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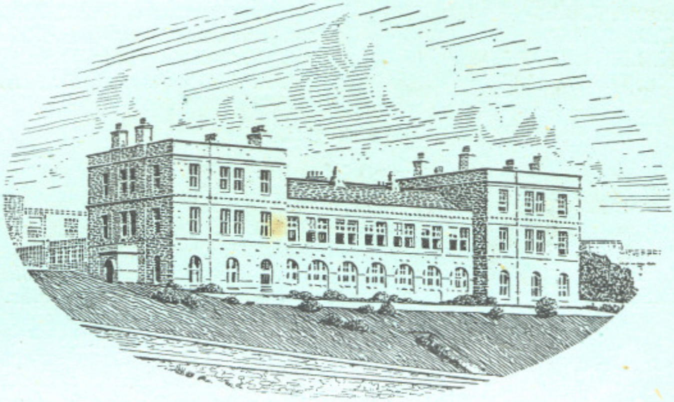

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THE SEASONAL CYCLE IN THE CORNISH PILCHARD, *SARDINA PILCHARDUS* WALBAUM

By C. F. Hickling, M.A.

Ministry of Agriculture and Fisheries

(Text-figs. 1–8)

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INTRODUCTION

From July 1935 to November 1938 research was carried out on the stock of pilchards (*Sardina pilchardus* Walbaum) which supplies the pilchard fishery of Cornwall.

During these forty-one months some ninety-nine samples were obtained from the Cornish fishing ports, or an average of between two and three samples per month; but the seasonal distribution of sampling was necessarily irregular in consonance with the great seasonal variation in the intensity of the fishery. Most of the samples were obtained in the months from July to October, the height of the fishery.

Some of the work was done at the Plymouth Laboratory, and I will here express my thanks to the late Director, Dr S. Kemp, F.R.S., and his staff for the facilities they provided.

Since the samples were obtained from the commercial fishing fleets, they do not necessarily represent the stock of pilchards in the north-western English Channel, or even in the vicinity of the Cornish coast, but only that part of it which is within reach of the fishing fleets and available for capture by the fishing gears used. The distinction may be important, for there are discrepancies between, for example, the spawning season, as deduced from the state of the gonads in commercially caught pilchards, and as proved by the presence of pilchard eggs in the plankton, which shows that the fishing fleets do not sample the whole pilchard stock.

The pilchard of Cornwall has been investigated by Fage (1920), le Danois (1929), le Gall (1930, 1937) and Hickling (1938, 1939). Le Gall showed that these pilchards consist mainly of fish of 18–26 cm., with an average length of about 23 cm., and of ages 2–8 or more, but chiefly 5 and 6. Both these points have been confirmed by Hickling (1939). As to the rate of growth, there is complete agreement among all these writers that growth is rapid in the first three years of life, so that a length of about 19 cm. is attained by the end of the third year of life, but that thereafter growth becomes very slow, a matter of 1 cm. or less per annum. Sexual maturity sets in during the third to fifth years of life, so that the reduction in the rate of growth coincides with the onset of maturity. The greatest length found among the 12,000 pilchards handled in the present research was 27·9 cm.

The pilchards of Cornwall, therefore, as they occur in the commercial catches, are large and old members of their species, which have already passed through their period of rapid growth before entering the fishery, and have become slow growers.

In the present research, each sample consisted of about 100 fish. Each fish in each sample yielded the following information:

Length from tip of lower jaw to end of the largest caudal fin ray.

Stomach contents, both the average weight of food per fish and the nature of the food.

Intestinal fat. The amount of intestinal fat was noted.

Gonads. The sex of the fish, the state of development of the gonads, and the weight of the gonads.

Weight. The weight of the gutted fish.

From each fish a scale was taken, and these have been used in the present paper in connexion with the growth of the fish and the scale.

On the minced flesh of a few pilchards, prepared as for canning with the head, tail and gut removed, an analysis was made of the fat, water and ash content. About five fish were taken from each of three groups of pilchards, namely, the small fish of less than 20 cm., the medium-sized fish of 20–23 cm., and the large fish of 23 cm. and upwards. In many samples, however, especially in winter and spring, small fish were lacking.

The fat content was estimated, during the first year's work, by digesting the minced flesh with hydrochloric acid, and then extracting the fat from the resulting soup with ether and petroleum ether. For the remainder of the time, however, the much handier Soxhlet method, as modified by Wimpenny (1938), was used, and it was therefore necessary to compare the results obtained by the two methods. For this purpose a number of determinations of the fat content of the same material was made by both methods; the results showed a very high degree of agreement, but the Soxhlet method gave consistently the higher figures for fat content. The correlation coefficient between the two series of determinations was +0·93, and the regression coefficient for the conversion of the bulk-extraction results to the Soxhlet results is given by:

(Percent. fat, Soxhlet) = 1·1 (percent. fat, bulk ext.) + 1·4.

By means of this formula the first year's results were converted so as to be comparable with the later years' results, and they are so presented in this paper. The word 'fat' will here be used to mean 'ether-soluble matter'.

The water content was estimated by prolonged evaporation on a steam bath, followed by drying to a constant weight in an electric oven at 80° C.

The ash content was estimated by combustion. Unfortunately, in samples containing an abundance of fat, it was often impossible to avoid the ignition of the melted and boiling oil, which was then liable to froth over the sides of the pot. A higher degree of experimental error is therefore to be expected in the estimations of ash, than in those of fat and water.

A residual percentage remains after the estimation of the percentage of water, fat and ash. It is obvious that most of this residue must consist of protein, but a test was made to see whether variations in this residue could be ascribed to variations in the protein. For this purpose, the table published by Lepierre & Rodriguez (1938) was used. These workers estimated the monthly percentage of fat, water, ash and protein in the Portuguese pilchard, over a period of nearly three years. Their data were extracted so as to compare the monthly variations in protein content with the monthly variations in the 'residue' remaining after summing the percentage of fat, water and ash and subtracting the sum from 100. The average percentage of protein was 19·04, of residue 19·60, and the coefficient of correlation between the variations in the two was +0·708, a very significant correlation. There would therefore seem to be justification for regarding the 'residue' as largely protein.

The Seasonal Variation in Mean Weight

Since for each fish in each sample the length and the gutted weight are known, it is an easy matter to calculate the mean weight of a gutted pilchard at each unit of length in each month during which the samples were collected. In Fig. 1 the mean monthly weights are shown graphically as they occur in pilchards of 19, 21 and 24 cm., representing respectively the small, medium and large pilchards. To show the remaining centimetre lengths would overcrowd the figure, and would be unnecessary, since they all show a similar seasonal variation.

Fig. 1 shows that the mean weight of a gutted pilchard of given length may fluctuate very widely. For example, in pilchards of 21 cm. the lowest mean weight was 66, the highest 88 g. Such a wide variation suggests that in the pilchard, as in the salmon and the herring, the flesh plays a very important part in the seasonal cycle of metabolism.

Within each year, the average weight tends to show a seasonal fluctuation; it is least in March and April, and then increases to a peak in June, July or August. Later, in the autumn, it decreases again, and then reaches a second and greater peak in November or December. Thereafter there is a rapid decline to the minimum in March or April.

In 1936, as compared with 1935 and 1937, the mean weight of the pilchard was low.

These results may be compared with those of Ramalho (1933, 1935) on the same species of pilchard caught off Portugal. He dealt with specimens much smaller than those which appear in the pilchard shoals off Cornwall, but found that in those also the minimum weight occurred towards the end of the winter, in March and April. From this minimum there was an increase to the optimum in October or November (as shown in his paper of 1933) or in the months from June to August (as shown in his paper of 1935). The two stocks of pilchards differ, therefore, in their annual cycle of fluctuations in mean weight, in that those of Portugal appear to reach their maximum mean weight some 2 or 3 months earlier than those of Cornwall, though both have their minimum mean weight at much the same season, and, secondly in that the pilchards of Cornwall have two peaks in their mean weight, in early summer and again in late autumn, whereas those of Portugal show one peak only, in late summer or autumn.

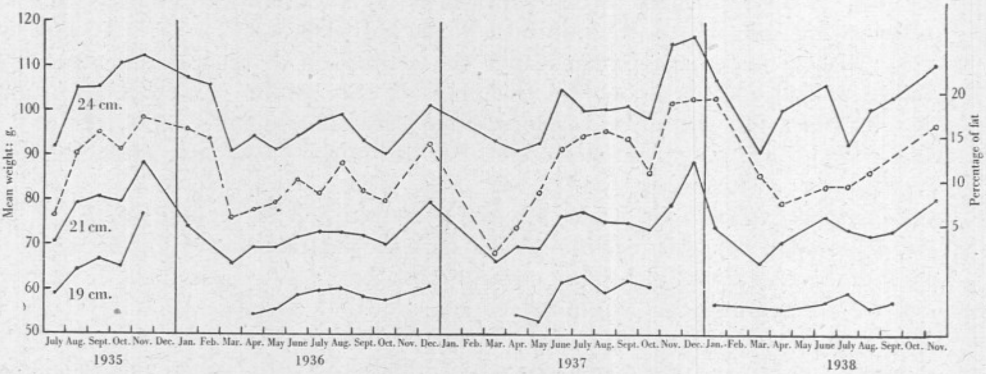

Fig. 1. Solid line: monthly mean weight in grams of gutted pilchards of 19, 21 and 24 cm. (scale on left). Broken line: monthly mean percentage of fat in pilchards of 20–22 cm. (scale on right).

THE COMPOSITION OF THE FLESH

In Fig. 1 the broken line shows the mean monthly variations in the percentage of fat in the wet weight of pilchards of medium size (20–22 cm.). The figure shows clearly that the seasonal variations in mean weight described above are very closely associated with the variations in the fat content. The fat content tends to be at its lowest in the months of March and April, and then to increase to a peak, first, in the summer, in June, July or August, and then to a second and greater peak in November and December. Moreover, just as, in 1936, the average weight of a pilchard of given length was lower than in the corresponding months of 1935, 1937 and 1938, so also was the fat content lower.

In the table below are shown the correlation coefficients between the variations in the monthly mean weight of pilchards of 19, 21 and 24 cm., and the variations in the monthly mean percentage of fat in pilchards of less than 20 cm., of 20–22 cm., and of 23 cm. and greater.

Correlation between weight of fish and fat content of fish				
of	of	Correlation coefficient	Degrees of freedom	P
19 cm.	<20 cm.	+0·65	18	<0·01
21 cm.	20–22 cm.	+0·80	30	<0·01
24 cm.	>23 cm.	+0·89	31	<0·01

The correlation coefficient becomes greater among the larger fish, but, according to the tables of probability in Fisher (1938), all three values are significant, in that a result equally good would be obtained by chance in uncorrelated material less than once in a hundred trials.

These results make it certain that the observed seasonal fluctuations in the mean weight of the fish, shown in Fig. 1, are largely due to fluctuations in the fat content. Wagner & Ramalho (1936) were able to show that in the Portuguese pilchard also there is a close correlation between the condition of the fish, expressed as the relation between weight and length, and the fat content. Moreover, when the results of Ramalho (1933, 1935) on the seasonal variations in mean weight of the pilchard are compared with those of Lepierre & Rodriguez (1938) on the seasonal variations in fat content, a close relationship is shown between the two.

In a short paper Hickling (1938) has shown the seasonal variations in the percentage of fat, water and ash as they occurred in pilchards of 20–22 cm. The variations in the fat content have already been reproduced in Fig. 1 of the present paper, and it has just been shown that the percentage of fat is correlated with the changes in mean weight in small, medium and large pilchards.

The water content fluctuates inversely with the fat content. Bruce (1924) showed this very clearly in the herring; in the pilchard the inverse relation is remarkably good. Below are given the correlation coefficients between the mean monthly percentages of fat and water as found in the present series of samples.

Correlation coefficients between fat content and water content of pilchards

Length cm.	Coefficient	Degrees of freedom	P
<20	−0·912	11	<0·01
20–22	−0·996	20	<0·01
>23	−0·978	20	<0·01

There is a very high degree of inverse correlation between the two, indeed, in pilchards of 20–22 cm. it would hardly be possible to expect a higher correlation coefficient in biological material.

The ash content tends to fluctuate directly with the water content and therefore inversely with the fat content. Below are given the correlation coefficients between the monthly mean variations in the fat content and the ash content.

Correlation coefficients between the water content and ash content of pilchards

Length cm.	Coefficient	Degrees of freedom	*P*
<20	−0·3320	11	>0·1
20–22	+0·5478	20	<0·01
>23	+0·5759	20	<0·01

The values for *P* show that, in pilchards of 20–22 and of 23< cm., there is a significant positive correlation between the variations in water content and ash content. In small pilchards of less than 20 cm. there is no correlation. But since these small pilchards are usually present in the samples only during the summer months, when the variations in fat and water content are not great, it may be that variations due to experimental error, which, for the reasons given earlier, may be great in the estimation of ash, are of the same order of magnitude. However this may be, in the medium- and large-sized pilchards, for which a more complete series is available, there is a significant positive correlation between the water content and ash content.

The average percentage composition of the pilchard at the time of maximum mean weight in November, December and January was:

Length cm.	Fat	Water	Ash	Residue
20–22	17·2	63·6	1·6	17·6
23	16·0	64·5	1·7	17·8

At the time of minimum mean weight in March and April the composition was:

Length cm.	Fat	Water	Ash	Residue
20–22	5·8	75·0	1·9	17·2
>23	5·1	75·9	2·0	17·0

The average composition throughout the whole series of samples, which approximates closely to the average composition at the height of the pilchard fishery is:

Length cm.	Fat	Water	Ash	Residue
<20	13·6	66·8	1·6	18·0
20–22	11·2	68·6	1·7	18·5
>23	9·4	70·2	1·8	18·6

These figures show that during the height of the pilchard fishery, when almost the whole of the year's catch is landed, the smaller pilchards are more valuable than the large ones from the nutritional point of view.

To sum up, therefore, in this series of samples of pilchards, the water and ash content varied inversely with the fat content, and therefore inversely with the mean weight of the fish.

If an increase in the weight of the fish is accompanied by a decrease in the percentage of water present, it follows that the actual weight of water present in a fish of given length must remain more or less stationary. In the present experiments, both the mean weight of the fish and the percentage of fat, water and ash are known, and it is therefore a simple calculation to find, in a fish of given weight, what is the actual weight of water, fat and ash present, and also, by subtraction, what is the weight of the 'residue' which, of course, is chiefly protein.

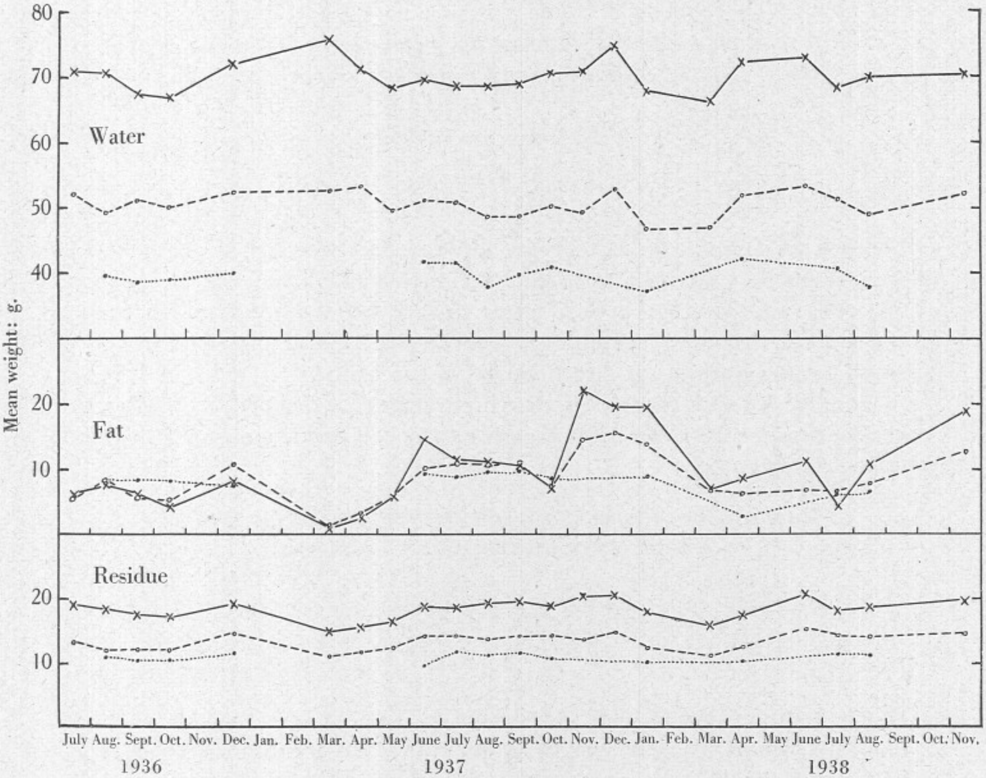

Fig. 2. Calculated monthly mean weight of water, fat and 'residue' in pilchards of three length groups.

...... 19 cm. ——— 21 cm. ——— 24 cm.

In Fig. 2, pilchards of 19 cm. are taken to represent the fish of less than 20 cm., pilchards of 21 cm. those of 20–22 cm., and pilchards of 24 cm. to represent those greater than 23 cm. Fig. 2, therefore, represents the seasonal variations in the calculated weight of fat, water, ash and protein present in pilchards of 19, 21 and 24 cm. respectively.

Fig. 2 shows that the amount of water present varies from sample to sample, but there is no regular seasonal variation, and there is no correlation between the weight of water present and the total weight of the fish. In the table below, the correlation coefficients between the weight of the fish and the weight of water present, are shown.

Correlation coefficients between the mean weight of the fish and the calculated weight of water present

Length cm.	Coefficient	Degrees of freedom	P
19	+0·4423	11	>0·1
21	+0·3248	21	>0·1
24	+0·3694	21	0·1

There is no significant correlation between the two, for an equally good relation could be obtained by chance in uncorrelated material at least once in ten trials, and therefore it can be concluded that the observed fluctuations in the amount of water present are due to chance and play no part in the seasonal fluctuations in the mean weight of the fish.

On the other hand, there is a very high degree of correlation between the seasonal fluctuations in the mean weight of the fish and those in the calculated weight of fat present.

Correlation coefficients between the mean weight of the fish and the calculated weight of fat present

Length cm.	Coefficient	Degrees of freedom	P
19	+0·8298	18	<0·01
21	+0·8609	30	<0·01
24	+0·9150	31	<0·01

The correlations are all very significant.

The fluctuations in mean weight of the entire fish are due therefore largely to fluctuations in the fat content and not to fluctuations in the water content. The ash content may be neglected, as it is too small to have much effect on the total weight of the fish.

But Fig. 2 also shows that the amount of 'residue', that is, mainly protein, shows a small seasonal variation, and that, among the larger fish at least, it is positively correlated with the fat variations.

Correlation coefficients between the seasonal fluctuations in the calculated weight of fat and of protein present

Length cm.	Correlation coefficient	Degrees of freedom	P
19	+0·094	11	>0·1
21	+0·571	20	<0·01
24	+0·663	20	<0·01

In the fish of 19 cm. there is no correlation between the seasonal variations in fat content and the variations in the quantity of 'residue', but there is a significant correlation in the case of the fish of 21 and 24 cm. This suggests that the small pilchards do not draw upon the reserves contained in the 'residue', but the larger fish do, and since the value of the correlation coefficient is greater in pilchards of 24 cm. than in those of 21 cm., the amount to which the 'residue' is drawn upon at the times when fat is also drawn upon is greater in the larger fish than in those of intermediate size.

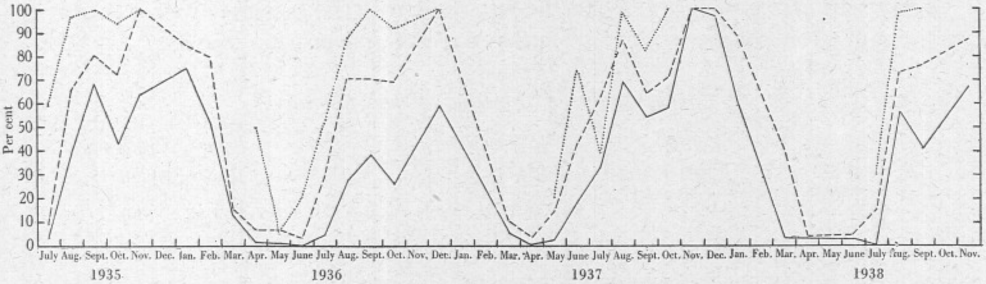

Fig. 3. Monthly mean percentage of pilchards of three length groups with abundant intestinal fat.

...... <20 cm. ——— 20–22 cm. ——— >23 cm.

So far the fat contained in the flesh has been dealt with, that is, fat present beneath the skin and between the muscles. But abundant fat is also stored in the mesentery. Fig. 3 shows the seasonal variations in the percentage of fish having abundant fat in the mesentery. In spite of the very arbitrary classification of the fish into 'fat' and 'not fat', the percentage of 'fat' fish shows a well-marked seasonal variation almost identical with that for the percentage of fat present in the flesh.

Correlation coefficients between the seasonal variations in the intestinal fat and the percentage of fat in the flesh

Length cm.	Coefficient	Degrees of freedom	*P*
<20	+0·4804	18	0·02–0·05
20–22	+0·8526	30	<0·01
>23	+0·7094	31	<0·01

The correlations are significant in pilchards of large and of medium size, but doubtfully so in small pilchards, since an agreement as good as that found could be obtained by chance in uncorrelated material between twice and five times in a hundred trials. But the correlation is a general one only; in the spring the body fat begins to regenerate before the intestinal fat, and in the autumn the intestinal fat is drawn upon to a greater extent than the body fat.

A series of four analyses showed that one gram of body fat is equivalent to 0·133 g. of intestinal fat in the seasonal variations of the fat content of the fish.

One other organ which, in many species of fish, is the main storage organ for fat, namely, the liver, remains to be considered. Lovern & Wood (1937) say of the liver of the herring that it is a small organ of little or no significance as a depot for fat. The same is true of the liver of the pilchard. It usually weighs between 1 and 2 g. only, and the two following analyses, made respectively in April, when the fat content of the fish as a whole is at its lowest, and in November, when the fat content of the fish as a whole is at its highest, show the percentage of fat, water, ash and residue present.

Composition of the liver of the pilchard

	Fat	Water	Ash	Residue
April	3·61 %	72·30 %	1·83 %	22·26 %
November	7·50 %	70·84 %	1·75 %	19·91 %

Clearly, the liver never contains much fat, and since the entire liver only weighs a gramme or two any fat stored in such small quantities in such a small organ may be neglected.

It would therefore appear that, as this section shows, the seasonal variations in the mean weight of a fish of given length described on p. 118 are due to the seasonal variations in the fat content, and, among the larger fish, to a slight extent to the seasonal variation in the content of 'residue'. The water content plays no part in the seasonal variation in mean weight of the fish, nor does the ash. The various constituents of the flesh of the pilchard may be likened to two, water and ash, which form a constant framework; one, fat, which is stored up in, and withdrawn from, this framework, the variations in fat causing the variations in mean weight; and finally, 'residue', no doubt mainly protein, which should probably be regarded as part of the permanent framework, but which can also be drawn upon to some extent. Besides the fat in the flesh, the intestinal fat is stored and replenished in the same way and should be added to the former.

Fig. 2 also shows that though the quantity of water increases rapidly with increase of length, the quantity of fat is approximately the same for fish of 19, 21 and 24 cm.

Actually there is a very slight increase in the calculated average weight of fat present, namely, from 7·8 g. in fish of 19 cm. to 8·4 g. at 24 cm. But when the data are tested statistically by the analysis of variance, the difference cannot be considered significant. This means that in relation to the weight of the fish, which continues to increase with increase of length, the quantity of fat must diminish.

THE SPAWNING CYCLE

In examining the factors which may account for the withdrawal of fat from the tissues of the fish, and its restoration, the easiest to attack is the spawning cycle, which accounts directly for the loss of a large amount of material, which must later be replaced.

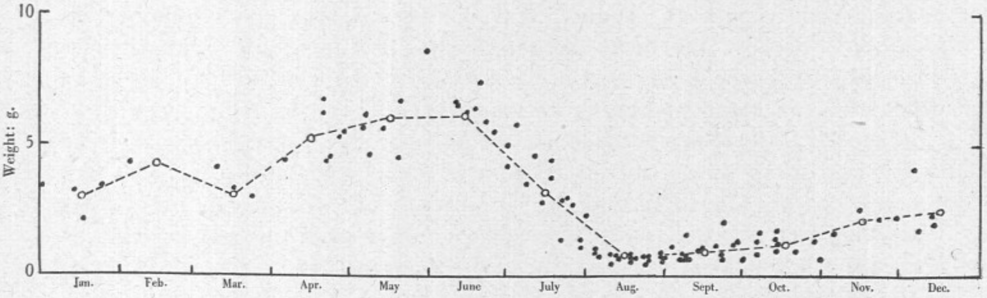

Fig. 4. Average weight of testis in each sample with (indicated by circles) calculated monthly averages.

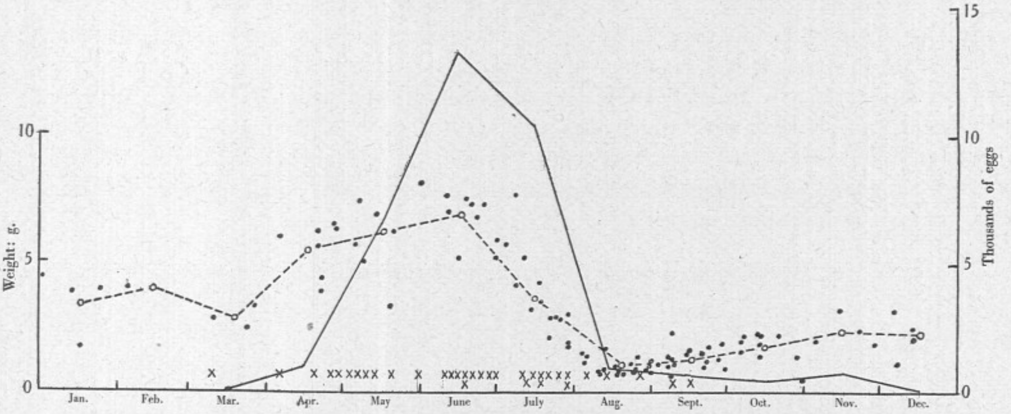

Fig. 5. Spawning of pilchards: females. Average weight of ovary in each sample, with monthly mean weights (scale on left), and average number of pilchard eggs taken per haul off Plymouth (scale on right).

● average weight of ovary.
○ calculated monthly average.
× spawning fish.
— monthly average number of pilchard eggs off Plymouth.

In Figs. 4 and 5 the average weights of the gonads of male and female pilchards, respectively, in each sample are plotted against the date of collection. Unlike the data as to mean weight and chemical composition, which differed from one year to another and so necessitated the setting out of the data by years, the course of the spawning cycle was practically identical in all the years covered by this research, and so it is possible to plot all the data as if they had been collected in a single year.

The broken line joins the monthly means.

It should here be said that, with very rare exceptions, all the pilchards dealt with have been mature fish. However, a few sterile fish have been found, in which the gonads have degenerated or have even disappeared entirely. In the latter case the fish may be 'capons', and enormously fat.

Figs. 4 and 5 show that the sexual cycle, as shown by the changes in mean weight of the gonads, is identical in males and females. Both have their lowest mean weight in August, and recovery begins in September and October. The very low mean weights found in August and September are due, not only to the exhaustion of the gonads of the mature fish, but to the very small gonads of pilchards which are about to mature for the first time.

From the time of minimum mean weight in August there is a very steady increase in mean weight to a maximum in June. Then follows a very rapid decrease to the August minimum. The month of July, in each of the four years, has seen this collapse of the gonads, for in each the gonads have had a high mean weight at the beginning of the month, and a low mean weight at the end of it.

The increase in weight of the gonads in preparation for spawning is accompanied by well-known changes in their naked-eye appearance. The shrivelled and semi-translucent spent testis loses its translucency and gradually becomes opaque and creamy white, until, at a certain indefinite point, a cut across such a testis will show the presence of ripe milt. Testes in this ripe condition have been found over the greater part of the year, as the table below shows. They occurred from January to September inclusive, though the highest percentages were found in the months from April to July. In June almost every testis was ripe.

Average percentage of spawning pilchards in each month

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
♂	3	7	16	53	86	97	54	6	1	0	1	0
♀	0	0	1	16	4	16	10	0·5	0·4	0	0	0

In the female the shrunken and translucent spent ovaries become opaque, and the ripening eggs begin to appear as minute white specks. The ovary continues to increase in size as these eggs enlarge, until the latter become pressed together and impart to the whole ovary a brilliant pinkish white colour. This is the penultimate stage of ripeness, and has been reached by a process as gradual and indefinite as the ripening of the testis.

But the final stage in the ripening of the ovarian eggs is quite definite. Some of the yolky eggs suddenly increase greatly in size and become translucent; they cause the whole ovary to become swollen, and ripe eggs will run from the vent at the slightest pressure. The change, as Milroy showed in 1898, is due to the absorption of water by the yolky eggs. 'The increase in volume is mainly due to the water, the total solids present in the immature and mature ova being practically the same.' This may also be illustrated in my pilchard material. Below are given the percentage of fat, water, ash and residue in ovaries in the penultimate stage of ripeness, and in the actually ripe condition.

	Fat	Water	Ash	Residue
Penultimate stage of maturation	1·72 %	75·89 %	1·70 %	20·69 %
Ripe condition	1·21 %	83·81 %	1·20 %	13·78 %

The water content is much higher in the ripe ovaries, and the values for fat, ash and residue are correspondingly depressed. But if the composition of the dry material is compared, it is seen that the final process of ripening has involved no great change in the composition of the 'solids'.

	Fat	Ash	Residue
Penultimate stage of maturation	7·1 %	7·0 %	85·9 %
Ripe condition	7·4 %	7·4 %	85·2 %

There is good reason to believe, that, from the rarity with which this final or spawning stage is found in teleosts, it is usually sudden and short-lived; the fish quickly sheds the ripe eggs and the ovary then returns either to the spent condition, or, if spawning is repeated, to a condition indistinguishable from the former penultimate stage of ripeness. In the Californian pilchard *Sardina caerulea*, for example, Clark (1934) found only four pilchards in this condition in eleven years' study. In the table on p. 126 it will be seen that the mean monthly percentage of female pilchards in this final stage of ripeness was never greater than about 16 %.

The table on p. 126 shows that female pilchards in the final, or actually spawning, condition occurred from March to September, and most frequently in the months from April to July. These are consequently to be regarded as the spawning months, and principal spawning months, respectively, of the Cornish pilchard as deduced from the present material. No significance is to be attached to the lower value found in May.

The same table further shows that the male pilchards are ripe for spawning over a longer period than the females; this appears to be almost universal among fishes.

Russell (1938, 1939) gives data as to the number of pilchard eggs occurring in the plankton off Plymouth in 1937 and 1938; in Fig. 5 a curve is drawn showing the average number of pilchard eggs per month per standard haul in the two years. The first eggs were taken in April; they were most abundant in June and July, and became scarce in August, though small numbers continued to occur until December.

The estimate of the principal spawning season, as deduced from the average weight of the gonads and the presence of spawning females, is in excellent agreement with the spawning season as proved by the presence of the eggs in the plankton; but the continued presence in the plankton of small numbers of pilchard eggs throughout October and November cannot be accounted for in the present material. It may be that a little belated spawning takes place far out to sea beyond the normal range of the fishing fleets, and this is confirmed by Cunningham (1893), who mentioned that spawning takes place late in the season in September, 10 miles south of the Eddystone, much farther out than the pilchard fleets normally work.

The Rate of Feeding

The contents of the stomachs of about fifty pilchards from each sample were squeezed out on to a filter paper and weighed. This weight, divided by the number of stomachs taken, gave the average weight of food per stomach. In Fig. 6 the average values are plotted against the date of collection, all years' results being put on to the same graph since, as I have shown elsewhere (1938), the feeding cycle is repeated with the greatest regularity each year. The calculated monthly averages are also shown, and are joined by the broken line.

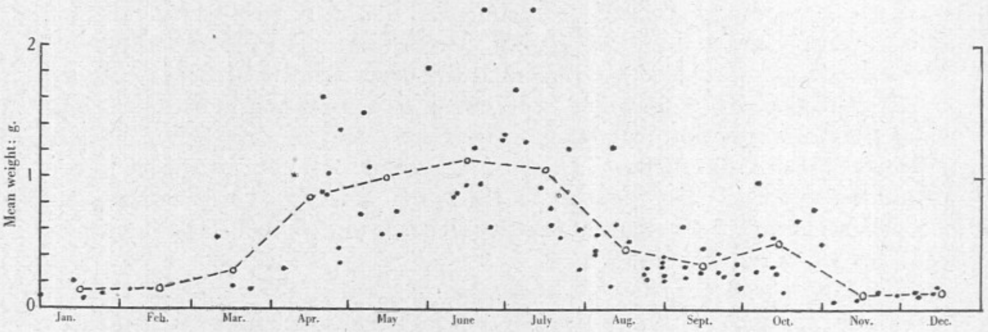

Fig. 6. Average weight of food per stomach in each sample, with monthly mean weights. Dots: average per sample of fifty stomachs 1935–8. Circles: calculated monthly averages.

The samples collected in November, December, January and February contained very little food, a nominal quantity of less than 0·1 g. per fish. In March, however, one sample contained an average of 0·27 g. per fish, and from April to October most of the samples gave evidence of active feeding. The heaviest individual average values were found in June and July, and in May, June and July every sample contained abundant food. In the latter part of August and in September the samples contained much less food, but in October there was a recurrence of samples containing more plentiful food.

The calculated monthly averages reflect these conclusions drawn from the individual samples; they show an increase in the average weight of food per stomach from February to a maximum in June. In July and August and September there is a decline, but a secondary increase occurs in October.

Clearly, the months of May, June and July are the principal months during which the pilchard feeds, with a secondary recovery in October, just before the winter fast sets in.

As far as I know, there have been no previous estimates of the seasonal rate of feeding in the pilchard. It is interesting to note, however, that in the herring, Savage (1935) found a very similar course of events. In that fish, however, the time of heaviest feeding was in May, with a secondary recovery in September. Fig. 6 shows that appreciable quantities of food are still being taken during August and September, which are the principal months of the commercial pilchard fishery. As this food is planktonic, the gut contents quickly liquefy, and for this reason pilchards cannot be despatched for long distances by rail. But if the gut is removed, this fish will travel as well as other species.

THE FOOD OF THE PILCHARD

A very rough analysis was made of the nature of the food of the pilchard throughout the year. The stomach contents of about fifty fish, after weighing, were shaken up in a jar of water and a few drops were withdrawn with a pipette and examined on a glass slide. One hundred 'unselected' organisms were classified under the six general headings, which were found to include all the most important and consistently recurring organisms:

(1) Copepods, including the adults and later developmental stages.

(2) Other Crustacea, including, beside adult ostracods, euphausiids, mysids and amphipods, the young and larval stages of many groups of Crustacea, including the earlier stages of copepods.

(3) Diatoms.

(4) Peridinians.

(5) Molluscs. Chiefly the larvae of lamellibranchs and gastropods, but also including, especially in June 1937, *Limacina*.

(6) Eggs. Including mainly the eggs of copepods, some of which, of course, may have been detached from the females after ingestion by the fish.

The results of the analysis are shown in Fig. 7. The percentages of organisms assigned to each of the six groups have been raised by the average weight of food per stomach in that sample, and all samples have been combined as monthly means. The reason for this treatment of the data is that the importance of each group of food organism is brought into relation with the general feeding cycle. The disadvantage of the method is that it does not, at the same time, indicate the relative importance of each group of organisms as food for the fish. One large crustacean larva or mysid may be equivalent in weight to several copepods, and one copepod to a great many diatoms or peridinians. Fig. 7, in fact, only shows which groups of organisms are of the greatest numerical importance in the different phases of the seasonal feeding cycle of the fish.

Besides the organisms grouped under the six main heads enumerated above, many others made occasional appearances; for example, tintinnids were frequent in one or two samples, while *Oikopleura*, *Sagitta* and very small fish were seen from time to time. But here attention will be confined to the six most important and constantly recurring groups.

The food of the Cornish pilchard is exclusively planktonic. It includes some very small forms, such as the diatom *Prorocentrum micans*, which was very abundant in some samples. But the gill rakers of the pilchard end in tufts of very fine processes (well figured by Schofield (1934) for the closely allied Californian pilchard, *Sardina caerulea*) and form a filtering apparatus much finer than that of the sprat, mackerel or even very small herrings, as I have found by examining these fish.

No analysis was attempted of the very small quantities of food present in the stomachs in winter. Much of it was unrecognizable, and may have been secretions from the walls of oesophagus and stomach, but the recognizable organisms included amphipods, a few diatoms and the nauplii of cirripedes.

Referring to Fig. 7, it will be seen that copepods were, numerically, one of the most important items in the food of the pilchard, and, when regard is had to their comparatively large size, they were in fact the most important. They reached their greatest importance numerically in May, June and July, at the time when the feeding of the pilchard was at its heaviest. Crustacea reached their maximum importance in May, but were an important item of food throughout the summer.

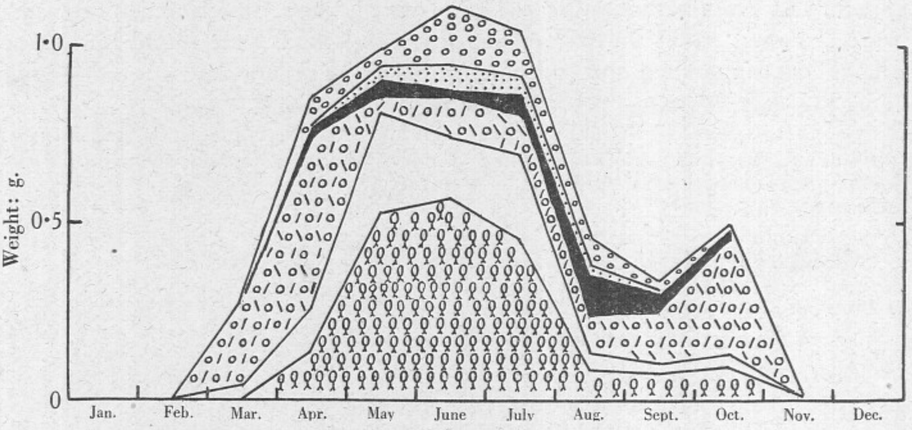

Fig. 7. Principal constituents of food of pilchard, calculated as monthly averages 1935–8.

♀♀♀ copepods.
☐ other Crustacea.
o\o\o diatoms.
■ peridinians.
∷∷ molluscs.
°°° eggs.

Diatoms showed two periods of greatest numerical importance. The first period was in the spring, and especially in April; the second in the autumn, and especially in October. The colour of the stomach contents of the pilchard in October was frequently green, and one or two of the samples were almost pure diatom. The food of the pilchard therefore closely reflects the well-known double nature of the annual diatom crop; indeed, the secondary recovery in the rate of feeding of the pilchard, in October, is almost wholly due to this autumn crop of diatoms. Lewis (1929) found that diatoms form a very important item in the food of the Californian pilchard also. Hart & Wailes (1932) found that this species feeds mainly on diatoms and crustacea, and only slightly on *Oikopleura*.

Peridinians had their greatest numerical importance in August and September, molluscs in May, June and July, and finally, eggs, chiefly copepod eggs, were most plentiful in June and July, a consequence, probably, of the maximum abundance of adult copepods, as shown by the stomach contents, in May and June.

Fage (1920) briefly summarized the previous work on the food of the pilchard. Cepède and Mangin both found young pilchards in the Channel and the Bay of Biscay feeding heavily on diatoms in September, though the larger specimens were not so exclusively feeding on them. Pouchet & le Guerre found adult pilchards with their stomachs containing an extraordinary number of peridinians, about 20 millions of *Peridinium polyedricum* Pouchet per specimen, apparently.

More recently Desbrosses (1933) has shown that, in the northern part of the Bay of Biscay, the food of the sardine or small pilchard consists, in July and August, of crustacea and especially copepods, though he also records gastropod larvae in July. But in September, October and November phytoplankton was predominant in the food, especially diatoms, and crustacea were very rare. These results are similar to those described above for the Cornish pilchard.

The food of the Cornish pilchard has been very carefully studied by Swithinbank & Bullen (1913). The summer pilchards, in Mount's Bay and Mevagissey Bay, were feeding mainly on copepods, chiefly *Pseudocalanus* and *Temora*, but in August, 1913, abundant phytoplankton was present in the stomachs. In October, phytoplankton was abundant in samples from Mevagissey Bay, with plentiful *Oikopleura* also, but in Mount's Bay *Oikopleura* was not detected, and the stomachs contained copepods, chiefly *Calanus*, and the mollusc *Limacina*. In January, a few fish larvae and eggs were found.

Comparing the stomach contents of the pilchard with plankton catches made at the same localities, Swithinbank & Bullen reached the conclusion that the pilchard is a selective feeder, for there were notable discrepancies between the organisms actually found in the stomachs of the pilchards and those taken by plankton nets in the vicinity. It would appear that, where both are available, the zooplankton is preferred to the phytoplankton, and this may even, according to the authors, affect the movements of the pilchard so that an abundance of phytoplankton on the usual fishing grounds may delay the arrival of the pilchards, as in August 1913.

The feeding cycle shown in Figs. 6 and 7 does indeed suggest that there is a considerable difference between the abundance of plankton and the amount of food in the stomach of the pilchard. For example, the average quantity of zooplankton taken appears to decline heavily after June, this decline being responsible for that of the average quantity of food as a whole, whereas there is no evidence that there is such a decline in the abundance of the zooplankton itself. On the contrary, at the nearby 'Seven Stones' lightship, according to Gough (1907) and Bygrave (1911) copepods, at least, remain abundant until November, and, more recently, Harvey, Cooper, Lebour & Russell (1935) show that, at a position 5 miles south of the breakwater at Plymouth, there is no decline in the abundance of zooplankton after June, but rather a continued increase to a maximum in August and September.

But after the month of June the pilchard shoals usually reach their maximum abundance and density in the coastal waters of Cornwall where the main fishery is carried on. Below are given, for the period covered by the present investigations, the average catch of pilchards per month per boat landing:

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Cwt.	7·6	1·8	9·2	7·7	6·9	9·8	7·7	19·5	20·5	13·2	6·5	5·0

In the months of August and September, and to a less extent, October, the average weight of pilchards per boat is much higher than at any other time of the year, clearly implying a much greater abundance of pilchards in these months than at other times. The available plankton must then be shared out among a much greater number of fish, resulting in a lowered average quantity for each.

The result, however, for the pilchards must be the same as an actual diminution in the abundance of plankton, namely, a lower average quantity of food available.

Wimpenny (1938) shows that there is a seasonal fluctuation in the fat (ether-soluble matter) in the plankton collected throughout the year at a series of stations off Flamborough Head. The lowest fat content was in February and April, and the maximum is reached in July. From July to September there was a decline in the fat content of the plankton, followed by a secondary increase in November and December. 'Biologically, these two maxima may be related to the spring and autumn outbursts of diatoms which are predecessors of fat storage by the zooplankton.'

In 1938 a few analyses were made of the fat content of the fresh food in the stomach of the pilchard. The results are given below as the percentage of fat in the dry weight of the food:

20 Apr.	20 June	4 July	11 July	18 July	17 Aug.	30 Aug.	15 Sept.
16·5 %	20·9 %	18·5 %	16·3 %	11·9 %	12·7 %	9·4 %	18·1 %

There was an increase in the fat content of the food from April to June, and then a steady decline through July to August, followed by an increase in September. It would appear, therefore, that, from June to September, not only is the quantity of food available to each pilchard decreasing, but that the food itself is becoming poorer in fat.

THE SEASONAL COURSE OF GROWTH

The scales of a fish have the function of covering the body, and since the number of scales does not increase, it follows that the existing scales must grow in proportion to the growth of that part of the body which they cover.

Where, therefore, there is evidence that the scale is growing, which it does by accretion at the margin, it can be assumed that the fish also is growing.

The upper surface of the scale, where this lies within the scale-pocket, is covered with fine striations, but these striations are interrupted or bent at the so-called winter rings, which run parallel to the margin of the scale. These rings provide fixed points by which an estimate can be made as to whether new material was being laid down at the margin of the scale at the time of collection.

For example, a large proportion of the scales collected in April and May show a winter ring just within the margin, with the first beginning of the resumption of the striated structure outside it, and it is reasonable to conclude that, in these samples, growth has just recommenced. From these months onward throughout the summer, the striations extend to the margin of the scale, but in the autumn and winter most of the scales have a structure at the margin which suggests that the winter ring is being formed there.

In the table below the average monthly percentages of scales examined which were estimated to have the winter ring at the margin are given. Only the scales of the smaller specimens were used, for in the scales of the larger specimens the winter rings become crowded near the margin and it becomes impossible to estimate the nature of the margin.

Percentage of scales with the winter ring at the margin

Jan.	86	Apr.	75	July	18	Oct.	82
Feb.	100	May	45	Aug.	28	Nov.	73
Mar.	79	June	10	Sept.	30	Dec.	92

Only in February (for which month, however, only two suitable scales are available) were the margins all of one type. In all other months both types of margins were found. But this lack of sharpness in the predominance of one type or the other is probably due to the difficulty of assessment already referred to.

The table shows that the scales have the winter ring at the margin from October to March, and to have the intermediate zone of striations at the margin from April to September. It follows that the scale grows from April to September, and this is confirmed by the finding of new striated growth at the margin of the scale, just outside the winter ring, in April and May.

Therefore the fish also probably grows in the months from April to September inclusive, but ceases to grow from October to March.

It also follows that only one winter ring is laid down each year, at least in the majority of the scales, so that a count of the winter rings allows of an estimate of the age of the fish in the pilchard, as in so many other species of fish.

DISCUSSION

It has been shown (p. 129) that the pilchard is exclusively a planktonic feeder and indeed has a feeding mechanism which enables it to feed on very small planktonic organisms. But the production of plankton in the sea is a strongly seasonal phenomenon and, therefore, the rate of feeding in the pilchard must always be strongly seasonal, as has been shown in Fig. 6. The whole metabolism of the fish must be adapted to the seasonal nature of its intake of material.

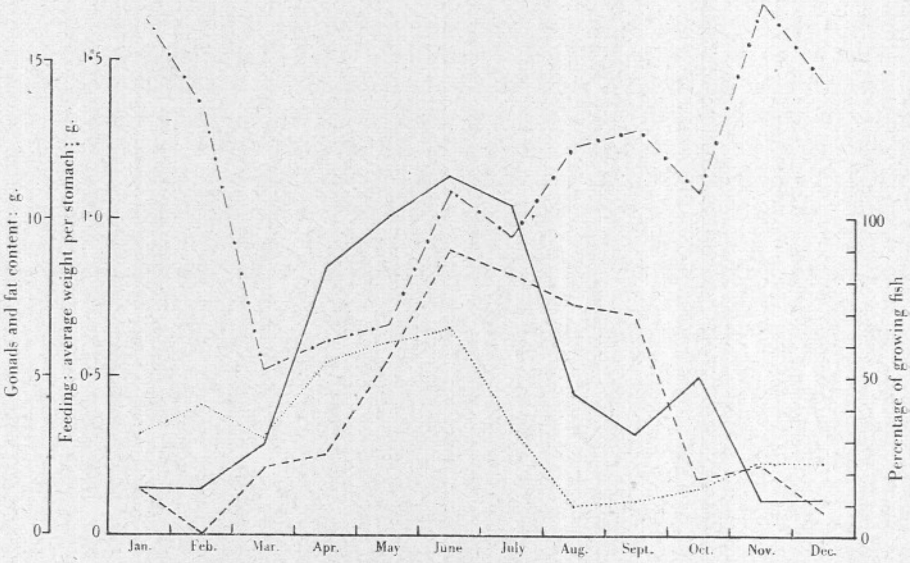

Fig. 8. The seasonal cycles of breeding, feeding, fat storage (scales on left), and percentage of growing fish (scale on right).

——— feeding. - - - - growth.
...... breeding. —·—— fat storage.

In Fig. 8 the results of all observations have been combined to show, as if in a single complete year, the seasonal course of the breeding cycle, the feeding cycle, the content of fat. The two factors named first are represented simply as monthly mean weights, for the course of these two cycles is so regularly repeated that they can be faithfully expressed in this way. But the content of fat has shown some variation from year to year and, therefore, in Fig. 8 the mean content of fat per month, calculated on the data of all years, gives a less satisfactory picture.

In Fig. 8 the breeding cycle is shown as the monthly mean weight of testis and ovary of fish of all sizes combined. The feeding cycle is expressed as the monthly mean weight of food per fish, and the fat cycle as the calculated monthly mean weight of fat present in fish of 19, 21 and 24 cm. combined. The data as shown in Fig. 8 are only intended to give a very general picture.

In Fig. 8 is also shown the seasonal cycle of growth, based on the table on p. 133.

The pilchard's year can be divided into three periods. In the first period, from April to July, feeding becomes vigorous, that is, the intake of material is great. But this is also the time of most active loss of material through spawning which is at its height in these months. As a result, however, of such active feeding, the fish is not only able to ripen its gonads but also to begin active growth and also to begin to replenish its store of fat. The figure shows, however, that the ripening of the gonads takes priority over both growth and fat storage.

The second period in the pilchard's year is from August to October. During this period feeding is less intense, and probably on a plankton poorer in fat than in the spring. But on the other hand, the gonads are quiescent and, therefore, the fish not only continues to grow but continues to lay in reserves of fat. In October feeding becomes brisker and on a plankton probably richer in fat; the gonads meanwhile are making no demands on the resources of the fish. Growth is mainly at an end for the year, and the result is a sudden and rapid accumulation of fat with which the fish can face its winter fast.

The third period of the pilchard's year is from November to March. During this period feeding is at a standstill, and the fish must draw upon its reserves for maintenance. Further, during this period the gonads show a slight but steady enlargement. The result is a heavy decline in the fat content of the fish, and a cessation of growth, which is marked on the scale as a winter ring.

It has been shown (p. 119) that the seasonal variations in the mean weight of a pilchard of given length are due chiefly to the seasonal variations in the weight of fat present, with the 'residue' contributing some part in the larger fish. The water and ash present were shown to play no part in this seasonal variation, being, as it were, the stable framework in which the variable constituents are stored. Therefore the same factors which bring about a seasonal variation in the reserves of fat present in the flesh of the pilchard cause a seasonal variation in the mean weight of a fish of given length.

The degree of exhaustion reached by the end of this period of fast depends on the amount of fat present when it began. In the table below are shown the mean weight of fat, including intestinal fat, present before the winter fast and at the end of the winter fast, in each year of the observations:

Year ...	1935–6	1936–7	1937–8
Wt. of fat before fast	18·87	12·06	24·57
Wt. of fat after fast	5·76	1·04	9·43
Loss of fat	13·11	11·02	15·14

In 1936–7, when the fast began with a lower fat content, the fat was almost all consumed by the end of the fast, but in 1935–6 and especially in 1936–7 there was a good balance remaining. One can only speculate as to what might happen if a year of poor condition, poorer even than that of 1936–7, were followed by a fasting period in which exceptional demands were made on the fat for maintenance.

In the pilchard of Portugal, as investigated by Ramalho (1933), Wagner & Ramalho (1936), and Lepierre & Rodriguez (1938), the course of the seasons is different, in that spawning takes place during the winter, and most intensively in February, March and April. The discrepancy already noted between the fat cycles of the Cornish and Portuguese pilchards is therefore probably due to the difference in time of the spawning cycle in relation to the feeding cycle. The Cornish pilchard tends to show a two-fold replenishment of fat reserves, a lesser one in the early summer, and a greater one in the late autumn, because the income of material due to the heavy feeding on the spring plankton is largely used in the ripening of the gonads, while that due to the autumn feeding can be devoted wholly to the replenishment of the reserves. The Portuguese pilchard, on the other hand, tends to show a single replenishment of fat, reaching a peak in the late summer, because the income of material due to the heavy feeding in the spring is not called upon by the gonads, while that due to the autumn feeding is more than counterbalanced by the demands of the developing gonads, resulting in the beginning of a loss of material at that time of the year in which the Cornish pilchard is at its fattest.

Fig. 8 shows that the breeding cycle and the feeding cycle both reach their peak in the months from April to July. This is contrary to the usual experience with fishes, for most fish are believed to fast during the spawning period. In June I have found pilchards containing at the same time an ovary running with ripe eggs, and a tolerably full stomach. But feeding is clearly a necessity for the pilchard at this time. The winter fast has left no reserves of food material on which to complete the function of the gonads, and the pilchard cannot afford to pass by the richest pasturage of the year, whatever the condition of its gonads.

Another illustration of how the breeding and feeding cycles interact to affect the fat content is furnished by the Sardinellas of Egypt (el Saby, 1937). The main feeding period is in the autumn, when there is a big growth of plankton due to the Nile floods. This period of heavy feeding occurs when the gonads are quiescent, and it results in a sudden and very heavy accumulation of fat, reaching a level as high as 28 or 29% of the wet weight of the fish by December and January. Spawning occurs during the late spring and early summer, and at this time the fat content may have fallen to less than 3%.

In a recent general account of the seasonal changes in the herring of the North Sea, Lovern & Wood (1937) show that the fat content of the various races of herrings tends to show two maxima, one in the spring, with its culmination in June to August, and one in the early winter (December). The feeding cycle appears to be the same for all herrings, and is most intensive in May and June, less so in July. This is confirmed by Savage (1935), who, further, shows that there is a secondary increase in the intensity of feeding in September.

Those races of herrings which spawn in autumn and winter show their greatest fat content from June to August, and thereafter a rapid loss of fat, for the demands of the gonads are then greater than the income due to feeding. Those races of herrings, however, which spawn in the spring, have their maximum fat content in the autumn, for, as in the pilchard, the spring feeding has been used to nourish the gonads, without leaving much surplus to replenish the reserves of fat.

SUMMARY

1. In the pilchard (*Sardina pilchardus* Walbaum) of Cornwall there is a substantial seasonal variation in the mean weight of a fish of given length. The weight is highest in late autumn and early winter, and least at the end of winter and the early spring.

2. These changes in weight are largely due to variations in the fat content of the fish, which are richest in fat at the beginning of the winter fast, and poorest at the end of it. But, especially among the larger fish, the 'residue', chiefly proteins, are drawn upon at the time of the exhaustion of the fat, and consequently at the time of minimum mean weight. The water and ash content show no seasonal variation, and therefore play no part in the observed seasonal variation in the mean weight of the entire fish.

3. The gonads have their lowest mean weight in August, increase in weight slowly throughout the winter, and are at their maximum state of development from April to July. The spawning season, as deduced from these samples, is from March to September.

4. The rate of feeding is greatest in the same months as the spawning months, namely, from April to July. From July to September the average weight of food per stomach decreases, probably not because the planktonic food is then less abundant, but because it is shared among a greater number of fish. In October there is a rally in the rate of feeding, but from November to February or March is a period of fasting, when very little food is taken.

5. The food of the pilchard is exclusively planktonic. In the spring, and again in the autumn, diatoms are abundant or even dominant in the food; in the summer, copepods and crustacea are the chief items of food.

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NOTES ON THE PYCNOGONIDA OF PLYMOUTH

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(Text-figs. 1–7)

The Pycnogonida of Plymouth have had very little attention and early records are few. Of the eight species recorded in the *Plymouth Marine Invertebrate Fauna* in 1904, two, *Nymphon gallicum* and *N. gracile*, are synonymous, and these two are also recorded in the 1931 edition which comprises only the same eight species. The scarcity of the records shows that little search was made for the members of this group, for on revising it at the present time it is found that thirteen species certainly occur, being five more than are shown in the *Marine Invertebrate Fauna*. Hodgson (1910) records thirteen species from Devonshire, but these are not all the same as the thirteen now recorded. He mentions eleven from Plymouth, three of which have not been found recently. These are *Pallene spectrum*, *Nymphon brevirostre* and *Ammothea laevis*.

The species recorded in the *Plymouth Marine Fauna* (1904, 1931) are:

Pycnogonum littorale Ström
Endeis spinosus (Montagu)
Anaplodactylus petiolatus (Krøyer)
Pallene brevirostris Johnston
Nymphon gracile Leach (with *N. gallicum* Hoek)
N. rubrum Hodge
Ammothea echinata (Hodge)

The species recorded by Hodgson (1910) from Devonshire are:

Pycnogonum littorale (Ström)
Endeis spinosus (Montagu)
Phoxichilidium femoratum (Rathke) (from south coast of Devonshire and Starcross only)
Anaphia (=*Anoplodactylus*) *petiolata* (Krøyer)
A. virescens (Hodge)
Pallene brevirostris Johnston
P. spectrum Dohrn
Nymphon rubrum Hodge
N. brevirostre Hodge
N. gracile Leach
Achelia (=*Ammothea*) *echinata* Hodge
A. laevis Hodge
A. hispida Hodge

Of these *Phoxichilidium femoratum* proper has not been found by me at Plymouth, although it must occur, for a specimen sent to me from the Dundee collection, kindly lent by Dr Calman, is labelled Plymouth. On the other hand, I find that a second species (almost certainly the *P. femoratum* of Hoek (1881) and of Loman (1907) from Holland) is common at Plymouth in certain localities and also occurs at Millport in the west of Scotland. There is little doubt that this species has been confused with *P. femoratum*. Sars (1891) has already suggested that Hoek's species was distinct, but the hint has not hitherto been followed up.

P. virescens was first found by Hodge at Polperro, Cornwall. It is usually regarded nowadays as an *Anoplodactylus*, but it clearly has a five-segmented oviger and, following most modern authorities, this shows it to be a *Phoxichilidium.* It is now found to be common between tide-marks in certain localities round Plymouth.

Pallene spectrum has only been found by Norman (1908). No details, except Plymouth as locality, are available.

Nymphon brevirostre, according to Hodgson (1910), has been found at Plymouth, but I have not seen it. Apparently it was taken at Plymouth and also at Starcross by Norman (1908).

In addition to these I have to add *Anoplodactylus angulatus* (Dohrn) to the British fauna. This species is very like *Phoxichilidium virescens*, but the oviger is composed of six segments.

Anoplodactylus pygmaeus, the *Pallene pygmaeus* of Hodge, is here shown to be identical with Dohrn's *Phoxichilidium exiguum.*

The following is a list of species seen by myself at Plymouth from inshore waters during the last three years:

Pycnogonum littorale Ström
Endeis spinosus (Montagu)
Phoxichilidium tubulariae n.sp.
P. virescens Hodge
Anoplodactylus angulatus (Dohrn)
A. petiolatus (Krøyer)
A. pygmaeus (Hodge) = *Phoxichilidium exiguum* Dohrn
Pallene brevirostris Johnston
Nymphon gracile Leach
N. rubrum Hodge
Ammothea echinata (Hodge)
A. longipes (Hodge) = *hispida* Hodge

In addition, *Phoxichilidium femoratum* is recorded from south Devon by Norman (1908), and, as is mentioned above, a specimen from Plymouth is in the Dundee collection, although I have not found it myself. If *Pallene spectrum*, *Nymphon brevirostris* and *Ammothea laevis* are added to this list, we have sixteen species, exactly double the number recorded in the fauna lists. These include a new species and a new British record. The fact that all the first twelve of these have been collected in very shallow waters in restricted areas close to the shore makes it likely that others will be found when facilities for collection in deeper waters are available.

My best thanks are due to Dr I. Gordon of the British Museum for allowing me to examine certain specimens from the Norman Collection, to Dr W. T. Calman for sending me a collection from Dundee, to Mr R. Elmhirst for much help in collecting specimens, to Prof. Hobson for sending specimens of *Phoxichilidium femoratum* from the Northumberland coast, to Miss E. Clay of the Plymouth Laboratory, who in her work with Dr M. Parke on seaweeds discovered a fertile field for pycnogonids at the bases of the thalli of *Ascophyllum* at Wembury, and to Dr Vera Fretter of the Royal Holloway College for collections from Kingsand.

The *Ascophyllum* from Church Reefs, Wembury, had short *Sertularia* growing on them near the base, and here were found many specimens of

Phoxichilidium virescens, *Anoplodactylus angulatus* and *Ammothea echinata*. These also occurred in the rock pools amongst corallines as they did in similar situations at Kingsand.

At Wembury *Phoxichilidium virescens* and *Anoplodactylus angulatus* were found spread out on the thallus of the *Ascophyllum* and were almost exactly the same colour. Most of them were also striped with purple, and this was accentuated in those from the corallines. It is interesting that Colman in his research at Wembury on the faunas inhabiting intertidal seaweeds (1940), specially notes that he found very few pycnogonids on *Ascophyllum*. The reason seems to be that he worked in an area which was not so fertile for the weed as that worked by Miss Parke and Miss Clay, although they were not far apart.

Another very good locality was found by Mr William Searle at the sides of Phoenix Wharf. Large tufts of the bryozoan *Bowerbankia* obtained from scrapings were found to be full of *Anoplodactylus pygmaeus* and dredgings from the Laira yielded tangles of weed, bryozoans and hydroids in which *A. petiolatus* as well as *A. pygmaeus* was found. *Ammothea echinata* and *A. longipes* occurred also in both localities as well as at Wembury.

Phoxichilidium tubulariae n.sp., also found at Millport, must have been confused for long with *P. femoratum*. It occurs almost exclusively on *Tubularia larynx*, especially on those growing on the experimental raft moored near the Plymouth Breakwater. It has also been found on the Millbay Pontoon. *Nymphon rubrum* and *N. gracile* are fairly common between tide-marks at Wembury and at Kingsand and are also taken in the Cattewater and at Millbay. As dredgings from the Sound were unobtainable in these years of the war, the above-mentioned localities were used almost exclusively.

COLOUR

The colour of the species is usually very characteristic, but it may vary to a large degree. *Phoxichilidium femoratum* is always red, usually a deep red. *P. tubulariae* n.sp., is usually colourless or pale yellowish and sometimes a sepia-brown; sometimes it is red or brown at the joints. *Nymphon rubrum* is red, whilst *N. gracilis* is colourless, yellowish or pink. *Endeis spinosus* may be colourless or yellowish, but sometimes has deep purple lines at the joints and the intestinal fluid may be a deep purple. *Anoplodactylus angulatus* is usually greenish with deep purple bands across the body and limbs and the intestinal fluid is green. Young specimens may be quite colourless. *Phoxichilidium virescens* is usually the same colour as *Anoplodactylus angulatus*, greenish with purple bands, the intestinal fluid being green. These two species often occur together. It is probable that *A. angulatus* has hitherto been confused with *Phoxichilidium virescens*.

I have not yet succeeded in correlating the colour of the intestinal fluid with any particular food or habitat, except in the young of *P. tubulariae* which live inside the gastral cavity of the hydroid and have the intestinal fluid of the same colour. As mentioned above *P. virescens* and *Anoplodactylus angulatus* closely approximate in colour to that of the *Ascophyllum* and the purple bands are like the corallines. It is interesting to find that varieties of other species occur with similar dark purple bands, and that these usually live among corallines or *Bowerbankia*. Thus on the tufts of *Bowerbankia* from Phoenix Wharf and from the Laira dredgings specimens of *Anoplodactylus pygmaeus* with deep purple bands were fairly frequent along with the pale coloured individuals in the proportion of about one in twenty. One specimen of *A. petiolatus* out of ten had a similar colouring, and one *Ammothea echinata* out of many. These pycnogons were frequently found in the autumn months when most hydroids had died down. *Sertularia*, however, in very short colonies was alive at this season, and, occasionally, small colonies of *Obelia*. It is difficult to be certain of the food in many cases, but *Phoxichilidium tubulariae* could easily be seen to eat the *Tubularia* on which it lives.

BREEDING

Most pycnogonids breed in spring and summer, but in addition to the usual breeding season males bearing eggs of *Anoplodactylus angulatus* and *Phoxichilidium virescens* were frequently found in autumn and winter, also, occasionally *Anoplodactylus pygmaeus* and *Phoxichilidium tubulariae* in autumn. *Endeis spinosus* occurred with eggs in January 1945. *Nymphon rubrum* was found with eggs early in March and others have been recorded in February. The growth of the hydroids is probably the chief factor of importance in the breeding. Larval *Ammothea* (almost certainly *A. echinata*) occur plentifully among *Obelia* in the summer.

It is chiefly in the family Phoxichilidiidae that the most interesting breeding habits occur. In this family the larvae live parasitically in the coelenterates. It has been shown (Lebour, 1917) that the larvae of *Anoplodactylus petiolatus* (= *Anaphia petiolata*) develop in the manubrium of medusae of *Obelia* and certain other related forms. Dogiel (1913), in his fine work on larval pycnogonids, states that the larvae of this species form galls on the hydroid *Syncoryne eximia* in the same way that *Phoxichilidium femoratum* does. As will be shown below it is now almost certain that the species on which Dogiel worked at Millport is not *Anoplodactylus petiolatus* but *Phoxichilidium virescens*. His *Anoplodactylus pygmaeus*, the larva of which occurs in *Obelia* hydroids, has been found in exactly the same habitat at Plymouth. The larvae of *Anoplodactylus petiolatus* (not of Dogiel) and of *A. pygmaeus* are much alike, both occurring in *Obelia*, but one in the medusa and the other in the hydroid. There is no doubt that they are separate species, although in my former work (1917) they were regarded as identical. Dogiel notes that the larva in *Syncoryne* is much more like *Phoxichilidium femoratum* than it is like *Anoplodactylus pygmaeus*, and his figures show that it is almost certainly *Phoxichilidium virescens*. The breeding of *Anoplodactylus angulatus* is not yet known, although its usual habitat on or near *Sertularia* seems to point to that hydroid as the host for the larva. It is hoped to prove this later on.

We thus have the British species of the Phoxichilidiidae with distinctive breeding habits and larval hosts as follows:

Species	Host
Phoxichilidium femoratum	*Syncoryne eximia*, in cysts (Hodge, 1863; Dogiel, 1913)
P. tubulariae n.sp.	*Tubularia larynx*, in gastral cavity (Loman, 1907; Lebour, in the present work)
P. virescens	*Syncoryne eximia*, in cysts (Dogiel, 1913)
Anoplodactylus petiolatus	*Obelia* medusa and related forms, in manubrium (Lebour, 1917)
A. pygmaeus	*Obelia* hydroid, in gastral cavity (Dogiel, 1913; Lebour, in the present work)
A. angulatus	Unknown, but possibly *Sertularia*

Numerous authors have described larvae of Phoxichilidiidae, but in most cases it is difficult to be certain about the identification of the species: detailed references are therefore omitted.

Notes on the Species

A list of the Plymouth species is given below with any notes that are relevant. The Phoxichilidiidae have been dealt with much more fully than the others, as certain important points have been discovered and with some of them changes in nomenclature have been found necessary. The new species *Phoxichilidium tubulariae* is described and compared with *P. femoratum*. *P. virescens* is removed from *Anoplodactylus* to *Phoxichilidium*; *Anoplodactylus pygmaeus* (Hodge) has been identified as synonymous with *Phoxichilidium exiguum* Dohrn, and *Anoplodactylus angulatus* has been added to the British fauna.

Family NYMPHONIDAE

Genus Nymphon Fabricius

Nymphon gracile Leach

Norman (1908) has shown that *N. gallicum* Hoek is the same species. Common between tide-marks and dredged in the Sound. For separate records see *Plymouth Marine Fauna* (1931). Breeding in February, May and June and probably throughout spring and summer.

A shore and shallow-water species, its distribution ranging from Denmark to the Mediterranean.

Nymphon rubrum Hodge

Common between tide-marks: Wembury, Millbay Pontoon, Kingsand; also dredged in the Sound. Breeding in spring (including March) and summer.

A shore and shallow-water species, its distribution ranging from Norway and Sweden to Holland and Belgium. On all the English coasts, Scotland and Ireland.

Nymphon brevirostre Hodge

Recorded by Norman (1908) and Hodgson (1910) from Plymouth Sound, Yealm River and Starcross. Not found within recent years.

A very small species, littoral to about 60 m. depth. Ranging from Norway and Sweden to the south of England.

Family PALLENIDAE

Genus Pallene Johnston

Pallene brevirostris Johnston

Not uncommon between tide-marks and dredged in the Sound. For separate records see *Plymouth Marine Fauna* (1931). Found recently in plankton from the Laira and between tide-marks among corallines, Wembury. Crawshay (1912) found a specimen 46 miles south-west of the Eddystone, in 49 fm. It occurs from the coast to fairly deep water.

Distribution ranging from Denmark, Norway and Sweden, Kiel and Naples to the Atlantic coast of north-east America.

Pallene spectrum Dohrn

Norman (1908) records this species from Plymouth. No data are available. Recorded elsewhere only from Naples.

Family PHOXICHILIDIIDAE

In the British representatives of this family the palpi are always absent, and in all the species the ovigerous legs are present only in the male. The family includes some of the most puzzling species in the British fauna and is also specially interesting because the larvae are adapted for parasitizing hydroids.

Three genera are British, but only two are common and recorded from Plymouth—*Phoxichilidium* and *Anoplodactylus*. Wilson (1878) founded the genus *Anoplodactylus*, separating it from *Phoxichilidium* by the number of segments in the ovigers (six in *Anoplodactylus*, five in *Phoxichilidium*) and by the (so-called) absence of auxiliary claws on the dactylus. The latter character, however, does not hold good, as Sars (1891) has already noted, for some *Anoplodactylus*, including *A. petiolatus* which Wilson himself refers to the genus, have small auxiliary claws quite as much developed as in some *Phoxichilidium* (for example, *P. virescens*).

Although the genus *Anoplodactylus* is recognized by most modern workers, it comes very close to *Phoxichilidium*, and except by the ovigers it is difficult to separate them. It is only in deference to these workers that I have kept them apart and because of the great increase in the number of species which makes the division convenient. Personally I do not think that the division is a natural one. Marcus (1940), dealing with this family, does not make things easier by disregarding the segmentation of the ovigers in the genus *Phoxichilidium*. In this genus he places Dohrn's *P. exiguum*, which is shown here to be synonymous with *Anoplodactylus pygmaeus* and is clearly closely related to *A. petiolatus*. Although he places *Phoxichilidium virescens*, rightly, in this genus he is evidently following Hoek, who apparently really had *Anoplodactylus angulatus* which is a true *Anoplodactylus*. However, he places in the genus *Halosoma* of Cole (1904) Dohrn's *Phoxichilidium robustum*, which is shown below to be so close to *P. virescens* that it is impossible to place them in different genera. Helfer & Schlottke (1935) place *Anoplodactylus exiguus* in the genus *Halosoma* and *Anoplodactylus pygmaeus* in *Anoplodactylus*, and these two species are obviously identical. Norman (1894, 1908) regarded *A. pygmaeus* and *A. exiguus* as synonymous with *A. petiolatus*. The explanation here is that he, among many workers, regarded Hoek's (1881) *Phoxichilidium pygmaeus* as the same as Hodge's species, whereas Hoek's species is certainly *Anoplodactylus petiolatus*, as can be seen from his figures. Norman is right in regarding Hoek's *pygmaeus* as synonymous with *A. petiolatus* but wrong in regarding *A. exiguus* as synonymous with that species. Bouvier (1923) regarded *Phoxichilidium virescens* and *P. robustum* as *Anoplodactylus* and *A. petiolatus*, *A. pygmaeus* and *A. exiguus* as distinct species. Like Norman, he was describing Hoek's *pygmaeus*. The matter is discussed further under the separate species.

It is shown here that there are two species hitherto included under the name *Phoxichilidium femoratum*, one of which must be given a new name, and for this *P. tubulariae* is proposed from its invariable habit of breeding inside the hydroids of *Tubularia larynx*. This is the species whose life history is described by Loman (1907) from Herdla as *Phoxichilidium femoratum*, and also, almost certainly, the *P. femoratum* of Hoek (1881) also from Herdla. It is to be noted once more that Sars (1891) had already queried the identity of Hoek's species, thinking it was probably different from *P. femoratum* and giving as his chief reason the armature of the propodus as described below. He regarded *P. femoratum* as a truly northern species, and probably Plymouth is almost its southern limit.

There are six species in the Plymouth area belonging to the Phoxichilidiidae, and they form three groups of two each:

(I) *Phoxichilidium femoratum* and *P. tubulariae*. These may be regarded as *Phoxichilidium* proper, having an elongated form, five segments in the oviger, short cephalon, and short ocular process, auxiliary claws placed dorsally and well developed, cement glands not opening in a funnel but in a series of depressions on the femur, or hardly raised from the surface. There are no tubercles on the lateral processes and no cutting lamella on the propodus.

(II) At the other extreme comes *Anoplodactylus* proper represented by *A. petiolatus* and *A. pygmaeus* (=*exiguus*) with six segments in the oviger, long or short cephalon with long ocular process, auxiliary claws short and placed laterally (*A. petiolatus*) or absent (*A. pygmaeus*), cement glands opening in a funnel on the femur. There are dorsal tubercles on the lateral processes and a cutting lamella on the propodus.

(III) Joining these two groups in the British species come *Phoxichilidium virescens*, so closely related to *P. robustum* that they might be forms of the same species, and *Anoplodactylus angulatus*, having five and six segments respectively in the oviger. Otherwise they are extremely alike and come nearer to *Phoxichilidium* than to *Anoplodactylus*, having a short cephalon and short ocular process, cement glands not opening in a funnel but in small openings along the dorsal surface of the femur, no lamellae on the propodus and no protuberances on the lateral processes. Unlike *Phoxichilidium*, however, they have small auxiliary claws placed laterally as in *Anoplodactylus petiolatus*.

Foreign species do not fall so readily into these groups. *Phoxichilidium australe* Hodgson (see Calman, 1915) is very like *P. virescens*, *Anoplodactylus cribellatus* Calman and *A. investigatorius* Calman (1923) come close to *A. angulatus*, but *A. saxatilis* Calman has a femoral gland tube, no lamina on the propodus and no protuberances on the lateral processes, thus coming between *A. angulatus* and *A. petiolatus*; an unnamed species from Burma (Calman, 1923) closely resembles *A. petiolatus*, but has no tubercles on the lateral processes. These are only a few examples of the variability of the species in the family which appear to be altering in countless directions. If it were not for the ever-growing number, it would perhaps be best to keep them all in one genus.

Genus Phoxichilidium Milne-Edwards

Phoxichilidium femoratum (Rathke)

(Figs. 1 *a–c*, 2 *a*)

This is the common northern species and well known since the time of Rathke. It is the species recorded by all the Scandinavian workers and occurs in Britain on all our coasts. Its larval stages are described by Hodge (1861) from the coast of Durham, in *Coryne* (= *Syncoryne eximia*). Later these were again described by Dogiel (1913) from Millport. The species is a dark and brilliant red which colours the whole cuticle. The description of Sars (1891) with figures cannot be bettered and his figures have been copied by most workers. It has been recorded from Starcross, Devon, and a specimen labelled 'Plymouth' occurs in the Dundee collection. I have not yet succeeded in finding it in the Plymouth area, although *Phoxichilidium tubulariae* is abundant. Both species are to be found at Millport, one chiefly on *Syncoryne* and the other on *Tubularia*. I am very grateful to Mr Elmhirst for information on this point and for specimens of both species.

Phoxichilidium tubulariae n.sp.

(Figs. 1 *d–g*, 2 *b*, 3 *a–c*)

Phoxichilidium femoratum (Rathke) Hoek, 1881.
Phoxichilidium femoratum (Rathke) Loman, 1907.
? *Phoxichilidium femoratum* (Rathke) Schlottke, 1932.

This species occurs at Plymouth in numbers among *Tubularia larynx*, especially where it grows on the experimental raft moored near the Breakwater and also on the Millbay pontoon. It is usually almost colourless or

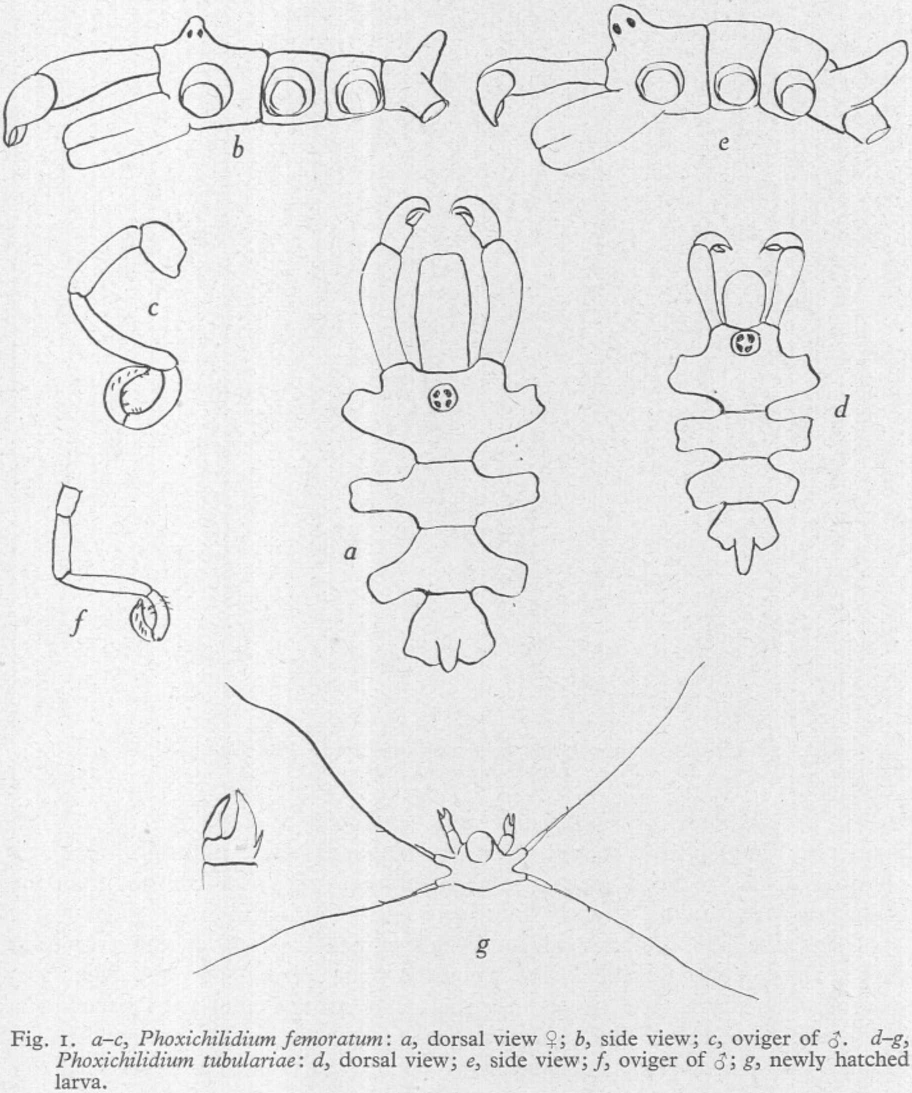

Fig. 1. *a–c*, *Phoxichilidium femoratum*: *a*, dorsal view ♀; *b*, side view; *c*, oviger of ♂. *d–g*, *Phoxichilidium tubulariae*: *d*, dorsal view; *e*, side view; *f*, oviger of ♂; *g*, newly hatched larva.

a pale straw colour, occasionally having red lines on the body sutures. It may also be brownish to sepia-brown. It may easily be seen eating the *Tubularia* heads, and its young are found in the gastral cavity of the hydroid. It is smaller and more slender in build than *Phoxichilidium femoratum*, its proboscis more or less swollen anteriorly and shorter in proportion to the body. The processes of the last abdominal segment are shorter and the abdomen longer. The body is about 1·5 mm. in length. The segmentation is distinct. The lateral processes are very distinct and separated by less than their own diameter. The cephalon is very short, the ocular tubercle blunt and reaching obliquely over the front margin. The proboscis is distinctly shorter than the chelophore, expanding slightly anteriorly and rounded in front. The oviger is of five distinct segments, the terminal segment as long as the preceding with a few recurved spines. The second coxa is longer than the other two together, the femur and tibiae subequal. The armature of the propodus is of the same type as in *P. femoratum*, but with fewer teeth at the base of the sole, usually two large teeth, followed by a pair slightly smaller. The auxiliary

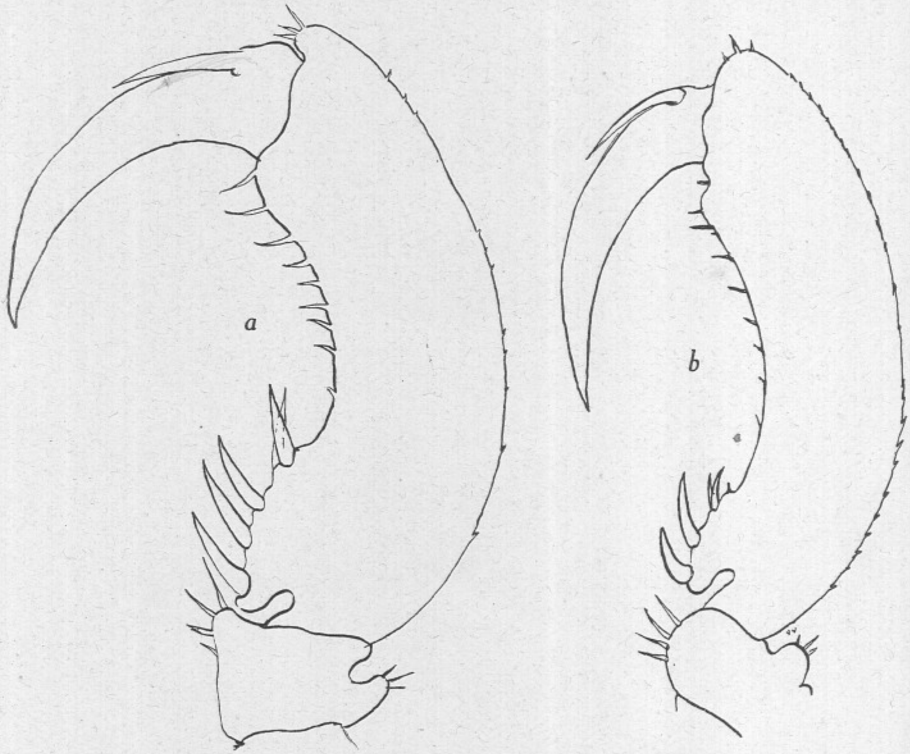

Fig. 2. *a, Phoxichilidium femoratum*, propodus and claw; *b, Phoxichilidium tubulariae*, propodus and claw.

claws are large and placed dorsally. Cement glands open on very inconspicuous pores placed dorsally on the femur.

A comparison of the two species is given below, showing the main points of difference:

Phoxichilidium femoratum	*Phoxichilidium tubulariae*
Length of body *ca.* 1·9–2 mm. Proboscis cylindrical, almost the same width throughout, end almost straight	Length of body *ca.* 1·4–1·5 mm. Proboscis wider anteriorly, shorter than in *P. femoratum*, end rounded, considerably shorter than the basal segment of the chelophores
Abdomen about the same length as the posterior abdominal processes	Abdomen nearly twice as long as the posterior abdominal processes
First two lateral processes with oblong spaces larger than the width of the processes themselves	Lateral processes with spaces narrower than the width of the processes themselves
Propodus usually armed at base with three or four large single and one pair of usually smaller teeth, number slightly variable	Propodus armed at base with two large single and one smaller pair of teeth, number slightly variable
Colour red	Colourless or straw colour, rarely brown or with red at sutures
Larvae in cysts in *Syncoryne eximia*	Larvae in *Tubularia*, in gastral cavity

The larvae of *P. femoratum* have been described by Hodge (1864) and by Dogiel (1913). They occur on *Syncoryne eximia* where they cause the hydroid to form cysts round them. Loman (1907) has found the larvae of *Phoxichilidium tubulariae* (as *P. femoratum*) in Holland in the polyps of *Tubularia*. Here they do not form cysts but live freely in the gastral cavity of their host. I have found these larvae in a similar habitat at Plymouth from spring to autumn. The *Tubularia* generally dies down in autumn, but wherever it is alive larvae may be found. As many as five advanced larvae may occur in

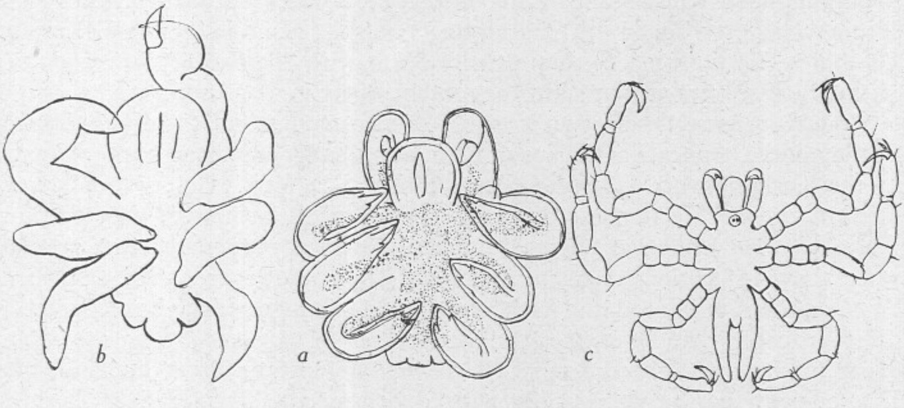

Fig. 3. *Phoxichilidium tubulariae*. *a*, penultimate larva from *Tubularia*; *b*, cast skin of same; *c*, last larva from cast skin. (About one-third scale of *a* and *b*.)

one polyp which, however, appears to be unharmed by them. The parasite remains in the polyp until the penultimate larval stage, when it emerges and casts its skin, the young pycnogon, with three pairs of legs and rudiments of the fourth pair, crawling about among the hydroids. The larva itself is colourless, but the intestinal fluid is a deep purple when seen by transmitted light and pink by reflected light. The newly hatched larva obtained from the parent measures 60–80 μ across the body, the length being about the same. It has conspicuous chelae and proboscis, the second and third appendages being drawn out into long threads at least five times the length of the body with a small tooth-like spine not far from the base. In one Plymouth larva there was a large accessory spine on the inside of the base of the chela, apparently an unusual feature.

Obviously these two species are closely related but distinct. The third species, *Phoxichilidium virescens*, is very different, and, except for the ovigers, it is much more like *Anoplodactylus angulatus*.

Phoxichilidium virescens Hodge

(Fig. 4 *a–f*)

This species was first described by Hodge (1864) from Polperro, Cornwall. I have examined his actual specimens and also one of Norman's from Plymouth and two from Starcross, Devon, from the Norman Collection. All of these are identical with those from Plymouth collected recently from Wembury and Kingsand. In the first locality they occur abundantly on *Ascophyllum* growing on the Church Reefs, in the second in rock pools among corallines. In both places they usually occur with *Anoplodactylus angulatus*, with which species at first sight they might easily be confused.

Hodge's original description is as follows: Rostrum stout, slightly thickened in the middle, truncate at the apex. Foot jaws slender and closely approximate at their origin, with 6–8 teeth. Legs moderately long. Colour pea green. Length $\frac{7}{100}$ in. He remarks that 'this species might at first be mistaken for *Phoxichilidium olivaceum* (Gosse); but the closely approximated foot jaws at once show its distinct character'. Gosse (1855), however, never described *P. olivaceum*, but figured it in such a way that it cannot certainly be recognized. It is probable that he had either this species or *Anoplodactylus angulatus*. Hoek (1881) records and figures *Phoxichilidium virescens* from Holland, but it is evident that he was dealing with *Anoplodactylus angulatus* for, besides the evidence of his figures, he states that he found a male of this species, which he lost, which had six segments in the oviger. Grube (1872) records *Phoxichilidium virescens* from Brittany and Bouvier (1923) from Cette. There are no good figures of it.

P. virescens measures about 1 mm. in length. It is usually described as pea green, but in the Plymouth specimens the animal itself is a dull greenish with the intestinal fluid bright green. Usually there are dark purple bands on the body and legs. Norman (1908) remarks that his specimens from

Starcross were still bright green after being kept for some years. These I have examined and they are still a uniform pale bright green. The body is completely segmented, the legs fairly slender, but having the same proportions and armature as *P. robustum* Dohrn. The body segments are broad and the spaces between the lateral processes narrow. The ocular process is extremely blunt and the cephalon broad. The abdomen is a short rounded knob, reaching obliquely slightly beyond the very short last lateral processes. The proboscis is bluntly truncate, showing signs of angles at the corners. There are no protuberances on the lateral processes. The chelae are armed with teeth.

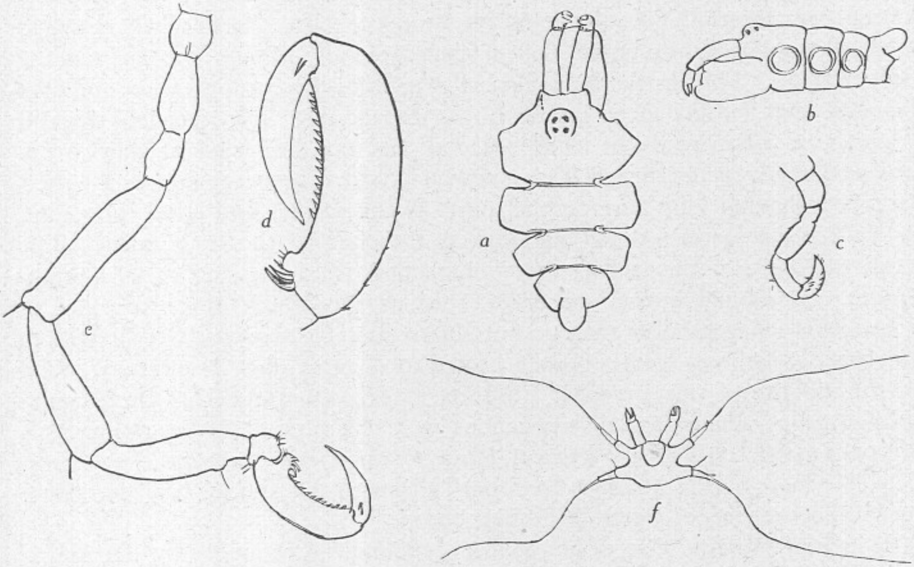

Fig. 4. *Phoxichilidium virescens.* *a*, dorsal view; *b*, side view; *c*, oviger; *d*, propodus; *e*, leg; *f*, newly hatched larva.

The legs have few setae, but a conspicuous seta mounted on a knob occurs distally on the femur and second tibia, a less conspicuous one on the first tibia. The second coxal segment is slightly longer than the third and the first is the shortest. The femur and tibiae are subequal. The propodus is armed with two or three, usually two, large spines at the base and a row of teeth on the sole. There is no cutting lamina. There are small auxiliary claws placed laterally. The ovigers have five segments, the last being flat and pointed and bearing two rows of reflected simple thorn-like spines. The second segment is slightly longer than the first, the third about twice as long as the second, and the fourth and fifth subequal. Very inconspicuous cement glands open by pores on the dorsal surface of the femur. Except for the very robust form and the distinct angles of the proboscis with an indentation behind the angles in *P. robustum* the characters of *P. virescens* and *P. robustum* agree in almost every particular.

Males of *P. virescens* carrying pink eggs were obtained from September to January, but probably breeding takes place also in spring and summer. The larvae hatched out, but the host was not discovered.

P. virescens is common at Millport between tide-marks, and it is almost certain that the larvae described by Dogiel (1913) as *Anoplodactylus petiolatus* belonged to this species. They occurred in *Syncoryne eximia* in which they inhabited cysts in much the same way as *Phoxichilidium femoratum*, and, as he remarks, were with difficulty distinguished from these. As the larva of *Anoplodactylus petiolatus* has already been found in the manubrium of *Obelia* medusae and similar forms (Lebour, 1917), it seems improbable that Dogiel's species was correctly identified, and his figures of the last larva newly emerged from the cyst are quite unlike that of *Anoplodactylus petiolatus* as are also the earlier stages. This last larva so closely resembles the form of *Phoxichilidium virescens* that I think there can be no further doubt. Moreover, the eggs of *P. virescens* when ready to hatch are pink and not colourless as they are in *Anoplodactylus petiolatus*, and the newly hatched larvae resemble Dogiel's figures in having long hairs at the joints of the second and third limbs and a small spine farther along the limb at the base of the long thread. The squarish body of the larva is very characteristic, measuring *ca.* 0·06 mm. across. As Dogiel himself observes, this larva is much more like that of *Phoxichilidium femoratum* than that of *Anoplodactylus pygmaeus*. He describes the latter, which is a species closely related to *A. petiolatus*. As a further proof of the identity of this larva Mr Elmhirst has kindly searched in the original locality from which Dogiel's specimens were taken, and the specimens collected consisted only of *A. pygmaeus*, *Phoxichilidium femoratum* and *P. virescens*. No *Anoplodactylus petiolatus* were found, although this species has been taken at Millport in deeper water (Elmhirst, 1911).

It is unfortunate that none of the specimens examined by Dogiel is available, but it may now, I think, be taken as correct that Dogiel's larvae from Millport which he named *Anoplodactylus petiolatus* were really *Phoxichilidium virescens*, and that his *Anoplodactylus pygmaeus* is correcty named and is synonymous with *Phoxichilidium exiguum* Dohrn.

An interesting point arises from Giltay's work (1928). He notes as a distinguishing character between *Phoxichilidium* and *Anoplodactylus* the position of the auxiliary claws—placed dorsally in the former and laterally in the latter. In *Phoxichilidium femoratum* and *P. tubulariae* they are dorsal and are well developed, whereas in *P. virescens* they are placed laterally and are very small, very much the same size as in *Anoplodactylus petiolatus* and *A. angulatus*. In *A. pygmaeus* they are absent altogether. In *Phoxichilidium australe* Hodgson and certain species of *Anoplodactylus* described by Calman mentioned above they are also small and lateral. Here, then, is another character which demonstrates the close linkage of the two genera and the intermediate feature in *Phoxichilidium virescens* and *Anoplodactylus angulatus*.

Phoxichilidium robustum Dohrn

This species, if indeed it be distinct from *P. virescens*, is not to be regarded as a member of the British fauna, since no specimens precisely resembling it have yet been found in British waters. I have, however, examined a specimen from the Norman Collection actually sent by Dohrn himself from Naples which is so like *P. virescens* that it is quite possible it should be regarded as a variety only. The two species are here kept apart because the more stumpy figure and distinctly angular proboscis of the Naples species does distinguish it. It is particularly interesting to find that in Norman's specimen of *P. robustum* from Naples the segmentation of the body is complete, whereas in Dohrn's description and figures there is no segmentation at all. Marcus (1940), who records and figures *P. robustum* (as *Halosoma*) from Brazil, describes his species as having the body segmented except for the last suture. In *P. virescens* the body is completely segmented. Marcus's figure is even more like *P. virescens*, and a figure of a leg by Giltay (1929) of *P. robustum* from Belgium is not nearly so robust as the original *robustum* although he describes the body as being non-segmented and the proboscis angular. The segmentation or otherwise of the body thus appears to be a variable feature, and the amount of compression of the segments apparently goes with it.

In the *P. robustum* described and figured by Dohrn the body is very much compressed and non-segmented, the legs plump and compact, and the proboscis with distinct angles, the surface below the angles indented. In the Norman specimens from Naples the body is segmented, but otherwise like the description and figures of Dohrn. Unfortunately, it is a female, but Dohrn's figures of the male show the ovigers of five segments and the proportions similar to Marcus's *P. robustum*. The latter is not quite so stumpy as Dohrn's specimen, and in *P. virescens* we have a fully segmented body, not quite so thick as *P. robustum*, with more slender legs, the ovigers being similar and also the armature of the legs, but the proboscis less angular. In all three the ocular process is very short and the abdomen short and rounded. They are so alike that it is impossible to place them in separate genera, and as is shown it is not certain that *virescens* and *robustum* are distinct species.

Many recent authors have removed *P. robustum* from *Anoplodactylus* and placed it in *Phoxichilidium*, but several have placed it in the genus *Halosoma* (regarded as a subgenus of *Anoplodactylus* by Loman (1908)). At the same time they place *Phoxichilidium virescens* either in *Phoxichilidium*, which is correct (Marcus, 1940[1]), or in *Anoplodactylus*, which is wrong (Norman, 1908; Bouvier, 1923) if we go by the ovigers. That is to say, the majority of workers place *Phoxichilidium virescens* and *P. robustum* in different genera, which is certainly wrong, as they resemble one another so closely.

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[1] Marcus was, however, really dealing with *Anoplodactylus angulatus* as he refers to Hoek's species.

Genus *Anoplodactylus* Wilson

Bouvier (1923) admits seven species from France in the present genus. Except for *A. massiliensis* these are all found at Plymouth, but the number must be reduced to three (*A. petiolatus*, *A. pygmaeus* and *A. angulatus*). As will be shown below, *A. pygmaeus* and *A. exiguus* are synonymous, and it has already been shown that *A. virescens* and *A. robustus* belong to *Phoxichilidium*.

There has always been difficulty over *Anoplodactylus pygmaeus*. Many workers, including myself (1917), following Norman (1894, 1908), regarded it as synonymous with *A. petiolatus*, possibly the young of that species. The prevailing opinion now is that it is distinct, which is certainly correct (Wiren, 1918; Carpenter, 1905; Giltay, 1928; Schlottke, 1932, etc.). Norman (1908) gives a long list of species which he regards as synonyms of *A. petiolatus* and before this (1894) states his reasons for regarding *A. pygmaeus* as probably the young of *A. petiolatus*. Having now found adults of both species at Plymouth, including males bearing eggs, I am certain that they are separate species.

Among the misconceptions which have arisen the first is that many workers have regarded Hoek's *Phoxichilidium pygmaeus* as synonymous with Hodge's *Pallene pygmaeus*, and not, as it undoubtedly is, with *Anoplodactylus petiolatus*, while, secondly, many have followed Norman in placing Dohrn's *Phoxichilidium exiguum* in the synonymy of *Anoplodactylus petiolatus*. Norman's list of synonyms of *A. petiolatus*, which includes Hoek's *Phoxichilidium pygmaeus*, is apparently right except for the inclusion of Hodge's *Pallene pygmaeus* and Dohrn's *Phoxichilidium exiguum*. These two, as will be shown below, are synonymous and quite distinct from *Anoplodactylus petiolatus*. Bouvier (1923), on the other hand, recognizes too many species and places *Phoxichilidium exiguum* (as *Anoplodactylus*) far away from *pygmaeus*, whilst the latter species he regards as closely related to *A. petiolatus*. His description and figures of *pygmaeus* are, however, taken from Hoek's form and actually represent *A. petiolatus*.

Having found at Plymouth a very large number of the small species which is the *Pallene pygmaeus* of Hodge (1864) and the *P. pygmaeus* of Dogiel (1913) from Millport (the larvae of which he describes), it was found that they correspond in every way with Dohrn's *Phoxichilidium exiguum* (1881). That they were synonymous was first noted by Norman (1894), who actually compared Hodge's type specimen from the Hancock Museum, Newcastle-upon-Tyne, with specimens of *P. exiguum* sent by Dohrn from Naples. Hodge's type specimen, unfortunately, cannot be found, but I have examined Dohrn's specimens from the Norman Collection, which are the same as the Plymouth and Millport species. Norman was wrong in supposing them to be the young of *A. petiolatus*, but this important observation as to their identity appears to have been overlooked by later workers who have continued to regard them as separate species, even sometimes placing them in different genera (Helfer

& Schlottke, 1935; Marcus, 1940). It can now be established that *A. petiolatus* and *A. pygmaeus* are separate but closely related species, and that *A. exiguus* is a synonym of *A. pygmaeus*.

The number of British species is thus reduced to three, excluding *A. oculatus* and *A. typhlops* dredged by Carpenter (1905) in deep water off the Irish coast. Of these three, *A. petiolatus*, *A. pygmaeus* and *A. angulatus*, the first two may be regarded as typical *Anoplodactylus*, with a more or less elongated ocular process, cement glands opening in a funnel on the femur, the propodus armed with a cutting plate and having protuberances on the lateral processes, whilst *A. angulatus* has a very short ocular peduncle, no funnel for the cement glands, no cutting plate on the propodus, and no protuberances on the lateral processes. *A. angulatus* thus links *Anoplodactylus* with *Phoxichilidium*.

Anoplodactylus angulatus (Dohrn)
(Fig. 5 *a–f*)

Phoxichilidium angulatum Dohrn, 1881.
P. virescens Hodge, Hoek, 1881.
Anoplodactylus angulatus (Dohrn) Bouvier, 1923.

This species is now added to the British fauna for the first time. At first sight it is so like *Phoxichilidium virescens* that it may well have been confused with that species. It does not, however, appear to occur with *P. virescens* at Millport, although the two are commonly found together at Plymouth, both on *Ascophyllum* and among corallines at Wembury and at Kingsand. They also occur in the Laira dredgings. Both were specially common among short *Sertularia* on the *Ascophyllum* at Wembury.

The species was first discovered at Naples by Dohrn and is recorded by Bouvier from Cette and by Giltay from Banyuls. Hoek's *Phoxichilidium virescens* from Herdla must be this species, as he mentions that there were six segments in the oviger of a male. A specimen from Naples, sent by Dohrn, which is in the Dundee collection, is undoubtedly the same as the Plymouth species. The very sharp angles on the proboscis distinguish it at once from *P. virescens*, but except for the ovigers (with six segments in *P. angulatus*, but only five in *P. virescens*) the species comes so near to *P. virescens* that it appears really to be more closely related to it than to *Anoplodactylus petiolatus* and *Phoxichilidium pygmaeus*. Both Norman (1908) and Bouvier (1923) knew this and regarded them both as belonging to *Anoplodactylus*, neither of them having apparently observed the differences in the ovigers.

Dohrn gives the length of the body as 1·5–2 mm. The Plymouth specimens are usually smaller and adults may be 0·96–1·3 mm. in length. The first body segment is broad, the second and third of moderate size, but the last is very much smaller with the lateral processes reduced to mere stumps. There are no protuberances on the lateral processes. The body in the Plymouth specimen is completely segmented, although Dohrn states that segmentation is absent between the third and fourth segments. In the specimens from Naples in the Dundee collection it was not possible to be certain on this point owing to its bad preservation. The cephalon is short and broad and bears a short rounded ocular tubercle slightly pointed at the tip which does not overlap the anterior margin of the cephalon. The abdomen is more than twice the length of the last lateral processes. The proboscis is stout, cylindrical, with conspicuous angles anteriorly. The spaces between the lateral processes are narrow but distinct. The legs are fairly long but stout, with long setae as in *Phoxichilidium virescens*, but without such distinct knobs. The chelae, which are toothed as in *P. virescens*, project well beyond the proboscis. The cement glands are situated on the femur as in *P. virescens*, but are very inconspicuous. The ovigers are shaped like those of *P. virescens* with the end pointed, but have six segments instead of five. The second segment is nearly double the length of the first and about two-thirds the length of the third, the fourth slightly shorter than the third, the fifth and sixth flattened and together slightly shorter than the fourth. The fifth bears two rows of tooth-like recurved spines as in *P. virescens*. The propodus is armed with two large teeth and three setae preceding a row of teeth on the sole. There is no lamina. There

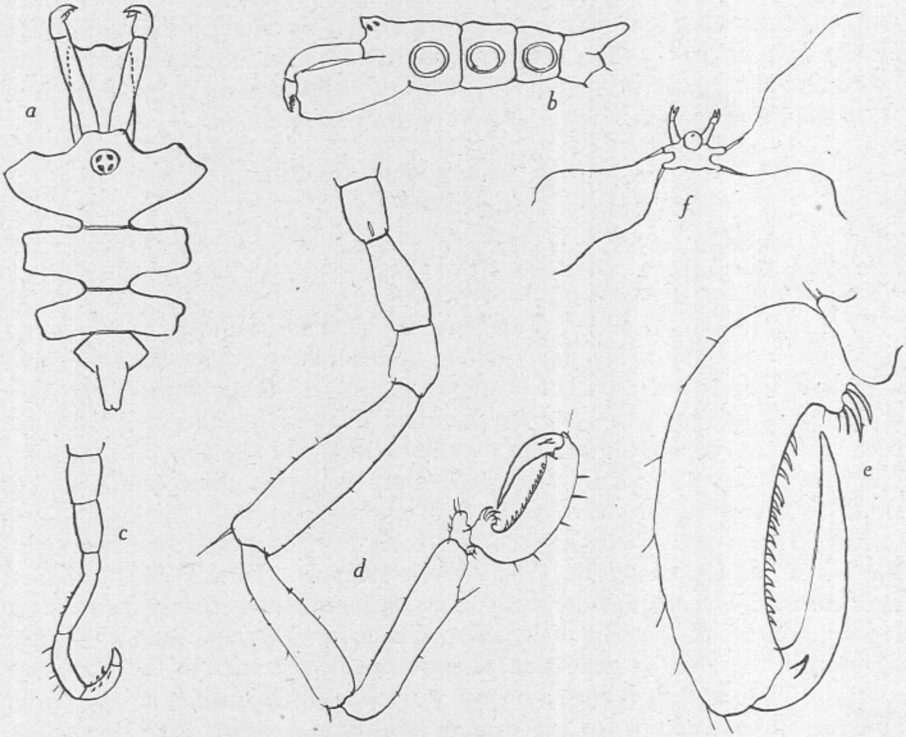

Fig. 5. *Anoplodactylus angulatus*. *a*, dorsal view; *b*, side view; *c*, oviger of ♂; *d*, leg; *e*, propodus; *f*, newly hatched larva.

are small auxiliary claws. The whole propodus is like *P. virescens.* Norman (1908) notes in his Naples specimen that there is a swelling at the base of the claw only to be seen when it is extended. This is sometimes, but not always, to be seen in the Plymouth specimen. It is usually not so pronounced as in Norman's figure. A trace of it is sometimes seen also in *P. virescens.*

Males carrying eggs were found in summer and autumn and larvae hatched out. It was not possible to rear them as the host was not ascertained. It is probable that the host is the *Sertularia* amongst which they lived on the *Ascophyllum,* but attempts to persuade the larvae to enter the hydroid were unsuccessful. The larva is like that of *Phoxichilidium tubulariae,* but smaller and with shorter appendages, and no teeth or hairs were visible at the base of the flagelliform threads. Eyes were present in these newly hatched larvae.

It is interesting to note that Marcus (1940) shows hairs on the legs in his *Anoplodactylus carvalhoi* and *A. strictus* which are similar to those in *Phoxichilidium virescens.*

In *Anoplodactylus angulatus* we have an *Anoplodactylus* which through *Phoxichilidium virescens* is closely related to *Phoxichilidium* proper as represented by *P. femoratum* and *P. tubulariae.*

Anoplodactylus petiolatus (Krøyer)

(Fig. 6 *a–h*)

Phoxichilidium petiolatum Krøyer, 1844.
Pallene attenuata Hodge, 1864.
Phoxichilidium petiolatum Krøyer, Hodge, 1864.
P. longicolle Dohrn, 1881.
P. pygmaeum (Hodge) Hoek, 1881.
Anoplodactylus petiolatus (Krøyer) Sars, 1891.
A. petiolatus (Krøyer) Bouvier, 1923.
Anaphia petiolata (Krøyer) Norman, 1908 (in part).
A. petiolata (Krøyer) Lebour, 1917.
Anoplodactylus pygmaeus (Hodge) Bouvier, 1923.

This well-known species occurs fairly commonly at Plymouth, but is never found in numbers. Its larva, however, is abundant in late spring and in summer in the manubrium of *Obelia* medusae and related forms in the plankton. It has already been recorded from Plymouth Sound by Norman (1908) and from Asia Shoal and Winter Shoal in *Plymouth Marine Fauna* (1931). Recently, I have found it in tangles of *Bowerbankia* and hydroids dredged from the Laira. Males with eggs were found in August and September 1944, and without eggs in October 1944. The young larvae have not yet been seen and, as shown above, Dogiel's larvae from Millport, which occurred in cysts in *Syncoryne,* are almost certainly *Phoxichilidium virescens.* The adult has been recorded from Millport (Elmhirst, 1911 and by Norman, 1908), but dredged in fairly deep water.

Dogiel (1911) states that he found this species at Cullercoats and followed its life history, the larvae inhabiting the polyps of *Campanularia flexuosa*

(Hincks). He remarks that the larvae 'were characterized by the uncommonly strong development of the last joint of the second and third pair of legs, and by the complete absence of eyes. The way in which the larvae enter the polyps was observed and the duration of the parasitic stage was found to be from 8 to 12 days. After this period the larva moults and leaves its host.' This account differs very much from his Millport observations and indicates still more strongly that he was dealing with different species. Unfortunately, no trace of the Cullercoats specimens can be found, and apparently these observations were not published in any more detail.

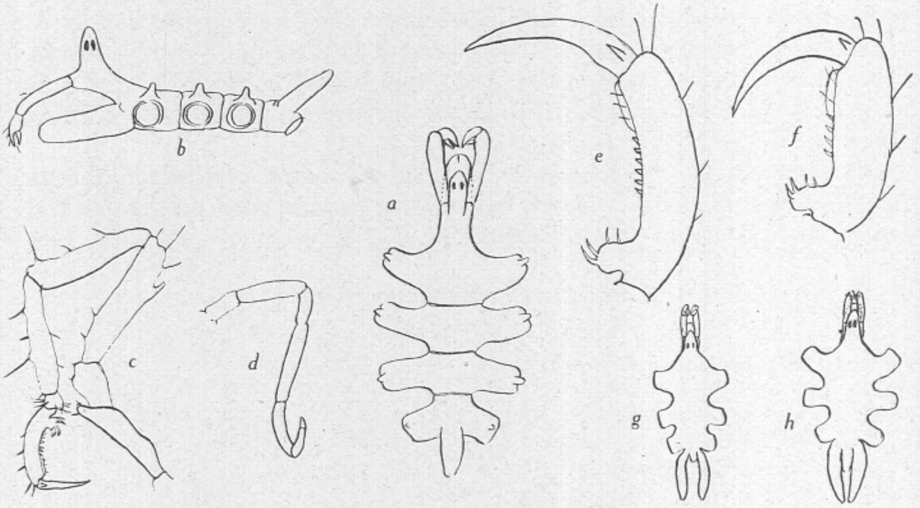

Fig. 6. *Anoplodactylus petiolatus*. *a*, dorsal view; *b*, side view; *c*, leg of ♂; *d*, oviger of ♂; *e*, propodus of adult; *f*, propodus of young form; *g*, last larval stage escaped from medusa; *h*, last larval stage a few days old.

The Plymouth specimens from the Laira agree exactly with the excellent descriptions and figures of Sars (1891) which are copied in nearly all recent works. They also agree with Dohrn's *Phoxichilidium longicolle*. It is to be noted here that Dohrn does not figure the protuberances on the lateral processes, except for a trace in the main figure, but I have examined specimens sent by Dohrn from Naples in the Norman Collection, and the protuberances were quite distinct and the specimens agree exactly with those from Plymouth. This species is the *Pallene attenuata* of Hodge (1864), who later in the same paper corrected it to *Phoxichilidium petiolatum* of Krøyer.

Anoplodactylus petiolatus is very slender and all its parts are elongated. The colour is pale yellowish or it is colourless. A specimen was found with deep purple bands similar to the variety of *A. pygmaeus*. The body is 1·2–1·5 mm. in length. The neck is very long, and the ocular process is long and reaches nearly to the end of the proboscis which is cylindrical and rounded at the end. The segmentation of the body is complete, the spaces between the lateral processes wide and rounded. There are conspicuous conical protuberances without hairs on the lateral processes. The abdomen is long and narrow, reaching well beyond the last lateral processes. In the ovigers of the male the third segment is very long, about twice the length of the second. The legs are elongated, the femur and tibiae subequal. The femur bears dorsally a conspicuous funnel for the opening of the cement glands. The propodus is armed internally with two large teeth and a smaller pair, with six teeth on the sole and a cutting lamella. In young forms, and sometimes in adults, there are only four teeth before the lamella as in Hoek's (1881) figures of *Phoxichilidium pygmaeum*, which is really *Anoplodactylus petiolatus*, and Bouvier's (1923) figure of *A. pygmaeus*, which is taken from Hoek. The claw is long and bears small auxiliary claws placed laterally.

It has been shown (Lebour, 1917) that the cephalon elongates with age and the young have a much shorter neck than the adults. This can be well seen in late larvae which have emerged from the medusae and then kept in bowls for a few days.

The distribution is wide, ranging from far north to the Mediterranean. Marcus (1940) records it, or possibly a closely related species, from Brazil.

Anoplodactylus pygmaeus (Hodge)

(Fig. 7 *a–l*)

Pallene pygmaea Hodge, 1864.
Phoxichilidium exiguum Dohrn, 1881.
Anoplodactylus pygmaeus (Hodge) Dogiel, 1913, larvae.
? *Anoplodactylus pygmaeus* (Hodge) Giltay, 1928.
Anoplodactylus exiguus (Dohrn) Bouvier, 1923.
A. pygmaeus (Hodge) Schlottke, 1932.

This species was first discovered by Spence Bate at Plymouth; he notices it in the *British Association Report*, Hull, 1853, and remarks on the larvae, but neither describes nor figures it. Hodge (1864) describes it and records it from the Durham coast. It is not the species described and figured by Hoek (1881) from Holland as *Phoxichilidium pygmaeum*, which, as Norman (1894, 1908) has rightly maintained, is *Anoplodactylus petiolatus*. It is, however, the species whose larvae are described by Dogiel (1913) in hydroids of *Obelia* from Millport; in this locality it appears to be common, and I have made a careful examination of specimens kindly sent to me by Mr Elmhirst. *Phoxichilidium exiguum* described and very accurately figured by Dohrn is also synonymous with this species.

Anoplodactylus pygmaeus occurs abundantly at Plymouth, in tufts of *Bowerbankia* and hydroids from Phoenix Wharf, in tufts of the same dredged from the Laira, on the Church Reefs at Wembury between tide-marks among corallines and hydroids, and in rock pools at Kingsand. It is now found to be one of the commonest shallow-water forms at Plymouth. It carries eggs from spring to autumn, and larvae were hatched and reared in *Obelia* hydroids in a bowl until they emerged in the last larval stage. These larvae and their habitat in the gastral cavity of the *Obelia* hydroid agree exactly with Dogiel's description.

Comparing the Plymouth and Millport specimens with Dohrn's (1881) description and figures of *Phoxichilidium exiguum* it is obvious that the species are identical. I have now examined specimens from Naples sent by Dohrn to Norman in the Norman Collection and confirmed this. Norman's mistake was to regard them as synonymous with *Anoplodactylus petiolatus*. The *A. pygmaeus* (Hodge) figured and recorded from Heligoland by Schlottke (1932) is correctly named and the species is correctly placed in the key to *Anoplodactylus* in the Nachtrag to *Die Tierwelt der Nord- und Ostsee* by Helfer (1935).

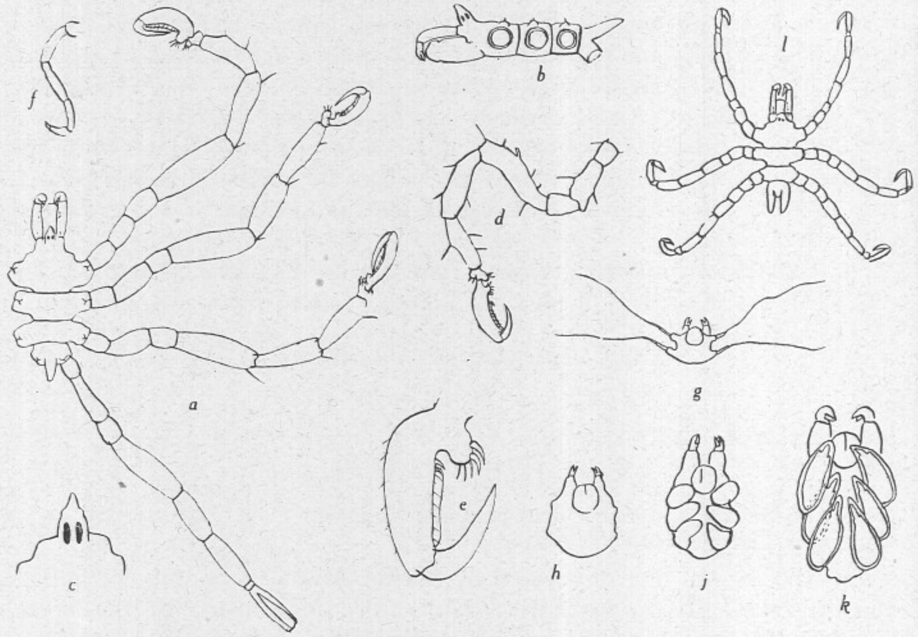

Fig. 7. *Anoplodactylus pygmaeus*. *a*, dorsal view; *b*, side view; *c*, ocular process; *d*, leg of ♂; *e*, propodus; *f*, oviger of ♂; *g*, newly hatched larva; *h*, early larva in *Obelia* hydroid; *j*, older larva in *Obelia* hydroid; *k*, penultimate larva in *Obelia* hydroid; *l*, last larva emerged from *Obelia* hydroid.

A. pygmaeus is a very small species, 0·65–1 mm. long. Although described by Dohrn as having the last two body segments fused, all the specimens I have examined, including those from Naples, are completely segmented, the division between the last two being sometimes difficult to see. The body is also completely segmented in Schlottke's (1932) figure. There are small protuberances on the lateral processes, each tipped with a hair. The spaces between the processes are narrow, but quite distinct. The cephalon is broader than long, but the ocular process overlaps it well in front and is pointed at the end. The proboscis is cylindrical, rounded anteriorly, with a constriction encircling it near the front. The abdomen is about twice as long as the last lateral processes and borne slightly obliquely. The legs are fairly long, not so slender as those of *A. petiolatus*, the femur of the male having a dorsal funnel for the cement glands. The propodus is stumpy with one or two teeth before the long lamina on the inside, fine hairs supporting the latter. The claw is about the same length as the sole of the propodus and there are no auxiliary claws. Perhaps the most important character is the segmentation of the ovigers. Because of the mistaken identity of Hoek's *Phoxichilidium pygmaeum* (which is really *Anoplodactylus petiolatus*) it has been thought that the third segment was very long, about twice as long as the second as it is in *A. petiolatus*. In reality the oviger of *pygmaeus* has the third segment fairly short. It is difficult to see in Dohrn's figure of *exiguum* on account of the eggs, but his description is quite clear on this point. In the oviger of *A. pygmaeus* the third segment is hardly longer than the second. There are no good figures of *A. pygmaeus* except Dohrn's (as *Phoxichilidium exiguum*) which are excellent. Nearly all authorities have taken Hoek's figures as representing this species. The colour is pale straw colour or it may be colourless. A certain number, about 20 % from the *Bowerbankia*, had dark purple stripes.

The chief differences between *A. pygmaeus* and *A. petiolatus* are summarized below:

A. petiolatus	*A. pygmaeus*
Body elongated, 1·2–2 mm. Lateral processes large and rounded	Body short, 0·65–1 mm. Lateral processes distinct, narrow
Protuberances on lateral processes unarmed	Protuberances on lateral processes armed with a hair at apex
Cephalon longer than broad	Cephalon broader than long
Proboscis cylindrical, without groove, rounded at apex	Proboscis cylindrical with circular groove near apex which is rounded and triangular
Oviger with third segment twice as long as the second	Oviger with third segment about equal to the second
Propodus long and narrow, armed with 4–6 teeth before the short lamina; small auxiliary claws	Propodus short, armed with one or two teeth before the long lamina; auxiliary claws absent
Larva in *Obelia* medusa and related forms	Larva in gastral cavity of *Obelia* hydroid

Marcus (1940) records *A. pygmaeus* from Brazil. His description and figures, however, show almost certainly that it is a different species. The ocular process is much shorter and blunter; there are no protuberances on the lateral processes, and the third segment of the oviger is much longer than in *A. pygmaeus*. The absence of auxiliary claws and the armature of the propodus, together with the funnel for the cement glands, show it to be closely related.

A. pygmaeus, as described by Dogiel (1913), feeds on and breeds in *Obelia*, the larva inhabiting the gastral cavity of the hydroid until it emerges in the last stage with three pairs of legs and rudiments of the last pair. I have hatched out the larvae at Plymouth, and by placing them on *Obelia* hydroids found them penetrating the polyps and growing inside them exactly as described by Dogiel. The larva is pale yellowish, and in the later stages is slightly smaller than those of *Anoplodactylus petiolatus* from the medusae, although in form it is much the same. There are no eyes, as Dogiel has already noted, whereas eyes are present in the later larvae of *A. petiolatus*. The last larval stage which emerges from the polyp is quite distinct from that of *A. petiolatus*, being smaller, with a much broader and shorter cephalon and much shorter legs. The length of the last larva, newly emerged from the *Obelia* polyp, is 0·4 mm.; that of *Anoplodactylus petiolatus*, newly emerged from the medusa, is 0·64 mm., and in each the spaces between the lateral processes show the features of the adult.

Dohrn (1881) has classified the Phoxichilidiidae by the form of the proboscis and the nature of the cement glands, thus separating *A. petiolatus* and *exiguum* (*pygmaeus*) from *A. angulatus* and *Phoxichilidium robustum*, which seems to be natural.

A key to the British Phoxichilidiidae including both *Phoxichilidium* and *Anoplodactylus* is given below:

I. Ocular process not projecting beyond cephalon. No funnel for cement glands. No protuberances on lateral processes. Propodus without cutting lamina.

  A. Ovigers with five segments.

  AA. Proboscis straight at end with more or less distinct angles at corners. Body and legs compact. Auxiliary claws small and placed laterally. *Phoxichilidium virescens*

  AAA. Proboscis rounded at end without angles. Body and legs elongated. Auxiliary claws fairly large and placed dorsally.

    a. Abdomen twice as long as last lateral processes. Proboscis wider anteriorly. *Phoxichilidium tubulariae*

    b. Abdomen hardly as long as last lateral processes. Proboscis cylindrical. *Phoxichilidium femoratum*

  B. Ovigers with six segments. Auxiliary claws small and placed laterally. *Anoplodactylus angulatus*

II. Ocular process projecting beyond cephalon. Cement glands opening in funnel on femur. Protuberances on lateral processes. Propodus with cutting lamella. Ovigers with six segments.

  A. Cephalon longer than broad, auxiliary claws small, placed laterally. *Anoplodactylus petiolatus*

  B. Cephalon broader than long. No auxiliary claws. *Anoplodactylus pygmaeus*

Family PHOXICHILAE

Genus Endeis

Endeis spinosus (Montagu)

This species is fairly common round Plymouth. One male with eggs found in July 1941 and one in January 1945 (for detailed records see *Plymouth Marine Fauna*, 1931). Young not fully developed were found clinging to medusae in the plankton, and larvae were found in *Obelia* hydroids (Lebour, 1917). The species occasionally to be found between tide-marks on the Church Reefs, Wembury, on the Millbay Pontoon, and in Laira dredgings.

A widely distributed species, inhabiting both shallow and deep water, ranging from Norway to the Azores and Mediterranean, north and south Atlantic coasts of America and the Sargasso Sea.

Family AMMOTHEIDAE

Genus Ammothea

Ammothea echinata (Hodge)

This is a very common species, found in *Bowerbankia* from Phoenix Wharf, Wembury and Kingsand and dredged in the Sound (for detailed records see *Plymouth Marine Fauna*, 1931). The species breeds in spring and summer.

A widely distributed species, ranging from Norway to the Mediterranean, Azores and Atlantic coast of America.

Ammothea longipes (Hodge)

Achelia hispida Hodge, 1864

Norman (1908) records this species from Starcross, Devon, but I cannot find any early records from Plymouth. It is fairly common with *A. echinata* between tide-marks both at Wembury and Kingsand and has also been found at Phoenix Wharf in *Bowerbankia*.

It is not nearly so plentiful as *A. echinata*.

Recorded from Naples and the coasts of Brittany.

Ammothea laevis (Hodge)

This species is recorded by Hodgson (1910) from the Eddystone Grounds, but I have not seen it and can find no further records from Plymouth.

It usually occurs from below low water to 40–60 m. and is recorded from Norway, north-west France and Belgium.

Family PYCNOGONIDAE

Genus Pycnogonum

Pycnogonum littorale (Ström)

This species is usually found below low-water mark. A dead specimen occurred high up on the Church Reefs, Wembury, among *Ascophyllum*. For details of records see *Plymouth Marine Fauna* (1931).

A widely distributed species from tidal zone to a depth of 800 m. It is recorded from Iceland and Greenland to the west coast of France, Mediterranean, northern Atlantic and the east coast of the United States.

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MARKING FISH WITH THE ELECTRIC TATTOOING NEEDLE

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Most fishery biologists have heard from time to time of experiments on marking fish by tattooing identification marks on them. The present usual methods of marking fish by attaching marks externally to the gill-cover, caudal peduncle, or other part of the body, have the disadvantage that a certain number of the marks are lost, and this uncertainty bedevils all those marking experiments designed to show rates of mortality or rates of capture.

Yet the only reference in the literature known to me is a very short paper by Gandolfi-Hornyold (1929). His most successful experiment consisted in marking six silver eels on the light ventral side with Indian ink (encre de Chine) introduced in the oriental fashion by a bundle of needles. Five of the six fish were alive some 6 weeks later with the marks as clearly legible as when first made. But I know of no further developments of this technique.

In August 1939, I made some experiments at the Plymouth Laboratory, by the courtesy of the late Director, Dr Kemp, F.R.S., and with the help of the staff, to all of whom I would express my thanks. Some thirty-two plaice, two soles, and twenty-five rays were placed in one of the big outdoor tanks for the experiments, and were all in good condition, though they had not been fed and were certainly overcrowded.

The electric tattooing needle used was bought from a professional tattooist, who also gave me a brief lesson on his art. In principle the needle is a small vibrator run from an ordinary torch battery. The vibrator is attached to a style enclosed in a tube, and a needle is secured to the end of the style, and is adjustable, so as to vary as may be required the length of needle point which projects from the enclosing tube. In use, the tube is held like a pen, and is repeatedly dipped in the pigment, as one dips a pen in ink. The writing is done slowly, with a moderate pressure on the skin, and the needle, which vibrates at high speed, makes a series of fine punctures in the skin into which the pigment is carried. The whole device is simple and effective.

On the first day I tried various settings of the needle and various slopes of the pen on dead fish, and then tried marking two small rays and a small plaice which had that day been brought in and placed in the shallow 'Drake's Island Tank' indoors. I found the plaice easy to mark, the rays difficult.

On the next day, 5 August, the marked plaice was dead, but so were two of the unmarked controls.

I found, to my surprise, that it is much easier to mark a living plaice or sole than a dead one. This is mainly because the fish responds to the irritation of the needle by producing much mucus, which washes away the surplus ink, and makes it easy to see how much of the work has entered the deeper skin, and therefore which of the strokes need to be repeated. I used three pigments, namely, Chinese ink, which I bought as a stick and ground myself for use as needed, natural sepia from cephalopods, and Windsor and Newton's best quality vermilion, which I mixed with water to make a very strong suspension. All marks were made on the white underside of the fish: they consisted of a letter and a number, e.g. E 37.

While it was easy to mark the plaice and the sole, I had the greatest difficulty with the rays. The skin of these fish has a leathery toughness which makes penetration to any depth a matter of great difficulty. Quite early in the experiments I came to the conclusion that the method would be of no use with rays, but I persisted in giving it a good trial. Yet a spotted dogfish, which I marked with a letter for a physiologist working on the reflexes of this fish, took the mark well.

The time taken to mark a plaice was about 70 sec.; but I was working single-handed and had to hold the fish as well as to manipulate the needle. No doubt the time would be less with an assistant. The rays took much longer, for owing to the difficulties mentioned above, the strokes of the needle had to be repeated again and again to get any impression. Yet none of the fish, of any species, seemed the worse for the marking; they usually lay quietly while being marked, and, on being restored to the water, at once fled to the bottom of the tank and endeavoured to hide their embarrassment under a shower of sand, or rather, of echinoderm spicules, for this was the only cover available.

On 10 August the experiment was ended, in its first stage, by clearing all the fish out of the big tank, and examining for general condition, wounds, and for the legibility of the marks. The plaice and the sole had then had the mark for 6 days, the rays for 4 days. The fish were inspected by Dr L. H. N. Cooper, who acted as referee, and judged the fish by a fairly strict standard. Below are given the results for the plaice and the sole.

			Condition			Legibility				
	No.	Died or dis-appeared	Very good	Good	Poor	Very good	Good	Moderate	Poor	Injured
					Plaice					
Marked	18	4	13	1	—	9	2	3	—	1
Controls	20	8	9	3	—	—	—	—	—	3
					Soles					
Marked	1	—	1	—	—	1	—	—	—	—
Control	1	—	—	—	1	—	—	—	—	—
					Rays					
Marked	12	7	4	1	—	0	3	1	1	3
Controls	17	3	6	5	3	—	—	—	—	6

Of the marked plaice, two died and two could not be found at the close of the experiments. Eight of the controls, however, died, and it will be clear that the deaths of the two marked plaice cannot with any certainty be ascribed to the operation of marking, for a much larger number of the untouched controls died. The general condition of the marked fish was also in no way inferior to that of the controls. As to the legibility of the mark, eleven were either very good, or good, and three only could be described as moderately good. In none did the referee fail correctly to read the number.

The sole took the mark very well, and was in perfect condition at the end of the experiment; the control sole was moribund.

The result with the rays was poor. Of the twelve rays marked, only five could be recognized as marked fish after 4 days. None died, though two of the controls died. Seven of the marked rays must therefore either have escaped from the tank, or have lost the mark. The latter is the most likely, for most of the rays were big specimens which could hardly hide themselves successfully in a dark corner of the tank; and, further, the referee passed over as 'controls' specimens which I knew to be marked fish, for I could still see traces of the marks.

Of the five rays recognized as marked fish, in not one was the mark classed as 'very good', three were 'good' only, and one was 'moderate', and one 'poor'. The general condition of the marked fish was at least equal to that of the controls, but wounds were very frequent, and I learnt that it is impossible to keep rays for very long in confinement in perfect condition.

Writing off the rays as a failure, there still remained the successful experiments with plaice and sole. Twelve of the marked plaice and the sole were put into the indoor tanks, where they were fed. A few days after the transfer, a ray, a plaice, and the sole died. The mark on the ray, which had been classed as 'good', was very feeble, that on the sole faint but legible, and that on the plaice very sharp and clear.

The outbreak of war caused the experiments to be ended on 26 September, when Mr G. A. Steven very kindly examined the fish for me and made a report.

After 7 weeks, the marks on the ten surviving plaice were classed by Mr Steven as follows: three fairly clear, three faint, and four extremely faint. Yet Mr Steven correctly read the writing on all but one of the fish. Four of the fish were in perfect condition, four had injuries to the tail, and two had abrasions on the underside of the head. None showed any injury around the mark.

It would seem from these experiments that tattooing has possibilities, but that the pigment injected is slowly dispersed or overlaid in the skin of the fish. It may be that branding with a hot instrument, or even scratching, will be more effective, for I would place it on record that on one of my trips on trawlers I saw caught a large halibut on which letters, apparently a man's initials, were clearly legible on the upper, coloured side. The letters were distorted in a direction which suggested that they were carved on the skin of the fish when small, and must have been carried for a long time. The letters appeared black, and the wounds, on healing, must have become surrounded by melanophores.

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THE MODE OF LIFE OF *ARENICOLA MARINA* L.

By G. P. Wells

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(Text-figs. 1–10)

CONTENTS

INTRODUCTION

Large, common, tough, the lugworm is an outstandingly good object for anatomical and physiological work. Its mode of life has not yet been clearly worked out, and one must know how an animal lives if one wishes to understand its structural and functional peculiarities. Burrowing as it does in muddy sand, the lugworm cannot be watched under natural conditions (except on the rare occasions when it shows itself on the surface). Existing accounts of its behaviour in the field are therefore practically confined to the form of the burrow which it excavates. The present paper attempts to synthesize, partly from field observations and partly from laboratory studies of the worm's activities, a coherent picture of its daily life.

The work was done in the summer and autumn of 1944, while the Zoology Department of University College, London, was evacuated to Bangor, North Wales. My warmest thanks are due to Professor Brambell and his staff, of the Zoology Department, University College of North Wales, for their friendly and helpful reception during that period.

The present content of the literature on the lugworm's burrow may be summarized in three statements: (i) according to the great majority of writers, the worm lives in a U-shaped burrow, open at both ends; (ii) a minority believe, however, that the open U is atypical, and that the usual burrow form is an L, in which a U-configuration is completed by a column of sand, distinguishable from the general mass, and rising from the lower end of the L to the surface; it is to this opinion that the present writer adheres; (iii) other burrow forms have been described from time to time, but appear in fact to be untrue, or true only in exceptional cases. The following are the main points in the history of the subject.

The first definite mention of the lugworm was by Belon (1555), who stated that it lives in mud, into which it can burrow rapidly, that it is dug for bait, and that its presence is indicated by masses of coiled excrements on the surface. For nearly three hundred years, practically nothing was added to this account of its mode of life. Detailed descriptions of the form of the burrow began to appear in the nineteenth century.

The U-shaped burrow was introduced by Audouin & Milne Edwards (1833) in the following words: the worms 'creusent des cavités cylindriques très profondes, qui communiquent ordinairement au dehors par deux extrémités'. Note the qualifying word 'ordinairement'. Milne Edwards repeated this description, with the qualification, in his revision of Lamarck (1838).

Stannius (1840) collected *Arenicola marina* at Heligoland, for anatomical study. He failed to find two openings to the burrow, and stated that the experience of fishermen, whom he questioned on the point, agreed with his own.

In spite of the dissentient voice of Stannius, the worm was described by the great majority of subsequent writers as living in a U-shaped burrow. Usually the statement was made without qualification, as if the open U were the only observable form. Fauvel (1927), to quote a recent example, described the burrow of *A. marina* as a 'galerie en U' without alternative.

An obvious question arises. If the lugworm lives in a U-shaped burrow, open at both ends, whence does it get the sand which it so copiously defaecates?

According to many of the earlier writers (e.g. Stannius, 1840; Gamble & Ashworth, 1898), burrowing and feeding are one and the same act; the lugworm burrows by eating its way into the sand. The view has, however, gradually grown up that the two performances are in fact distinct, and it was recently shown that very little sand, if any, is swallowed during burrowing (Wells, 1944 *b*). Those who believe that the open U is the typical burrow form generally state that the worm ascends to feed from the surface layer of the sand, which is especially rich in micro-organisms and detritus.

The first hint of this came from Cunningham & Ramage (1888): 'sand is ejected in a cylindrical rod from the anus, and this forms a spiral coil on the surface of the shore; near the "cast" is usually a wide hole, from which the head is protruded when the tide is up.'

Gamble & Ashworth (1898) made an almost identical statement. They distinguished, on anatomical grounds, between two varieties of *A. marina*. The large 'Laminarian' variety was described as living in a long vertical shaft (p. 175). The worms of the commoner 'littoral' variety 'sink their U-shaped burrows to a depth of from one to two feet below the surface. One end of the burrow is marked by a casting, the other by a "countersunk" hole, through which the head of the lugworm is protruded when the tide comes in.'

Wesenberg-Lund (1905) was more specific. He described the burrow as horseshoe-shaped, with a faecal pile at one end and a funnel-shaped depression at the other. At low tide, the worm lies at the bottom of the burrow. When the tide comes in, carrying and depositing fresh material, the worm ascends and sucks surface sand from the region of the funnel. This is how the funnel is formed.

Blegvad (1914) watched the worms on the beach, when the sand was covered by a shallow layer of water. 'At the bottom of a little funnel-shaped depression of the sand the proboscis may be seen moving up and down, swallowing the matter drawn down from the sides and circumference of the funnel.'

In the light of these various observations, the open U is seen as a workable burrow form, in which the worm could live and maintain itself. The writer believes, however, that the U is exceptional, occurring only in a particular type of situation, and he doubts whether the worm ever actually feeds at the surface, even when its head moves about in the funnel. As we shall see, it may be doing something else.

The first clear account of the L is by Bohn (1903), who worked at Wimereux. He believed that many varieties of *A. marina* exist, with different habits, but he gave details of two only. One of these was described as making a reticulate burrow (p. 175). The other was found on a bank of sand exposed at low tide. When the sea was just leaving the bank, and the surface sand was soft and semi-fluid, he saw the formation and disappearance of fugitive funnels. The level of the water in the funnels oscillated rhythmically, and sometimes dropped abruptly, as if sucked down from below. The worms' heads did not appear at the surface. As the sand dried and hardened, the funnels became fixed. Only in exceptional cases was there an opening at the bottom of the funnel. The burrows were nearly always oblique or L-shaped, with their blind ends dilated (Fig. 1 b_1, b_2). The head of the worm was at the blind end, 10–15 cm. below the surface, and vertically below the funnel. As the head moved rhythmically and swallowed sand, the column of sand above it was kept in pulsing and slowly subsiding motion, and the funnel at the surface resulted from this activity.

Ashworth (1912) mentioned L-shaped burrows as an occasional alternative to the open U.

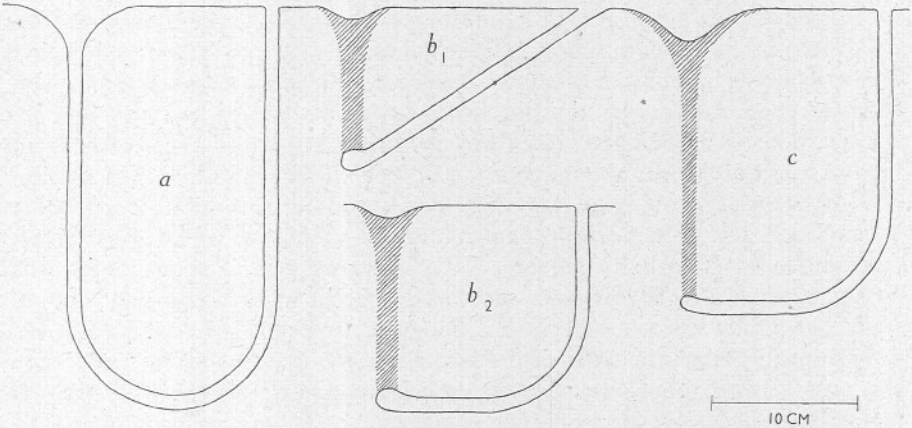

Fig. 1. Diagrams of *Arenicola* burrows from the literature. *a* is the open U. b_1, b_2 are of Bohn's low-tide variety; the shaded area is a column of rhythmically moving sand over the animal's head. *c* is Thamdrup's typical form; the shaded area is the 'Saugsäule', continually consumed below and renewed by sedimentation and subsidence from above.

The fullest description of the L is that of Thamdrup (1935), who worked on beaches in Denmark, in Holland, at Plymouth and at Millport, and wrote that he had examined many hundreds of lugworm burrows, all of which conformed to the same essential plan. His account is in many ways the best yet available; nevertheless certain of his results will be disputed below, and it is therefore necessary to summarize his conclusions in some detail.

Thamdrup's main points are as follows. Starting from the faecal pile, a gallery descends vertically, or in a gentle curve, to a depth of 20–28 cm., where it turns to run horizontally for a variable distance. It thus forms an L. This L does not necessarily lie in a plane, but may bend to one side or the other. In exceptional cases, the blind end of the gallery may rise 1–5 cm. towards the surface. The worm is generally found with its head in the lower part of the burrow, and its tail towards the opening. Vertically above the blind end of the burrow, there is in most cases a conical depression on the surface of the sand. This is connected with the end of the burrow by a narrow, perpendicular column of yellow sand, the 'Saugsäule', contrasting in colour with the grey-black of the general mass (Fig. 1 *c*). The column arises as follows. The worm eats sand at the blind end of the gallery. New sand slides downwards to replace the old, as fast as it is consumed. The surface therefore subsides to form a funnel, in which fresh material is deposited by the tide. Thus a continually descending column of surface sand originates and is maintained. Sometimes the worm tunnels a horizontal branch from the lower part of the burrow, and sets up a new 'Saugsäule' at the end of it.

Thamdrup adds a tantalizing sentence: 'Diese ganze Auffassung von der Bildung der Röhre und dem Entstehen des Trichters und der Saugsäule durch die Nahrungsaufnahme wurde beim Auslegen rotgefärbten Sandes auf die Oberfläche kontrolliert; hierdurch war es möglich, die Bewegung des Materials durch den Trichter und die Saugsäule hindurch Schritt für Schritt zu verfolgen, bis es als Kothaufen wieder an die Oberfläche gelangt.' No further details are given on this point—nothing except the passage just quoted. This is unfortunate; the concept of the 'Saugsäule' will be criticized below, and more information about the reddened sand might be illuminating.

Why, if the burrow is of this form, have so many authorities described it as an open U? Thamdrup's explanation is as follows. The gravity-feed mechanism only works if the sand is sufficiently moist to slide downwards. In some situations, at low tide, the water content of the sand may become such that, while the material in the 'Saugsäule' continues to descend as fast as consumed below, the sides of the funnel are too dry to slide in and renew the supply from above. In this case, a large part, or even the whole, of the material in the 'Saugsäule' may be removed by the worm. The 'Saugsäule' may thus be converted into an open shaft, completing the U, 'als ob der Wurm seinen Gang unter der Bildung eines U an die Oberfläche geführt hatte. In solchen Fällen kann man auch ab und zu sehen, wie der Wurm sich in dem so gebildeten Gang hinaufstreckt.'

Thamdrup's whole story is clear and attractive, and rests on a great number of field observations. Nevertheless, there are facts which it fails to explain. Why, for instance, when an accident of desiccation has converted the L into an open U, should the worm stretch up towards the funnel? As we have seen, the worm's head has been described as appearing actually at the funnel by Cunningham & Ramage (1888), by Gamble & Ashworth (1898), by Wesenberg-Lund (1905) and by Blegvad (1914); this impressive series of observations suggests that it is something more than a chance phenomenon. One may also ask how a worm, living in such a burrow as Thamdrup describes, obtains an oxygen supply.

It will be shown below that the lugworm's burrow is typically an L with a column of 'specialized' sand completing a U-configuration, but the column is the resultant of a number of different factors; its form is more variable than Thamdrup's account suggests, and it is set up and maintained by several distinct activities of the worm.

Besides the open U and the L, a few other burrow forms have been described; they appear, however, to occur in exceptional cases only, if they occur at all.

Oken (1817) stated that the lugworm lives, head upwards, in a vertical shaft, about as long as the worm itself. Nothing like this has been observed by anybody else.

Gamble and Ashworth (1898) distinguished between two varieties of *A. marina*, differing in structure, in habitat and in habit. The common 'littoral' variety was described as living in an open U. The second 'Laminarian' variety 'occurs on the Lancashire coast at the upper part of the Laminarian zone...the burrows are of considerable length, three feet or more, and are not U-shaped, but simply vertical'. As Fauvel (1899) suggested, a worm living in such a shaft would have to get food and oxygen by means quite unlike those employed in a U or an L, and so great a difference of habit is hard to conceive. The description of Gamble & Ashworth was later revised by Ashworth (1912), who placed the worms of the 'Laminarian' variety either in vertical shafts or in L-shaped burrows, the latter being the more usual form. The writer believes that all of the vertical shafts were in fact L's whose horizontal parts had eluded the observers. In digging in the Laminarian zone, to a depth of 'three feet or more', the holes would readily fill with water, and this, as he can testify, makes careful study difficult. Richter (1926) included the vertical shaft among the possible burrow forms of *A. marina*, but he apparently based this statement on the work of Gamble & Ashworth, and not on his own observation.

Irregular networks of galleries, branching out from the bottom of the burrow, were briefly described by Bohn (1903) as occurring in aquaria, and by Richter (1924) as occurring in the field.

THE FORM OF THE BURROW, AS OBSERVED IN THE NEIGHBOURHOOD OF BANGOR, NORTH WALES

My field observations were made from July to October 1944, at several localities in the neighbourhood of Bangor, North Wales.

The technique varied with the circumstances. If the sand was firm enough, it was caused to split in the plane of the burrow. If this was impossible, the sand was sliced with a trowel or a large knife, or the burrow was followed with a long probe of bicycle valve tubing.

Owing to the great variability of the burrow, the following account is illustrated as far as possible by scale drawings of individual burrows. The drawings were carefully made on graph paper on the beach, after measuring up the burrows with a ruler, and subsequently traced on to Bristol board. To facilitate comparison, the drawings have been turned round when necessary, to bring the faecal end always to the right.

The burrows generally curve somewhat to right or left, and are drawn as if straightened out to lie in the plane of the paper.

In every case where an individual burrow was drawn, the worm was found and roughly measured. The outlines of the worms have been included to scale in the drawings, though, for clarity, they have not been put in place in the burrows.

The Three Divisions of the Burrow

In the great majority of burrows, a tunnel descends vertically from just below the pile of faeces on the surface and then swings round to run horizontally. So far everything is plain; most authorities agree up to this point, and the roughly L-shaped tunnel is very easily demonstrated on the beach. The worm is found in the tunnel, with its tail towards the faecal opening, and, on careful inspection, certain distinguishing marks can be seen, which differentiate the upper few centimetres of the tunnel from the rest. The short, upper portion will be termed the *tail shaft*, and the longer portion, which descends from the lower end of the tail shaft and then curves to become horizontal, will be termed the *gallery* (Fig. 10, p. 204).

It is at the lower end of the gallery that the difficulties, and most of the interest, begin. This end of the gallery is connected with the surface by a zone which will be termed the *head shaft*. The characters of the head shaft are exceedingly variable, from burrow to burrow and, probably, in a single burrow from time to time. Sometimes a clear channel continues upwards from the end of the gallery to the surface of the sand, in which case the burrow is an open U. More often, the U-configuration is completed by a column of specialized, or 'worked' sand, rising from the deep end of the gallery, and broadening, more or less regularly, and more or less rapidly, as the surface is approached. Shafts of this type are often difficult to expose and study.

The simpler, less variable parts of the burrow will be described first.

The Gallery

The gallery—the longest of the three divisions of the burrow—is a cylindrical passage along which the worm moves to and fro, always with its head in the same direction.[1] The inner surface of the wall is firm and well smoothed, except that it generally shows a fine transverse striation, presumably due to the worm's neuropodia.

If the burrow runs through grey or black mud, the gallery is seen to be surrounded by a yellow-brown layer, often several millimetres thick. This layer is generally firmer than the surrounding mud, due, apparently, to mucus exuded by the worm. Its colour is largely caused by the oxidation of black iron sulphide in the mud to yellow oxide, but sometimes it exhibits greenish or rusty orange tints, to which coloured secretions from the worm probably contribute.

The gallery usually drops more or less vertically for some distance from the lower end of the tail shaft, and then curves gradually round to become horizontal. Occasionally, however, one finds a burrow which descends obliquely, at about 45°, from the defaecation point.

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[1] By narrowing itself, and repeatedly extruding its proboscis along its own ventral surface, a lugworm can turn longitudinally in a glass tube which, at other times, it seems comfortably to fill. This may also occur in sand. I have noted on several occasions that worms kept in the laboratory can turn in their burrows, thereafter defaecating from the upper end of the head shaft. Once or twice, in the field, I saw faecal cylinders in the middle of funnels, suggesting that the worms had reversed themselves in their burrows. Reversal appears, however, to be an infrequent event, involving reconstruction of the burrow to suit the new orientation.

The Tail Shaft

Periodically, the worm moves backwards to the surface to defaecate. This it does by shooting out, at great speed, a single faecal cylinder. The caudal end of the burrow therefore becomes surrounded by a number of cylinders, each resulting from one such excursion. If there is little wave disturbance, the cylinders may pile up into a heap several centimetres in height.

Defaecation usually occurs with the tip of the tail just at the surface of the sand—at least, the faecal cylinders usually end at the very mouth of the burrow. Occasionally, however, one finds a cylinder extending for a few millimetres down a burrow.

The tail shaft is that part of the burrow which is occupied by the tail at the moment of defaecation. It is generally strictly vertical (except for the uppermost few millimetres). It differs from the gallery in being slightly narrower, and, since it is never occupied by the chaetigerous part of the worm, in showing no transverse, neuropodial striations.

The uppermost extremity of the tail shaft may open simply and directly at the surface of the sand. More often, it bends sharply, so that the upright part of the shaft is not vertically below the orifice (Fig. 5 *b*). Very commonly, it divides into two or more branches which open separately, and through any one of which the worm may defaecate (Fig. 3). Clearly, these passages must have been excavated and moulded by the tail itself.

The Head Shaft

As already stated, the head shaft is extremely variable. I have chosen for description the commonest and most representative types, and also one or two out of many exceptional or unique cases; the latter were selected, partly to show the range of variation encountered, and partly because they throw light on the activities of the worms.

The examples chosen will be grouped according to the kind of bottom in which they were found.

In rapidly drying sand. At Aber, when the tide is out, a flat expanse of sand stretches seawards for several miles. The surface undulates gently, and varies in moisture relations from place to place. Vast areas keep a certain amount of water on the surface, even after hours of exposure, and these are densely populated by large lugworms. Here and there, however, a stretch is found which dries soon after the tide has receded. The worms on such patches are few and, perhaps because they are young, or perhaps because the environment is unfavourable, they are never of large size. The surface of these patches is firm and ripple-marked. As one digs, no water appears in the holes, and it is often obvious, at least after an hour or so of tidal exposure, that the worms in the burrows are living in damp air.

The burrows in such places are very easy to study. If one inserts the spade vertically beside a funnel, on the side away from the casting, and then gives a quick heave, the sand often splits in such a way as to expose the whole burrow in section. Other types of bottom are less amenable. Rapidly drying sand will therefore be taken first, even though the small size and sparse distribution of the worms suggest that the habitat is not as favourable for the inhabitants as it is for the observer.

The positions of the head shafts are generally indicated, on the surface of the dry sand, by shallow conical depressions. Sometimes there is a hole, a few millimetres across, at the bottom of the cone; sometimes there is no trace of any opening. The hole, when present, suggests that the burrow is an open U, but this inference is dangerous; as we shall see, the hole may lead into a blind cavity; the only way to establish the presence of an open U is to expose it along its whole length. Occasionally, a head shaft ends above in a ragged hole, a centimetre or so across, and lying flush with the surface, i.e. without any surrounding depression.

The commonest type of burrow is that illustrated by the two examples in Fig. 2 *a*, *b*. In both there is a shallow cone ending below in a small opening; this opening leads into an irregularly shaped cavity whose walls are apparently smoothed. From the bottom of this cavity, a tubular passage descends to continue into the lower end of the gallery. In Fig. 2 *a*, this passage is empty, and the burrow is therefore an open U. There is, however, a difference between the gallery and the passage ascending the head shaft. The wall of the gallery is firm and transversely marked by the worm's neuropodia. As the burrow curves upwards into the head shaft, these signs disappear, and the ascending passage has coarse, powdery looking walls. In Fig. 2 *b*, the general plan is similar, but the upper end of the passage is filled with a cylinder of fairly firm sand (stippled in the drawing) which can quite easily be tumbled out of it.

Such burrows were found in great numbers. The sand cylinder may be short, or it may descend as far as the boundary between head shaft and gallery; sometimes it continues above into a mass of sand filling the lower part of the irregular cavity below the funnel. The passage up the head shaft has the same diameter as the gallery, from whose lower end it curves smoothly upwards; it differs from the gallery only in the coarse texture of its wall; it has evidently been excavated and traversed by the worm. The sand cylinder seems to have been drawn down into it.

The most reasonable explanation of these appearances is, I think, the following. At high tide, when the surface sand was soft, the worm ascended and worked, by some means, on the sand in the region of the irregular cavity below the funnel, mixing it with water and making it semi-fluid. The worm then retired backwards to the gallery, drawing the softened sand down as a cylinder. This gives Fig. 2 *b*. To get Fig. 2 *a*, one must suppose that the cylinder was consumed from below.

As already stated, Fig. 2 *a*, *b* show the most usual type of burrow found in dry sand. Sometimes, however, one finds a head shaft consisting of a broad cone of yellowish, 'worked' sand. Two examples of this are drawn in Fig. 2 *c*, *d*.

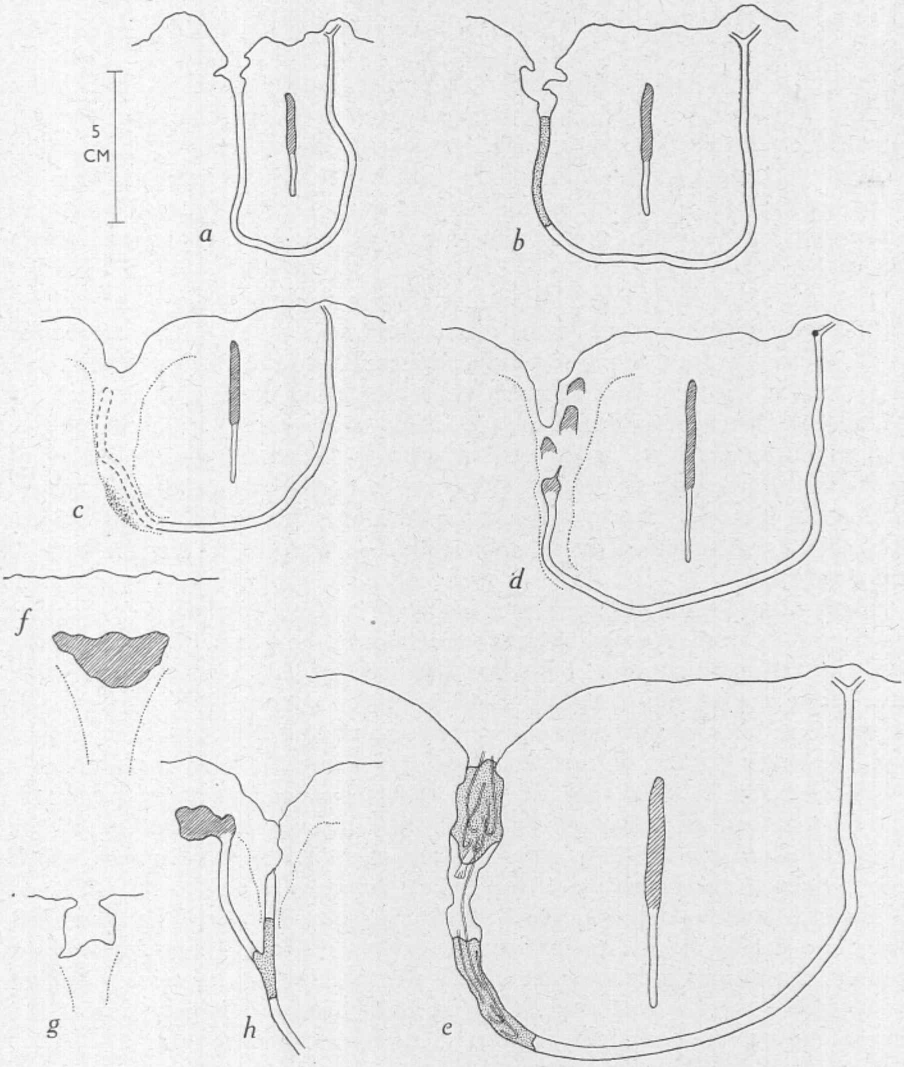

Fig. 2. Burrows and head shafts from rapidly drying sand, Aber. *a–e*, whole burrows, with the worms inset to scale; *f–h*, head shafts. The scale applies to all the figures.

In Fig. 2 *c*, the head shaft is a broad column of yellow sand (dotted outline), fine in texture except at its lower end, where it is coarse and gritty (stippled). The lumen of the burrow continues up this column to end blindly near the base of the surface depression, but, as before, the part which ascends the column (dashed outline) has coarse, powdery walls and is less permanent in appearance than the gallery. The sand in the column was probably worked up and softened by the worm at high tide; the ascending tunnel represents a single upward excursion of the worm, made while the sand was still fairly soft.

In Fig. 2 *d*, the head shaft is again a tapering column of yellow sand (dotted outline). Within it, four cavities (shaded) appeared when the sand was split open. The cavities have fairly smooth walls; the lowest one continues into a descending passage, which meets the gallery below; this passage lacks the usual gallery markings. The cavities appear to result from successive upward excursions of the worm, during which the sand was eaten or dragged downwards.

Fig. 2 *e* shows a unique, but rather illuminating, burrow. The position of the head shaft is marked on the surface by a wide cone. A broad, irregular space curves up from the lower end of the gallery to the bottom of the cone. The walls of this space are apparently smoothed, but not as firm and definite as those of the gallery. Within the space, and completely blocking it, are two masses of rather moist, 'pasty' sand (stippled). There are also a number of filaments of green weed (double lines), mostly curled up in the sand masses, and, at the bottom of the upper mass, the skeleton of the tail of a small shrimp. The worm was found in the usual position, i.e. with its head at the base of the head shaft.

Fig. 2 *e* can, I think, be interpreted in one way only. The smoothed, irregular cavity results from repeated upward excursions of the worm. The moist sand, with its various inclusions, has somehow been pulled down into the shaft. As the tide recedes, bits of algae and similar objects are often left in the funnels of lugworm burrows; if the worm were to ascend and drag the moist surface sand downwards, such objects would be drawn into the head shaft too.

These examples show that previous writers have tended to over-simplify the burrow, and the behaviour by which the burrow is produced.

To conclude this section, some further examples may be noted, which throw light on the formation of the conical depressions on the surface.

Fig. 2 *f* shows a condition which I only encountered once. The head shaft ends above in a closed, smooth-walled cavity (shaded). This cavity lies a couple of centimetres below the surface, which shows no depression or sign of the presence of a head shaft. This shaft belonged to a large worm, as the worms on dry sandbanks go; its overall length was about 9·5 cm.

Fig. 2 *g* shows a not uncommon condition. The head shaft leads up to an irregular cavity whose roof has apparently collapsed in the middle. This condition can clearly be derived from that just described, if it be supposed that the worm had worked rather nearer the surface. The appearance, as seen from above, of a ragged hole without a surrounding depression indicates a shaft of this type; by inserting a probe, one can generally satisfy oneself that the hole leads into a fairly extensive, blind cavity.

Finally, Fig. 2 *h* illustrates an exceptional condition, which I saw only twice out of many burrows examined—a forked head shaft. The vertical branch ends just below the funnel, to which a fine crack runs from its blind end. The side branch ends beside the funnel, in a cavity with rather smoothed walls (shaded). This may have been the beginning of a second funnel. Sand (stippled) has been dragged down to the fork, apparently from the original funnel. The worm's overall length was about 4 cm.

In wet sand (*the* '*typical form*'). As already described, the distribution of lugworms on the Aber sands is somewhat patchy. The areas densely populated with large worms have the following characteristics: the sand surface is fairly firm and ripple-marked; the receding tide generally leaves water in the troughs of the ripples and the hollows marking the positions of *Arenicola* head shafts. This water may remain for hours, or it may slowly dry or drain away, but even in the latter case the deeper sand is obviously wetter than on the 'rapidly drying' patches described above. Water collects in the holes as one digs, making observation difficult.

The burrows in wet sand conform to a fairly simple and uniform pattern. For this reason, and because the worms are large and abundant, the wet-sand form will be termed the 'typical' one.

I studied the typical form at Aber and at Bangor, on the beach below the lane called Gorad-y-Gyt. In the latter situation, much of the sand contains shell fragments, which lead to complications described in another section. If, however, one walks out along a stream which crosses the sands to the right (north-east) of a disused oyster bed, one finds, near low-tide mark, a patch where the shell is practically absent and the burrows conform to the simple, typical pattern.

The presence of a head shaft in wet sand is usually marked by a saucer-shaped depression of the surface, several centimetres across. In most cases, these depressions retain water as the tide recedes, and fragments of weed and similar objects collect in them. Sometimes a hole, about 1 cm. across, opens at the bottom of the saucer. This is no proof that the burrow is an open U; in every case examined by myself, the hole led into an irregular, blind cavity, as in Fig. 3.

On exploring the saucers with the finger, one notices (i) that the bottom of the saucer, which is usually flat, is softer than the general sand, and (ii) that, at a certain point, the finger can be pushed downwards into a tapering shaft, encountering practically no resistance; the shaft is often long enough to admit the whole forefinger, and several centimetres wide at the top; it feels as if full of a fluid or semi-fluid mixture of sand and water.

Owing to the wet consistency of the sand, one can seldom expose the head shafts by causing it to split. One has to slice away the sand with a trowel or a large knife, and study the shafts in horizontal or vertical section. The burrow drawn in Fig. 3 was fortunately placed in a bank of sand beside a stream, and could therefore be dissected from the side and drawn to scale.

The upper part of the head shaft consists of a more or less gradually tapering cone of pasty or fluid sand. This is the part that one can probe with the finger, as just described. It leads below into an approximately vertical column of rather firmer sand, which descends to meet the gallery. This column has the following characteristics. It is yellow in colour, contrasting with the grey or black of the surrounding sand; its boundary is sharp, but completely devoid of any special wall, like the mucus-impregnated wall of the gallery; its diameter varies in different cases from about 7 to a little over 20 mm.; it enlarges, and becomes irregular in form, at the point where it meets the gallery.

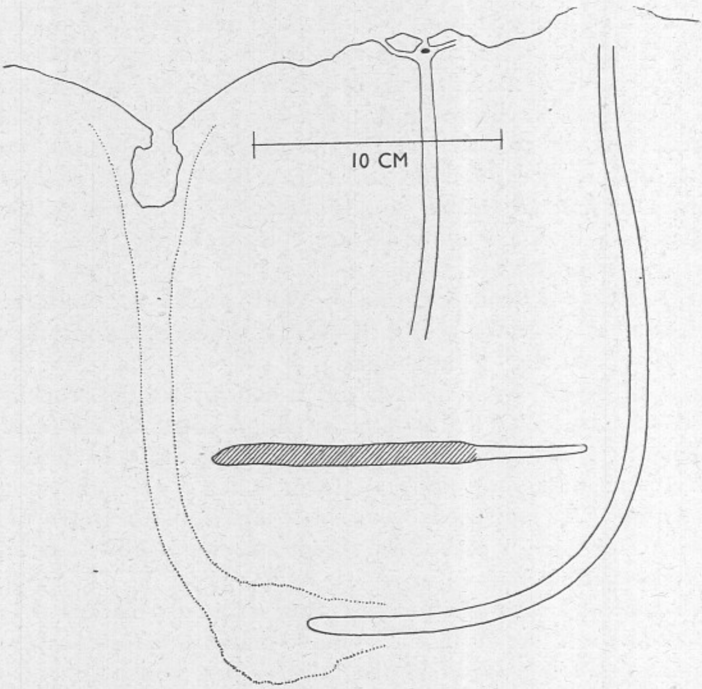

Fig. 3. A burrow of the 'typical form' from wet sand, Bangor, with the worm inset to scale. This burrow was probed from the faecal end, then laid open. The details of the tail shaft were destroyed while inserting the probe. The caudal end of a burrow from wet sand, Aber, has been inserted between the two orifices of the main burrow; the black spot is the beginning of another outlet running away from the observer; the scale line is drawn at the boundary between tail shaft and gallery.

The yellow column is obviously the 'Saugsäule' of Thamdrup (1935). His suggestion that its component sand is continually consumed below, and therefore continually moving downwards, is supported by the following observations. Bits of weed and similar objects (including dead leaves, on the Bangor beach in autumn) often collect in the saucers on the surface.

Sometimes one finds a piece of weed or a leaf, still quite fresh in appearance, embedded in the sand at some point along the shaft. Finally, in the enlarged region where the shaft meets the gallery, there is often a considerable accumulation of weed, shell, leaves and so forth, mostly packed against the sides of the yellow area. They seem to be drawn in above and to travel down with the sand, to be rejected by the feeding worm, and so to collect at the point where feeding takes place.

On the other hand, there are facts which make it impossible to accept Thamdrup's hypothesis as the whole truth. Sometimes one finds a shaft dropping perpendicularly to the end of the gallery, as his hypothesis requires (Fig. 1 *c*). Very often, however, the shafts are curved. Sometimes the end of the gallery begins to rise, and the head shaft smoothly continues the curve. Once or twice, I saw a gentle sigmoid curvature of the shaft.[1] These curves make it impossible that the shafts could have originated, and improbable that they could be maintained, by gravitational subsidence alone. Subsidence is undoubtedly important, but other factors must be at work in giving the shaft its form.

Three facts suggest that the worm tunnels up nearly to the surface as a first stage in the setting up of the head shafts. First, the narrowest head shafts observed were just about equal in diameter to the galleries. Secondly, they often curve upwards, in such a way as smoothly to continue the line of the gallery. Thirdly, I once found the following appearances: a cone of soft sand, 10 cm. deep and 6 cm. across at its upper end, tapered below into a shaft, slightly over 1 cm. across; in the upper end of the shaft, there was a long cylindrical cavity, of the diameter of a fair-sized worm's body, ending above in a slight dilation at the bottom of the cone, and continuing for some distance down the shaft; unhappily, my excavation filled with water as I was working and I could neither determine whether the cavity traversed the whole shaft nor find the responsible worm, but it seems clear that the worm had ascended the shaft to the cone, while the latter was full of sand.

These evidences suggest that the narrower head shafts originate in much the same way as that of Fig. 2 *b*. The worm ascends nearly to the surface, 'works up' and softens a cone of sand, and then retires, drawing the softened sand into the shaft after it. Such a sand column could then operate for some time as suggested by Thamdrup, sliding down as consumed below. The wider head shafts, which range up to about 2 cm. across, might originate as narrow ones, and then be widened, either by parallel workings of this type or by other factors to be discussed in a later section.

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[1] Once I followed a column, about 1 cm. in diameter, which ran as follows: starting from the lower end of a cone of very wet sand, 4 cm. deep, it (i) descended for 6 cm. through black muddy sand, then (ii) passed downwards for a further 10 cm. through a layer of sand closely packed with small shell fragments, during which part of its course it curved gently round the edge of a larger shell and returned to the original perpendicular, and finally (iii) swung, pretty sharply, through a right angle, to meet the gallery, where the head of a large worm (overall length 16 cm., and plump in proportion) was found.

The presence of a saucer on the surface indicates a well-established head shaft. Sometimes one sees other appearances which (as shown by laboratory observations, described below) are preliminary stages in the development of saucers. The following are examples: (i) one or two cracks, running circularly and marking out an area a couple of centimetres across, which is flush with and otherwise indistinguishable from the general surface; (ii) a roughly circular area of surface sand, a couple of centimetres across, which has dropped about 1 cm. and so forms the flat bottom of a pit surrounded by vertical walls; (iii) an irregular hole, 1–2 cm. in diameter, leading into a blind cavity much as in Fig. 2*g*.

Such incipient shafts are always to be seen here and there among the saucers. Once, at Bangor, after several days of stormy weather, I found that the saucers were few and small while most of the head shafts were marked by appearances like those just described. Deeper in the sand, I found the usual yellow columns; probably the storm had disturbed the surface sand only, and it was the uppermost portion of each shaft which was being redeveloped.

In shelly sand. At Bangor, below Gorad-y-Gyt, most of the sand contains numerous shell fragments, which lead to curious complications. I studied the shelly burrows mainly on a patch to the left (south-west) of the old oyster bed, near the inshore margin of the sand flat.

The sand here is very wet, muddy and soft. The worms are large and abundant. The surface signs of a head shaft are like those described for wet sand; the most usual one is a shallow, water-filled saucer, with pieces of weed and so forth left in it by the receding tide.

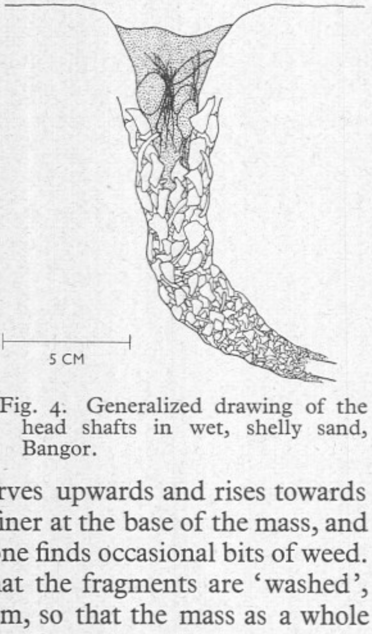

Fig. 4. Generalized drawing of the head shafts in wet, shelly sand, Bangor.

If one follows a burrow, starting from the faecal end, one finds that it descends and turns horizontally in the usual way. One then encounters a roughly cylindrical mass of closely packed shell fragments, which curves upwards and rises towards the surface (Fig. 4). The shell fragments are finer at the base of the mass, and become coarser as one ascends; among them one finds occasional bits of weed. The most curious thing about the mass is that the fragments are 'washed', and have very little sand or silt between them, so that the mass as a whole is loose in texture and crumbles very readily. Sometimes the lumen of the burrow can be traced for some little distance into the shelly mass, sometimes not; it is here, at the base of the mass, that the worm is usually found.

In most cases, a cone of soft, fluid sand can be seen to descend from the saucer at the surface into the shelly mass. As in the case of the wet-sand shafts, this cone can be probed from above with the finger. It often contains shells, or pieces of shells, or weed; these are still unwashed, or muddy, and appear to be descending with the sand from the surface. A cluster of such objects is shown in Fig. 4.

Once or twice, I was able to find a narrow cylinder of fairly firm sand, descending through the shelly mass from the point of the cone. In such a case, the head shaft can be described as one of the typical wet-sand form, surrounded by a shelly sheath. If the worm works the shaft by tunnelling upwards and then dragging softened sand down, one can see that coarse shell fragments might be pushed aside by the ascending worm and so form a sheath. Rejection of the finer fragments could occur during feeding from the bottom of the shaft. More often than not, however, I failed to find the sand cylinder; there seemed to be nothing but a wet cone above, a gallery below, and, in between, the crumbling, baffling mass of miscellaneous fragments.

The fact that the fragments are washed is probably due to the action of the current of water with which the worm irrigates its burrow, to get a supply of oxygen. This current, as will be shown in a later section, ascends the head shaft, and could carry the lighter particles away.

Because of the fluidity of the sand cone, and the friability of the shelly mass, the head shafts cannot be neatly exposed and dissected. Fig. 4 is a generalized drawing, made after digging out and examining a great number of shafts.

A raised bank crosses the patch where most of these observations were made, running roughly parallel with the shore. The sand on the bank is very shelly, and as firm as rapidly drying sand, which it also resembles in the paucity and small size of its worms. I was able, by splitting the sand on the edge of this bank, to expose in section the two burrows drawn in Fig. 5 *a*, *b*. Their general form is not unlike that of the dry-sand burrows in Fig. 2 *c*, *d*, but they are greatly complicated by the presence of shell fragments.

In Fig. 5 *a*, the lumen of the burrow vanishes into a conical region, composed below of sand and fine shell bits, and above of rather larger, silt-free fragments. Resting on top of the shell is a mass of moist, yellow sand (fine stippling in the figure). On dissecting with a knife, I failed to find any upward extension of the lumen, or downward extension of the sand, into the shelly mass. It was, however, very difficult to examine.

In Fig. 5 *b*, the lumen is traceable (to the left of the thick ascending line in the figure), first past a collection of fine, neatly packed shell fragments (dashed), then through a mass of coarser, washed shell. At the upper end of this passage (which is walled, most of the way up, simply by clean, loosely packed shell pieces) there lies, across its top, a large shell (drawn as a thick, oblique line). Curving to the left of this shell, the passage ends at the foot of a cone of yellow sand (fine stippling). The sand may have extended for some distance down the passage as a cylinder; unhappily, the other half of the split sand broke up and could not be examined. This shaft might have arisen by the means postulated above. The coarse shell could have been thrust aside while the worm was working up and down in the shaft, then washed by the ascending water current. The collection of fine fragments below could have resulted from rejection during feeding.

In any case, it is clear enough that the burrows fail to conform with any of the simple patterns to be found in the literature, and must have been set up by complicated activities of the worms. The fact that the worms are large and numerous on the wetter parts of the area shows that the observations cannot be dismissed as trivial. In places the head shafts, active and abandoned, are so plentiful that their horizontal portions (which are often longer than in Fig. 4) form an irregular layer of almost slit-free shell, about 15 cm. from the surface—a very definite contribution by the lugworm population to the architecture of the beach.

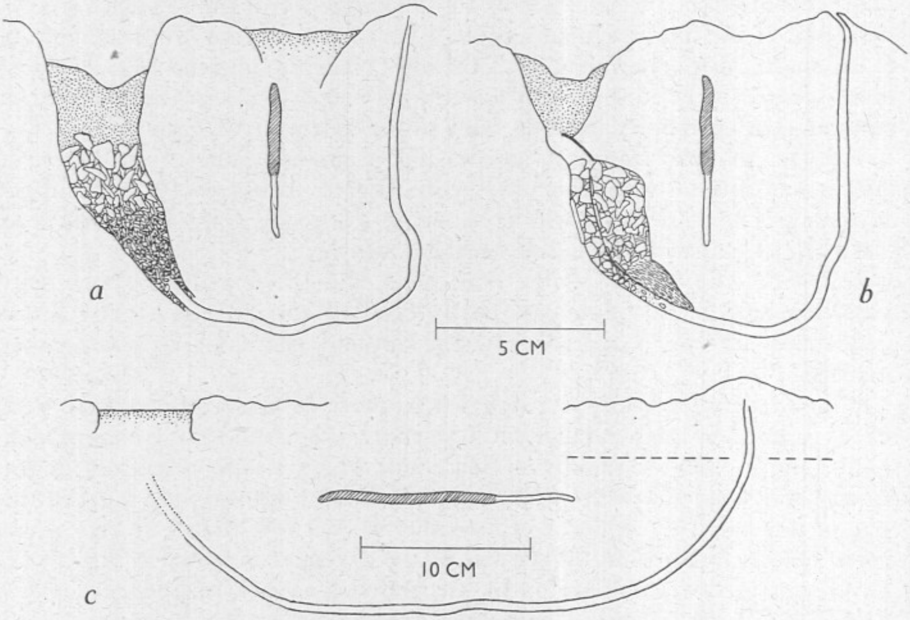

Fig. 5. *a*, *b*, burrows from firm, shelly sand, Bangor; *c*, burrow from gravelly sand, among stones, Pwllfanog.

In gravelly and stony situations. We conclude with an atypical habitat, which is interesting as showing what a lugworm can do.

Near a disused slate factory at Pwllfanog, on the Anglesey side of the Menai Straits, a mass of rock and large pieces of slate stretches out into the tidal zone. The whole is overgrown with *Fucus*. Here and there, among the rocks and slate slabs, small patches with a sandy surface appear, and on these one occasionally sees the casts of quite large *A. marina*. The burrows can be traced downwards, using a long, flexible probe, into a layer of gravelly sand with numerous stones and small pieces of slate.

I found the burrows, and especially the head shafts, impossible to expose completely. One has continually to remove stones, and, as one does so, the structure of the loose, gravelly material breaks up. My most successful attempt is shown in Fig. 5 *c*. The details of the faecal end were destroyed by the insertion of the probe. From this point, the burrow dropped vertically through about 4 cm. of coarse sand, then (at the dashed line) entered a gravelly layer, in which it swung round to become horizontal. The gravelly layer consisted mainly of fine stones, 2–3 mm. across, but there were many smaller grains and larger objects, including stones 5 cm. or so across.

The horizontal part of the burrow ran over the surface of a firm, compact stratum. It was crescent- or banana-shaped, as viewed from above, and has been 'straightened out' in the drawing. It ended by curving upwards, and here a large worm was found.

The worm's head was vertically below a flat area of sand, several centimetres across and surrounded by largish stones; this area was the upper end of the head shaft. The sand below it was about 3 cm. deep, and lay on a layer of loosely packed gravel in which the gallery ended; surface sand and bits of *Fucus* appeared to have been pulled downwards between the stones by the worm.

Though very imperfect, this description shows that the animal could not possibly have set up a 'Saugsäule' in the manner described by Thamdrup. It must have maintained itself by working its way up through the gravel and either eating the surface sand *in situ* or dragging material down for consumption below.

Once, at Pwllfanog, I found a large *A. marina* in a thin layer of silty material between two large, flat, horizontal slabs of slate. Unfortunately, the form of its burrow could not be determined.

Conclusions from the field observations. The main conclusions, drawn from the above examples, will now be summarized.

(i) The open U is an atypical burrow form. It was encountered in rapidly drying sand only, a situation where the worms were few and small. Very often, in other situations, small round holes were seen at the bottoms of funnels; a casual observer might take this appearance as evidence of a U-shaped burrow; in most cases, however, the hole leads into a blind cavity, and the only way to establish the existence of an open U is to expose it along its whole length.

Moreover, the two limbs of the U, when it occurs, have distinct characteristics. The ascending passage in the head shaft differs markedly from the gallery in the loose, 'powdery' appearance of its walls, and in the absence of neuropodial markings. It seems to be of less permanent nature than the gallery.

(ii) The most typical form of head shaft is an ascending column of yellow sand, spreading out into a cone below a saucer-shaped depression of the surface (Fig. 3). That the shafts are fed from at their lower ends, and consequently subside gradually, is shown by the accumulations of pieces of weed and similar objects which are often found at their bottoms, and by the surface saucers, which are evidently due to subsidence. Nevertheless, the head shaft cannot originate or be shaped, as Thamdrup suggested, by these means alone. The shafts are sometimes curved, even in wet, shell-free sand, and the worms can live and maintain themselves in shelly and gravelly situations where the setting up of a shaft by deep feeding and subsidence would be quite impossible. The narrowest head shafts seen in wet sand, and the upward passages in the open U's, correspond in diameter with the gallery, and there is no reason, on Thamdrup's hypothesis, why this should be so.

(iii) There is abundant evidence that the worms actually ascend the head shafts from time to time. Passages obviously left by the worms were often seen in rapidly drying sand, and once in wet sand. In the latter situation, the head shafts seem, from their diameters, to be formed in the first place by upward excursions of the worms. The appearance of a shelly sheath surrounding a cylinder of sand, sometimes seen on the shelly beach, suggests that the shell was thrust aside during the upward excursions. The conclusion seems inescapable, that the worm ascends the head shaft to 'work up' and manipulate the sand. Such head shafts as those in Figs. 2 *a*, *b* and *e*; 5 *a*, *b* and *c* could only have arisen in consequence of complicated 'working' operations.

THE WORKING OF THE HEAD SHAFT

In explaining the appearances seen in the field, the worm was supposed to 'work up' and soften the sand in the head shaft, and, in some cases, actively to draw it downwards. We turn now to a laboratory study of the means by which the worm could do these things.

The Irrigation of the Burrow, and the Effects of Water Currents on the Sand

As many observers have remarked, a lugworm resting in a glass tube drives water through the tube by means of special waves travelling along its body, usually from tail to head (Just, 1924; van Dam, 1937, 1938). This is so invariable a component of the worm's behaviour in the laboratory that its normality—i.e. its occurrence at high tide in the field—can hardly be doubted. The current is generally regarded as a means of irrigating the burrow, and so securing a supply of oxygen.

This is all very well if the burrow is an open U. Often, however, the open part of the burrow is L-shaped, and the U is completed by a column of sand. Problems therefore arise. Can a closed burrow be irrigated at all? If so, what happens to the stream at the blind end of the L, where the worm's head usually lies? Sea water being lighter than sand, the current will presumably make its way upwards, and may therefore have an important effect on the architecture of the head shaft.

To explore this possibility, I made a number of experiments of the following kind. Glass vessels were filled with muddy sand from an *Arenicola* beach at Bangor, and currents of sea water were then discharged into the sand near the glass, so that their subsequent course and their effects on the sand could be watched.

Measurements of the amount of water pumped by lugworms were made by van Dam (1938). He put the worms in glass tubes. In most of his experiments, the worms were driving water from one vessel to another, and the levels in the two vessels were equalized by a system of siphons, i.e. the worms were not pumping against a measurable pressure head. He found, under these conditions, (i) that the worms pumped intermittently; thus, in a protocol which he cites in detail, a worm pumped for about 10 min., then rested for about 20 min., and so on; (ii) that the waves could be reversed, so that the current could be driven in either direction along the body, but it 'practically always goes from tail to head'; (iii) while a worm was pumping, about 8 waves travelled along its body per min., and each wave drove slightly over 1 c.c. of water down the tube. He also made the following remark: 'I observed that *Arenicola* is able to force water through its tube against a pressure of 10 cm. water.' This is not given as a maximum value, but simply as an incidental observation. The maximum pressure obtainable was not determined, and no measurements were made of the volumes pumped when working against pressure heads.

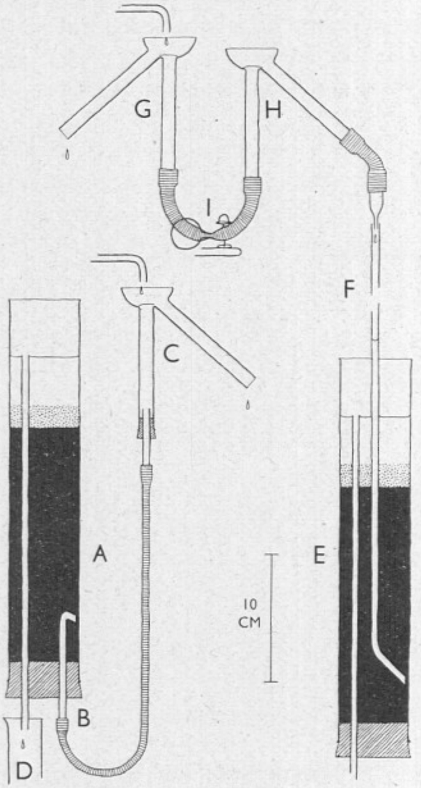

Fig. 6. Apparatus for studying the effects of artificial irrigation currents on the sand. Explanation in the text.

Experiments with controlled pressure. My first experiments were made at constant pressures, using the apparatus shown on the left in Fig. 6. In a typical experiment, the apparatus is filled with sea water, and muddy sand from the beach is added to glass cylinder *A* (internal diameter 5·5 cm.) and gently stirred, then allowed to settle for an hour or so. There results a column of muddy sand, pretty firmly packed (black in Fig. 6), with a layer of light material, which sediments slowly, above it (stippled). Sea water is then allowed to flow in through inflow tube B (internal diameter 0·7 cm.), which opens about 2 mm. from the side of the cylinder, so that the course of the stream can be observed. The percolation pressure is regulated by adjusting the height of overflow vessel C, and the rate of percolation is measured by means of graduated cylinder D.

The results were curious; the flow was almost 'all or none'. For instance, an experiment in which the inflow hole was 10 cm. below the top of the mud gave the following results. The 'percolation pressure' is the difference between the water levels in A and C. With percolation pressures up to 5·5 cm., no displacement of the sand occurred, and there was no flow. With 6·0 or 6·5 cm., fine cracks appeared, running irregularly upwards, through which the water filtered very slowly, at about 0·2 c.c./min. At the threshold pressure (7·0 cm.), the water blasted itself an upward channel, through which it rushed at 250 c.c./min. The channel is drawn to scale in Fig. 7 *a*, as seen through the glass. The circle indicates the inflow hole, about 2 mm. back from the glass. The cylinder was filled with muddy sand up to the dotted line, and a layer of light sediment, resting on this, up to the continuous line. The channel ends above in a 'volcano'. The 'crater' is surrounded by a rim of upblown sand (stippled). The lower part of the channel has been blown entirely clear of sand; the 'crater' cone contains a violent swirl of the heavier sand grains (not drawn)—falling, then being blown upwards again, and so on—and the lighter, muddy components have been completely swept away.

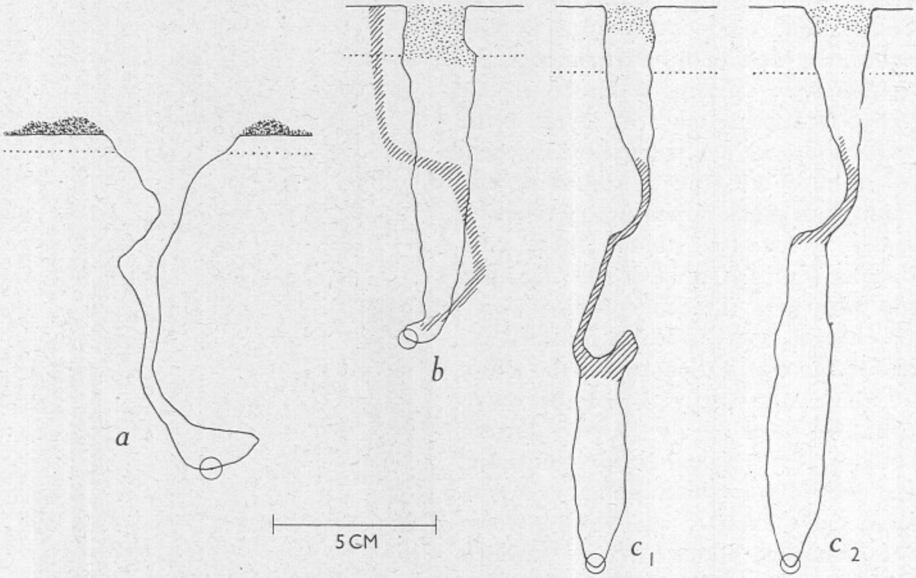

Fig. 7. Channels made with the apparatus of Fig. 6. Explanation in the text.

With greater depths of sand, similar 'all or none' flow was obtained. The pressure required to blast a channel was usually about equal to the depth of the sand; thus, with 20 cm. sand over the inflow hole, a percolation pressure of 19 cm. gave a slow trickle of 0·5 c.c./min., while 21 cm. pressure blasted a channel and produced a violent flow.

Experiments with controlled flow rate. A flow of 250 c.c./min. is beyond the capacity of any *Arenicola.* I therefore made a second series of experiments, in which the flow rate was controlled instead of the pressure. The current was made to flow in pulses, in imitation of the irrigation waves, so that it should resemble the output of a lugworm as closely as possible.

The apparatus is shown in Fig. 6, on the right. Glass cylinder *E* is filled with muddy sand as before. Sea water is admitted through vertical tube *F* (internal diameter 0·6 cm.). Tube *F* receives the water from the 'pulsing flow' device. Overflow vessel *G* is connected to a similar vessel *H*, set slightly below it, by wide rubber tubing closed by pinchcock *I*. The lower flange of the pinchcock is soldered to a brass rod, rigidly held in a stand. Its upper flange bears a hoop of copper wire, through which a length of leather belting (not drawn) is passed. The ends of the belt pass downwards and are tied below a crank on an axle of a Palmer power table. With every revolution of the crank, the belt is pulled down and so opens the pinchcock, allowing *G* to discharge into *H*, and so over into *F*.

The crank revolved once every 7 sec. The heights of *G* and *H* were set to give 1 c.c. at each discharge. These quantities were based on the results of van Dam (1938) on living lugworms, cited above.

Several experiments were made, with sand columns ranging in height from 10 to 25 cm. The following sequence of events was always observed. On starting the apparatus, sea water piled up in *F* until it reached a height (over the water level in *E*) equal to, or slightly greater than, the sand depth. It then blasted a narrow, rather tortuously ascending channel through the sand. As this happened, the pressure head in *F* fell to about half its previous height, where it remained, with a slight rise at each pulse. The ascending channel slowly widened and straightened as the water continued to flow up it, and acquired a very characteristic appearance. The flow rate was insufficient to blow the channel clear of sand. The channel was therefore full of eddying material which soon became roughly sorted and graded, with the heavier particles below and the lighter above. The system finally reached a steady state, with the perfusion pressure, in centimetres sea water, equal to about half the depth of the inflow hole below the mud surface.

The results of two typical experiments are reproduced.

In Fig. 7 *b*, the inflow hole (circle) was 10 cm. from the sediment surface. The stream blasted a tortuous channel (shaded), which slowly straightened and broadened. After 1 hr. it had acquired the outline drawn as a continuous line. Its contents were roughly graded, with coarse sand below, finer sand next, and a layer of floccules of light sediment (stippled) at the top; the whole was in continual pulsing, eddying motion. The system had settled down to run at a pressure which rose from 4·5 to 6·0 cm. at each pulse.

Fig. 7 *c* shows an experiment in which the inflow hole was 17 cm. below the mud surface. The first drawing (c_1) was made 1 hr. after the experiment started. There were wide columns of graded material above and below; in the middle (shaded), the channel was still narrow and tortuous, and blew clear of sand at each pulse; the percolation pressure at this stage was 5–6·5 cm. The second drawing (c_2) was made after a further 2 hr.; the channel had straightened itself considerably, and the system was running at 7–8·5 cm. pressure.

If, in these experiments, the flow was stopped for 10 min. or so after a steady state had been reached, the material in the channel settled and packed itself, with the heavier particles still below and the lighter above. On starting the apparatus again, the pressure head in *F* rose to a height a few centimetres above the steady-state level (though not as high as the initial blast level) before flow was resumed. The system rapidly returned to the previous steady-state pressure.

The density of the wet, muddy sand is roughly 2. The pressure head required for the initial blast is roughly equal to the depth of sand. These facts suggest that blasting consists essentially of the bodily raising of a column of sand extending from the inflow hole to the surface. When the column is lifted, it cracks and breaks up, and the lighter, muddy components are swept upwards. Thereafter, the lower part of the channel is filled with washed sand, which coheres less than the original mixture of sand and mud.

Remarks on the experiments. The following points emerge.

(i) To maintain an upward stream, in material of the kind used in these experiments, the worm must pump steadily at a pressure equal, in cm. H_2O, to half the height of the sand over its head. According to van Dam (1938), it can produce pressures of 10 cm. or more; according to Thamdrup (1935), it burrows to a depth of 20–28 cm.; evidently, then, it could irrigate an L-shaped burrow, once the initial blast had been achieved.

(ii) To produce this initial blast, twice the above pressure would be required. The maximum pressure that a pumping worm can produce is not known, and an enquiry into the point would be somewhat academic; the worm could reduce the necessary effort by tunnelling upwards, and there is plenty of evidence from field observations that it sometimes does so.

(iii) The upflowing water might well oxidize the iron sulphide in the mud and thus produce a yellow colour. Therefore, a yellow column, rising from the end of a lugworm's burrow, does not necessarily consist of surface sand.

(iv) The shaft produced by the water current would be vertical (except that it could curve round large stones and shells) and, to judge by the above experiments, some 1·5–2 cm. in diameter. As the head shafts found by the writer in the field were often much slenderer than this, and might be gently curved in the absence of obvious obstacles, it follows that other factors must play a part in their establishment and formation.

(v) The upward current would have an undesirable incidental effect, for its tendency would be to sweep the lighter particles upwards, leaving washed sand by the worm's mouth, and the lighter particles include the nutritious ones. This suggests that a conflict might arise between the means of oxygen supply and food supply.

In glass tubes, lugworms sometimes pump water in the reverse direction, from head to tail, and one might think that the conflict could be resolved if such reverse irrigation were the normal method under natural conditions. The following evidence, however, tends to exclude this possibility: (i) After many observations on worms in glass tubes, van Dam (1938) concluded that the current 'practically always goes from tail to head' in undisturbed worms, and that reverse flow appears to be a result of recent disturbance; Just (1924), who also watched worms in glass tubes, saw only the forwardly running waves; (ii) in the experiments with worms in sand-filled tanks, described below, I often saw swift currents flowing upwards in the head shafts, but I never saw any evidence of irrigation in the opposite direction; (iii) reverse irrigation in the field would draw sand between the worm's body and the wall of its burrow, and, except for the head shaft, a lugworm's burrow is always beautifully clear and open.

Evidently, we have two antagonistic processes at work. There is the downward movement of muddy sand, produced by feeding at the base of the head shaft, and the upward movement of water, which tends to wash the more valuable components away. We have now to see how these two processes can be reconciled.

The 'Working Up' of the Sand by the Worm

In another context (Wells, 1937) I devised a glass 'observation tube' in which lugworms lived for days or weeks, and their activities could be watched. Since then, I have put worms in observation tubes from time to time, and have noticed movements which may be of great importance in the working of the head shaft.

The observation tube is U-shaped, and of internal diameter 7–8 mm. (Fig. 8). Near its upper end, a narrow cross-tube connects the two limbs, so that the worm can circulate the contained sea water. Aeration is by means of a narrow capillary inserted into one limb, which is also widened above to facilitate the initial introduction of the worm.

The 'drag' cycle. To understand this performance, we must first note a feature of the worm, to which attention has only recently been drawn (Wells, 1944 *a*). The chaetigerous annuli of the more anterior segments have a special musculature, by means of which they can be raised into sharp, backwardly-directed flanges. The movement is best shown by the first three chaetigerous annuli; it also appears, to a progressively diminishing extent, in the next three or four. It is abrupt and vigorous; at one moment an annulus is flat, in the usual configuration; at the next, its whole circumference is raised, and the annulus itself seems to be distended with body fluid. All of these annuli rise and fall simultaneously (Fig. 8, inset).

In July 1942 I was watching a worm in an observation tube. It lay quietly at first, with its head at the bottom of the U and its tail up one limb. Suddenly it became restless, and crept forwards until its head was well up the other limb, and most of its body consequently vertical. It then repeatedly performed the following cycle of operations: (i) it gave three or four powerful extrusions of the proboscis, moving upwards a little as it did so, and lengthening and stretching the front part of its body exceedingly, as if to get its head as far up the tube as possible; (ii) it elevated its chaetigerous annuli, and slowly and steadily shortened itself, pulling its head down again; (iii) the annuli dropped back into the usual, flat configuration, and it began to work its head upwards again, so returning to stage (i). The whole cycle was carried out some half-dozen times.

Now, what was the worm trying to do? My first impression was that it wanted to grip the wall of the tube with the raised chaetigerous annuli, and so pull itself up. This interpretation was soon abandoned, for the same worm could creep up or down the tube in the usual way, forwards or backwards, with ease. Moreover, the hinder segments gripped the tube, and so acted as a fixed point, during the downward drag of the head. Clearly, the cycle could be used for a quite different purpose—to pull something down into a burrow.

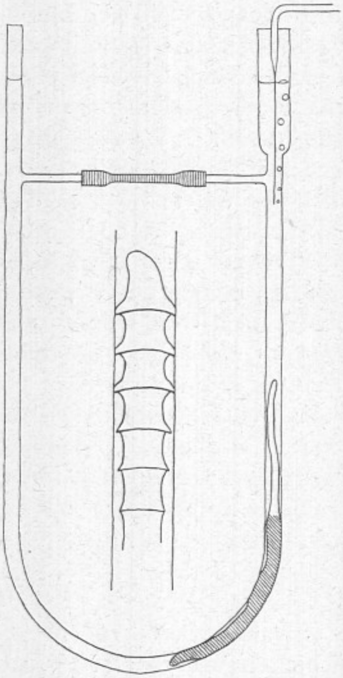

Fig. 8. Observation tube for studying the movements of *Arenicola marina*. Inset: the elevation of the anterior chaetigerous annuli.

I have seen the same action on several subsequent occasions. Sometimes the head is stretched out, beyond the end of the tube, into the air; then the annuli are raised and it is slowly pulled back.

The cycle could evidently be used to scrape and drag surface sand into an open funnel. As already noted (p. 172), several observers have described the worm's head as appearing actually at the funnel. From their accounts, this seems to occur only, or chiefly, when the burrow is submerged and the surface sand therefore soft. The worm might ascend, as Wesenberg-Lund (1905) and Blegvad (1914) suggested, to eat from the sides of the funnel; alternatively, it might collect surface sand by means of the drag cycle and pull it down into the shaft for subsequent consumption at leisure. As the proboscis is used in stage (i) of the drag cycle, the two possibilities would be hard to distinguish from each other in the field. In a predatory world, the second course would perhaps be the wiser one.

But the drag cycle could also be used in another way—to mix deeper material, softened by the ascending irrigation current, and so to combat the tendency of the current to sweep the lighter and more nutritious particles upwards. The broader of the head shafts found in the field (e.g. Fig. 2 *c*, *d*) can be supposed to be 'worked up' by the softening action of the water current coupled with mixing and stirring by the drag cycle.

Moreover, if the sand contains pebbles or large shell fragments, a rough sorting could be carried out by means of the drag cycle. The worm's head, as it drives upwards, would tend to push such objects sideways, and so to deposit them as a sheath around the central column of worked sand. Indications that this occurs were found while studying the burrows in wet, shelly sand (Fig. 4).

'*Piston*' *action.* I have sometimes watched worms in plain U-tubes, lacking the cross-tube shown in Fig. 8. Under these conditions, I have often noticed that the worm, while creeping forwards or backwards along a tube, may also occlude it; as the worm travels, one meniscus rises and the other falls; differences of pressure of 10 cm. or more can thus be set up.

This gives us an approach to the narrower of the head shafts found in the field. Such shafts are found both in rapidly drying and in wet sand. They consist of a tunnel or a sand column, of about the same diameter as the worm, rising to spread into a conical region below the funnel or saucer on the surface. The facts can be accounted for by supposing that the worm ascends to a point a few centimetres below the surface, then softens and mixes a cone of sand by means of the irrigation current and the drag cycle, then retires and pulls the semi-fluid sand into the passage along which it ascended, by means of piston action.

Indeed, all of the field appearances can be explained as resulting from the interaction of three factors—the softening of the sand by the irrigation current, the mixing and manipulation of the sand by the processes just described, and the subsidence of the worked-up material in consequence of feeding at the lower end of the shaft. The rejection of unsuitable materials will occur, partly (as just pointed out) during the drag cycle, and partly at the lower end of the shaft during feeding. It is in the latter situation that the smaller and the more flexible of the unwanted objects, which would not be thrust aside during the drag cycle, generally accumulate.

Burrows made in the Laboratory

In the hope of seeing these various factors at work, I kept a number of worms separately, each in a glass tank of wet sand. Fairly large worms were chosen (overall length 10–14 cm.) and the volume of sand was small; by this means, the worms were induced to set up head shafts against the glass, where they could be observed in detail.

The tanks had a horizontal sectional area of 11 × 17 cm. and were filled with muddy sand to a depth varying in different cases from 14 to 19 cm. The sand was stratified, to make the conditions as normal as possible; most of it was grey-black material, dug fairly deeply from the beach, but a layer of yellow surface sand was put on top. Finally, the whole was covered with a couple of centimetres of sea water, so that the worms could irrigate their burrows.

Beyond aerating the sea water, and occasionally adding distilled water to compensate for evaporation, no further precautions were taken. The worms lived actively in the tanks for many weeks. My records cover (i) four worms, kept under observation for 30 days, and (ii) confirmatory experiments on five others, kept for various periods (up to 3 months) and observed from time to time.

The worms themselves were seldom seen. Their behaviour was inferred (i) from the position and amount of their faeces, which were cleared away whenever they were noted, to facilitate further observation, and (ii) from the forms and changes of the head shafts.

The faeces. In most cases there was a preliminary period of 'settling down', lasting for 24–48 hr., when a worm was first put in a tank. During this time, no faeces appeared.

After this period, the worms, with one exception, defaecated at least once a day, and generally much more often. The single exception defaecated little and seldom, and sometimes missed out a day altogether. This peculiarity was kept up throughout the month of observation. There seemed to be considerable individual differences in this matter; other worms consistently distinguished themselves as abundant defaecators.

At the same time, the frequency of defaecation often fluctuated in any one worm. A vigorously active individual would regularly produce a cylinder every 25–45 min., for many hours, and this could be kept up day after day. Sometimes, however, a worm defaecated every half hour or so on one day, but rested for three or four hours at a stretch on the next.

The position at which the faeces appeared was very constant. Of the four worms studied for a month, the first always defaecated at the same point; the second changed its position once by reversing the burrow, the faeces thereafter appearing at the top of the old head shaft; the third made two changes, reversing its burrow on one day and returning to the old orientation 3 days later; the fourth changed three times, once by reversal and twice, on consecutive days, by breaking new ground.

Few of the investigators of the form of the burrow have concerned themselves with its permanence. The most direct observations on this point are by Schwarz (1932) and by Thamdrup (1935). The former pointed out that the funnels and faecal piles may become very large in situations sheltered from wave action, suggesting that the worm lives in the same burrow for a considerable time. According to the latter, the permanence of the burrow depends to some extent on its situation; if the sand is not much disturbed by wave action, the burrow is inhabited at least for weeks on end; this conclusion rests on observations of worms in a large aquarium, on the watching of marked burrows on the beach, and on the dimensions of funnels and faecal piles in sheltered situations; the burrows are probably changed more frequently in places where the surface is often disturbed. My own aquarium observations confirm this general conclusion, as regards the faecal ends of the burrows; we shall see later that the head shafts were changed rather more often.

Head shafts seen in section. Head shafts were made, sometimes against the glass and sometimes away from it. In the former case they were seen as it were in section.

I never saw an open, ascending passage, ending above in a funnel, as required by the 'open U' form of burrow. The head shafts were broad, typically vertical columns of 'worked' sand, often very like those produced by the artificial irrigation currents described above. Ascending streams of water were frequently seen in the shafts.

A typical example is shown in Fig. 9 *a*, with the outline of the worm included to scale below. This shaft was set up in the corner of the tank, so the page should be imagined as folded backwards at right angles along the vertical line.

The first observed signs of this shaft were a conical depression of the surface, and an irregular cavity, with a domed roof, about 9 cm. below it. This stage is shown by thick outlines in the figure, the cavity being shaded.

On the following day the shaft had assumed its definitive form. It was now very like an artificial irrigation channel, and consisted of loosely packed sand, with a layer of light sediment, 3 cm. deep, at the top. It differed from the artificial channels in that a funnel had developed at its upper end, due to the animal's feeding from the substance of the shaft. This stage is drawn as a thin outline, the horizontal line being the top surface of the sediment.

The worm continued to work this shaft for a fortnight, at the end of which time it had acquired the outline shown as a dotted line in the figure. The processes actually seen during this period were (i) crumbling away of sand from the sides of the funnel, (ii) upward streaming of the irrigation current, now on one side of the shaft and now on the other, (iii) slight erosion of the side walls of the shaft by the stream, causing gradual broadening of the column, and (iv) on one occasion, pulsing movements of the sand suggesting that the drag cycle was being carried out somewhere within it. The worm itself was never seen. At the end of the fortnight, the whole column had acquired a striking yellow colour, like that of the surface layer of the sand, into which it appeared to continue. This coloration was doubtless due, in part at least, to oxidation by the irrigation current.

Several shafts, resembling this one in general pattern, were set up during these experiments. The first signs of their formation were (i) slight subsidence of the surface, accompanied by (ii) the appearance of irregular cavities, often with vigorous upward currents in them, further down. Sometimes black silt, obviously swept up from below, appeared on top of the yellow surface layer of the sand. From the first, then, it seems that feeding and irrigation were at work together.

The shafts soon settled down into broad, rather loosely packed columns, with light sediment above, and with funnels round their upper ends. The sand grains in the columns did not grade themselves as perfectly as did those in the artificial irrigation channels; except for the top layer of sediment, the substance of a column was pretty homogeneous. This probably resulted from two factors. First, the worm drove the upward stream, now on one side of the column and now on the other, and this seemed to have a stirring effect. Secondly, on several occasions, pulsing movements of the sand were noticed, suggestive of the drag cycle. To my sorrow, however, the worms were never actually seen to carry out the cycle. On the rare occasions when parts of the worms were visible, they were working at the lower ends of the shafts.

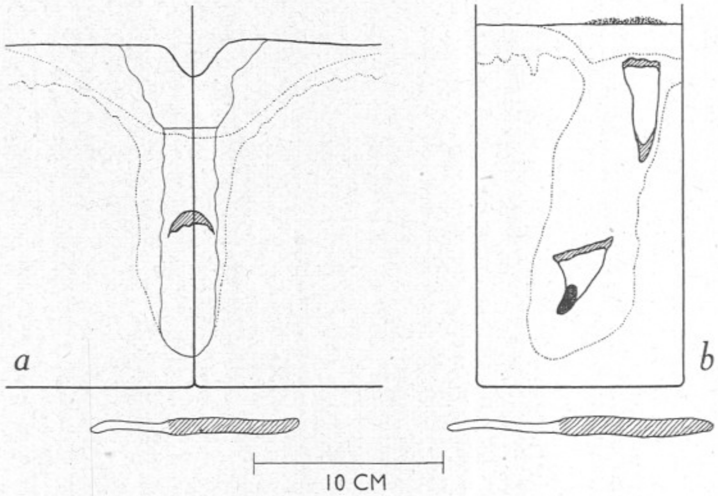

Fig. 9. Stages in the development of head shafts in glass tanks. The worm responsible for each shaft is drawn to scale below it.

Irrigation was always intermittent. When a worm began to drive water upwards, the level of the top of the column rose several millimetres, due, presumably, to the forcing of water in among the sand grains with consequent increase in volume of the column. It sank again when irrigation ceased. Bohn (1903) saw very similar oscillations of level in funnels on a sand bank, as the tide was just flowing off it.

On probing the head shafts, their texture was found to be exceedingly soft, as one might expect; in this respect, they resembled the upper parts of the head shafts found in wet sand in the field.

An interesting, if rather atypical, shaft is shown in Fig. 9 *b*. The first observed stage is drawn with thick outlines, the cavities being shaded. Below, there was a triangular area of 'worked' sand with a cavity at its upper side and a glimpse of the worm's head (black) at its apex. Nearer the surface was a second triangular area with clefts at both ends. Vigorous upward currents were seen in the substance of both areas. Finally, there was a thin layer of upblown black sediment (stippled) on the surface. These various signs clearly indicate an irregular, somewhat oblique shaft, partly against and partly away from the glass. Its obliquity is interesting, and suggests that the worm had tunnelled upwards nearly to the surface as a preliminary stage in its establishment. The setting up of a shaft appears, then, to involve all of the three factors, feeding, irrigation and upward excursion.

This shaft was worked for three weeks, during which period upward currents and occasional clefts appeared in various places. The final result was a wide area of yellowish, 'worked' sand, still rather oblique, whose boundary is drawn as a dotted line in the figure. This shaft was made by the worm which defaecated little and seldom, hence the comparatively slight depression at the surface.

Head shafts seen from above. When head shafts were set up away from the glass, they presented the appearance, as seen from above, of gradually enlarging and deepening saucers, often with a flat bottom of fine sedimentary material, and closely resembling those seen so often on the beach.

The irrigation current escaped either diffusely (in which case the water in the saucer was often hazy or cloudy in appearance) or through 'blow holes', i.e. circular areas, a few millimetres across, walled by low parapets of upblown material, and containing sediment in intermittent, eddying motion. A blow hole would appear at some point in a saucer, to disappear after several hours and perhaps be replaced by another elsewhere. Similar blow holes are often seen in the saucers in wet sand on the beach.

The first stages in the formation of a saucer were very variable. An area, a couple of centimetres across, might be outlined by two or three fine cracks, and then gradually subside to form the bottom of a saucer; or a ragged hole, 1 or 2 cm. across, with steep walls and a cloudy, turbid interior, might be the first sign, the saucer later developing by inward crumbling of its margin. Once again, these observations are paralleled by others made on the beach (p. 184).

General remarks on the head shafts. The head shafts were changed rather more frequently than the defaecation points. For example, after the worm had worked the head shaft of Fig. 9 *a* for 2 weeks, it became restless and, in the next 5 days, it set up three new head shafts, at the sides of the old funnel. It continued, however, to defaecate from the old point. The phenomenon of changing the head shaft while retaining the old defaecation point was often noted during these experiments. It has also been observed in the field, both by Thamdrup (1935) and by myself (Fig. 2 *h*).

Occasionally, a worm defaecated copiously for a day or so, during which no sign of a head shaft could be seen, either against or away from the glass. The longest period for which such behaviour continued was 4 days. I have no explanation to offer for this observation.

It was suggested, in a previous section, that the main factors in the working of a head shaft are feeding and subsidence, the irrigation current, and upward 'working' excursions of the worm. In the experiments now described, whose main purpose was to test that statement, the importance of the first two was clearly demonstrated—of feeding and subsidence by the gradual development of the funnels at the upper ends of the shafts, and of the irrigation currents (which were frequently seen) by the general structure of the shafts and their top layer of light sediment. The existence of upward excursions was inferred, on rather less solid grounds, from the obliquity of the shaft in Fig. 9 *b*, from occasional pulsing movements of the sand suggestive of the drag cycle, and from the imperfect grading of the sand in the shafts.

In comparing the results with those of the field observations, it must be borne in mind that the tidal factor was lacking in my experiments. There was no supply of fresh material at the upper ends of the shafts (except for insignificant depositions of faecal matter when the faeces were periodically destroyed) and the worms were able at all times to irrigate their burrows. The latter consideration may be important; the behaviour of the worms, and the consequent structure of the head shafts, may be greatly affected by the periodic 'cutting out' of irrigation at low tide, with its inevitable effects on the mechanical properties of the sand.

The experimental results may be regarded as a model of the worm's normal high-tide behaviour, while the field observations were naturally made at low tide. The worm's life is an alternation of the two modes. We may suppose that the submerged worm works up and softens the sand by the processes already described. In the case of the wider shafts, the whole, or a large part, of the shaft may be so treated. In the case of the narrower ones, the working may be confined to the upper, conical portion and followed by the drawing downwards of a narrow column of softened sand. At low tide, feeding and a certain amount of working up may continue if the sand is soft and wet, but these activities will presumably be greatly slowed or altogether stopped if the sand dries and hardens. With the return of the tide, irrigation can be resumed, and the head shafts can be extensively reconstructed if necessary.

NOTES ON FOOD SUPPLY AND OXYGEN SUPPLY

The following notes arise from observations made incidentally during the course of the work.

The Food of the Lugworm

Lugworm faeces are generally yellow, like the surface sand, but black or grey-black faeces sometimes occur. While working in the field, both at Bangor and at Aber, I always noticed a sprinkling of dark castings among the much commoner yellow ones. The worms kept in tanks, as described in the last section, usually produced yellow faeces, but sometimes black or grey faeces appeared.

The colour of the faeces presumably depends on that of the sand on which the worm happens to be feeding. It would be difficult to explain the following laboratory observation in any other way. A worm, which was setting up a new head shaft, produced a cylinder consisting of 4 cm. of yellow matter followed by 3 cm. of black, the two separated by a sharp boundary though both forming parts of the same faex. Twenty minutes later, it shot out an even more remarkable one—2 cm. black, then 1 cm. yellow, then 2 cm. black, and finally 2 cm. yellow—again with sharp boundaries. The subsequent faeces were all yellow. The worm must have fed alternately from black and yellow sand, and refrained from mixing its successive ingestions as they passed down its gut.

The occasional black faeces seen in the field indicate, then, that the worms sometimes consume the deeper sand. In the laboratory experiments, the appearance of black faeces generally coincided with a change in the configuration of the burrow, such as the establishment of a new head shaft. During the early stages of formation of a head shaft (e.g. those shown by thick outlines in Fig. 9), the deep material is still black, and its consumption is demonstrated by surface subsidence and the appearance of cavities deep in the sand. Worms feeding from well-established head shafts nearly always produced yellow faeces. Exceptions, however, occurred; thus, one worm produced copious masses of grey-black faeces every day for a fortnight, for most of which time it was apparently working a single head shaft, set up away from the glass, but plainly visible as a gradually deepening, saucer-shaped depression of the surface.

A yellow casting—and the ones in the field are mostly yellow—shows that the worm has eaten yellow sand. It also suggests that the worm has eaten surface sand, but this inference is less secure than the first, since the ascending irrigation current might turn the deeper sand yellow. In fact, however, a well-established head shaft seems to be, in the main, a descending column of surface sand; downward motion is shown by the shelly and vegetable fragments which frequently collect at the lower end, and by the subsidence of the funnel; renewal from the surface and by sedimentation must take place if the shaft is to be maintained. A certain amount of deeper material may get mixed in with it, partly owing to the activities of the ascending and descending worm, and partly owing to the eroding action of the irrigation current on the walls of the column; the shafts seen in the laboratory tanks slowly widened, and a similar widening probably occurs in the field.

The frequent collections of fine shell fragments, pieces of weed, dead leaves and so forth at the bottoms of the head shafts are evidence that selection occurs at the moment of feeding, even if it is limited to the rejection of mechanically unsuitable objects. Sometimes, however, quite large pieces of animal or plant material are swallowed. Ashworth (1912) states that pieces of seaweed are occasionally found in the alimentary tract of *A. marina*, and Saint-Joseph (1894) remarks: 'dans le corps d'un exemplaire j'ai trouvé une Néréide entière presque digérée.' Whether these soft objects were accidentally engulfed with the sand, or whether they were deliberately selected, is not known. One would have to examine the contents of a large number of specimens, preferably from different situations and at different seasons of the year, before deciding whether such ingestions occur with dietetically significant frequency.

Oxygen supply: aerial respiration

Lugworms can absorb oxygen either from water or from air. The latter point is emphasized by van Dam (1938): 'in my tests *Arenicola* was seen to live for several days in damp air of room temperature.'

At high tide, both ends of the burrow are submerged. We have seen that the worm can irrigate the burrow under these conditions, so securing an adequate oxygen supply, even if the burrow is not an open U.

At low tide, the conditions vary with the situation. I found, on rapidly drying sand patches, that the water drained away to such a depth that the burrows were completely air-filled. There will be no great difficulty in this case, provided the air is damp. More often, on the other hand, the burrow is wholly or partly filled with water, which the worm is unable to circulate. This water will lose its oxygen, partly to the worm and partly, perhaps, to the surrounding sand, and the worm may therefore find itself exposed to oxygen lack. What will it do?

Lindroth (1938) showed that *Nereis* (*diversicolor* and *virens*), in a U-tube of water deficient in oxygen, draws air bubbles between its body and the tube and holds them there. Van Dam (1938) discussed the possibility of spontaneous aerial respiration in *Arenicola*, but was unable to demonstrate it: 'if, however, animals were put into a glass U-tube partly filled with water, they did not creep into the air of the tube even after a number of hours; at most they protruded their head or tail about 1 cm. above the water.'

I was more fortunate. On putting worms into U-tubes partly filled with sea water, which they were unable to circulate, I repeatedly saw what appears to be a method of aerial respiration. After an hour or so, they crept backwards to the surface of the water, with their tails curled up into a pretty tight screw (as if to make them as short as possible); they then drew air down between their dorsal surfaces and the tube, and held it there. The 'trapped' bubble usually covered several pairs of gills. This behaviour was not invariably obtained. The most successful experiments were done within 24 hr. of the collection of the worms, and in a light so dim that one could only just see what the worms were doing. Probably a bright light has an inhibiting effect on the behaviour of *A. marina*.

Clearly, 'bubble-trapping' could be very useful in wet sand at low tide. It could conceivably alternate with other activities, the haemoglobin being used for oxygen storage. Thus, the worm might oxygenate its haemoglobin after each defaecatory excursion, then go down again to resume feeding.

In the above remarks, it was assumed that the worm is in a well-established burrow. Special conditions will arise while a burrow is being constructed or altered. On putting the worms into the experimental tanks described above, they vanished into the sand, and 24–48 hr. often elapsed before any faeces, or any sign of a head shaft, were seen. It would be interesting to know how they secured an oxygen supply during that time.

SUMMARY

The Form of the Burrow

1. The burrows were studied in various situations (rapidly drying sand, wet sand, shelly sand, gravelly and stony places), all in the neighbourhood of Bangor, North Wales.

2. The burrow typically consists of a gallery, a tail shaft and a head shaft (Fig. 10, 204).

The gallery is a roughly L-shaped tunnel, whose walls are impregnated by the worm's secretions and marked by its neuropodia. The worm moves to and fro in the gallery, with its tail towards the upper end.

The tail shaft is a short portion connecting the upper end of the gallery with the exterior, and housing the worm's tail at the moment of defaecation. It may have two or more orifices, and it lacks neuropodial markings.

The head shaft connects the lower end of the gallery with the surface, and is exceedingly variable in structure. The most typical form occurs in wet sand. In this case the head shaft is a column of yellowish sand, one to three times as wide as the gallery, rising towards the surface and there spreading into a cone below a saucer-shaped depression. In other situations many variations are encountered; the shaft may, for example, be a broadly spreading cone of sand; it may include an open passage, of the same diameter as the gallery; it may be complicated by the presence of shell fragments or other objects.

3. In the second of these variations, the burrow is an open U. Such burrows were found only in rapidly drying sand, and appear therefore to be exceptional. Moreover, the ascending passage in an open head shaft lacks

the mucus-impregnated wall and neuropodial markings of the gallery, and seems to be of less permanent nature.

4. Evidence that the worm feeds at the lower end of the head shaft is given by the frequent accumulations of weeds, dead leaves and so forth at the bottom of the shaft. These objects are left in the surface saucer by the receding tide, travel down the shaft, and are rejected by the feeding worm below.

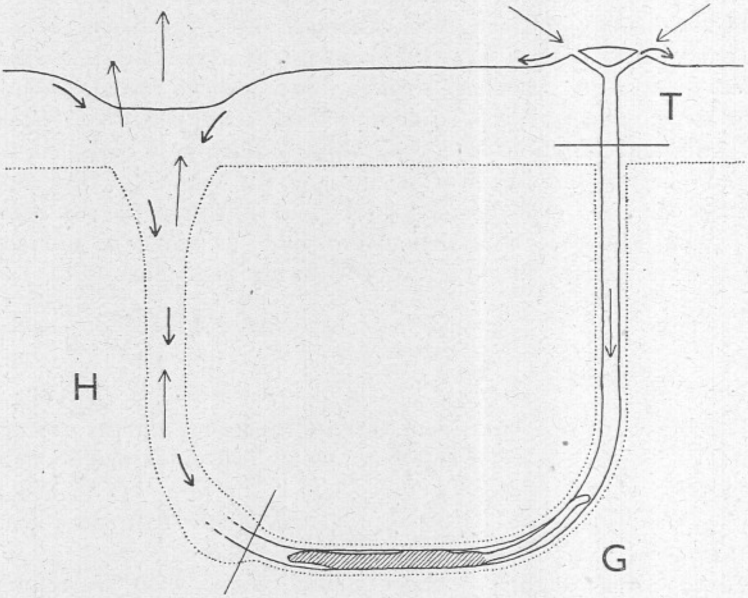

Fig. 10. Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

According to Thamdrup (1935), the head shaft is a column of down-sliding sand which originates and is maintained by the worm's feeding at the lower end. Doubt is thrown on this suggested mode of origin by two facts: (i) the head shafts, even in wet, shell-free sand, are often slightly curved, and (ii) worms can live in shelly and gravelly situations where the setting up of a shaft along these lines would be quite impossible.

5. Many signs show that the worm ascends the head shaft from time to time. Obvious ascending tunnels, of the same bore as the gallery, were frequently found in rapidly drying sand. That the typical, wet-sand head shafts are shaped in the first place by upward excursions of the worm is suggested (i) by the fact that the narrowest head shafts have about the same

diameter as the gallery, and (ii) by a single case in which a wet-sand shaft contained an impress of the worm's body near its upper end.

6. The head shafts encountered in shelly and gravelly situations cannot have arisen by deep feeding and subsidence alone; they must have been produced by complicated 'working' activities of the worms.

The Working of the Head Shaft

7. A laboratory study has been made of the processes by which *Arenicola* works its head shaft.

8. The worms drive water through their burrows by means of special waves travelling forwards along the body. Water currents were liberated into muddy sand and their course and effects on the sand were noted. The results show that a lugworm could irrigate an L-shaped burrow; the water would rise from the blind end of the L and form a vertical shaft, about 1·5–2·0 cm. across; the shaft would consist of graded material, with coarse sand below and fine sediment above, and it might be yellowed by the ascending stream.

Such water currents might be important in softening the sand in the head shaft, but the shapes of head shafts found in the field show that they cannot have been formed by the irrigation current alone.

9. While watching worms in glass tubes, two types of movement were seen, which are probably of great importance in the working of the head shaft. They are (i) the 'drag' cycle, in which the head is thrust upwards, then the anterior chaetigerous annuli are raised into flanges and the head is pulled slowly back again, and (ii) 'piston' action, in which the worm creeps along a tube, at the same time occluding it, and so drawing water through the tube.

10. The various head shafts seen in the field can be explained as arising from the interaction of three factors: (i) the softening of the sand by the irrigation current, (ii) upward excursions of the worm, with special activities like those just described, and (iii) feeding from the base of the head shaft.

11. A number of worms were kept individually for many weeks, each in a glass tank of muddy sand under sea water. When head shafts were set up away from the glass, their appearance resembled in every way those seen on the beach. When head shafts were set up against the glass, they were seen to be columns of sand, continually perfused by the ascending irrigation current; they gradually broadened and yellowed; conical depressions developed at their upper ends, due to the feeding of the worms from their substance; occasional pulsing movements of the sand suggested that the worms were carrying out the drag cycle somewhere inside the shafts.

12. In the tank experiments, the defaecation points were seldom changed; the positions of the head shafts were changed rather more often. These results confirm the conclusion of Thamdrup (1935), that a lugworm inhabits a single burrow at least for weeks at a stretch, if the conditions are favourable.

Notes on Food Supply and Oxygen Supply

13. The occasional occurrence of black faeces, both in the laboratory and in the field, shows that *Arenicola* sometimes consumes the deeper sand, although its chief diet seems to be the downwardly moving surface sand in the head shaft.

14. In a U-tube of stagnant water, *Arenicola* often rises backwards to the water surface and draws air bubbles down into contact with its gills, thus proceeding spontaneously to aerial respiration. This behaviour could be useful at low tide, when the burrows are often filled, or partly filled, with stagnant water.

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MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1943–44

The Council and Officers.

During the year the Association has lost the services of two distinguished marine biologists, Prof. W. M. Tattersall and Mr A. C. Gardiner. Prof. Tattersall was a member of Council at the time of his death on October 5th and Mr Gardiner, who died on August 29th, had been a member in former years. The Council also notes with regret the death of Mr L. R. Crawshay, a former member of the staff, who had worked regularly in the laboratory since 1934, and that of Mr P. R. Crimp, a Student Probationer at Plymouth before the war, who died on active service in North Africa.

The Royal Society has appointed Prof. A. V. Hill as the Society's representative on the Council in place of Sir Sidney Harmer. Sir Sidney Harmer, who has been a member of the Association since 1885, has served for long periods on the Council and has represented the Royal Society continuously since 1925.

Four ordinary meetings of the Council were held during the year, three in the rooms of the Royal Society in London and one at Plymouth. At these the average attendance was 14. The thanks of the Association are due to the President and Council of the Royal Society for their kindness in giving accommodation for the London meetings.

The Plymouth Laboratory.

During the year considerable progress has been made with the plans for the restoration of the laboratory premises. At the April meeting of Council Mr J. M. Easton of the firm of Stanley Hall & Easton and Robertson was appointed Architect to the Association. Mr Easton visited Plymouth in June, when he made a thorough inspection of the laboratory buildings.

The District Inspector of Fisheries, S.W. Area, has been given temporary office accommodation in the laboratory.

The Ship and Motor Boat.

The *Salpa* remains under requisition by the Admiralty, and has not been available for the service of the laboratory. The motor boat *Gammarus* is in good condition and has continued her work. The dinghy belonging to the Association was considerably damaged in the air-raids on Plymouth and has now become unserviceable; it has been replaced by another obtained from H.M. Dockyard at Devonport.

Arrangements for the collection of marine animals on board one of the trawlers working from Plymouth has resulted in improved supplies of specimens to University departments.

The Staff.

The Director has accepted an invitation to serve as a member of the Colonial Fisheries Advisory Committee which has been formed under the chairmanship of the Duke of Devonshire.

Mr E. Ford has been promoted to Flight Lieutenant in the R.A.F.V.R.

Dr W. R. G. Atkins and Dr H. W. Harvey have continued their work on the Marine Corrosion Committee of the Iron and Steel Institute.

Occupation of Tables.

The following have occupied tables at the Plymouth laboratory during the year:

Miss M. E. BENNETT, Northampton (Algae).
The late L. R. CRAWSHAY, Plymouth (Sponges).
Dr S. P. CHU, Ray Lankester Investigator (Nutritional requirements of phytoplankton).
E. W. EWER, Great Missenden (*Sabella pavonina*).
Dr V. FRETTER, London (Reproductive system of Nudibranchs and Protobranchs).
Mrs J. FROUD, London (Parasites in *Melinna adriatica*).
Dr J. O. GAVRONSKY, London (Utilization of common algae for obtaining solvents by fermentations).
Dr T. J. HART, Discovery Committee (Falkland Islands' fisheries).
Dr M. KNIGHT, Liverpool (Algae).
A. G. LOWNDES (Density of aquatic organisms).
Dr M. PARKE and Miss E. CLAY (Algae).
R. B. PIKE, Reading (*Galathea*).
Mr A. N. SCOTT, Bristol (General zoology).
Prof. T. A. STEPHENSON, Aberystwyth (Drawings of marine fauna).
Prof. C. M. YONGE, Bristol (General zoology).

No vacation courses were held during the year. In April Mr A. H. Lewis brought four boys from Wellington College to work at the laboratory, and in May Mr A. Gillespie and Miss N. Elcock brought fifteen boys on a visit from Blundell's School. On several occasions boys from Kelly College have worked at the laboratory under Mr A. G. Lowndes.

Prof. C. Singer, Mr C. F. Hickling, Mr W. G. Atkins of the Indian Jute Mills Association, and Capt. W. B. Dowson, who is studying Nigerian fisheries, have paid visits to the laboratory.

Scientific Work of the Laboratory Staff.

Dr W. R. G. Atkins, who has a temporary research appointment in the Meteorological Office, has not spent much time at the laboratory during the year. On two occasions he was engaged in testing instruments for the Meteorological Office, and he has continued some work on methods of preserving ropes and nets with the assistance of Mr F. J. Warren.

Dr H. W. Harvey has been mainly occupied with experiments concerning conditions which prevent the attachment and growth of marine organisms. It was observed that some copper soaps possessed marked antifouling properties and provided particularly adherent coatings which lasted well under water, but allowed some growth of weed and animals. Their partial antifouling effect appears to be due to the fatty acid rather than to the copper content, because their copper leaches into the sea too slowly to exert any preventive action and, moreover, coatings of some fatty acids have been found to prevent the growth of organisms. Thus a coating of lauric acid has remained clean for several months while a similar coating of stearic acid kept in the sea alongside it fouled within a fortnight.

Most of the experiments have been concerned with increasing the antifouling action of copper soaps by adding slowly soluble metallic or organic poisons and with means of obtaining lasting adherence and toughness of the paint films—this has led to paints which kept clean for nine months in the sea and show some prospect of further development. The effect of temperature, hydrogen-ion concentration and turbulence of the water on the rate at which added copper leaches from these copper soap films has been investigated.

Several coatings relying on their naphthalene content for antifouling action have been made and found to keep clean for several months in the sea; although these are not practicable for use on ships' bottoms, the experiments indicate that 'fat solvents' which leach slowly into the water prevent attachment and growth of organisms. The aim has been to throw light on the mechanisms by which surfaces may be kept free from marine growths rather than to develop an antifouling paint, in the hope that such knowledge may open up new methods. Close contact has been maintained with the group investigating various aspects of the problem for the Marine Corrosion Committee of the Iron and Steel Institute.

Some preliminary work has also been carried out concerning the cycle of phosphorus in the sea, which has since been extended by Dr S. P. Chu's investigations of the utilization of phosphorus by diatoms.

Miss Lebour has published her paper on the larvae of the genus *Porcellana* and related forms in the current number of the Association's Journal. She has continued to study the inshore plankton, and has added largely to the breeding records of many species, special attention being paid to decapod and mollusc larvae. A very young float of *Velella*, captured in February, 1943, after violent storms, indicated that the species was in the district.

Continuing her work on *Teredo* and its relatives she has examined drift wood from Wembury Bay and from outside trawlers which yielded large numbers of *Teredo megotara* and *Xylophaga*. It was possible to study the breeding of these to a certain extent and it was established that both have very small and numerous eggs and that it is unlikely that either of them keeps the embryos in the gill pouches as does *Teredo navalis*. Successful fertilizations were made of *Xylophaga*, but the embryos did not live more than a few days.

A critical survey has been begun of the Plymouth Pycnogonida, the species of which are very much confused. It was discovered that the well-known *Phoxichilidium femoratum*, hitherto unrecorded from Plymouth, consists of two distinct species, one of which is common at Plymouth. The true *P. femoratum* of Rathke is apparently a more northerly form. Apart from very distinct life-histories the two species differ in colour and in many small anatomical characters. The species of *Anoplodactylus* are also being specially studied and are yielding interesting results.

Mr D. P. Wilson has kept a close watch on his cultures of *Nitzschia closterium* with a view to discovering any regular seasonal variation which they may show in comparison with previous years. For the third successive autumn there has been a rise in the percentage number of triradiates which are in process of eliminating one of the horns by a method of gradual reduction. This rise, however, has not again reached the striking proportions it had when it was first observed in 1941. Formation of the oval form without horns has been shown by simple experiment to take place most readily in a relatively strong light, while in a dim light they are rarely produced. During the year a remarkable cruciform type, regular in shape, appeared independently in a few cultures. It was at first very rare, one cruciform among several thousand other cells, but it increased slightly in abundance and attempts were made to get it into pure culture. At one time cultures were obtained with between thirty and fifty per cent of their cells cruciform, but the type appears to be somewhat unstable and apparently reverts fairly readily to a simpler condition. Cultures with cruciform cells in some abundance are, however, still living.

During the year Mr Wilson has worked out a technique for the photomicrography of living plankton organisms. These have always presented special difficulties to the photomicrographer and satisfactory pictures have rarely been secured by photographic means. Mr Wilson has succeeded in obtaining several series of photographs of high quality illustrating the development of certain marine animals; and the technique promises to be useful in the future.

Mr Wilson has devoted much of his time to plans for the post-war reconstruction and extension of the laboratory buildings, improving in detail on those mentioned in the last report and providing for additional accommodation where needed. He has also made reports on the biological condition of various materials which are being tested against underwater deterioration.

The work, which is being carried out for industrial firms, is concerned with the rotting of textiles and the fouling of painted surfaces.

Mrs Sexton has continued her work on the Amphipod *Jassa falcata* (Montagu), analysing the results of the breeding experiments carried out in the laboratory. She has figured the moults of many of the F_1 and F_2 to show the changes which take place in the growth stages, particularly in the males. From these it can be seen that many of the so-called 'species' attributed to the genus *Jassa* are in fact only the various developmental stages of the one species, *J. falcata*. Such forms occur in one and the same brood, and differ greatly from each other and from the full-grown males—particularly in the shape of the hands of the second gnathopods, and in the structure and sensory armature of the lower antennae.

Special Research.

The research work on brown algae, which is being undertaken by Dr M. Parke with the assistance of Miss E. Clay, has been vigorously continued during the year. The experimental work is being carried out at Wembury and on the west coast of Scotland and is conducted in collaboration with Dr M. Knight, who is engaged on similar research in the Isle of Man. Two years have now elapsed since the algal investigations began; areas which were cleared at the outset now show satisfactory re-growth and it has thus been possible to make useful observations on plants of known age. Preliminary attempts to follow growth below low-water mark by laying slabs of concrete on the bottom were frustrated through the loss of marking buoys in heavy weather, and the study of the deep-water *Laminaria Cloustoni* is for this reason less advanced. It is of interest to note that *Saccorhiza polyschides* is frequently one of the first plants to establish itself on a cleared area, and by its rapid growth quickly outstrips any species of *Laminaria* in thallus production; this species is, however, only an annual and thus disappears at the end of the season.

It is expected that, with the possible exception of *Laminaria Cloustoni*, most of the important points in the life cycle and process of regeneration in the commoner species of brown algae will be ascertained during the coming year; but in the course of the work very extensive data have been accumulated and some time must elapse before the full results are ready for publication.

The Library.

The library has remained in store near Tavistock throughout the year. The arrangement is most inconvenient since it is rarely possible to find books needed in the laboratory work. It is hoped that the coming year will bring improved conditions which will allow the library to be re-established at Plymouth.

The thanks of the Association are due to those institutions and authors who have presented books or papers.

Published Memoirs.

Vol. xxv, No. 4, of the *Journal* of the Association was published in September 1943. This part contains an obituary notice of the late Dr E. J. Allen written by the President.

The following papers, outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

Atkins, D., 1943. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part VIII. Notes on gill musculature in the Microciliobranchia. *Quart. Journ. Micr. Sci.*, Vol. lxxxiv, pp. 187–255.

Atkins, W. R. G., 1943. Determination of the water content of wood and other substances by means of ternary azeotropic mixtures. *Nature*, Vol. 151, p. 449.

Earland, Arthur and Jepps, Margaret W., 1943. A note on an abnormal specimen of *Elphidium crispum* (L.). *Journ. Roy. Micr. Soc.*, (3), Vol. lxiii, pp. 43–7.

Ewer, D. W. and Ewer, R. F., 1943. Osmotic regulation in *Sabella pavonina*. *Nature*, Vol. 152, pp. 598–9.

Holmes, William, 1943. Innervation of crustacean muscles. *Nature*, Vol. 151, pp. 531–2.

Lebour, M. V., 1943. The Crab. *School Sci. Rev.*, No. 94, pp. 319–27.

Lebour, M. V., 1944. Shrimps and Prawns. *School Sci. Rev.*, No. 96, pp. 209–16.

Lebour, M. V., 1944. The rearing of marine animals in captivity. *Rep. & Trans. Plymouth Institution & Devon & Cornwall Nat. Hist. Soc.*, Vol. xviii, for the years 1936–43.

Lowndes, A. G., 1943. The term *Tractellum* in flagellate organisms. *Nature*, Vol. 152, p. 51.

Lowndes, A. G., 1943. Some applications of the displacement method of weighing living aquatic organisms. *Proc. Zool. Soc.*, A, Vol. cxiii, pp. 28–43.

Lowndes, A. G., 1944. The swimming of unicellular flagellate organisms. *Proc. Zool. Soc.*, A, Vol. cxiii, pp. 99–107.

Lysaght, Averil M., 1943. The incidence of larval trematodes in males and females of the gastropod *Littorina neritoides* (L.) on the Plymouth Breakwater. *Parasitology*, Vol. xxxv, pp. 17–22.

MacKay, Donald C. G., 1943. Relative growth of the European edible crab, *Cancer pagurus*. II. Growth of the abdomen. *Growth*, Vol. vii, pp. 217–26.

MacKay, Donald C. G., 1943. Relative growth of the European edible crab, *Cancer pagurus*. III. Growth of the sternum and appendages. *Growth*, Vol. vii, pp. 401–12.

Myers, Earl H., 1943. Life activities of Foraminifera in relation to Marine Ecology. *Proc. Amer. Phil. Soc.*, Vol. lxxxvi, pp. 439–58.

Pantin, C. F. A. & Pantin, A. M., 1943. The stimulus to feeding in *Anemonia sulcata*. *Journ. Exp. Biol.*, Vol. xx, pp. 6–13.

Membership of the Association.

There have been no changes in the list of Vice-Presidents. The number of Associate members is now 5, and the total number of annual members on 31 March 1944 was 309, the same number as at the corresponding date in 1943. The number of life members at the end of the year was 51.

Finance.

Grant from the Development Fund. The Council has again to express its thanks to the Development Commissioners for their continued support of the Plymouth laboratory.

Private Income. The Council gratefully acknowledges the following generous grants for the year:

From the Fishmongers' Company (£575), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the laboratory: The Universities of Cambridge (£105), London (£105), Oxford (£52. 10*s*.), Bristol (£25), Manchester (£10. 10*s*.), Leeds (£10. 10*s*.), Sheffield (£5); the British Association (£50), the Physiological Society (£30), the Ray Lankester Fund (£20) and the Imperial College of Science and Technology (£10).

President, Vice-presidents, Officers and Council.

The following is the list of those proposed by the Council for election for the year 1944–45.

President

G. P. Bidder, Sc.D.

Vice-Presidents

The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholas Waterhouse; K.B.E.
The Lord Moyne, P.C., D.S.O.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. Peel, D.S.O., M.C.
Lord Mildmay of Flete, P.C.
Col. Right Hon. Sir Reginald Dorman Smith, M.P.
Sir Joseph Barcroft, Kt., C.B.E., F.R.S.
Prof. J. Stanley Gardiner, F.R.S.
Prof. Walter Garstang, D.Sc.

COUNCIL

To retire in 1945

Prof. H. Graham Cannon, Sc.D., F.R.S.
The Hon. Miriam Rothschild
C. Forster-Cooper, M.A., Sc.D., F.R.S.
Prof. A. C. Hardy, D.Sc., F.R.S.

To retire in 1946

Prof. F. E. Fritsch, D.Sc., F.R.S.
Morley H. Neale
Miss Margery Knight, D.Sc.
Michael Graham
J. E. Smith, Ph.D.

To retire in 1947

Prof. F. W. Rogers Brambell, D.Sc
Prof. H. Munro Fox, F.R.S.
O. D. Hunt
L. Harrison Matthews, Sc.D.
Prof. James Ritchie, M.A., D.Sc.
J. F. Danielli

Chairman of Council

Prof. James Gray, M.C., Sc.D., F.R.S.

Hon. Treasurer

Major E. G. Christie-Miller, 71 Park Street, London, W. 1

Secretary

Stanley Kemp, Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Sc.D.
The Lord Moyne, P.C., D.S.O.
A. T. A. Dobson, C.B., C.V.O., C.B.E. (Ministry of Agriculture & Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.
  Major E. G. Christie-Miller
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
H. G. Maurice, C.B. (Zoological Society)
Prof. A. V. Hill, O.B.E., Sc.D., F.R.S., M.P. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1944

				£	s.	d.	£	s.	d.
SUNDRY CREDITORS:									
Accrued Expenses				52	15	2			
Subscriptions received in advance				13	13	0			
Grant received in advance				125	0	0			
							191	8	2
AQUARIUM GUIDE PRINTING FUND:									
As at 31st March 1943							22	1	6
SPECIAL APPARATUS FUND:									
As at 31st March 1943							10	4	11
MACKEREL RESEARCH FUND:									
As at 31st March 1943				39	7	10			
Less: Expenditure				39	7	10			
							–	–	–
BIOLOGICAL INVESTIGATIONS ON ALGAE:									
Grant Received				1604	3	9			
Less: Balance as at 31st March 1943	15	11	9						
Expenditure	1480	14	9						
Table Rent credited to Income and Expenditure Account	100	0	0						
				1596	6	6			
							7	17	3
E. T. BROWNE BEQUESTS FUNDS:									
Building Fund, as at 31st March 1943	1122	5	0						
Interest on Investment	34	3	9						
				1156	8	9			
Library Fund, as at 31st March 1943	991	9	8						
Interest on Investment	30	4	1						
				1021	13	9			
Special Apparatus Fund, as at 31st March 1943	2254	2	10						
Interest on Investment	68	13	6						
				2322	16	4			
Scientific Publications Fund, as at 31st March 1943	1690	11	10						
Interest on Investment	51	10	0						
				1742	1	10			
							6243	0	8

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at Valuation as estimated by the Director as at 31st March 1941:						
S/S "Salpa"	2000	0	0			
Motor Boat "Gammarus"	100	0	0			
Nets, Gear and General Equipment	30	0	0			
				2130	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at Valuation as estimated by the Director as at 31st March 1941 plus additions at Cost:						
As at 31st March 1943				4050	0	0
LIBRARY, at Valuation of Mr Ridgill Trout in January 1941 plus additions at Cost:						
As at 31st March 1943				16000	0	0
STOCKS ON HAND, as valued by the Director:						
Specimens	800	0	0			
Chemicals	150	0	0			
Journals	400	0	0			
				1350	0	0
SUNDRY DEBTORS:						
Sales of Specimens and Journals, etc.	187	10	2			
Ministry of War Transport—Hire of S/S "Salpa"	67	0	0			
Ministry of Agriculture and Fisheries—fourth instalment of Grant from Development Fund for 1943/44	1678	0	0			
				1932	10	2
PREPAYMENTS				17	12	8
GENERAL FUND INVESTMENT, at market value as at 31st March 1931:						
£352. 2*s*. 3*d*. Local Loans 3% ... ... (Market Value at date £330. 19*s*. 9*d*.)				232	7	10
E. T. BROWNE BEQUESTS FUNDS INVESTMENT, a tcost:						
£6331. 11*s*. 2*d*. Conversion Loan 3% ... ... (Market Value at date £6497. 15*s*. 3*d*.)				6243	0	8
"SALPA" DEPRECIATION FUND INVESTMENTS, at cost:						
£590. 6*s*. 0*d*. Local Loans 3%	506	10	9			
£4151. 10*s*. 3*d*. Conversion Loan 3% ... ... (Market Value at date £4815. 7*s*. 6*d*.)	4226	13	5			
				4733	4	2
REPAIRS AND RENOVATIONS FUND INVESTMENT, at cost:						
£370. 9*s*. 9*d*. Conversion Loan 3% ... ... (Market Value at date £380. 4*s*. 3*d*.)				377	17	5

"SALPA" DEPRECIATION FUND:		
As at 31st March 1943	4271 7 6	
Add: Amount receivable from Ministry of War Transport on account of Hire	402 0 0	
Interest on Investments	126 16 8	
		4800 4 2
REPAIRS AND RENOVATIONS FUND:		
As at 31st March 1943	316 19 11	
Add: Transfer from Income and Expenditure Account	50 0 0	
Interest on Investment	10 17 6	
		377 17 5
COMPOSITION FEES FUND:		
As at 31st March 1943		252 0 0
CAPITAL RESERVE ACCOUNT:		
As at 31st March 1943		21688 8 2
SURPLUS ACCOUNT:		
As at 31st March 1943	3592 16 5	
Add: Surplus for the year as per Income and Expenditure Account	253 0 3	
		3845 16 8
		£37,438 18 11

COMPOSITION FEES FUND INVESTMENTS, at cost:		
£18. 8*s*. 6*d*. Local Loans 3%	15 15 0	
£231. 10*s*. 6*d*. Conversion Loan 3%	236 5 0	
(Market Value at date £254. 18*s*. 4*d*.)		252 0 0
CASH AT BANK AND IN HAND:		
Coutts & Company	52 10 2	
Lloyds Bank Limited	39 8 7	
Cash in Hand	23 14 0	
		115 12 9
RECOVERABLE EXPENDITURE:		
M. Parke Fund:		
As at 31st March 1943	12 0 8	
Less: Amount Recovered	12 0 8	
		– – –
Cellon Account:		
Expenditure during the year		4 13 3
		£37,438 18 11

C. M. YONGE
STANLEY KEMP } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1944 according to the best of our information and the explanations given to us and as shown by the books of the Association.

5 St Lawrence Road, Plymouth.
23rd May, 1944.

PRICE, WATERHOUSE & CO.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1944.

	£	s.	d.	£	s.	d.
To Salaries, including the Association's Contributions to Superannuation and War Bonuses				5718	2	2
,, Laboratory and Boats' Crews' Wages, including National Insurance, Contribution to Superannuation Scheme, War Bonuses and Employers Liability Insurance ...				3878	2	11
,, Upkeep of Library				148	18	3
,, Scientific Publications, Less Sales				340	4	0
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	19	1	9			
Electricity, Oil, Gas, Coal and Water ...	309	13	10			
Chemicals and Apparatus	188	0	7			
Fire Insurance, Tithe, Ground Rent and Rent of Store	79	14	2			
Travelling Expenses	101	11	5			
Stationery, Postages, Telephone, Carriage and Sundries	268	13	8			
Specimens	339	3	3			
				1305	18	8
,, Maintenance and Hire of Boats:						
Petrol, Oil, Paraffin, etc.	15	9	1			
Maintenance and Repairs with Nets, Gear and Apparatus	26	15	0			
Purchase of Materials for Nets, etc. for Sale	6	5	3			
Boat Hire and Collecting Expenses	3	0	11			
Third Party Insurance	5	0	0			
				56	10	3
,, Bank Charges				8	17	4
,, Transfer to Repairs and Renovations Fund				50	0	0
,, War Time Expenditure:						
War Damage Contributions	93	12	6			
War Risk Insurance	27	8	4			
Storage of Library	25	4	0			
Payment of Firewatchers	20	11	0			
				166	15	10
,, Balance, Being Surplus, for the Year ...				253	0	3
				£11,926	9	8

	£	s.	d.	£	s.	d.
By Grants:						
Ministry of Agriculture and Fisheries Grant from Development Fund	9478	0	0			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				10168	0	0
,, Subscriptions (excluding Subscriptions received in advance)				297	0	11
,, Donation				25	0	0
,, Fees for Tests of Materials				76	8	0
,, Sales:						
Specimens	835	11	2			
Nets, Gear and Hydrographical Apparatus ...	8	16	6			
				844	7	8
,, Table Rents (including University of Cambridge £105; Bristol £25; London £105; Oxford £52. 10*s.* 0*d.*; Leeds £10. 10*s.* 0*d.*; Manchester £10. 10*s.* 0*d.*; Sheffield £5; Imperial College £10; Trustees of Ray Lankester Fund £20, and £100 transferred from Biological Investigations on Algae) ...				496	2	6
,, Interest on Investments				18	1	2
,, Sale of Dr M. V. Lebour's Book					11	11
,, Sale of "Plymouth Marine Fauna" ...					17	6
				£11,926	9	8

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

The Association was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Marine animals and plants are supplied to educational institutions and as soon as possible arrangements will be made for the resumption of the courses for advanced students formerly held at Easter and in September.

Research work at sea is undertaken by a motor boat, and, in normal times, by a steam drifter, and these also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

CONTENTS

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