers, 41, <i>Mincing Lane, E.C.</i> 3	£500
The Worshipful Company of Fishmongers, <i>London Bridge, E.C.</i> 4	£18,105
The Zoological Society of London, <i>Regent's Park, N. W.</i> 8 .....	£500
Bayly, Robert (the late) .....	£1000
Bayly, John (the late) .....	£600
Thomasson, J. P. (the late) .....	£970
*G. P. Bidder, Esq., Sc.D., <i>Cavendish Corner, Cambridge</i> .....	£3008
*E. T. Browne, Esq., B.A., <i>Anglefield, Berkhamsted</i> .....	£1035

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1884	The Royal Microscopical Society, 20, <i>Hanover Square, W. 1</i> .....	£152 10s.
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1884	Gassiott, John P. (the late) .....	£100
†1884	Lankester, Sir E. Ray, K.C.B., F.R.S., 44 <i>Oakley Street, Chelsea, S.W. 3</i> .....	£101
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1884	Moseley, Prof. H. N., F.R.S. (the late) .....	£100
1884	The Rt. Hon. Lord Avebury, F.R.S. (the late) .....	£100
1884	Poulton, Prof. Edward B., M.A., F.R.S., <i>Wyleham House, Oxford</i> .....	£105
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1884	Worthington, James (the late) .....	£100
1885	Derby, the late Earl of .....	£100
1887	Weldon, Prof. W. F. R., F.R.S. (the late) .....	£100
1888	Bury, Henry, M.A., <i>The Gate House, 17 Alumdale Road, Bournemouth</i> <i>West</i> .....	£100
1888	The Worshipful Company of Drapers, <i>Drapers' Hall, E.C.</i> .....	£315
1889	The Worshipful Company of Grocers, <i>Poultry, E.C. 2</i> .....	£120
1889	Thompson, Sir Henry, Bart. (the late) .....	£110
1889	Revelstoke, The late Lord .....	£100
*1890	Riches, T. H., B.A., <i>Kitwells, Shenley, Herts</i> .....	£430
1902	Gurney, Robert, <i>Ingham Old Hall, Stalham, Norfolk</i> .....	£107 1s.
1904	Shaw, J., K.C., <i>Kentchurch Court, Hereford</i> .....	£113
1909	Harding, Colonel W., <i>The Hall, Madingley, Cambridge</i> .....	£115 15s.
1910	Murray, Sir John, K.C.B., F.R.S. (the late) .....	£100
1912	Swithinbank, H., F.R.S.E., F.R.G.S., <i>Denham Court, Denham, Bucks.</i> .....	£100
1913	Shearer, Dr. Cresswell, F.R.S., 4, <i>Fitzwilliam Road, Cambridge</i> .....	£100
1913	Heron-Allen, E., F.R.S., F.L.S., F.R.M.S., F.G.S., <i>Large Acres,</i> <i>Selsey Bill, Sussex</i> .....	£125 15s.
1920	McClean, Capt. W.N., 1, <i>Onslow Gardens, S.W. 7</i> .....	£100
1920	Berry, H. Seymour, <i>Merthyr Tydfil, Glam.</i> .....	£105
1920	Llewellyn, D. R. .....	£105
1921	Harmer, F. W. (the late).....	£100
1923	Worth, R. H., 42 <i>George Street, Plymouth</i> .....	£115 15s.
1924	The MacFisheries, Ltd., 125 <i>Lower Thames Street, E.C. 3</i> .....	£100
1924	Murray, Lady, 7 <i>Egerton Gardens, London, S.W. 3</i> .....	£100
1925	The Institution of Civil Engineers, <i>Great George Street, Westminster,</i> <i>S.W. 1</i> .....	£100

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- 1900 Aders, Dr. W. M., *Zanzibar, East Africa* .....£5 and Ann.  
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 1889 Alward, G. L., *Enfield Villa, Humberstone Avenue, Waltham, Grimsby* Ann.  
 1910 Ashworth, Prof. J. H., D.Sc., F.R.S., *The University, Edinburgh* ..... Ann.  
 1921 Askwith, The Rt. Hon. Lord, K.C.B., D.C.L., *5 Cadogan Gardens, London, S.W. 3* ..... £5  
 †1911 Astor, Viscount, *4, St. James' Square, London, S.W. 1* .....£10 and C.  
 1910 Atkinson, G. T., *Fisheries Office, Esplanade, Lowestoft* ..... Ann
- 1920 Baker, J. R., *New College, Oxford and The Dell, Malvern Wells*...£1 and C.  
 1923 Barnard, K. H., *South African Museum, Cape Town*..... £10  
 1923 Barnard, T. T., *King's College, Cambridge* ..... £11  
 1923 Barnes, H. F., *South-Eastern Agricultural College, Wye, Kent*..... Ann.  
 1919 Bateson, Prof. W., F.R.S., *The Manor House, Merton, S.W. 19* £2 2s. and Ann.  
 1919 Bawcomb, J. .... Ann.  
 1884 Bayly, Miss Anna, *Seven Trees, Plymouth* ..... £60  
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 1885 Beck, Conrad, *68, Cornhill, E.C. 3* ..... C.  
 1884 Beddington, Alfred H., *8, Cornwall Terrace, Regent's Park, N.W. 1* ... C.  
 †1907 Bedford, His Grace the Duke of, K.G., *Endsleigh, Tavistock* ...£10 and C.  
 1919 Behrens, Lt.-Col. T. T., *United Service Club, Pall Mall, London, S.W. 1* ..... Ann.  
 1925 Berrill, N. J., *Southlands, Knowle, Bristol* ..... Ann.  
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 1910 Bidder, Mrs. M. G., *Cavendish Corner, Cambridge* ..... Ann.  
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 1910 Bloomer, H. H., *75-77, Colmore Row, Birmingham* ..... Ann.  
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 1922 Blundell, Mrs. H. Moss, *Callipers Hall, Chipperfield, King's Langley, Herts* ..... Ann.  
 1910 Borley, J. O., O.B.E., M.A., *Fisheries Laboratory, Lowestoft* £1 1s. and Ann.  
 1918 Borradaile, L. A., Sc.D., *Selwyn College, Cambridge* .....£1 1s. and Ann.  
 1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W. 8* ... Ann.  
 \*1884 Bourne, Prof. Gilbert C., M.A., D.Sc., F.R.S., *Twynning Manor, Tewkesbury* .....£8 3s. and Ann.  
 1898 Bowles, Col. Henry, *Forty Hall, Enfield* ..... Ann.

- 1924 Bowman, Dr. A., *Marine Laboratory, Wood Street, Torry, Aberdeen* ... Ann.
- 1910 Bradford, Sir J. Rose, K.C.M.G., M.D., D.Sc., F.R.S., 8, *Manchester Square, London, W. 1* ..... Ann.
- \*1920 Brand, W. T., 58, *Eaton Place, London, S.W. 1* ..... £40 10s.
- 1920 Buchanan, J. Y., F.R.S. .... £45
- 1902 Brighton Public Library (Henry D. Roberts, Chief Librarian) ..... Ann.
- 1924 Brightwell, L. R., *Wakeford Lodge, High Street, Hampton Hill, Middlesex* Ann.
- 1918 Brindley, H. H., *St. John's College, Cambridge* ..... £2 2s. and Ann.
- 1886 Brooksbank, Mrs. M., *Leigh Place, Godstone, Surrey* ..... C.
- 1884 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants* ..... £20 and C.
- 1924 Brown, W. Hargreaves, c/o Messrs. Brown, Shipley and Co., *Founder's Court, Lothbury, E.C. 2* ..... £10 10s.
- 1892 Browne, Mrs. E. T., *Anglefield, Berkhamsted* ..... £35 and Ann.
- 1923 Browne, F. Balfour, *Gonville and Caius College Cambridge* ..... £5
- 1920 Burne, R. H., M.A., *Royal College of Surgeons, Lincoln's Inn Fields, London, W.C. 2* ..... £5 and Ann.
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The late Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the late Duke of ARGYLL, the late Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr. CARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY, the late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000. Since that time investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the hire and maintenance of fishing-boats, and the salary of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council, by an Honorary Secretary and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances. The reader is referred to page 4 of the Cover for information as to membership of the Association.



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