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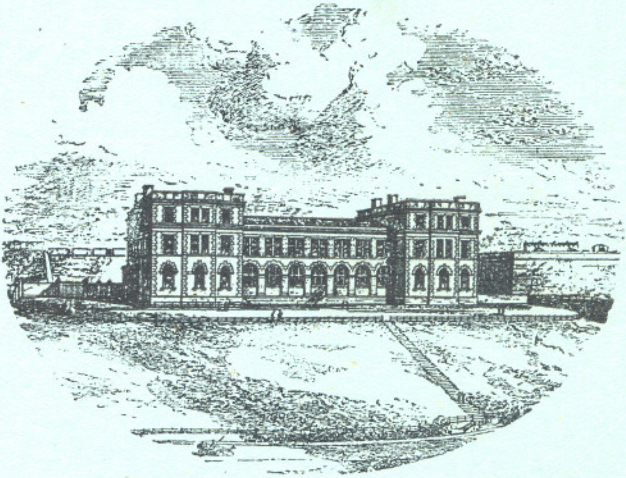

THE PLYMOUTH LABORATORY.

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Herring Investigations at Plymouth. V. The Plymouth Winter Fishery during the Season 1927–28.

By

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Naturalist at the Plymouth Laboratory.

With 7 Figures in the Text.

CONTENTS

DURING the winter of 1927–28 the progress of the herring fishing at Plymouth was followed for the fourth consecutive season. A diary of market events was again kept by Mr. A. J. Smith of the Laboratory staff, while statistics of commercial landings and of the number of visiting drifters were kindly supplied by Mr. T. Edser of the Statistical Department, Ministry of Agriculture and Fisheries, and by Mr. E. C. Nelder of the Sutton Harbour Improvement Company, respectively. In the examination of age and growth of random samples of herrings, Mr. F. J. Warren, Laboratory Assistant, again acted as recorder. Details of the methods of treatment of the data collected will be found in Part I of this series of Reports (Ford, **1**).

THE WINTER FISHERY OF 1927–28.

The season was in several ways a notable one. It will be seen from the following table that in spite of a marked reduction in the number of boats fishing, particularly in the case of steamers, the total quantity of herrings landed created a record :—

Season Dec.-Jan.	Number of East Country steamers.	Number of West Country (Cornish) motor drifters*	Total Quantity of Herrings landed. cwt.	Quantity landed by steamers only. cwt.	Quantity landed by motor drifters† only. cwt.
1918–19	33	139	8,624	7,628	996
1919–20	30	156	29,425	12,728	16,697
1920–21	26	182	40,263	20,973	19,290
1921–22	31	155	16,922	10,494	6,428
1922–23	68	142	54,839	40,941	13,898
1923–24	59	161	98,684	57,519	41,165
1924–25	86	176	113,585	83,647	29,938
1925–26	153	158	105,643	82,780	22,863
1926–27	129	169	63,138	45,932	17,206
1927–28	77	145	122,419	82,803	39,616

The Steam Fishery.

There has been an appreciable decline in the number of steamers visiting Plymouth during the past two seasons, due, probably, to the fact that the fishery had experienced several indifferent seasons in succession. In the months of December, 1927, and January, 1928, however, the seventy-seven steamers made a total of 1789 landings of an average weight of 46·6 cwt. This result was a welcome improvement on the averages for the corresponding months of the seasons 1925–26 and 1926–27 (23·1 cwt. and 16·6 cwt. respectively), as well as on the average of 26·6 cwt., covering the longer period of nine seasons from December, 1918, to January, 1927.

Whether or no the steamers, by ceasing fishing towards the end of January, leave the district when fishing might yet prove profitable, is a question worthy of investigation. The work of the past few years has created the impression that to the westward of Plymouth there may be an assemblage of well-grown, comparatively later-spawning herrings which are not every year fully exploited. Some of the small local drifters, when weather permits, certainly continue to make catches until well on into March, while the study of fishes landed during February and March has shown that an appreciable proportion of them have yet to spawn. Wallace (**4**, p. 35), too, has shown that later spawning of considerable intensity does occur in westerly waters in the neighbourhood of Gribbon Head. In such a season as the one now under review, when consistently good catches to the eastward are made, there is a decided tendency to bring the fishery to a close as soon as the easterly shoals show signs of exhaustion. In consequence of this, the late westerly fish are liable to be almost entirely neglected.

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* A small number of Plymouth motor drifters take part in the fishery, numbering on average about twelve.

† These figures are inclusive of the landings by Plymouth boats.

The Motor Fishery.

The total weight of fish landed by the motor drifters during December, 1927, and January, 1928, was the heaviest since the record season of 1923–24. This satisfactory aggregate, however, in contrast with that of the steamers, was chiefly due to a considerable rise in the total number of landings made, rather than to an increase in the average weight per individual landing. Thus, although the total number of landings was the greatest recorded since the Ministry's more modern system of statistics was adopted in 1906, the average weight of 24·6 cwt. per landing did not greatly exceed the average of 22·6 cwt. for the nine-year period from December, 1918, to January, 1927.

As in past seasons, a considerable weight of fish was landed by the steamers on days when the motor drifters made no landings. Thus, on 22 days (inclusive of 6 Sundays) during December, 1927, and January, 1928, a total of 29,708 cwt. was landed by steamers, while there were no landings at all by motors.

Value of the Fishery.

The total value of the fishery during each of the past twenty-two seasons is shown in the following table, together with the average price per 1 cwt. :—

Season (Dec.–Jan.)	Total Weight landed. (cwt.)	Total Value. £	Average Price per 1 cwt. shillings and pence.
1906–07	32,913	8,040	4 11
1907–08	23,957	6,583	5 6
1908–09	4,257	2,521	11 10
1909–10	52,544	16,105	6 1
1910–11	37,741	17,048	9 0
1911–12	39,167	18,158	9 3
1912–13	8,171	3,594	8 10
1913–14	28,886	13,933	9 8
1914–15	7,585	6,021	15 11
1915–16	11,582	13,062	22 7
1916–17	24,293	35,901	29 6
1917–18	38,108	88,453	46 5
1918–19	8,624	15,160	35 2
1919–20	29,425	40,045	27 3
1920–21	40,263	42,752	21 3
1921–22	16,922	14,792	17 6
1922–23	54,839	26,326	9 8
1923–24	98,684	65,290	13 3
1924–25	113,585	109,294	19 3
1925–26	105,643	89,334	16 11
1926–27	63,138	47,539	15 1
1927–28	122,419	65,451	10 8

It will be seen that during the season 1927–28, although a record total weight of fish was landed, the average price per 1 cwt. was, with the solitary exception of the season 1922–23, easily the lowest realised since the pre-war season of 1913–14. Thus, it is only necessary to refer back to the season 1925–26 to discover a total financial yield exceeding that of 1927–28.

It is of some local interest to note that the seasonal average price per 1 cwt. realised at Plymouth has almost always been greater than the yearly average price of herrings of British taking generally. This fact is brought out in the following table and in Fig. 1 :—

	Herrings. British Taking. Average Price per 1 cwt.		Herrings. Plymouth only. Average Price per 1 cwt.		
Year.	shillings.	pence.	shillings.	pence.	Season Dec.–Jan.
1906	8	1	4	11	1906–07
1907	5	1	5	6	1907–08
1908	5	7	11	10	1908–09
1909	6	0	6	1	1909–10
1910	7	8	9	0	1910–11
1911	5	11	9	3	1911–12
1912	6	2	8	10	1912–13
1913	6	4	9	8	1913–14
1914	6	9	15	11	1914–15
1915	16	5	22	7	1915–16
1916	21	11	29	6	1916–17
1917	22	10	46	5	1917–18
1918	24	6	35	2	1918–19
1919	14	1	27	3	1919–20
1920	11	11	21	3	1920–21
1921	4	7	17	6	1921–22
1922	7	1	9	8	1922–23
1923	7	11	13	3	1923–24
1924	11	4	19	3	1924–25
1925	10	5	16	11	1925–26
1926	8	7	15	1	1926–27
1927	9	5	10	8	1927–28

The daily returns of landings and market prices at Plymouth during December, 1927, provide a good illustration of the fact that the ruling price on the market is to a greater or lesser extent dependent upon the quantity of fish available. In the following table, daily landings have

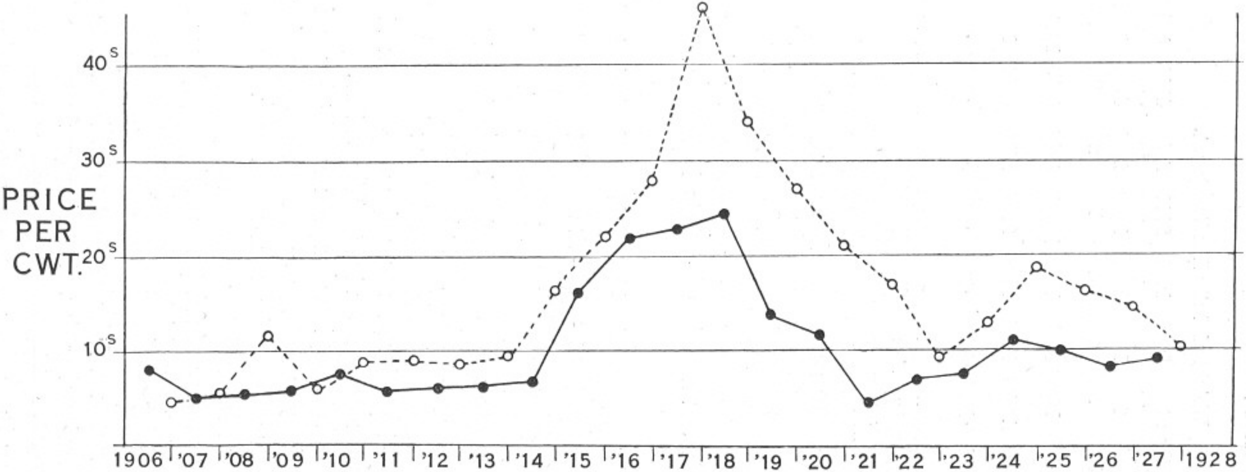

FIG. 1.—Market price per 1 cwt. of Herrings.

Continuous line —— Herrings of British taking throughout year.
Broken line .... Herrings landed at Plymouth during Dec. and Jan.

been grouped into convenient classes and the average price per 1 cwt. calculated for each class :—

Weight of Daily Landing (cwt.).

	Less than 500	500 to 999	1000 to 1499	1500 to 1999	2000 to 2499	2500 to 2999	4000 to 4499	5000 to 5499	5500 to 5999	7000 to 7499
No. of Days	5	2	3	4	7	2	2	3	1	1
Total weight landed (cwt.)	1336	1409	3581	7140	15311	5750	8600	15818	5650	7010
Average weight (cwt.) per day	267	704·5	1194	1785	2187	2875	4300	5273	5650	7010
Average price per 1 cwt. (£)	1·186	·9645	·6782	·596	·566	·433	·483	·367	·256	·320

In Fig. 2 the average price per 1 cwt. for the average weight in each class has been plotted, and the smooth curve AB drawn freehand to provide a reasonably good representation of the general downward trend of the average price as the size of the daily landing increases. It is seen that this curve falls steeply at first, but less and less rapidly later. By erecting perpendiculars from the correct points along the base line, to cut the curve AB, it is possible to read off the average price per 1 cwt. for landings of given size. The following data have been obtained in this manner :—

Weight of landing (cwt.)	500	1000	2000	3000	4000	5000	6000	7000
Approx. average price per 1 cwt. (shillings and pence)	20/–	15/–	11/6	9/11	8/6	7/4	6/3	5/4
Approx. average price per 1 lb. (pence)	2·1	1·6	1·2	1·1	·9	·8	·7	·6

It is also of interest to note that during December, 1927, on 15 out of the total of 30 days on which fish were actually landed, a total of 48,085 cwt., representing about 67% of the total weight landed throughout the month, was sold at a daily average price varying from 10s. to 5s. per 1 cwt. ; that is, at the rate of from 1d. to ½d. per 1 lb.

In applying these statistics, however, it must be borne in mind that they are *averages ;* they smooth over those differences in price, often appreciable, between different sales on the same day. Every prospective buyer knows his own immediate requirements, and bids accordingly. One needs a given quantity of fish of the finest quality procurable for which he is prepared to pay a high price. Having secured these fish, he is indifferent to all subsequent sales. On the other hand, a second buyer is not likely to compete for fish until the price has fallen to a certain figure, but he will then buy heavily. The average figures for the day used in the foregoing considerations thus represent the mean of individual sale prices which may differ to a marked degree, so that in drawing comparisons such as that between prices at the source and those paid by the consumer these averages must be applied with great caution, if at all.

So far as actual fishing and marketing operations are concerned, however, they are instructive. By utilising the data derived from the curve AB on Fig. 2 we can determine the approximate total market value of a day's catch of given weight; thus:—

Weight of landing (cwt.)	500	1000	2000	3000	4000	5000	6000	7000
Approx. average price per 1 cwt. (shillings and pence)	20/–	15/–	11/6	9/11	8/6	7/4	6/3	5/4
Approx. total value of landing (£)	500	750	1150	1485	1700	1835	1875	1875

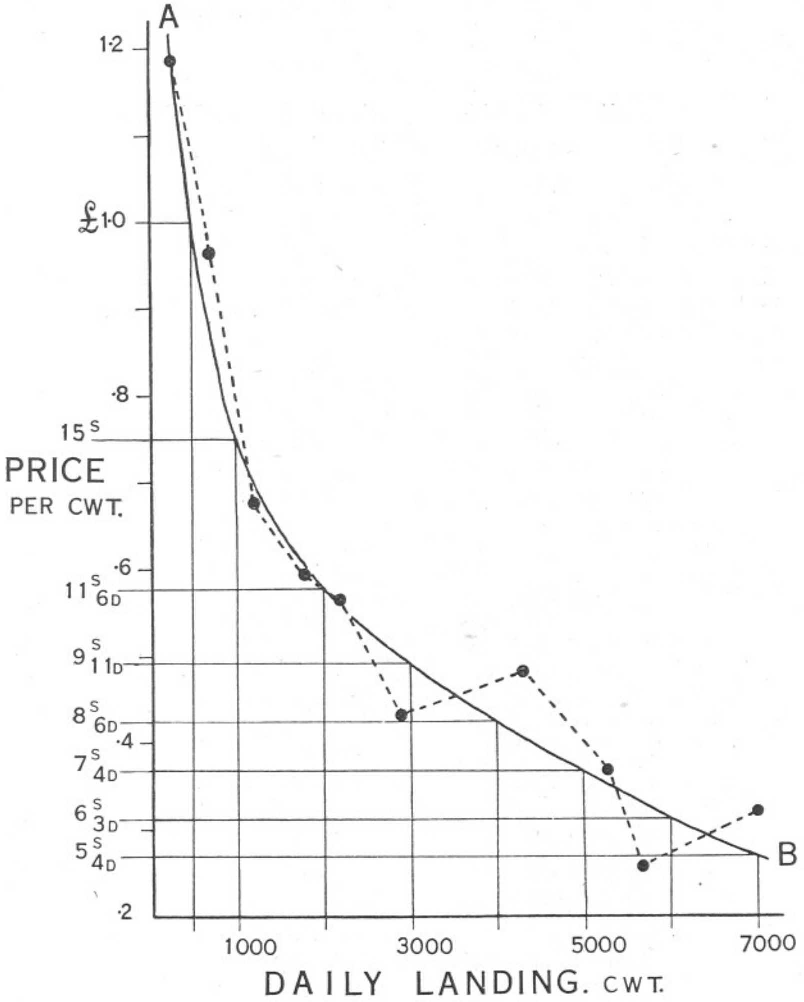

Fig. 2.—Market price per 1 cwt. of Herrings landed by steamers during Dec., 1927.

The continuous curve AB is drawn freehand as an approximate fit to the observed values, and from it the price per 1 cwt. for a daily landing of given size may be estimated.

To the mind of the fisherman these figures mean that during December, 1927, in increasing the total weight of fish landed in a day from 1000 cwt. to 2000 cwt., he received £400 for the additional 1000 cwt., whereas in raising the daily total from 4000 cwt. to 5000 cwt., the remuneration he received for the additional 1000 cwt. had dwindled to £135. And what is more, any amount of fish in excess of 5000 cwt. per day was literally given away.

These figures also suggest that during this period buyers were not prepared to spend much more than £1800–£1900 on daily catches aggregating 5000 cwt. or over.

THE CHARACTERS OF THE FISHES LANDED.

Eleven samples from commercial landings between October 17th, 1927, and March 3rd, 1928, were examined for length, sexual condition, age, and growth. The possession of corresponding data for the three preceding seasons undoubtedly adds to the interest and value of the present records, enabling useful comparisons to be made from which a more intelligent view of events from year to year can be obtained.

Average Length.

In Table I on page 23 the values of the median length (Q_2), the quartiles (Q_1 and Q_3), and the upper and lower limits of size for each sample are given. Corresponding data for previous seasons were given in Part III (Ford, **2**, p. 301). The means of the individual values of Q_1, Q_2, and Q_3 for each season provide a rough indication of the length distribution, and in the following table these means for the period November to January during the four consecutive seasons are shown :—

	Mean of sample values for the following seasons (Nov.–Jan.).			
	1924–25.	1925–26. (cm.).	1926–27.	1927–28.
Q_1 . . .	26·4	26·4	25·6	24·7
Q_2 . . .	27·3	27·4	26·5	25·8
Q_3 . . .	28·2	28·3	27·8	27·0

It is seen that the appreciable depression of length during 1926–27 was followed by a further drop during 1927–28. It is true that considerable differences in average size can be occasioned by changes in the size of mesh in the drift-nets used (*vide* Hodgson, **3**), but in the present instance this is not thought to be the important factor. The account of the age-composition of the samples, given later, will demonstrate convincingly that the 1927–28 samples included a very much larger percentage of young fishes than those of 1925–26 or even 1924–25. Further discussion of the length data will be found on page 12 in conjunction with those on age.

Age Composition of Samples.

The age composition of the 1927–28 samples is given in the form of percentages in Table II on page 24. These results are also shown graphically in Fig. 4 on page 11, while, for convenience, the corresponding results for previous seasons have been republished in Fig. 3. It will be noticed that the principle used during the seasons 1924–25 and 1925–26, namely, of including all fishes definitely older than " 6 zones 6 rings " in a composite year-group, has been reverted to. Where interest is chiefly centred on the percentages of well-represented year-classes which either form the mainstay of a current fishery or will become increasingly important in the near future, it is hardly necessary to estimate precisely the age of a few older fishes.

By determining the mean of the individual sample percentages of each year-group, we can arrive at an average composition which will serve as a working summary for the season. Admittedly, such a summary is an approximation, but it facilitates the comparison of results from season to season ; it is not intended to stand as an accurate assessment of the age-stock on the grounds. The summary for 1927–28 is as follows :—

Season (Nov.–Jan.).	Percentage Composition by Age.										Older than 6
	2	2–3	3	3–4	4	4–5	5	5–6	6	6–old	
1927–8	—	—	16·5	0·2	19·2	1·2	30·4	1·8	11·1	1·1	18·2

As an alternative, sample age-data may also be summarised as percentages of definite year-classes, thus :—

Season (Nov.–Jan.).	Percentages of Year-classes.				
	1925	1924	1923	1922	1921 & earlier.
1927–28 . .	16·5	19·2	30·4	11·1	18·2

It is seen that the 1923 year-class, now as 5-zoned 5-ringed fishes, definitely dominated with a percentage of 30·4. This is in accordance with the expectation expressed in Part III (Ford **2**, p. 291) when the previous season's results were under review. Two other facts should be noted at this stage. In the first place, there was an unusually high percentage of 3-zoned 3-ringed fishes (1925 year-class), the significance of which will be dealt with later. Secondly, the year-class 1920, so dominant a constituent of the samples from the landings of the three previous seasons, no longer formed an important element.

The Year-class 1920.

It has previously been shown that fishes of the year-class 1920 were much in evidence during the seasons 1924–25, 1925–26, and 1926–27 (Ford, **2**, p. 289). As 5-zoned 5-ringed fishes in 1924–25 they comprised

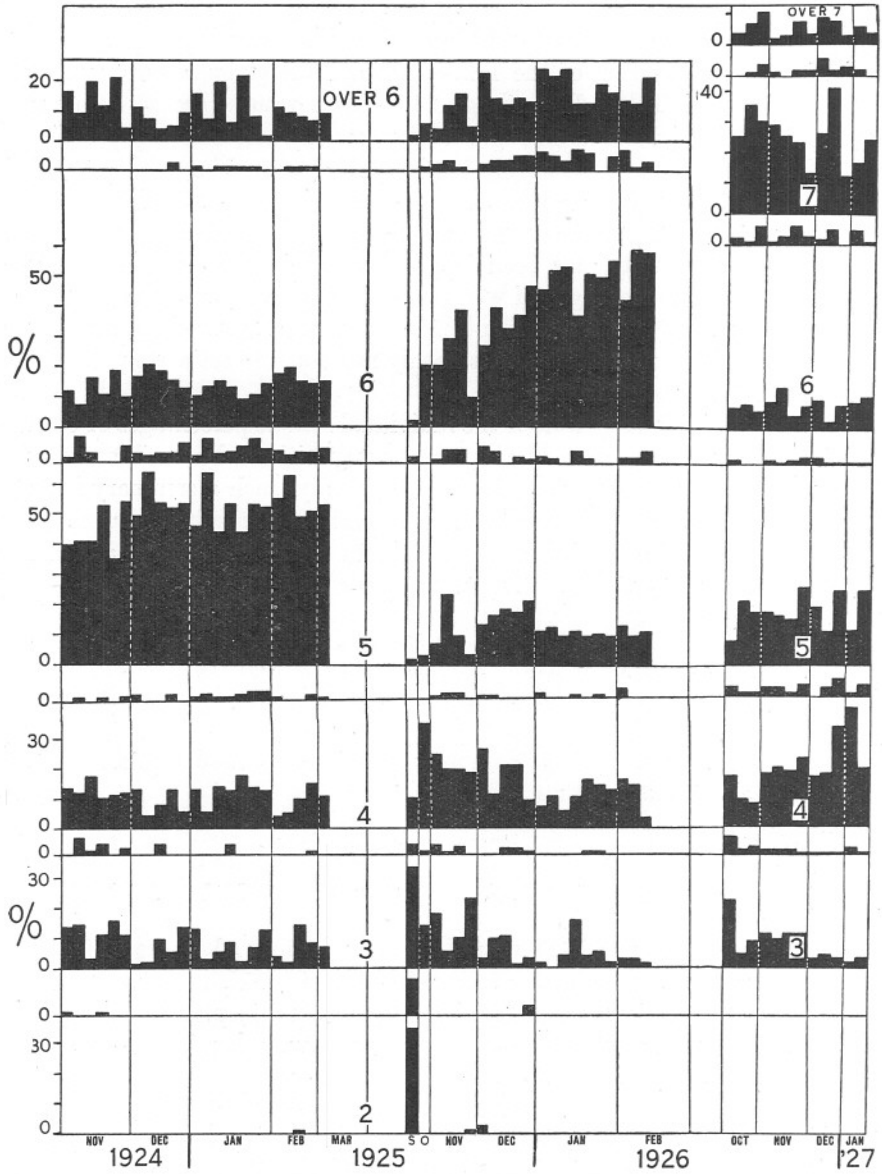

Fig. 3.—Age composition of samples of Plymouth Herrings.

Sample percentages are shown as small vertical blocks. The age-classes are as follows:

2	2-zoned 2-ringed.
3	3-zoned 3-ringed.
4	4-zoned 4-ringed.
5	5-zoned 5-ringed.
6	6-zoned 6-ringed.
7	7-zoned 7-ringed.

The "interval" classes are obviously 2 or 3, 3 or 4, 4 or 5, etc.

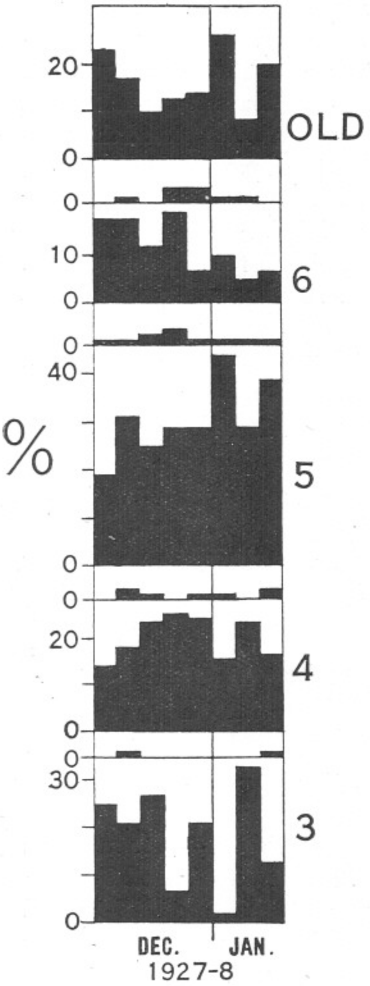

FIG. 4.—Age composition of samples of Plymouth Herrings landed during season 1927–28.

Figure constructed in same way as Fig. 3. The age-class "OLD" includes all fishes definitely older than 6-zoned 6-rings.

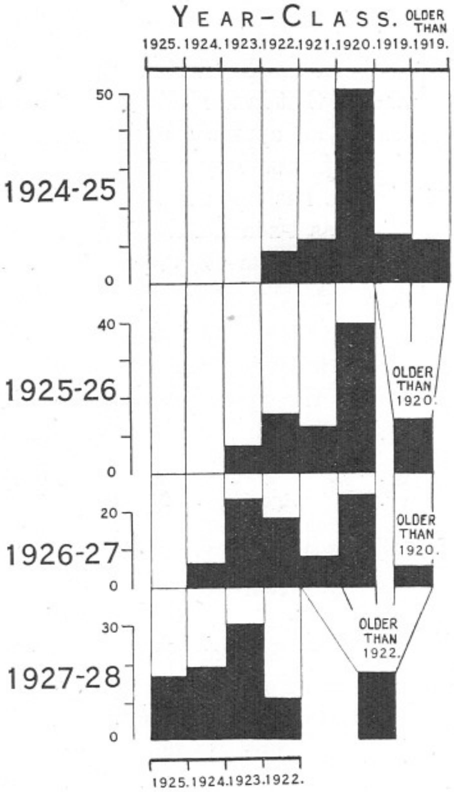

FIG. 5.—Summary of age composition during four consecutive seasons at Plymouth. The average seasonal percentage of each year-class is shown as a small vertical block.

more than 50% of many samples; as 6-zoned 6-ringed fishes in 1925–26 they again greatly outnumbered those of any other year-class, while as 7-zoned 7-ringed individuals in 1926–27 they were still a leading element although not so heavily represented as in previous years. But now, in 1927–28, as 8-zoned 8-ringed fishes they no longer form a dominant constituent of the samples, having been replaced by the members of younger year-classes. It is, naturally, a little disappointing that the available data do not go sufficiently far back actually to cover the whole period throughout which this successful year-class 1920 had formed part of the Plymouth catches. Judging from recent experience, it seems extremely unlikely that more than an occasional well-grown individual of this class would have been caught in 1921–22 as a 2-zoned 2-ringed fish. It is possible, however, that in the following season of 1922–23, the catches would have included an appreciable percentage of the 1920 year-class as 3-zoned 3-ringed fishes. Furthermore, when as a result of a further year's growth their size has become well within catchable range, the percentage in 1923–24 as 4-zoned 4-ringed individuals might easily have exceeded that of any other year-class represented.

Length for Age.

In the following table the average length and individual variation for fishes of the year-classes represented during the season 1927–28 are given :—

Year-class.	Age.	No. of fishes in each of 10 length-groups (cm.).										Total No.	Average length. cm.
		21	22	23	24	25	26	27	28	29	30		
1925	3-zoned 3-ringed	4	18	57	71	34	4	1	1	–	–	190	24·2
1924	4-zoned 4-ringed	–	2	26	49	66	32	9	3	1	1	189	25·3
1923	5-zoned 5-ringed	–	–	2	25	120	105	44	5	–	–	301	26·1
1922	6-zoned 6-ringed	–	–	–	7	27	31	31	8	5	–	109	26·7

These averages are lower than the corresponding ones for previous seasons (cf. Ford, **2**, p. 293), particularly those of the 3-zoned 3-ringed and 6-zoned 6-ringed fishes. The fact that fishing during 1927–28 was conducted almost entirely on the more easterly grounds may account for this (*vide* Ford, **2**, p. 287).

PREDICTIONS OF FUTURE FISHERIES.

No one with any practical experience of the annual fluctuations to which the herring fisheries are subject, will be likely to underestimate the difficulties which have to be overcome before there can be any hope of giving reliable forecasts of future fisheries. In the pages which follow an attempt has been made to indicate how the results of the investigations during the past few seasons may be brought to bear directly upon this practical question. In the face of so formidable a problem, any worker might reasonably hesitate to advance suggestions after such a short period of study ; it should, therefore, in fairness to the present writer, be clearly recognised that the attempted forecasts are given primarily as illustrations of the way in which the limited data may prove helpful, and, secondarily, as trial predictions which can ultimately be substantiated or disproved. Even if such forecasts do eventually prove poor, they should not necessarily be regarded as a condemnation of the whole work ; the discrepancies between forecast and reality ought rather to be examined most carefully in an endeavour to discover why they have arisen.

If we examine the data of landings by steamers over a period of years at Plymouth we are at once impressed by three facts :—

1. The average weight per landing varies greatly from one season to the next.
2. In some years the heaviest landings are made in December, whereas in others, in January.
3. Fishing operations are adversely influenced by bad weather conditions.

Of these three facts, the present work can only deal with the first two ; the influence of meteorological conditions is outside its scope, important as it may be. We have thus to discuss how the systematic study of the fishes landed during the past four seasons, and of a set of temperature records in the Plymouth area over the same period, can help us to predict the yield of a future fishery, as well as the "earliness" or "lateness" of the fishery in that season.

We have already seen that the 1920 year-class of fish formed a marked percentage of the landings in recent years. Let us, therefore, first notice the state of the fishery during those seasons when this year-class was represented in the landings. In the following table, the values of the average weight per landing by steamers are shown against the corresponding age and percentage of fishes of the 1920 year-class :—

Season (Nov.–Jan.).	1920 Year-class. Age. Zones.	Rings.	Percentage.	Average Weight per Landing by Steamers. cwt.
1921–22	2	2	Practically unrepresented	13·8
1922–23	3	3	No data available	25·8
1923–24	4	4	No data available	37·8
1924–25	5	5	50·5	40·0
1925–26	6	6	39·6	23·0
1926–27	7	7	24·2	16·0
1927–28	8	8	<10	46·6

We see that the average weight per landing rose each season from 1921–22 to 1924–25, but then fell away for two seasons in succession. During the same period the percentage of the 1920 year-class rose and fell in a corresponding manner. It is not unreasonable to argue that this is no mere coincidence and that the high average landings during 1923–24 and 1924–25 were the result of the maximum representation of a highly successful year-class 1920. From this observation we could reasonably contend that had we in 1922–23 appreciated the coming importance of this year-class we could have predicted the good catches in 1924–25 and 1925–26.

Clearly, then, as an initial step towards forecasting, we must examine our data on age composition, in order to get as much information as possible concerning the various year-classes represented.

Age Composition of Samples during the four Seasons from 1924–25 *to* 1927–28.

In the following table, and in Fig. 5 on page 11, the average age composition for each of the four seasons 1924–25 to 1927–28 is given. The seasonal averages are in each case the mean of all the sample percentages of that season, and they are tabulated according to the year-class :—

Season	Average Percentage of different Year-classes.							
(Nov.–Jan.)	1925	1924	1923	1922	1921	1920	1919	Earlier than 1919
1924–25	—	—	—	8·2	11·8	50·5	12·8	11·0
1925–26	—	0·25	7·2	15·7	12·6	39·6	14·2	
1926–27	—	6·3	23·2	18·9	8·6	24·2	5·2	
1927–28	16·5	19·2	30·4	11·1	18·2			

3-zoned 3-ringed
4-zoned 4-ringed
5-zoned 5-ringed
6-zoned 6-ringed

Before proceeding to examine the actual data given in the above table, it will be helpful to point out the three leading ways in which the data may be read :—

1. By reading along a horizontal line we obtain the percentage of each year-class during the same season.
2. By reading down a vertical column we learn how the percentage of a given year-class changes from one season to the next.
3. By reading across the diagonal rows we learn the percentage of fishes in each season having a given number of zones and rings.

Turning now to the data themselves, we see, in the first place, that a year-class usually makes its initial appearance in the samples when 3-zoned 3-ringed. The 1924 year-class was an exception, but even then only an occasional 2-zoned 2-ringed fish occurred in 1925–26. Bearing in mind the relatively small size of fishes when 3-zoned 3-ringed, it is probable that as yet only the bigger representatives are caught, the smaller ones avoiding capture by passing through the mesh of the net.

In the second place, the percentage of a year-class tends to rise until its members have become 5-zoned 5-ringed. For example, in 1925–26, the percentage of year-class 1923, then 3-zoned 3-ringed, was 7·2%; in the following season, when the fishes were 4-zoned 4-ringed, the percentage rose to 23·2%; in 1927–28, when the fishes had become 5-zoned 5-ringed, the percentage had again risen to 30·4%. Year-classes 1921, 1922, and 1924 show a similar tendency (see Fig. 5 on p. 11).

Thirdly, the percentage of a year-class tends to decline when its members have passed the age of 5-zones 5-rings. Thus, in 1924–25, the percentage of year-class 1920 was 50·5%, the fishes being 5-zoned 5-ringed; in 1925–26 the percentage of the same year-class, now 6-zoned 6-ringed, had dropped to 39·6%; in 1926–27, when the fishes were 7-zoned 7-ringed, the percentage had dropped still farther to the low level of 24·2%; in 1927–28 the percentage of year-class 1920 had become so reduced that by including with it the percentages of all older year-classes, as well as that of year-class 1921, the aggregate was only 18·2%. The percentages of year-classes 1919, 1921, and 1922 also showed a decline after the age of 5-zones 5-rings was reached (see Fig. 5, p. 11).

Let us now return to the 1927–28 data. Five distinct age-groups are concerned, viz.: the four year-classes 1925, 1924, 1923, and 1922, and the composite group which includes all fishes of the years prior to 1922. Arguing on the indications arrived at above, we can make some progress if asked to predict what will happen during the next few seasons. We will consider each age-group in turn:—

(A) Year-class 1925.

Members of this class, as 3-zoned 3-ringed individuals, formed 16·5% during the season 1927–28. It will be observed that this percentage was considerably greater than that for similar-aged fish in any of the preceding seasons, indicating that the year-class 1925 is likely to prove a highly successful one. We should expect that during the season 1928–29, when the fish will be 4-zoned 4-ringed, the percentage will prove appreciably higher—perhaps from two to three times that shown in 1927–28. In the following season of 1929–30, when the members of this same year-class will be 5-zoned 5-ringed, we may look for a percentage greater even than that of 1928–29—perhaps amounting to 50% of the total sample. In the next season (1930–31), when an age of 6-zones 6-rings will be reached, we may expect to witness the beginning of a decline in importance, which decline will in subsequent seasons become more and more pronounced.

(B) Year-class 1924.

Members of this class, as 4-zoned 4-ringed individuals, formed 19·2% during the season 1927–28, a value which compared fairly favourably with that for fishes of corresponding age in previous seasons. We should expect in 1928–29 a somewhat increased percentage, say approaching 25%. In the following season (1929–30) the first evidence of a falling-off in numbers would be anticipated, for the fishes will then have become 6-zoned 6-ringed. In the next season (1930–31) the percentage will probably have become reduced to an amount hardly large enough to be considered an important element of the catches.

(C) Year-class 1923.

Fishes of this class, as 5-zoned 5-ringed individuals, comprised 30·4% during the season 1927–28. This percentage must be regarded as the highest likely to be reached by this year-class. The first signs of depletion are to be looked for in 1928–29, although the percentage then reached should still form an appreciable constituent of the samples. In 1929–30, a further reduction would be expected, while in 1930–31 this year-class will probably cease to be more than nominally represented.

(D) Year-class 1922.

This year-class had already passed its zenith in 1927–28, so that in 1928–29 it cannot be expected to enter much into the landings.

(E) Year-classes of 1921 and earlier years.

As with year-class 1922, these year-classes had in 1927–28 already passed out of the stage when they could be considered likely to continue as important constituents of the landings.

If we take as a criterion of relative importance a percentage of 10%, we can, from the observations made under (A) to (E), suggest the future season during which each of the year-classes represented in 1927–28 will cease to be an important element of the samples :—

Year-classes of 1921 and earlier years	During	season	1928–29
Year-class 1922	,,	,,	1928–29
Year-class 1923	,,	,,	1929–30 or 1930–31
Year-class 1924	,,	,,	1930–31
Year-class 1925	,,	,,	1931–32 or 1932–33

Thus by 1932–33, i.e. five seasons hence, practically the whole of the stock represented in this season of 1927–28 will have been replaced by new stock.

It is important to realise, however, that no consideration of the sample data for any given season can yield the slightest information concerning the proportion of new year-classes which will appear in the future. But, by watching the actual percentage of 3-zoned 3-ringed fishes in each season, we can obtain advanced warning of the part likely to be played by a newly arrived year-class. If the percentage of 3-zoned 3-ringed fishes is unusually high, we may expect fishes of that year-class to become a leading constituent of the landings during the next two seasons at least ; if, on the other hand, 3-zoned 3-ringed fishes are relatively few, we shall not expect great subsequent yield from that year-class.

Age Composition in Relation to Density of Landings.

In the preceding section we endeavoured to predict the proportions of the different year-classes in samples of future seasons. We have next to discuss the probable effects of these changes in proportion on the density of commercial landings. At this stage it is necessary for us to recall that in our age-estimates we are dealing with percentages and not absolute values. Thus to determine the numerical abundance of fishes of a given year-class in a particular season, we must interpret our age-percentages in terms of the absolute density of fish—in our case, the average weight per landing by the steamers. With these two sets of data available, let us try first to sum up the situation during the season 1927–28, when the average weight per landing rose to a new high level. (See table on p. 13.) We can safely conclude that the good landings in that season were not due to the year-classes 1920 and 1921, for the former had at that time become seriously depleted, while the latter had been poorly represented during the two previous seasons when most would be expected from it. Evidence seems in favour of the view also, that year-class 1922 was of minor importance ; had it been one of appreciable success we should not have expected the average weight per landing in 1926–27, when fishes of this class were 5-zoned 5-ringed, to have fallen so low as 16 cwt. Our attention is thus attracted particularly to year-classes 1923, 1924, and 1925. Of these three, year-class 1923 had already given promise in 1926–27 of being a more important one than its immediate predecessors of 1921 and 1922, and the possibility of an increase in its significance in 1927–28 was suggested in an earlier Report. (Ford, **2**, p. 291.) Here again, however, the low average landing in 1926–27 does not support the view that year-class 1923 was an outstanding success like that of 1920, although it must be regarded as a considerable improvement on year-classes 1922 and 1921 on account of its importance during 1927–28.

Turning next to year-class 1924, we note that its members, as 4-zoned 4-ringed fishes during the season 1927–28, contributed 19·2% towards the high average landing of 46·6 cwt. We must therefore regard this year-class as of at least average importance, and expect it to yield a satisfactory quota to catches of the immediate future. The percentage of 6·3 in 1926–27 when the fishes of the class were 3-zoned 3-ringed, however, did not arouse unusually high expectations.

The third of the classes to be considered is that of 1925 which appeared for the first time in appreciable numbers in 1927–28. Here we have very real hopes of a new highly successful group which in the first year of appearance constitutes a percentage of 16·5% of a high seasonal yield.

We are now in a position to attempt a forecast for the forthcoming season of 1928–29. On the indications considered above, we should expect the following :—

1. A decline in the abundance of the fairly rich year-class 1923.
2. An increase in the fairly rich year-class 1924.
3. An increase in the rich year-class 1925.

We should, under the circumstances noted, expect that the total increase resulting from (2) and (3) would more than counterbalance the decrease due to (1). That is to say, so far as the old stock is concerned, there should be a better available supply of fish in 1928–29 than in 1927–28. Furthermore, an additional new element, the 1926 year-class, should appear as 3-zoned 3-ringed fishes, but no forecast can, at present, be offered concerning the extent to which this may be expected. Altogether, then, so far as the available supply of fish is concerned, the prospects for the season 1928–29 would appear favourable.

Early and Late Seasons.

It is well known that at Plymouth, as elsewhere, the season is sometimes early, sometimes late. Any form of observation which would give a reliable indication of the time at which good fishing might be expected in an impending season, would, therefore, be of material practical utility.

We know that, at Plymouth, the shoals which arrive in the winter are concentrating for spawning. It is reasonable to think that such a physical factor as the temperature of the sea will influence the development and ultimate maturation of the roes and milts, and, in consequence, will have its effect on the time at which the fishes approach the spawning-grounds. Since the year 1921, regular observations of temperature at certain hydrographical stations in the Plymouth area have been made by Dr. Atkins and Mr. Harvey of the Laboratory Staff. We may safely use the data on temperature at a depth of 10 metres at Station E_1 (ca. 10 miles S.W. of the Eddystone) as an approximation to the temperature conditions prevailing over the Plymouth herring fishing-grounds (*vide* Ford, **2**, p. 287). In Fig. 6 the temperatures during the winter months are expressed in the form of smoothed curves drawn to fit the data.

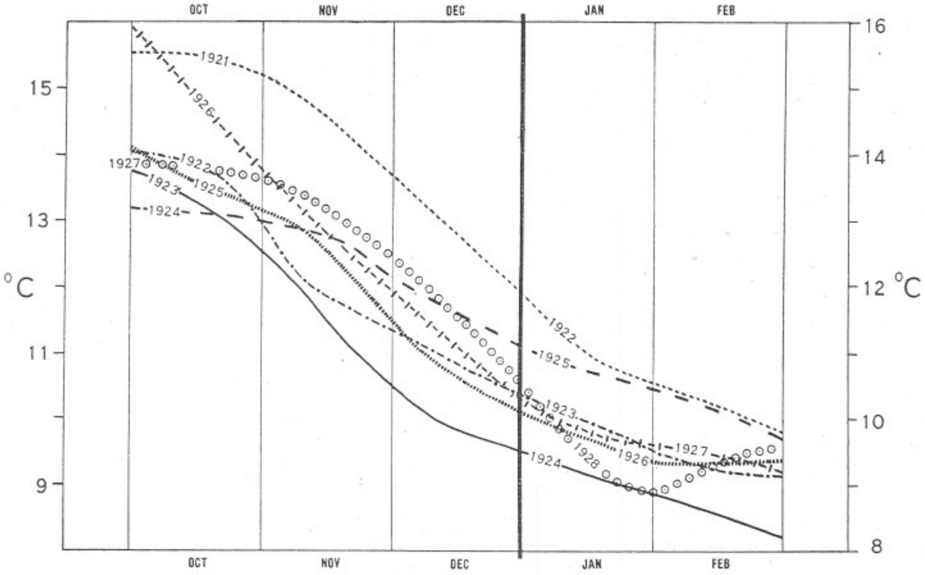

FIG. 6.—Temperatures at 10 metres depth at Hydrographical Station E_1.

From the curves in Fig. 6, the following average values for the seven seasons have been determined :—

Date.	Nov. 1st.	Dec. 1st,	Jan. 1st.	Feb. 1st.
Average temp. (°C)	13·5	11·9	10·5	9·6

Comparing the records for individual seasons with the above averages, we see at once that during 1921–22 the temperatures were much above the normal throughout the months of November, December, and January, whereas during 1923–24 they were consistently below the normal. It is of immediate interest to examine the monthly landings of herrings during these two markedly abnormal years. For this purpose, the landings by motor-drifters are the more convenient, for these vessels are at work during November, whereas the steamers rarely arrive in numbers until December. Here are the data of landings by motor-drifters during the two seasons 1921–22 and 1923–24 :—

	Total Weight of Fish Landed by Motor-Drifters. (Cwt.)		
Season.	November.	December.	January.
1921–22	293	2,103	4,325
1923–24	23,492	23,840	17,325

The contrast between these two sets of data is striking. In the first place it is seen that the total landed during November was almost negligible in 1921–22 but of real importance in 1923–24. This observation becomes of additional interest when it is realised that in the month of November, during each of the remaining five of the series of seven seasons, the total weight landed never once exceeded 9000 cwt., nor was it less than 4000 cwt. In the second place it is seen that in 1921–22 the greatest quantity of fish was landed as late as January, whereas in 1923–24 the best catches were taken in November and December.

There appears to be no evidence that these two facts can be entirely explained by differences in intensity of fishing due to the number of vessels working in the two seasons, or to varying weather conditions. Turning to the temperature records, therefore, it is interesting to notice that the temperature range during January, 1922, corresponded with that prevailing during the greater part of November, 1923. From this we may well suppose that catches are likely to be considerably better in waters *below* 12° C. than in waters *above* 12° C. in temperature.

Referring once more to Fig. 6, we see that the temperatures prevailing during the season 1924–25 are interesting in that the curve, like those for 1921–22 and 1923–24, is a departure from the normal, although of a different character. The water during late December and the whole of January was appreciably warmer than usual. Thus on January 1st, 1924, the temperature was about 11·1° C. compared with the normal of 10·5° C., and on February 1st it was still as high as 10·5° C., compared with the normal of 9·6° C. Comparing the average weight of fish per landing by the steamers during December, 1924, and January, 1925, we find that the average was higher during the latter month (Dec., 1924=20·3 cwt., Jan., 1925=50·7 cwt).. That is to say, superior catches coincided with a temperature lower than about 11·1° C.

From these observations concerning three seasons abnormal so far as temperature is concerned we may, therefore, draw up an experimental progress report regarding the yield of the fishery with respect to the temperature of the sea :—

Temperature °C.	Expected Yield.
Above 13	poor.
13–12	improving.
12–11	fair.
Below 11	good.

Assuming that this report is sound, we can, from the temperatures representing the average conditions for the seven seasons (given on p. 19), deduce a hypothetical "normal" time table of fishing. In Fig. 7, a smooth curve has been drawn to pass through the calculated average temperatures, from which we can determine the dates at which the criterion temperatures are reached :—

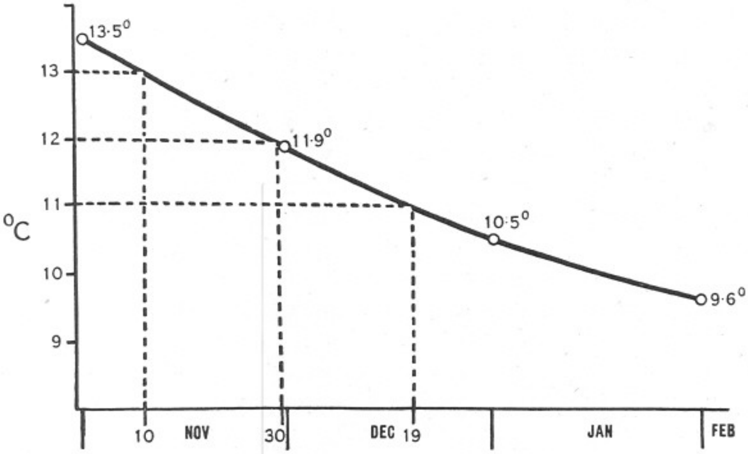

FIG. 7.—Average temperatures at 10 metres depth at Hydrographical Station E_1, based on the seven seasons' data given in Fig. 6. The dates at which 13° C., 12° C. and 11° C. are reached are indicated.

13° C.	12° C.	11° C.
November 10th.	November 30th.	December 19th.

We should therefore expect fishing normally to be poor until November 10th ; improving from November 11th to November 30th ; fair from December 1st to December 19th, and to become really satisfactory on December 20th.

Future Investigations.

In the above sections an attempt has been made to demonstrate the application of the study of the age of herrings, and the temperature conditions on the fishing-grounds to the question of the prediction of future fisheries. It has been shown that advanced knowledge of the probable abundance of fish in a future season can be obtained by the study of the age of fishes in earlier years in conjunction with statistical data on market landings. Clearly, then, similar work should be carried out in the seasons which are to come in order to verify or improve upon the conclusions so far reached. With regard to the prediction of a "time table" of fishing, there is good reason to advocate the observation of temperature over the fishing-grounds at short intervals, from, say, the beginning of November onwards, so that more precise data may be obtained concerning the coincidence of fishing results with water temperature.

It is hardly necessary to point out that there are factors likely seriously to influence local fishing which in these pages have not been taken into account at all, such as variations in strength and direction of winds; the changing tides, or the phases of the moon. While we know with certainty that gales frequently prevent the smaller vessels from leaving harbour, and that wind and tide materially affect actual fishing operations, we do not, as yet, possess much knowledge concerning the effect of such factors on the fish themselves. Conceivably, it is possible that fish may be present in the vicinity in good quantity, although few can be caught. For instance, do fish react to a period of calm sea over the time of "dead" tides ?—Do they, as one experienced skipper suggests, keep to the bottom owing to the resulting clearness of the water ? If a wind now arises, will it "stir the fish" and so cause better fishing ? Is an offshore (north-easterly) wind bad for fishing ? Does the light of a full moon induce the fish to take to the deeper layers ? Such questions as these remain to be solved, but the solutions will be hard to accomplish on account of the practical difficulties in observation.

There is also the question of the particular local grounds on which fish are plentiful in one year, or during one part of the season, and not in another. Why, for example, are fish located comparatively far up Channel towards Brixham, in one season, and away down Channel to the westward of Plymouth in another ? Can these variations be accounted for and thus predicted ? It is suggested that the study of growth from scale-measurements, and the comparisons between fishes from different parts of the Channel and south-western district will lead to a fuller knowledge of the origin and movements of the herring shoals visiting Plymouth, and that this information should ultimately indicate the particular local grounds likely to be frequented by shoals of known character. This accomplished, the further work of anticipating the future stock for these particular grounds can be undertaken. In this connection the study of fishes landed at Brighton, Brixham, Mevagissey, Newlyn, Padstow, and Milford, during the past few years has provided data of immediate value.

Finally, there remains the study of the circumstances which control the survival of the yearly broods of young herrings resulting from the spawning of the visiting shoals, for until we are fully acquainted with these facts, we cannot foretell what amount of new stock will arrive in a future season. This necessitates the detailed investigation of the history of the fish from the egg until the age of three years is reached, and, also, of the physical and other conditions which determine the number of fishes which will survive to enter the adult shoals. It is only in this way that we can arrive at an explanation of the amazing success of some year-classes and the complete failure of others; while, as has already been shown, knowledge in advance of outstanding year-classes is also knowledge in advance of fishing prospects.

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3. Hodgson, W. C. "Preliminary Note on Experiments concerning the Selective Action of Drift Nets." Journal du Conseil., Vol. II, No. 3, 1927.

4. Wallace, W. "First Report on Young Herring in the Southern North Sea and English Channel—Part I." Min. Agric. Fish., Fishery Invest., Ser. II, Vol. VII, No. 4, 1924.

TABLE I.

Length Distribution (cm.).

Sample.	Date. 1927	Total No. of Fishes	Lower Limit.	Lower Quartile Q_1	Median Q_2	Upper Quartile Q_3	Upper Limit.
1	Oct. 17	100	23·5	24·6	25·4	26·2	28·5
2	Nov. 10	110	24·5	26·0	26·6	27·5	30·5
3	Dec. 2	110	21·5	25·0	26·0	27·1	30·5
4	Dec. 8	110	23·5	24·9	25·9	27·4	29·5
5	Dec. 14	100	22·5	24·4	25·6	26·6	29·5
6	Dec. 21	100	22·5	24·1	25·2	26·5	29·5
7	Dec. 30	100	22·5	24·4	25·3	26·6	30·5
	1928						
8	Jan. 2	110	24·5	25·9	26·7	27·6	29·5
9	Jan. 17	100	21·5	23·5	24·7	26·1	30·5
10	Jan. 28	100	22·5	24·1	26·0	27·4	29·5
11	Mar. 3	100	22·5	25·2	26·4	28·1	31·5

TABLE II.

		PERCENTAGE AGE COMPOSITION.											
Sample.	Date. 1927	2	3	3–4	4	4–5	5	5–6	6	6-old.	Older than 6	?	Total No. of Fish in Sample.
1	Oct. 17	4	41	–	14	–	23	1	8	–	9	–	100
2	Nov. 10	–	–	–	15	4	29	5	14	–	32	1	100
3	Dec. 2	–	25	–	14	–	19	1	18	–	23	–	100
4	Dec. 8	–	21	1	18	2	31	1	8	1	17	–	100
5	Dec. 14	–	27	–	23	1	25	2	12	–	10	–	100
6	Dec. 21	–	7	–	25	–	29	3	19	3	13	1	100
7	Dec. 30	–	21	–	24	1	29	1	7	3	14	–	100
	1928												
8	Jan. 2	–	1·8	–	15·5	0·9	43·6	0·9	10·0	0·9	26·3	–	110
9	Jan. 17	–	33	–	23	–	29	1	5	1	8	–	100
10	Jan. 28	–	13	1	16	2	39	1	7	–	20	1	100
11	Mar. 3	–	11	–	12	–	36	1	8	4	27	1	100

Herring Investigations at Plymouth. VI. Winter Herrings Caught off the Sussex Coast and in the Great West Bay during the Years 1924 to 1927.

By

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Naturalist at the Plymouth Laboratory.

With 2 Figures in the Text.

CONTENTS.

INTRODUCTION.

As explained in Part I of this series of Reports (Ford, **1**, p. 238) it was thought that the study of herrings landed at other ports would provide information bearing upon the question of the origin and migrations of the shoals visiting Plymouth during the winter. The examination of the appreciable number of such samples obtained, however, has yielded results which are of interest in themselves, apart from their application to the question of the Plymouth fishery. In this paper, an account is given of the study of herrings landed at Hastings and Brighton from off the Sussex coast, and at Brixham from the Great West Bay. It is necessary to point out that the sampling was not specifically designed for such a study, so that due allowance for this fact must be made in drawing conclusions as to the progress of the local fisheries.

I am indebted to the following gentlemen for their kindness in forwarding samples to Plymouth :—

	Samples from
Mr. Edward Page, Chief Fishery Officer, Sussex. .	Hastings.
Mr. H. W. Jordan of Brighton	Brighton.
Mr. T. B. Lovell of Brixham	Brixham.

HERRINGS CAUGHT OFF THE SUSSEX COAST.

During the months of October, November, and December, herrings caught in drift or standing nets in local waters by small craft are landed at ports or on beaches along the Sussex coast. A total of 9 samples taken in this area during the seasons 1924 to 1927 was examined, and data collected regarding length, age, growth, sexual condition, and average number of vertebræ.

Condition of Gonads (Roes and Milts).

The examination of the gonads showed that the samples consisted overwhelmingly of " full " fishes, with occasional ripe, spent or immature individuals. Actual spawning, therefore, would hardly be expected to occur until at least the end of December. The youngest fishes (3-zoned 3-ringed) possessed well-advanced gonads, so that it is reasonable to suppose that first spawning may commonly occur during the third winter of life in the scaled condition.

Average Length.

The values of the median (Q_2) and quartiles (Q_1 and Q_3) for each sample are given in Table I on page 39. The range in length of the middle 50% (Q_3–Q_1) may again be used as a convenient index of the commonest sizes (cf. Ford, III, p. 287). It is seen that Q_1 varied from 22·1 cm. to 23·2 cm., and Q_3 from 23·8 cm. to 24·7 cm. ; that is to say, fishes of the 22, 23, and 24 cm. groups always comprised at least 50% of each sample. It was shown in Part III (Ford, **1**, p. 287) that the Plymouth winter fishery is centred chiefly upon herrings of the 25, 26, 27, and 28 cm. groups, so that here on the Sussex coast the fishery is based upon much smaller fishes.

Age Composition of Samples.

The estimates of age from scale readings are given in Table II on page 40 in the form of percentages and in graphic form in Fig. 1. It is clear that, throughout, the bulk of a sample was made up of 3-zoned 3-ringed or 4-zoned 4-ringed fishes. This suggests that, in each season, the landings include a considerable proportion of new stock, and, also, that much of the old stock remaining from a previous season either does not subsequently return to the district or evades capture by the local nets.

It will be seen that whereas in 1924, 1925, and 1926, 4-zoned 4-ringed herrings were appreciably more numerous than the 3-zoned 3-ringed ones, in 1927 the reverse was the case, for in a sample taken on November 1st, 1927, at Brighton, 70% consisted of year-class 1925. The abundance of herrings of this particular year-class during the winter of 1927 is an interesting observation, for the same phenomenon was observed at Plymouth.

Length for Age.

In view of the importance of the 3-zoned and 4-zoned fishes, the average length and individual variation of individuals in these two age-groups are given below :—

Age.	Date.	Port of Landing.	No. of fishes in each of the following 7 length groups (cm.).							Total No.	Average length. cm.	Year. class.
			20	21	22	23	24	25	26			
3-zoned 3-ringed	Dec. 9th 1924	Plymouth*	–	2	23	8	1	–	–	34	22·7	1922
	Oct. 19th, 1925	Brighton	–	8	5	1	–	–	1	15	22·3	1923
	Nov. 10th, 1925	Brighton	–	3	5	2	2	–	–	12	22·75	1923
	Dec. 1st, 1925	Brighton	–	11	12	7	3	–	–	33	22·6	1923
	Nov. 1st, 1926	Brighton	–	4	9	7	2	–	–	22	22·8	1924
	Nov. 4th, 1926	Brighton	–	4	13	6	1	–	–	24	22·7	1924
	Dec. 2nd, 1926	Brighton	–	3	6	4	–	–	–	13	22·6	1924
	Dec. 10th, 1926	Hastings	–	–	13	5	2	–	–	20	22·95	1924
	Nov. 1st, 1927	Brighton	–	1	15	39	14	1	–	70	23·5	1925
4-zoned 4-ringed	Dec. 9th, 1924	Plymouth*	–	–	6	9	9	–	–	24	23·6	1921
	Oct. 19th, 1925	Brighton	–	8	21	29	10	–	–	68	23·1	1922
	Nov. 10th, 1925	Brighton	1	2	15	29	9	2	2	60	23·4	1922
	Dec. 1st, 1925	Brighton	–	–	9	10	6	1	–	26	23·5	1922
	Nov. 1st, 1926	Brighton	–	–	11	23	16	3	–	53	23·7	1923
	Nov. 4th, 1926	Brighton	–	–	8	23	22	2	–	55	23·8	1923
	Dec. 2nd, 1926	Brighton	–	–	5	30	22	3	–	60	23·9	1923
	Dec. 10th, 1926	Hastings	–	–	1	23	28	6	1	59	24·2	1923
	Nov. 1st, 1927	Brighton	–	–	2	8	3	2	–	15	23·8	1924

* Caught off Newhaven.

It is sufficient at this stage to point out that the average lengths shown above are markedly less than the corresponding values for herrings landed at Plymouth (cf. Ford, **1**, Part III, p. 293).

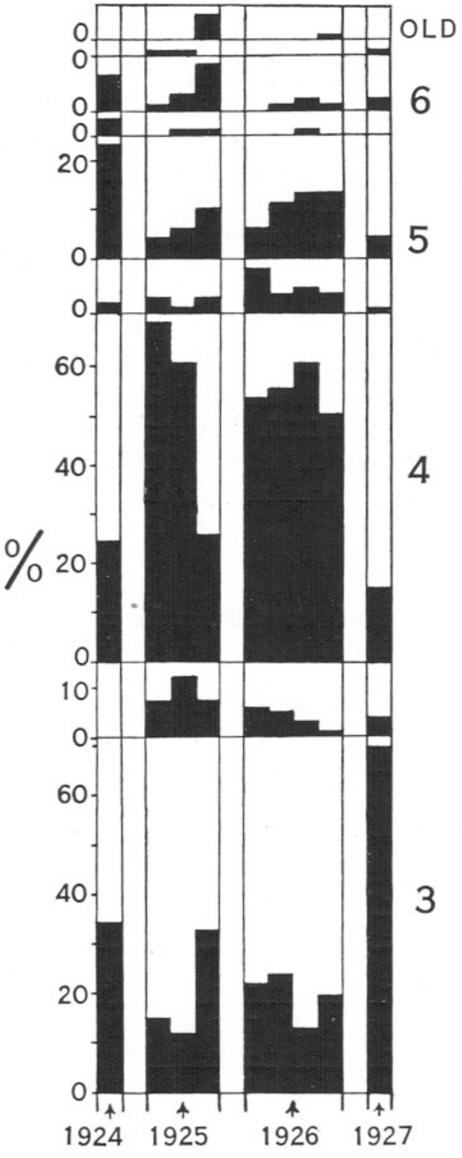

FIG. 1.—Age composition of samples from off Sussex coast.

Samples percentages are shown as small vertical blocks. The age classes are as follows :—

3	3-zoned 3-ringed.
4	4-zoned 4-ringed.
5	5-zoned 5-ringed.
6	6-zoned 6-ringed.
old	Zones and rings exceeding 6.

The "interval" classes are 3 or 4, 4 or 5, etc.

Length at Formation of First Winter-ring.

In the consideration of herrings taken in the Sussex district, data on the length (l_1) at the formation of the first winter-ring are of particular interest, for such information bears directly upon the question of the degree to which the herring stock is indigenous to the English Channel or is augmented from the Southern North Sea. Moreover, as already emphasized in previous reports, precise knowledge of the magnitude and variation of l_1 is essential if reliable comparisons of growth are to be made. In Tables III and IV on pages 40, 41, values of l_1 for 3-zoned 3-ringed fishes and 4-zoned 4-ringed fishes are given. The variation, not only from individual to individual, but from sample to sample, is seen to be large in both series. Under such circumstances there appears little justification for attaching great significance to the absolute value of any form of average.

We will examine the data for the 4-zoned 4-ringed fishes. It is evident that the dispersion of the variates over the total range of variation in l_1 differs appreciably from season to season. The samples of 1925 are distinct from those of other years in that they contain a high proportion of herrings with l_1 say from 7 cm. to 9 cm. Now it will be recalled that Hodgson (**2**, p. 16) recognises a "Southern North Sea Type" of herring (l_1=8 cm.), which he regards as distinct from "Channel" herrings (l_1=12 cm.). In January, 1926, from his study of the scales of herrings landed at Boulogne (*vide* Hodgson, **3**, p. 342), Hodgson concluded that North Sea fish of his Southern Type were spawning along with Channel fish at that time. Under this hypothesis of two distinct types of herrings in the eastern section of the English Channel, it is conceivable that, periodically, Southern North Sea Type herrings may visit the English side of the Channel as well as the French. Such, for instance, would account for the high proportion of fish with l_1 from 7 cm. to 9 cm., in the above Sussex samples during the winter of 1925. Possibly, in other years, this phenomenon is not so marked in extent. A yearly variation in the proportions of the two types would also account for the seasonal differences in dispersion of the variates over the total range in l_1 among the samples taken. This question will, however, receive further attention at a later stage.

Growth subsequent to Formation of First Winter-ring.

In Part I (Ford, **1**, p. 249) it was shown that the data on the growth of 4-zoned 4-ringed fishes caught off the Sussex coast during the seasons 1924 to 1926 could be summarised in the form of five mathematical equations :—

$$l_2 = \cdot 59 l_1 + 11\cdot 70 \quad \ldots\ldots\ldots \quad (1)$$
$$l_3 = \cdot 504 l_2 + 12\cdot 80 \quad \ldots\ldots\ldots \quad (2)$$
$$l_4 = \cdot 774 l_3 + 6\cdot 71 \quad \ldots\ldots\ldots \quad (3)$$
$$l_3 = \cdot 277 l_1 + 18\cdot 92 \quad \ldots\ldots\ldots \quad (4)$$
$$l_4 = \cdot 221 l_1 + 21\cdot 28 \quad \ldots\ldots\ldots \quad (5)$$

An illustration was also given of the way these equations might be used to compare the growth of the Sussex fishes with that of fishes of a similar age from a different locality. In the present instance, they will be utilised to compare the data with the growth-characters of Hodgson's "Southern North Sea Type." In **2**, page 16, Hodgson shows diagrammatically the size at each year, which is :—

cm.

l_1	l_2	l_3	l_4
8	16	20–21	23

Using equation (1) above, we find the value of l_2 for l_1 of 8 cm. :—

$$l_2 = \cdot 59 l_1 + 11\cdot 70 \quad \ldots\ldots\ldots \quad (1)$$
$$= \cdot 59(8) + 11\cdot 70 \quad \ldots\ldots\ldots \quad (2)$$
$$= 16\cdot 4 \text{ cm. (compare with Hodgson's } l_2 = 16 \text{ cm.).}$$

Using equation (4) above, we find the value of l_3 for l_1 of 8 cm. :—

$$\begin{aligned} l_3 &= \cdot277 l_1 + 18\cdot92 \ldots\ldots\ldots \quad (4) \\ &= \cdot277(8) + 18\cdot92 \\ &= 21\cdot1 \text{ cm. (compare with Hodgson's } l_3 = 20\text{–}21 \text{ cm.).} \end{aligned}$$

Using equation (5) above, we find the value of l_4 for l_1 of 8 cm. :—

$$\begin{aligned} l_4 &= \cdot221 l_1 + 21\cdot28 \ \ldots\ldots\ldots (5) \\ &= \cdot221(8) + 21\cdot28 \\ &= 23\cdot0 \text{ (compare with Hodgson's } l_4 = 23 \text{ cm.).} \end{aligned}$$

These results are sufficiently in accord to say that fishes with $l_1 = 8$ cm. caught off the Sussex coast are remarkably similar in growth to those on which Hodgson based his " Southern North Sea Type."

Let us now consider Hodgson's " Channel Type." A total of 36 4-zoned fishes of length 24 cm. examined by him from Brighton on January 4th, 1924, was found to show an average l_1 of 12·34 cm. Using equation (5) above, we find the value of l_4 for l_1 of 12·34 cm. :—

$$\begin{aligned} l_4 &= \cdot221 l_1 + 21\cdot28 \ \ldots\ldots\ldots (5) \\ &= \cdot221(12\cdot34) + 21\cdot28 \\ &= 24\cdot0 \text{ cm. (compare with Hodgson's } l_4 = 24\cdot0 \text{ cm.).} \end{aligned}$$

This provides reason for arguing that fishes with l_1 about 12 cm. caught off the Sussex coast resemble those of the " Channel Type " of Hodgson. Thus both Southern Northern Sea Type and Channel Type are satisfied by the same growth equations. In other words, so far as growth is concerned, the initial difference between the values of l_1 is, of itself, sufficient to account for the subsequent differences between the values of l_2, l_3, and l_4 in the two types. Expressing this in another way, it may be said that the particular growth conditions which induce 8 cm. whitebait to develop into 4-zoned 4-ringed fishes of the Southern North Sea Type would induce 12·35 cm. whitebait to develop into 4-zoned 4-ringed fishes of the Channel Type ; there is no necessity to assume any difference between growth conditions.

Movements of Shoals.

It is convenient to discuss the movements of the shoals by commencing the migratory cycle with the fish on the local grounds in the winter. We have seen that, here, they are " full " fishes approaching maturity. We may, therefore, assume that they will eventually move off to spawn. The observations of Wallace (**5**) and Hodgson (**3**) indicate a spawning region in the neighbourhood of Cap d'Antifer, this locality being not unduly remote from the Sussex coast. Fishes actually spawning were obtained by

Hodgson (3) in January, 1926. After spawning, however, facts are less clear. If we follow le Gall (**4**) we shall now draw a distinction between the Channel Type and the Southern North Sea Type of fish ; we shall contend that the latter retire into the North Sea while the former remain within the English Channel. Regarding this phase, some interest is attached to a sample of fishes caught off Brighton on May 22nd, 1926. Of a total of 65 there were 32 showing 5-zones and 4-rings to the scale. These 32 individuals, then, had obviously been 4-zoned 4-ringed fishes in the winter of 1925, and at the time of capture had commenced their 5th summer zone. In length they varied from 22 cm. to 25 cm, about a mean of 23·9 cm., and their values of l_2, l_3, and l_4 closely approximated to those of the Southern North Sea Type. Thus, while we may freely admit the possibility of an interchange of fish between the North Sea and the English Channel, as le Gall suggests, we must also admit that fishes of the Southern North Sea Type of growth can and do remain within the Channel after spawning.

We have now to consider the nature of the shoals which arrive off the coast of Sussex in the winter. To what extent are they composed of stock which had previously visited the area, and from whence comes any new stock ? We have seen that each season, the bulk of the fishes caught are either 3-zoned 3-ringed or 4-zoned 4-ringed individuals. Thus, the 4-zoned 4-ringed fish do not subsequently return, or at least, are not captured. The 3-zoned 3-ringed ones, may, however, do so in the next year constituting the 4-zoned 4-ringed fishes of the new season. In addition, there must certainly be an important influx of new stock. It is possible that 4-zoned 4-ringed fishes which have never previously visited the area may arrive, conceivably in part from the North Sea, while undoubtedly 3-zoned 3-ringed individuals approaching first maturity will make their appearance for the first time.

Racial Considerations.

As stated in Parts I and II, the methods adopted in the present series of studies enable the worker to investigate growth and migrations without thought of " races " or " racial composition " ; at any rate, in the initial stages. Probably no better illustration could be given of the great practical difficulties to be faced by an investigator who sets out to determine the races represented, than that afforded by the situation in the area under consideration. Here, in brief, are the facts as they are known at present:—

(A) Off the Sussex coast during the winter.

There is a mixed assemblage of " full " fishes which, judging by the values of l_1 deduced from scale measurements, had grown from " whitebait " varying from 5 cm. to 17 cm. in length. There is no uniformity from sample to sample or from season to season as regards the proportions of the fishes from the different whitebait; sometimes those derived from small whitebait are the more numerous, at other times, those derived from the larger.

(B) On the spawning-ground in the neighbourhood of Cap d'Antifer.

Here, again, there is a mixed assemblage of fishes actually spawning together (Hodgson, **3**). The scale-characters of the spawners are similar to those of the fishes mentioned under (A) above. The larvæ resulting from this spawning may or may not be direct crosses between fishes with small l_1 and those with large l_1. The larvæ themselves may be transported by water movements through the Straits of Dover into the North Sea, and thence to the Thames Estuary where they enter into the composition of the shoals of whitebait along with young herrings from the North Sea itself (Wallace, **5**, p. 7).

(C) Off the Sussex coast during the summer.

Shoals of herrings comparable in growth with those of (A) and (B) above may be met with, still providing evidence of mixture.

In view of these facts it would seem essential that in accumulating statistical material for racial analysis, the age, total length, magnitude of l_1 and stage of maturity would all have to be taken into account. Furthermore, if the "race" data are to be statistically reliable, the number of individuals in each statistical class must be fairly large. This means that the original samples of the mixed catch, taken at random, must be very large. An instance may be given from present records. A random sample of 100 fishes taken off Brighton on November 10th, 1925, included 60 of age 4-zone 4-rings. Of these 60, there were 29 having a total length of 23 cm. The values of l_1 for these 29 individuals were :—

l_1 (cm.).

7·5	8·5	9·5	10·5	11·5	12·5
2	12	8	4	–	3

Thus, if we wished to obtain reliable data (e.g. on Average No. of Vertebræ or No. of Keeled Scales) concerning 4-zoned 4-ringed fishes of length 23 cm., for different values of l_1, the original random sample would need to be many times larger than the one actually taken. To complete the amount of additional routine work occasioned by thus largely increasing the size of the random sample, especially when sampling itself must be frequent, would be beyond the capacity of a single investigator.

HERRINGS CAUGHT IN THE GREAT WEST BAY.

The herrings landed at Brixham during the winter form an interesting study, but care must be taken to ascertain the particular locality from which the fishes have been landed. In some seasons the shoals upon which the Plymouth steam fishery is being concentrated are located well up Channel off Start Point and a certain number of East Country steamers may elect temporarily to use Brixham as their port of landing. Apart from this, however, drift and standing nets are every year worked still farther to the eastward in the Great West Bay, and it is concerning these fish that information is given below. Between November, 1925, and January, 1927, eight samples were sent to Plymouth from Brixham, where they were submitted to the usual routine examination.

Condition of Gonads (Roes and Milts).

The following is a summary of the data on the degree of maturity of the gonads :—

		No. of Fishes in each of the 4 following classes :—				
Sample.	Date.	Immature. Hjort's Stage 1.	Full. Hjort's Stages IV & V.	Ripe. Hjort's Stage VI.	Spent. Hjort's Stage VII.	Total No. of Fishes.
5.	Oct. 27th, 1926	–	109	1	–	110
1.	Nov. 9th, 1925	–	75	2	2	79
2.	Nov. 26th, 1925	3	114	3	–	120
6.	Nov. 23rd, 1926	–	116	2	–	118
3.	Dec. 16th, 1925	–	56	34	5	95
7.	Dec. 14th, 1926	–	113	4	3	120
4.	Jan. 4th, 1926	–	9	12	43	64
8.	Jan. 20th, 1927	–	17	93	–	110

These samples indicate that we have to deal with December and January spawning fishes. Sample 8, of which about 90% were fully mature ♂ and ♀ fishes, was from a total catch of 20 crans made by a motor-drifter off Exmouth, so that it is reasonable to suspect that actual spawning occurred at no great distance from this locality. As in the case of the Sussex herrings, the youngest fishes (3-zoned 3-ringed) gave evidence that they would spawn in their third winter of life in the scaled condition.

Average Length.

It will be seen from the values of Q_1, Q_2, and Q_3 given in Table V on page 41, that there are appreciable differences in length distribution between samples. Thus, on November 26th, 1925, the middle 50% (Q_3–Q_1) included fishes of the 22 cm., 23 cm., and 24 cm. length groups, whereas on January 4th, 1926, it comprised those of the 25 cm., 26 cm., and 27 cm. groups. Sample 3, taken on December 16th, 1925, on the other hand, is bimodal as regards length. No very useful purpose, therefore, is served by conducting a more detailed analysis of the raw length data as they stand. There is, however, one point of interest which was referred to in Part III (**1**, p. 287). It was there shown that in the Plymouth samples there was a tendency for the average length to be lower towards the eastwards. (i.e. from Plymouth towards Start Point). The present series of samples was taken from catches made in waters still farther to the eastward, and it will be observed that there is a further depression in the lower quartile length (Q_1). That is to say, a larger proportion of smaller fishes is likely to be landed from the Great West Bay than from the area covered by the Plymouth fishery. It is thus possible that in the intermediate waters to the eastward of Plymouth some overlap of fish-population may occur.

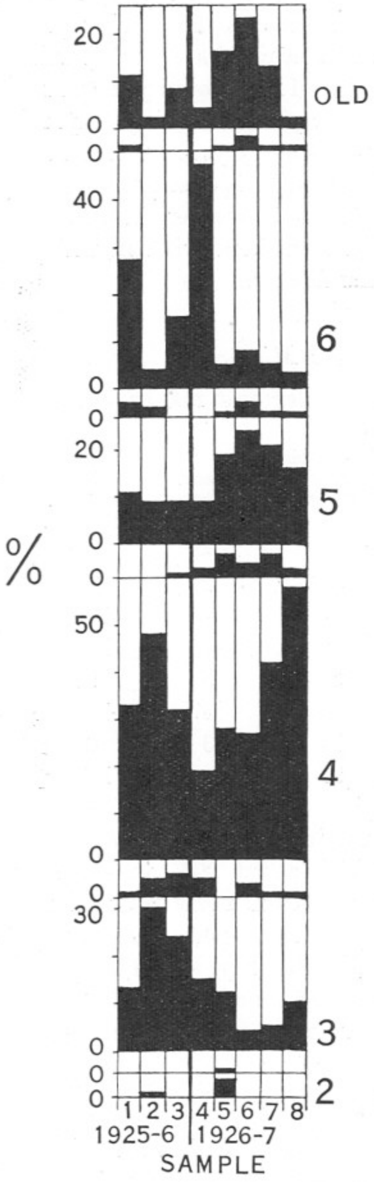

Fig. 2.—Age composition of samples from Great West Bay.
Details as in Fig. 1 (page 28).

Age Composition of Samples.

Estimates of age from scale-readings, expressed in the form of percentages, are given in Table VI on page 42, and recorded graphically in Fig. 2.

In the first place it will be noted that the 4-zoned 4-ringed class was always well represented; in 7 of the total of 8 samples it was actually the dominant constituent. The samples of the season 1925–26 also showed an appreciable percentage of 3-zoned 3-ringed fishes. In this heavy proportion of young fishes, then, the situation resembles that experienced off the Sussex coast (*vide* p. 27).

Unlike the Brighton and Hastings samples, however, the present ones include an appreciable percentage of individuals older than 4-zones 4-rings. Of these older individuals, those of the year-class 1920, as 6-zoned 6-ringed fishes, were important during the season 1925–26, and again as 7-zoned 7-ringed fishes in the following season, 1926–27. On the other hand, fishes of the 1921 class were scarce either as 5-zoned 5-ringed in 1925–26 or as 6-zoned 6-ringed in 1926–27. In these respects, the situation is reminiscent of Plymouth during the corresponding period (*vide* Ford, **1**, Part III, p. 289).

The contribution each season made by the year-classes concerned is shown in convenient summary form below :—

Season.	Date of sample.	Percentage of sample in each of 5 year-classes.									
		1920		1921		1922		1923		1924	
1925–26	Nov. 9	26·6	as 6-zoned 6-ringed fishes.	11·4	as 5-zoned 5-ringed fishes.	32·9	as 4-zoned 4-ringed fishes.	12·7	as 3-zoned 3-ringed fishes.	—	
	Nov. 26	4·0		9·0		48·0		30·0		—	
	Dec. 16	15·3		9·4		31·8		28·2		—	
	Jan. 4	47·2		9·4		18·9		15·1		—	
1926–27	Oct. 27	11·0	as 7-zoned 7-ringed fishes.	5·0	as 6-zoned 6-ringed fishes.	19·0	as 5-zoned 5-ringed fishes.	28·0	as 4 zoned 4-ringed fishes.	12·0	as 3-zoned 3-ringed fishes.
	Nov. 23	20·0		8·0		24·0		27·0		4·0	
	Dec. 14	10·0		5·0		21·0		42·0		5·0	
	Jan. 20	2·0		3·0		19·0		58·0		10·0	

In Part III (Ford, **1**, p. 291), in summarising the evidence to be drawn from the results of age-estimations on Plymouth fishes during the season 1926–27, the following was stated : " . . . that the 1920 class showed definite signs of a decline in intensity, and that the 1921 class gave no signs that it would ever become important, while of the younger classes, that of 1923 was the most promising."

An examination of the data summarised in the table above shows that this might equally well be written concerning the samples from the Great West Bay.

Length for Age.

Fishes of the same age differ so much in total length that little practical significance can be attached to the average length calculated from the lumped sample data throughout one season for a given year-class. Interesting evidence, however, is to be obtained from the data for individual samples :—

3-ZONED 3-RINGED FISHES.

Season.	Date.	No. of Fishes in each of 8 Length groups (cm.). 20	21	22	23	24	25	26	27	Total No.	Year-class.
1925–26	Nov. 9	–	–	1	1	1	3	2	2	10	1923
	Nov. 26	2	2	12	8	4	1	1	–	30	
	Dec. 16	–	4	7	10	2	1	–	–	24	
	Jan. 4	–	–	3	–	–	1	4	–	8	
1926–27	Oct. 27	–	–	3	4	1	1	2	1	12	1924
	Nov. 26	–	–	–	–	–	2	1	1	4	
	Dec. 16	–	–	1	1	–	–	3	–	5	
	Jan. 20	–	1	2	4	1	2	–	–	10	

It is seen that there is a tendency for the individuals to group themselves in two parts of the total range in length, viz. in the 22 and 23 cm. groups and again in the 25 and 26 cm. groups. This is instructive, for if we turn to the Sussex samples (p. 27) we see that the 3-zoned 3-ringed fishes largely fall into the 22 cm. and 23 cm. length groups; on the other hand, if we refer to the Plymouth samples of 1926–27 (Ford, **1**, Part III, p. 293) we see that the 3-zoned 3-ringed fishes largely fall into the 25 and 26 cm. length groups.

4-ZONED 4-RINGED FISHES.

		No. of Fishes in each of 9 Length groups (cm.).									Total	Year-
Season.	Date.	21	22	23	24	25	26	27	28	29	No.	class.
1925–26	Nov. 9	–	2	1	5	4	8	5	–	1	26	1922
	Nov. 26	1	11	15	13	4	4	–	–	–	48	
	Dec. 16	–	11	5	3	4	3	1	–	–	27	
	Jan. 4	–	–	1	2	4	2	1	–	–	10	
1926–27	Oct. 27	–	1	1	20	5	1	–	–	–	28	1923
	Nov. 26	–	–	1	13	5	7	1	–	–	27	
	Dec. 16	–	–	8	16	14	3	1	–	–	42	
	Jan. 20	–	2	13	33	9	1	–	–	–	58	

In this age-group, fishes group themselves in different parts of the total length range in different samples. Here again it is interesting to compare the data with those from Sussex and Plymouth. In the Brixham sample of November 26th, 1925, of a total of 48 individuals, 39 fall into the 22, 23, and 24 cm. length groups. This compares favourably with a sample of sixty 4-zoned 4-ringed fishes taken off Brighton on November 10th, 1925, of which 53 fall into the same length groups. In contrast with this, it is to be noted that during the season 1925–26 at Plymouth, 4-zoned 4-ringed fishes grouped themselves largely in the 25, 26, and 27 cm. groups, whereas here in the Great West Bay samples, fishes of a similar age exceeding 26 cm. in length are few in number.

5-ZONED 5-RINGED FISHES.

As already stated above, fishes of this age (1921 year-class) were relatively unimportant during the season 1925–26. In the following season, however, when the members of the 1922 year-class had become 5-zoned 5-ringed fishes, the proportion was appreciable. The length-distribution was as follows:—

		No. of Fishes in each of 6 Length groups (cm.).						Total	Year-
Season.	Date.	23	24	25	26	27	28	No.	class.
1926–27	Oct. 27	3	6	6	1	3	–	19	1922
	Nov. 26	–	2	12	3	5	2	24	
	Dec. 16	1	3	9	5	3	–	21	
	Jan. 20	2	6	9	2	–	–	19	

Compared with the Plymouth fishes of the same year-class during the same season (*vide* Ford, **1**, Part III, p. 293) the above are distributed over a lower part of the length-range.

6-ZONED 6-RINGED FISHES.

Members of the 1920 year-class as 6-zoned 6-ringed fishes were of considerable importance in three of the four samples taken during the season of 1925–26. Data on length are as follows :—

Season.	Date.	No. of Fishes in each of 7 Length groups (cm.).							Total No.	Year-class.
		25	26	27	28	29	30	31		
1925–26	Nov. 9	1	3	10	3	2	–	1	21	1920
	Nov. 26	–	1	3	–	–	–	–	4	
	Dec. 16	2	5	4	1	1	–	–	13	
	Jan. 4	3	6	5	7	4	–	–	25	

The fishes of the 1920 year-class caught during the season 1925–26 at Plymouth (*vide* Ford, **1**, Part III, p. 293) were largely grouped in the 26, 27, 28, and 29 cm. length groups, and of an average length of 27·9 cm.

7-ZONED 7-RINGED FISHES.

During the season 1926–27, a fair proportion of the 1920 class, now as 7-zoned 7-ringed individuals, was present in the samples :—

Season.	Date.	No. of Fishes in each of 4 Length groups (cm.).				Total No.	Year-class.
		25	26	27	28		
1926–27	Oct. 27	–	1	6	4	11	1920
	Nov. 26	–	8	10	2	20	
	Dec. 16	3	7	–	–	10	
	Jan. 20	–	2	–	–	2	

The above are certainly distributed over a lower part of the length range than corresponding fishes landed at Plymouth.

From the foregoing considerations of length for age it seems permissible to draw two conclusions concerning the herrings landed from the Great West Bay :—

(*a*) Of the fishes of the younger age-groups (3-zoned 3-ringed and 4-zoned 4-ringed) many are of a length similar to that for fishes of corresponding age caught off the Sussex coast.

(*b*) Herrings of the older age-groups (5-zoned 5-ringed and older) are generally distributed over a lower part of the total length range than similar aged fishes taken in Plymouth waters during the same period.

Length at Formation of First Winter-ring (l_1).

In view of the relative importance in the catches of 4-zoned 4-ringed fishes, the lengths l_1, l_2, and l_3 have been calculated from scale-measurements. The data on l_1 for each sample are as follows :—

4-ZONED 4-RINGED FISHES.

Season.	Date	L1. Central values of 12 classes (cm.).												Total No. of fishes.	Year-class.
		6·5	7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5	17·5		
1925–26	Nov. 9	–	2	3	1	4	1	2	6	2	2	1	1	25	1922
	Nov. 26	2	5	13	10	4	4	–	2	1	–	–	–	41	
	Dec. 16	1	2	9	1	2	1	1	3	1	–	–	–	21	
	Jan. 4	–	–	2	1	1	3	1	1	1	–	–	–	10	
1926–27	Oct. 27	–	2	5	3	2	2	3	5	4	1	–	–	27	1923
	Nov. 26	–	–	2	1	5	2	3	3	5	5	–	1	27	
	Dec. 16	–	1	–	3	7	2	7	3	6	7	2	–	38	
	Jan. 20	–	–	2	4	10	5	7	6	8	6	4	1	53	

Thus, as has been seen at Brighton and Plymouth, the value of l_1 for fishes in the Great West Bay varies over a considerable range. The sample of November 26th, 1925, is interesting in that there was an appreciable number of fishes with l_1 from 7·5 to 9·5 cm. This reminds us of the situation at Brighton. More frequently, however, l_1 is comparatively large, often exceeding 12·5 cm., and in this respect, the samples are in closer agreement with those of similar-aged fishes landed at Plymouth.

Average Number of Vertebræ.

Data on the number of vertebræ for herrings of the samples under consideration have already been given in Part II (Ford, **1**). If we refer to Fig. 1 on page 274 of that paper, we see that the average number of vertebræ for these Great West Bay fishes is intermediate between that for Plymouth and that for Sussex herrings. This fact is instructive in view of the results of age and growth comparisons described above.

From the results discussed in the preceding pages, then, we see that the herrings landed from the Great West Bay during the winter present an interesting problem for further study. Efforts must be directed towards an understanding of why, on the one hand, there is a measure of similarity to the Sussex fish, and, on the other, to those landed at Plymouth. By a detailed systematic sampling it should be possible to arrive at a fuller knowledge of the migratory cycles of the herrings frequenting the English Channel generally, and, incidentally, therefore, to throw light on these movements as they concern the Plymouth shoals in particular.

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TABLE I.

Herrings caught off Sussex Coast.

				Length Distribution (cm.).				
Sample No.	Date.	Port of Landing.	Total No. of Fishes.	Lower Limit.	Lower Quartile Q_1.	Median Q_2.	Upper Quartile Q_3.	Upper Limit.
	1924							
1.	Dec. 9	Plymouth*	161	21·5	22·6	23·6	24·7	26·5
	1925							
2.	Oct. 19	Brighton	128	20·5	22·1	23·0	23·8	26·5
3.	Nov. 10	,,	100	20·5	22·8	23·5	24·3	27·5
4.	Dec. 1	,,	118	21·5	22·4	23·4	24·7	29·5
	1926							
5.	Nov. 1	Brighton	120	21·5	22·9	23·5	24·2	26·5
6.	Nov. 4	,,	100	21·5	22·9	23·6	24·3	25·5
7.	Dec. 2	,,	100	21·5	23·2	23·9	24·6	25·5
8.	Dec. 10	Hastings	120	22·5	23·2	24·0	24·6	26·5
	1927							
9.	Nov. 1	Brighton	102	21·5	23·1	23·9	24·6	25·5

* This sample was from a steamer landing at Plymouth. Nets were shot off Newhaven on the journey westward to Plymouth from Lowestoft.

TABLE II.

Herrings caught off Sussex Coast.

percentage age composition (zones and rings).

Sample No.	Date.	3	3–4	4	4–5	5	5–6	6	6–old	Older than 6.	Total No. of Fish.
	1924										
1.	Dec. 9	34	–	24	2	23	3	7	–	–	100
	1925										
2.	Oct. 19	15	7	68	3	4	–	1	1	–	100
3.	Nov. 10	12	12	60	1	6	1	3	1	–	100
4.	Dec. 1	33	7	26	3	10	1	9	–	5	100
	1926										
5.	Nov. 1	22	6	53	9	6	–	–	–	–	100
6.	Nov. 4	24	5	55	4	11	–	1	–	–	100
7.	Dec. 2	13	3	60	5	13	1	2	–	3	100
8.	Dec. 10	20	1	59	4	13	–	1	1	–	100
	1927										
9.	Nov. 1	70	5	15	1	4	–	2	–	–	100

TABLE III.

Herrings caught off Sussex Coast.

3-zoned 3-ringed Fishes.

Sample.	Date.	L_1. Central Valves of 10 Length classes (cm.).									
		7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5
	1925										
2.	Oct. 19	–	1	–	3	–	3	2	5	–	–
3.	Nov. 10	–	–	1	–	2	3	3	2	–	1
4.	Dec. 1	–	–	2	3	10	5	4	2	4	1
	1926										
5.	Nov. 1	–	–	–	2	6	4	2	3	3	–
6.	Nov. 4	–	–	3	3	5	6	4	1	2	–
7.	Dec. 2	1	1	1	1	4	3	1	–	1	–
8.	Dec. 10	–	–	2	2	3	3	1	3	4	1

TABLE IV.

HERRINGS CAUGHT OFF SUSSEX COAST.

4-ZONED 4-RINGED FISHES.

L_1. Central Valves of 13 Length classes (cm.).

Sample.	Date.	5·5	6·5	7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5	17·5
	1924													
1.	Dec. 9	–	–	2	1	5	4	5	6	1	–	–	–	–
	1925													
2.	Oct. 19	1	1	10	24	9	9	7	3	2	–	–	–	–
3.	Nov. 10	–	1	6	22	13	8	2	5	–	–	1	–	–
4.	Dec. 1	–	1	2	7	5	–	2	5	1	–	–	–	–
	1926													
5.	Nov. 1	–	–	3	5	5	9	15	4	3	1	2	–	–
6.	Nov. 4	–	–	1	3	4	12	15	5	5	–	–	–	–
7.	Dec. 2	–	–	–	4	6	11	11	8	6	6	5	1	–
8.	Dec. 10	–	–	–	3	7	2	12	11	8	5	3	2	1

TABLE V.

HERRINGS CAUGHT IN THE GREAT WEST BAY.

			LENGTH DISTRIBUTION (CM.).				
Sample No.	Date.	Total No. of Fishes.	Lower Limit.	Lower Quartile Q_1.	Median Q_2.	Upper Quartile Q_3.	Upper Limit.
	1925						
1.	Nov. 9	79	22·5	25·8	27·0	28·0	31·5
2.	Nov. 26	120	20·5	22·7	23·7	24·9	28·5
3.	Dec. 16	94	21·5	22·75	24·0	26·4	29·5
	1926						
4.	Jan. 4	64	22·5	25·1	26·6	28·1	29·5
5.	Oct. 27	110	21·5	24·2	25·1	27·1	29·5
6.	Nov. 23	118	23·5	25·3	26·2	27·2	28·5
7.	Dec. 14	120	22·5	24·5	25·4	26·1	27·5
	1927						
8.	Jan. 20	110	21·5	23·9	24·6	25·25	26·5

TABLE VI

Herrings caught in the Great West Bay.

PERCENTAGE AGE COMPOSITION (ZONES AND RINGS).

Sample No.	Date.	2	2–3	3	3–4	4	4–5	5	5–6	6	6–old	Older than 6	Total No. of Fish.
	1925												
1.	Nov. 9	–	–	12·7	1·3	32·9	–	11·4	2·5	26·6	1·3	11·4	79
2.	Nov. 26	1	–	30	4	48	–	9	2	4	–	2	100
3.	Dec. 16	–	–	28·2	5·9	31·8	1·2	9·4	–	15·3	–	8·3	85
	1926												
4.	Jan. 4	–	–	15·1	3·8	18·9	1·9	9·4	–	47·2	–	3·8	53
5.	Oct. 27	4	1	12	–	28	5	19	1	5	3	16	100
6.	Nov. 23	–	–	4	3	27	3	24	3	8	2	23	100
7.	Dec. 14	–	–	5	1	42	5	21	1	5	2	13	100
	1927												
8.	Jan. 20	–	–	10	1	58	2	19	1	3	–	2	100

Herring Investigations at Plymouth. VII. On the Artificial Fertilisation and Hatching of Herring Eggs under known Conditions of Salinity, with some Observations on the Specific Gravity of the Larvæ.

By

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Naturalist at the Plymouth Laboratory.

INTRODUCTION.

IT has previously been shown (Ford, **1**, p. 284) that herrings with fully ripened roes or milts form a considerable proportion of the landings by commercial drifters at Plymouth during December and January. Although naturally-deposited spawn has rarely been obtained from the sea-bottom in the district, the fact that newly-hatched larvæ occur in abundance provides evidence that actual spawning occurs locally. It has also been shown that from the end of September onwards, ripe fishes may be taken in stop-nets in Plymouth Sound, and even in sprat-seines in the estuarine waters of the River Tamar. A number of interesting and important questions is suggested by these observations. For example, do the ripe herrings which frequent the River Tamar actually spawn there, and if so, are they morphologically identical with those which spawn at sea, or are they of a different character ? Would eggs deposited in the river be successfully fertilised and able to endure the periodic freshening of the water ? Are the morphological characters of the offspring in any way dependent upon the environmental conditions under which they are developed ?

It is a comparatively simple process to express the eggs from a recently-dead ripe female on to glass plates, and then to fertilise them with the milt from a ripe male. The fertilised eggs develop quite normally in sea-water and give a good yield of apparently healthy and active larvæ. Unfortunately, however, it seems impossible at present to rear these larvæ beyond the stage at which the yolk-sac is absorbed. Thus, while we can readily obtain a batch of larvæ from the artificial crossing of parents of known character, we cannot, as yet, rear the young to the stage at which they exhibit the adult characters used to define the parents. It will be realised that this fact is a serious hindrance to progress along the lines of investigation under consideration, and it is to be hoped that some worker will soon be able to devote time to discover how successfully to rear herring larvæ. The problem will need undivided attention ; it is not one likely to be solved as an incidental to other investigations.

There are, however, important initial points which can be cleared up by experiments in artificial fertilisations alone. During the winter of 1928–29 some preliminary tests were made, having as their object the determination of the effects of changing salinity as one leading environmental factor. The nature of the experiments and the results obtained are discussed below.

EXPERIMENT A.

During the evening of January 14th, 1929, eggs from a ripe female herring 27·5 cm. in length were expressed on to four glass plates and fertilised by the milt of a ripe male 27·3 cm. in length. Laboratory tank-room sea-water was used throughout the fertilisations, at a temperature of 7·5° C. On the morning of January 15th the plates with the developing eggs were transferred, one to each of the following tanks :—

Tank 1. 8000 cc. Laboratory tank-room sea-water.
Tank 2. 4000 cc. ,, ,, +4000 cc. fresh-water from tap.
Tank 3. 2000 cc. ,, ,, +6000 cc. ,, ,,
Tank 4. 1000 cc. ,, ,, +7000 cc. ,, ,,

The salinities of these tanks, determined by titration against silver nitrate solution according to the method recommended by Harvey (**2**, p. 37), were as follows :—

Tank 1.	37·8
Tank 2.	18·8
Tank 3.	9·34
Tank 4.	4·75

Rough sketches of the disposition of the eggs on each plate were made, indicating unfertilised eggs. These sketches provided a means of ascertaining at a glance if any eggs died subsequent to transference to the test tanks. Each tank was aerated continuously throughout the experiment. On January 25th, larvæ began to hatch out in Tanks 1 and 2, and, on the following day, in the remaining Tanks 3 and 4. No eggs had apparently died during the experiment. Within the next two or three days the whole of the eggs in Tanks 1 and 2 hatched out, but in Tanks 3 and 4, particularly the latter, many of the larvæ appeared rather weakly, for although they broke through the egg-envelope, they were unable to wriggle entirely free from it. On February 4th, ten days after the first larvæ were hatched, a few individuals still remained alive in all four tanks.

There was, however, a greater percentage of survivors in Tanks 1 and 2 than in Tanks 3 and 4.

Thus, eggs fertilised in tank-room sea-water will survive exposure to freshened sea-water of a salinity at least as low as 5, and give rise to living larvæ, some of which will remain alive in that water until the absorption of the yolk has reached an advanced stage.

EXPERIMENT B.

On January 22nd an attempt was made to obtain successful fertilisations, not only in sea-water of normal salinity, but in different mixtures of salt and freshwater. A female of 28·5 cm. and a male of 28·3 cm. were used for the experiment and operations conducted in water of from 9°–10° C. The following were the results :—

Plate No.	Water used. Sea-water.	Fresh (tap).	Salinity.	Result.
1	2000 cc.	—	37·8	Successful fertilisation.
2	1000 cc.	1000	19·0	,, ,,
3	250 cc.	1750	4·8	,, ,,
4	125 cc.	1875	2·4	One or two eggs fertilised, remainder unfertilised.
5	—	2000	—	Failure.

Thus, actual fertilisation seems certainly possible in water of salinity of 4·8, and may even be possible in still fresher water down to a salinity of 2·5.

Plates 1, 2, and 3 carrying the successfully fertilised eggs were placed in tanks of water of the following salinities :—

Plate No.	Tank. Sea-water.	Fresh (tap).	Salinity.
1	2000 cc.	—	37·8
2	1000 cc.	1000	19·0
3	250 cc.	1750	4·8

On February 4th larvæ hatched from the eggs on all three plates. That is to say, eggs fertilised in water of salinity as low as 5 will develop in that water and give rise to living larvæ.

Now although the results of these experiments need confirmation and elaboration, they are of immediate local application. If the eggs of herrings taken from the sea are capable not only of being fertilised, but also of undergoing successful incubation in water varying in salinity from 37·8 to 4·8, it is perfectly logical to believe that, so far as salinity is concerned, the fishes experimented with could, if they had been free to choose, have spawned on any suitable ground either outside or within Plymouth Sound or at places some considerable distance up the rivers Tamar and Lynher, with fair chances of a satisfactory brood of larvæ.

SPECIFIC GRAVITY OF LARVÆ.

Herring larvæ in an aquarium filled with ordinary sea-water, when not actually swimming, tend to sink at an appreciable rate. During the course of experiments A and B above, the impression was gained that larvæ in diluted sea-water sank more quickly than those in undiluted, and, in consequence, were more often at the bottom of the aquaria than at the surface. It was therefore decided to make some comparisons between larvæ incubated and reared in different strengths of sea-water, regarding their specific gravity. The method was to determine by trial and error the particular one of a series of brines of known strength in which a larva would remain in equilibrium, neither rising nor falling.

The standard brine used was 100 grammes of common salt dissolved in 500 cc. of tap-water, and the following series of test brines was made up at a temperature of 12° C. :—

Test Brine No.	Standard Brine cc.	Tap-water cc.	Actual Strength of Test Brine.
1	50	50	10 grm. NaCl per 100 cc.
2	47·5	52·5	9·5 ,, ,, ,,
3	45	55	9·0 ,, ,, ,,
4	42·5	57·5	8·5 ,, ,, ,,
5	40	60	8·0 ,, ,, ,,
6	37·5	62·5	7·5 ,, ,, ,,
7	35	65	7·0 ,, ,, ,,
8	32·5	67·5	6·5 ,, ,, ,,
9	30	70	6·0 ,, ,, ,,
10	27·5	72·5	5·5 ,, ,, ,,
11	25	75	5·0 ,, ,, ,,
12	22·5	77·5	4·5 ,, ,, ,,
13	20	80	4·0 ,, ,, ,,
14	17·5	82·5	3·5 ,, ,, ,,

The number of larvæ available for experiment was limited, and no opportunity presented itself later to make further fertilisations, so that the results obtained are tentative. Some difficulty, also, was experienced in actual practice, on account of the intermittent swimming of the larvæ in the test brines; in future tests it might be profitable to employ an anæsthetic.

It soon became evident that the specific gravity of the larva depended upon the amount of unabsorbed yolk in the yolk-sac, newly-hatched larvæ remaining in equilibrium in much stronger brine than larvæ some 10 days old. In the following table the results are given for tests of larvæ of different ages. The larvæ used were all hatched from eggs fertilised and incubated in sea-water of salinity 37·8 :—

Age of larvæ.	No. of larvæ remaining in equilibrium in following test brines :—																		
	2	2–3*	3	3–4*	4	4–5*	5	5–6*	6	6–7*	7	7–8*	8	8–9*	9	9–10*	10	10–11*	11
6 hours or less after hatching	2	1	1	3	2	1	–	4	–	–	–	–	–	–	–	–	–	–	–
24 hours or less after hatching	–	1	1	1	–	3	1	6	3	3	1	–	–	–	–	–	–	–	–
2nd day after hatching	–	–	–	1	1	1	–	1	–	1	1	1	1	1	1	–	–	–	–
3rd day after hatching	–	–	–	–	–	–	–	1	–	2	1	2	1	1	1	1	–	–	–
4th day after hatching	–	–	–	–	–	–	–	–	–	1	1	–	–	1	1	1	–	–	–
9–10 days after hatching	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	3	2	–	–
10–12 days after	–	–	–	–	–	–	–	–	–	–	–	1	–	1	1	1	3	1	2

In consequence of this difference of specific gravity due to the quantity of unabsorbed yolk, it will be appreciated that, in attempting to draw comparisons between larvæ fertilised and/or incubated in different strengths of sea-water, it is essential that the larvæ compared should be of similar age and of the same parentage. In the present series, such material was limited, but the results tabulated below are interesting and suggestive although they need confirmation :—

LARVÆ FROM EXPERIMENT B (ABOVE).

Age of larvæ.	Larvæ hatched from eggs fertilised and incubated in water of following salinity.	No. larvæ remaining in equilibrium in following test brines.														
		2	2–3	3	3–4	4	4–5	5	5–6	6	6–7	7	7–8	8	8–9	9
Maximum of 24 hrs. after hatching	37·8	1	2	–	2	1	–	–	2	–	–	–	–	–	–	–
	19·0	–	–	–	–	–	–	1	1	2	1	–	3	–	1	–
	4·8	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1

LARVÆ FROM EXPERIMENT A (ABOVE).

Age of larvæ.	Larvæ hatched from eggs fertilised in sea-water of salinity 37·8 but incubated and reared in water of following salinity.	No. larvæ remaining in equilibrium in following test brines :—												
		7–8	8	8–9	9	9–10	10	10–11	11	11–12	12	12–13	13	13–14
9–10 days after hatching.	37·8	1	–	1	1	3	2	–	–	–	–	–	–	–
	19·0	–	–	–	2	1	1	–	–	–	–	–	–	–
	4·8	–	–	–	–	–	–	–	–	1	1	–	1	1

---

* The interval classes 2–3, 3–4, etc., indicate that the larvæ concerned do not remain in equilibrium in any one of the series of brines. Thus, a larvæ entered in Class 2–3 rises in brine 2 and falls in brine 3.

These results suggest that by incubating eggs in freshened water and allowing the newly-hatched larvæ to develop under the same salinity conditions, the specific gravity becomes reduced at a rate dependent upon the degree of freshening of the water.

The phenomenon of changing specific gravity of larvæ, due either to the gradual absorption of yolk during development or to the fact that incubation was carried out in freshened water, or both, would seem to merit attention. Herring larvæ being appreciably heavier than the water in which they live will tend to sink to the sea-bottom unless they persistently swim towards the surface; upward progress will be less easy for newly-hatched larvæ than for older ones on account of their higher specific gravity and their inferior swimming power. Questions relating to horizontal and vertical distribution of herring larvæ at different ages may well be affected by such factors.

In the second place, the differences of specific gravity induced by freshening of the water may conceivably have its effect on the metabolism of the larva, with a resulting morphological reaction. Such would be a highly important matter in all questions relating to racial investigations.

The results of these preliminary experiments, therefore, suggest that a fuller investigation along the lines indicated would be most profitable.

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1. Ford, E. "Herring Investigations at Plymouth. III. The Plymouth Winter Fishery during the Seasons 1924–25, 1925–26, and 1926–27." Journ. Mar. Biol. Assoc., Vol. XV, No. 1, February, 1928.

2. Harvey, H. W. "Biological Chemistry and Physics of Sea-water." Cambridge, 1927.

The Reproductive Organs of the Herring in Relation to Growth.

By

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With 4 Figures in the Text.

THE different organs of an animal do not all grow at one speed. Some develop precociously, and others, like the reproductive system, are delayed for a considerable time in their development, though ultimately they may become very large. In a mature herring about one-fifth of the entire weight consists of reproductive tissues. The different organ-growths are integrated into the growth of the whole body, and one kind of curve will represent both the parts and the whole.

In the herring there are great seasonal changes consequent upon spawning. The weight of the gonads reaches a maximum and then falls abruptly to zero, after which it increases again to the next maximum at the following spawning season. The amplitude of this fluctuation is an increasing one; and, at the suggestion of Dr. J. H. Orton, I have made the following analysis to discover whether a time comes ultimately when the increasing tax of spawning brings about the animal's death. If the successive gonad-maxima go on increasing after the general body-growth has slowed down, this may be the case; on the other hand, if the growth-rate of the gonads is not greater than that of the body in old fishes, it may be assumed confidently that death is due to other causes.

While at Port Erin in 1925 I made a series of weighings and age-determinations which provided data exactly suited to the investigation of this point, on which this paper is based.

MATERIAL.

The samples of herrings used fall into two series, one from the Irish Sea within a radius of twenty miles of the Chickens Lighthouse, to the south of the Isle of Man, locally called *Calf Herrings;* the other from inshore shoals off Port Erin bay, known as *Low Herrings*, which spawn slightly earlier. The principal part of this paper deals with the Calf samples, which were more numerous and extend over the whole spawning season. They were obtained from Scottish steam-drifters at Port St. Mary between August 18th and September 25th, 1925.

Within a few hours of landing the fish were measured and weighed, the gonads removed and weighed also. At the same time scales taken from each fish were placed in numbered watch-glasses, and from these age-determinations were made. Scales with more than seven dark winter-rings were regarded as unreliable in age-determination, and have been disregarded in curve-fitting.

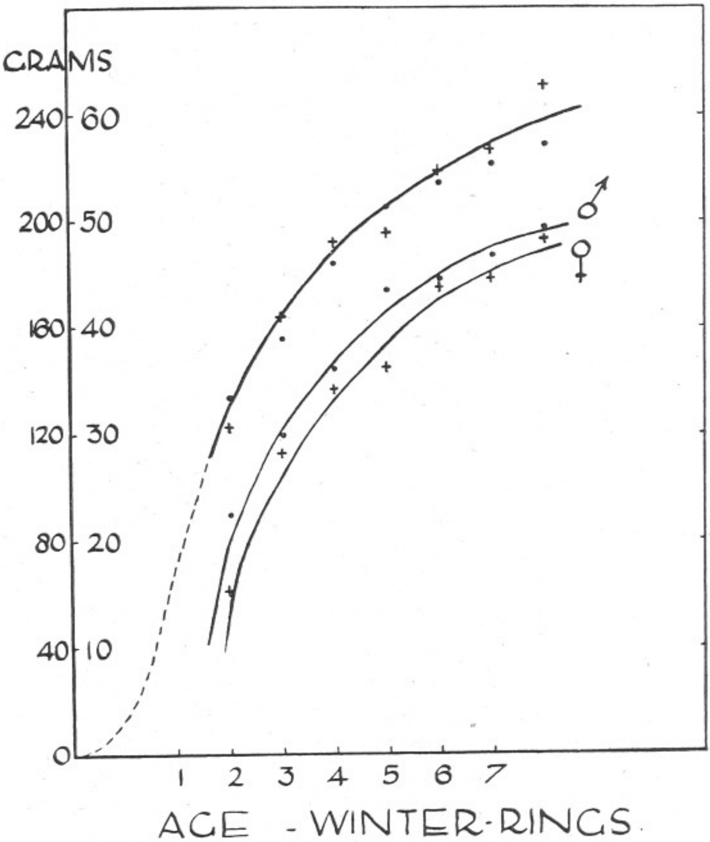

FIG. 1.—Total Body-Weights (upper curve) and Gonad-Weights (lower curves) of Calf herring, plotted against age.

Data for males represented by dots, and for females by crosses.

Fish in other than stages V and VI of maturity could not of course be used, and this, together with the separation of the sexes, reduces the data materially. Tests have been made, however, to show that where conclusions have been drawn, they are mathematically justified. The fact that the curves are not smooth does depend to some extent upon the numbers available, but also very largely on the natural diversity of different year-classes of herrings from the same shoals. From the numbers of each year-class obtained by sampling it is clear that different years offer different chances of survival at least, and probably also of growth; complete homogeneity would not be realized, however great the sample might be.

AGE-FREQUENCY OF CALF HERRINGS.

Year of birth	1918	1919	1920	1921	1922
Frequency	83	83	54	61	80

Subsequent sections refer to the *Calf* samples, unless otherwise stated.

BODY-WEIGHT.

The rate of growth is at its maximum when the fish is about two years old; that is, the point of inflexion of the S-shaped growth-curve occurs at this time. Consequently all the material considered here is situated in the upper portion of the curve, where the growth-rate is continually decreasing. This growth-curve is similar to that of autocatalysis, and has been studied by Pearl (**3**). No attempt has been made here at curve-fitting, so that it is not possible to say whether the growth of the two sexes can be represented by a single curve, or whether they form two distinct curves. It appears from Fig. 1 that they are, at any rate, very close together, if not identical. The females attain a greater weight in these samples, and apparently a greater age also.

GONAD-WEIGHT.

The growth of the gonads, like that of any other organ, can be represented by a curve similar to that for the whole animal. In Fig. 1 the curve for gonad-weight is on four times the scale of the body-weight curve. The former is displaced to the right, owing to the initial delay in gonad development, and is at first steeper than the body-growth curve, but after about seven years (five winter-rings) it maintains a fairly constant relation to the body-weight.

The gonad curve is really discontinuous once spawning has occurred for the first time. At this and subsequent spawning times the gonad-weight falls abruptly to zero, whence it re-develops to reach the next datum on the curve in the following season (Fig. 2). These successive maxima fall on a smooth curve which is independent of the total weight of the body.

The gonads are not the only organs which undergo an annual cycle.

Mr. E. Ford has kindly placed at my disposal extensive data on the liver-weight of the mackerel, which passes through a similar cycle, the maxima appearing just before the spawning season. These maxima also lie on an S-shaped curve. Owing to the difficulty of catching herrings of the same class at all seasons of the year, no investigation has been made of the changes which take place in other tissues of the body, except just before and during the spawning season (Bruce, **1**). It appears, however, that even the muscle tissue is depleted to some extent at this time, and that its growth may also be represented by a rhythmic curve with rising maxima. Thus at least two periodic fluctuations are taking place in the body, whose amplitudes are independent. The total body-weight represents the sum of a differential system of organ-growth.

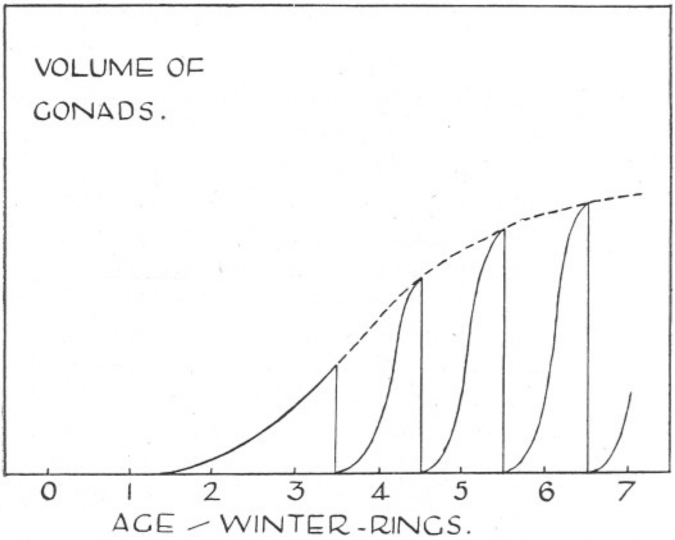

FIG. 2.—Diagram illustrating the discontinuity of gonad development.

RELATION OF GONAD-WEIGHT TO BODY-WEIGHT.

The data were divided into weight-groups at 10 gm. intervals. The figure given for the weight is the mid-point of the group, and differs slightly from the mean within the group (Tables V and VI). In Figs. 3 and 4 it will be seen that the points, though somewhat scattered, show a high correlation between gonad-weight and total body-weight, and that the line which fits the points most closely is nearly straight, The correlation coefficients which are worked out below, approach sufficiently near to unity to enable a straight line to be used as a working approximation.

The relation which is important here is that of gonad-weight to body-weight. Subsequently it will be necessary to deduce approximate gonad-weights from body-weights, so that the line to be determined is the regression of gonad-weight on body-weight. Gonad-weight is the dependent and body-weight the independent variate. This relation, called the regression function, is given by the formula (Fisher, **2**) :—

$$y=\bar{y}-b(x-\bar{x}),$$

where y is the gonad-weight with mean $\bar{y}$, x is the total body-weight with mean $\bar{x}$; and b is a constant to be determined, called the regression coefficient. It gives the slope of the curve.

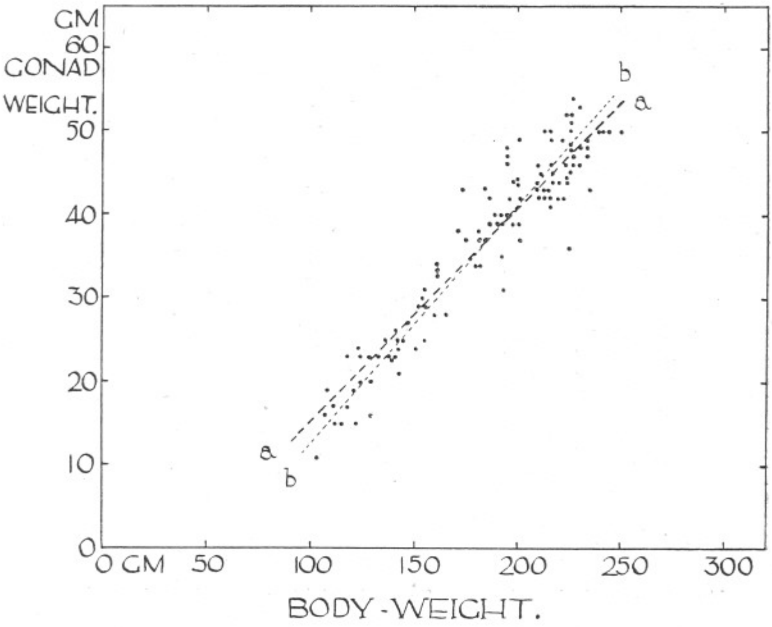

FIG. 3.—Correlation diagram of gonad-weights and body-weights for males of Calf type.

aa. Regression line of gonad-weight on body-weight.
bb. Regression line of body-weight on gonad-weight.

It is important to notice that the regression of body-weight on gonad-weight is not the same as the regression of gonad-weight on body-weight. It would be if the correlation between the two variates were complete (i.e. unity), which it is not. In Figs. 3 and 4 both regression lines are drawn, illustrating the difference. The fact that the regression line evaluated and used below does not appear to fit the points perfectly is liable to deceive unless this distinction is realized.

For the males it is found that

$$^{\sigma}y=\pm 2{\cdot}189\times 5 \text{ gm.} \qquad \bar{y}=37{\cdot}26 \text{ gm.}$$
$$^{\sigma}x=\pm 3{\cdot}973\times 10 \text{ gm.} \qquad \bar{x}=186{\cdot}5 \text{ gm.}$$

The coefficient of correlation (r) between y and x is 0·949. The regression coefficient (b) is estimated by the formula

$$b=r\frac{^{\sigma}y}{^{\sigma}x}=0{\cdot}949\times\frac{2{\cdot}189\times 5}{3{\cdot}973\times 10}=0{\cdot}261$$

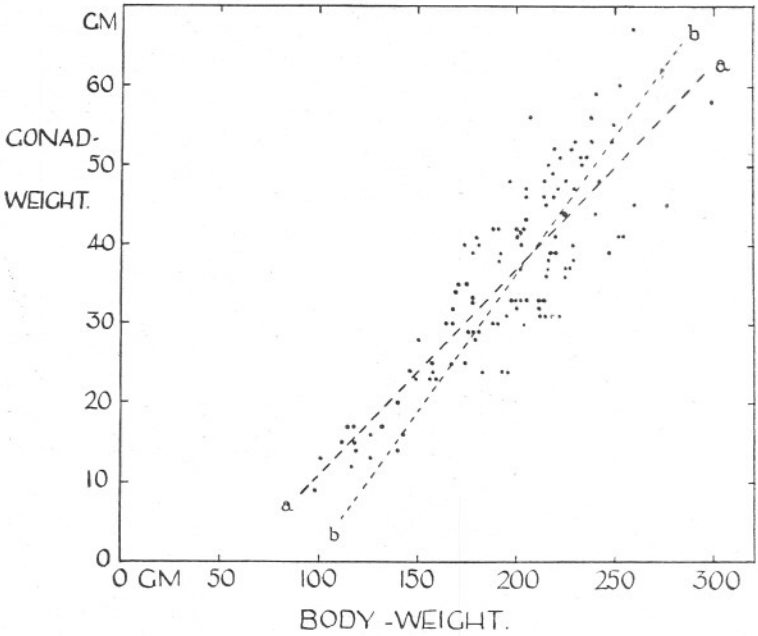

FIG. 4.—Correlation diagram of gonad-weights and body-weights for females of Calf type.

Lettering as in Fig. 3.

Therefore

$$y=37{\cdot}26+0{\cdot}261\,(x-186{\cdot}5)$$
$$=0{\cdot}261x-11{\cdot}5 \text{ gm.}$$

For the females,

$$b=r\frac{^{\sigma}y}{^{\sigma}x}=0{\cdot}876\times\frac{(2{\cdot}407\times 5)}{(3{\cdot}959\times 10)}=0{\cdot}266$$

Therefore

$$y=36{\cdot}33+0{\cdot}266\,(x-197{\cdot}25)$$
$$=0{\cdot}266x-16{\cdot}2 \text{ gm.}$$

Though the very close agreement between the regression coefficients of males and females may be fortuitous, there cannot possibly be a significant difference between the two growth-rates. The constants 11·5 and 16·2, which indicate how far the lines are displaced to the right along the x-axis, differ by nearly 5 gm., and it will be necessary to test the significance of this.

Two 25-gm. groups of values were selected where the mean total weights of males and females are the same.

Take $x=222\cdot5$ gm. (range of weight from 213–237 gm.).

TABLE I.

y		Males.				Females	
gm.	Deviation (d)	Frequency (f)	$f\times d$	$f\times d^2$	f	$f\times d$	$f\times d^2$
30	−15	. .	. .	. .	4	−60	900
35	−10	1	−10	100	6	−60	600
40	− 5	6	−30	150	6	−30	150
45	. .	16	. .	. .	8	. .	. .
50	+ 5	13	+65	325	10	+50	250
55	+10	2	+20	200	2	+20	200
		$n=38$	+45	775	$n=36$	−80	2100
Divided by $(n-1)$ since the numbers are small .			. 1·216	20·95		−2·29	60·00
Correction for mean .			.$(1\cdot216)^2$	1·48		$(-2\cdot29)^2$	5·23
Correction for grouping .			(25× ·0833)	2·08			2·08
Corrected estimate of variance				=17·39			=52·69

Standard Error of the means of y_1 (males) and y_2 (females)$=s$.

$$s^2=\frac{17\cdot39}{38}+\frac{52\cdot69}{36}=0\cdot458+1\cdot463,$$

$$\therefore s=\sqrt{1\cdot921}=\pm1\cdot39 \text{ gm.}$$

Mean $y_1=46\cdot22$ gm. ; and mean $y_2=42\cdot71$ gm.

$$\therefore y_1-y_2=3\cdot51 \text{ gm.}$$

Thus in this case the mean difference between testes and ovaries is about 3·5 gm. The points therefore lie closer together than the average (4·7 gm.); yet this difference is about 2·5 times its own standard error, so that it may be regarded as definitely significant.

Taking two other pairs of values, where $x=199$ gm., we find the difference of the mean gonad-weights to be 6 gm., with a standard error of 1·56 gm. P is therefore rather more than 0·0001, which means that such figures could be explained by coincidence in only one out of ten thousand trials, assuming the samples to be random.

The mean gonad-weights of the whole sample (♂ 37·26, ♀ 36·33 gm.) differ by less than a gram. For this reason it might still be thought that the male and female regression lines of gonad-weight on body-weight are virtually identical. Such confusion arises from the fact that, though the ovaries are lighter than the testes in comparable fishes, the females reach a greater absolute size. The range of ovary weight is thus extended beyond that of testis weight, bringing the mean relatively higher. The total body-weights at which the mean gonad-weights occur (♂ 186·5, ♀ 197·2 gm.) make this clear.

Since the regression functions are used extensively in the following pages, and considerable importance attaches to their reliability, tests have been made to show whether or not the departures from straightness of the lines are significant. These are given in an appendix at the end of the paper. I have to thank Dr. R. A. Fisher for his assistance at this point. His methods have been used throughout this paper, and the sums and calculations are drawn up as nearly as possible on the lines of the examples given in his book (Fisher, **2**). In both sexes of the Calf herring which have been tested, the probability of any departures from linear regression being significant is well below the formal limit (5 per cent.).

Conclusions from Regression Functions.

Certain deductions may be made from this analysis. The males and females have been found statistically distinct in so far that the testes occupy a greater proportion of the total weight than do the ovaries in comparable fishes. The rates of growth of the gonads with respect to body-weight are, however, the same.

The regression lines obtained are approximations to the facts over the range considered. It is not legitimate to produce them to cut the x-axis at 44 and 61 gm., since the real lines are certainly not straight as will be shown below. It is clear, however, that the female gonads lag behind the male at the initiation of development, a lag indicated by $61-44$ gm. For if the two sexes were simultaneous in this respect, either the regression lines would be identical, or they would diverge from a common initial point, with different regression coefficients. This is contrary to the observations made previously.

Nor can the observed sexual difference be due to a difference in specific gravities of testicular and ovarian tissue. If this were the case, the coefficients b_1, b_2 could not be the same. The regression lines would again diverge for increasing values of x, even if they did not have a common origin.*

If the regression equation is applied to the sigmoid gonad curve in Fig. 1, it will be seen how the approximation breaks down if extended beyond the range of observations. By putting successively $y=0$, $x=0$, we should have a curve asymptotic to $-11{\cdot}5$ at the lower end, and reaching the value 0 gm. when $x=44{\cdot}0$ gm. (for the males). This is of course impossible, but it is easily shown that the origin of the curve is near this point, when $x=41$ gm. For instance, if the ratio $\frac{y}{x}$ is calculated, the observed ratios are less than the theoretical values at first, which is to be expected if the origin of the real curve is near this point.

TABLE II.

Age (winter rings)	2	3	4	5	6	7
Observed $\frac{y}{x}\%$	16·46	18·9	19·4	21·2	20·7	21·06
Theoretical $\frac{y}{x}\%$	17·4	18·7	19·9	20·5	20·7	20·9

The gonads thus start to develop in the summer after the first winter ring is laid down, when the males reach a weight of 35 to 50 gm. It is possible that the females have reached a greater size at this time, which would account for the initial difference in gonad-weight, or that the development of their gonads may be delayed somewhat longer. Spawning fishes were not found amongst the Manx herring less than 95 gm. in weight, or having scales with fewer than two winter rings.

"Low" Herrings.

In confirmation of these results, data obtained from samples of the inshore or *Low herring* have been examined in the same way. The data are not so extensive as those for the Calf type, and were collected rather before the height of the spawning season, from July 21st to 29th. They comprise 234 fish, of which 161 were in Stage V, and thus available for comparison with the other samples; 110 were males, and 51 females.

In the same way as before the regressions of gonad-weight on body-weight have been determined. These are not thought to be very reliable,

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* The specific gravities of the fresh gonads of six male and six female herrings about to spawn (Stage V) have been determined from Plymouth material. If anything, the testes are lighter than the ovaries. Sp. Gr. of Testes= 1·07(5); Sp. Gr. of Ovaries= 1·08(4).

particularly in the case of the female, but they offer an excellent check upon those found for the other data. The regression functions are :—

for the males, $y=0{\cdot}21(7)x-10{\cdot}45$ gm.,

and for the females, $y=0{\cdot}21(9)x-20{\cdot}3$ gm.

These are also statistically distinct. The coefficients are again almost the same, though the very slight difference observed is certainly due to coincidence. They are considerably smaller than the same coefficients in the Calf samples, due largely to the earlier stage of maturity found in the present case. Stage V is elastic, embracing for 200 gm. fishes a range of male gonad-weight between 30 and 50 gm. ; for this reason there is a notable difference between the earlier and final grades of ripeness found within it.

AGE.

The rate of growth of the gonads decreases with advancing age ; and in this sense their increase can be correlated with the number of times the fish has spawned. The more numerous the spawnings, the smaller the annual increase of gonad-weight. Such a correlation would, however, be a false one ; for the growth-rate of the gonads is intimately concerned with that of the whole body, which also becomes smaller with advancing age. There is no other connection with the number of spawning seasons. For, if a number of fish of the same weight are taken, their ages will vary over a small range ; and it is possible to show that among these the older fish, which have spawned more often, have gonads just as large as, and no larger than the younger ones, allowances being made for the variations of different year-classes. A comparison of fishes of roughly the same weights, but of different ages, is the only method of approach to this question.

In the following Table the two 25-gm. weight groups (200 and 225 gm.) have been combined to illustrate this point. The range of weight is from 188 to 237 gm. The mean observed ratio $\frac{y}{x}$ is given, and also the theoretical ratio, calculated from the regression formulæ. The differences between these are slight, and there is no marked increase in the observed values in the older year-groups, such as would be expected if the size of the gonads went on increasing after the general growth had practically ceased.

It may be noticed in addition that the material annually spent in building up the gonad is completely made up before the next season.

For four years after spawning the relative size of the gonad continues to increase (see Table on p. 57) ; there it remains almost constant, and its actual weight increases in linear proportion to the body-weight.

The end of these four preliminary seasons, during which the relative fecundity is rising, is not a turning-point in the death-rate, as far as can be ascertained from the numbers in these and subsequent year-classes.

TABLE III.

Age (winter rings)	3	4	5	6	7	8 & above
MALES						
Frequency	—	7	21	20	9	4
Observed $\frac{y}{x}\%$	—	19·8	20·9	20·8	21·2	20·9
Expected $\frac{y}{x}\%$	—	20·4	20·7	21·0	20·9	21·1
Difference	—	−0·6	0·2	−0·2	0·3	−0·3
FEMALES						
Frequency	2	8	14	22	12	3
Observed $\frac{y}{x}\%$	18·3	17·0	18·9	19·6	18·9	17·7
Expected $\frac{y}{x}\%$	18·2	18·2	18·7	19·0	18·9	19·1
Difference	0·1	−1·2	0·2	0·6	0·0	−1·4

TABLE IV.

Age (winter rings)	2	3	4	5	6	7	8 & above
Frequency	80	61	54	83	83	36	37

Both five- and six-ring groups are particularly numerous.

Thus it appears that spawning does not draw on the resources of the fish to a greater extent than can be replaced, with interest, each year. There is no indication of an increasing tax which the fish cannot make up, the effects of which continue to pile up until ultimately they cause its death, in a way that has sometimes been suggested. The growth of the gonads is in harmony with that of the other organs.

There is a notable difference in the absolute sizes of the two sexes. For the Calf type, the mean weight of the females is 197·25 gm., and for the males 186·5 gm. This, however, does not approach the great difference found in the flat-fishes or the whiting. Owing to the uncertainty of age-determination when the rings become crowded, it is not possible to say whether the females attain a greater age also.

I wish to thank Mr. E. Ford for his constant advice, and Dr. R. A. Fisher, F.R.S., for his kindness in going over the manuscript.

SUMMARY.

From two series of samples of different populations of herrings from the neighbourhood of the Isle of Man, data were obtained of the lengths, weights, gonad-weights, and ages of 396 mature fishes. The growths of the whole body and of the gonads were represented by the upper portions of S-shaped curves. The male and female body-weights are nearly the same at any age over the range considered, but the testes of the male are always heavier than the ovaries of the female in such comparable fishes. The females attain a greater size than the males.

The weight of the gonads bears a linear relationship (as a first approximation) to the total weight of the fish over the range of size considered. The regression functions evaluated for the two sexes are

$$y=0{\cdot}261x-11{\cdot}5 \text{ for the males, and}$$
$$y=0{\cdot}266x-16{\cdot}2 \text{ for the females,}$$

where y is the gonad-weight and x the total weight of the fish, both in grams. The difference between the weights of testes and ovaries in male and female fishes of the same size is therefore about 4·7 gm., which is shown to be significant. It cannot be due to specific gravity of growth-rate differences, since the regression coefficient (0·26) is the same for both sexes.

It is suggested that the reproductive organs start to develop in the summer following the laying down of the first winter ring on the scales ; and that the initial handicap in female gonad-weight may be due to the males being smaller than the females at this time.

Confirmation of the conclusions drawn from the Calf herring is given by a similar analysis of the Low herring samples.

By a comparison of fishes of the same weight but of varying ages, it is shown that the annual loss of tissue at spawning is completely made up during the next twelve months, and that death cannot be due to the increasing tax of spawning ultimately exceeding the animal's powers of recovery.

REFERENCES.

1. Bruce, J. R. Biochemical Journal, **18**, Nos. 3 and 4, 1924.
2. Fisher, R. A. Statistical Methods for Research Workers. 2nd Ed., Edinburgh, 1928.
3. Pearl, R. Studies in Human Biology. Baltimore, 1924.

TABLE V.

Correlation Table of Gonad-weight and Total Body-weight for Males of the "Calf" Type.

Total Body-weight. (Grams) = x.

Gonad-weight (grams) = y	105	115	125	135	145	155	165	175	185	195	205	215	225	235	245	255	Total.	Frequency × Deviation.	Frequency × (Deviation)^2.
10	1																1	-5	25
15	1	4	2														7	−28	112
20	1		3		1												5	−15	45
25		1	3	4	6	2											16	−32	64
30						4	2			1							7	−7	7
35							3	1	4	1	1		1				11	0	0
40								1	4	6	2	5	2				20	20	20
45								1	1	3	4	7	8	3			27	54	108
50										1	1	3	7	3	3	1	19	57	171
55													1	1			2	8	32
Total $-n_p$	3	5	8	4	7	6	5	3	9	12	8	15	19	7	3	1	**115**	+52	584
Total excess	−12	−18	−23	−8	−15	−8	−2	+3	+6	+14	+13	+28	+43	+19	+9	+3	+52		
Mean excess	−4·000	−3·600	−2·875	−2·000	−2·143	−1·333	−0·400	+1·000	+0·667	+1·167	+1·625	+1·867	+2·263	+2·714	+3·000	+3·000	0·4522		
Product	48·00	64·80	66·12	16·00	32·14	10·67	0·80	3·00	4·00	16·33	21·12	52·27	97·31	51·57	27·00	9·00	23·51		
Frequency × Deviation	−24	−35	−48	−20	−28	−18	−10	−3	0	12	16	45	76	35	18	7	+23		
Frequency × (Deviation)^2	192	245	288	100	112	54	20	3	0	12	32	135	304	175	108	49	1829		
$n_p(x-\bar{x})(y-\bar{y})$	96	126	138	40	60	24	4	−3		14	26	84	172	95	54	21	951		

Note.—All calculations are made in grouping units, i.e. 10 grams for x and 5 grams for y.

TABLE VI.

CORRELATION TABLE OF GONAD-WEIGHT AND TOTAL BODY-WEIGHT FOR FEMALES OF THE "CALF" TYPE.

TOTAL BODY-WEIGHT. (GRAMS) $= x$.

GONAD-WEIGHT (GRAMS) $= y$	100	110	120	130	140	150	160	170	180	190	200	210	220	230	240	250	260	270	280	290	300	Frequency Total × Deviation		Frequency × (Deviation)²
10	1		1																			2	−10	50
15	1	1	4	3	2																	11	−44	176
20					1																	1	−3	9
25						2	4	4	1	1	1											13	−26	52
30						2		3	2	2	3	3	2									17	−17	17
35								2	5		4	3	2	3								19	0	0
40								1	3	4	5		3	3		3						22	22	22
45												2	3	4	1		1		1			12	24	48
50											1	1	4	4	2							12	36	108
55														2	2	2						6	24	96
60															1	1		1			1	4	20	100
65																	1					1	6	36
Total	2	1	5	3	3	4	4	10	11	7	14	9	14	16	6	6	2	1	1	0	1	**120**	+32	714
Total excess	−9	−4	−21	−12	−11	−6	−8	−10	−1	0	+3	+4	+19	+31	+21	+16	+8	+5	+2	0	+5	+32		
Mean excess	−4·500	−4·000	−4·200	−4·000	−3·667	−1·500	−2·000	−1·000	−0·091	0·0	+0·214	+0·444	1·357	1·937	3·500	2·667	4·000	5·000	2·000	0·0	5·000	0·2667		
Product	40·50	16·00	88·20	48·00	40·33	9·00	16·00	10·00	0·09	0·0	0·64	1·78	25·78	60·05	73·50	42·67	32·00	25·00	4·00	0·0	25·00	8·533		
Frequency × Deviation	−20	−9	−40	−21	−18	−20	−16	−30	−22	−7	0	+9	28	48	24	30	12	7	8	0	10	−27		
Frequency × (Deviation)²	200	81	320	147	108	100	64	90	44	7	0	9	56	144	96	150	72	49	64	0	100	1901		
$n_p(x-\bar{x})\ (y-\bar{y})$	90	36	168	84	66	30	32	30	2	0	0	4	38	93	84	80	48	35	16	0	50	986		

NOTE.—All calculations are made in grouping units, i.e. 10 grams for x and 5 grams for y.

APPENDIX.

These tests of the straightness of the regression lines follow the method given by Fisher (**2**, pp. 216–223). The steps of the calculation are arranged consecutively, and are intended to be read in conjunction with Dr. Fisher's book. where a similar case is described in full. Tables 50 and 51 in his example correspond to Table V for the males and Table VI for the females in mine.

(*a*) *Males.*

TABLE VII

	Estimate.	Correction for Mean.	Corrected Estimate.
$\Sigma(y-\bar{y})^2$	584	$-\frac{52^2}{115}$	560·5
$\Sigma(x-\bar{x})^2$	1829	$-\frac{23^2}{115}$	1824·4
$\Sigma(x-\bar{x})(y-\bar{y})$	951	$-\frac{52\times23}{115}$	940·6

From Table V,

Sum of Products in first 16 arrays $=520\cdot14$
Product in final array $=23\cdot51$

$$\Sigma[n_p(\bar{y}_p-\bar{y})^2] = 496\cdot63$$

From Table VII, $\Sigma(y-\bar{y})^2 = 560\cdot5$

TABLE VIII.

Variance.	Degrees of Freedom.	Sum of Squares.	Mean Square.
Between Arrays	15	496·6	..
Within Arrays	99	63·9	0·645
Total	114	560·5	

$$\Sigma(x-\bar{x})^2 = 1842\cdot4$$

$$\Sigma(x-\bar{x})(y-\bar{y}) = 940\cdot6$$

$$\therefore \frac{[\Sigma(x-\bar{x})(y-\bar{y})^2]}{\Sigma(x-\bar{x})^2} = \frac{(940\cdot6)^2}{1824\cdot4} = 485\cdot0.$$

TABLE IX.

Variance between Arrays due to :—	Degrees of Freedom.	Sum of Squares.	Mean. Square.
Linear regression	1	485·0	. .
Deviations from regression	14	11·6	0·83
Total	15	496·6	

TABLE X.

Mean Square.	Natural Log.	$\frac{1}{2}$ Log.
0·83	−0·1863	−0·093
0·645	−0·4385	−0·219
	Difference (z)	=0·126

Thus z is 0·126, and since the 5 per cent point is about 0·29 (**2**, p. 212), there is absolutely no significant departure from linear regression.

(*b*) *Females.*

TABLE XI.

	Estimate.	Correction for Mean.	Corrected Estimate.
$\Sigma(y-\bar{y})^2$	714	$-\frac{32^2}{120}$	705·5
$\Sigma(x-\bar{x})^2$	1901	$-\frac{(-27^2)}{120}$	1894·9
$\Sigma(x-\bar{x})(y-\bar{y})$	986	$+\frac{32\times 27}{120}$	993·2

From Table VI,

Sum of Product in first 21 arrays =558·54
Products in final array = 8·53
$\Sigma[n_p(\bar{y}_p-\bar{y})^2]$ =550·01
From Table XI, $\Sigma(y-\bar{y})^2$ =705·5

TABLE XII.

Variance.	Degrees of Freedom.	Sum of Squares.	Mean Square.
Between Arrays	20	550·0	. .
Within Arrays	99	155·5	1·571
Total	119	705·5	

$$\Sigma(x-x)^2 = 1894{\cdot}9$$

$$\Sigma(x-\bar{x})(y-\bar{y}) = 993{\cdot}2$$

$$\therefore \frac{[\Sigma(x-\bar{x})(y-\bar{y})]^2}{\Sigma(x-\bar{x})^2} = \frac{(993{\cdot}2)^2}{1894{\cdot}9} = 520{\cdot}6.$$

TABLE XIII.

Variance between Arrays due to :—	Degrees of Freedom.	Sum of Squares.	Mean Square.
Linear regression	1	520·6	. .
Deviations from regression	19	29·4	1·547
Total	20	550·0	

TABLE XIV.

Mean Square.	Natural Log.	½ Log.
1·547	0·436	0·218
1·571	0·452	0·226
	Difference (z)	$=-0{\cdot}008$

The probability that any departures from the female regression line are significant is therefore infinitesimal.

Note on a Sailfish (*Istiophorus americanus* Cuvier and Valenciennes) new to the British Fauna.

By

J. R. Norman.

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With 2 Figures in the Text.

About 9 a.m. (flood tide) on 17th August, 1928, a large sailfish was captured in a dying condition in the main channel of the Yealm estuary, South Devon, opposite the Yealm Hotel, about a mile above the Yealm Bar. The fish was carefully packed up by Mr. V. C. Wynne-Edwards, and promptly despatched to the British Museum (Natural History), where the plaster cast shown in the accompanying illustration (Fig. 1) was prepared by Mr. S. Stammwitz. The specimen was then cut into two pieces and preserved in alcohol.

Owing to the difficulty of preserving these large fishes in museums, except as stuffed skins, and to the marked changes which they appear to exhibit at different stages of growth, our knowledge of the group which includes the swordfishes, sailfishes, and spearfishes is decidedly limited, and the identification of species is a matter of some difficulty.*

In a recent monograph,† Jordan and Evermann distinguish nine species of *Istiophorus*, of which five are said to be new to science. The descriptions of four of these new species are based solely on photographs, the fifth being described from a plaster cast in the museum at Honolulu. As suggested by the authors themselves, some of the characters used by them in their key to the species may be "matters of age not indicating specific distinction." According to this key, the present specimen from Devonshire would appear to be referable to one of their new species—*I. maguirei* from the West Indies, but, so far as I am able to judge from the description and photograph, there seems to be no valid reason for separating this from *I. americanus*, which is found on the Atlantic coast of America from Brazil northwards to Cape Cod and beyond.

The first mention of the species in question, indeed, the first allusion to a sailfish, is to be found in Piso's *Historiæ Rerum Naturalium Brasiliæ*

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* For a complete summary of our knowledge of the group up to that date, see Goode, Rep. U.S. Fish. Comm. (1880), 1883, pp. 289–386, pls. I–XXIV.

† Occ. Papers Calif. Acad. Sci., XII, 1926, 113 pp., 20 pls.

. . . printed at Amsterdam in 1648. In this work a few lines of description and a crude but recognisable figure are given by Marcgrave (p. 171), who gives the fish the name of "*Guebucu brasiliensibus.*" No species of this genus was systematically described until 1786, when Broussonet* published a description based on a specimen and a drawing made by Sir Joseph Banks, giving the fish the name of *Scomber gladius.* The type of this species, a stuffed skin eight feet in length, is preserved in the collection of the British Museum, and was said to have come from "La Mer des Indes." In 1802, Lacepède† established the genus *Istiophorus* for this species. In 1831, Cuvier and Valenciennes‡ founded the species *I. americanus* on the figure in Piso and Marcgrave's work, and redescribed the Indian species as *I. indicus*, ignoring for some unknown reason Broussonet's earlier name. According to Cuvier and Valenciennes, *I. americanus* occurs also on the Atlantic coast of Africa, and they mention a specimen seven feet in length figured by Barbot, which had been caught off Commendo. This is the only reference I have been able to trace of the species occurring on the eastern side of the Atlantic, unless the young specimen caught between France and the Cape of Good Hope, and described by Cuvier and Valenciennes§ as *Histiophorus pulchellus*, should prove to be identical with *I. americanus.*

Several authors have expressed doubt as to whether *I. americanus* is specifically distinct from *I. gladius*, and the two species were united by Günther and Lütken. No attempt has been made previously to compare specimens of similar size, and I take this opportunity of publishing a description of the specimen from Devonshire, and also of Broussonet's type specimen of *I. gladius*, which I regard as representing a distinct species.

Istiophorus americanus, Cuv. & Val. (Figs. 1, 2).

Depth of body about 6½ in the length (from tip of sword to base of caudal), length of head nearly 3. Distance from tip of sword to anterior margin of eye about twice the length of rest of head; diameter of eye 3½ in postorbital part of head, interorbital width 1⅜. Sword narrow, regularly tapering, nearly twice as broad as deep, its upper and lower surfaces both rounded. Maxillary extending to a little beyond eye; jaws with bands of minute, conical teeth, which extend forward on to the lateral and ventro-lateral surfaces of the sword. Dorsal XXXV (+VIII), 7; the whole fin depressible into a deep groove which extends nearly to the origin of the soft dorsal; origin of spinous dorsal above operculum; outline of fin irregular, the longest spines about middle of fin, 1⅓ in length of head; last visible spine followed by eight short, stiff, stub-like spines,

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* Mem. Acad. Sci., 1786, p. 454, pl. 10.

† Hist. Nat. Poiss., III, p. 374.

‡ Hist. Nat. Poiss., VIII, p. 293.

§ *l.c.*, p. 305.

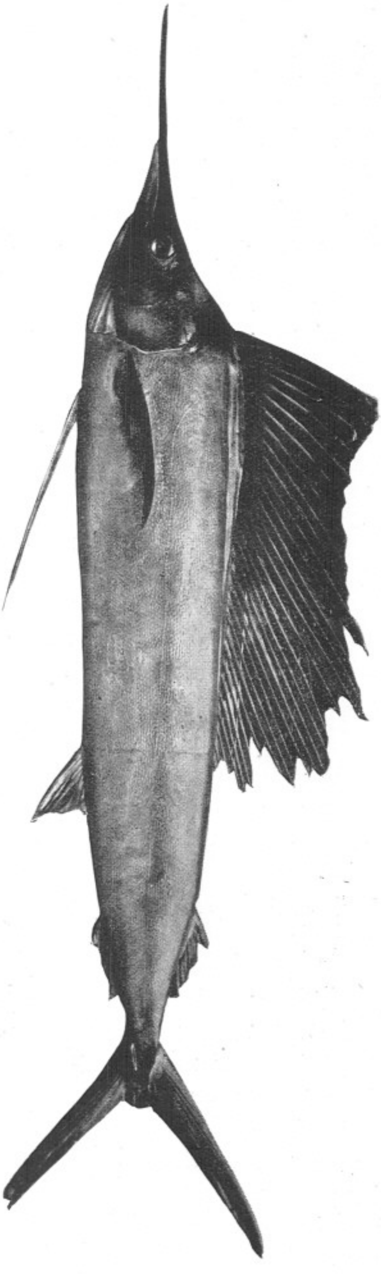

FIG. 1.—Plaster cast of specimen of Sailfish (*Istiophorus americanus*) from the Yealm Estuary, South Devon.

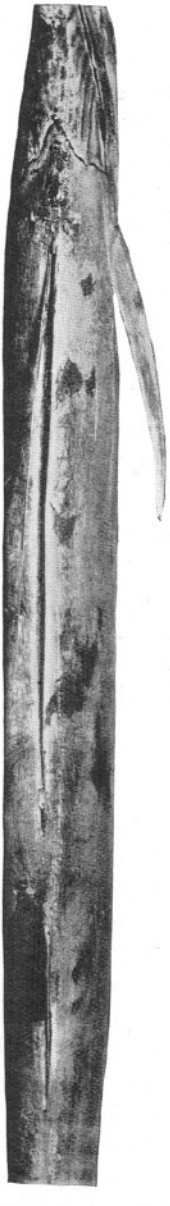

FIG. 2.—Ventral view of the fresh specimen, showing the groove for the reception of the pelvic fins.

which are completely hidden in the groove, and decrease in size posteriorly; soft dorsal separated from the last stub-like spine by a distance which is a little greater than diameter of eye. Anal 9+7 ; origin of first anal fin, which is depressible into a groove, below 33rd dorsal spine ; origin of second anal about level with that of soft dorsal. Pectoral a little less than $\frac{1}{2}$ length of head. Pelvic slender, tapering, about $1\frac{2}{5}$ in length of head, depressible into a deep groove which extends backwards nearly to the vent (Fig. 2). Upper lobe of caudal $1\frac{3}{5}$ in length of head. Caudal peduncle with two strong, parallel keels on either side. Brownish above, silvery grey below ; all the fins greyish brown, the spinous dorsal with a number of small, round, dark spots on the membrane between the spines.

The principal dimensions of the specimens are as follows :—

Total length	2260 mm.
Length to base of caudal	1882 mm.
Greatest depth of body	290 mm.
Total length of head	647 mm.
Length from tip of sword to anterior margin of eye	429 mm.
Diameter of eye	47 mm.
Interorbital width	100 mm.
Length of first dorsal spine	315 mm.
Length of longest dorsal spine	485 mm.
Length of pectoral	305 mm.
Length of pelvic	450 mm.

Istiophorus gladius (Broussonet).

Depth of body 6 or 7 times in the length, length of head nearly 3. Distance from tip of sword to anterior margin of eye nearly $2\frac{1}{2}$ times the length of rest of head ; diameter of eye $3\frac{1}{2}$ in postorbital part of head, interorbital width $1\frac{2}{3}$. Sword and teeth similar to those of *I. americanus*. Dorsal XLV, 7 ; origin of spinous dorsal above operculum ; outline of fin apparently irregular, the longest spines about middle of fin, longer than head ; all the spines are visible, and decrease gradually in length posteriorly ;* origin of soft dorsal separated from last spine by a distance which is little greater than diameter of eye. Anal 14 (or 13)+7 ; origin of first anal fin below 35th dorsal spine ; origin of second anal about level with that of soft dorsal. Pectoral about $\frac{1}{2}$ length of head. Pelvic slender, tapering, $1\frac{1}{4}$ in length of head. Upper lobe of caudal nearly $1\frac{1}{2}$ in length of head. Caudal peduncle with two strong, parallel keels on either side.

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* The depth of the grooves for the reception of the fins, and the extent to which the posterior dorsal spines are hidden, is not apparent in this stuffed skin.

The principal dimensions of the specimen are as follows :—

Total length	2458 mm.
Length to base of caudal	2058 mm.
Greatest depth of body	270 mm.
Total length of head	705 mm.
Length from tip of sword to anterior margin of eye	500 mm.
Diameter of eye	50 mm.
Interorbital width	90 mm.
Length of first dorsal spine	345 mm.
Length of highest dorsal spine	820 mm.
Length of pectoral	356 mm.
Length of pelvic	520 mm.

This species differs from *I. americanus* chiefly in the longer sword, larger spinous dorsal fin, with higher posterior rays, longer anal fin, and in the longer pelvics.

Galatheascus striatus—a New Rhizocephalan.

By

Dr. H. Boschma,

Zoological Laboratory of the University, Leiden.

With 6 Figures in the Text.

A specimen of *Galathea strigosa* (L.) with a parasite of fairly large size at the abdomen was collected at the Looe–Eddystone Grounds near Plymouth on June 11th, 1913. Since then the decapod with its parasite has been in the collection of the Laboratory of the Marine Biological Association. The specimen is different from all other parasites known to infest the species of the genus Galathea : at a first superficial inspection no mantle opening could be detected, and consequently it remained

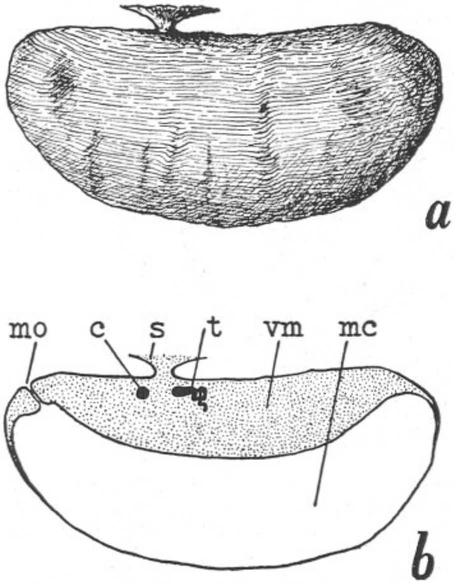

Fig. 1.—*Galatheascus striatus*. *a*, the animal from the left side ; *b*, semidiagrammatic longitudinal section in which the genital organs of one side are shown also ; *mo*, mantle opening ; *c*, colleteric gland ; *s*, stalk ; *t*, testis ; *vm*, visceral mass ; *mc*, mantle cavity. ×3.

doubtful whether the parasite belonged to the Rhizocephala or to some other group of Crustaceans. At my request Dr. E. J. Allen kindly put the animal at my disposal for further investigation. Fortunately the mantle cavity contained an enormous mass of nauplius larvæ, which proved that the parasite belongs to the Rhizocephala, as these larvæ have well-developed frontal horns (Fig. 6).

After some fragments of the mantle had been cut off for the study of its chitinous coverings a series of transverse sections was made from the whole animal. The study of its internal anatomy shows that the specimen is closely allied to Peltogaster and consequently has to be classified in the family Peltogastridæ. There are, however, sufficient characteristics which distinguish the specimen from the species of the genus Peltogaster to establish a separate genus, which may be called *Galatheascus*. The diagnosis of this genus is as follows :—

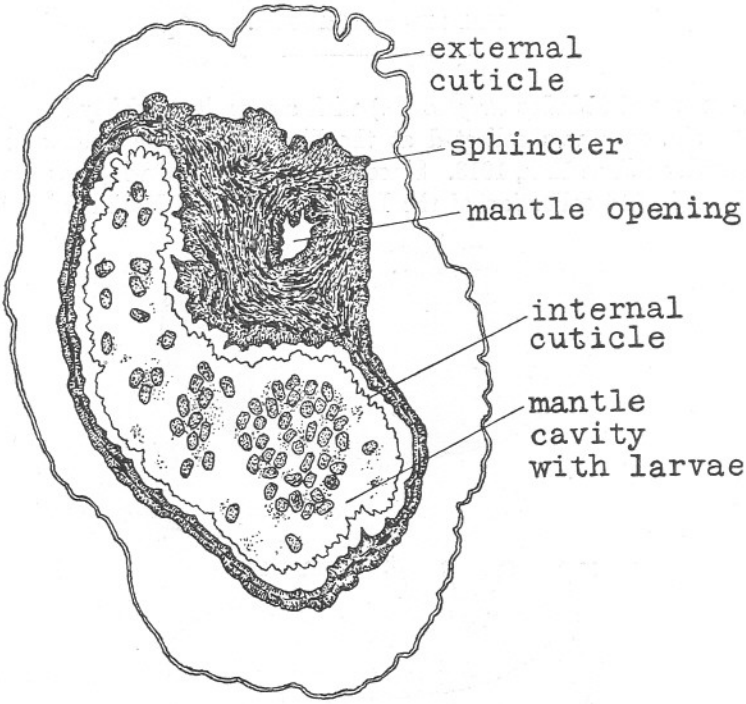

FIG. 2.—Transverse section through the anterior part of the body of *Galatheascus striatus*. The chitinous sheaths of both surfaces of the mantle have loosened from the muscular part. × 18.

Galatheascus n. g. Body elongate oviform, mesentery very broad, extending from the anterior to the posterior extremity. Stalk in the anterior half of the body. Mantle opening extremely narrow. Colleteric glands small, simple, in the neighbourhood of the stalk. Testes consisting of a very small straight part at each side of the median plane and a strongly coiled portion which passes into the vasa deferentia; the whole of the male genital organs in the region of the stalk.

The type species of this genus may be characterised especially by the structure of the chitinous parts of the mantle. So the following diagnosis of the species can be given :—

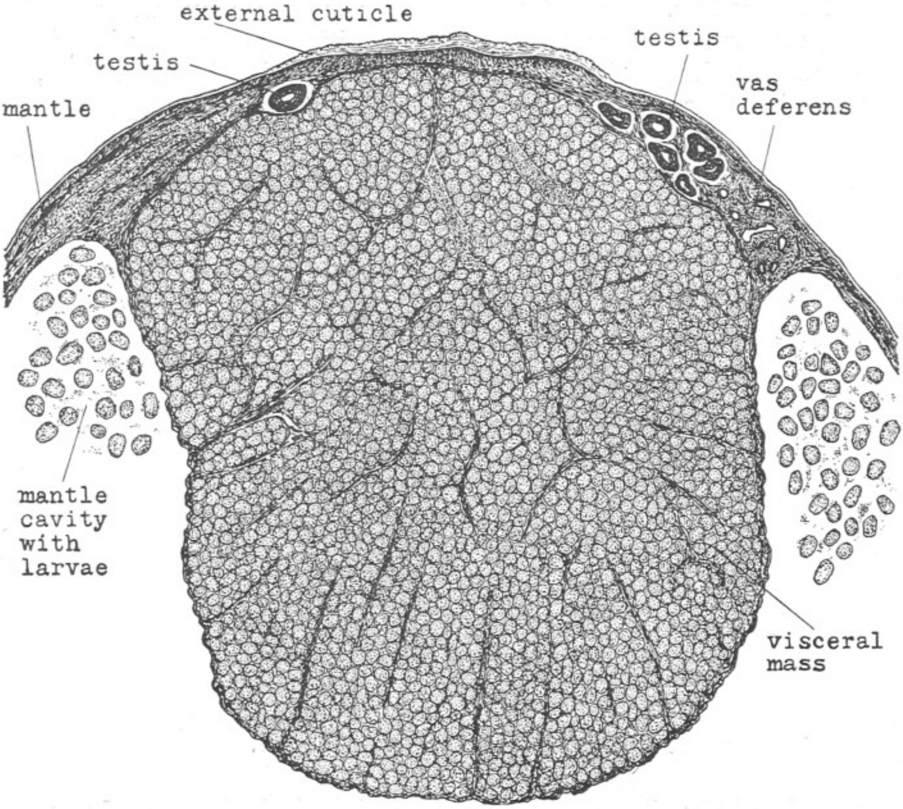

Fig. 3.—Transverse section through the region of the stalk of *Galatheascus striatus*. × 20.

Galatheascus striatus n. sp. External cuticle of the mantle smooth, with shallow grooves extending over the surface in longitudinal direction. These grooves are about 0·2 mm. apart. The internal cuticle bears retinacula containing one to three spindles each. These spindles have a length of 20 to 25 μ.

A more elaborate description of the peculiarities of the only available specimen is given below.

The parasite was attached to the ventral surface of a specimen of *Galathea strigosa* (L.), between the second and the third abdominal segment. Its longitudinal axis had a direction perpendicular to that of its host; the anterior pole of the parasite was directed toward the right side of the host. The mantle opening is so small (diameter less than 0·5 mm.) that it escaped notice until the parasite could be studied in the series of sections. One of the most striking differences from the species of the genus Peltogaster is caused by the position of the stalk, which in Galatheascus is found in the anterior half of the dorsal surface (Fig. 1 *a*, *b*), whilst in Peltogaster the stalk is inserted to the mantle in the posterior part of the body. In Galatheascus the stalk itself is slender, about 1 mm. thick, and very short. It is surrounded by an inconspicuous shield-like thickened part of the external cuticle; in Fig. 3 this thicker part of the chitin is visible. Muscles are present especially in the dorsal part of the animal and in the mantle. Moreover, the small mantle opening and the narrow tube connecting this opening with the mantle cavity are surrounded by an extremely strongly developed sphincter (Fig. 2). Besides these there is a thin layer of muscles enveloping the visceral mass. Between the groups of eggs in the ovary, which occupies almost the whole of the visceral mass, there are sparsely distributed muscular elements (cf. Fig. 3).

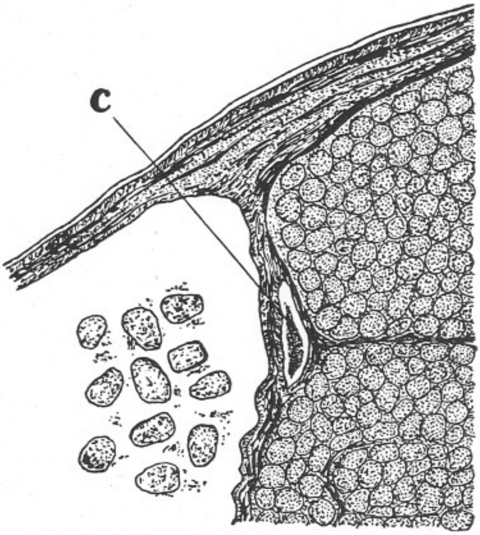

Fig. 4.—Part of a transverse section through *Galatheascus striatus*, slightly nearer to the anterior pole than that of Fig. 3, showing the colleteric gland (*c*). ×36.

In the neighbourhood of the stalk the genital organs are found (cf. Fig. 1 *b*). The structure of the testes does not differ in any significant detail from those of Peltogaster; the course of these organs, however, is different. Their closed extremity is directed toward the anterior pole; along a short distance they are straight, but soon the tubes continue their course in a very irregular coiled manner. As a result in sections through this region the lumen of the testis appears several times. One of the testes lies slightly behind the other, consequently in Fig. 3 the posterior part of one and the anterior part of the other testis is visible. After the coiled part of the testis this organ passes into the vas deferens, which has a much thinner wall and is less conspicuous; this part of the male genital organs also has a strongly irregular course. It terminates with the male genital opening which opens into the mantle cavity.

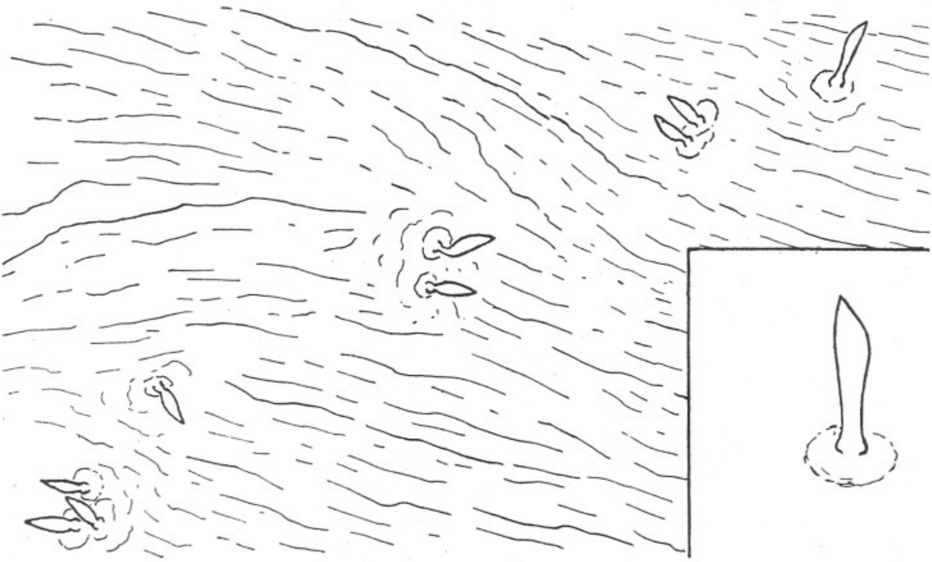

FIG. 5.—Retinacula on the internal cuticle of *Galatheascus striatus*. × 380. In the right-hand corner of the figure one retinaculum more strongly enlarged (× 880).

The colleteric glands have a very minute size: their diameter is less than 0·5 mm. They have an approximately circular lumen which is flattened in a lateral direction. On each side of the visceral mass, close to the insertion of the mantle, one of these organs is found. Inside the glands contain a coagulated mass, obviously the product of secretion of the gland cells. In general the colleteric glands of Galatheascus are built on the same plan as those of Peltogaster; they are probably even more simple than those of the latter genus.

With the exception of the shield-like part round the stalk the external cuticle of the mantle is comparatively thin (8–11 μ). In many parts of the mantle it has loosened from the muscular elements (e.g. in the anterior part; cf. Fig. 2). The same holds true for the internal cuticle. The surface of the external cuticle is smooth except for the shallow longitudinal grooves mentioned above.

The internal cuticle of the mantle possesses a great number of retinacula (Fig. 5). Many of these consists of a single spindle, others have two, and others again three. The spindles are slender, pointed at the top, and do not bear barbs. In general they are like those of *Peltogaster paguri*, though they are of somewhat larger size (in *P. paguri* about 16 μ, in Galatheascus 20–25 μ).

The larvæ (Fig. 6) are strongly reminiscent of those of Peltogaster (cf. Nilsson-Cantell, 1921); they also have approximately the same size, the total length on an average amounting to 250 μ. In the nauplius of Galatheascus the lateral horns are directed more strongly backwards than in those of Peltogaster. For more particulars on the shape of the legs, etc., I refer to the figure. Probably on account of the insufficient state of preservation, the mouth parts and the frontal filaments could not be found. The eye also is invisible, so in all probability in the living larvæ it was devoid of pigment.

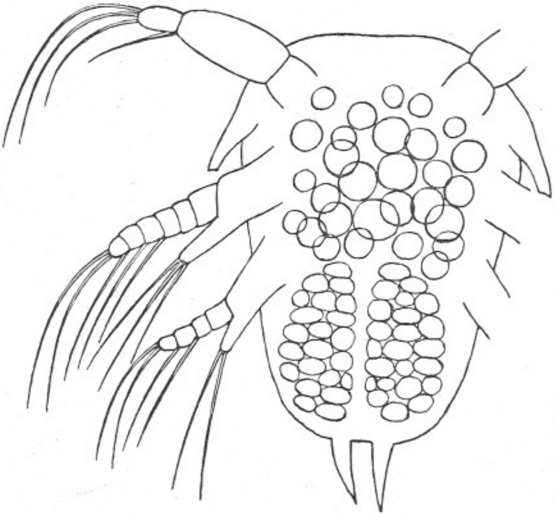

FIG. 6.—Nauplius larva of *Galatheascus striatus*, ventral view. × 250.

Galatheascus striatus is the first Peltogastrid known to infest a host belonging to the Galatheidæ. Other Rhizocephalid parasites are known to occur on Galatheidæ, but these are representatives of the genus Lernæodiscus (family Lernæodiscidæ, cf. Boschma, 1928). The only

Rhizocephalid hitherto known as a parasite of *Galathea strigosa* is the form designated by Smith (1906) as the new species *Lernæodiscus strigosæ*, the diagnosis of which, however, is very incomplete. According to Smith it differs from *Lernæodiscus galatheæ* by having a very wide "anterior" hinge of the mesentery.

The position of *Galatheascus striatus* to its host differs from that in the other Peltogastridæ: the long axis of Galatheascus is perpendicular to that of its host. Consequently the diagnosis of the family Peltogastridæ as given in a previous paper (Boschma, 1928) has to be amended, the statement "long axis parallel to long axis of host" cannot remain in this diagnosis.

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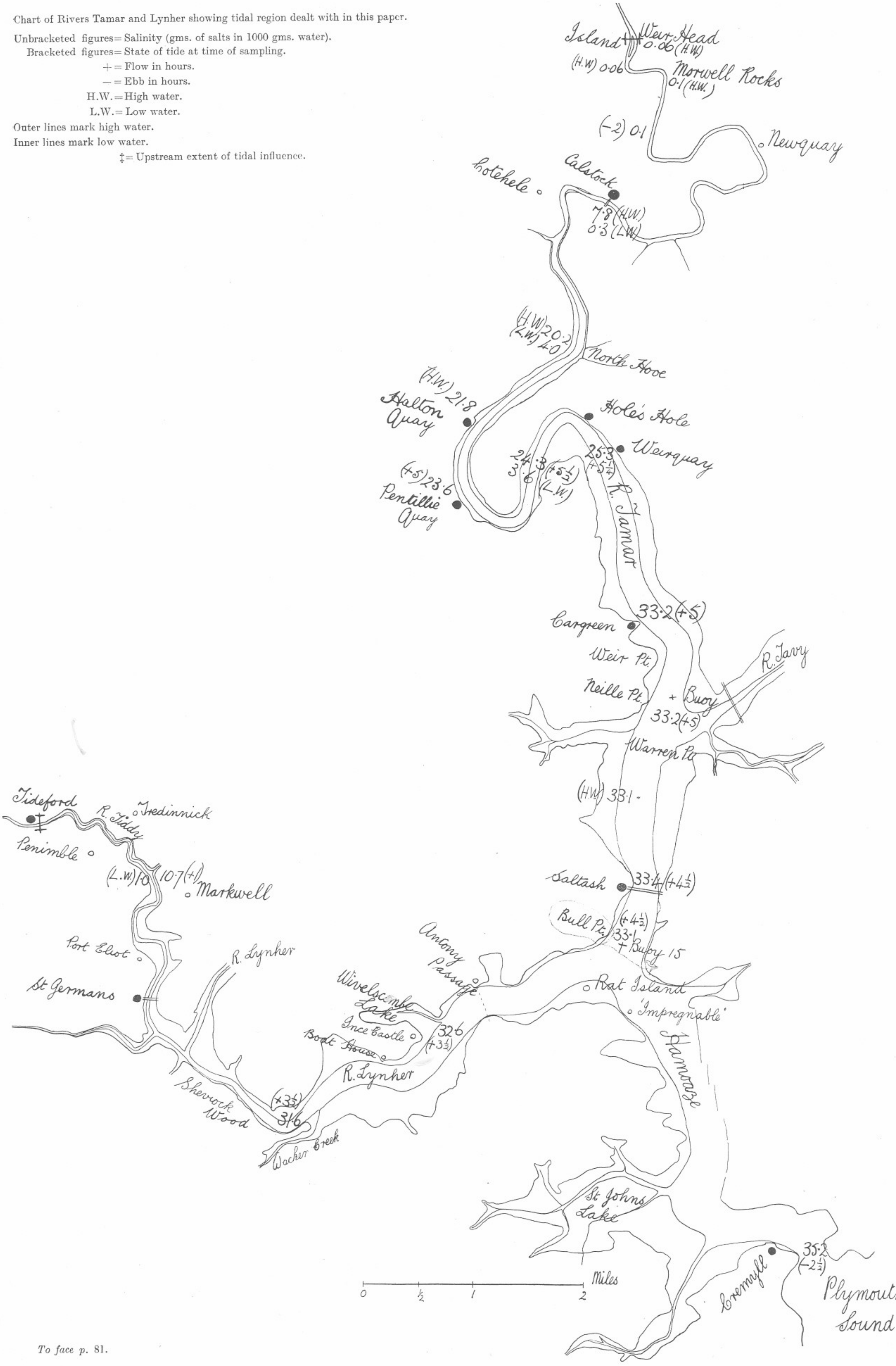
NILSSON-CANTELL, C. A. 1921. Cirripeden-Studien. Zool. Bidrag f. Uppsala, Bd. 7.

SMITH, G. 1906. Rhizocephala. Fauna und Flora des Golfes von Neapel, 29. Monographie.

Chart of Rivers Tamar and Lynher showing tidal region dealt with in this paper.

Unbracketed figures = Salinity (gms. of salts in 1000 gms. water).
Bracketed figures = State of tide at time of sampling.
+ = Flow in hours.
— = Ebb in hours.
H.W. = High water.
L.W. = Low water.
Outer lines mark high water.
Inner lines mark low water.
‡ = Upstream extent of tidal influence.



A Report on the Fauna of the Estuaries of the River Tamar and the River Lynher.

By

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With 1 Figure in the Text and 1 Chart.

THE following is an account of a faunistic investigation covering those parts of the Rivers Tamar and Lynher which are affected by the tide, and was carried out during a period of six months from June to November, 1928.

DESCRIPTION OF THE AREA.

The Tamar forms a portion of the boundary between Devon and Cornwall and flows in a southerly direction along a more or less winding course. (Chart.) The extent of the stream dealt with is from Plymouth Sound to Weir Head, some 19 miles inland measured along the water-course. For about 6 miles downstream from Weir Head, the valley is rather narrow with rock exposures at different places on the convex side of bends, the water being confined to a well-defined channel with steep sides, which are uncovered by the vertical contraction of the stream at low water. The remainder of the river, down to the sea has, generally, a mud-bank on each side, except at occasional bends where rock is present, which is exposed at low water by the lateral contraction due to reduction in level. The upper 4 miles of this region has narrower mud-banks than has the lower portion. These mud-banks or -flats are for the greater part more or less plane surfaces, which may slope gradually into the bed of the main channel, as happens in the lower portion of the area, or they may slope suddenly downwards at the edge, thus forming a well-marked bank to the main channel. In many cases their landward edges lie below high-water neap tide, but in others they slope imperceptibly into the adjoining land surface. In the former cases there is often a low cliff of about 2 feet bordering salt-marsh.

The constitution of the deposit has not been examined, but superficial observation shows that it is generally greyish to black mud of varying consistency, from tough clay-like material into which a man of 168 lbs. may sink to a depth of about 6 inches, to thin " slurry " into which he may sink to a depth of about 3 feet. The greater part of the area examined has mud into which he may sink to a depth of from 9 inches to 18 inches. The thinner mud is generally greyish, and the tougher usually black. St. John's Lake and a flat above Saltash Bridge on the left bank have a flora of Zostera, growing on a mud of medium consistency in which walking is difficult.

The banks in the upper 4 miles of the mud-flat region, where there is an abrupt slope into the main channel, are of interest on account of a change in character of the deposit along the sharp slope. The fine mud extends downwards roughly half-way, to about half-tide mark, and below there is a change to a coarse-grained material, in some cases having grains of about 1·5 mm. diameter. Such a substratum is quite hard and clearly sandy. The reason for this is largely to be sought in the effect of the rising tide, which passes along the channel with considerable force and lifts the deposit up. The fine material is carried along upstream, and, as further rising goes on, the stream, at about half-tide, commences to spread laterally over the banks, so that a reduction in forward movement is effected with a corresponding fall in the transporting power of the current. Thus suspended material is precipitated in graded series, the fine material being laid on the broad mud-flat and the coarse on the lower part of the slope. The spreading of the water over the upper surface of a mud-flat is a gentle process, and although there is erosion it is only relatively slight, apparently a very thin layer being involved. Some time before high-water most of the lifted material is redeposited, and the turbid stream at the beginning of the tidal flow ultimately becomes relatively clear.

In the lower 9 miles or so, where the mud-flats slope gently into the main channel, this strong scouring does not appear to take place, and the water spreads gently over the banks with disturbance of little more than the merest superficial layer.

On the convex side of bends with rocky ground there is usually a thin layer of mud, which is lifted at the flow and deposited at slackening of the tide. These places are usually not densely populated, since conditions are changing too violently. If *Fucus vesiculosus* is present there is always a fauna, but if it is absent then the fauna is scanty.

Rocky shores are found at places in the upper 6 miles, at the large double bend above Hole's Hole to Pentillie, at Neille Point, and along the shores of the Hamoaze, below Saltash. Alongside the rock in several places the depth of water may be 20 feet to 30 feet. From the Saltash region downwards the depth is considerably more.

The portion of the River Lynher, or St. Germans River,* which is

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* The Lynher, which is the longer, flows into the St. Germans River about half a mile east of St. Germans.

dealt with, consists of a length of about 8 miles extending downwards in a roughly south-easterly direction for about 4 miles, and then approximately north-easterly for the same distance, when it joins the Tamar about 3¾ miles from the Sound. It also shows two quite well-marked regions, the lower one being about 6½ miles long and the upper (St. Germans), having the characters of the upper 6 miles of the Tamar, extending about 1½ miles, as far as Tideford. The lower 6½ miles have mud-banks corresponding in character with those of the Tamar, i.e. with sharply sloping margins forming the banks of the channel, or with gently sloping surfaces, which gradually pass into the main channel.

The lower 4 miles present a fairly uniform appearance, the fall being slight, but the upper has very rapid transitional stages from the freshwater region to the brackish area, as the fall is much more marked, the whole tidal length of the St. Germans being 8 miles from Bull Point to Tideford, as compared with about 16 miles from Bull Point to Weir Head. Judging from the fauna, the 4 miles or so from Sheviock Wood to Tideford corresponds with the length of the Tamar upwards from half a mile below Pentillie Quay, a distance of about 9 miles. The same general agreement is seen in the physical nature of the two regions.

Where there are well-marked bends there are usually deposits of plant detritus on the concave side of the bend. These are known locally as "Point-stuff," and serve as sources of manure. They also play a part in the nutrition of many animals, which live on and about them. Beds of "Point-stuff" occur more commonly in the Tamar above Hole's Hole. In the river above St. Germans, the bends are short and, although plant detritus is found, it is not nearly so extensive as in the other river.

OBSERVATIONS ON THE SALINITY* OF THE WATER.

Water samples were taken at various times and places. Owing to the circumstances which governed the work it was not possible to sample the two rivers on the same day. The tidal flow is rapid, high water at Calstock, 13 miles up, being about 23 minutes later than at Plymouth. The result of this was that samples taken at different places on the same day were not comparable, since the state of the tide was different at any two places visited. An attempt was made to obtain approximately comparable results by visiting stations at, as nearly as possible, the same state of the tide. During the present summer, when sampling was carried out, the rainfall was negligible, 3·38 inches being registered at Plymouth during 86 days, so that any disturbance due to excessive fresh water was eliminated. The chief disturbing factor was the variation in the size of the tide, not only from spring tide to neap tide, but in the

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* Total weight of salts in grammes per 1000 gms. of sea-water.

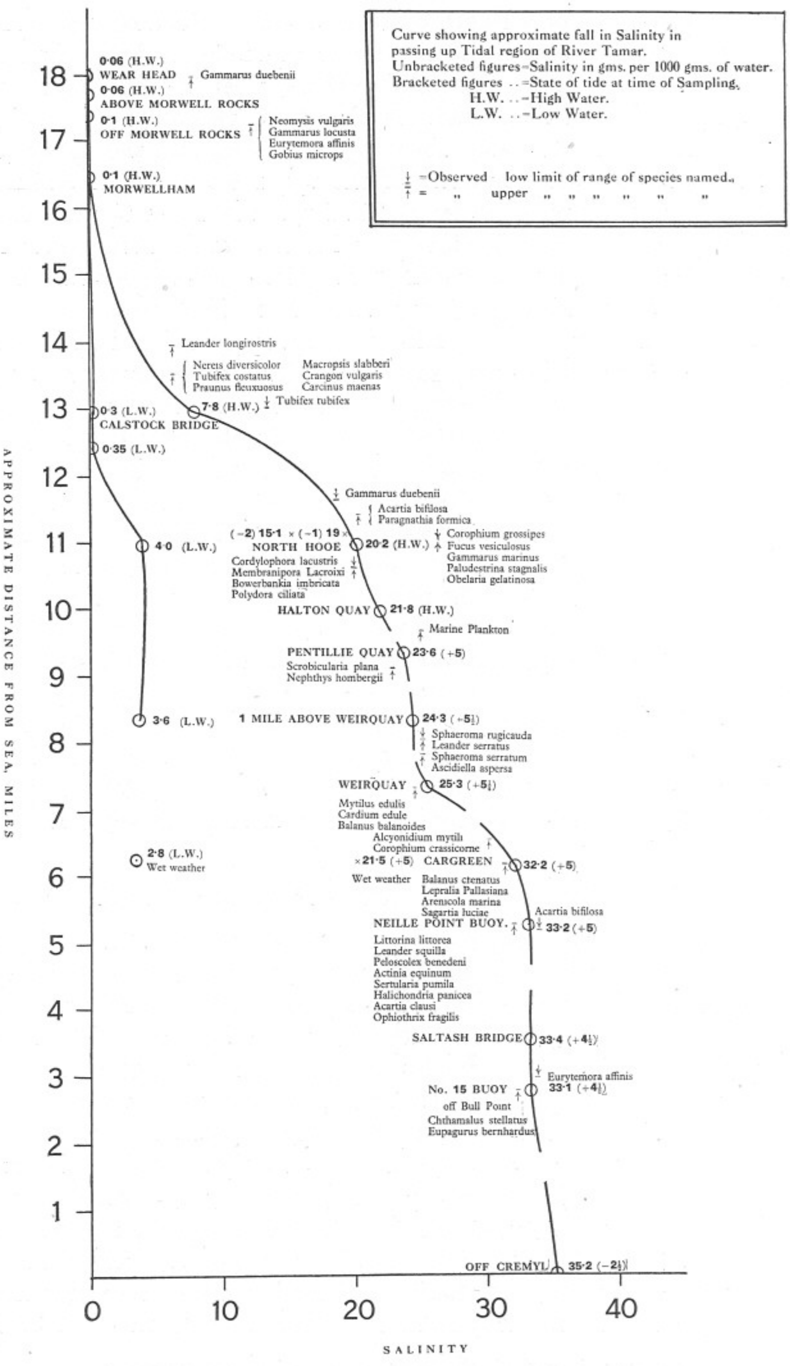
Curve showing approximate fall in Salinity in passing up Tidal region of River Tamar.
Unbracketed figures=Salinity in gms. per 1000 gms. of water.
Bracketed figures ..=State of tide at time of Sampling.
H.W. ..=High Water.
L.W. ..=Low Water.
↓ =Observed low limit of range of species named.
↑ = " upper " " " " " "
0·06 (H.W.) WEAR HEAD
Gammarus duebenii
0·06 (H.W.) ABOVE MORWELL ROCKS
0·1 (H.W.) OFF MORWELL ROCKS
Neomysis vulgaris
Gammarus locusta
Eurytemora affinis
Gobius microps
0·1 (H.W.) MORWELLHAM
Leander longirostris
Nereis diversicolor
Tubifex costatus
Praunus fleuxuosus
Macropsis slabberi
Crangon vulgaris
Carcinus maenas
7·8 (H.W.)
Tubifex tubifex
0·3 (L.W.) CALSTOCK BRIDGE
0·35 (L.W.)
Gammarus duebenii
Acartia bifilosa
Paragnathia formica
(−2) 15·1 × (−1) 19 ×
NORTH HOOE
20·2 (H.W.)
4·0 (L.W.)
Corophium grossipes
Fucus vesiculosus
Gammarus marinus
Paludestrina stagnalis
Obelaria gelatinosa
Cordylophora lacustris
Membranipora Lacroixi
Bowerbankia imbricata
Polydora ciliata
HALTON QUAY 21·8 (H.W.)
Marine Plankton
PENTILLIE QUAY 23·6 (+5)
Scrobicularia plana
Nephthys hombergii
3·6 (L.W.)
1 MILE ABOVE WEIRQUAY 24·3 (+5½)
Sphaeroma rugicauda
Leander serratus
Sphaeroma serratum
Ascidiella aspersa
WEIRQUAY 25·3 (+5½)
Mytilus edulis
Cardium edule
Balanus balanoides
Alcyonidium mytili
Corophium crassicorne
2·8 (L.W.) Wet weather
×21·5 (+5) CARGREEN 32·2 (+5)
Wet weather
Balanus ctenatus
Lepralia Pallasiana
Arenicola marina
Sagartia luciae
Acartia bifilosa
NEILLE POINT BUOY. 33·2 (+5)
Littorina littorea
Leander squilla
Peloscolex benedeni
Actinia equinum
Sertularia pumila
Halichondria panicea
Acartia clausi
Ophiothrix fragilis
SALTASH BRIDGE 33·4 (+4½)
Eurytemora affinis
No. 15 BUOY 33·1 (+4½)
off Bull Point
Chthamalus stellatus
Eupagurus bernhardus
OFF CREMYL 35·2 (−2½)
APPROXIMATE DISTANCE FROM SEA, MILES
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
10
20
30
40
SALINITY

FIG. 1.

size of the various springs and neaps, since the amount of salt water coming up was not the same at two corresponding phases of the tidal month. However, this can be neglected, as the intention was to obtain merely an approximate idea of the salinity of the stream.

The high-water salinity curve (Fig. 1) shows a gradual fall as far as Cargreen, after which there is a rapid decline to Weir Quay, about 1½ miles further up. From there to Pentillie, round the two bends, the fall is again gradual, while from Halton Quay it increases until there is again a marked drop between North Hooe and Calstock, a distance of about 2 miles. Above Calstock, to Weir Head where the fresh water is met, the fall per unit distance appears to decrease towards the upper limit of the tidal region. Determinations of low-water salinity indicate that the greatest variation between low- and high-water concentrations is found between North Hooe and the Weir Quay district. As will be noticed later, this is the region where a large number of marine species reach their limit of existence.

Indications of the movement of sea-water were also seen in the distribution of marine plankton. There was a rapid reduction in the variety of species in passing from the junction of the Lynher and the Tamar to the junction of the Tamar and the Tavy. From this latter region upwards there were few species, the chief being *Sagitta bipunctata*, *Euterpina acutifrons*, and *Aurelia aurita*, which were found to have their upper limit about half-way between Pentillie Quay and Halton Quay. Along this length, as is mentioned above, there is a marked fall in the salinity about high water. Similarly there is a reduction in the number of bottom species. It would appear that the main body of incoming sea-water does not pass Cargreen. A considerable portion goes into the Lynher and the Tavy and covers the mud-flats on each side between Saltash and Neille Point. A further large quantity is held over the flats between Neille Point and Hole's Hole.

During observations at Calstock, July 11–13, with hot dry weather, there was a scum of unicellular algæ covering the river and exposed banks at low water. This extended downwards for about three-quarters of a mile. With the incoming of the tide, this scum was pushed upstream, almost unbroken, until it lay, at high water, along a length of about 1¼ miles immediately below Weir Head. Here the salinity was low, varying from $0{\cdot}06^{\circ}/_{\circ\circ}$ to about $0{\cdot}3^{\circ}/_{\circ\circ}$, and the mass of water was evidently largely derived from that portion which, at low water, extended down to the Cotehele locality. The place of this water would be taken by that pushed up from the lower region down to the Halton Quay–Pentillie Quay neighbourhood. This is suggested after a consideration of the low-water salinities at the places named. Support is added by results obtained at a point off Markwell, about 1 mile above St. Germans

Bridge, where indications of movement of water were obtained, as follows :—

2 p.m. salinity $1{\cdot}7^{\circ}/_{\circ\circ}$
2.30 p.m. ,, $1{\cdot}7^{\circ}/_{\circ\circ}$
3.20 p.m. ,, $1{\cdot}9^{\circ}/_{\circ\circ}$ first indication of flow.
3.50 p.m. ,, $2{\cdot}4^{\circ}/_{\circ\circ}$
4.10 p.m. ,, $10{\cdot}7^{\circ}/_{\circ\circ}$

Reference will be made later to these data, when the movements of organisms are considered.

The influence of wet weather on the salinity of these rivers has not been studied, but a sample at Cargreen showed a fall from $32{\cdot}2^{\circ}/_{\circ\circ}$, during dry weather, to $21{\cdot}5^{\circ}/_{\circ\circ}$ on a fine day but after a rainfall of 2·14 inches during the previous 7 days.* Both samples were taken at 5 hours of flow.

Few salinity determinations have been made in the River Lynher, but the results show that the concentration at high water, as far as Sheviock Wood, is quite high, $31{\cdot}6^{\circ}/_{\circ\circ}$ at 3½ hours' flow. About St. Germans and Port Eliot there was a very abrupt change in salinity from low water to high water, as is indicated above, when the tide begins to flow strongly. Here the number of species is small.

The interesting shore plants, which have been noticed, are *Fucus vesiculosus*, *Atriplex portulacoides*, and *Phragmites communis*. They extend to about North Hooe, Fucus and Atriplex upstream, and Phragmites downstream. The two latter meet about North Hooe, with a well-defined junction, while Fucus suddenly ceases. The seaweed is very poorly grown from Pentillie upwards, the vesicles and fronds being dwarfed.

THE COLLECTION OF ORGANISMS.

Besides the usual methods employed in shore-collecting and the use of the fine tow-net, the plankton-net devised by Russell (**41**) was found to be very efficient in taking the larger plankton. The net used was of stramin, and had a mouth of rectangular shape 3 feet by 9 inches. This was attached to an Agassiz frame 1 foot high, having two posterior bars 9 inches apart to which the mouth of the net was lashed. The mouth of the net was thus about 1½ inches from the bed of the stream when the frame was resting on the bottom. The nature of the ground rendered unnecessary the provision of a protecting outer bag. On the mud-banks and on the hard ground the apparatus worked very satisfactorily, but tended to dig up the beds of " Point-stuff." It was also used at various depths while the boat was anchored, the net being suspended against the

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* Plymouth rainfall.

tide. In order to sample at definite depths, an extra bridle was attached to two "eyes" at the back of the frame, and when the whole apparatus was lifted by this bridle, the frame and net hung down so that the mouth was quite efficiently closed.

Generally it was quite sufficient to make collections in this way while the boat was at rest, but when the tide slackened, at high or low water, towing was necessary.

FAUNISTIC NOTES.

Species belonging to various parts of the Animal Kingdom have been taken from the two rivers. They fall into a number of groups in so far as their distribution is concerned, viz. :—

1. Those coming in from the sea, either planktonic or benthic, which are intolerant of the changing conditions, and disappear rapidly, especially between Neille Point and Weir Quay.
2. Those coming in from the sea tolerant of considerable change in conditions, and persisting (a) to Halton Quay–North Hooe, (b) to Calstock district.
3. Brackish-water species, which replace some of the marine species. These appear between Pentillie and Hole's Hole.
4. Freshwater species tolerant of slight salinity.

By far the greatest number falls into Group 1, a very much smaller number into Group 2, Group 3 is also small, while only two, *Tubifex tubifex* and *Sphærium casertanum*, have been found in Group 4.

In considering the distribution of the various species, notice must be taken of the local variations in the conditions which determine their presence or absence. Sessile organisms requiring a solid substratum are not normally found on the mud-banks. The occurrence of odd specimens of *Cereus pedunculatus* attached to occasional small stones, and of *Metridium senilis* and *Sagartia troglodytes* living on small pieces of wood on mud-flats, shows forcibly the dependence of such animals upon suitable substrata. The distribution of burrowing animals is also partly dependent upon the nature of the substratum, those requiring tough mud being rarely found in very soft deposits. Generally speaking the latter type of sediment has been found to carry an exceedingly scanty macrofauna.

The channels scoured by the strong tides are poorly populated by sessile organisms, except when there is a solid bed, such as a rock exposure or a piece of masonry. Occasionally Fucus obtains a foothold in a sandy bed, and the fronds may carry Polyzoa and Hydroids, along with a number of Harpacticids.

It is to be noticed that the fauna so far recorded consists, chiefly, of littoral species which are adapted to withstand the rapidly varying circumstances of estuarine life. The largest number of plankton species is found in the most saline region, while the brackish water has only a very few species.

PROTOZOA.

This part of the animal kingdom has not been studied and *Polystomella crispa* only has been recorded. It is very common in the more saline part of the river.

PORIFERA.

The sponges have been found to be limited to the water which is highly saline at high water, not extending at most beyond Cargreen. There is a great development of *Halichondria panicea* on the mussel-bed off Neille Point. The low-water spring-tide depth at this place was about 12–15 inches, and the bed was not observed ever to be exposed. Dr. G. P. Bidder, to whom I am indebted for its determination, describes it as of the estuarine metamp.

CŒLENTERATA.

Obelaria gelatinosa is the dominant marine cœlenterate, it being present in great quantity, especially below half-tide mark. After Hole's Hole it becomes more scanty and dwarfed, while its vertical extent becomes limited to low-water mark. *Obelia geniculata* has a very much more restricted range, not having been found past Weir Quay (Sal. H.W. about $25^\circ/_{oo}$, $+\frac{1}{4}$ hr. $18{\cdot}8^\circ/_{oo}$).

The gymnoblastic hydroids lie in two groups, *Clava squamata* and *C. multicornis*, which are the marine types disappearing past Cargreen, and *Cordylophora lacustris*, a brackish-water species living in the upper part of the stream, from about New Quay down to the neighbourhood of Halton Quay. The salinity range is extensive, varying, at high water, from about $0{\cdot}1^\circ/_{oo}$ above Calstock to about $22^\circ/_{oo}$ near Halton Quay. The densest growth is on Calstock Bridge and on the rocks at Ashburton Turn, where the vertical extent is up to half-tide. Towards the extremes of the Cordylophora region the vertical range becomes reduced to low-water mark.

The upper end of the range of *Obelaria gelatinosa* overlaps the lower end of that of Cordylophora.

None of the Anthozoa has been found where the high-water salinity is normally less than $33^\circ/_{oo}$.

Aurelia aurita breeds extensively in the asexual stage on the mussel-bed off Neille Point. The medusæ regularly invade the river during the summer months, and have been taken up as far as near Pentillie Quay.

NEMERTINI.

Lineus ruber has been taken most commonly. None has been found in water having a high-water salinity of less than about 33°/₀₀.

ANNELIDA.

The class Polychæta provided the largest number of species in this phylum, most of them disappearing before Cargreen or when the salinity began to fall rapidly about this region. The most numerous and widely spread species found were *Nereis diversicolor*, *Polydora ciliata*, *Heterocirrus zetlandicus*, and *Heteromastus filiformis*. *Arenicola marina* occurs in the more saline area, and especially in the Lynher up to Ince Castle and in St. John's Lake. It soon disappears when the salinity begins to fall. The last specimens seen in the Tamar were at Cargreen. *Kefersteinia cirrata* and *Magalia perarmata* are common on the Neille Point mussel-bed, but extend very little further. The widest range is that of *Nereis diversicolor*, which persists into a region with a tidal variation of about 7·8°/₀₀ salinity at high water to about 0·4°/₀₀ at low water. It is extremely abundant in the stiffer muds, and at all levels where the banks slope gently into the main channel. Where there is an abrupt slope into the main channel, the animal is usually absent below half-tide mark, the deposit here being sandy. Above half-tide mark the sediment rapidly becomes fine, so as to produce a substratum in which the worm can easily burrow.

Polydora ciliata has been found as far up as a region having a tidal salinity variation of from about 20°/₀₀ to 4°/₀₀. Although, in the Saltash district, it has been taken chiefly from its normal habitat, shells, in other places it has been found living in mud, and very commonly in mud tubes constructed in narrow cracks in rock. During the summer the plankton, from as far up as North Hooe, was found to contain large numbers of the larvæ of Polydora.

Of the Oligochæta, *Tubifex costatus* and *Clitellio arenarius* have a range similar to that of *Nereis diversicolor*. They are both abundant in the stiffer mud and beneath stones in muddy places. *Peloscolex benedeni* is associated with them until the salinity begins rapidly to fall. *Tubifex tubifex* extends from the fresh water into the upper brackish region. It may be regarded as succeeding *T. costatus*.

CRUSTACEA.

The Cladocera are recorded only from the highly saline area.

Of the *Copepoda Gymnoplea* the species of greatest interest are *Acartia Clausi*, *A. bifilosa*, and *Eurytemora affinis*. *A. Clausi* is abundant in the

Hamoaze, diminishing in numbers above Saltash and finally disappearing about the confluence of the Tamar and the Tavy. *A. bifilosa* makes its appearance about this point, becomes numerous about Hole's Hole, and disappears somewhere near the Cotehele district. It has not been seen in the plankton from Calstock. *Eurytemora affinis* is scarce in the Saltash area, increases by Hole's Hole, forms the greater part of the plankton upwards along the river, until at Calstock it is present as almost a pure culture. Shortly after this point the numbers fall off rapidly, disappearance taking place near Morwell Rocks.

The salinity range at high water for *E. affinis* was determined to be approximately $33°/_{oo}$ to $0{\cdot}1°/_{oo}$.

The brackish-water Gymnoplea were found to be much more numerous at the beginning of November than at any other time during the summer, there being indications of an autumn–winter maximum. The adult females were all carrying eggs, and an enormous number of larvæ and young adults were found. It is noteworthy that, in a series of collections made between Neille Point and Morwell Rocks (7.11.28), the samples from the upper part of the river contained only adults with all the females carrying eggs, while those from the lower portion contained many larvæ and young adults, and relatively fewer egg-bearing females.

The Harpacticidæ are mostly littoral species, and do not appear to extend beyond a lower salinity limit of about $20°/_{oo}$ at high water. The weed on the buoys in the Hamoaze and off Neille Point carries a very dense fauna, consisting chiefly of *Idya furcata*, *Thalestris longimana*, and *Parathalestris Clausi*. *Notodelphys Allmani* is coextensive with its host *Ascidiella aspersa*, which is restricted to the region of high salinity.

The distribution of the four species of *Cirripedia Thoracica* shows *Chthamalus stellatus* to have the narrowest range, *Balanus balanoides* and *B. crenatus* extending further up, but being restricted to a lower salinity limit of about $33°/_{oo}$, and *B. improvisus* occurring furthest up in the region of great salinity variation, between low and high water.

In the up-river localities there were indications that additions to the barnacle population were made very occasionally since, at Cargreen, above Halton Quay and at St. Germans Bridge, there were no examples seen which could be regarded as having been deposited this year. All the specimens were very large, and apparently aged. During the summer, large numbers of Balanus nauplii from 5–12% of the total catch, were taken in the region of the mouth of the River Lynher, but none was seen in collections made off Neille Point.

Sacculina carcini has a limited distribution. No specimens of infected *Carcinus mænas* were taken above Neille Point. The nauplii were very abundant in plankton taken in the Hamoaze, but none appeared to get up to the Neille Point district.

The Schizopoda contributed four species, of which *Schistomysis ornata* had the shortest range and the least significance from the point of view of number. The most abundant Mysid was *Neomysis vulgaris*, *Macropsis slabberi* was somewhat less, on the whole, and *Praunus flexuosus* much less than either. Neomysis and Praunus were usually found at or near the bottom, feeding on detritus. Of the mobile organisms the Mysids may be regarded as of the utmost importance in the conversion of detritus into animal matter. This importance, in the estuaries, can hardly be exaggerated.

Macropsis is usually found swimming freely in the more open water, and may be considered as a pelagic animal. Collections at different depths showed generally that it was most abundant in the upper portion of its vertical range, and was only occasionally taken within 1 foot of the bottom. On the other hand, Praunus and Neomysis were almost always thick within 1 foot of the bottom, and either absent or very poorly represented higher up. In shallow water, of about 1 fathom or less, the three species would be found well mixed down to the bottom. Occasionally, as when much fresh water was coming down, Neomysis and Praunus were taken near the surface. At such times there was a fair amount of turbidity.

The Mysids in the estuaries are moved about very much by the tide. Observations above St. Germans, near Markwell, gave the following data, collections being made with the stramin net resting on the bed, 10-minute hauls, in a stream, at most, 1 foot deep, the net being placed mouth upstream :—

	1.30 p.m., a few minutes before L.W.	2.40 p.m., during L.W. period.	3.25 p.m. after 10 mins. flow.
Neomysis vulgaris	40	10	6970
Crangon vulgaris	11	—	4
Gammarus locusta	1	1	1

Reference to the notes on salinity changes at this place (p. 86) will show that the rise in salinity commenced after 3.20 p.m., and was very marked at 4.10 p.m. As the water moved upstream the swarms of Mysids could be seen, in the shallow water along the edge, to form a thick soup, and the water surface here was bespattered with splashes, caused by the jumping of the myriads of overcrowded animals. This phenomenon was observed regularly, at the turn of the tide and for some time afterwards, until they were more thinly distributed over the substratum. A similar concentration takes place along the edge of the tide, as it ebbs from the mud-banks.

It is noticeable that the Mysid fauna at the edge of the tide is, in effect, a Neomysis fauna. The vertical distribution of Neomysis and Macropsis, in the deeper parts, may be fairly generally expressed by the following table :—

Off Sheviock Wood R. Lynher.	2 ft. deep. % of total.	7 ft. deep. % of total.	13 ft. deep. % of total.	20 ft. deep. % of total.	Bottom 24 ft. % of total.
Macropsis slabberi	98·5	29	67	64	—
Neomysis vulgaris	—	8·4	18	14·2	47
Praunus flexuosus	—	43	4	—	—
Crangon vulgaris	—	—	—	—	27

The table does not show the usual distribution of Praunus, but in all other collections, whether singly from the bottom or in vertical series, this animal has been taken chiefly within the lowest foot or so of the bed. It and Neomysis are to be taken in great numbers among Fucus.

The three species are capable of suffering a very wide range of salinity changes ; especially is this the case with Neomysis, which extends from the sea up to Morwell Rocks, with a high-water salinity of about 0·1°/₀₀. The other two do not persist far beyond Calstock, where the high-water salinity was 7·8°/₀₀ and low-water 0·3°/₀₀.

Neomysis was observed breeding throughout the summer and into November, while Praunus and Macropsis were not taken with full brood-pouches later than the beginning of September.

Three species of Isopoda claimed special attention, viz. : *Sphæroma serratum*, *S. rugicauda*, and *Paragnathia formica*. The first is a marine species, which extends up the Tamar to about half-way between Hole's Hole and Pentillie Quay, where the high-water salinity was 24°/₀₀ ; *S. rugicauda* succeeded it and persisted to a region a little above Calstock. The same succession was observed in the Lynher, the junction of the two ranges being near Sheviock Wood. *S. rugicauda* was found almost at the upper limit of the tidal zone, near Tideford. This species provided examples having one to three notches on the postero-lateral border of the exopodite of the uropod, collected at Calstock and St. Germans.

Paragnathia formica was also common in both rivers. In the Tamar, the determined range was from Neille Point to a piece of hard ground opposite the hamlet of Boheterick, a little distance below Calstock, with a high-water salinity of well below 20°/₀₀. It was collected from the edge of salt marshes near high-water mark, in circumstances such as were described by Omer–Cooper (**36**), and from beneath stones at about half-tide. The praniza stage was often taken in the stramin net at various depths.

The *Amphipoda* have presented interesting examples of species range and succession.

Three species of Gammarus have been taken commonly, *G. marinus*, *G. locusta*, *G. duebenii*. The first was found to be co-extensive with *Fucus* *vesiculosus*, and was not found further up than North Hooe. *G. locusta* was found to be very common and extended up to Morwell Rocks. *G. duebenii* was met with first opposite Cotehele Woods, below Calstock, and was common up to Weir Head, where the water was apparently fresh (H.W. Sal. $0{\cdot}06^{\circ}/_{\circ\circ}$). It was abundant in the moss *Eurhynchium rusciforme.*

G. marinus was usually found among Fucus and under stones, *G. locusta* was also taken swimming freely, chiefly near the bottom, and was very abundant, in company with Neomysis and Praunus, on the banks of vegetable debris ("Point-stuff"), which formed at bends. *G. duebenni* was taken in similar circumstances to those of *G. locusta,* and may be regarded as succeeding the latter in brackish water.

Corophium crassicorne extends from the sea to about half-way between Cargreen and Weir Quay, where the salinity undergoes a considerable fall. It is very abundant among the weed growing on buoys in the Hamoaze and further upstream, and along the shore. *Corophium grossipes* succeeds it in the upper part of the stream, it having been met with first near North Hooe. This species burrows in the earthen banks and in the stiffer mud, and forms U-shaped earthen tunnels under stones. In the Calstock district it is very abundant and replaces *Nereis diversicolor* in the banks. A similar relation between the worm and the amphipod was seen in the River Tiddy, between St. Germans and Tideford. The upper limit was not discovered in the Tamar, but in the Tiddy it was coincident with the end of the tidal zone.

Seven species of Decapoda were recorded of which six may be considered. The genus Leander provided three species, viz., *L. serratus,* which extends almost up to Pentillie Quay, it being most abundant in the region of higher salinity, and is commercially exploited about Saltash and the lower district; *L. squilla,* which was not taken above Neille Point, but probably extends somewhat further, since it was common at this place; and *L. longirostris,* which occurs frequently in the Lynher and Tiddy, and in the Tamar above Hole's Hole, extending as far as about a mile above Calstock. A few juvenile specimens of this last species were taken in St. John's Lake. Gurney (**18**) records the taking of young stages of this species off Plymouth. *L. serratus* and *L. squilla* are also common in the Lynher.

Palæmonetes varians has been found abundantly about St. Germans, both in pools on the salt marsh, and in the side streams communicating with the river. It was taken also in the Tamar, a little above Calstock. On the whole, this species is much less abundant in the main stream than in the small lateral diverticula. It thrives well in a salinity change of from less than $0{\cdot}3^{\circ}/_{\circ\circ}$ to $29{\cdot}6^{\circ}/_{\circ\circ}$.

Crangon vulgaris and *Carcinus mænas* have a range about the same as that of *Nereis diversicolor*, and are both common. In the upper portion of the Tamar, about Calstock, they appear to be smaller than nearer the sea. Large numbers have been taken from the beds of "Point-stuff," in company with Neomysis, Praunus, and *Gammarus locusta*.

MOLLUSCA.

The common molluscs are few in species. In spite of the fact that there is a considerable amount of rock exposed within the observed range of *Patella vulgata*, this species has been found only rarely. *Littorina littorea* and *L. obtusata* are both common as far as Sheviock Wood and Neille Point, on both hard and soft ground. Old dead shells of *L. obtusata* were picked up beside Cargreen, but no signs of living examples were seen. The egg-capsules of *L. littorea* were taken in the plankton, half a mile above St. Germans Bridge. *Paludestrina stagnalis* was found swarming over the mud-flats which carry Zostera, viz.: St. Germans Lake and the flat next above Saltash Bridge, on the left bank. Its numbers diminish rapidly past Cargreen and it is found only occasionally above Pentillie. *Mytilus edulis* and *Cardium edule* have a commercial value about Saltash, many being collected up as far as Warren Point on the left bank, and Neille Point on the right. The mussel-bed off the latter point is quite extensive, lying in water from 12 inches to 18 inches at low tide. *Ostrea edulis* has been taken from the mussel-bed, and is said to be abundant in the vicinity. *Scrobicularia plana* is the only other mollusc which has been taken commonly. It is found in the stiff mud of St. John's Lake, of the Lynher as far as Port Eliot, and in the Tamar as far as Pentillie. It tends to decrease in number as the mud becomes softer or more sandy, and also as it is followed into the less saline waters.

POLYZOA.

Membranipora Lacroixii and *Bowerbankia imbricata* were taken up as far as half a mile above Halton Quay, where the salinity range from high to low water was approximately $21°/_{\circ\circ}$ to $4°/_{\circ\circ}$. The latter species is exceedingly abundant as far up as Cargreen, covering the Fucus fronds, in some cases, almost completely. Membranipora is also common, especially on stones and shells. *Lepralia Pallasiana* and *Alcyonidium mytili* both cease a little way beyond Cargreen, where the high-water salinity begins rapidly to decrease. They also are very abundant.

TUNICATA.

Oikopleura dioica moves with the tide and does not appear to pass Saltash. *Ascidiella aspersa* is the common species, it being very abundant on the mussel-bed off Neille Point, and becoming rapidly scarcer until it ends about Hole's Hole in the Tamar, and about Sheviock Wood in the Lynher.

PISCES.

For the purpose of these notes only *Gobius microps* will be considered here. It is present in great quantity and ranges up to Morwell Rocks. At Calstock it formed in three samples, taken with the stramin net, 10·4%, 15%, and 25% respectively of the total (29.6.28). Large numbers are to be found, at low water, in the small channels traversing mud-banks, and in pools. Along the edge of the tide, immediately after the Mysids have passed, they may be taken in abundance. When the mud-flats are covered by the tide, Gobius spreads out over the bed similarly to Neomysis and Praunus, but not in such quantity. It feeds chiefly upon Mysids and Copepods, and is to be regarded as a serious competitor of the young Clupeoids which live in the estuaries (**15**).

I wish to record my indebtedness to Dr. E. J. Allen, F.R.S., and the staff of the Marine Biological Laboratory, Plymouth, for valuable assistance and continued interest, to Dr. G. P. Bidder, Miss S. L. Garstang (Mrs. A. C. Hardy), Mr. W. Edgar Evans, Mr. R. Gurney, and Professor W. M. Tattersall, who have decided certain species for me, and to the Council of the University of Leeds who gave me leave of absence to carry out the investigation.

NOTE ON HETEROCIRRUS ZETLANDICUS.

The worm which is recorded here under this name, although answering in most of its characteristics to the description of the species, differs from the type in not possessing crochets. All the setæ are capillary bristles, but in cases where they are broken the stumps have a resemblance to those figures of crochets given in Southern, Clare Island Survey, Proc. Roy. Irish Acad., XXXI–2, 1914, Pl. XII, Fig. 29 J.K. It agrees closely with stage B, *loc. cit.*, pp. 47, 117, 118, and the possibility suggests itself that the crochets described and figured by Southern were broken capillary bristles, damaged either recently or at a more remote period.

FAUNISTIC LIST (Compare with lists in **1**, **2**, **3**, **37**, **38**).*

PROTOZOA FORAMINIFERA :

Polystomellinæ

Polystomella crispa L. (**53**). Common in Tamar ; taken up to ½ mile above Cargreen. Common among tow-nettings and dredgings.

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* Figures in thick type refer to the list of References on p. 107.

METAZOA PORIFERA:

Haplosclerid æ.

Halichondria panicea Pallas (**6**). Rat Island and Hamoaze; massive growth on Neille Point mussel-bed.

Axinellidæ.

Hymeniacidon sanguineum Grant (**6**). Rat Island; Weir Point.

GYMNOBLASTEA.

Clavidæ.

Clava multicornis Forskål (**4**). Occasional, on wood and stones in main channel off Cargreen.

Clava squamata O.F.M. (**4**). Relatively common in main channel off Cargreen.

Cordylophora lacustris Allman (**4**). Abundant above, at, and below Calstock; massive growth on Calstock Bridge, and on rocks below Cotehele Woods. Extends down to within ½ mile of Halton Quay.

CALYPTOBLASTEA.

Campanulariidæ.

Obelia geniculata L. (**22**). On Fucus, as far as Cargreen in Tamar, and hard ground, by boathouse near Ince Castle in Lynher.

Obelaria gelatinosa Pallas (**22**). Abundant in Tamar, extending to North Hooe; abundant in Lynher, extending to Port Eliot.

Gonothyraea Lovéni Allman (**22**). On Fucus near Warren Point, R. Tamar; on Fucus near boathouse by Ince Castle, R. Lynher.

Sertulariidæ.

Sertularia pumila L. (**22**). On Fucus up to Neille Point, and to boathouse by Ince Castle.

Eucopidæ.

Phialidium hemisphaericum Gronovius (**29**). Taken in plankton up to within 1 mile of Pentillie Quay, R. Tamar, and up to Sheviock Woods, R. Lynher. Very abundant in Hamoaze and adjacent waters during summer.

DISCOMEDUSÆ.

Ulmaridæ.

Aurelia aurita Lamarck (**29**). Medusæ taken to within 1 mile of Pentillie Quay, R. Tamar; Scyphistomæ abundant on Neille Point mussel-bed, also at Cargreen Hard, and above Antony Creek, R. Lynher.

ZOANTHARIA.

Actiniidæ.

Actinia equina L. (**17**). On Rocks up to Neille Point, R. Tamar; up to boathouse near Ince Castle, R. Lynher.

Metridium senilis L. var. *pallidum* (**17**). On piece of wood ½ mile above Saltash Bridge.

Sagartia luciæ Verrill (**30**). On rocks at Bull Point, Hamoaze; Neille Point and Cargreen Hard, R. Tamar.

Sagartia troglodytes Gosse var. *ornata* (**17**). On piece of wood, ½ mile above Saltash Bridge; mussel-bed off Neille Point, R. Tamar.

Cereus pedunculatus Pennant (**17**). Rat Island; St. John's Lake.

Diadumene cincta T. A. Steph. (**51**). Mussel-bed off Neille Point, R. Tamar.

NEMERTINI.

Amphiporidæ.

Amphiporus lactifloreus Johnston (**25**). Under stones, between Saltash Bridge and Warren Point.

Tetrastemmidæ.

Prostoma melanocephalum melanocephalum Johnston (**8**). Under stones, between Saltash Bridge and Warren Point; Rat Island.

Lineus bilineatus Renier (**8**). Mussel-bed off Neille Point.

ROTIFERA.

Synchæta gyrina Hood (**34**). Common in plankton between Neille Point and Cotehele (Nov.).

POLYCHÆTA.

Syllidæ.

Syllis gracilis Grube (**12**). Rat Island.

Syllis prolifera Krohn (**12**). Bull Point, Hamoaze; mussel-bed off Neille Point.

Odontosyllis ctenostoma Claparède (**12**). Mussel-bed off Neille Point.

Exogone gemmifera Pagenstecher (**12**). Shore, by boathouse near Ince Castle, R. Lynher.

Autolytus prolifer O.F.M. (**12**). In plankton from Hamoaze, off Bull Point.

Hesionidæ.

Kefersteinia cirrata Keferstein (**12**). Rat Island; common in mussel-bed off Neille Point.

Magalia perarmata Marion and Bobretsky (**12**). Common on mussel-bed off Neille Point; Cargreen Hard.

Aphroditidæ.

Lagisca extenuata Grube (**12**). Mussel-bed off Neille Point.

Harmothoë impar Johnston (**12**). Mussel-bed off Neille Point.

Pholoë minuta Fabr. (**12**). Cargreen Hard.

Phyllodocidæ.

Phyllodoce maculata L. (**12**). Rat Island.

Nereidæ.

Leptonereis glauca Clap. (**12**). Mussel-bed off Neille Point.

Nereis (Perinereis) cultifera Grube (**12**). Rat Island.

Nereis (Hediste) diversicolor O.F.M. (**12**). Dominant animal in mudbanks, extending to ½ mile above Calstock, and to about 1 mile below Tideford.

Nephthydæ.

Nephthys Hombergii Lamarck (**12**). Widely distributed in mud, up to Pentillie Quay, and to lower end of Sheviock Wood.

Glyceridæ.

Glycera alba Rathke (**12**). Rat Island, in mud.

Spionidæ.

Scolecolepis fuliginosa Clap. (**13**). Neille Point, in small pool.

Nerine foliosa Aud. et M-Ed. (**13**). Rat Island, in mud.

Pygospio elegans Clap. (**13**). Shore, by boathouse near Ince Castle.

Polydora ciliata Johnston (**13**). Widely distributed up to ½ mile beyond Halton Quay and to Port Eliot. In mud, in clefts in rock, and in shells of Ostrea and Balanus.

Polydora hoplura Clap. (**13**). Mussel-bed, Neille Point.

Cirratulidæ.

Audounia tentaculata Montagu (**13**). St. John's Lake; Rat Island.

Cirratulus cirratus O.F.M. (**13**). Rat Island; shore, by boathouse near Ince Castle.

Heterocirrus zetlandicus McIntosh (**13**). Common in stiff mud, up to Neille Point; Rat Island.

Streblospio Shrubsolii Buchanan (**13**). Occasional, in mud off Port Eliot, and up to ½ mile above Halton Quay.

Terebellidæ.

Lanice conchilega Pallas (**13**). St. John's Lake; Rat Island; shore, by boathouse near Ince Castle.

Ampharetidæ.

Ampharete Grubei Malmgren (**13**). St. John's Lake.

Melinna palmata (**13**). Wivelscombe Lake; Rat Island.

Capitellidæ.

Heteromastus filiformis Clap. (**13**). Common in stiff mud, in R. Tamar up to Neille Point, and in R. Lynher up to Sheviock Wood.

Capitella capitata Fabr. (**13**). Rat Island; shore, by boathouse near Ince Castle.

Arenicolidæ.

Arenicola marina L. (**13**). Up to Cargreen, and to confluence of R. Lynher and R. Tiddy.

Sabellidæ.

Dasychone bombyx Dalyell (**13**). St. John's Lake.

Serpulidæ.

Pomatoceros triqueter L. (**13**). Up to Hole's Hole, and to Sheviock Wood. Commoner nearer the sea.

Spirorbis spirillum L. (**13**). Off Neille Point on stones.

Spirorbis borealis Daudin (**13**). Rat Island on Fucus and stones.

OLIGOCHÆTA.

Naididæ.

Chætogaster diaphanus Gruith (**31**). Among moss at Weir Head; a freshwater species in company with brackish-water forms.

Nais elinguis Müller, Oerstedt. (**31**). In moss with Chætogaster.

Tubificidæ.

Tubifex costatus Clap. (**32**). Widely distributed and common in mud, and under stones on mud and muddy sand, up to ½ mile beyond Calstock Bridge, and to mud-flats above St. Germans Bridge.

Tubifex tubifex Müller (**31**). Extending from fresh water down to about ⅓ mile above Calstock. In R. Tiddy near Tideford.

Clitellio arenarius Müller (**32**). In stiff mud and muddy sand, and under stones, up to ½ mile above Calstock Bridge, and to shore, by boathouse near Ince Castle.

Peloscolex Benedeni Udeken (**32**). Up to Neille Point and Port Eliot, in stiff mud and muddy sand. Common.

Chætognatha.

Sagitta bipunctata Quoy and Gaimard (**19**). R. Tamar. Occasional specimens in plankton, ½ mile beyond Pentillie Quay.

BRANCHIOPODA.

Podon intermedius Lilljeb. (**34**). In Plankton, up to Neille Point, and to Sheviock Wood.

Evadne Nordmanni Lovén (**34**). In plankton, off *Impregnable*.

Chydorus sphaericus O.F.M. (**26**). Near lower end of Weir Island, Weir Head, in water carrying brackish-water forms. A freshwater species.

COPEPODA.

Calanidæ.

Calanus finmarchicus Gunnerus (**44**). At mouth of Hamoaze.

Pseudocalanidæ.

Pseudocalanus elongatus Bœck (**44**). In plankton off *Impregnable.*

Centropagidæ.

Centropages typicus Kröyer (**44**). Up to mouth of R. Tavy.

Temoridæ.

Temora longicornis O.F.M. (**44**). Up to mouth of R. Tavy.

Eurytemora affinis Poppe (**16**). From about *Impregnable* to Morwellham Quay and to Port Eliot. Common in brackish water.

Eurytemora velox Lilljeb. (**16**). In shallow pool on salt marsh above St. Germans.

Parapontellidæ.

Parapontella brevicornis Lubbock (**44**). In Hamoaze off *Impregnable.*

Acartiidæ.

Acartia Clausi Giesbr. (**44**). Common in Lynher, and in Tamar up to Neille Point.

Acartia bifilosa Giesbr. (**16**). Common in Tamar from Neille Point to near Cotehele.

Cyclopidæ.

Oithona helgolandica Claus (**46**). Up to Neille Point and to Antony Passage. Common.

Cyclopina longicornis Bœck (**46**). Up to Saltash. Common.

Harpacticoida.

Longipedia minor Scott (**45**). Neille Point; Hole's Hole, amongst weed and on mud.

Ectinosoma melaniceps Bœck (**47**). Cargreen Hard.

Euterpina acutifrons Dana (**45**). In plankton, to Halton Quay.

Harpacticus chelifer Müller (**45**). In weed, on Neille Point buoy.

Harpacticus gracilis Claus (**45**). Up to Halton Quay and to Sheviock Wood, in plankton and on bottom. Common.

Harpacticus flexus Brady (**45**). Up to Hole's Hole. Common.

Alteutha interrupta Goodsir (**45**). On Neille Point buoy, and in townettings from off Wivelscombe Lake.

Idya furcata Baird (**45**). Common on buoys and on shore, also in tow-nettings. Up to Hole's Hole, and boathouse by Ince Castle.

Thalestris longimana Claus (**45**). Up to Neille Point buoy. Common on buoys.

Parathalestris harpacticoides Claus (**45**). On No. 15 Buoy, Hamoaze.

Parathalestris Clausi Norman (**45**). On buoys up to Neille Point. Common.

Dactylopusia thisboides Claus (**45**). Rat Island; up to Neille Point buoy.

Dactylopusia vulgaris G. O. Sars (**45**). Neille Point, in pool at half-tide.

Dactylopodella flava Claus (**45**). Rat Island.

Laophonte proxima G. O. Sars (**45**). Cargreen Hard; Hole's Hole. On Bowerbankia.

Laophonte similis Claus (**45**). On shore, by boathouse near Ince Castle.

Laophonte Strömi Baird (**45**). Common on buoys up to Neille Point.

Laophonte abbreviata G. O. Sars (**47**). Half a mile above Cargreen, on mud.

Enhydrosoma propinquum Brady (**45**). In tow-nettings, off *Impregnable* and near Sheviock Wood.

Cymbasoma longispinosum Bourne (**48**). In tow-nettings, up to Sheviock Wood, and to Neille Point buoy.

Corycæidæ.

Corycæus anglicus Lubbock (**7**). In plankton, off *Impregnable.*

Notodelphydæ.

Notodelphys Allmani Thorell (**48**). In *Ascidiella aspersa*, up to Hole's Hole, and Sheviock Wood.

Ascidicola rosea Thorell (**48**). In *Ascidiella aspersa*, Sheviock Wood.

CIRRIPEDIA.

Balanidæ.

Balanus balanoides L. (**10**). Up to shore by boathouse near Ince Castle, and to Cargreen. Common.

Balanus crenatus Bruguière (**10**). Up to shore by boathouse near Ince Castle, and to Cargreen. Fairly common.

Balanus improvisus Darwin (**10**). Half a mile above Halton Quay; St. Germans Bridge.

Chthamalus stellatus Poli (**10**). Bull Point, Hamoaze.

Peltrogastridæ.

Sacculina carcini Thompson (**52**). On *Carcinus mænas* up to Neille Point.

SCHIZOPODA.

Mysinæ.

Praunus flexuosus Müller (**34**). Common up to ¼ mile above Calstock, and to ½ mile above St. Germans Bridge.

Schistomysis ornata G. O. Sars (**34**). Up to Sheviock Wood.

Macropsis Slabberi v. Beneden (**34**). Abundant. Up to ½ mile above Calstock, and 2 miles above St. Germans.

Neomysis vulgaris Thompson (**34**). Very abundant. Up to Morwell Rocks, and to Penimble, R. Tiddy.

ISOPODA.

Anthuridæ.

Anthura gracilis Montagu (**35**). Occasional. Rat Island; off Port Eliot. In mud.

Sphæroma serratum Fabr. (**49**). Up to 1 mile above Weir Quay, and to Wivelscombe Lake.

Sphæroma rugicauda Leach (**49**). From ½ mile below Pentillie Quay to ½ mile above Calstock; from Sheviock Wood to Tideford. Abundant.

Dynamene rubra Leach (**49**). Shore at Bull Point, Hamoaze.

Limnoriidæ.

Limnoria lignorum Rathke (**43**). In log, on mud-flat ½ mile above Cargreen.

Gnathiidæ.

Paragnathia formica Hesse (**33**). Neille Point to 1 mile below Calstock; about junction of R. Lynher and R. Tiddy and main stream. Common. Got from edge of salt marsh about H.W., and in tow-nets.

Janiridæ.

Jæra marina Fabr. (**43**). Common at Bull Point, Hamoaze; shore, by boathouse near Ince Castle.

Idotheidæ.

Idothea baltica Pallas (**43**). St. John's Lake among Zostera; off Ince Castle.

Ligiidæ.

Ligia oceanica L. (**43**). In rocks by Ince Castle; in wall above Saltash Bridge.

Cryptoniscinæ.

Hemioniscus balani Spence Bate (**52**). In *Balanus balanoides* from St. John's Lake and Bull Point.

AMPHIPODA.

Hyperiidæ.

Hyperia galba Mont. (**42**). One mile below Pentillie Quay, *Aurelia aurita* also taken.

Orchestiidæ.

Orchestia littorea Mont. (**42**). Up to North Hooe, and to Ince Castle.

Calliopiidæ.

Apherusa Jurinii M.Edw. (**42**). Corner opposite *Defiance*, right bank. Ovigerous females, and small half-grown animals (19.8.28).

Gammaridæ.

Gammarus locusta L. (**42**). Very common up to Morwell Rocks, and to Tredinnick, below Tideford.

Gammarus marinus Leach (**42**). Common to North Hooe, and to junction of Lynher and Tiddy.

Gammarus duebenii Lilljeb. (**42**). From about 1 mile below Calstock to Weir Head; from Sheviock Wood to Penimble, below Tideford.

Melita palmata Mont. (**42**). Up to Weir Quay, usually on hard ground.

Podoceridæ.

Podocerus (Jassa) falcatus Mont. (**42**). In weed on buoys, up to Neille Point and up to Sheviock Wood. Taken from bottom and in nets. Common.

Podocerus odontonyx G. O. Sars (**42**). No. 15 Buoy off Bull Point, Hamoaze. Fairly common.

Corophiidæ.

Corophium crassicorne Bruzel (**42**). Up to ½ mile above Cargreen. Common on buoys and on mussel-bed.

Corophium grossipes L. (**42**). Common from North Hooe towards Morwellham; R. Lynher from Wacker Creek* to Tideford.

Caprellidæ.

Pseudoprotella phasma Mont. (**9**). Off lower end of Sheviock Wood, 1 specimen.

Pariambus typicus Kröyer (**9**). Off lower end of Sheviock Wood, 1 specimen.

MACRURA.

Palæmonidæ.

Leander serratus Pennant (**52**). Up to Pentillie Quay, and to confluence of Lynher and Tiddy. Common.

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* Near Antony, after which the author has named it, *passim*.—Ed.

Leander longirostris H.M.-Ed. (**52**). From St. John's Lake to ¼ mile above Calstock Bridge. In Lynher to ¼ mile above St. Germans Bridge.

Leander squilla L. (**52**). Up to Neille Point, and to boathouse near Ince Castle.

Crangonidæ.

Crangon vulgaris L. (**52**). Up to ¼ mile above Calstock, and to ¼ mile above St. Germans Bridge. Common.

ANOMURA.

Paguridæ.

Eupagurus bernhardus L. (**5**). St. John's Lake; Bull Point; Hamoaze.

Porcellanidæ.

Porcellana longicornis L. (**5**). Mussel-bed, Neille Point.

BRACHYURA.

Portunidæ.

Carcinus mænas Pennant (**5**). Common up to ¾ mile above Calstock Bridge, and to Tredinnick.

INSECTA.

Thysanura.

Petrobius maritimus Leach (**39**). Up to Port Eliot, and to Warren Point.

Trichoptera.

Leptocerus annulicornis Steph. (**40**). Larvæ in moss, with brackish-water forms, below Weir Head. A freshwater larva.

PROSOBRANCHIATA.

Patellidæ.

Patella vulgata L. (**24**). Occasional specimens on stones, on mud-bank; St. John's Lake, and left bank above Saltash Bridge.

Littorinidæ.

Littorina littorea L. (**24**). Common up to Neille Point, and to Sheviock Wood.

Littorina obtusata L. (**24**). Common up to Neille Point, and to Sheviock Wood.

Littorina rudis Maton (**24**). St. John's Lake; by boathouse near Ince Castle.

Assimineidæ.

Paludestrina stagnalis Baster (**24**). Common up to North Hooe, and to Sheviock Wood.

Cypraeidæ.

Trivia europæa Mont. (**14**). Mussel-bed, Neille Point, 1 specimen.

PELECYPODA.

Mytilidæ.

Mytilus edulis L. (**14**). Common up to Weir Quay, and to Sheviock Wood.

Scrobiculariidæ.

Scrobicularia plana da Costa (**14**). Common in stiff mud. Up to Pentillie Quay, and to Port Eliot.

Tellinidæ.

Macoma baltica L. (**14**). Shore, by boathouse near Ince Castle. Dead shells near Hole's Hole.

Veneridæ.

Tapes pallustra Mont. (**14**). Rat Island.

Cardiidæ.

Cardium edule L. (**14**). Common. Up to Hole's Hole, and to St. Germans.

Cycladidæ.

Pisidium casertanum Poli (**50**). In fine clean sand, down to lower end of Morwell Rocks. Freshwater species among brackish-water forms.

POLYZOA.

Membraniporidæ.

Membranipora Lacroixi Audouin (**23**). Common. Up to ½ mile above Halton Quay, and to St. Germans Bridge.

Escharidæ.

Lepralia Pallasiana Moll (**23**). Common. Up to Cargreen, and to Sheviock Wood.

Alcyonidiidæ.

Alcyonidium mytili Dalyell (**23**). Common. Up to ½ mile above Cargreen, and to shore, by boathouse near Ince Castle.

Vesiculariidæ.

Bowerbankia imbricata Adams (**23**). Very abundant. Up to ½ mile above Halton Quay, and to confluence of Lynher and Tiddy.

Pedicillinidæ.

Pedicillina cernua Pallas (**23**). Mussel-bed, Neille Point.

ECHINODERMATA.

Ophiothricidæ.

Ophiothrix fragilis Abildgaard (**27**). Mussel-bed off Neille Point.

TUNICATA.

Appendiculariidæ.

Oikipleura dioica Fol. (**34**). In plankton. Hamoaze up to *Impregnable.*

Molgulidæ.

Molgula manhattensis De Kay (**20**). St. John's Lake; lower end of Sheviock Wood. Occasional.

Ascidiidæ.

Ascidiella aspersa O.F.M. (**21**). Common. Up to ½ mile above Hole's Hole, and to Sheviock Wood.

Ciona intestinalis L. (**21**). Occasional. Shore, by boathouse near Ince Castle.

Botryllidæ.

Botryllus Schlosseri Pallas (**20**). Up to Hole's Hole on *Fucus.*

Botrylloides rubrum M.-Ed. (**21**). Rat Island.

Didemnidæ.

Distalpia sp. Shore, by boathouse near Ince Castle.

CYCLOSTOMATA.

Petromyzontidæ.

Petromyzon marinus L. (**11**). Weir Head.

PISCES.

Salmonidæ.

Salmo salar L. (**11**). In Tamar and tributaries.

Murænidæ.

Anguilla vulgaris Turton (**11**). Up to Weir Head.

Syngnathidæ.

Syngnathus acus L. (**11**). Up to Hole's Hole, and to Sheviock Wood.

Mugilidæ.

Mugil chelo Cuvier (**11**). Up to Weir Head. Common.

Pleuronectidæ.

Pleuronectes flesus L. (**11**). Up to Weir Head, and to Port Eliot.

Gobiidæ.

Gobius microps Kröyer (**11**). Very abundant. Up to Morwell Rocks, and to Port Eliot.

Agonidæ.

Agonus cataphractus L. (**11**). Mussel-bed, Neille Point.

Blenniidæ.

Blennius pholis L. (**11**). Rat Island.

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On some Factors Limiting the Habitat of *Arenicola marina.*

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CONTENTS.

INTRODUCTION.

In connection with a certain problem in Palæontology (**1**) it became necessary to learn in what manner the marine burrowing worms of the past (but not the tubicolous worms) were likely to have behaved with regard to red oxide of iron in the amorphous state. Some of the sands (now rocks) in which those worms burrowed contained a large amount of iron oxide, others contained practically none at all. Owing, however, to certain differences and one particular common feature shown by the rocks in question, the following experiments were instituted in the hope that the habitat of the present-day worms might throw some light on the conditions of the past.

Type of Habitat of *A. marina*.

Curiously enough, despite all that has been written about *A. marina* no accurate details can be found dealing with either the nature of the ground material nor with the minimum density of the water tolerated by the organism.

With regard to the minimum density Benham (**2**) says, "*A. marina* lives equally well in water of very different density," and Ashworth (**3**) states that it occurs far up certain estuaries which, in times of flood at least, are of much less density than sea-water. He also quotes Bohn to the effect that the absence of *A. marina* from the northern parts of the Baltic may be due to the same cause.

The information dealing with the ground material is much more plentiful. The researches of Allen and Todd (**4**, **5**) in the Salcombe and Exe estuaries would seem to show that *A. marina* in that locality is confined to a ground material consisting of mud and sand, mud and gravel, but very seldom, if ever, occurring in pure sand or pure mud. Ashworth (**3**) simply says that, " all species of Arenicola burrow in sand or gravel." Ferronnière (**6**) in his exhaustive survey of the Loire Estuary says that *A. marina* is found in sand containing an admixture of mud, but not in fresh deposits of mud where the water is flowing, although they were found in fœtid mud. Here, I think it is necessary to draw some distinction between the different kinds of mud. Fœtid mud must contain some organic matter, while mud formed by silt may contain very little organic matter and can hardly ever become fœtid.

My own limited investigations have shown that Arenicola does not occur in very pure sand. Where such appears to be the case, digging almost invariably shows that the pure top layer overlies a bed of sand mixed with mud.

From the work of Davidson (**7**) it will be seen that the top layer of sand must be more or less purified since the worms pass vast quantities through their bodies annually and, in the process, remove the organic matter.

MATERIAL AND APPARATUS.

The material used in this work consisted of a number of specimens of *Arenicola marina* supplied by the Marine Biological Station at Plymouth, quantities of sea-sand and sea-water and the following substances in a very finely divided state which were not known to have lethal properties :—

Ferric oxide.
Calcium carbonate.
Magnesium carbonate.
Stourbridge clay.
Kaolin.
Kieselguhr.

The apparatus consisted of a number of wide-mouthed bottles of 150 c.c. capacity and several " gas jars," 10 inches high and 2 inches in internal diameter.

Aeration was effected by means of a filter-pump fixed to a water-supply tap and connected by rubber tubing via a 4-way pipe to the various jars.

The jars were fitted with rubber stoppers and two glass tubes. Aeration of the water was, therefore, caused by suction and not by blowing as is more usual. This method was found to be highly satisfactory and, by careful adjustment of the size of the pipes, no great head of water was necessary to ensure a constant supply of air.

A. Experiments with Ferric Oxide.

Three gas jars were used for this experiment. Each contained 300 gms. of fresh sea-sand and 250 c.c. of sea-water.

The control worm was placed in its jar (A1). It immediately burrowed into the sand where it remained throughout the course of the experiments.

To jar (A2) was added 2 gms. of ferric oxide. This was allowed to settle, and then, by means of a glass rod, was stirred into the sand to a depth of about one and a quarter inches. This layer represented about 1 gm. of the oxide to 50 gms. of sand. When this had stood for an hour and very little oxide remained in suspension a worm was introduced. It immediately showed every sign of discomfort, wriggling into knots and everting and introverting its pharynx.

It made no attempt to burrow other than to place its anterior extremity against the sand and remove it almost immediately. When its movements began to slacken in vigour the organism was removed from the jar and revived in pure sea-water.

Fifty grammes of fresh sand were then poured evenly over the top of the sand and oxide, the water was pipetted off and a fresh supply added, thus ensuring that there was practically no iron oxide in suspension nor in direct contact with the water.

The same worm was again introduced. At first it remained quite still, but soon it began to burrow. The burrow extended down vertically only as far as the surface of the layer of oxide when it tended to run parallel to it, but never pierced it.

Jar (A3). A specimen of *Arenicola marina* was placed in a jar containing sand with a layer of iron oxide overlaid with $\frac{3}{4}$ inch of pure sand. The worm immediately started to burrow. On reaching the oxide it withdrew from the sand. This burrowing down to the oxide and complete withdrawal on coming in contact with it occurred several times. Ultimately, however, the burrow was continued along the surface of the oxide.

After a time, since the worm showed no sign of piercing the oxide, it was removed and placed in a jar containing only pure sand and sea-water. It was noticed that a small amount of the oxide had adhered to the anterior end of the worm. At first it made no attempt to burrow, but after lying quiescent for about three hours (after which time the oxide, although still there, was more in the nature of a layer of mucus containing iron oxide than a direct layer of the oxide on the worm), it burrowed completely.

Jar (A4). The conditions in this experiment were exactly similar to those in the previous experiment. Again the worm burrowed down to the surface of the oxide, but it did not withdraw from the burrow. After a certain amount of hesitation it continued the burrow parallel to the surface of the oxide. When no further effort was made to burrow vertically the worm was removed and placed in a jar of pure sand and sea-water. The anterior end of this worm had only a trace of oxide adhering to it. Burrowing commenced in just over an hour.

Jar (A5) was similar to (A1) in composition except that the sand contained 1 gm. of ferric oxide evenly distributed throughout. On top of this mixture a very thin layer of pure sand was spread. When a worm was introduced it almost immediately pierced the pure sand, but hesitated when it came into contact with the underlying mixture. However, after a few abortive attempts it ultimately burrowed right down until it was completely immersed. Its behaviour differed from that of the control in as much as while the control remained buried this specimen soon protruded its posterior end from the burrow and remained in that position until stimulated by tapping the jar or by shutting off and turning on the air supply suddenly. From these results it will be seen that *Arenicola marina* found the presence of ferric oxide repellent under two conditions only, viz. :—

1. When the water contained it in suspension.
2. When mixed with sand in a high proportion (1 gm. oxide to 50 gms. sand).

Since it appears to be more likely that Arenicola under natural conditions would come into contact with the ferric oxide in suspension in water, rather than the oxide-sand mixture, a further set of experiments were set going in order to find out the effect of the suspension on the worm.

To this end a suspension was made up of 0·5 gm. of the oxide in 100 c.c. sea-water. When a worm was introduced it immediately showed symptoms of acute discomfort in the usual way, i.e. by violent wriggling, etc. After six hours this worm ceased to show any movement and could not be revived.

B. Experiments with other Substances.

These results, of course, merely suggest that ferric oxide is abhorrent to Arenicola, so the following experiments were undertaken to find if the substance were lethal, and if so, in what quantity. The apparatus used was essentially the same as formerly, except that wide-mouthed bottles of 150 c.c. capacity were used instead of jars.

Three such bottles were fitted up as follows: water 140 c.c., with

	Ferric oxide.	Worm, size.
B1	0·00 gm.	Medium.
B2	0·05 gm.	Large.
B3	0·03 gm.	Small.

Almost immediately after introducing the oxide to bottles B2 and B3 it had completely enveloped both worms in a thin layer, but with this difference, worm B2 had practically all the available oxide adhering to it while worm B3 had only a portion of the available oxide adhering to it, although it was as completely enveloped as B2. (This, of course, was owing to its smaller size.)

The oxide, it may here be explained, was caught and retained by the mucus secreted by the worm.

In the case of worm B2, after 20 hours, the movements of the organism caused the oxide-laden sheath of mucus to be formed into a band about 1 cm. wide towards the anterior end, and from this time onwards the worm began to revive.

B3, however, was not so happily situated. No sooner did the mucous sheath begin to shorten than the parts so exposed collected a further coat of the oxide not previously collected. This coat it did not survive.

From this it can be concluded that ferric oxide in the amorphous state is not necessarily an active poison as far as *Arenicola marina* is concerned, but that it is lethal only when it can form with the mucus secreted by the organism a coat to shut off contact with the surrounding water for a sufficiently long period, and so inhibit respiration.

The difference between the case of A3 and B3 (when A3 lived in sand containing 0·3% of the oxide in sand while B3 was killed by 0·021%) may be explained by the fact that by burrowing through the sand the layer of oxide is scraped off with the mucus used to support the walls of the burrow.

If, as has been said, ferric oxide is lethal only in virtue of its physical properties, other substances of similar physical properties ought to act in the same way towards Arenicola.

To this end the B group of tests were repeated in exactly the same manner with (1) Calcium carbonate, (2) Magnesium carbonate, (3) Stourbridge clay, (4) Kaolin and (5) Kieselguhr. The results were so near those got with ferric oxide that it would merely be repetition to give details of the individual results, although it was noted that the kaolin appeared to be more intensely irritating to the worm than any of the others.

At the suggestion of Dr. Orton (to whom I am deeply indebted) these experiments were repeated in order that any alteration in hydrogen ion concentration might be checked.

The original sea-water was pH 7·95. The hydrogen ion concentration at the end of the experiment was found to have increased in the case of the control to pH 8·05. At the death of the worms it was pH 8·15 except in the case of the calcium carbonate where it reached the maximum of pH 8·35.

These results seem to prove, therefore, that it is the physical form and not the chemical composition of the substance which the organisms find intolerable.

Degree of Salinity.

Although the foregoing results would seem to show that *Arenicola marina* is unlikely to be found living in places where a large amount of fine sediment is brought down in suspension, it was found desirable to secure some data as to the degree of salinity of the water which would be necessary for the life of the organisms in estuaries. In this connection the jars each contained 100 gms. fresh sand.

C1 was used as a control with pure sea-water. C2–C5 contained respectively diluted sea-water, 75%, 50%, 30%, and 20%.

After four days no difference could be detected between the condition of the worms in C1, C2.

C3 and C4, however, were very much less active and showed no inclination to burrow, although they moved about in a feeble manner.

C5 remained almost motionless except for very inconspicuous rhythmic contractions. The condition of the organisms (C3–C5) may best be described as of such extreme turgidity that they were quite unable to exercise any power of locomotion, so that as burrowing worms they had ceased to exist.

An attempt was then made to find to what extent *Arenicola marina* could be slowly acclimatised to reduced salinity. Sea-water of salinity 35·2‰ was used as standard (pH 7·95).

Three 150 c.c. bottles were used.

C6 . .	Control.
C7 . .	50 pts. sea-water to 50 pts. fresh.
C8 . .	Normal sea-water.

Ten c.c. distilled water was added every 24 hours at first, but owing to the condition of the worm less frequent additions were made towards the end. (On several occasions the bottles became too full and some of the mixture had to be poured off.)

C7 became rather turgid when placed in the mixture, but moved about slightly. On the addition of more fresh water it practically ceased to move and only its turgid state indicated the condition of life. On the fifth day, however, it died—becoming quite flaccid—and the salinity was found to be 3·10‰ (pH 7·65).

C8 lived normally for the first four days after which, though never showing so much turgidity as C7, its movements slowed down and it died on the eighth day when the salinity of the water was 14·39‰ (pH 7·85).

While these experiments were going on the control worm of the previous experiment in its bottle was still being aerated, and at the same time evaporation was going on so that the salinity was gradually increasing. It was not noticed that the worm as a whole became any thinner or less active, but the effect on the caudal end was most marked. The latter did not become generally attenuated, but became reduced in length and constricted at three places, more or less equidistant, so that the part appeared as a series of knots. At the death of this worm (after evaporation had been going on for 12 days) the salinity was found to be 37·4‰ and the pH 8·05.

From C7 and C8, taken in conjunction with the previous lot of experiments, it would appear that *A. marina* does not tend to adapt itself to any great change in salinity, its range probably lying between 35‰ and 25‰ for, although it may actually live beyond those limits in the Laboratory, it could not do so under natural conditions.

Also, it should be noted that no sand was placed in the vessels with the worms during the latter experiments because of the fact that no guarantee could be given that the sand contained water of the same salinity as that above the sand.

SUMMARY.

In the foregoing work it was found that: *Arenicola marina* was repelled and could not burrow in sand containing 2·0% of ferric oxide in the amorphous state.

That 0·021% ferric oxide in suspension in sea-water was lethal owing to its forming with the mucus of the organism an envelope which prevented contact with the surrounding air-carrying water.

That calcium carbonate, magnesium carbonate, Stourbridge clay, kaolin, and kieselguhr had the same effect as the ferric oxide in suspension.

That although able to live for a short time in water of salinity 3·10‰, *Arenicola marina* tended to become so turgid in water of 14·32‰ as to be unable to burrow.

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Notes on the Rate of Growth of *Tellina tenuis* da Costa in the Firth of Clyde.

By

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With 5 Figures in the Text.

CONTENTS.

I. Foreword.

The material on which the present paper is based was collected from the Millport Marine Biological Station. I am indebted to the Superintendent, Mr. Elmhirst, for facilities for making the collections.

The biology of *Tellina tenuis* in the Cumbrae and neighbourhood was investigated during the autumn of 1926 and in 1927 (**2**), and the present paper is a direct continuation of that work. On several points in the earlier work, especially on the rate of growth of the species, it was felt that confirmatory evidence was necessary. A comparison of the size-frequency curves for the autumn of 1926 and 1927 showed that while on the 1926 curve there were only two modes, there were three on the 1927 curve, and that the mid mode of 1927 fell midway between those of 1926. This meant either, that rate of growth of the intermediate group in 1927 had been only half of that of the corresponding group in the previous year, or that on the 1926 curve one or more year groups were unrepresented. The latter explanation was considered at the time to be the more satisfactory one, and the work of the present year seems to confirm that view.

In the earlier investigation samples were collected at five intertidal stations, and at several stations below L.W.M., but for the present study it was not deemed necessary to re-examine all these, and regular collecting was restricted in the intertidal zone to Stations 5 and 2 (at L.W.M. springs and 40 yards below H.W.M. neaps respectively), and below L.W.M. to Stations 6 and 7 (2 and 3 fathoms respectively). In the earlier investigation the amount of sand sieved at the intertidal stations was a standard cut of a $\frac{1}{4}$ sq. metre dug to a depth of about 15 cm.,* but during 1928, in addition to this standard cut, extra cuts were sieved to increase the collections, especially for the older groups. For comparison with Kames Bay one station on the Hunterston Sands was examined. All stations were visited three times during the year, in March, June, and the end of September.

II. RATE OF GROWTH AT STATIONS 2 AND 5.

STN. 5 (Figs. 1–2. Table VI).

A comparison of the figures for October, 1927, with those of March, 1928, shows that, as in the previous year, there had been no growth during the winter months. There had been, however, a considerable mortality amongst the smallest individuals (1927 spat), the proportion of the population at 3 mm. having fallen from 20·7% to 14·8%.

By the beginning of June, 1928, only a little growth was apparent, the mode at 7 mm. having shifted to 8 mm. and that at 11 mm. to 12 mm., but there was no sign of any growth amongst the smaller sizes, the mode remaining at 3 mm.

By the end of September, 1928, the mode at 8 mm. in June had moved to 9 mm., but the group represented by the mode at 12 mm. in June, although still present, no longer formed a distinct group.

The greatest change had taken place amongst the smaller sizes in which the mode at 3 mm. in June had moved to 6 mm. and the young spat had appeared at 3 mm.

Compared with 1927 growth had been rather less and, amongst the smaller sizes, more erratic. For example, in 1927 the mode at 3 mm. in April moved to 5 mm. in June and to 7 mm. by the beginning of October, while in 1928 the mode at 3 mm. in March was still at the same figure in June, but reached 6 mm. by the end of September.

On the size-frequency curve for September, 1928, there are three modes at 3 mm., 6 mm., and 9 mm., representing respectively :

0+ group	1928 spat.
1+ ,, ...	1927 ,,
2+ ,, ...	1926 ,,

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* Contracted in the rest of the paper to "$\frac{1}{4}$ sq. m."

as we know from measurements since September, 1926. On the curve for October, 1927, there were also three modes at 3 mm., 7 mm., and 11 mm. respectively, which were considered to represent the 1927 spat, 1926 spat, and 1924 spat respectively (**2**, p. 690).

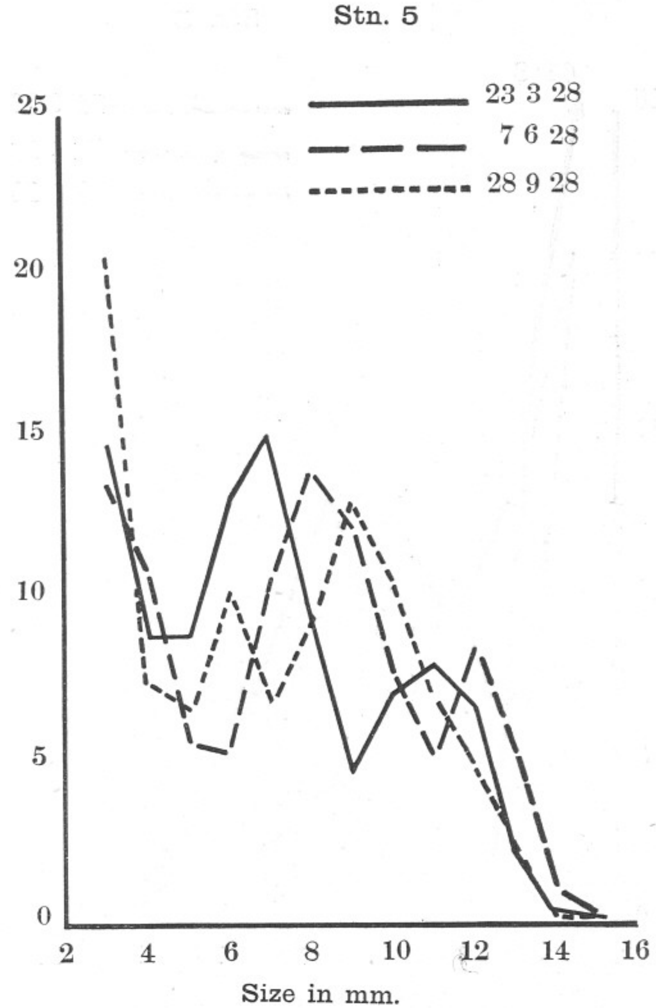

FIG. 1.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 5 in March, June and Sept., 1928.

The view that a year group (1925 spat) was unrepresented on the curve for 1926 seems justified when we consider that the rate of growth during 1928 was of the same order as during 1927 and that there was in September, 1928, a mode at 9 mm., the figure at which, in the earlier paper, it was considered that a year group should have been present on the curve for September, 1926 (**2**, p. 690).

The various year groups did not form equal proportions of the population. Since 1926 the spat of that year has continued as a dominant group, and as the 2+ group in September, 1928, even with the natural rate of mortality of two years, it formed a large proportion of the population (Fig. 2). If we take the numbers from 8 mm. to 11 mm.

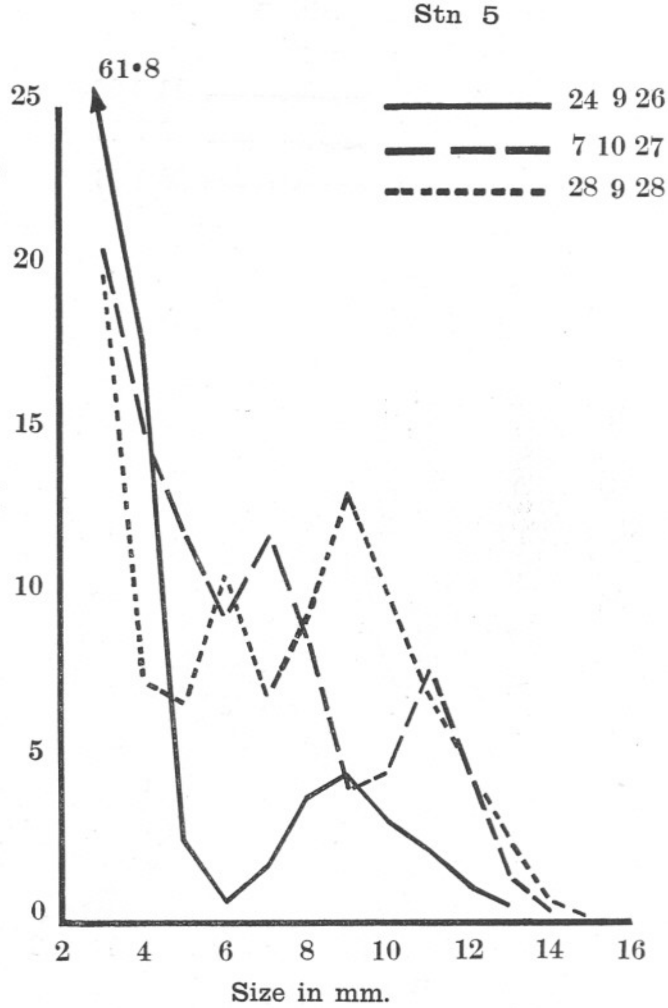

FIG. 2.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 5 in Sept. 1926, Oct. 1927, and Sept. 1928.

as representing the group, the proportion was 40% and the actual numbers per "¼ sq. m." 304.

These figures also indicate that in Kames Bay the species can be subject to little interference, for it is unlikely that if this were to any extent a feeding-ground for fish the 1926 spat could have survived in such numbers.

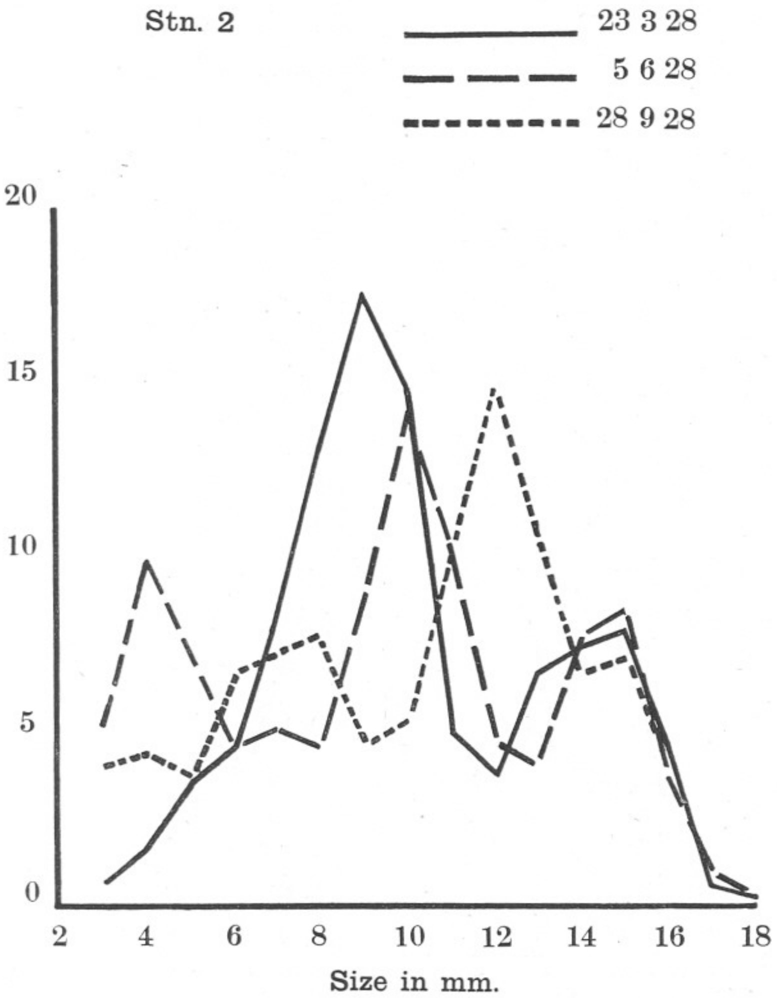

Fig. 3.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 2 in March, June and Sept. 1928.

Stn. 2 (Figs. 3–4. Table VI).

As at Station 5, there was no growth during the winter months, the size-frequency curve for March, 1928, being very similar to that of October,

1927. Again, the maximum concentration of the individuals 3 mm. in length occurred in late spring, not in autumn as at Station 5.

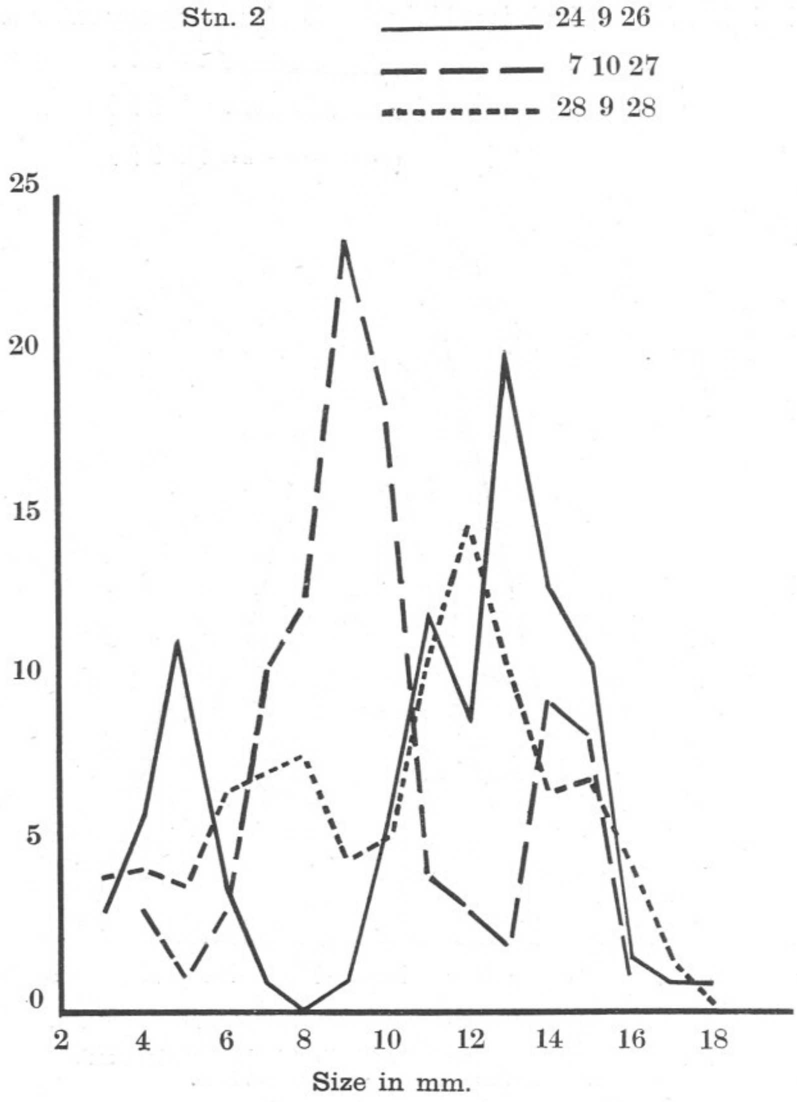

FIG. 4.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 2 in Sept. 1926, Oct. 1927 and Sept. 1928.

On the size-frequency curve for March, 1928, there were modes at 9 mm. and 15 mm. By June that at 9 mm. had moved to 10 mm., but that at 15 mm. remained at the same figure. At the other end of the curve the spat of 1927 was showing as a distinct group at 4 mm. By the end of September the mode at 4 mm. had moved to 8 mm., that at 10 mm. to 12 mm., while that at 15 mm. remained stationary.

Compared with 1927 growth was rather less, the modes for 1928 being about 1 mm. behind the corresponding ones for 1927.

In 1927 also the rate of growth from March to June was greater than that from June to the beginning of October, but in 1928 the position was reversed.

The results at this station again confirm the view of a missing year group on the curve for 1926, the rate of growth during 1928 having been of the same order as in 1927.

The 1926 spat was a prominent group at this station, as at Station 5. If we take the figures from 10 mm. to 15 mm. as representing it, the proportion of the population belonging to it was 52·5% and the actual numbers were 108 per "¼ sq. m."

STN. 6 (Table VI).

The collection made at this station in the end of September, 1928, was similar to those of the preceding years. The individuals were all very small and few exceeded 7 mm. in length.

There were no signs of any growth or of year groups as at Stations 2 and 5. There had been, however, a steady decrease from 325 in September, 1926, to 128 in September, 1928, per 20 cm. cube, as the following table shows.

TABLE I.

Table showing the decrease in the numbers of *Tellina tenuis* per 20 cm. cube at Station 6 from September, 1926, to September, 1928.

Date.	No. of *Tellina tenuis*
6.10.26	327
13.4.27	355
13.8.27	254
8.10.27	194
23.3.28	167
28.9.28	128

STN. 7 (Table VI).

Again, as on previous occasions, the individuals at this station were only of very small size, the majority ranging from 3 mm. to 6 mm. As at Station 6, there had been practically no signs of growth during the whole year, but again there had been a very heavy mortality as the following table shows.

TABLE II.

Table showing the decrease in the numbers of *Tellina tenuis* per 20 cm. cube during 1928.

Date.	No. of *Tellina tenuis*.
8.10.27	143
23.3.28	66
28.9.28	18

The results from Stations 1 to 5, that is from that part of the range of the species from H.W.M. to L.W.M., are straightforward. The size-frequency curves show modes which move forward regularly and the course of events is orderly and logical.

At Stations 6 to 8, that is from that part of the range of the species below L.W.M., the results do not fit into the same scheme. When first examined in September, 1926, the specimens of *Tellina tenuis* were all fairly small (**2**, p. 701), and they appear to have remained at practically the same size ever since. Now elsewhere we find the species below L.W.M., although only in small numbers, but the size of the individual is often much greater than here. What, then, is the explanation of the state of affairs in Kames Bay ? The most satisfactory explanation is that in the summer and autumn of 1926 huge numbers of spat settled on the ground from Stations 6 to 8, causing overcrowding to such an extent that the food supply has proved insufficient. Under such circumstances a species, after holding the ground for some time would, in the natural course of events, begin to die off, and this is exactly what has been taking place to a very marked extent during the present year (Tables I and II).

III. RATE OF GROWTH OF *TELLINA TENUIS* ON THE HUNTERSTON SANDS.

It was decided to make an exact comparison during 1928 between the rate of growth of *Tellina tenuis* in Kames Bay and in one of the other sands. A station near L.W.M. on the Hunterston Sands, Ayrshire Coast, was chosen and was examined at the same times as Kames Bay.

HUNTERSTON SANDS AT PERCH (Fig. 5. Table VII).

On the size-frequency curves there were in April two modes at 3 mm. and 9 mm. By June that at 3 mm. had moved to 5 mm. and that at 9 mm. to 10 mm. By the end of September the curve had greatly changed, for, as at Station 5, the group represented by the 10 mm. mode in June had practically disappeared. Now this result was not due to insufficient sampling but represented the actual condition of affairs, for in view of such a marked change the matter could not be left undecided, and two repeat samplings were made, with exactly the same result.

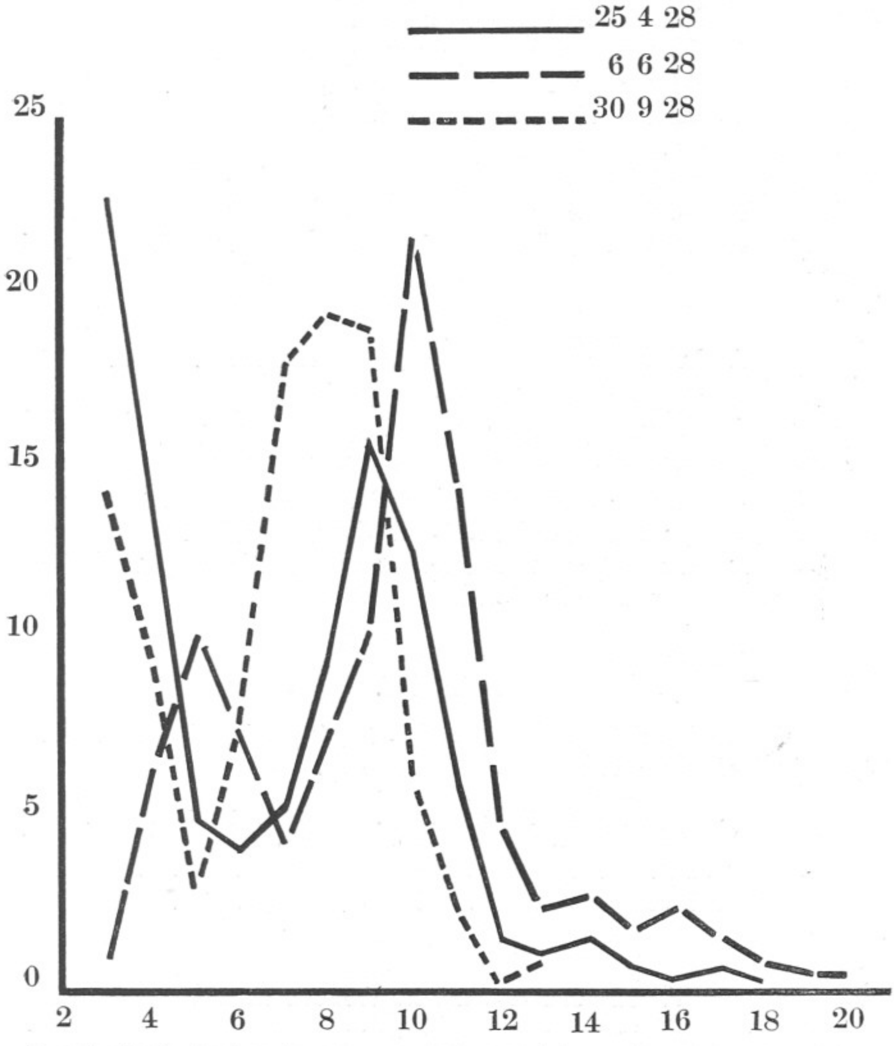

FIG. 5.—Graph showing the percentage (ordinate) of the catch at each mm. for the Hunterston Sands at L.W.M. in April, June and Sept. 1928.

To return to the curve, the mode at 5 mm. in June had moved to 8 mm. and the new spat had appeared at 3 mm. in September. The two modes on the September curve represent the 0+ group (1928 spat) at 3 mm.

and the 1+ group (1927 spat) at 8 mm. The 2+ group (1926 spat), which is still the dominant year group in Kames Bay and was, till June, here also, has gone. When picking over the samples the empty valves, whole and therefore not taken by fish, were found in large numbers, but what was the cause of the heavy mortality here, and to a lesser extent at Station 5 in Kames Bay, was not apparent.

If we take the April curve as roughly corresponding to the size-frequency distribution at the end of the previous autumn, growth, as in Kames Bay, has been rather less in 1928, the second mode being at 8 mm. as against 9 mm. last year.

The position of the mode at 8 mm. indicates that the rate of growth at this station is of the same order as that at Stations 2 or 3 in Kames Bay, and not as at Station 5, as the position on the beach would lead us to suppose.

IV. DISTRIBUTION OF SIZES PASSING THE 2 MM. SIEVE.

So far we have only dealt with the specimens retained by the 2 mm. sieve. In the earlier investigation the distribution and relative frequency of the sizes passing the 2 mm. sieve but retained by the 1 mm. sieve were also dealt with, and for comparison a similar set of observations was made at Stations 2, 5, 6, and 7 in 1928. Compared with 1927 there has been a marked reduction in the numbers at all stations by the end of 1928, as the following table shows.

TABLE III.

Table showing the numbers of *Tellina tenuis* passing the 2 mm. sieve but retained by the 1 mm. sieve in Kames Bay.

	Contained in a 20-cm. cube.		Contained in a ¼ sq. metre.	
	Stn. 7.	Stn. 6.	Stn. 5.	Stn. 2.
Sept. 1927	167	85	102	20
Sept. 1928	0	3	60	0

V. AMOUNT OF SPAT IN VARIOUS YEARS.

There is good evidence that the spat which settled on the bottom and survived until the autumn varied during the years 1926–8. The year 1926 stands out as one of unusual abundance. If we consider the individuals of 3 mm. and 4 mm. in the end of September as representing the spat, the numbers per ¼ sq. m. at Stations 2 and 5 for each year were as follows.

TABLE IV.

Table showing the numbers of specimens 3 mm. and 4 mm. in length at Stations 5 and 2 in September of each year per $\frac{1}{4}$ sq. m.

	Stn. 5.	Stn. 2.
1926	655	12
1927	272	13
1928	213	26

So far as the collections made by the 2 mm. sieve are concerned 1927 and 1928 seem to be about equal, but when the figures in Table III are taken into consideration 1928 appears the poorer.

VI. HISTORY OF THE 1926 SPAT.

It has already been pointed out how the 1926 spat has survived as a dominant group, and it is possible to trace its history since 1926.

The group was found as spat in September, 1926, and was present in large numbers from Station 7 to half-tide, and in small numbers to H.W.M.

In September, 1928, below L.W.M. it still remained on the ground, but showed little growth, and had steadily declined in numbers. At Station 7 a few remained and the numbers had fallen to a third at Station 6.

At, and above, L.W.M. the modes remained at a standstill during the winter months, but showed progress during the summer months, the shift of the mode being least at Station 5 and proportionately greater at each station nearer H.W.M. The halts and progress of the modes are clearly seen in Table V.

TABLE V.

Table showing the position of the modes of the 1926 spat, from September, 1926, to September, 1928, for each time of collecting, for Stations 2 and 5.

Date.	Stn. 5.	*Yearly increment.*	Stn. 2.	*Yearly increment.*
24.9.26	3 mm.			
13.4.27	3 ,,	4 mm.	3 mm.	6 mm.
20.6.27	5 ,,		6 ,,	
13.8.27	6 ,,		8·5 ,,	
7.10.27	7 ,,		9 ,,	
23.3.28	7 ,,	2 mm.	9 ,,	3 mm.
7.6.28	8 ,,		10 ,,	
28.9.28	9 ,,		12 ,,	

In 1927 the mode shifted from 3 mm. to 7 mm. at Station 5 and from 3 mm to 9 mm. at Station 2. During 1928 the shift at Station 5 was from 7 mm. to 9 mm., and at Station 2 from 9 mm. to 12 mm. In other words, the movement during 1928 was exactly half of that during 1927 at both stations. This result is in accord with that which Orton (**1**) has found for *Cardium edule*. In that species, for four years, each annual increment was approximately half of the preceding year.

If, in the case of the Lamellibranchs, it can be assumed that the annual increment is even approximately half that of the preceding year, an important point is established, which may give a means of estimating the age of the numerous small, but from the economic point of view important, species. In these species it might be possible to measure the first full year's increment, but it would probably be very difficult to follow subsequent growth.

Table VI.

Stn. 2.

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total specimens.
23.3.28	0·7	1·6	3·7	4·7	8·0	13·1	17·5	14·8	5·0	3·8	6·7	7·4	7·9	4·6	0·5	0·2	674
5.6.28	5·1	9·8	7·2	4·4	5·1	4·7	9·0	13·9	10·4	4·8	4·1	7·7	8·4	3·9	0·9	0·2	662
28.9.28	4·1	4·4	3·8	6·7	7·3	7·7	4·7	5·3	10·7	14·9	10·5	6·6	7·3	4·5	1·4	0·2	684

Stn. 5

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	13	14	15	Total specimens.
23.3.28	14·8	8·9	8·9	13·1	15·1	10·0	4·8	7·1	8·0	6·7	2·3	0·4	0·1	2002
7.6.28	13·6	10·9	5·6	5·3	10·7	13·9	12·2	7·7	5·1	8·7	5·3	1·2	0·2	1351
28.9.28	20·6	7·5	6·7	10·4	6·8	9·4	13·1	10·5	7·0	4·9	2·5	0·3	0·2	1519

Stn. 6.

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	Total specimens.
29.9.28	20·9	22·1	20·9	14·6	13·2	5·0	1·9	0·6	0·0	0·6	158

Stn. 7.

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	Total specimens.
29.9.28	32·3	22·6	29·0	12·9	3·2	31

TABLE VII.

Hunterston Sands (at Perch).

Percentages of catch at each mm. length.

mm.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Total specimens.
25.4.28	22·7	13·9	4·9	4·1	5·3	9·3	15·8	12·7	5·9	1·3	1·0	1·2	0·7	0·3	0·7	0·2	–	–	589
6.6.28	0·9	6·3	10·1	7·5	4·2	7·3	10·1	21·8	14·5	4·9	2·3	2·6	2·1	2·3	1·4	0·7	0·5	0·5	427
30.9.28	14·3	9·5	2·8	7·7	18·0	19·3	18·8	6·0	2·2	0·4	1·0	–	–	–	–	–	–	–	496

VII. SUMMARY.

1. The present paper is a direct continuation of the work done at Millport during 1926 and 1927.

2. As before, *Tellina tenuis* showed no growth during the winter months.

3. As before, the rate of growth at L.W.M. was less than that near H.W.M.

4. Below L.W.M. there seemed to have been no growth during the year, but there had been a heavy mortality during 1928.

5. Above L.W.M. the rate of growth during 1928 was of the same order as that of 1927, and the view that a year group was unrepresented on the 1926 curve seems justified.

6. At the end of September, 1928, the 1926 spat still formed a large and well-marked group.

7. The history of the 1926 spat is traced, and the annual increment found to be halved in succeeding years.

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On Methods of Reproduction as Specific Characters.

By

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With 11 Figures in the Text.

CONTENTS.

INTRODUCTION.

The primary aim of this paper is to show that among certain Actinians investigated, the species are sharply differentiated by their divers methods of reproduction; and to point out that the general question of species is one which is worthy of the attention of experimental biologists. Arguments supporting these contentions will be found in Section 7.

I should like to make the following acknowledgments. I have received a grant, which has made the work described possible, from the Department of Scientific and Industrial Research. I have received interest and advice from Prof. Watson, and invaluable assistance (detailed below) from Mr. W. Edgar Evans. The whole cultural side of the work was carried out by my wife, who also provided Text-Figs. 2 and 3, and the sections from which they were drawn. I am very much indebted also to the Plymouth staff and to Miss M. Delap, of Valencia, and Mr. Elmhirst, of Millport, for the collection of the large amount of material required.

1. THE METHODS OF REPRODUCTION PREVALENT AMONG ACTINIANS.

The sea-anemones which have been specially studied for this part of the paper are the following :—

1. *Sagartia lacerata* (Dalyell).
   [*S. coccinea* of Gosse, but not *Actinia coccinea* Müller].
2. *S. elegans* (Dalyell).
   [Various colour-varieties were used].
3. *S. anguicoma* (Price).
   [More usually known in this country as *S. viduata* (Müller). It is not, however, identical with the latter, which is non-British.]
4. *S. troglodytes* (Price).
   [Both varieties of this species were used, the typical form (var. *decorata* Stephenson) and the var. *ornata* (Holdsworth)].
5. *S. sphyrodeta* Gosse.
6. *Cereus pedunculatus* (Pennant).
   [Commonly known as *Sagartia bellis* (Ellis)].
7. *Diadumene cincta* Stephenson.
8. *D. luciæ* (Verrill).
   [Also known as *Sagartia luciæ* Verrill].

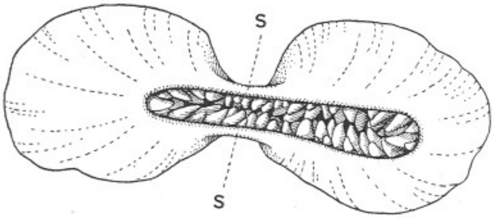
In the above-mentioned species the following methods of reproduction occur.

1. *Oviposition, etc.*

The deposition of either sperms, ova, or both, has been observed in several of the species under consideration; but data relating to this are scanty, and are insufficient to permit us to form any adequate idea as to the extent to which the various species deposit ova in the wild state. Further information is badly needed about the breeding-seasons of anemones and about the life-history of their gonads. From the point of view of this paper, however, it may be taken as probable that all or most of the species concerned deposit ova on occasion. The oviparous habit therefore, being general, is not considered in detail here. It could only be of interest to the issue involved if it could be shown that the viviparous species never deposit ova. This, however, is not the case. In *Sagartia troglodytes* the animal is hermaphrodite, and has been seen to discharge ova and spermatozoa simultaneously, or one a short time after the other; and this probably occurs in nature as well as under aquarium conditions, although the species is habitually viviparous. In the other viviparous form, *Cereus pedunculatus*, the animal is also hermaphrodite, and here I am not aware of cases in which it has been seen to deposit ova. Specimens undergoing irritation have been known to discharge early embryos (observed by Signor Jucci at the Plymouth Laboratory), but this is not, as far as I know, a normal occurrence.

2. *Viviparity* (*Sagartia troglodytes* and *Cereus pedunculatus*).

In the viviparous forms, which are sometimes (perhaps always) hermaphrodite, fertilisation is internal, and the embryos develop in the cœlenteron of the parent, achieve their metamorphosis, and are fully-formed small anemones by the time they escape from the parent. This does not necessarily apply to all the ova of any given specimen; and although fertilisation in the case of the young which are retained is certainly internal, it does not follow that it is effected by spermatozoa belonging to the individual which produced the ova. An anemone with some of its viviparous young* is illustrated in Text-Fig. 5.



TEXT-FIG. 1.—*Sagartia sphyrodeta*. A specimen in the act of dividing into halves. The base, column-wall, and throat have actually ruptured, and the two parts are held together by the sphincter (S) and by part of the oral disc (not visible in the sketch). Enlarged more than 5 diameters.

3. *Longitudinal Fission* (*Sagartia sphyrodeta* and *Diadumene luciæ*).

In this method the animal elongates in one direction, the two halves of the base moving away from each other. Rupture results, and each of the halves heals up and forms a new individual. The halves may be equal or unequal in size, but each normally possesses tentacles, so that a complete new set does not have to be regenerated by either half. The fission tears the base and the column-wall, and also involves the throat, in many cases if not always. These statements do not apply to all cases of fission among Actinians, since there are apparently instances in which

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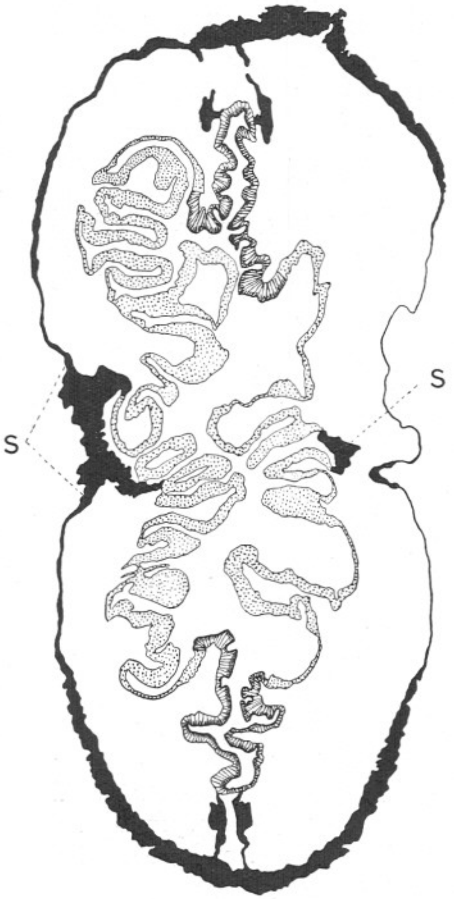
* For the sake of brevity the term viviparous young has been used throughout to denote viviparously produced young.

a gradual separation of parts takes place ; but they apply to the normal fissions in the species here dealt with, where the process is one of rupture, and is of relatively brief duration, often lasting for a matter of hours only. In some cases more than two pieces arise from a fission.

In the interesting and instructive paper recently published by Matthai (1926), on colony-formation in Astræid corals, this author concludes from his studies, with full justification, that true fission, involving division of the throat, does not occur among the Astræidæ, and that there is no evidence of it among the Madreporaria.* This being so, it may be relevant to emphasize the fact that it *does* occur among the Actiniaria. I have personally witnessed a number of instances of its occurrence in anemones (and many other examples of the allied process of laceration), and in one case I was fortunate in catching a specimen of *Sagartia sphyrodeta* at a stage in the process at which the base and throat had been torn completely in two, but only part of the body-wall had given way. The two halves were still connected by the sphincter and by part of the oral disc. A sketch of this specimen, from the living animal, is shown in Text-Fig. 1. It was fixed immediately after it had been sketched and was subsequently sectioned. Two sections from the series are illustrated in Text-Figs. 2 and 3. In the section shown in Fig. 2 the body-wall and oral disc of the two



TEXT-FIG. 2.—*Sagartia sphyrodeta*. A transverse section of the specimen shown in Text-Fig. 1, after fixation. See text. Column-wall and directive mesenteries black ; tentacles and oral disc stippled ; throat shaded with strokes. S, sphincter, cut through in two places. All mesenteries are omitted save the directives.

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* In this connection it should be remembered that in Corynactis fission certainly does occur, and may involve the mouth (an observation confirmed by Evans, who has seen fission many times in *C. viridis*). I have tried to show elsewhese (1921, p. 510) that Corynactis is probably an aberrant Madrepore which secretes no skeleton, and not an anemone. But this does not affect the question of the typical Madreporaria.

sides are continuous, and part of the throat is seen in each half. In the other section, Fig. 3 (cut at a lower level than the first), the base, the body-wall, and throat of each half have been torn away completely from the other half.

That fission should occur frequently among the Actiniaria and not among the skeleton-building Madreporaria serves only to emphasize the essential difference in tendency between these groups. In the Actiniaria we are dealing with non-colonial organisms which are typically muscular creeping-forms (no other group of the Cœlenterates offers a parallel to this creeping habit of the Actinians), secreting no skeleton, and inclined to divide by means of fission or laceration. In the Madreporaria, on the other hand, it is a question of animals which are frequently colonial, entirely sedentary, nearly always building a skeleton, and reproducing asexually by means of budding of one kind or another, and not by fission; budding is not characteristic of Actiniaria, although cases of it are on record.

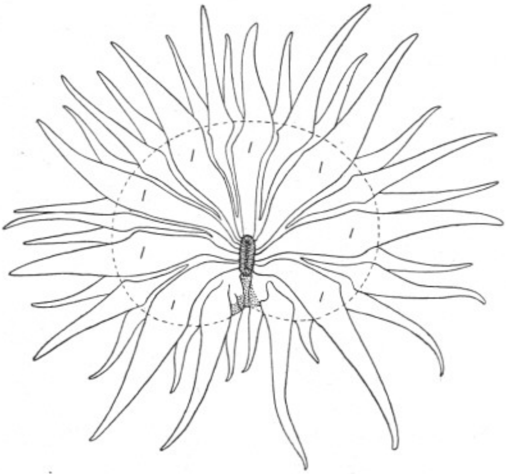
In *Gonactinia prolifera* and *Aiptasia couchii*, *transverse fission* takes place; but this is a process of rare occurrence among anemones and not found in the species studied here. In *Gonactinia* the process is one resembling in some respects the strobilisation of a scyphistoma.

Text-Fig. 3.—A section from the same series as that from which was taken the section shown in Text-Fig. 2; this one is cut at a lower level. See explanation beneath Text-Fig. 2, and also the text. B, base—the animal was somewhat curled up after fixation, so that in the lower part base and column-wall come into the same section on either side.

Lastly it may be noted that in almost any collection of specimens of *Sagartia sphyrodeta* or *Diadumene luciæ* freshly brought in, it is possible to detect a certain proportion of individuals which show unmistakable signs of having recently undergone fission. This is revealed by the presence of a sector of regenerating tissue, of different colour from the rest. A sketch of an expanded specimen which had recently divided is shown in Text-Fig. 4.

4. *Laceration by Tearing* (*Sagartia elegans* and *Diadumene cincta*).

In this method no division of the animal occurs so long as it remains stationary (except in the event of its putting out a basal extension and afterwards withdrawing this in such a way that a rupture occurs), but if it begins to creep away there may be left behind a larger or smaller fragment, attached to the substratum. The separation of the piece is an actual tear involving a stretching of the region of rupture ; it may take place on a perfectly smooth surface, or it may occur when the animal climbs over a rough place or an edge ; in animals kept in finger-bowls a laceration is often produced if the anemone climbs over the edge of the bowl. In my experience the piece torn off is never large enough to contain any portion of the disc and tentacles of the parent, although it includes part of the base, the body-wall, and the lower ends of mesenteries, and may be more than a centimetre in diameter. In *Diadumene cincta* the animal, after having produced a laceration which has become almost separated from it, occasionally tries to recall the laceration and heal it up again. In the cases observed this resulted in death.



TEXT-FIG. 4.—Outline of a specimen derived from a recent fission. The shape of the disc (the edge of which is indicated by a dotted line) is modified. The regenerating region (approximately) is stippled. The primary tentacles are marked I. Enlarged about 10 diameters.

An example in which six lacerations had separated from a single specimen of *Sagartia elegans* is illustrated in Text-Fig. 6.

5. *Laceration by Constriction* (*Sagartia lacerata*).

Here the parent anemone usually (though not necessarily) remains stationary, and from the expanded edge of its base small capes and islands become constricted off (Text-Fig. 8). These may remain quite close to the parent, or may move away to some distance from it, often remaining connected with it for a time by a thin stolon before complete separation takes place. Here, as in laceration by tearing, the fragments contain base, body-wall, and mesenteries only; and they are usually small, a few millimetres only in diameter, whereas by the other method rather large pieces are sometimes torn off. A specimen from which a number of lacerations had separated is illustrated in Text-Fig. 7.

2. DATA RELATING TO THE SUBJECT COLLECTED BY W. E. EVANS.

For some years Mr. W. Edgar Evans, B.Sc., of the Royal Botanic Garden at Edinburgh, has maintained in his house a private marine aquarium of an unusual type. The whole construction and mode of maintenance of his aquarium are excellent, and during the period when Mr. Evans was able to give a considerable amount of attention to it, the health of the animals contained in it was of an extremely high order, such as I have seen equalled nowhere else. For some time now, the tanks have been used almost exclusively for sea-anemones, and all the available British species have been under observation in them at one time or another. Details of the construction and method of maintenance of this aquarium will be found in *Discovery*, Vol. VII, No. 74, 1926, p. 51.

The methods of reproduction detailed in the last section have been known to naturalists for many years, but the general idea connected with them seems to have been that they are of somewhat erratic occurrence among Actinian species, and that one anemone is as likely to undergo fission, for instance, as another. Although it has been quite clearly understood by certain workers (see p. 154) that some of the methods are characteristic of given species, no special study has been devoted, so far as I am aware, to reproductive methods considered purely as specific characters. While observing the anemones in his collection over a period of several years, Mr. Evans noticed that no one species (save *Aiptasia couchii*) ever employed more than a single method of reproduction (apart from the deposition of sperms and ova), and some of his notes are given below. The value of his observations lies partly in the fact that his aquarium has been one of quite exceptional efficiency, and partly in that, though his records cover but few specimens, many of these were under continuous observation for several years.

The details are as follows. The calculation of times is up to June 27th, 1926. In the majority of cases a separate account of each specimen was kept in an aquarium notebook.

Sagartia troglodytes.

The records available cover 22 specimens, and 21 were still alive on the date to which the calculations run. Of these, three had been under observation for between 4 and 5 years (two for nearly 5), five for between 3 and 4 years, three for between 2 and 3 years, and the rest for less than a year.

During this time, reproduction by fission or laceration was never seen or even suspected, whilst the production of viviparous young was so normal and frequent in well-fed specimens that it was not as a rule entered in the aquarium notebook, although recorded on certain occasions. Damage to specimens while collecting in the wild usually resulted in the escape of viviparous young. A sample of the entries in the notebook is as follows :—

Colour-Variety.	Obtained.	Died.	Locality.	Remarks.
ornata	7.9.25	Living	Valencia, Co. Kerry	Viviparous young at intervals.
scolopacina	29.5.22	31.5.24	Longniddry, Forth	Viviparous young produced
ornata	1.4.23	Living	Torquay	Viviparous young occasionally.
lilacina	8.10.22	Living	Joppa, Forth	No reproduction observed.

Sagartia elegans.

The records available cover 14 specimens, and 7 were still alive on the date to which the calculations run. Of these, two were under observation for between 3 and 4 years, five for between 2 and 3 years, four for between 1 and 2 years, and the rest for less than a year. In this species reproduction by laceration was found to be so constant a characteristic of well-fed specimens that again only a certain number of instances were actually entered in the notebook. No healthy specimen was ever kept which did not undergo laceration. Neither fission nor the production of viviparous young was ever observed. A sample of the entries in the notebook is as follows :—

Colour-Variety.	Obtained.	Died.	Locality.	Remarks.
ornata*	2.11.23	12.5.25	Millport, Clyde	Laceration often. Over 10 pieces before 14.12.24.
venusta	20.1.25	Living	Valencia, Co. Kerry	Laceration occasionally.
venusta	20.9.22	8.25	Tenby	Laceration began 23.12.22, next occurred 9.1.23, later often.
nivea	20.9.22	Living	Tenby	Laceration frequently.

Sagartia anguicoma.

The records available cover 6 specimens, and 5 were still alive on the date to which the calculations run. Of these, one was under observation for between 4 and 5 years, one for between 3 and 4 years, the others for less than a year. During this period fission and laceration were never seen or even suspected; production of viviparous young was suspected (not seen) on one occasion, but subsequently definitely disproved.

Beyond the above data general notes are available to the effect that in *Cereus pedunculatus* viviparous young were produced at all seasons; that in *Sagartia sphyrodeta* fission was observed at various times, e.g. 10.12.22. and 29.3.25; that in *S. lacerata* laceration occurred at all seasons; that in *Diadumene luciæ* fission occurred at all seasons if the animals were well fed; and that at *D. cincta* laceration at all seasons was observed.

Further observations by Mr. Evans, on species not specially dealt with in this paper, are given below in Section 6. For the moment, however, it is enough to say that the results above recorded fit in exactly with those derived from the experiments detailed in the next section.

3. ACCOUNT OF EXPERIMENTS AT PLYMOUTH.

I was at first unwilling to agree with the conclusions reached by Evans as a result of his aquarium observations; but subsequently I became much interested in the subject, and decided to undertake some experiments, in the hope of putting the matter upon a more satisfactory basis. I was able to carry out these experiments during five months' residence at Plymouth, January to June, 1927. I regret that I was unable to carry them on for a longer period, because the reproductive processes are slow, and a run of two or three years would have been much better than a few months. Again, the total number of experimental animals (over 400) was not as large as I should have wished, but

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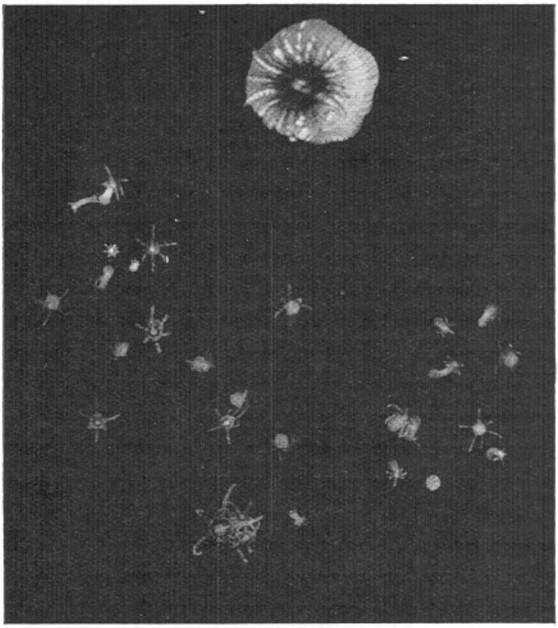
* *Sagartia elegans* and *S. troglodytes* both possess a variety named "*ornata*."

since many of these had to be accommodated each in a separate finger-bowl, the question of accommodation and maintenance became serious. The time required for keeping clean and feeding individually as many specimens as this is considerable.

The method of experiment was as follows. In the first place it was desired to isolate a number of individuals of each of the species (see p. 148) chosen for experiment, so that a detailed record could be kept of the activities of each animal. This was done by placing each individual in a separate finger-bowl, and awaiting results. The conditions were kept as uniform as possible for all the species, and the finger-bowls were cleaned and their occupants fed at regular intervals. Great care was taken to provide as adequate aeration as possible, and to keep the animals healthy. The whole of them were inspected daily and notes made of anything which occurred. The general mortality was so low as to be negligible except in two difficult species (*S. sphyrodeta* and *D. luciæ*) which could not be maintained as satisfactorily as the others with the facilities available. It was necessary to use ordinary tank-water, and this is not

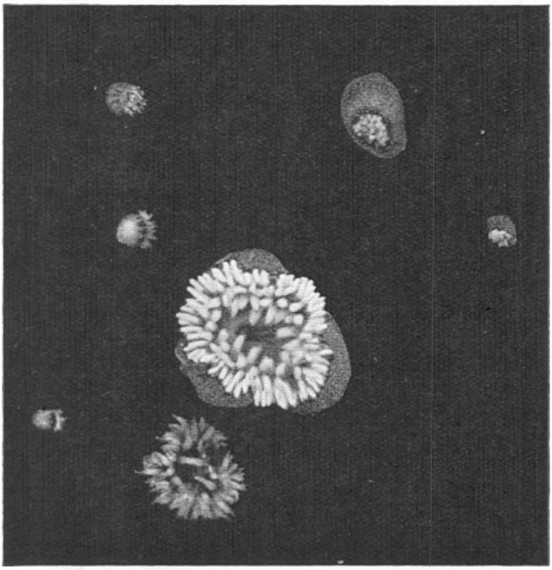


TEXT-FIG. 5.—From a photograph of a specimen of *Bunodactis verrucosa*, with a number of viviparous young which it had recently produced. The parent is in a partially contracted condition. Slightly reduced.

of the very best quality for delicate species, which also require special conditions in other respects.

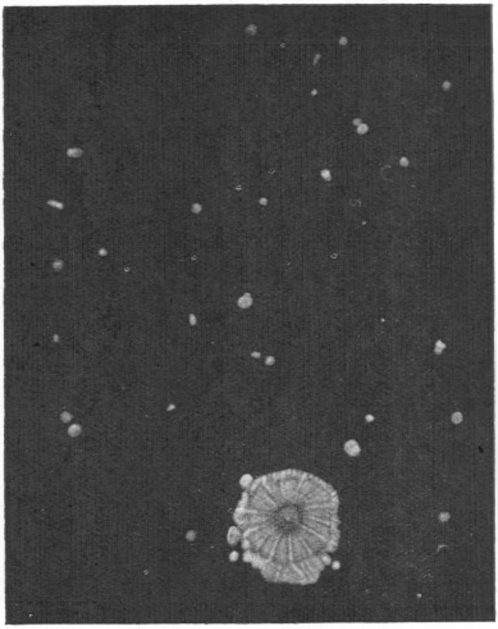
In the case of many of the finger-bowls, it was found sufficient to stand them on the slate slabs underneath some of the tanks, and to aerate them for a certain period, daily, by means of a special apparatus which changed the water at the same time.

Other finger-bowls were kept in running water in a tank, the water-level being kept below the tops of the finger-bowls so that their isolation was maintained; these were aerated by flooding them once a day. A further number of bowls was kept under water which was in circulation; these were not, therefore, fully isolated from one another (e.g. spermatozoa could escape from one bowl to another), but from the point of view of laceration, fission, and viviparous young, the isolation was adequate.



TEXT-FIG. 6.—From a photograph of a specimen of *Sagartia elegans*, with six smaller specimens round it. The latter were all produced as lacerations torn away from the parent when it moved from one place to another; all of them have regenerated. Slightly reduced.

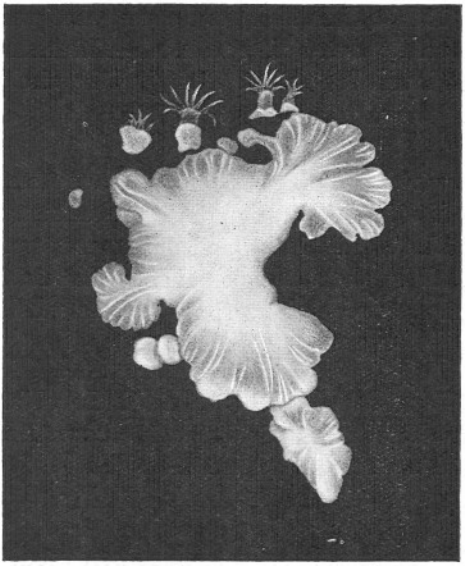
For a considerable part of the period of experiment, about half the specimens of several species were kept in special finger-bowls which had been entirely lined with a mixture of Portland cement and gravel, sometimes with stones and shells fixed in it. This was in order to provide a rough surface for the animals, with the idea that lacerations might be produced more freely on this than on glass. It also gave an excellent opportunity to species which do not normally lacerate, to do so—and thus acted as an additional control. It was found, however, that the kinds which do not lacerate showed not the least tendency to do so on the rough surface; these creatures will glide over edges which would often provide an irresistible opportunity for lacerating, in the other species, without doing so. Moreover, the lacerating species seemed little, if at all, more inclined to tear themselves on the rough surface than on the smooth. These cement bowls are useful for various purposes, but have to be soaked first in fresh and later in sea-water, and scrubbed free from the crystals which form on the cement, for some time before they are fit for use. In the detailed records of the experiments no distinction is made between cases in which the animals were in glass bowls for the whole period, and those in which they were at first in glass bowls and later in cement ones; because it was found that the change had no effect on



Text-Fig. 7.—From a photograph of a specimen of *Sagartia lacerata*, also showing a number of small individuals, all produced as lacerations (by the constrictional method) from the one parent. Both the parent and such of the young as possessed them had withdrawn their tentacles, as is usual in this species when exposed to daylight. Slightly reduced.

the essential conditions of the experiment. Most of the cement bowls were kept under circulation.

In the second place it was desired to ascertain whether, in species which do not reproduce by any asexual method under natural conditions, portions cut off artificially would regenerate as readily as in the case of species which lacerate of their own accord. For this purpose four species were chosen, two belonging to each category. Prior to each operation, a healthy adult anemone was allowed to settle comfortably in a finger-bowl, or on a glass slide; when it had become firmly attached, small portions were separated from the edge of its base by tangential cuts with a small, sharp, sterilised scalpel. After the cuts had been made the parent anemone was removed and the glass cleaned, this leaving behind the separated pieces attached to the bowl. The bowls containing the pieces were kept under circulation in a tank, and the pieces allowed to regenerate. Plymouth tank-water is not an ideal medium for such experiments, because it contains a soft sediment which settles continually in the bowls and on the regenerating pieces, so that it is not easy to keep them sufficiently clean; if the sediment is allowed to



TEXT-FIG. 8.—A specimen of *Sagartia lacerata* which had attached itself to glass; viewed through the glass from below the base. Several pieces are becoming or have become separated from the edge of the base, and in four of these tentacles are visible. Slightly enlarged.

accumulate for too long the pieces die. Nevertheless, the general results were satisfactory. The details are as follows :—

A. EXPERIMENTS ON THE NATURAL METHODS OF REPRODUCTION.*

I. *Sagartia elegans.*

Experiment 1.

32 specimens were used (30 to begin with, the other two to replace specimens which died). The duration of the experiment was 21 weeks and 5 days (January 13th to June 14th), and during that period 52 lacerations were produced, all by the tearing method. The number of specimens which underwent laceration was 21 (65·6% of the whole number).

Experiment 2.

26 specimens were used (25 to begin with, the other one to replace a specimen which died). The duration of the experiment was 14 weeks and 2 days (March 6th to June 14th), and during that period 8 lacerations were produced, all by the tearing method. The number of specimens which underwent laceration was 5 (19·2% of the whole number).

Other data.

From about 30 specimens which were not included in the main experiments, but were kept in other vessels, 20 lacerations were produced during the period of the main experiments.

Summary.

From over 80 specimens of *S. elegans* there were produced 80 lacerations during the course of the experiments ; by no means every specimen produced a laceration during this period, but some specimens produced more than one, so that the total number produced averages about one laceration to each individual used.

II. *Sagartia lacerata.*

Experiment 1.

15 specimens were used. The duration of the experiment was 20 weeks and 5 days (January 15th to June 9th), and during that period 172 lacerations were produced, all by the constrictional method. All the specimens underwent laceration, the respective number of lacerations produced by the different individuals being as follows : 1, 6, 11, 8, 13, 15, 9, 28, 8, 13, 40, 1, 8, 1, 7.

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* In this account of the experiments it is to be understood that no method of reproduction occurred in any experiment except the one recorded.

Experiment 2.

21 specimens were used. In this case all were contained in a single bowl, and the lacerations were removed as formed. Between February 11th and June 14th (17 weeks and 4 days), 116 lacerations were produced. One adult was removed on April 19th.

Summary.

From 36 specimens of *S. lacerata* there were produced 288 lacerations in the course of the experiments.

III. *Sagartia sphyrodeta.*

Experiment 1.

27 specimens were used (21 to begin with, 6 to replace specimens which died). Other specimens died before the end of the experiment, and were not replaced—total deaths 12. The duration of the experiment was 21 weeks (January 12th to June 8th), and during that time 7 specimens underwent longitudinal fission, two of these being further subdivisions of the halves resulting from a previous fission.

Experiment 2.

11 specimens were used (7 to begin with, 2 to replace specimens which died, and 2 added later). Other specimens died before the end of the experiment, and were not replaced—total deaths 5. The duration of the experiment was 16 weeks and 1 day (February 15th to June 8th), and during that period no fission occurred.

Other data.

Two specimens not included in the above experiments were observed to undergo longitudinal fission, and from among other specimens collected 9 showed unmistakable evidence of having recently undergone fission, the regeneration-zone being clearly marked.

Summary.

Among the 38 experimental specimens 7 cases of fission occurred during the period of observation; two other cases were observed in specimens outside the experiments. Nine further specimens collected had recently undergone fission.

IV. *Sagartia troglodytes* var. *decorata.*

Experiment 1.

16 specimens were used (15 to begin with, one to replace a specimen which escaped). The duration of the experiment was 20 weeks and 6 days (January 19th to June 14th), and during that period none of the

specimens underwent any form of asexual reproduction, nor did any of them produce viviparous young. The gonads appeared to be ripening towards the end of the experiment, so that the time for the production of viviparous young in these specimens would be later in the year. This is the only negative result reached which should have been positive; for there is ample evidence from other quarters to show that this form is viviparous.

V. *Sagartia troglodytes* var. *ornata*.

Experiment 1.

15 specimens were used. The duration of the experiment was 21 weeks and 3 days (January 15th to June 14th), and during that period 20 viviparous young were produced. These were produced by 6 of the specimens, the rest (60% of the whole number) producing nothing.

Experiment 2.

In this case 48 specimens were divided out among three vessels. Between February 2nd and April 9th (9 weeks and 3 days) they produced among them 56 viviparous young.

Other data.

7 viviparous young were produced by specimens received from Millport on April 24th—produced on April 25th.

Summary.

63 specimens produced among them 76 viviparous young during the period of observation. Seven other viviparous young were produced by further specimens (number unknown) of the species, on April 25th. The period of the experiments did not cover the prolific season of production.

VI. *Sagartia anguicoma* ("*viduata*").

Experiment 1.

15 specimens were used. The duration of the experiment was 21 weeks and 3 days (January 15th to June 14th), during which time no asexual reproduction of any kind occurred, nor were any viviparous young produced.

VII. *Cereus pedunculatus* (*Sagartia bellis*).

Experiment 1.

15 specimens were used. The duration of the experiment was 21 weeks and 3 days (January 15th to June 14th), during which time 110 viviparous young were produced. These young were produced by 11 of the

parents, the other four producing none. The numbers produced by the 11 adults in question were respectively 19, 2, 11, 16, 6, 37, 3, 5, 1, 3, and 7.

Experiment 2.

In this case 24 specimens were kept together in a tank, and the young removed as born. Between March 26th and June 16th (11 weeks and 5 days), 104 viviparous young were produced.

Other data.

One specimen not in either of the above experiments produced 12 viviparous young between April 19th and June 14th.

Summary.

40 specimens produced among them 226 young during the period of observation.

VIII. *Diadumene cincta.*

Experiment 1.

16 specimens were used (15 to begin with and one to replace a specimen which died). These were at first placed each in a separate finger-bowl, as usual, but later on some of them were transferred to a single square dish containing stones and gravel, so that they could be given a type of aeration which suited them better. The duration of the experiment was 21 weeks and 4 days (January 14th to June 14th), and during that time 8 lacerations were produced, all by the tearing method. In two cases the animal tried to recall the laceration before it had quite separated off; this resulted in death.

Other data.

A specimen outside the above experiment produced a laceration by the tearing method on March 22nd.

IX. *Diadumene* ("*Sagartia*") *luciæ.*

Experiment 1.

We were unable to obtain good material for this experiment. The few specimens available were all very small, and not in first-rate condition. This accounts for the poor result. Moreover, such small specimens (a few millimetres only in diameter) are difficult to keep, under the conditions of the experiment, and although 22 specimens in all were used (15 to begin with, the others to replace those which died), only 3 were still alive after May 22nd. The experiment started January 12th–20th. During the experiment 5 specimens underwent longitudinal fission.

Other data.

A specimen collected on April 19th had recently undergone fission.

The net result of the above experiments and observations is summarised in the following table, which shows the total number of new animals produced by any method in each of the species used, within the period of observation (about 21 weeks). In the cases of *S. sphyrodeta* and *D. luciæ* the collected specimens which had recently undergone fission are included. The result is discussed on page 159.

Species.	Fission.	Laceration by Tearing.	Laceration by Constriction.	Viviparous Young.
Sagartia elegans	—	80	—	—
S. lacerata	—	—	288	—
S. sphyrodeta	18	—	—	—
S. troglodytes var. decorata	—	—	—	—
S. troglodytes var. ornata	—	—	—	83
S. anguicoma	—	—	—	—
Cereus pedunculatus	—	—	—	226
Diadumene cincta	—	9	—	—
D. luciæ	6	—	—	—

B. Experiments in Artificial Laceration.

The results of these experiments are summarised in the table on the opposite page.

The pieces were not all cut off on the same date, because it was impossible to obtain enough material in suitable condition for operation, at any single time early in the period of experimentation. The experiments therefore lasted longer for some pieces than for others, the minimum time being 6 weeks and 5 days; but it must be remembered that the experiment for any given piece may be regarded as being over when that piece has attained full development, so that in this sense some of the experiments were complete long before the end of the whole period of experimentation. The variation in date of starting makes no essential difference to the result, because the highest mortality normally occurs shortly after the operation, and it may be taken that if an amputation survived for the minimum period mentioned it would, in the ordinary course of events, ultimately become fully developed even if it had not already done so by the end of the experimental period.

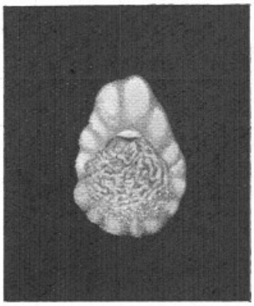
Species.	Number of specimens used.	Number of pieces cut off.	Number which survived until end of experiment.	Time taken to regenerate tentacles.			Time taken to acquire mouth and disc as well as tentacles.		
				Minimum.	Maximum.	Average.	Minimum.	Maximum.	Average.
Sagartia elegans	23	60	55 (91·7%)	2 weeks 1 day	9 weeks 1 day	4 weeks 6 days 54	4 weeks 5 days	14 weeks 6 days	8 weeks 5 days 36
Sagartia troglodytes var. decorata	21	76	22 (28·9%) 32 made some attempt at regeneration, but 2 only became fully developed	5 only achieved tentacles 5 weeks 3 days	8 weeks 4 days	7 weeks 3 days 4	2 only achieved mouths, they were perfect after 12 weeks 4 days.		
Sagartia anguicoma	18	67	39 (58·2%)	3 weeks 2 days	13 weeks 3 days	8 weeks 4 days 36	6 weeks 4 days	15 weeks 5 days	11 weeks 5 days 22
Sagartia lacerata (summary of all experiments)	A considerable number (not exactly recorded)	62	51 (82·3%)	3 weeks 2 days	13 weeks 2 days	10 weeks 20	4 weeks 3 days	17 weeks 1 day	10 weeks 3 days 10
Sagartia lacerata (the best experiment only)	Several	20	20 (100%)	3 weeks 2 days	3 weeks 2 days	3 weeks 2 days 4	4 weeks 3 days	8 weeks 2 days	5 weeks 5 days 4

In the above table the number in the lower right-hand corner of each of the rectangles containing an *average*, represents the number of pieces from which the average was calculated. There is no implication that specimens not included in this number failed to regenerate properly—the implication is that the time in which they regenerated could not be determined.

The essential part of these results may be better understood by their concentration in a further table as follows :—

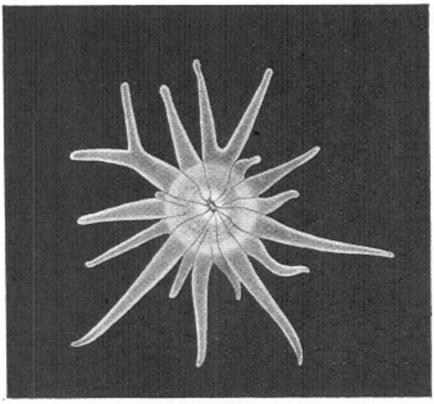
Species.	Number of pieces cut off.	Percentage reared (to nearest whole number).	Average time in which tentacles were regenerated.	Average time in which animal became fully formed.
Sagartia elegans	60	92%	4 weeks 6 days	8 weeks 5 days.
S. troglodytes var. decorata	76	29% lived 3% became fully formed	7 weeks 3 days	12 weeks 4 days.
S. anguicoma	67	58%	8 weeks 4 days	11 weeks 5 days.
S. lacerata (one experiment only)	20	100%	3 weeks 2 days	5 weeks 5 days.

These tables call for further comment. The records of the times taken for regeneration of tentacles and for the regeneration of the whole animal cannot be taken too seriously, because they are approximate, and may be partly misleading ; but they are recorded for what they are worth.



TEXT-FIG. 9.—A specimen of *Sagartia anguicoma*, produced from a small piece cut from the edge of the base of a large specimen. Regeneration is well advanced, and the regenerated tissue is clearly distinguishable from the old tissue as a pale crescent. Tentacles were present, but were retracted at the time when the sketch was made. Magnified nearly 5 diameters.

In these regenerating pieces (except in the case of *Sagartia troglodytes*, where the regenerating tentacles are non-retractile) the tentacles are usually retractile from the beginning, and consequently may be hidden from view at the time of the periodic observations. This means that it is very difficult to tell the exact date upon which tentacles or mouth first came into being in any given piece, and that data could not be obtained for all the pieces under observation. On the other hand, if a specimen is contracted at the time of one observation it is often expanded the next time, so that in the majority of cases the figure gained probably gives an approximation to the truth, allowing a fairly wide margin of error. The net result is that the minimum times given are probably the most valuable ; the averages are probably too high ; and the maximum times mean very little, since they probably represent the individuals which were either contracted most often or were abnormally backward in development. Notwithstanding the above, I think the data are sufficiently satisfactory to make valid the conclusion that under the conditions of the experiment pieces of *S. lacerata* and *S. elegans* (the forms which lacerate naturally) regenerated more rapidly, in the main, than those of *S. troglodytes* and *S. anguicoma*.



TEXT-FIG. 10.—One of the two specimens of *Sagartia troglodytes* which regenerated fully from an artificially separated basal fragment. One tentacle is forked at the base, another higher up. Enlarged about 12 diameters.

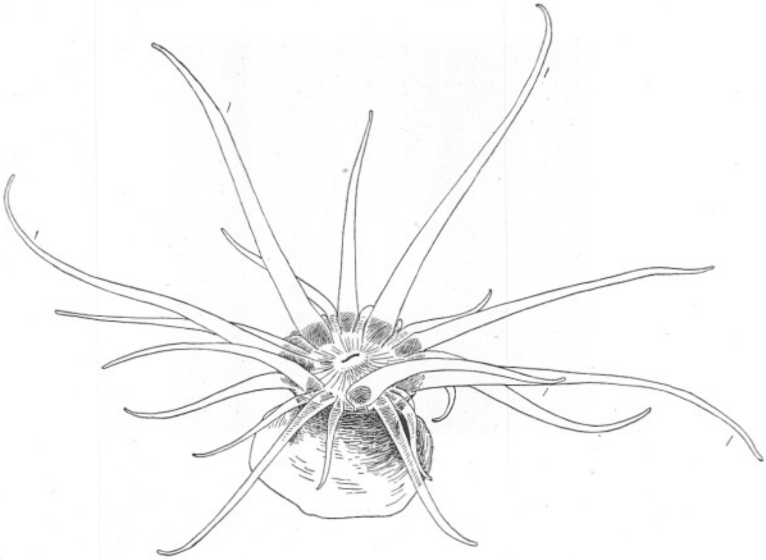
The more important side of the result, however, is that upon which the information is precise, i.e. the percentage of pieces which were able to regenerate into fully-formed animals in the various species. Here a separate note on each form will be advisable.

Sagartia elegans.

In this species the pieces regenerate easily and often rapidly. The percentage reared (92%) is actually too low, since the remaining specimens (5) were mostly lost, and did not actually die. One can expect to rear something like 100% of any good batch of pieces detached from individuals of this species.

S. troglodytes.

The remarkable fact here emerges, that of 76 pieces, only 2 came to maturity (one of these is illustrated in Text-Fig. 10); 32 pieces made some attempt at regeneration, but in only 5 did this reach even the grade of tentacles. The regeneration was slow and obviously difficult, and often abnormal and imperfect. It is quite clear that the pieces did not regenerate at all easily under the conditions provided. This may be accounted for as follows. In the rearing of basal fragments, the probability of success depends on three factors: (1) the firmness with which the piece is attached to the glass, (2) the amount of mucus which it secretes, and (3) the degree to which it can be kept clean. In *Sagartia* the degree of firmness with which the animal adheres to foreign surfaces varies distinctly according to species, although individual exceptions may always be found to this rule. In the main, for instance, *S. troglodytes* adheres much less tightly than do *S. anguicoma* or *S. elegans*. This means that pieces cut away from *troglodytes* are often but lightly attached, or may come loose altogether; and in rearing pieces it is a rule that mortality among loose or nearly loose fragments is very much higher than among such as are well attached. Again, the amount and quality of the daily secretion of mucus in *Sagartia* varies, and this variation, of course, occurs in the fragments. *S. troglodytes* secretes a tougher and



TEXT-FIG. 11.—A fully regenerated specimen of *Sagartia anguicoma*, produced from an artificially separated basal fragment. The primary tentacles are marked I. Magnified about 9 diameters.

more tenacious mucus than do *S. anguicoma* and *S. elegans*, and in the case of the fragments this often forms a dense cap or ring round the piece, from which the fragment cannot free itself, and this cap forms an admirable site for the accumulation of sediment and bacteria. To anyone who has reared such pieces these reasons are adequate to explain the difficulty of rearing *troglodytes ;* but in addition it seems in itself a delicate species, and by watching the course of regeneration one receives the impression that its regenerative ability is not strong.

S. anguicoma.

In this case, although the proportion of pieces reared (58%) was lower than in *S. elegans*, it was evident that the species possesses strong regenerative ability, and the pieces usually regenerate well and cleanly, although with less certainty than do those of *elegans*. This is doubtless partly due to the fact that they usually adhere very firmly, and secrete mucus of a less offensive nature than that of *troglodytes ;* but they seem to be also stronger and of a firmer texture in themselves. A regenerating fragment of this species is illustrated in Text-Fig. 9, and an expanded specimen fully regenerated in Text-Fig. 11.

S. lacerata.

In this species the result should theoretically be as good as those in *S. elegans*, since *S. lacerata* fragments more freely in nature than any other form. In fact, however, except in the best experiment, they fell below expectation ; but it is possible to account reasonably for this. In the earlier experiments, most of the pieces cut off were very small (*S. lacerata* is usually a small species, and they were mostly smaller than in the other species used), and did not regenerate very well. I believe this may be due to the fact that laceration in this species, when it occurs naturally, is a gradual process of constriction, and does not involve a large open wound as does the ripping incurred by *S. elegans*. In a small piece cut off suddenly, on the other hand, a wide open wound is involved, and this does not seem to suit the species. Consequently, after this had been realised, 20 pieces of slightly larger average size, but still not more than a few millimetres in diameter, were cut off from a set of adults, and all of these regenerated and survived.* Taking all the experiments together the percentage is lowered to 82%, which even then is higher than in *S. anguicoma*.

Conclusion.

If " outside " water in quantity had been available, probably a higher percentage of pieces of *S. troglodytes* and *S. anguicoma* would have been

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* It is just possible (but not probable) that one or two of these pieces included tentacles when first cut off.

reared than in tank-water; and probably the same would be true in nature. This consideration notwithstanding, the marked differences which occurred under identical conditions in the four species certainly mean something, and it may be concluded that the regeneration of pieces takes place more readily in the species which lacerate in nature than in those which do not. At the same time those which do not naturally lacerate are *able* to regenerate from fragments, though to a different degree in different cases. This renders the more remarkable the fact that they do not normally lacerate in the wild state.

4. EVIDENCE DERIVED FROM THE LITERATURE.

It is hardly necessary to give a complete summary of the data available in the literature which bear on the subject at issue, for reasons which will appear (note on exceptions, in Section 7). I give, however, a selection of facts extracted from the considerable amount of literature which exists on the subject. Some of these supplement my own results, especially in the cases of *Diadumene luciæ* (where my results are scanty) and *Cereus pedunculatus*. The other extracts are designed to illustrate the type of observations which have been made by other authors.

Fission, laceration and regeneration in Actinians have been studied by a number of authors—by Carlgren, Dalyell, Andres, Cary, Davis, Child, Parker, Hammatt, Torrey, Hazen, Loeb, and others. Many of the observations of these authors are relevant to the present question, although the aim of their studies has usually been distinct from that of this paper. Several of them, for instance Dalyell, Carlgren, and Davis, have clearly realised that in forms with which they were dealing a stated method of reproduction was characteristic of given species. The data quoted below, from Dalyell, makes this evident, in his case. Carlgren, in his 1904 paper on regeneration, deliberately selected for certain experiments species which do not habitually reproduce asexually, in order to avoid the introduction of complicating factors into his work; and in many other ways it is clear that he is aware of the state of affairs. The present paper, however, is the first study, as far as I know, devoted to the consideration of the specific value of reproductive methods as such.

The observations made in his aquarium by Sir John Dalyell possess great value, and the following data, extracted from his *Rare and Remarkable Animals of Scotland*, concern us here.

Actinia equina. Specimens were kept in captivity for as long as 13 and 20 years. Dalyell was fully aware that the normal habit of the species is to produce viviparous young; he also observed the production of embryos prior to metamorphosis, but these were rarely liberated by the parent, and such an occurrence was regarded by Dalyell as accidental and non-typical. One specimen in his possession for 20 years produced 334 young during that time; another which he kept for over four years produced 200 young in 14 days. The first of these specimens produced further young after Dalyell's death (see Ashworth and Annandale, 1904). In other cases young individuals were reared. One of these first produced viviparous young when between 14 and 15 months old, and by the time it was 4 years old had produced 64 of them. Another lived for nearly 5 years; at 3 years old it had produced 28 young, the first of which had appeared at between 13 and 14 months; subsequently it produced many more, 7 one night and 15 another. A third produced its first young at a year old, produced 60 in three years, and more afterwards; this one lived 10 years. A fourth began to breed at 14 months old, and was prolific; two depositions of young containing 60 and 43 respectively; this specimen, a double one, was accidentally torn in half at about six years old, and one half produced further young after this. In this species viviparity has also been observed by many other workers.

Sagartia elegans. Here there is an observation made by Dalyell to the effect that specimens kept by him for three years produced no viviparous young; this confirms my own and Evans's results.

S. troglodytes (the "*Actinia explorator*" of Dalyell). Dalyell was aware that this species is viviparous, and records the production of over 60 young in a night by two small specimens.

S. lacerata. In the case of this species Dalyell showed that laceration is the characteristic mode of reproduction. On page 228 he remarks: "Amidst the numerous embarrassments obstructing the discrimination of species and varieties of the Actinia" (i.e. of Actiniæ), "it is fortunate to meet certain immutable features, so prominent as to distinguish some of them, so definitely from all others, as to leave no liability to error." This remark refers, partly at least, to the habit of laceration. One of Dalyell's specimens produced over 70 young by laceration in the course of a year, and one laceration which was reared began to lacerate itself after nine months, and produced 40 lacerations in 80 days. Specimens were kept for over three years; no viviparous young were ever observed. Lacerations sometimes achieved tentacles 15 days after the appearance of the basal irregularities which produced them.

Finally, Dalyell realised that among anemones the animal "propagates by two distinct fashions, as seen in different species"—this refers to viviparity and laceration by constriction, other methods (apart from the production of ova) not having come to his notice.

Next we may consider a paper by Davis (1919) on asexual multiplication and regeneration in *Diadumene luciæ*. This paper deals mainly and in detail with the morphological results of fission, but a large amount of material was used by the author, and it emerges clearly from his study that longitudinal fission involving the tearing of mouth and throat is a characteristic and frequent occurrence in the species; and the author remarks on page 167: "There is no suggestion of a division resembling that known as basal fragmentation. Any other method of asexual reproduction than that described above" (i.e. fission), "must be very rare in the adult form of this species." That fission is habitual in the species is confirmed from various quarters, by the observations of Davenport, Hargitt, Hausman, Walton, etc., as well as those of Evans and myself. It has also been suggested that the species can bud and lacerate (Davenport 1903, Hausman 1919), but these suggestions are not, so far as I know, founded upon actual observations, and if they are correct these processes must, as Davis remarks, be quite exceptional.

In 1911 Cary published a paper on pedal laceration in Actinians, giving an account of this occurrence in *Cylista leucolena* and in three species of *Aiptasia* (none of these forms is British). Among 1300 specimens of *C. leucolena* examined, 1234 had given rise to lacerations; the same is true of 78 out of 150 specimens of *Aiptasia pallida*, of 187 out of 220 of *A. tagetes*, and of 20 out of 52 of *A. annulata*. For details reference should be made to the paper.

The observations made by Miss Jessie Nelson, and later by Ashworth and Annandale (1904), and by Evans, on some specimens of *Cereus pedunculatus*, are interesting in this connection. The specimens in question are 16 in number, and have now been in captivity for some 66 years; their actual age must be at least 70 years, and may be considerably more. These specimens (referred incorrectly by Ashworth and Annandale to *S. troglodytes*) are still in good health, and during their captivity have produced countless viviparous young, some of which have been reared and have been prolific in their turn, which applies again to the grandchildren. The original specimens are mostly still breeding freely, and have never, so far as I know, produced anything but such young.*

Further papers dealing with asexual reproduction and regeneration are enumerated in the list of literature at the end of this paper, and the case of *Metridium* is mentioned on page 162. The above examples will serve to illustrate the sort of material which may be gleaned from the literature, and the only other point which need be noted at the moment is that there exist records which contradict the conclusions of this paper; these are dealt with on page 161.

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* One of the original specimens was removed from the tank containing the others on May 27, 1925; in the 123 days succeeding its isolation it produced 102 young. Since then it has produced none up-to-date (May, 1928). This suggests that it had been fertilised from sperm of another individual before isolation—although no emission of sperm had been seen. Some specimens of the species are undoubtedly hermaphrodite, but it does not follow that it is self-fertilising.

5. THE EFFECT OF THE MODE OF REPRODUCTION UPON THE MORPHOLOGY.

A considerable body of knowledge exists as to the effect of asexual reproduction on the morphology of Actinians, and as to the morphological conditions which follow the regeneration of artificially separated portions of these animals. For details reference must be made first and foremost to the very important papers of Carlgren (1904, 1909, 1909a), and also to that of Davis (1919) above mentioned, as well as those of Cary (1911), Davenport (1903), Hargitt (1914), Parker (1897, 1899), Torrey (1898, 1902), Hammatt (1906), A. F. Dixon (1888), G. Y. and A. F. Dixon (1889 and 1891), Hahn (1905), etc.

The point I wish to make here is that there is quite enough evidence to show that anemones with more or less irregular symmetry (i.e. those which depart from the typical condition possessing 2 siphonoglyphs, 2 pairs of directives, 6 primary pairs of mesenteries, and 6 primary tentacles, all bilaterally arranged) are generally specimens which in one way or another have been produced asexually. These specimens may have a varying number of siphonoglyphs and directives, a number of primary tentacles and mesenteries other than six (4, 5, 7, 8, 9, 10, 11, 12, 13, 14), and no definite bilateral symmetry. This is the general rule; but it does not imply either (a) that asexually produced specimens are never hexamerous and bilateral, nor that (b) sexually produced specimens are never irregular. Both these conditions do exist, for specific causes. But our knowledge is sufficient to make it a very probable assumption that if, in any given species, a high proportion of the individuals exhibit irregular symmetry, this is a species in which asexual reproduction is frequent. If, in such a case, we have even a few actual records of asexual reproduction, the assumption that it is general becomes still more likely. Conversely, the result of my own and other observations shows that in the case of viviparous species the young are normally symmetrical and hexamerous; so, consequently, are the adults; and if, in a species whose reproductive habit is not known, the adults are found to be regular and hexamerous, it is probably one in which either viviparity or at least the absence of asexual reproduction is prevalent. There do arise cases in which individuals of sexual origin are irregular; but this can be due to reparation of injured parts and similar causes, and does not affect the general rule. My own study of a wide range of material has shown that the above remarks apply to the species specially dealt with in this paper—i.e. in *Sagartia elegans*, *S. lacerata*, *S. sphyrodeta*, *Diadumene luciæ*, and *D. cincta*, the adult symmetry is often or usually more or less irregular, whereas in *S. troglodytes*. *S. anguicoma*, and *Cereus* *pedunculatus* (viviparous or oviparous forms) the symmetry is normally regular and hexamerous. In this latter connection it may be noted that in a paper published in 1898, Clubb records an anatomical examination of 165 specimens of the viviparous *Actinia equina.* All of these were hexamerous; and 158 of them were bilaterally symmetrical, with 2 syphonoglyphs and 2 pairs of directives.

6. REPRODUCTION IN THE BRITISH SPECIES AS A WHOLE.

I am at present unable to give a complete collection of records of reproduction in British species from the literature, because I am on the eve of departure for a year's research in Australia; but in the following list I give a contribution towards these records, from the observations of Evans and myself. In some cases the data given are merely additions to, or confirmation of, facts already known; in others the data are new. The letters E and S indicate whether the observation is due to Evans or myself; and species in which we have seen no reproduction are not included. "Sperm, 2.27" means "Sperm emitted, February, 1927"—and so on.

Gonactinia prolifera. Transverse fission (S).

Milne-Edwardsia carnea. A young specimen taken from a Ctenophore (*Bolina* sp.) upon which it was parasitic, in October, 1926, was reared by Miss Delap, of Valencia, and sent to us. We both confirm it as this species, having seen it alive and sufficiently grown for an accurate determination. We have also seen young specimens creeping about stones inhabited by the adult.

Halcampa chrysanthellum. Sperm, 2.27 (S).

Ilyanthus mitchellii. Ova, 26.10.26; 9.27 (E). The ova are extremely large.

Actinia equina. Viviparous young habitual (E and S).

Anemonia sulcata. Longitudinal fission, 25.9.22; 28.4.24; 2.4.25; 1.9.23 (E).

Bolocera tuediæ. Ova, July, 1925, and in 1926 (E).

Tealia felina. Sperm, 5.11.22. etc. (E).

Bunodactis verrucosa. Viviparous young habitual (E and S). A brood of 27 young (produced under the action of menthol) was seen, 30.5.27 (S), the same individual producing more young later. This specimen and some of its young are illustrated in Text-Fig. 5.

Anthopleura thallia. Longitudinal fission frequent (E). The prevalent irregular symmetry of this species supports these observations.

Diadumene cincta. Laceration by tearing fairly frequent (E and S).

D. luciæ. Longitudinal fission habitual (E and S).

Aiptasia couchii. Transverse fission, 10.25 (E); viviparous young, 8.25 (E).

Metridium senile. Laceration habitual (E and S). Ova, 4.8.22; sperm and ova at other times (E).

Calliactis parasitica. Sperm, 9.22 (E).

Adamsia palliata. Ova, 29.10.25, and on several occasions since (E).

Cataphellia brodricii. Viviparous young in quantity from specimens collected at Salcombe and Wembury (Devon) in March and April, 1927. Several adults produced young, the total number of the latter amounting to 231; the three largest broods contained respectively 68, 85, and 51. Since the adults and young are normally regular and hexamerous, it is probable that viviparity is habitual (S). Specimens sent to Edinburgh at the time mentioned produced further young individuals afterwards (E).

Hormathia coronata. Viviparous young, 15.3.25; 7.5.25; 10.6.25; 7.4.27 (E). The species is normally regular and hexamerous, and there are French records which state that it is viviparous; probably, therefore, it is habitually so.

Paraphellia expansa. Ova probably belonging to this species have been seen (E).

Gephyropsis dohrnii. Laceration, 15.11.25 (E), and at other times (S).

Sagartia elegans. Laceration by tearing habitual (E and S).

S. anguicoma. Sperm, 11.25 (E).

S. troglodytes. Viviparity habitual (E and S). Sperm, 11.6.22; ova, 9–10, 6.23 (E), and at other times (E and S).

S. lacerata. Laceration by constriction habitual (E and S).

S. sphyrodeta. Longitudinal fission habitual (E and S).

Cereus pedunculatus. Viviparity habitual (E and S).

Phellia gausapata. Laceration observed in each of 5 specimens; one or two lacerations produced by each (E).

7. DISCUSSION.

It has been sought to establish that

(1) In the species selected for study, the deposition of ova may occur in any of them (except that in *Cereus pedunculatus* the ova normally, and perhaps always, develop within the cœlenteron of the parent).

(2) Apart from this, there are two principal methods of propagation in these species, viviparity and asexual reproduction; and only one of these methods normally occurs within a single species.

(3) In the forms which reproduce asexually, only one out of three possible methods (total longitudinal fission, laceration by constriction, or laceration by tearing) normally occurs in any one species.

Can the above statements be regarded as proved ? In this connection the following points may be noted.

(1) It is a striking fact that there is not, in my experiments, a single exception of any kind to the rules postulated. The same applies to the observations of Evans, and to my own general experience of living anemones, which has spread over some fourteen years. This distinctly enhances the results. The most difficult point to establish is the negative observation that certain species do *not* reproduce asexually ; but since asexual reproduction occurs at any time of the year, and fairly freely where it does take place, there should have been at least some exceptions if a negative conclusion were incorrect.

(2) There are other series of data available beyond the experiments, which confirm the above results.

A. Observations by various workers recorded in the literature. It so happens that in some instances where my own results are scanty, the gap can be filled either from the literature or from Evans' observations.

B. There are data available relating to the morphology of considerable numbers of specimens of many of the species concerned, which add confirmation to the experimental results.

(3) For the above reasons I believe that, although my experiments taken alone would be insufficient to prove the case, when all the available data are taken into account, the conclusions outlined above are justified. Moreover, I have reason to think that the numbers yielded by my experiments understate the case rather than otherwise, since the processes observed went on rather more slowly under the Plymouth conditions than has been the case with many of the specimens in Evans' aquarium.

The question of exceptions must be next considered. I do not wish to maintain that in any species such never occur ; they may well do so, even though they have not come under my notice ; but even if they do, the general contention is not invalidated. In species which have *not* been specially studied here, moreover, it may be true that different conditions occur, and that combinations not represented in those here selected are present. It is quite possible that just as in morphology it is found that some species are stable and others are unstable, so in the matter of reproduction it may be true that some species (such as those investigated) are stable or almost stable, others more variable. I suspect that Metridium may be somewhat variable in this respect, although laceration is certainly its prevalent method. Again, in *Aiptasia couchii*, although we do not know enough about the species to be sure what are its normal habits, it appears to be established that the species is viviparous and that it also undergoes, at times, a curious form of transverse fission.

Nor must the possibility be forgotten that within the same species the method of reproduction may vary with locality. I am not aware that this applies to any of the British species within the British area, but it *may* apply, for instance, to their Norwegian or Mediterranean representatives. In the case of *Actinia equina*, Gravier has found that the species is still viviparous at the island of S. Thomé, near the Equator. In *Sagartia troglodytes*, however, the viviparous habit has not been observed by Carlgren in Scandinavian waters (this species is in any case oviparous as well), although of course it may occur. Carlgren's observations on *S. troglodytes* confirm my own, that it does not reproduce asexually, and the same applies to *S. viduata*, a northern species closely allied to *S. anguicoma*.

There are a number of records in the literature which definitely contradict my observations. It is very difficult to tell whether these have any serious bearing on the question, because frequently either sufficient precision is lacking in the records, or they apply to isolated instances only. It must be remembered that the phenomena exhibited by Actinians have not always been understood at all clearly. When, for instance, we are told that in some species *budding* has been observed, it is much more likely that what was actually seen was either a subsidiary tuft of tentacles (sometimes including a disc and throat as well) on the side of the anemone, produced as the result of a small wound, or as the consequence of the regeneration of an atypical laceration ; or some other similar phenomenon. Such formations resulting from wounds certainly do occur, and have nothing to do with asexual reproduction. Some records of " buds " are due to a regenerating laceration which has not been fully detached from the parent. True budding is probably very rare among Actinians, if it occurs at all. Again, at one time it was generally assumed that double-headed anemones, or specimens with two bases, were necessarily stages in fission. Carlgren and others have shown that permanent double-monsters *can* originate from arrested and incomplete fission ; but that many of them are double from an early embryonic stage, or arise from some other reason, and their condition has nothing to do with ordinary asexual reproduction.

Further, in the early days an isolated record of the production of viviparous young, in the species in which we know that they do not normally occur, might well apply to basal fragments which had not been noticed until they had formed tentacles. When, as was often the case, the actual birth of the young was not witnessed, this is the probable explanation, and I know of one instance in which it actually occurred. In other cases records are rendered valueless because we cannot be certain that the specimens under observation really belonged to the species to which they were assigned; several species of Sagartia live in the same localities and have often been confused one with another. For the above reasons, although I am aware, to give instances, that viviparity has been recorded in *S. elegans* (Gosse 1860, pp. 46 and 71), that laceration has been recorded in *Actinia equina* (Landauer 1924), *Cereus pedunculatus* and *Bunodactis gemmacea* (Andres 1881), and so on, I am confident that the majority of such records are either mistakes, or that they refer to the results of injury, to double individuals, or to similar conditions. Some of them, no doubt, refer to genuine exceptions, but there is no evidence to show that these exist in sufficient amount to invalidate in any way the conclusions of this paper. Such records for the genus Sagartia are but few.

The case of Metridium is worthy of a little further attention, since much research has centred round it. Papers dealing partly or entirely with Metridium have been published by Carlgren (1904, 1909), Verrill (1922), McMurrich (1901, 1911), Hausding (1914), Parker (1897, 1899), Torrey (1898, 1902), Hammatt (1906), G. Y. and A. F. Dixon (1891), Hahn (1905), etc. Carlgren, Parker, Torrey, and Hahn especially have studied the influence of asexual reproduction on the morphology, among them giving many details of variation in siphonoglyphs, number of perfect mesenteries, and general symmetry, and dealing with the question of double-monsters, etc. Torrey (1902) emphasises that although fission and budding occur in the species, neither of these has more than a trifling influence on the number of individuals, since laceration is frequent, rapid, and universal. Among 2662 individuals, less than 2·5% were suspected of fission or budding, and if the origin of the so-called " fission " and " budding " could be fully studied it would doubtless be found that many or most of the instances were really due to double-monsters, injuries, etc. Double specimens are normally permanently double and the halves do not separate. Whether fission of the type found in *Sagartia sphyrodeta* occurs at all in Metridium is doubtful. Consequently, although there may be more variation in the reproductive processes here than in other cases, there is certainly less than might at first sight appear. (The above remarks refer indiscriminately to *Metridium senile*, *M. fimbriatum*, and *M. marginatum*; it is held by some authors that these are all the same, by others that they are not. The question is not finally soluble at the moment.)

Lastly, I would like to make a comment on the situation; but wish to make it quite clear that the following remarks make no claim to represent a discussion of the species-problem in general. I hope to discuss this problem at a later date ; but for the moment I am giving an indication of the sense in which the word " species " is here used, in order that the facts concerning methods of reproduction as specific characters may be fitted into their place with relation to our existing knowledge of species.

There exists, as is well known, an unfortunate division of zoologists into systematic and general workers. Systematic work is regarded, not without reason, by the ordinary zoologist, as at the best a necessary evil, and it is hardly possible to mention the word " species " without causing an unfavourable reaction in one's audience ; the very word conjures up visions of dullness. For this state of affairs the systematists cannot be held guiltless, since their work represents, only too often, a purely academic study of certain aspects of organisms, and is divorced from any general interest in the field of zoology as a whole. On the other hand, it is unfortunate that the question of species receives as little attention as it does from zoologists in general. The subject of evolution is one of the central problems of biology, and it is a problem which is intimately bound up with that of species. It will hardly be denied by anyone that work which sheds light upon the question of evolution is a live issue. At the present time, when experimental methods of research are so much to the fore, there is an excellent opportunity for a fresh attack upon the species-problem, from an angle distinct from the classical one. It is not enough to " leave it to the systematists," since this will not lead to any advance in our knowledge ; the field must be explored by biologists with general knowledge and interests.

If, then, we are to approach the problem along new lines, one of the steps which must first be taken is this, that species must be studied intensively, and everything about them must be taken into account. Not only must we know that A differs from B in the possession of a different number of hairs on its legs, but we must also know the whole of its morphology, its life-history and habits, its methods of reproduction, and whether it possesses distinctive physiological characteristics unlike those of B. When this has been done we shall at least know more about the potentialities of species than is at present the case.

At this point there arises the question " What is a species ? " This is a matter of definition too involved for detailed discussion in the present paper, but it will be advisable to give some indication of the sense in which the term is here employed.

The Actinians which have been specially studied here present a case in which, despite the general belief to the contrary, it is possible to recognise the species (from living specimens) quite distinctly by taking into account morphology, markings, and colouration ; and no specimen comes to hand of which one cannot say "this anemone belongs to such-and-such a species, and it is clearly different from any other kind of anemone." So much is this the case, that it is often possible to identify an anemone from a detached fragment of its basal margin.

For the purposes of the present stage of this discussion, therefore, the word "species" may be regarded, in the first place, as a term covering all existing specimens of any animal which is not of the same kind as any other animal; the criteria of distinction being a series of differences which are visibly expressed throughout the entire morphology. But since the factor of time must also be considered, this definition requires the qualification that a species now living also includes many individuals which are extinct, and many which are yet to come. Its limits in time lie between

(a) The time when the animal type in question first became recognisably distinct from any other.*

(b) The time when this same type, by splitting up into others, or by becoming extinct, will cease to exist as such.

Hence, it is clear that a species, although it may persist for a long time, is transitory. Moreover, if it is one which is to split up ultimately into others, there will be a period at the beginning and another at the end of its history during which it will be difficult to distinguish it from parallel or derived forms. Consequently, the limits of a species *in time* can never be precisely fixed, although its morphological limits for a certain period of its history may be sharply marked. It may be true, moreover, that at the present time a number of species are not in the phase of evolution during which they are recognisably distinct, as in the case of the Actinians in question, but are in a state of flux. If such forms exist, one would expect to find groups of forms, evidently allied, among which races (linked perhaps by numerous hybrids) can be distinguished with more or less accuracy, but among which the species cannot be determined with the degree of precision which is practicable among the anemones. I feel that such an explanation may account, for instance, for the state of affairs which prevails in the genus Dactylorchis, a group of plants which I have studied somewhat extensively in the field. If, therefore, there are cases in which it is possible accurately to determine specific limits, and others in which it is not possible; and if in any case the limits of a species in time are not sharply marked; it is evident that the conception of a species is at present lacking in precision. But in the following paragraphs the word may be understood to mean, as nearly

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* By "recognisably distinct" is meant "distinguished by a series of differences which are visibly expressed throughout the morphology"; i.e. recognisably distinct as an animal type from any other animal type. In other words, although a red animal is "recognisably distinct" from a black one (and the difference may depend upon a Mendelian factor), this does not necessarily mean that the two are specifically distinct.

as the above qualifications will allow, an animal type which is different from all other animal types.

Having explained the interpretation to be placed upon the word "species" for the purpose of this discussion, it may next be pointed out that, in the methods of reproduction which have been studied in these anemones, we have a criterion for specific distinction of a nature different from the usual morphological standard. It is evident that in dealing with a sharp distinction between a species which does, and another which does not, habitually reproduce asexually, we are dealing with a marked difference between the physiological constitutions of the forms in question. The fact that any species *can* regenerate from artificially separated fragments merely renders more striking the apparently complete abstinence of certain species from doing so. Now, in the species in question there is no doubt about the morphological distinctions between them; but we can hardly speak of a reproductive method as "morphological." It is true that morphological distinctions are the expression of different series of physiological processes, and that the "morphological" and the "physiological" are interdependent, and merge into one another when philosophically considered; but for ordinary purposes of terminology it is necessary to draw a line between the two, and a method of reproduction must lie on the physiological side of that line.

This raises the question of "physiological species" in general. In this connection it may be noted that in the higher animals (e.g. the mammals) the morphological differences between species may be considerable, whereas marked physiological differences of a grade comparable to the differences in reproductive physiology exhibited by the anemones, are not present. The interest of the anemones lies in the fact that among them there may exist side by side a slight degree of morphological distinction between two species, accompanied by a very marked physiological difference. If, in this respect, it is true that the anemones represent a stage intermediate between the highest and the lowest animals (as indeed from general considerations might be anticipated), we should expect to find that on a still lower grade there might be morphological identity between species which would then be distinguishable only by physiological tests; and this state of affairs appears to be realised, for instance, in the bacteria and in the moulds. To such cases as these last, the term "physiological species" may very appropriately be applied; but it should be remembered that such species are of the same essential nature as those which occur among anemones or mammals, whether the criteria which most readily distinguish them be morphological or physiological. In other words, so long as a species is understood in the sense of this discussion, it is immaterial whether the adjective applied to it be "morphological" or "physiological." It follows from this, that the word "species" should not be applied to cases in which it is possible, within the limits of a single species (in the accepted sense), to distinguish groups of individuals (e.g. blood-groups) which exhibit different physiological reactions of certain kinds. Such differences as these (which can be paralleled on the morphological side) do not necessarily indicate specific difference at all. It may be that some of them are the forerunners of far-reaching changes which will in time differentiate one species into more than one; but until such differentiation has taken place these groups cannot validly be termed species.

The addition of the bacteria, etc., to the list of organisms amongst which species can be recognised, involves the emendation of the definition of a species given below, to the effect that the criteria which distinguish organisms of one kind from those of another may be physiological instead of morphological.

In conclusion it may be noted that the case of the Actinians is not an isolated one. In Ascidians, as Berrill (1928) has shown, species may be distinguished according to whether or not they have a tadpole-stage in their development. In regeneration among invertebrates, distinct methods of behaviour after injury, characteristic of species, are probably widespread, as demonstrated, for instance, by the work of Nusbaum and Oxner on Lineids. In the anemones themselves, there are specific differences in the power with which the base adheres to foreign substances; in the quality and amount of mucus which the animal secretes; and in its irritability—e.g. in the readiness with which it will shoot forth acontia when provoked. These last-quoted cases, however, are much less sharp and less easily measurable than the methods of reproduction; and they may vary very considerably from one individual to another, and according to the type of environment which an individual has inhabited, prior to collection. They are, in fact, differences of tendency rather than absolute distinctions such as method of reproduction, mode of early development, or behaviour during regeneration.

8. SUMMARY.

1. Eight species of Actinians (enumerated on p. 148) have been specially studied with regard to their reproductive processes.

2. Among these forms five methods of reproduction occur—longitudinal fission; laceration by tearing; laceration by constriction; production of young viviparously; deposition of ova.

3. Deposition of ova may co-exist with any other method, except perhaps in certain viviparous forms.

4. Apart from this, one method only prevails in any one of the selected species—

A. Longitudinal fission in *Sagartia sphyrodeta* and *Diadumene luciæ*.

B. Laceration by tearing in *Sagartia elegans* and *Diadumene cincta*.

C. Laceration by constriction in *Sagartia lacerata*.

D. Viviparity in *Sagartia troglodytes* and *Cereus pedunculatus*.

5. In *Sagartia anguicoma* neither viviparity nor asexual reproduction occurs.

6. The viviparous forms studied do not reproduce asexually; nor are those which reproduce asexually viviparous.

7. In the experiments and observations of the author and of W. E. Evans, no exceptions to the above statements occurred. The question of exceptions is discussed on page 161.

8. Four of the above species were selected for regeneration experiments. Pieces were cut off from the margin of the base in each (artificial laceration).

9. In *Sagartia elegans* (which lacerates naturally) it was found that nearly 100% of such pieces would regenerate easily; in *S. lacerata* the same was true in the best experiment.

10. In *Sagartia troglodytes* (which does not lacerate naturally) only two pieces out of 76 regenerated fully, and the regenerative ability of the species appeared to be weak. In *S. anguicoma*, however, the percentage of pieces which regenerated fully (and did so strongly) was very much higher, though not reaching that of *S. elegans*.

11. Regeneration was probably more rapid, in the main, in the species which lacerate naturally than in the others.

12. It is maintained that sharp distinctions between species, such as those mentioned above, are of interest from the point of view of the general problem of species.

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On the Nematocysts of Sea Anemones.

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With 1 Plate and 10 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE main object of this paper has been to determine whether or no it is possible to differentiate the species and genera of Actinians by employing as criteria the characteristics of their nematocysts.

I wish to acknowledge that I have received a grant from the Royal Society which has very greatly assisted the work described. The figures in Plate I have been published before in my Ray Society monograph on the British anemones; but their repetition here is essential for the adequate illustration of this paper. Figs. 1 and 4 on this plate are copied from Will's paper on spirocysts (1909a, Pl. 3, Figs. 4 and 9).

1. MATERIAL AND METHODS.

The material for this study was mostly obtained at Plymouth, this being supplemented by specimens from other places where necessary. The whole of the observations apply to fresh material studied before fixation, unless otherwise stated.

The object of the research was to take measurements of the capsules of nematocysts and to make observations on the distribution of the different patterns of nematocyst among various species ; for this purpose it was not necessary to make permanent preparations, and such were not attempted.

When the nematocysts to be studied are contained in an acontium belonging to a species which emits acontia readily, or when they are situated in a tentacle, it is easy to isolate a small piece of one of these tissues for study. Similarly, if a sample of nematocysts from the body-wall be required, a small amount of ectoderm containing them can readily be scraped off. If, however, nematocysts are required from the mesenterial filaments, throat, peristome, acrorhagi, etc., it is advisable to anæsthetise the anemone with menthol, until it ceases to respond to tactile stimuli. It can then be cut up without undue contraction, and accurate samples of the tissues required may be extracted.

For purposes of measurement and general observation fresh preparations of nematocysts may usually be employed without staining. In certain cases, however, and for the observation of particular details, these preparations may be stained directly. The best stains for general purposes are methylene blue (a 1% solution, or weaker) and acid fuchsin (1%). Spirocysts have a strong affinity for acid fuchsin, and some kinds of nematocysts, or perhaps all nematocysts under given conditions, for methylene blue—and it is possible to stain a preparation containing both so that the spirocysts appear bright crimson, and the nematocysts deep blue ; usually, however, the stains are employed separately. I have tried various other stains—picronigrosin, hæmatoxylin, eosin, picro-indigo-carmine, methyl green, neutral red, Janus green, etc. Some of these are useful for staining nematocysts or spirocysts in sections, but for fresh material nothing I have used equals the methylene blue and fuchsin ; other workers have found the same. In some cases the details of the barbs and spirals on the threads of the nematocysts can be seen to more advantage by introducing them into a medium of high refractive index. A medium which I have found serviceable is one described by Lee (*Microtomist's Vade-mecum*, 1921 Edition, p. 224)—a saturated solution of potassium iodide and biniodide of mercury in distilled water. The solution is made by grinding up the two materials together with a little water in a small mortar ; the amount of these which dissolves in a small quantity of water is considerable, and a syrupy solution of a clear greenish yellow colour results. This solution can be either used at full strength or in various dilutions, according to the index required. When adding it to a fresh preparation it is best to acclimatise this by introducing a drop of a dilute solution before a higher concentration is used. The action of methylene blue for the demonstration of detail is altered and sometimes enhanced by the addition of a very little potassium hydroxide (in a 5% or 10% solution) to the preparation. If the mercury medium is also employed, this should be added after the KOH and methylene blue, which may with advantage be mixed (provided proper proportions are used) immediately before they are added to the preparation. The results with such preparations are sometimes excellent, but very transitory.

Fresh preparations are made as follows. A small piece of the tissue to be studied is placed on a slide in a drop of sea-water. It is chopped into very fine fragments with a small needle-knife. All fragments are then eliminated save those of the finest grade, and a cover-slip is added. The cover-slip should be a large one, almost completely covering the slide, and the drop of fluid beneath it should be small. This ensures that the film between slide and cover-slip shall be very thin, so that the cover-slip is held tightly down. Consequently the nematocysts in the preparation do not move about in the fluid; they cannot, of course, be measured unless they are perfectly stationary. After the addition of the cover-slip, the preparation may be further dissociated by holding the slip down at one corner, between finger and thumb, and rubbing its surface firmly with the blunt end of a small scalpel, especially over the spots where little masses of tissue occur. In good preparations of this nature there should be many isolated nematocysts both exploded and otherwise, free from surrounding tissue. The smaller the amount of tissue used the better—sometimes it is enough to rub a fragment of tissue in a drop of water on a slide, remove the tissue, and use the nematocysts left in the drop. Larger masses of tissue, dissociated by being firmly pressed out, are useful for certain purposes, but not if one desires to see detail in the capsules. The method here outlined is not a refined one, but quite adequate for the object in view.

The microscope employed for the work was a Leitz binocular, with interchangeable binocular and monocular body (the monocular being used for measuring). It was used with a thorium-lamp, achromatic condenser, and a bull's-eye between the lamp and the mirror. Various objectives (oil-immersions) and eye-pieces, including compensating-oculars, were tried, but for general purposes it was found that No. 2 eye-pieces and a 10 water-immersion objective (Leitz) gave the best results.

2. ACCOUNT OF THE OBSERVATIONS MADE.

The measurements recorded below were made with a Leitz eye-piece-micrometer, No. 2 eye-piece, and 10 water-immersion objective (very rarely a $\frac{1}{12}$ inch oil-immersion).

A cnida, be it a nematocyst or a spirocyst (see p. 187 for further details), consists of a hollow refringent capsule, with one end of which a hollow thread is continuous. The thread is inside the capsule before explosion takes place, outside afterwards; and in changing from one


A
B
C
D
E
F
G
H
K
M

position to the other it evaginates or turns completely inside out, as one may turn a glove-finger. The dimensions of the capsule are less variable and much easier to obtain than those of the thread, and are therefore taken as the standard of size.

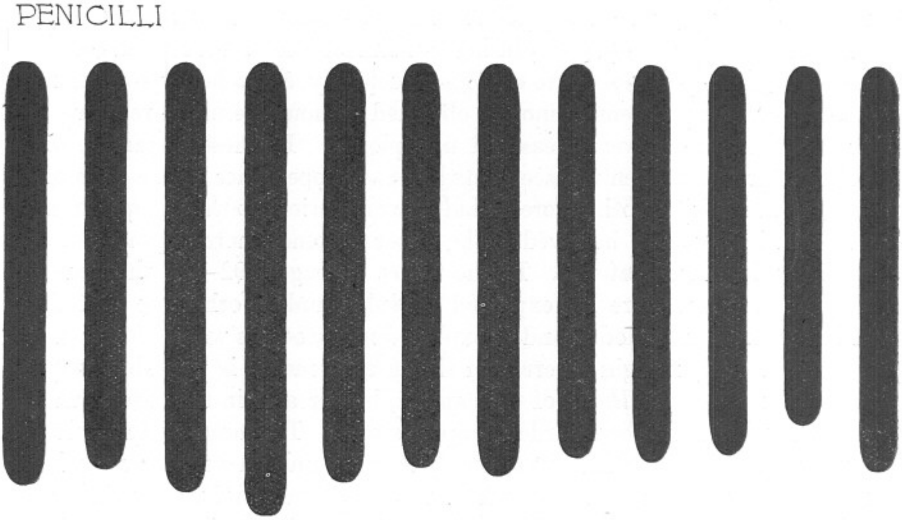
All the measurements given below, therefore, refer to the capsule, measured on fresh preparations in sea-water (unless otherwise stated), unstained and free from reagents, so that no distortion of the natural dimensions has been introduced. The capsules were measured after the eversion of the thread, wherever possible, because it is always easier to recognise the pattern of a capsule after evagination than before, and thus one avoids any question of confusing two similar kinds. In certain cases, however, the capsules seem to explode reluctantly, and a large proportion of evaginated specimens cannot be obtained without the use of reagents; in such cases they were measured unexploded. In these instances, of course, care was taken to ascertain the exact appearance of the type of capsule in question both before and after evagination, so that no question of confusing types is involved. The latter becomes more important in dealing with fixed material. In the tables on pages 192–198, therefore, the measurements are on exploded capsules, unless otherwise stated. A comparison of exploded and unexploded nematocysts will be found on page 198. The margin of error in the measurements is probably very slight as regards the *length* of the capsule, but greater in the case of the breadth, which must be regarded as approximate. The number of samples of any one tissue examined was usually 2 or 3, sometimes more; a single sample was used only in cases where very little material was available.

It should be noted that all the statements in this paper refer to the types of nematocysts which *predominate* in any tissue. In many cases there exist, in one and the same tissue, majority-forms and minority-forms. The latter are usually smaller than the former, and although they are sometimes rather numerous, they are generally present in much smaller numbers than the majority-forms. It is difficult to estimate their numbers and importance, and also to make out their structure, and in the present study they have been left out of account. In adequate fresh preparations there is no difficulty in determining which are the majority-forms.

TEXT-FIG. 1.—Sketches showing the general appearance of some Actinian nematocysts (for more detailed drawings see Pl. I). Figs. A, B, C, and F are penicilli of different varieties; the others are spirulæ, their barbs erect in some cases, reversed in others. Fig. H (*Metridium*) is a spirula, but only the enlarged basal part of the thread is shown, this part being unusually long here. A, *Sagartia troglodytes* var. *ornata* (acontium); B, *Phellia gausapata* (tentacle); C and K, *Phellia gausapata* (acontium); D and G, *Gephyropsis dohrnii* (acontium), two nematocysts of the same kind in different conditions; E, *Paraphellia expansa* (acontium); F, *Peachia triphylla* (mesenterial filament); H, *Metridium senile* (acontium); M, *Peachia triphylla* (throat).

A. VARIABILITY OF THE CAPSULES WITHIN A SINGLE SPECIES.

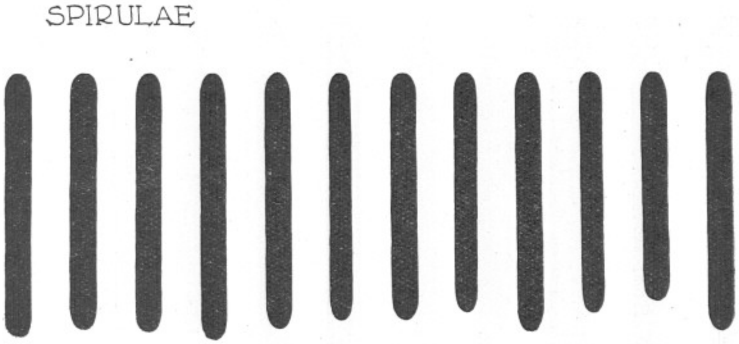
The first step was to gain some idea of the degree to which the size of the capsule varies in a single tissue of one and the same species. For this purpose a variable species (*Sagartia elegans*) was chosen, and the nematocysts from the acontia of specimens from different localities (Plymouth and Valencia) were studied. Twelve specimens were used, belonging to various colour-varieties (*venusta*, *venustoides*, *nivea*, *niveoides*, *rosea*, *roseoides*, and *miniata-ornata*), and the figures given are based on measurements of 30 capsules of each pattern from each specimen. These numbers are not large, but the measurements take a long time to make, and it is consequently impracticable to make them on a very extensive scale.



TEXT-FIG. 2.—Diagrams illustrating the average size of the capsules of the penicilli in the acontia of twelve specimens of *Sagartia elegans*. In this figure, and in Text-Figs. 3, 5–7, and 9–10, each diagram represents the average length and breadth of the capsules of a given type from a single tissue of a single individual anemone ; these figures are further explained in the text. A conventional shape has been adopted for all these diagrams, and all are drawn to the same scale ; they are not intended to illustrate the actual shapes of the various capsules, and they are slightly more approximate than the figures given in the tables at the end of the paper.

In the acontia of certain Actinians two types of nematocyst are plentiful. The first of these, a *penicillus*, is a capsule bearing a short, stout thread, barbed like a bottle-brush ; examples of this type are illustrated in Plate I, Figs. 5–7, and in Text-Fig. 1. In this type there is sometimes a slender terminal thread, which may be long or may be short and wisp-like, at the end of the "bottle-brush" (as in Pl. I, Fig. 6, and in Text-Fig. 1, F); in other cases there is no terminal thread. The minor varieties within the type are characteristic of different species. The second type usually but not invariably possesses a smaller capsule, but a very much longer and more slender thread, the basal portion of which is either somewhat enlarged or bears well-developed barbs, or both; this is known as a *spirula*, and is illustrated in Plate I, Figs. 2 and 3, and in Text-Fig. 1. Both of these types occur in *S. elegans*.

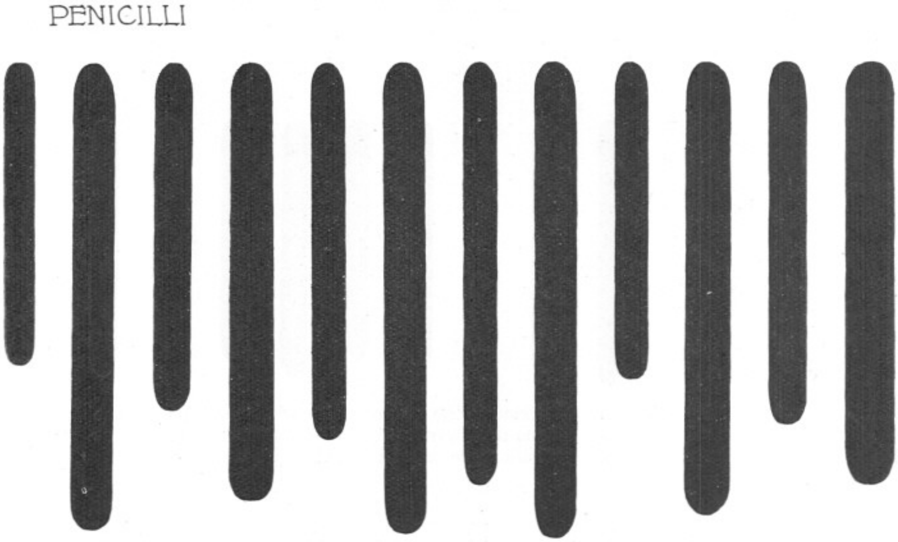
The figures for *S. elegans* are given in Table I on page 192; and in Text-Figs. 2 and 3 the average sizes of the capsules are represented graphically. From these figures it can readily be seen that the average length of the capsule varies considerably from one specimen to another, but not within very wide limits. In these figures the diagrams are arranged in a graded series, so that the one representing the capsules of the largest specimen used is on the left, and that representing those of the smallest is on the right. From this it is evident that there is no strict relation between the size of the individual and the average size of its nematocysts. Text-Fig. 4 gives the maximum and minimum sizes of penicilli which were found in six of the twelve specimens, instead of the average.



TEXT-FIG. 3.—Diagrams illustrating the average size of the spirulæ in the acontia of twelve specimens of *Sagartia elegans*—the same specimens as those from which the penicilli represented in Text-Fig. 2 were taken.

B. CONNECTION BETWEEN THE SIZE OF THE ANIMAL AND THE SIZE OF THE NEMATOCYSTS.

The second point to be ascertained was how far, within a single stable species, the size of the nematocysts changes as the animal grows larger. It is impossible to tell the age of an anemone from its size, since size in these animals depends on the amount of food recently received, and not upon age. But in a viviparous form one can at least distinguish new-born young from older individuals. The species chosen for this purpose was *Cereus pedunculatus*, and measurements were made from two new-born young and from 5 adult specimens forming a graded series from a small to a very large one. The acontia were used again here, and measurements were made from 30 examples of each of the two types of capsule contained therein. The figures are detailed in Table II on page 192, and the result is represented graphically in Text-Fig. 5, the diagrams being arranged in order of size of the specimens from which the capsules were taken; the diagram representing those of the largest specimen is on the left. From this it will be seen that although the nematocysts of the new-born young are distinctly smaller than those of the adults of any size (and this was confirmed by further measurements from 4 other new-born young not detailed here), the size varies relatively little between the five adults, although these represent extremely different sizes of animal, No. 1 being many times the bulk of No. 5. Nor does the nematocyst-size increase regularly with the body-size.



TEXT-FIG. 4.—Diagrams illustrating the maximum and minimum sizes of penicillus found in the acontia of six specimens of *Sagartia elegans*. The diagram on the extreme left refers to the same specimen as the one next to it; and so on, in pairs.

C. THE NEMATOCYSTS IN THE ACONTIA OF THE SPECIES OF SAGARTIA.

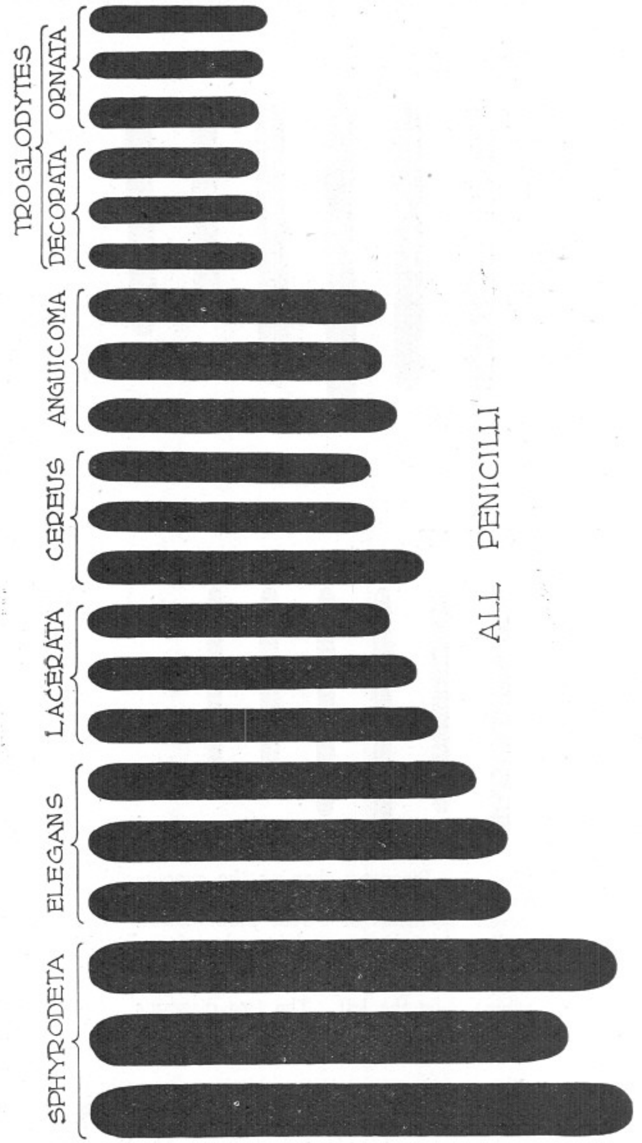
The third stage in the investigation was to find out in what manner nematocysts vary in a given tissue from one species of a genus to another.

the genus Sagartia being used as a test-case. The acontia again were used, and nematocysts from three specimens of each Sagartian species were studied. By this time it had been realised that 20 measurements of any one type of capsule are enough to give a sufficient idea of the range of variation. In the measurements above recorded for *S. elegans* the average is very little different if calculated from the first 20 capsules measured, than if calculated from the whole 30. Consequently in the observations recorded from this point onward, the figures are taken from measurements of 20 specimens of each kind of capsule, except

Text-Fig. 5.—Diagrams showing the average size of the penicilli and spirulæ in the acontia of seven specimens of *Cereus pedunculatus*. The diagrams are arranged in order of size of the anemone from which they were taken; that representing the capsules from the largest specimen is on the left. The two disgrams on the right represent capsules from new-born specimens.

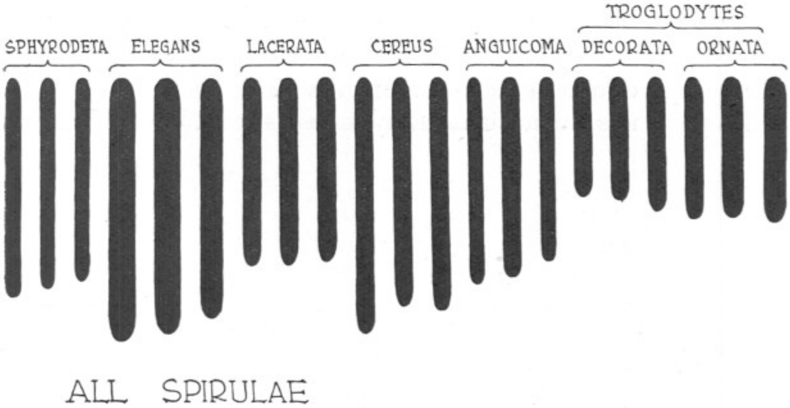
in cases where for some special reason a smaller number only was practicable.

The figures relating to 4 species of Sagartia are recorded in Table III on page 193, and the average sizes of the capsules are indicated by diagrams in Text-Figs. 6 and 7 ; these latter include also *Sagartia elegans* and *Cereus pedunculatus* (which is very closely related to the Sagartias).



Text-Fig. 6.—Diagrams illustrating variation in the average size of the penicilli in the acontia of five species of Sagartia (*S. sphyrodeta*, *S. elegans*, *S. lacerata*, *S. anguicoma*, and *S. troglodytes*) and of *Cereus pedunculatus*.

From Fig. 6 it will be clear that the penicilli of *Sagartia sphyrodeta* (a small species) outstrip those of all others in size, and that the penicilli of *S. troglodytes* (both varieties) are much the smallest. There would therefore be no difficulty in separating individuals of *S. troglodytes* from those of *S. sphyrodeta*, in a mixed collection, on the strength of these capsules; nor, indeed, would there be much difficulty in separating one of these species from any others, given well-grown specimens. If, however, one were to attempt the same feat with a mixed batch of *S. lacerata*. *S. anguicoma*, and Cereus, it would be quite another matter. These could, of course, be sorted out on other grounds; but from the penicilli of their acontia they could not, since the range of variation in one would overlap the range in another, the size being distinctly similar in all. In order to make this still clearer, I made an additional series of measurements of the penicilli of a specimen of each of these species, and I measured also those of two specimens of *S. elegans*, measuring in this case 100 of each, so that curves might be drawn from the measurements. The result is shown in Text-Fig. 8, from which it may be seen that the curves for *C. pedunculatus* and *S. anguicoma* (extremely distinct species) are very similar; so are those for *S. lacerata* and a small specimen of *S. elegans*, which again are very different in other respects. In this particular figure the curves for *S. anguicoma*+*C. pedunculatus* are separated by a gap from those for *S. lacerata*+small *S. elegans*; but the gap between the small and the large *S. elegans* is greater. Moreover, it may be stated that by choosing one's specimens carefully these gaps could be filled in, and a graded series of curves produced, though the curves for the other species would hardly reach up to the level of the curve for the



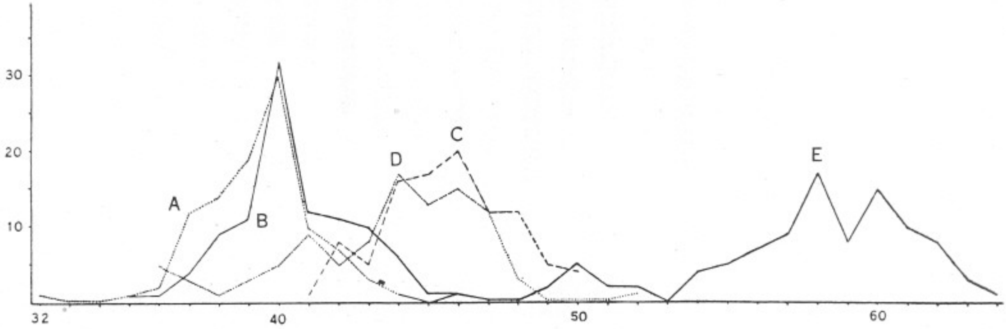
Text-Fig. 7.—Diagrams illustrating the average size of the spirulæ in the acontia of the same specimens as those from which the penicilli represented in Text-Fig. 6 were taken.

large *S. elegans*, since this species does really tend to have larger penicilli than the others. But it must be evident from the contemplation of these curves that it would be quite unsafe to attempt to distinguish the species involved on the basis of the size of the penicilli of their acontia. Even if it be true that the capsules of each tend to occupy a given range of size, the ranges for the several species are very close to one another.

An important point which is demonstrated by the above table is that in all the species of Sagartia, as well as in Cereus, there are both penicilli and spirulæ in the acontia; and the former are larger than the latter.

D. The Nematocysts in the Acontia of other Genera.

It was next desired to ascertain in what manner the nematocysts occur in the acontia of other genera of anemones which possess these organs, and this point was studied in as many forms as could be obtained alive.



Text-Fig. 8.—Curves illustrating variation in the length of the penicilli of the acontia in specimens of three species of Sagartia and in *Cereus pedunculatus*. Each curve is plotted from measurements of 100 capsules. The numbers along the abscissa represent the lengths of the capsules in μ; those along the ordinate represent the number of capsules of each length (to the nearest whole number) in each 100 measured. A, *Sagartia anguicoma*; B, *Cereus pedunculatus*; C, *S. lacerata*; D, *S. elegans* (small specimen); E, *S. elegans* (large specimen).

The result is detailed in Table IV on page 194, and in Text-Figs. 9 and 10. From these observations several facts emerge. The most important is that in the genera Phellia, Diadumene, and Aiptasia the acontia contain both penicilli and spirulæ in abundance, whereas in all the other genera spirulæ alone are present. No genus which I have studied possesses penicilli only. This confirms the idea which has been gained from other sources, that all the genera with spirulæ only are closely related, and that Diadumene and Aiptasia are more or less closely related to each other, but show less affinity to the other series of forms. As to Phellia, it is a genus of obscure standing, which I will deal with more fully in another paper. Another point which becomes clear is that in the genera with spirulæ only (except Metridium) these are of very similar dimensions all the way through (see also Text-Fig. 9), and therefore their size is not of great value for purposes of identification.

The *details* of the nematocysts in these forms vary from one species to another—most distinctive are the large spirulæ of *Metridium senile*, which are unlike any other capsules I have seen. In these, the capsule itself is long, the thread is very long, and its specialised basal part, which is slender where it leaves the capsule, gradually widens to a maximum, then ceases abruptly ; this part is sometimes more than twice as long as the capsule. In the penicilli there is sometimes a slender terminal thread, which may be quite short, on the end of the "bottle-brush" portion (Aiptasia, Diadumene, *Sagartia sphyrodeta*), in other cases little or no trace of any such thread. Such differences, in some cases, are probably characteristic of species only ; in others they perhaps characterise genera.

E. The Nematocysts of Tissues other than Acontia.

Finally, a short study was made of nematocysts occurring in tissues other than acontia, and in anemones possessing no acontia. In the latter, special attention was paid to acrorhagi, which, like acontia, are special stinging-batteries. I should have liked to extend this section of the work much further than time allowed.

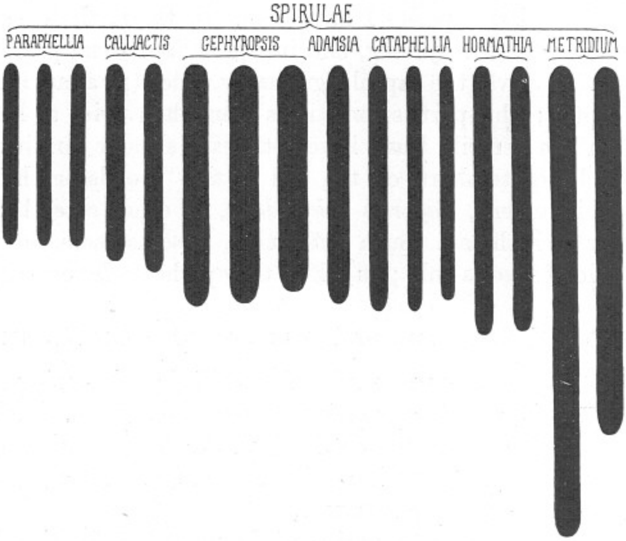
The tables relating to this section of the work (Tables V to VII) will be found on pages 195–197. The points which may be deduced from them are as follows :—

(1) In *Anthopleura ballii* and *A. thallia* the acrorhagi contain a special type of nematocyst not found, so far as I know, elsewhere in the body. To what type these capsules belong I am not certain, but I think that in *A. thallia*, at least, they may be spirocysts of a particular kind, and not nematocysts at all.

(2) *Bunodactis verrucosa* has the same nematocysts in the "acrorhagi" as in the rest of the body-wall ; the acrorhagi are therefore not special stinging-batteries in this case, but come under the heading of "pseudo-acrorhagi."

(3) In Peachia the prevalent nematocysts in the ectoderm of column-wall and tentacles, and the epithelium of the throat, are spirulæ of identical type, but of slightly different sizes. In the mesenterial filaments, however, there are three very distinct kinds of capsule ; one is a penicillus of a curious kind, one a large capsule of special type, with the basal part of the long thread very little differentiated (probably a modified spirula) ; the third an ordinary spirula. It is curious that the same general distribution of types occurs in the tissues of *Anthopleura ballii*, a form very different from Peachia.

(4) In *Phellia gausapata* both penicilli and spirulæ occur in the epithelium of column, tentacles, and throat, as well as in the acontia; those of the acontia are unlike the rest, and minor variations appear from one tissue to another.



TEXT-FIG. 9.—Diagrams illustrating the average size of the spirulæ in the acontia of anemones of several genera.

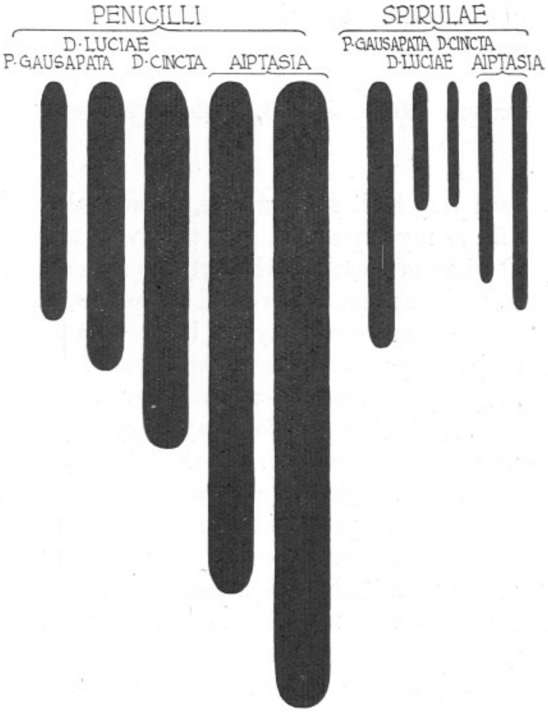
F. OTHER DATA.

There has been discussion as to whether the capsule of a nematocyst is larger before explosion than afterwards. I have made a certain number of measurements on exploded and unexploded cysts of the same kind, from the same tissue and usually from the same sample; the results are given in Table VIII.

This table includes both spirulæ and penicilli, and these from more than one tissue. In all cases there is a diminution of volume after the explosion, although sometimes it is very slight. I have very few data to offer with regard to the effect of reagents on the size of the capsule. In a specimen of *Peachia triphylla* I measured a few capsules of each of the three types which occur in the mesenterial filaments, some in the fresh condition, others after fixation in formalin.

Type.	Average Size before Fixation.	Average Size after Fixation.
1.	$24{\cdot}8\times 4{\cdot}2\ \mu$	$24{\cdot}8\times 4{\cdot}0\ \mu$
2.	$46{\cdot}0\times 5{\cdot}2\ \mu$	$46{\cdot}1\times 5{\cdot}4\ \mu$
3.	$26{\cdot}5\times 3{\cdot}9\ \mu$	$26{\cdot}0\times 3{\cdot}7\ \mu$

In this instance, therefore, the fixation made no appreciable difference. I believe, however, that spirit affects the capsule more than formalin, and that nematocysts in sections are sometimes very considerably shrunken.



TEXT-FIG. 10.—Diagrams illustrating the average size of the penicilli and spirulæ in the acontia of *Phellia gausapata*, *Diadumene luciæ*, *D. cincta*, and *Aiptasia couchii*.

3. SUMMARY AND CONCLUSIONS.

The cnidæ or explosive capsules of the Actiniaria comprise two distinct kinds.

(1) *Spirocysts* (Pl. I, Figs. 1 and 4). Thin-walled capsules with a thread which is closed at the end, and which bears spirals but no barbs. They stain readily with acid fuchsin, but the capsular content does not stain. Found in the tentacles and peristome only, in most species; in other tissues exceptionally. The spiral bands on the thread swell up in sea-water, and on contact with foreign bodies spread out into a network of strands; the thread is therefore adhesive, and may not be poisonous. The thread, prior to evagination, is coiled in a neat spiral within the capsule.

(2) *Nematocysts* (Pl. I, Figs. 2, 3, 5–7, and Text-Fig. 1). Thick-walled capsules with a thread which is often open at the end and normally bears barbs. They typically stain with methylene blue, and the capsular content often becomes stained. Widely distributed in the tissues. Poisonous and penetrating. The thread, prior to evagination, may be variously arranged within the capsule.

The present paper deals particularly with the following points :—

(1) *Spirocysts.*

These have been very little studied here, because their distribution is limited, and as far as my experience goes they vary a good deal in size in the individual, and not greatly in character from genus to genus. The only suggestion I wish to make with regard to them is, that the ordinary and well-known type of spirocyst may not be the only kind in existence, and that there may be capsules intermediate in type between nematocysts and spirocysts. I suspect that the special capsules in the acrorhagi of certain species (e.g. *Anthopleura thallia*) may be spirocysts of an unusual kind, and I have seen in the ectoderm of the lower part of the body of *Sagartia anguicoma* and *S. troglodytes* enormous oval capsules of a peculiar sort. These have a thin collapsible wall, a stout and apparently unarmed thread which, before explosion, is coiled up spirocyst-wise within the capsule ; they stain with fuchsin (although less deeply than ordinary spirocysts), and I think they must be a form of spirocyst. Moreover, although I have not studied this point in detail, I think that nematocysts are more variable in their action towards methylene blue than is generally supposed.

(2) *Nematocysts.*

With regard to these capsules, it is evident that two general patterns of cyst are widely distributed among Actinians. These two types, the *penicillus* and the *spirula* (described on pp. 178–179, and figured in Pl. I, and Text-Fig. 1) are easily distinguished from one another, although each contains varieties ; and their distribution among the genera is of taxonomic importance. In one and the same tissue of an anemone there may be found spirulæ only, or both penicilli and spirulæ may be present together (possibly penicilli alone occur in certain cases). Furthermore, there may be present, for instance, two varieties of spirulæ as well as penicilli. Again, one or more of these kinds of capsule may be present in great quantity, others being more or less scarce (see note on p. 177). The following data refer to majority-forms only.

A. In the acontia of those Actiniaria studied which possess them, the nematocysts occur in two fashions ; in the first, the acontia contain spirulæ only, in the second they contain both spirulæ and penicilli in abundance (i.e. there are 2 majority-forms of capsule).

B. Among the forms examined, the species belonging to a single genus have the same type or types of capsule in the acontia throughout, although the details may vary. Different genera, however, are in some cases sharply distinguished from one another by the nature of the nematocysts in their acontia; in other cases this is not so.

C. In *Phellia gausapata*, a species containing both penicilli and spirulæ in its acontia, both of these types occur in other tissues as well. In Peachia and in *Anthopleura ballii*, the prevalent capsules are spirulæ throughout most of the tissues, but in the mesenterial filaments three types, including penicilli, occur.

D. The *size* of the nematocysts in the acontia is useful in some cases as a specific distinction. This applies to *Sagartia troglodytes* and *S. sphyrodeta*, which are separable from the other British Sagartias on the basis of the size of the penicilli in their acontia.

E. In other cases the size of the capsules in one species is so nearly similar to that in another, that no distinction of the two forms is possible on the basis of this character. This applies to the penicilli of *Sagartia anguicoma*, *S. lacerata*, *Cereus pedunculatus*, and in lesser degree to those of *S. elegans*.

F. The size of the nematocysts in the acontia is sometimes very uniform from one genus to another, and in such cases gives very little help for generic determinations. This applies to Adamsia, Calliactis, Gephyropsis, Paraphellia, Hormathia, and Cataphellia, a closely related series of forms, all possessing spirulæ only in their acontia.

G. The variation in size of the capsules within a species is indicated by an example in Text-Figs. 2–4.

H. The size of the animal has not very much effect on the size of the nematocysts, except in extreme cases (Text-Figs. 2, 3, 5, and Tables I and II).

The general conclusion which may be drawn from the above data is that the distribution of different types of capsule may be very important in dealing with generic (and perhaps family) distinctions; and that the size of the capsule is useful as a *specific* character in certain cases, but useless in others. A good example of the ease with which genera are in some cases separable in this way is the case of Metridium and Diadumene. The young of *M. senile* and the adult of *D. cincta*, although perfectly distinct, are sufficiently similar in colour and facies to be confused with one another by an inexperienced observer. In the acontia of the Metridium, however, there are large spirulæ of a peculiar type, in abundance; whereas in those of the Diadumene both spirulæ and penicilli abound ; and it is not difficult to make a preparation which will reveal these facts.

It is therefore evident that, as in the case of every other character connected with Actinian morphology, the nematocysts provide valuable diagnostic features in some cases and not in others ; and this emphasises once more that in dealing with such animals the species cannot be understood unless the whole of the characteristics of the organism, and not a single series of features, be taken into account.

Carlgren has maintained for many years that no description of an Actinian is complete unless it includes details of the nematocysts, and that we cannot construct a final classification until we know enough about their occurrence in the group. He has provided measurements of the capsules in his own descriptions for some time. I am glad, as a result of the above study, to express my agreement with Carlgren in this matter, especially as I did not hold this view originally.

It is more difficult to deal with the nematocysts from preserved than from fresh material, because, although dissociated preparations can easily be made, one mostly sees the capsules unexploded or damaged, and it is not always possible to tell exactly to what type they may belong. As the *number of types present* is a factor often more important than the size, it is advisable to procure fresh material wherever possible.

In the various tables given on pages 192–198, the maximum and minimum dimensions which occurred among the capsules measured, as well as the average size, are stated. This gives a better idea of the situation than if one of these series of data only be quoted. Carlgren in his descriptions usually quotes the range ; personally I should prefer the average, since it is my impression that the majority of capsules are of sizes not very far from the average, and that although it is useful to know the maximum and minimum, these are less significant than the average.

The reason why acontia have been so much used in this paper is that it was thought probable that in these special stinging organs, if anywhere, differences of diagnostic value would appear. I think the result justifies this idea. Probably the state of affairs in the acontia gives a key to that in the rest of the tissues—if we may judge by *Phellia gausapata*.

Since the above work was finished, Carlgren has kindly sent me particulars of a similar study, not yet published, which he has made on Actinian acontia. He has observed as I did, that in Hormathia, Calliactis, Paraphellia, Adamsia, and Gephyropsis there are nematocysts of one type only in the acontia ; and to my list he adds the genera (mostly non-British) Actinauge, Phelliactis, Paracalliactis, Chondrophellia, Allantactis, Cricophorus, Stephanauge, Acraspedanthus, and Phelliogeton. Carlgren finds also the two types of capsule in the acontia of Sagartia (including Thöe), Phellia, Cereus, Diadumene and Aiptasia (with allied forms), and adds to this list Artemidactis, Choriactis, Parathöe, Sagartiogeton, Andvakia, and Isophellia. Moreover, in two peculiar genera (Kadosactis and Sagartiomorphe) he has observed penicilli only in the acontia; if these alone are present in quantity we have here a third type which I have not seen myself.

These investigations re-open the question of the classification of the anemones with acontia. I do not propose to discuss this subject in detail at present, but am willing to modify the scheme which I suggested in 1920, in the light of new knowledge. A provisional scheme which would meet with the views of both Carlgren and myself would be as follows.

1. Diadumenidæ, as defined by Carlgren, 1924, page 234. Acontia with both penicilli and spirulæ.
2. Aiptasiidæ, as defined by Carlgren, 1924, page 237. Acontia with both penicilli and spirulæ.
3. Metridiidæ. Including the Metridiidæ and Chondractiniidæ as defined by me in 1920, pages 526 and 533 (but omitting Sagartiomorphe and the Aiptasia group). For forms possessing spirulæ only, in the acontia; base and basilar muscles; mesenteries not divided into macro- and microcnemes; usually six or about six pairs of perfect mesenteries. Cinclides present or not. Sphincter mesoglœal. Primary mesenteries often sterile.
4. Sagartiidæ. Including Sagartiidæ and Choriactidæ of my 1920 paper. The acontia possess both penicilli and spirulæ in abundance. Base and basilar muscles present; mesenteries not divided into macro- and microcnemes, usually more than six pairs perfect. Cinclides present as a rule. Sphincter mesoglœal. Primary mesenteries typically fertile.
5. Carlgren suggests the possible addition to these of new families, Kadosactidæ (for Kadosactis and Sagartiomorphe) and Acraspedanthidæ (for Acraspedanthus and Phelliogeton). These forms I do not know personally, so cannot yet form an opinion.
6. Phelliidæ. I hope to deal with this family shortly, in a separate paper.
7. Forms with no base or basilar muscles must perhaps (certainly according to Carlgren) be classified separately. I will return to this later.

TABLE I.

Number, variety and locality of specimen.	Diameter of base of specimen used.	Type of Nematocyst.	Range of variation in size.	Average size.
1. venusta (Valencia)	2·1 cm.	Penicilli	48–56×5–6·5μ	53·3×5·1μ
		Spirulæ	30–36×2·6–4μ	32·5×3·1μ
2. venustoides (Plymouth)	1·6 cm.	Penicilli	40–57×4–6μ	51·6×4·9μ
		Spirulæ	29–35×2·6–3·5μ	31·6×2·9μ
3. roseoides (Valencia)	2·6 cm.	Penicilli	44–58×4–6μ	52·7×5·1μ
		Spirulæ	30–39×2·6–4μ	33·9×3·3μ
4. miniata (Plymouth)	2·8 cm.	Penicilli	40–62×4–6μ	55·9×5·3μ
		Spirulæ	31–38×3–4μ	34·3×3·5μ
5. venusta (Plymouth)	1·1 cm.	Penicilli	39–56×4–5·6μ	47·4×4·9μ
		Spirulæ	24–33×2·6–4μ	29·8×3·3μ
6. nivea (Plymouth)	2·1 cm.	Penicilli	42–60×4·6–6μ	55·4×5·4μ
		Spirulæ	26–38×3–4·5μ	33·7×3·7μ
7. rosea (Valencia)	2 cm.	Penicilli	50–58×5–6μ	54·4×5·5μ
		Spirulæ	29–36×3–4μ	32·7×3·5μ
8. nivea (Valencia)	2·7 cm.	Penicilli	50–62·6×4·6–6·5μ	57·1×5·5μ
		Spirulæ	28·6–37×3–4μ	34·0×3·4μ
9. miniata (Valencia)	1·0 cm.	Penicilli	45·2–59×4·6–6μ	53·6×5·1μ
		Spirulæ	31–38×3–4μ	33·9×3·4μ
10. venustoides (Valencia)	1·9 cm.	Penicilli	42–59×4–6μ	51·9×5·1μ
		Spirulæ	26–35×2·6–4μ	31·4×3·2μ
11. niveoides (Valencia)	2·6 cm.	Penicilli	46–58×5–6μ	54·1×5·4μ
		Spirulæ	28–37×3–4μ	33·5×3·5μ
12. miniata (Plymouth)	2·7 cm.	Penicilli	56–63×4·6–6·6μ	59·8×5·7μ
		Spirulæ	32–38×3–4μ	35·2×3·5μ

TABLE II.

Number of specimen.	Diameter of expanded tentacular crown.	Type of Nematocyst.	Range of variation in size.	Average size.
1	4·1 cm.	Penicilli	40–48·6×4–5μ	44·5×4·5μ
		Spirulæ	29–36×2·4–3·4μ	33·6×2·7μ
2	3·2 cm.	Penicilli	38–44×4–5μ	41·9×4·3μ
		Spirulæ	30–38×2·4–3·4μ	33·9×2·9μ
3	2 cm.	Penicilli	33–42×3·8–5·4μ	38·2×4·1μ
		Spirulæ	28–33×2·2–3μ	30·2×2·5μ
4	1·7 cm.	Penicilli	36–46×3·6–5μ	40·8×4·2μ
		Spirulæ	29–36×2·4–3μ	32·7×2·6μ
5	1·1 cm.	Penicilli	34–42×3·6–4·6μ	37·4×4·0μ
		Spirulæ	28–35×2–3μ	30·6×2·6μ

Number of specimen.	Diameter of expanded tentacular crown.	Type of Nematocyst.	Range of variation in size.	Average size.
6	·5 cm.	Penicilli	25·2–31·2×3·2–4μ	29·1×3·6μ
	(New born)	Spirulæ	25–30×2–2·6μ	27·1×2·3μ
7	·35 cm.	Penicilli	30–35×3·4–4μ	31·2×3·6μ
	(New born)	Spirulæ	23·2–29×2–2·4μ	26·5×2·2μ

TABLE III.

Species.	Number and locality of specimen.	Diameter of specimen.	Type of Nematocyst.	Range of size.	Average size.
Sagartia sphyrodeta	1	2·2 cm.	Penicilli	62–86×6–7·2μ	72·2×6·9μ
	Plymouth	(flower)	Spirulæ	24–32×1·6–2μ	28·6×1·8μ
	2	2·2 cm.	Penicilli	58–71·2×6·6–8μ	63·7×7·1μ
	Plymouth	(flower)	Spirulæ	24–29×1·6–2μ	27·4×1·8μ
	3	1·4 cm.	Penicilli	60–77×6–8μ	69·8×6·9μ
	Plymouth	(flower)	Spirulæ	24–29×1·6–2μ	26·7×1·9μ
S. anguicoma	1	4 cm.	Penicilli	38·6–43·2×4–5μ	41·1×4·6μ
	Plymouth	(base)	Spirulæ	23–31×2–2·6μ	27·0×2·2μ
	2	3·8 cm.	Penicilli	35–42×4–4·5μ	38·8×4·8μ
	Plymouth	(base)	Spirulæ	23–30×2–2·6μ	25·9×2·4μ
	3	2 cm.	Penicilli	34–44×4–4·6μ	39·5×4·4μ
	Plymouth	(base)	Spirulæ	19–26×2–2·6μ	23·9×2·2μ
S. troglodytes var. decorata	1	4 cm.	Penicilli	21–24×3·4–4μ	23·2×3·7μ
	Valencia	(base)	Spirulæ	13–17×2–2·6μ	15·3×2·4μ
	2	3·8 cm.	Penicilli	20–26×3·4–4μ	22·9×3·6μ
	Valencia	(base)	Spirulæ	14–17×2–2·6μ	15·8×2·3μ
	3	·9 cm.	Penicilli	20–25·4×3·2–4μ	22·7×3·8μ
	Torquay	(base)	Spirulæ	16–20×2·4–2·8μ	17·7×2·5μ
S. troglodytes var. ornata	1	·8 cm.	Penicilli	21·2–24×3·2–4·6μ	22·4×3·9μ
	Locality unknown	(base)	Spirulæ	17–21×2·2–2·6μ	18·5×2·5μ
	2	·9 cm.	Penicilli	21–25×3·4–4μ	23·1×3·6μ
	Millport	(base)	Spirulæ (unexploded)	16–20·6×2·6–3μ	18·7×2·8μ
	3	·9 cm.	Penicilli	21–26×3·2–3·8μ	23·6×3·5μ
	Locality unknown	(base)	Spirulæ (unexploded)	16–21×2·4–3·4μ	18·9×2·8μ
S. lacerata	1	1·8 cm.	Penicilli	41–51·2×4–5·4μ	46·7×4·6μ
	Plymouth	(base)	Spirulæ	22–27·2×2–2·6μ	24·4×2·4μ
	2	1·8 cm.	Penicilli	40–49×4–5μ	43·5×4·6μ
	Plymouth	(base)	Spirulæ	22–28×2–2·6μ	24·3×2·4μ
	3	1·2 cm.	Penicilli	38–44×4–5μ	40·2×4·4μ
	Plymouth	(base)	Spirulæ	23–26×2–2·6μ	24·0×2·3μ

TABLE IV.

Species and locality.	Number and size of specimen.	Type of Nematocyst.	Range of size.	Average size.
Paraphellia expansa (Plymouth)	1 2·8 cm. (base)	Spirulæ	22–26×2–2·6μ	24·2×2·2μ
	2 2·8 cm. (base)	Spirulæ	22–26×1·8–2μ	23·8×2·0μ
	3 slightly smaller than 1 and 2	Spirulæ	22–26×1·8–2·4μ	23·9×2·0μ
Cataphellia brodricii (Salcombe)	1 (base) 1·3 cm.	Spirulæ	30–35·2×2–2·6μ	32·5×2·3μ
	2 1·3 cm. (base)	Spirulæ	30–37×2–2·4μ	32·6×2·1μ
	3 ·9 cm. (base)	Spirulæ	27–36×2–2·6μ	31·1×2·1μ
Hormathia coronata (Plymouth)	1 2·25 cm. (column)	Spirulæ	33·6–37×2·6–3μ	35·6×2·7μ
	2 1·3 cm. (column)	Spirulæ	33–38×2·4–3μ	35·1×2·7μ
Gephyropsis dohrnii (Plymouth)	1 1·0 cm. (base)	Spirulæ	28–43×3·2–4μ	31·8×3·7μ
	2 1·0 cm. (base)	Spirulæ	28–34×3·8–4·6μ	31·5×4·1μ
	3 1·0 cm. (base)	Spirulæ	28–32×3·2–4μ	30·3×3·8μ
Adamsia palliata (Plymouth)	1 4·8 cm. (flower)	Spirulæ	28–35·2×2·4–3μ	31·7×2·8μ
Calliactis parasitica (Plymouth)	1 8·5 cm. (flower)	Spirulæ	24·6–29×2·4–2·8μ	27·4×2·6μ

Species and locality.	Number and size of specimen.	Type of Nematocyst.	Range of size.	Average size.
	2 8·5 cm. (flower)	Spirulæ	24–28×2·4–2·6μ	26·1×2·5μ
Metridium senile (Plymouth)	1 column 7 cm. high (adult)	Spirulæ	56–68×3–3·8μ	62·1×3·5μ
	2 base ·9 cm. across (young)	Spirulæ	45·2–52×2·6–3·8μ	48·4×3·4μ
Phellia gausapata (Wick)	1 large specimen	Penicilli	30–33×3–3·6μ	31·5×3·3μ
		Spirulæ	33–37×3·4–3·8μ	34·8×3·5μ
Diadumene luciæ (Plymouth)	1 ·5 cm. (base)	Penicilli	31–42·6×4·6–6μ	38·2×5·2μ
		Spirulæ (unexploded)	15–19×1·6–2·2μ	16·8×2·0μ
Diadumene cincta (Plymouth)	1 1·4 cm. (base)	Penicilli	44–52·6×5·4–7·4μ	48·3×6·1μ
		Spirulæ (unexploded)	15–18×1·4–2μ	16·4×1·7μ
Aiptasia couchii (Plymouth)	1 1 cm. (flower)	Penicilli	57–78×5·4–7·4μ	67·5×6·0μ
		Spirulæ	24–30×1·8–2·4μ	26·6×2·0μ
	2 1·3 cm. (column)	Penicilli	74–90×6–8·4μ	82·6×7·4μ
		Spirulæ	26–33×1·8–2μ	29·9×2·0μ

TABLE V.

SPECIES WITH ACRORHAGI, ETC.

1. Anthopleura ballii, a Valencia specimen. Diameter of flower 4·5 cm. All capsules measured unexploded.

Tissue.	Type of capsule.	Range of size.	Average size.
Acrorhagi	Type 1. Form characteristic of the Acrorhagi	34–42·6×2·2–3μ	38·4×2·7μ
	Type 2 Spirulæ	22–26×2–2·6μ	23·5×2·3μ
	Type 3 Spirulæ	16–21×1·9–2·4μ	18·7×2·1μ
Ectoderm of column wall	Spirulæ	16–19×2–2·4μ	16·6×2·0μ
Ectoderm of tentacle	Spirulæ	22–27·2×2–2·6μ	24·5×2·4μ

Tissue.	Type of capsule.	Range of size.	Average size.
Mesenterial filament	Type 1. Penicilli	16·6–20×3·8–4·6μ	17·9×4·4μ
	Type 2. Large special kind	33·2–42×4–4·4μ	39·0×4·1μ
	Type 3. Spirulæ	16–17×2μ	16·7×2μ
Epithelium of throat	Spirulæ	28–31×2·6–3μ	29·2×2·9μ

2. Anthopleura thallia, a Torquay specimen. Height of animal 3·6 cm. Capsules measured unexploded.

Tissue.	Type of capsule.	Range of size.	Average size.
Acrorhagi	Type characteristic of Acrorhagi (Spirocysts also are present ; so are Spirulæ)	36·6–45·6×4–5·4μ	40·6×4·7μ

3. Bunodactis gemmacea, a Plymouth specimen. Diameter of column 1·5 cm. Capsules measured unexploded.

Tissue.	Type of capsule.	Range of size.	Average size.
Pseudo-acrorhagi	Type 1. Rod-like kind	25–41·6×1–1·2μ	31·0×1·1μ
	Type 2. Spirulæ	11·2–14×1·6–2·2μ	12·8×1·9μ
Ectoderm of column wall	Type 1. Rod-like kind	25·2–38×1–1·2μ	32·3×1·0μ
	Type 2. Spirulæ	12–15×1·6–2μ	13·2×1·9μ

TABLE VI.

PEACHIA.

1. *Peachia hastata.* A Port Erin specimen. Total length (contracted) 2·2 cm. Capsules measured unexploded except in throat. Measured on one specimen except those of the tentacles, which were taken from another similar example.

Tissue.	Type of Nematocyst.	Range of size.	Average size.
Epithelium of throat	Spirulæ	21–25×2·6–3·6μ	22·7×3·2μ
Ectoderm of column wall	Spirulæ	13·2–16×2·6–3·4μ	14·8×2·8μ
Ectoderm of tentacles	Spirulæ	18–25·2×2·6–3·6μ	21·1×3μ
	Spirocysts	18–24×2·4–3μ	20·2×2·8μ
Mesenterial filaments (measured after fixation in formalin)	Type 1. Penicilli	16–18×3·8–4·6μ	16·9×4·1μ
	Type 2. Large kind	24–42×5·2–6·6μ	33·7×5·8μ
	Type 3. Spirulæ	20–27·2×3·4–4μ	24·2×3·7μ

Further measurements were made on 2 larger preserved specimens of *P. hastata* from Port Erin. I. Formalin specimen 5·6 cm. long. Filaments, Type 1, range 17–19·6×4μ, average 18·4×4μ; Type 2, range 26–41×4·6–7·4μ, average 31·4×5·4μ. II. Spirit specimen 6·5 cm. long. Filaments, Type 1, range 20–22×3–3·8μ, average 20·8×3·3μ.

2. *Peachia triphylla.* A Plymouth specimen. Total length (contracted) 4·1 cm. Capsules measured unexploded except in throat.

	Type of Nematocyst.	Range of size.	Average size.
Epithelium of throat	Spirulæ	24–28×3·4–5μ	26·0×4·1μ
Ectoderm of column wall	Spirulæ	15·6–19·6×2·2–3·4μ	17·7×2·6μ
Ectoderm of tentacles	Spirulæ	19–28×2·2–3·2μ	23·6×2·7μ
	Spirocysts	16–28×3–3·8μ	23·1×3·2μ
Mesenterial filaments	Type 1. Penicilli	23–27×4–4·6μ	24·8×4·2μ
	Type 2. Large kind	42–50×4–6μ	46·0×5·2μ
	Type 3. Spirulæ	24–28×3·8–4μ	26·5×3·9μ

TABLE VII

PHELLIA GAUSAPATA.

A large specimen from Wick, Caithness. Capsules measured unexploded except in acontia.

Tissue.	Type of Nematocyst.	Range of size.	Average size.
Acontia	Penicilli	30–33×3–3·6μ	31·5×3·3μ
	Spirulæ	33–37×3·4–3·8μ	34·8×3·5μ
Ectoderm of tentacles	Penicilli (commonest form)	14–18×3·2–4μ	16·4×3·5μ
	Spirulæ	16·6–21×2–2·4μ	19·7×2·1μ
	Spirocysts	14·6–29×2–4·6μ	22·9×3·3μ
Ectoderm of scapulus	Penicilli	16–18×3·6–4μ	16·9×3·7μ
Ectoderm of scapus (low down)	Penicilli	17–20×3·8–4μ	18·1×4μ
	Spirulæ	14–17·6×3·2–3·8μ	16·3×3·5μ
Epithelium of throat	Penicilli	21·2–25×3·8–4·6μ	23·5×4·1μ
	Spirulæ	24·6–29×2–2·6μ	26·8×2·2μ

TABLE VIII.

Species.	Tissue.	Type of capsule.	Average size before explosion.	Average size after explosion.
Paraphellia expansa	Acontia	Spirulæ	25·9×2·4μ	24·2×2·2μ
Cereus pedunculatus	Acontia	Penicilli	49·5×5·6μ	44·5×4·5μ
		Spirulæ	36·6×3·3μ	33·6×2·7μ
Peachia hastata	Epithelium of throat	Spirulæ	26·1×4μ	22·7×3·2μ
	Ectoderm of column wall	Spirulæ	14·8×2·8μ	14·0×2·4μ
Peachia triphylla	Epithelium of throat	Spirulæ	27·2×4·2μ	26·0×4·1μ
	Ectoderm of column wall	Spirulæ	17·7×2·6μ	16·4×2·5μ
Calliactis parasitica	Acontia	Spirulæ	29×2·9μ	27·4×2·6μ
Phellia gausapata	Ectoderm of tentacles	Penicilli	16·4×3·5μ	14·7×3·2μ
	Ectoderm of scapulus	Penicilli	16·9×3·7μ	14·8×3·2μ
Sagartia elegans	Acontia	Penicilli	67·2×6·9μ	59·8×5·7μ

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PLATE I.

FIG. 1.—A completely evaginated spirocyst from *Tealia felina*, very highly magnified. After Will, 1909a, Pl. 3, Fig. 4 (slightly modified). Here the spiral bands have partially disappeared, their substance having swelled and become drawn out into strands in places. Anastomosis has taken place between some of the strands.

FIG. 2.—An evaginated nematocyst (of the spirula type) from an acontium of *Sagartia elegans*. The long terminal part of the thread is not shown, and the barbs have fallen off, revealing clearly the spiral bands. The enlarged basal part is rendered wider than usual here by the medium employed (mercury medium ; see text).

FIG. 3.—A partially evaginated nematocyst (spirula type) from an acontium of *Hormathia coronata*. The distal part of the thread is still inside the capsule. The individual barbs are not shown here, only the general effect produced ; they are actually inserted in the manner shown in Fig. 7, but point the other way.

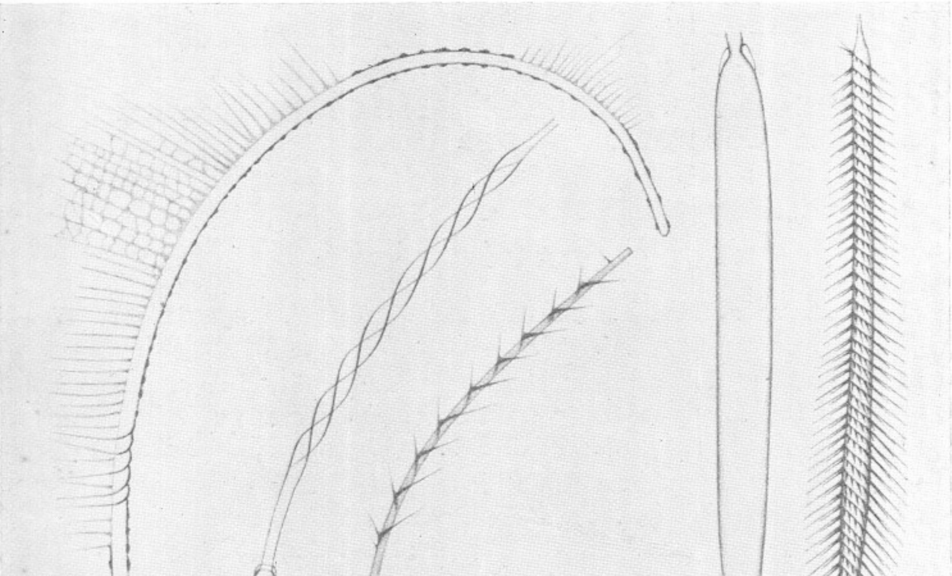
FIG. 4.—Spirocyst of *Tealia felina*, very highly magnified. After Will, 1909a, Pl. 3, Fig. 9. The thread is only partially evaginated. The spiral bands are clearly visible on the wide evaginated part ; on the narrow portion which is not yet extruded the series of diagonal strokes represents the continuation of the spiral bands on the inner wall of this portion.

FIG. 5.—The capsule of an evaginated nematocyst (of the penicillus type) from an acontium of *Sagartia sphyrodeta*. Oc. 2, obj. 10.

FIG. 6.—The thread belonging to the capsule shown in Fig. 5, drawn to same scale. Slightly diagrammatic. The terminal portion of the thread is not shown, but was short and slender. The barbs were actually continued (though becoming more delicate) almost to the base of the thread, but were rendered barely visible in the lower part by the stain and medium employed (methylene blue used with potassium hydroxide and followed by mercury medium ; see text). Oc. 2, obj. 10.

FIG. 7.—Diagrammatic enlargement of the terminal part of the thick region of the thread from another nematocyst similar to that shown in Fig. 6.

PLATE I.



On a Fungus Allied to the Saprolegniaceæ found in the Pea-crab *Pinnotheres.*

By

D. Atkins, B.Sc.

With 13 Figures in the Text.

INTRODUCTION.

In the course of work on *Pinnotheres*, a fungus, which from its general characters would appear to be allied to the Saprolegniaceæ, was noticed in pea-crabs taken from mussels (*Mytilus edulis*) coming from beds in the estuary of the Camel near St. Issey Cliff (Padstow), from the estuary of the Yealm, and from near the junction of the Tamar and Tavy (Weir Point). Although the pea-crab lives in estuarine situations where the water is brackish, yet it may be taken in bivalves dredged in rather deep water on the coast (**1**, p. 123); those in the Laboratory were kept in the sea-water in ordinary circulation in the tanks and it was under these conditions that the fungus was seen to grow and produce reproductive elements. This fungus therefore attacks a marine invertebrate and, as far as I have been able to ascertain, it is the first member of the Saprolegniaceæ which has been so described. Some members of the family which occur on living freshwater fish are *Saprolegnia parasitica* Coker* on salmon, trout, etc.—stated by Patterson (**13**, p. 5) to be unable to grow in sea-water—*Achlya Hoferi* Harz on Bohemian mirror carp (**8**, p. 201; **2**, p. 145), *A. Nowickii* Raciborski on a sink carp (**2**, p. 147), and *A. polyandra* and *A. prolifera* on various fish (**9**, p. 108), while two which are found on freshwater plankton-crustaceans are *Leptolegnia caudata* de Bary on *Leptodora Kindtii* in Denmark (**14**, p. 511) and *Pythiopsis cymosa* de Bary on *Holopedium gibberum* in Lake Malmagen in Sweden (**14**, p. 511).

The mycelium of the *Pinnotheres* fungus may penetrate deeply into the body of the pea-crab, surrounding the organs, and may occasionally extend into the appendages, mouth parts, and even the eye-stalks, while it is generally found in the gills (Fig. 1). Such deep penetration of the tissue of the host would appear to be somewhat unusual among the Saprolegniaceæ, but it may also be effected by the salmon fungus where

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* Coker (**2**, p. 58) considers that the fungus described from salmon and certain other fish as *Saprolegnia ferax* is distinct from that species, and he names it *S. parasitica*.

the way is prepared by *Bacillus salmonis pestis*, the bacteria breaking down the tissue which the fungus is then able to invade (**13**, p. 7), and by *A. Hoferi* of the Bohemian mirror carp, which is also probably preceded by bacteria (**2**, p. 145 ; **8**, p. 201). In these cases the fungus may penetrate the entire dermis with the exception of the muscles. The mycelium of *L. caudata* which attacks and kills *Leptodora* in large numbers, sometimes almost exterminating them from certain lakes in Denmark, is said by P. E. Müller to envelop the organs. Petersen (**14**, p. 512) thinks that the mycelium usually enters round the mouth opening and, spreading rapidly, kills the animal, while it finally envelops both the mother individual and the eggs with a thick meshwork of hyphæ.

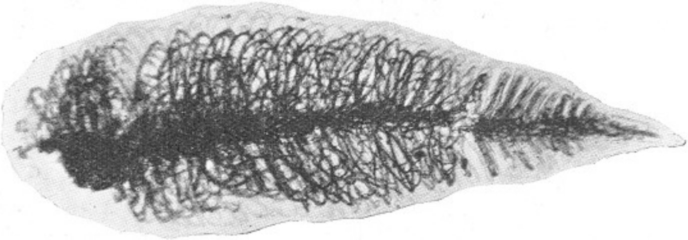

FIG. 1.—Photograph of a gill infested with the fungus, fixed in Flemming's fluid. × ca. 29.

DESCRIPTION OF THE FUNGUS.

Mussels were obtained from Padstow on the following consecutive dates, November 25/27, February 24/28, April 25/28, August 1/28, and September 14/28, and a certain number of the pea-crabs taken from them on arrival at the Station either showed signs of the disease at the time or developed it later, but crabs obtained from mussels from the same place on October 11/28 were apparently free, for they did not develop it although many were kept together in bowls for about 6 weeks. Crabs which also developed the disease were obtained from near the junction of the Tamar and Tavy on March 22/28, April 10 and 20/28, and from the Yealm on July 21/28. The fungus would therefore seem to attack crabs during the greater part of the year in the comparatively mild climate of the south-west of England and is not restricted to the period of July to about the middle of September as are apparently the attacks of *Leptolegnia* on *Leptodora* in Denmark (**14**, p. 512). In some few instances it is certain that the crabs were already infected when taken from the mussels on arrival from the beds, and against the possibility of their acquiring the infection from the water circulating in the tanks in the Laboratory is the fact that crabs kept for over a year separately in mussels for rearing experiments have not developed the disease.

The presence of the fungus is mostly indicated some days before the death of the crab either by opaque white patches showing through the chitin of its body and abdomen, or else more rarely by the opaqueness of the gills, though a crab may die of the disease without any outward indication. The patches in the body generally occur over the gill chamber, especially the posterior region, though as the disease progresses the whole of the roof of the gill chamber may become involved. A white line is sometimes seen along the junction of the carapace with the abdomen, and patches may also occur in the abdomen, where they are generally to be found round the junction of two segments. The white appearance due to the presence of the fungus can readily be distinguished from that due to parasitisation by a Sarcosporidian identified by Dr. Pixell Goodrich; in the latter case the muscles only become an opaque white. The white patches of the fungus probably surround the original point of infection, and from their position it will be realised that the fungus enters the crab either where the chitin is extremely thin or along the fine chitinous membrane which unites the segments of the abdomen, and the posterior border of the carapace to the abdomen. The white patches are

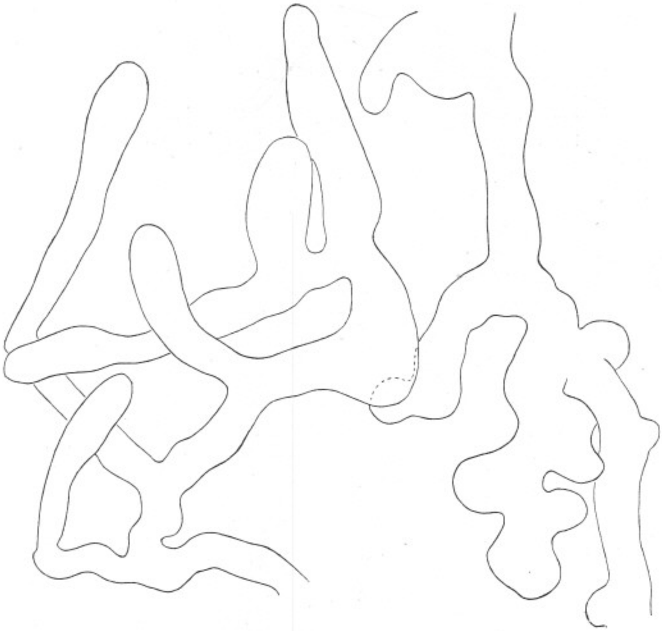

FIG. 2.—Broad, uncrowded hyphæ from roof of gill chamber. The protoplasmic contents are not shown, they were very finely granular with indication of vacuoles. × ca. 253.

This figure and all following ones were drawn from living material.

an intricately branched felt-like mycelium of fine hyphæ averaging about 9μ in width; occasionally very broad, uncrowded hyphæ up to about 32μ in width are found in the roof of the gill chamber (Fig. 2).

It appears that when the fungus enters through the exceedingly fine chitin roofing the gill chamber, it spreads for some distance in the tissue between it and the thicker chitin of the dorsal surface of the carapace, while it sends branches into the gills and sometimes the mouth parts. The fungus is most easily seen in these situations, but probably in some, if not all cases, it also extends into the body of the crab. Perhaps the easiest way of following the hyphæ, but only possible if the crab is small and thin-shelled, is to lift off the carapace, puncture the abdomen in several places, and fix the animal in Flemming's fluid. The oil globules, often present in great numbers in the hyphæ, are blackened by the osmic acid, and the branches of the fungus can be traced after clearing the crab in glycerine. By this means the fungus was seen without dissection in the body of three small crabs.

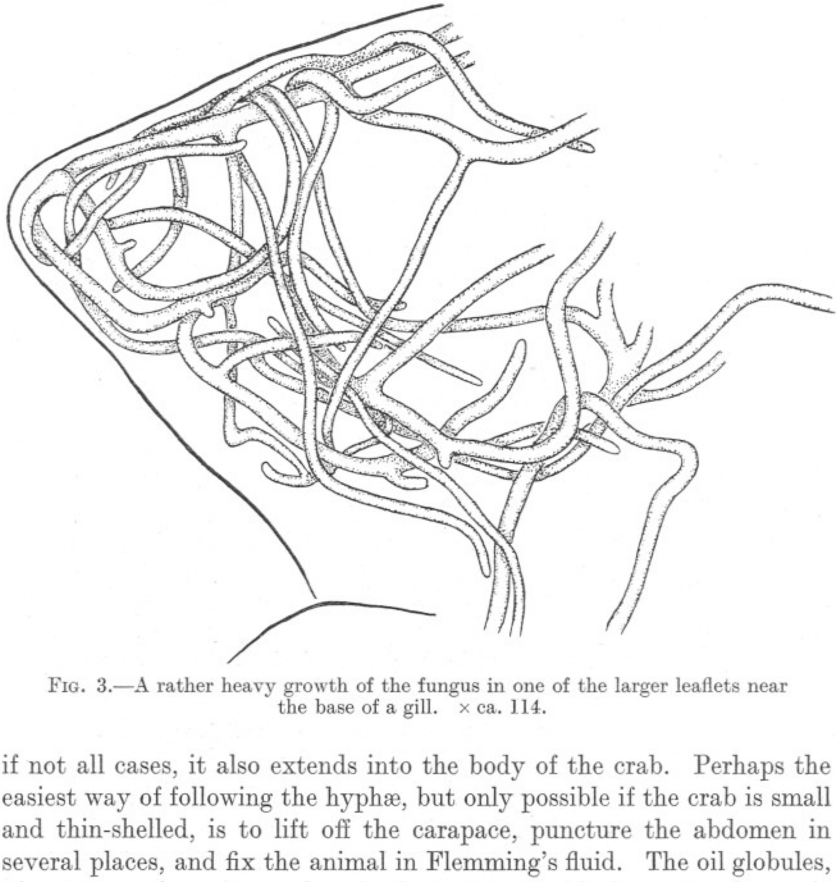

FIG. 3.—A rather heavy growth of the fungus in one of the larger leaflets near the base of a gill. × ca. 114.

When the fungus has once entered the gills it soon absorbs the tissue and death of the pea-crab is rapid. It is an interesting possibility that in this case death may be due to asphyxiation.

In examining crabs for the presence of the fungus, when the white patches are absent, an inspection of the gills only has usually been relied on. A crab may die, however, when only one gill out of the six is infected, and therefore it would appear that in such a case there must be a considerable growth of the fungus in the body, unless laboratory conditions, which possibly included for these crabs shortage of food, markedly weakened them.

The fungus is most easily studied in the gills where the delicate chitinous covering is so thin as to be transparent (Fig. 1). The hyphæ would seem to enter through the base of the gill from the infection area in the roof of the gill chamber and pass down the axis of the gill, giving off branches into the gill leaflets, both the axis and the leaflets soon becoming crowded with richly branched hyphæ (Fig. 3). At least in the young stages of the fungus the hyphæ keep within the leaflet, passing up one edge, curving very regularly round the tip, and passing down the other edge and so into the main axis, giving off branches on the way.

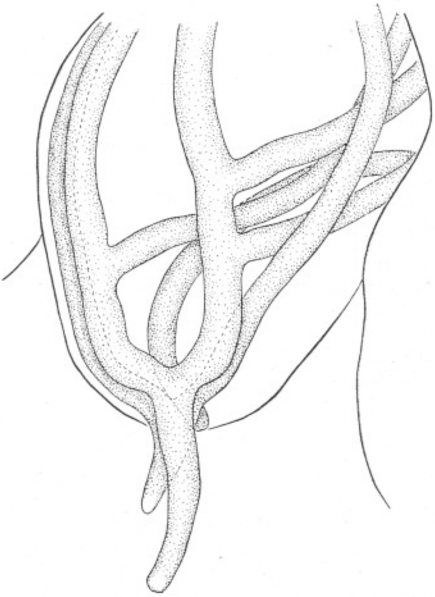

FIG. 4.—Sketch to show the very regular mode of growth of the hyphæ within the gill leaflet. The papillæ for discharging the spores are well developed but intact. The protoplasm is indicated by stippling, but no attempt has been made to show its structure. The thick lines show the outline of the gill leaflets. × ca. 253.

The whole of the contents of the hyphæ in the gills of the host gradually divide into zoospores and no marked sporangia are formed. This fungus resembles *Aphanomyces* (**2**, p. 160) and *Leptolegnia* (**14**, p. 522) in that the sporangia are formed from unchanged hyphæ. Cross walls arise, but the portion cut off may be of considerable length with several branches ; it may include a length running along the axis of the gill with loops into the gill leaflets, but apparently with only one exit. When the abdomen of the crab has areas of infection, hyphæ may pass into the pleopods and there become sporangia. A characteristic of this fungus is that the spore-producing filaments occur within the crab, though they would appear to be restricted to the gills and pleopods, the hyphæ in the roof of the gill chamber and in the body being purely vegetative. The reproductive hyphæ are generally stouter than the vegetative and are remarkably regular, tapering gradually to the tip with very clear and definite outline (Fig. 4). They vary in width from about 10μ to 20μ. Gills and pleopods

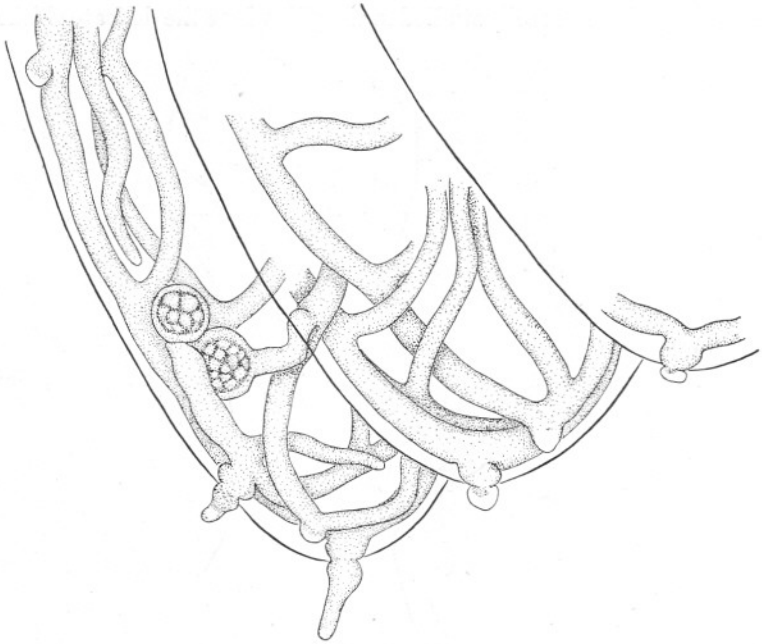

FIG. 5.—Sketch to show the fungus in three overlapping gill leaflets. Discharging papillæ are developing and show a bulge at the point of penetration of the chitin of the gill. The sketch was made at 8 p.m. ; the next morning the filaments were empty, as was also the larger of the two reproductive bodies ; the smaller, which had a wall dividing it from the hypha, was still full. The protoplasm is indicated by stippling, but no attempt has been made to show its structure, except in the two round reproductive bodies. The thick lines show the outline of the gill leaflets. × ca. 253.

may be seen with a network of hyphæ empty except for a comparatively few spores which, unable to escape for some reason, have encysted there. The tissue of such gills and pleopods generally has disappeared entirely. It would seem that the filaments which enter these structures are entirely reproductive, though where infection takes place directly on the gill there is a tiny opaque patch of vegetative hyphæ. It may be that in the comparatively confined space of the gill or pleopod the tissue is soon consumed, and under these conditions spore formation naturally follows.

FIG. 6.—Sketches to show the development of a secondary discharging papilla when the tip of the first one has not given way. × ca. 342½.

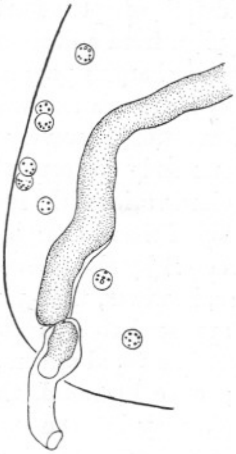

FIG. 7.—Hypha growing up within an old sporangium after the *Saprolegnia* type of proliferation; it is much reduced in size where it penetrates the gill chitin. The tip of the hypha is of almost clear protoplasm. A few spores are lying free on the surface of the gill leaflet, the outline of which is shown by a thick line. × ca. 342½.

Klebs in 1899 showed that sporangia are formed only when the food-supply is quickly and markedly decreased (**15**, p. 484).

When spore formation is about to take place a small branch or papilla arises either from the end of a hypha (Figs. 7, 8A) or along its length (Figs. 4, 5, 9, 12) and the tip becomes applied to and penetrates the chitin. There is a slight bulging of the tip of the papilla, before the chitin is penetrated (Fig. 5). The branches to the exterior are mostly quite short, ranging between 0·03 mm. to 0·12 mm. It is by these short branches or papillæ that the zoospores pass to the exterior and, with very few exceptions, this is the only part of the fungus which extends into the sea-water. In one interesting case where the long blade-like exopodite of the second pleopod of one side was infected, the long hairs were absent towards the tip, only their circular bases remaining, and the tips of the hyphæ were protruding through the centre of these cup-like bases. Branched discharging papillæ may occur where the tip of the original papilla has apparently failed to give way and a lateral branch has arisen through which discharge has taken place (Fig. 6).

Occasionally a new sporangium may grow up within an old one, as sometimes occurs in *Leptolegnia* (**2**, p. 157) and is typical in *Saprolegnia*, but the most that has been seen is one within another (Fig. 7).

The details of spore formation have not been observed. A gill which when pulled from a dead crab at night shows no sign of spore formation or of the discharging papillæ will the next morning be seen with a quantity of empty sporangia and with others in the process of discharging spores; spore formation, however, occurs in gills in situ. Spore discharge seems most commonly to occur at night. The number of spores in a row in a sporangium varies with the width, from several to one or two.

The tip of the discharging papilla is mostly rounded; it would seem to be forced off by the pressure of the zoospores packed behind it; in one instance, however, the tip was flattened, with a fine membrane across it which appeared to dissolve. When the tip first gives way the zoospores pour out in a rapid stream, but when pressure is relieved they swim out singly; once liberated, they swim off rapidly. Zoospores within the sporangia may be seen trying the various branches until they find the exit. If the exit should be blocked by an encysted spore, or if the sporangium is very long and branched, a considerable number of spores may be retained, becoming encysted.

The time during which the first zoospores may remain active varies considerably. They are apparently very susceptible to changes in the environment, for the placing of a cover-slip over a drop containing motile spores, just out of a sporangium, causes rapid encystment. Both within the sporangium and outside, zoospores may come to rest while still irregular in shape; this is probably due to sudden change in the environment, such as increasing salinity on the slide. On the other hand, zoospores seen coming from a sporangium at 9.30 p.m. were taken up in a fine pipette and put on a cover-slip as a hanging drop; many were still active 50 minutes later. The length of time during which the zoospores may remain active seems unusually long for the first zoospores, which in the Saprolegniaceæ apparently encyst after 5 to 15 minutes.

The first zoospores are of two sizes, large and small, as in *S. anisospora* de Bary (**2**, p. 33); the small are, however, comparatively rare. The small ones are about 8μ in length, the large about 14μ. Fig. 8 A and B shows sporangia from different parts of the same gill, one containing a few small zoospores, the other containing large ones; the smaller appear to be more regular in shape. Zoospores of intermediate size occur. The zoospores within the sporangia vary considerably in shape, especially in different sporangia. They may be oval, pear-shaped, or very elongated, almost rod-shaped, and may be rather irregular in outline, while some have a distinct protoplasmic tail. The zoospores appear capable of changing their shape to some extent, are slightly amœboid (Fig. 9). They are considerably flattened, as may be seen when they turn up an edge in swimming. It is probable that when free in the water they become a more regular pear-shape. Zoospores swimming in the sporangia always keep the same end foremost, but in some cases the fore end is blunt, in others rather pointed, though generally all in the same sporangium swim with the same end foremost. The free zoospores have many shining droplets, and a small vacuole near the apex; they are biciliate but swim rapidly enough to make the number of the cilia and their attachment very difficult to discern. They move with the pointed end foremost and tend to swim in wide circles. The smaller zoospores, which seem to have a more regular shape, swim in a more straightforward manner and more rapidly. They often swing round in their tracks; this *volte-face* could be more easily understood if there were an anteriorly and a

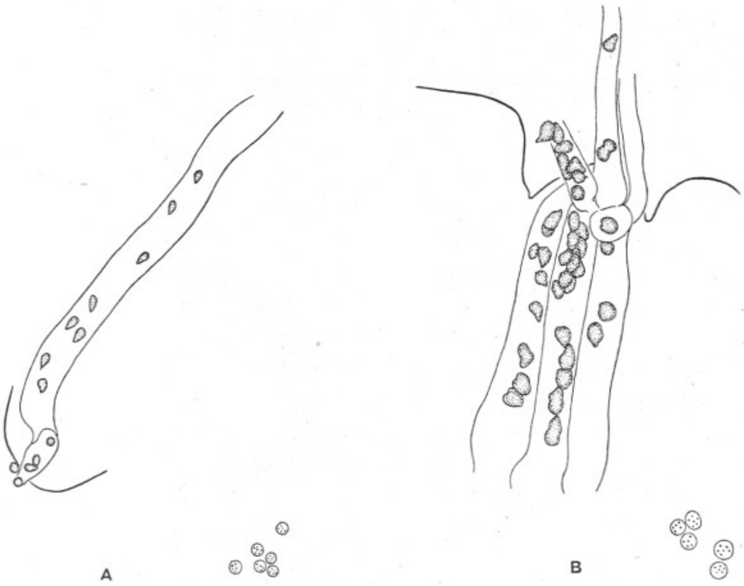

FIG. 8,—A. Zoosporangium with small zoospores. In the lower right-hand corner are cysts formed from some of these spores within the sporangium. B. Zoosporangium with large zoospores. In the lower right-hand corner are cysts formed from some of the spores within the sporangium. × ca. 253.

posteriorly directed cilium. One apically attached cilium can be seen clearly, a second is sometimes glimpsed but is much more difficult to distinguish. A possible explanation is that this one, though also apically attached, is normally posteriorly directed and therefore often hidden by the body of the zoospore. In an attempt to make certain of the point of attachment of the cilia, zoospores were fixed in vapour of glacial acetic acid, then treated with iodine, but drops of sea-water containing the zoospores were also swarming with bacteria, which were particularly thick round the spores and often tended to arrange themselves on fixing, end to end in crinkled lines, sometimes touching the spores, so that any cilia were entirely hidden.

An interesting case was noted of spores emerging from a sporangium by way of a tiny discharging papilla which was markedly constricted where it penetrated the chitin of the gill. The emerging zoospores took a considerable time to pass through, they were almost pinched in half and detained there for perhaps 30 seconds. After passing through they halted at the exit for a few seconds as though held up by a posterior cilium or protoplasmic process adhering to the wall of the papilla; they would fling themselves sideways in an effort to become free.

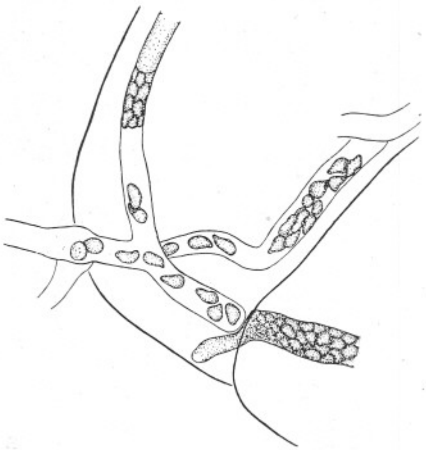

FIG. 9.—Sketch showing slightly amœboid zoospores within sporangia. A spore has encysted in the discharging papilla of one sporangium making it difficult for the zoospores to pass. × ca. 342½.

As mentioned previously the length of time before encystment varies considerably, as does also the time taken actually to encyst. They may take several minutes in the process, swinging round and round in small circles and becoming more and more rounded until at last movement ceases; or a zoospore may stop abruptly when swimming rapidly, and, as it were, tucking in the pointed end, become rounded in a second. When rounded the spore often swings round for a short time, and at least one cilium can be seen lashing. The spore comes to rest, a shining droplet appears on the tip of the cilium as it gradually shortens, and while still of some length it breaks off and floats away. This process of events was seen very clearly perhaps a dozen times and the path of the drifting cilium followed for a second or so. Generally only one cilium has been clearly seen during this process. The shortening of the cilia with the appearing of a droplet was noted by Butler in the encysting zoospores of *Pythium de Baryanum* Hesse (Pythiaceæ) (**6**, p. 94). On one occasion a zoospore of the *Pinnotheres* fungus, seen when about to encyst, had two apical cilia which curled in towards each other, then broke off and floated away. The cysts vary from about 6μ to 10 or 11μ in diameter; they contain several shining globules. A fine germ tube is put out, but since no nutritive medium was supplied, as the tubes grew in length the part next the cysts was gradually left empty and after a time the plant died. Small swollen structures occur along the germ tube (Fig. 10), some nearly as large as the original cyst, as though there was an attempt at re-encystment (**3**, p. 283).

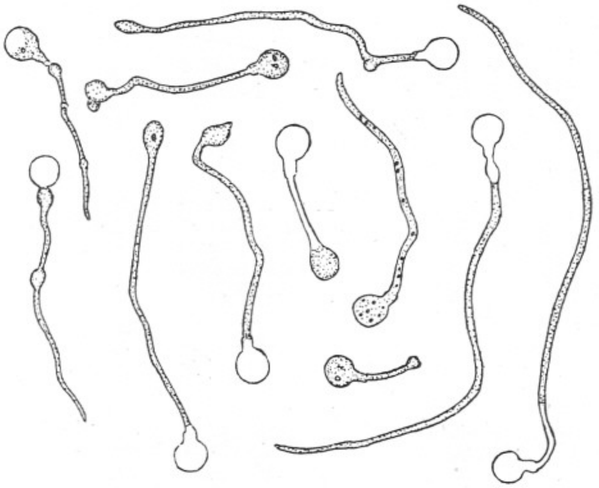

FIG. 10.—Germinating cysts. Some have small swellings along the length of the germ tube and one seems to be attempting to re-encyst. × ca. 685.

The question of the structure of the zoospores and as to whether there are two motile phases has had to be left, at least for the present, in a very unsatisfactory state. Owing to lack of time no attempt was made to obtain pure cultures and, as already mentioned, it was found impossible otherwise to obtain a drop containing zoospores that was not swarming with bacteria, hiding the cilia. A second zoospore has not been observed emerging from a cyst, all that can be brought forward in favour of the existence of two motile phases in this fungus is, firstly, the finding of empty cyst cases with tiny exit tubes: the empty cases showed up quite clearly owing to the thick zone of bacteria collected round them. Secondly, the occurrence of a few zoospores of a definite bean-shape with two cilia which appeared to be laterally inserted, answering to the description of the second zoospores of the Saprolegniaceæ. These came from a sporangium, but may have emerged from spores encysted there.

Difficulty was experienced with growing the fungus in hanging drops of sea-water; it was found that the development of the fungus in the gills in such drops was arrested after a day or two, but that development would go forward and spores form if they were changed into a bowl of sea-water, even if growth had been at a standstill for 14 or so days. A somewhat similar state of affairs has been described by Lechmere (**11**, p. 318) for a species of *Saprolegnia*. The cysts formed in some of the hanging drops, probably owing to artificial conditions, did not develop and after a few days became enlarged, while their contents shrunk away from the wall, in some cases stretching in a band across the cell.

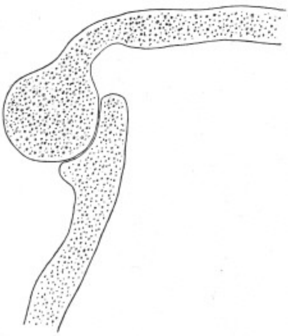

Fig. 11.—Young oogonium with applied antheridium (?). × 400.

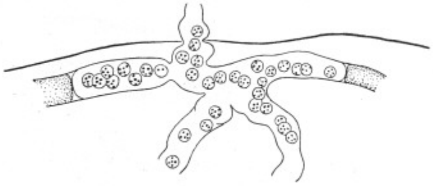

Fig. 12.—Sketch to show part of a branched sporangium with a single aperture; a number of zoospores have encysted within it. The thick line shows the outline of the gill leaflet. × ca. 253.

Fig. 13.—Sketch to show the highly vacuolated nature of the protoplasm in hyphæ which very occasionally grow out from the gill into the sea-water. × ca. 342½.

The infection and death was observed of a tiny nematode worm which had accidentally become fixed by its posterior extremity near the edge of a hanging drop made with an infected gill. The spores settled in the first place on the motionless tail of the worm; the rest of the body was writhing vigorously for over 16 hours.

Sexual organs have not been definitely identified. Fig. 11 shows what appears to be a young oogonium about 32μ in diameter with an applied antheridium of diclinous origin. In gills fixed in Flemming's fluid a very few round bodies containing many black globules of varying size have been seen. Similar bodies are shown in Fig. 5 which was sketched from fresh material. They appeared as shown at night, the next morning the larger one and the hyphæ were empty, the smaller still full. On two or three occasions two round bodies have been seen in proximity as in this figure. There is a possibility that they may be oogonia or gemmæ, but in any case they are exceedingly rare and are formed on spore-producing hyphæ.

LIFE-HISTORY (SO FAR AS KNOWN).

The mycelium enters the pea-crab in places where the chitin is extremely thin, and round the point of infection the hyphæ form a densely woven patch. In cases where the entrance is effected through the roof of the gill chamber, some strands pass into the body while hyphæ invade the gills and mouth parts. When the tissue of the gills is partly absorbed and the death of the crab is imminent, the hyphæ in these parts turn into zoosporangia, swarms of zoospores being liberated. These remain active under laboratory conditions for a period of a few up to at least 50 minutes, when they encyst. After encystment a second motile period may occur. Infection probably occurs during one or other of the motile phases. Organs which have been recognised as possibly sexual would appear to be rare.

DISCUSSION OF RELATIONSHIPS.

The *Pinnotheres* fungus has the general characters of the Saprolegniaceæ, the hyphæ, which are freely branched and unconstricted, are aseptate until the approach of the reproductive stages, and the asexual spores are biciliate. The zoosporangia are formed from unchanged hyphæ, as in *Aphanomyces* (**2**, p. 160) and *Leptolegnia* (**14**, p. 522); they are mostly branched (Fig. 12) as Coker (**2**, p. 159) observed for the sporangia in old cultures of *Leptolegnia* which may become very complex from the extension of a single sporangium into a number of adjoining branches. In both *Aphanomyces* and *Leptolegnia*, however, the spores are typically formed in a single row, while in the *Pinnotheres* fungus the number varies with the width of the sporangium. Very occasionally a second sporangium is formed within an empty one, a feeble development of the "nested" arrangement found in *Saprolegnia* and sometimes in *Leptolegnia* (**2**, pp. 22, 157). The biciliate zoospores on emerging from the sporangia swim actively away as in *Saprolegnia*, *Leptolegnia*, and *Isoachyla* (**2**, pp. 22, 157, 81; **6**, p. 83), and it is possible that after encystment a second zoospore emerges as also occurs in those genera. As previously mentioned, the first zoospores are probably of two sizes, large and small, with intermediate sizes as in *S. anisospora* de Bary.

The *Pinnotheres* fungus is distinguished from species of Saprolegniaceæ growing on freshwater animals and apparently from all other members of the family (**6**, p. 82) by being almost entirely an internal parasite, the discharging papillæ of the sporangia only, with very rare exception, penetrating the chitin of the host and reaching the exterior. It is extremely rare for there to be any growth of the fungus, apart from the discharging papillæ, external to the host, but an exceedingly slight external growth was noticed on three occasions on gills. Such filaments are very different in appearance from the normal internal hyphæ from which they arise, they are very fine and exceedingly vacuolated, the squarish vacuoles stretching across the width of the hyphæ (Fig. 13). Similar very slender, highly vacuolated hyphæ were seen extending from a few well-developed embryos of *P. pisum ;* the hyphal threads radiating from the embryos had the appearance of a halo. These were found on August 21st and 12 days later the female, which was carrying the embryos, was found dead with white opaque patches on the abdomen and with the gills infested with the usual fungus.

Dead infected crabs, left in sea-water, show no external growth of the fungus and it seems probable that it dies soon after the crab. This is in striking contrast to the heavy external growth formed by *S. parasitica* on dead salmon and other fish, dead flies, beetles, etc. (**10**, pp. 321, 331), indeed this latter species is said by Patterson (**13**, p. 1) to show a richer growth on dead than on living salmon, indicating that dead tissue is much more suitable for its growth than the living fish. The apparent inability of the *Pinnotheres* fungus to form a growth on dead crabs may seem to argue in favour of its truly parasitic nature, but putrefaction of *Pinnotheres* is somewhat rapid and it may be that the number of bacteria, etc., present, check the growth of the fungus and kill it (**14**, p. 506 ; **10**, p. 331).

The question as to whether it is a true parasite or only invades tissue which has been broken down by parasitic bacteria, as does *S. parasitica* of the salmon (**13**, pp. 2, 7 ; **4**, p. 200 ; **7**, p. 29) and perhaps *A. Hoferi* of the Bohemian mirror carp (**2**, p. 145), has not been gone into : there is quite a possibility that this may be so, for gills infested with the fungus are almost always swarming with bacteria of several kinds. If it is a true parasite it would seem to be ill adapted to its host, for its penetration into the gills must soon cause the death of the host.

It is very probable that death occurs more rapidly under laboratory than under natural conditions. In the case of the crabs, of which details are given in Table I, they had been taken from mussels, being themselves parasites (**12**), and were isolated free in batches varying in number from

TABLE I.

MORTALITY OF PEA-CRABS, INFECTED WITH THE FUNGUS, WHEN KEPT TOGETHER IN BOWLS.

Number of crabs in a bowl, all of which died with the infection.	Date of placing in bowl.	Date of 1st and of last death.		Number of days before 1st death.	Number of days between 1st and last death.	Number of days between placing in bowl and last death.
5 (4 adult ♀+1 ♂) from Weir Point, April 10/28	April 10, 1928	April 28	May 18	18	20	38
12 (♀ adult) from Padstow, April 25/28	April 25	May 22	June 6	27	15	42
13 (♀ adult) from Padstow, April 25/28	April 27	May 12	May 25	15	13	28
7 (♀ adult) from Padstow, April 25/28	May 8	May 26	June 8	18	13	31
3 (♀ berried) from Padstow, April 25/28	May 8	June 4	June 13	27	9	36
7 (♀ adult) from Padstow, April 25/28	May 9	May 28	June 15	19	18	37
21 (♀ adult) from Padstow, April 25/28	May 10	May 22	June 11	12	20	32
18 (♀ adult) from Padstow, Sept. 14/28	September 17	October 6	October 20	19	14	33
				Average 19·4	Average 15·2	Average 34·6

5 to 21 in bowls of sea-water and therefore possibly able to obtain little food. When a number of crabs were kept together in a large glass dish, as in the eight instances given in Table I, they gradually died of the disease, one after the other succumbing. Mortality was very much lower among those crabs kept singly in finger bowls, indicating that the disease is extremely infectious. All crabs in the Laboratory had their water renewed every day or every other day.

The death of the host is generally sufficiently rapid, at least in the Laboratory, for the gonad—so far as appears outwardly—not to be affected. This is a condition contrary to that which occurs in infection by a Sarcosporidian identified by Dr. Pixell Goodrich, and in infection by *Pinnotherion vermiforme* Giard and Bonnier (**5**). In some few cases, mostly crabs which when taken from the mussels were seen to be infected, the crabs were rather orange or milky orange in colour. This possibly indicates that they may resist the fungus longer under natural conditions and there is time for them to draw on the gonad. In one dead crab examined, which had been a milky orange for some time, the fungal threads were found among degenerating ova in the gonad. The main axis of each of the gills was full of a bright yellowish orange substance, which looked like yolk globules, but did not blacken with the osmic acid in Flemming's fluid, and was doubtless derived from the degenerating ova.

SUMMARY.

A fungus, most probably allied to the Saprolegniaceæ, has been found infecting *Pinnotheres*. Pea-crabs so infected always die, but there is not as yet sufficient evidence to determine whether the fungus is pathogenic or only invades tissue which has been destroyed by parasitic bacteria. Although having the general characters of the family it apparently differs from all members so far described in that it occurs in a marine invertebrate and is almost entirely internal in habit, the zoosporangia occurring within the tissue of the host.

ACKNOWLEDGMENTS.

The work was carried out at Plymouth while holding a Miss Busk studentship of Bedford College. I wish to thank the College authorities for allowing me to work at the Marine Station, and the London University for granting me the use of their table. My thanks are also due to the Director and Staff for their kindness, and I am especially indebted to Dr. J. H. Orton for criticism and advice throughout the work. Miss G. L. Naylor most kindly read the manuscript. I am in addition indebted to several members of the Staff, and especially to Mr. A. J. Smith for the photograph in Fig. 1.

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The Larvæ of the British Sabellarians.

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With 9 Plates and 5 Figures in the Text.

CONTENTS

1. INTRODUCTION.

The larvæ of Sabellarians are some of the commonest of plankton organisms, and especially in the spring and summer months are present in abundance around our coasts. They have frequently been figured and described from plankton catches made in different parts of the world, but in nearly every case they have been regarded as larvæ of some form of Spionid, in spite of the fact that de Quatrefages (**18**) as long ago as 1848, Horst (**12**) in 1881, and von Drasche (**5**) in 1885 all obtained the early stages from artificial fertilisations of a species of Sabellaria. In 1914 Caullery (**3**), by comparing larvæ which he had caught in the plankton with the figures published by these three workers, and by calling attention to certain chætæ found in his oldest specimens was able to point out the chief differences between the larvæ of Spionids and those of Sabellarians. In the same year Ziegler (**21**) again obtained the early stages of *Sabellaria spinulosa* by means of artificial fertilisations, but since then no further researches on these larvæ have been made. As yet no satisfactory account of the development of any Sabellarian exists, and the present paper gives for the first time a fairly full description of the development of the external features in two species of Sabellaria, and includes the first observations which have been made on the metamorphosis and early bottom stages of these remarkable creatures. All measurements are given in the legends to the text-figures or in the explanation of the plates.

It is a pleasant duty to have to thank Dr. Allen and the members of this Laboratory for their encouragement and help in this work. Dr. Lebour and Mr. A. J. Smith have both kindly attended to my plunger jars on occasions when I have been away.

2. METHODS.

In the early spring of 1927 a number of common and familiar larvæ were picked out from plankton catches and placed in bowls of sea-water. They were then thought to be Spionid larvæ, Caullery's paper not having been seen at that time. These larvæ after some weeks metamorphosed into what was, with some surprise, recognised to be the young of a species of Sabellaria. Two species of this genus are common in the Plymouth district, one, *S. alveolata* Linnæus forming large honeycomb masses of sandy tubes attached to the rocks on the shore at Whitsand Bay, the other, *S. spinulosa* Leuckart building separate sandy tubes attached to stones and shells on the bottom of the Sound, and elsewhere below low-water mark. Living specimens of both were collected, and artificial fertilisations made. Mature individuals of both species, and especially of the former, can be obtained during the greater part of the year, and they shed their genital products as soon as they are removed from their tubes. The early larval stages are easily obtained, and it is these which have previously been described by von Drasche and others. The early larvæ were placed in plunger jars or in finger bowls. The water used was obtained well out to sea, and was passed through a Berkefeld filter to remove any organisms it contained. A few drops of a culture of Nitzschia (kindly supplied by Dr. Allen) was added to each plunger jar or bowl, and this served as food. Numerous attempts to rear the larvæ in this manner were made, and some of these were successful. On the whole those in the plunger jars did best, but in several cases excellent results were obtained in the finger bowls. In warm weather those plunger jars which stood in an aquarium tank and were cooled and protected from rapid changes of temperature by running water gave the best results. It was also found important to protect the jars from too strong a light, otherwise the diatoms became too numerous. The spines of the very young larvæ became attached to anything of a sticky nature, such as clumps of diatoms, and many larvæ often stuck to the same speck of debris, from which they were rarely able to free themselves. Older larvæ were powerful enough to pull themselves away. It is thus very important that the water should be perfectly clean. The water as a rule remained unchanged throughout each experiment.

There are two stages through which it is especially difficult to rear the larvæ. The first is the growth stage between the trochophore with nine or ten bristles in each bundle, and the considerably larger early metatrochophore with two or three trunk segments and a telotroch. Once that stage has been passed growth continues fairly readily until the larvæ are ready for metamorphosis. They then frequently die off, sometimes first making an abortive attempt to metamorphose. It was only after numerous attempts that artificially fertilised larvæ were reared to early bottom tube-building stages.

All the drawings, except where otherwise stated, are from living larvæ, confined in cavity slips but perfectly free to move about, so that the body was not distorted in any way. Proportions were obtained with the aid of a square-net micrometer in the eyepiece, drawing in the first place on to squared paper. Larvæ were also mounted in the usual manner for the better examination of the chætæ.

3. THE DEVELOPMENT OF *SABELLARIA ALVEOLATA* LINNÆUS.

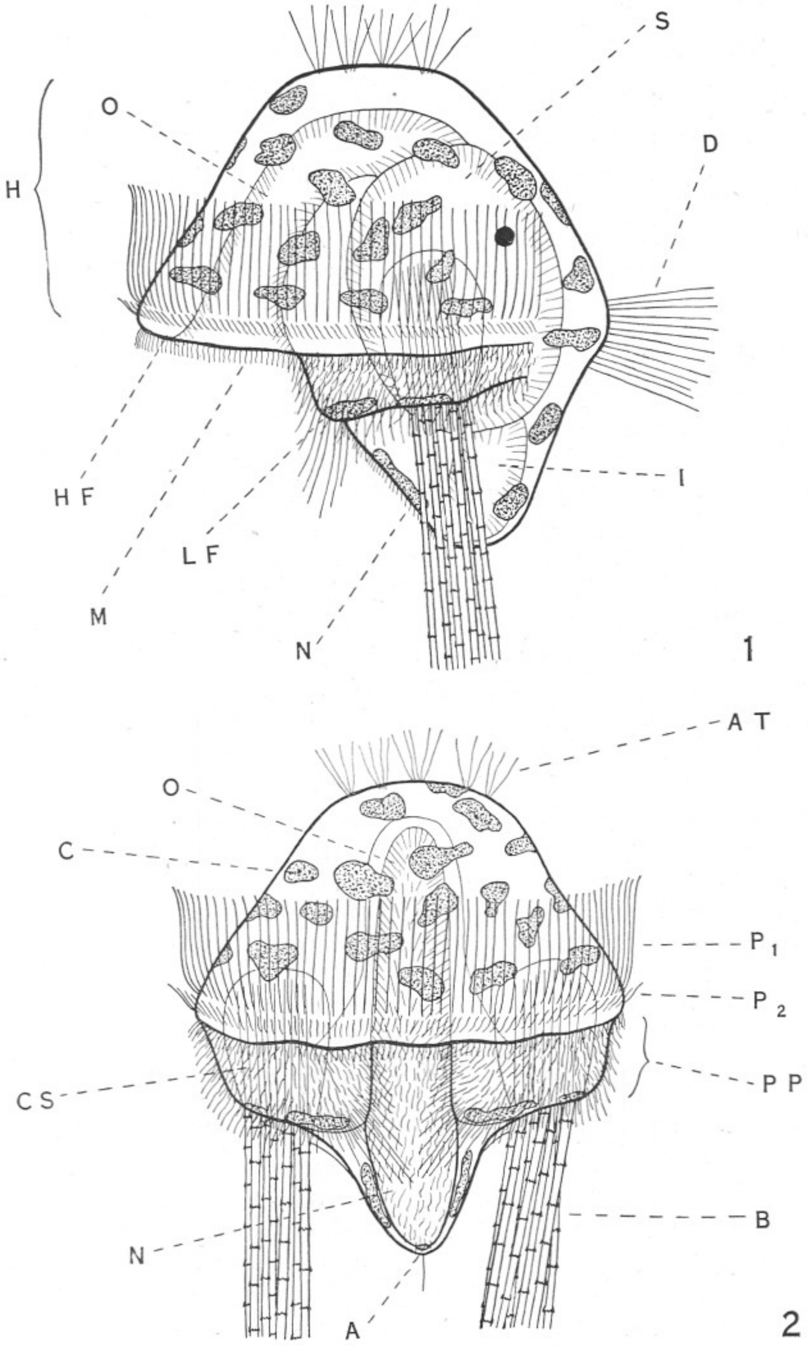
(*a*) *The pelagic stages.*

When seen in the mass by reflected light, the freshly spawned ova of this species are purplish in hue. A conspicuous germinal vesicle is present and the eggs are very irregular in shape. If not fertilised, healthy ova will remain in this condition for several hours, but if sperm be added they round up and throw off a crumpled fertilisation membrane and the germinal vesicle disappears. After a time polar bodies are extruded and segmentation commences. Eighteen or twenty hours later the embryos show the first signs of movement. Fig. 1, Plate I, is a drawing of an embryo twenty-seven hours after fertilisation. The outline is rather irregular, and the embryo is densely granular and opaque. The colour is similar to that of the freshly spawned ova. It is surrounded by the crumpled fertilisation membrane through which cilia project. Just posterior to the equator there is a complete ring of very short fine cilia, the first sign of the prototroch. At the anterior pole a few very fine long cilia form an apical tuft. The movements are rather feeble, but as the prototrochal cilia lengthen and become more powerful, the embryo begins to swim actively forwards, rotating on its longitudinal axis. The cilia of the apical tuft are usually directed forwards and twisted together. As the embryo develops its outline loses its irregularity, and, owing to a slight increase in size, it fills up the space inside the fertilisation membrane, smoothing out the wrinkles (Plate I, Fig. 2). This fertilisation membrane persists as the skin of the larva and is present up to the latest stage observed. It forms a rather close-fitting envelope separated from the "surface" of the larva by a narrow space. As this membrane is never tightly stretched, and as it is always of about the same thickness whatever the size of the larva may be, it is obvious that the original fertilisation membrane must be added to by secretion during growth. In only one culture out of many in which special attention was paid to this point, has the fertilisation membrane been observed to be actually thrown off. In this case, when a stage a little later than that shown in Fig. 2, Plate I, was reached, in many of the larvæ, but by no means in the majority, the membrane split right round in the line of the prototroch and was cast off in two pieces, one anteriorly and one posteriorly. This left the larva covered by a very delicate pellicle, and for two or three days it was possible, with a high power, to distinguish two kinds of larvæ in the bowl, those which had retained the membrane and those which had cast it off. Soon, however, it was no longer possible to do this; all the larvæ had a typical membrane round them, which must mean that either those which cast it off had all died (many of both kinds of larvæ died), or had secreted another membrane indistinguishable from the true fertilisation membrane. In either event it is highly probable that the loss of the membrane was an exceptional occurrence.

About forty-six hours after fertilisation the embryo reaches the stage shown in Fig. 2, Plate I. It is slightly elongated in an anterior posterior direction, and is opaque and granular in general appearance. With a high power the gut can be seen to be differentiating. The prototroch consists of a single row of fine cilia completely surrounding the body just behind the equator; the long apical tuft is as in the previous stage, but at the posterior end a single extremely fine cilium, which persists for some considerable time (see figures), has appeared. A slight depression in the region of the future mouth deepens a little, and fifteen hours later is as shown in side view in Fig. 4, Plate I. By that time one long and one short provisional bristle have appeared on each side (Plate I, Fig. 3) and the general colour is an unevenly distributed yellowish green by transmitted light. Otherwise there has been little change. Shortly afterwards, however, the mouth appears as a small well-ciliated invagination situated just behind the prototroch in the slight ventral depression previously mentioned. About the same time the prototroch acquires a second and posterior row of very short cilia and becomes interrupted by a gap on the dorsal surface. First one and then another bristle appears in each bundle, and the yellowish green pigment, together with specks of brown, begin to be aggregated into chromatophores. The ventral depression deepens slightly, and the prototroch is raised up on a backwardly projecting fold which runs round the ventral surface just in front of the mouth and passes up on each side, but does not extend on to the dorsal surface. A neurotroch of short cilia appears on the ventral surface, and the forwardly directed œsophagus becomes ciliated and is a conspicuous feature of the ventral view. The apical tuft loses its longest cilia but persists as tufts of short fine cilia throughout pelagic life. Thus thirty hours after the last stage it reaches the condition shown in Figs. 5 and 6, Plate I. The larva is now much less granular and more transparent than previously, but there are still a great number of oily globules in the tissues.

About forty hours later, just over five and a half days after fertilisation, the larva reaches the stage shown in Fig. 7, Plate I. As this is the stage which has previously been specially figured by Horst, von Drasche, and Ziegler, and past which they failed to rear their larvæ, it is worth describing it in some detail. Text-Figs. 1 and 2 represent lateral and ventral views of a slightly older individual, but the only marked difference between it and the above-mentioned larva is that it possesses a few more bristles. Thus the following description, with that exception, applies to both.

The young Sabellarian has now reached what can be regarded as the fully developed Trochophore stage, and it has commenced to feed. The most striking feature is the backwardly projecting fold overhanging the mouth in front and passing round each side until it is lost as it merges into the dorsal surface. The whole of the region anterior to this fold can conveniently be referred to as the "hood." Behind this hood-fold there is on either side of the mouth a second rather similar fold or ridge which in later stages becomes more prominent. This structure will be called the "lip-fold." The diagrammatic section (Plate IX, Fig. 19) indicates the extent of the folding at this stage, while Text-Fig. 5, of the same but more highly developed structures in a larva which is probably that of Pallasia, gives a fair idea of the formation of this region in Sabellarian larvæ generally. The prototroch is carried near the edge of the hood-fold, it is complete ventrally but there is a large dorsal gap. It consists of an anterior row of long and rather strong driving cilia which form the chief swimming organ of the larva at this stage. Immediately behind a second row of shorter cilia occurs. In each of these rows the cilia are almost in single file, but as their points of attachment are not quite in line but are scattered a little, there is a slight tendency to form a very narrow band. Behind the second row there is a third line of short cilia along the edge of the hood-fold and more cilia occur in the groove formed by the hood-fold, and also on the lip-folds. On the latter the cilia are usually grouped into two or three irregular bands running parallel with the edges of the folds. These cilia can be regarded as a posterior prototroch ; they are longest near the posterior edges of the lip-folds and especially at the posterior corners by the mouth. They probably form a food-collecting area, but attempts to prove this have been unsuccessful, largely on account of the minute size. The long cilia on the lip-fold corners are held more or less stiffly in the position figured and undergo vibratory movements. This distribution of the protrochal cilia is unaltered during the later pelagic stages, but in the drawings on the plates it has not been possible to indicate it very clearly owing to the relatively small size of the scale used. On the ventral surface between the mouth and the anus there is a rather deep wide groove, which is well ciliated by a broad neurotroch. The mouth leads into a ciliated œsophagus which runs forward, to open near the anterior end of the hood into a large globular stomach, also ciliated. A short ciliated intestine passes to the anus which is situated on the ventral surface close to the posterior end of the larva. On the anterior extremity of the hood, some tufts of fine apical cilia occur, while at the posterior extremity of the body a single fine cilium projects backwards. In the dorsal gap of the prototroch there is a prominent dorsal hump, and this carries a number of long fine but rather stiff cilia which occasionally vibrate. Four long provisional bristles (except in Text-Figs. 1 and 2, where there are more) project from a conspicuous chæta-sac situated on each side, and they pass out below the lip-folds. The chæta-sacs are moved by a series of muscles in such a way that they can direct the bristles in many directions. The structure of the bristles is very characteristic, they are surrounded by rings of teeth, the points of which are directed towards their distal extremities. Owing to the minute size and transparency it is extremely difficult, even with an oil-immersion, to make out the real nature of these rings. They appear to be collars arising from the bristle shaft with the free border of the collar toothed or serrated. The teeth are longer on one side of the collar than on the other (Plate IX, Fig. 11). The collars are arranged at intervals of about $8{\cdot}5\mu$, but the distance apart varies. The larva is fairly transparent and has a considerable number of oily globules in its tissues. A conspicuous feature are the fairly numerous irregular chromatophores scattered over the hood (except on the anterior-dorsal region), on the dorsal hump, on the lip-folds, at the posterior end of the body, and one along each side just lateral to the ventral groove. The chromatophores have a fairly sharp irregular outline with a greenish yellow ground-colour, over which are scattered many irregular dark brown specks. One red eye-spot has appeared on the left side in front of the place where the prototroch stops short (out of sight in Fig. 7,



TEXT-FIGS. 1 and 2.—Lateral and ventral views of a trochophore larva of *Sabellaria alveolata* Linnæus. From life, slightly diagrammatic, × 624. Actual length (excluding bristles and apical cilia) approx. 100μ.

A, anus; AT, apical tufts of cilia; B, bristles, cut short; C, chromatophore; CS, chæta-sac; D, cilia on dorsal hump; H, hood; HF, edge of hood-fold; I, intestine; LF, edge of lip-fold; M, mouth; N, neurotroch; O, œsophagus; P$_1$, anterior or first row of prototroch; P$_2$, second row of prototroch; PP, posterior prototroch, or cilia on lip-folds; S, stomach.

Plate I). This and the eye-spots that develop later lie deeper in the tissues than do the chromatophores.

After the larva has reached the fully developed trochophore stage represented in Fig. 7, Plate I, no further differentiation of the soft tissues is apparent for some little time. The organism merely acquires more and more bristles until there are nine or ten in each bundle. During this period, which lasts for several days, sometimes about a week, the body of the larva remains the same size, or at most only becomes very slightly larger. At the end of the period it begins to grow and a constriction appears just in front of the chromatophores which are situated on each side of the ventral groove. The region behind this constriction becomes the telotrochal swelling (see p. 248 for reasons for using this term). At this period the telotroch is arising; the grasping-cilia (see p. 231) soon becoming quite prominent, but the driving cilia remain for some time fine, slender, and few in number. Meanwhile two more eye-spots have appeared, both on the right side. The second of these to develop arose posterior to and nearer the mid-dorsal line than the first. The fourth eye-spot does not develop until the larva has almost reached the stage shown in Fig. 10, Plate I, and it then appears posterior to and nearer the mid-dorsal line than the eye-spot on the left side, which was the first to appear. This curious order in the development of the eye-spots was constant in a large number of larvæ examined from different cultures, except that occasionally supernumerary ones might develop. Each eye-spot consists of numerous reddish globules (oily ?) aggregated into a cluster.

The larva drawn in Figs. 8 and 9, Plate I, was twenty days old, and it is definitely a metatrochophore. The telotrochal swelling and two or three trunk segments are marked out, but the limits of the segments are rather indistinct. The telotroch is present, but at this stage possesses a ventral gap, through which the neurotroch passes to the anus. There are three eye-spots, one on the left and two on the right side. Each bristle-bundle contains fifteen to seventeen bristles, one or two of them being quite short. In other details the creature closely resembles the trochophore, except that it is larger and the hood and lip-folds are more prominent. Growth continues and new trunk segments appear in front of the telotrochal swelling. A six-weeks'-old larva is shown in Figs. 10 and 11, Plate I, but many larvæ by this time are much more advanced. There is a great variation in the rate of growth of individual larvæ from the same culture, and reared in the same bowl or plunger jar. At the stage shown in these drawings, irregular pigment bands are present on the dorsal anterior part of some of the trunk segments, and they extend round the sides of the body to about as far as the borders of the wide ventral trough in which the neurotroch lies. These pigment bands ordinarily have a black appearance, but they are really composed of a large number of very dark brown granules crowded together. Four red eye-spots are present in the positions indicated. The chromatophores have the same appearance as before, but they are confined to the hood, lips, dorsal hump, and the telotrochal swelling. On the hood they form a more or less regular line in front of the prototroch; elsewhere they are more scattered, but are absent from the anterior-dorsal area and from an area on each side just lateral to the eye-spots. The telotroch has either a ventral gap, or its cilia in that region are indistinguishable from the neurotrochal cilia which pass through it. In the ventral view the telotrochal swelling is represented as being turned slightly forwards; it is characterised by a number of clear vesicular-like "cells" that are present in addition to the chromatophores, which are rather darker than those on the hood. The larva is fairly transparent and very active.

Fig. 1, Plate II, shows in lateral view a larva from the same culture and plunger jar as the last, but only two days older. It was one of the more advanced larvæ referred to above. The trunk is much bigger in proportion to the hood than formerly. The three parathoracic segments are clearly defined, but as yet bear no parapodia. Behind them the first three abdominal segments have appeared; these bear slight lateral lobes, the first appearance of the dorsal uncinigerous processes of the parapodia. Between the parathoracic segments and the hood is a region more or less undifferentiated which will subsequently form into the two anterior thoracic segments of the adult. The most striking new feature, however, is the development of a pair of tentacles, one on each side of the dorsal hump at the place where the hood-fold edge merges into the dorsal surface. The attachment is almost in line with the end of the prototrochal row. These tentacles subsequently form the structures in the adult which are referred to as palps by many authors (e.g. Fauvel, **6**). Just ventral to each chæta-sac two small lobes have arisen, the largest of which will grow out into what may be called the ventral cirrus. The neurotroch is still a broad band of fine cilia, but cannot be seen in lateral view owing to the shallow trough in which it lies.

Another larva from the same culture, drawn seven days later, is shown in Fig. 2, Plate II. The dorsal parapodial lobes of the parathoracic segments have appeared, and each has two short bristles projecting from it. The uncinigerous lobes of the abdominal parapodia are larger, and now possess a number of uncini (Plate IX, Fig. 18); the first pair have four or five each, the second pair two each, and the third pair one each. The second pair of these uncinigerous lobes is situated more ventrally than the first and third pair. An important new feature is the appearance of a few special chætæ among the bases of the long provisional bristles. These chætæ will subsequently form some of the first crown chætæ of the metamorphosed larva. Three kinds are present, one each of two sorts of bristles and a few paleæ of a curious broad flattened form (Plate IX, Figs. 13, 14, and 12). The tentacles are longer and are thickly ciliated on their ventral surfaces, but the cilia are not yet very active. They are not contractile (or very slightly so) and are held stiffly in the position shown. The cirrus ventral to the chæta-sac is quite long; on it are a number of sensory cilia. The great chæta-sacs are passing backwards into a more posterior position. A horseshoe-shaped area around the posterior border of the mouth is becoming glandular; it is the first appearance of the building organ. The ciliation is the same as described for younger larvæ except that there is no ventral gap in the telotroch. The driving cilia of the telotroch are longest at the dorsal ends of the row next to the grasping-cilia, and they gradually decrease in size and power as they approach the mid-ventral position.

The larva shown in Fig. 3, Plate II, was seven and a half weeks old, but was from another culture reared in the autumn of 1927, the larvæ of the previous drawings having been reared in the spring, but all died before this stage was reached. In its main features this larva is very similar to the preceding stage, but the body is more massive and the parapodia more distinct. Each dorsal bundle of the parathoracic parapodia consists of two prominent spear-headed bristles (Plate IX, Fig. 16) and two finer bristles (Plate IX, Fig. 17) which do not project much. In addition the third pair each has a long slender barbed bristle. Ventral bundles have also appeared on these segments, and have two fine bristles to a bundle. These cannot be seen in dorsal view, but are shown in Fig. 2, Plate III, which is a ventral view of a slightly later stage. The uncinigerous lobes of the first pair carry about ten uncini each, the second pair about five and the third pair about four. The numbers, however, vary considerably and need not be the same on either side. There are about thirty-five provisional bristles in each of the great bundles, and among them there are twelve to fourteen primary crown paleæ of the flattened type (Plate IX, Fig. 12) as well as the two short pointed bristles (Plate IX, Figs. 13 and 14) which were present in the previous stage. Owing to the greater growth of the body in comparison with the hood, the mouth and lip-folds are now well exposed. The building organ has increased in size, and the rudimentary parapodia of the two anterior thoracic segments are appearing. Fig. 2, Plate III, gives a good idea of the ventral surface of the anterior end, but in this drawing the structures are a little more advanced. There has been no change in the general ciliation except that the first signs of a nototroch are present on the first parathoracic segment. The tentacles are of considerable length, and are thickly ciliated ventrally. Chromatophores similar to those on the hood are present on their dorsal surfaces. The anus is situated on the apex of a slight cone. The larva is rather opaque, the general body-colour being brownish. The chromatophores are darker brown than formerly, particularly those on the telotrochal swelling. The eye-spots have also become darker.

The larva has now reached the end of its pelagic development, but before describing the metamorphosis it will be well to consider the swimming movements.

(b) *Swimming movements and the "grasping-cilia."*

Sabellarian larvæ do not show a very active reaction towards light, but they do tend to keep on the side of the bowl or dish furthest from the window whenever the light is strong. This is most noticeable with the earlier stages after they have got one or more of their eye-spots. Polydora larvæ, under similar conditions, will be found on the side of the bowl nearest to the light (see Wilson, **20**, p. 577). They swim with the hood anterior to the direction of movement, and when watched in a plunger jar they will be seen, as a rule, to keep themselves orientated so that the hood is uppermost, i.e. in the position in which the figures are drawn. But they frequently depart from this upright position to swim in any direction, often moving along with the body placed horizontally. While swimming the two bundles of provisional bristles are kept close to the sides and the distal tips of the bundles meet one another above and behind the telotrochal swelling. The bristles pass through the dorsal gap in the telotroch and are held by the "grasping-cilia." The telotroch passes up the sides of the swelling on to the dorsal surface, and there the row of cilia turns abruptly forwards to form a longitudinal row on each side of a large dorsal gap. The cilia of these longitudinal rows project laterally and rather dorsally. They always remain more or less curved at their extremities, and although they undergo vibratory movements, they never actually beat. Their function is to curl round and grasp the long provisional bristles while the larva is swimming. Cilia with a similar function are present at the ends of the nototrochs—but not on the telotroch—of Polydora, and have already been described (Wilson, **20**, p. 577). In Sabellaria these cilia are much stronger and more conspicuous. Their function is probably twofold: (1) they help the larva's progress by holding in the bristles to the stream-line, and (2) their action must give increased rigidity to the larva as a whole and to the telotrochal swelling in particular, thus increasing the efficiency of the telotroch as a driving organ. In the later stages the driving cilia of the telotroch are longer and stronger than those of the prototroch, and possibly finally supersede the latter as a swimming organ. Under such circumstances anything which helps to make the soft body of the larva rigid will be to its advantage. The correctness of this interpretation appears to be supported by the appearance, during the later stages, of the single long barbed bristle from each of the parapodia of the third parathoracic segments. These appear at a time when owing to the growth of the body the telotrochal swelling has been carried so far back that the grasping cilia can only just reach the tips of the provisional bristles. The two long bristles from the third parathoracic segment project further back than they do and are also held by the grasping-cilia. This will give rigidity to the body at a new point. In the latest stages, just before metamorphosis, it frequently happens that the long ringed bristles no longer reach as far back as the grasping-cilia unless the larva contracts its body. Fig. 3, Plate II, shows the body slightly contracted; it is frequently more stretched in the swimming larva, and then the grasping-cilia can only take hold of the barbed bristles from the third parathoracic segment. These bristles are lost during metamorphosis. It is interesting to recall the fact that in the development of the telotroch the grasping-cilia develop faster than the driving-cilia and are used for grasping the bristles while the latter are still fine and weak.

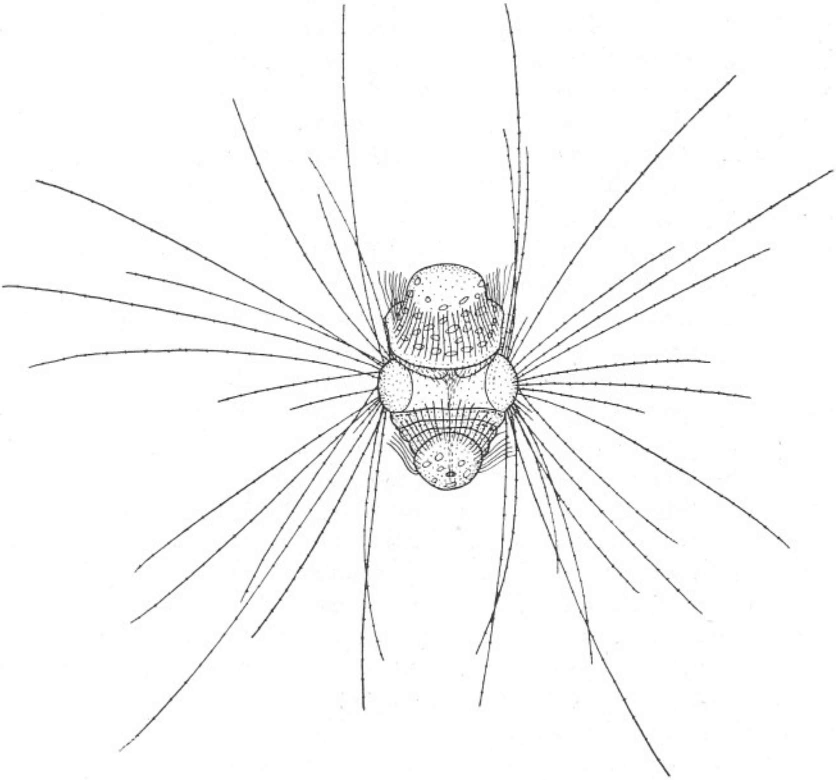
While swimming, a larva will every now and then suddenly flex the body ventrally so as to bring the telotrochal swelling close to the hood in the region of the mouth. At the same time the bristles are spread to point in all directions (Text-Fig. 3). This occurs when it bumps up against anything or is otherwise irritated. Tiny fishes have been seen to take larvæ into their mouths and immediately spit them out again with their spines erect. Some of these larvæ were afterwards examined; they appeared to be uninjured. This power of spreading the spines is acquired about the stage shown in Fig. 6, Plate I. The spines may also have a suspensory function, but this is difficult to prove. The larvæ frequently swim for long periods without erecting them and rarely have been seen to keep them spread for long, and then only while they were continually being irritated.

In all the figures, for the sake of clearness, the spines have been drawn in the partially erect condition. In Fig. 7, Plate V, the grasping-cilia are shown partially in action.

(c) *Metamorphosis and the early bottom stages.*

The duration of pelagic life varies within wide limits. Reared larvæ take from six weeks to three months from the time of fertilisation before they are ready to metamorphose. It is likely that the shorter period most nearly represents the time taken in the sea.

After a larva has reached the stage drawn in Fig. 3, Plate II, it shows an increasing tendency to crawl about on the bottom. This it does head downwards by applying the mouth to the substratum, on which the lips are spread out and flattened, the building organ being pushed back and stretched aside to allow of their full protrusion, so that their ciliated surfaces, which are normally just inside the mouth opening, come into contact with the ground. The tentacles are turned outwards and forwards so that their ciliated surfaces also come into contact with the substratum. They are not, however, kept pressed against it, but are repeatedly raised up a little and put down again in a manner suggestive of feeling. In this way the larva glides forwards, the tentacles preceding and possibly testing the ground over which it travels. The hold is tenacious, a larva can resist quite strong squirts of water, and if it is clinging to the inside of a pipette is very difficult to dislodge. After crawling about for some time a larva may suddenly take to swimming again, settling down later on.



Text-Fig. 3.—Ventral view of a formalin-preserved Sabellaria larva showing bristles erect. ×156. This is the position assumed when the larva is irritated and is characteristic of the larvæ as seen in preserved tow-nettings.

The change in habits is accompanied by changes in structure. The hood commences to shrink and the lips and mouth are exposed more and more fully (Plate III, Fig. 2). The building organ is enlarging rapidly, and the first two thoracic segments begin to be defined by the growth of their parapodial rudiments. The body lengthens and the telotrochal swelling is flexed somewhat ventrally, while the cone bearing the anus grows out into a long process which turns forwards ventrally to form the characteristic caudal region of the adult. Ventral bristles appear on the abdominal segments and more nototrochs develop dorsally. Meanwhile great changes have been taking place in the head region. The hood has continued to shrink and the prototrochal cilia gradually disappear although some may persist for some time. The tentacles are in process of turning forwards permanently, and are becoming very contractile and wrinkled. In some cases a secondary tentacle is growing out on each side close to the anterior lateral corner of the mouth. These are probably the first filaments of what is sometimes called the palp (e.g. Benham, Camb. Nat. Hist., Vol. II). They are indicated as showing through the transparent tentacles in Fig. 1, Plate III, and are clearly shown, but are more highly developed in Plate IV. The great chæta-sacs have become fully exposed and have rotated a little so as to bring the ventral cirri into a lateral position. A second cirrus is present on the border of each chæta-sac close to the inner ventral corners. These secondary cirri were present as small swellings in the larva drawn in Fig. 3, Plate II, but they were then hidden between the bristle bundles and the back of the larva. The latter has now the appearance shown in Fig. 1, Plate III, and the long provisional bristles are rapidly falling out. The great chæta-sacs and the associated tissues turn upwards and forwards, at the same time shedding any provisional bristles which may remain. They finally take up a position projecting forwards and rather dorsally, and thus come to form the peduncular crown of the adult. These observations of the metamorphosis thus confirm the assumptions of descriptive morphologists that " les deux gros pédoncules operculaires représentent très probablement les rames dorsales fusionnées des deux premiers pièds rejetés en avant du prostomium " (Fauvel, **6**, p. 205).

The time taken to metamorphose varies, but appears to be normally about two days ; it is often longer.

The specimen represented in ventral view in Plate IV was just over seven weeks old, and had probably metamorphosed a week or ten days previously. It was living in a little tube of mucus and debris on the bottom of the plunger jar. As this is, unfortunately, the most advanced stage to which the larvæ have been reared, it will be well to describe it in some detail. The peduncles project forwards and rather dorsally. On each twelve to fourteen primary crown paleæ (Plate IX, Fig. 12) are arranged in a circular row spread out fanwise from the centre. The circle is interrupted by a large gap on the side immediately facing the opposite peduncle. This is similar to the arrangement of the crown paleæ of the adult. Inside the curve of the row and close to the gap are situated the two pointed bristles previously mentioned. These are shown in Figs. 13 and 14, Plate IX, the former being placed immediately lateral to the latter. Another pointed and curved bristle (Plate IX, Fig. 15) has appeared on the inner side of each peduncle below the level of the crown paleæ. The two cirri are prominent and probably represent the first of the numerous papillæ which in the adult form a row just below and outside the outer row of crown chætæ. In a median position, just ventral to the gap between the peduncles, is a strongly ciliated conical process, formed in front of the eye-spots during the shrinkage of the hood. The four eye-spots are still present, but the anterior pair (indicated in Plate IV) are closer together than in the larva. The eye-spots are almost black with a reddish tinge. The tentacles project forwards and outwards; they are strongly wrinkled and contractile, and have thickly ciliated ventral surfaces. Along their edges there is on every wrinkle a pair of specially stout cilia, and there are a number of these cilia on the tip. Just ventral to their place of attachment a dark brown swelling represents the remains of the hood. The brown pigment is a concentration of the brown specks of the chromatophores, the latter having shared in the general shrinkage of the hood. The prototroch disappeared long ago. The lip-folds form prominent ciliated lateral lips. Close to the anterior lateral corners of the mouth are a pair of wrinkled " tentacles " ciliated on their anterior surfaces in a similar way to that in which the ventral surfaces of the tentacles are ciliated. These " tentacles " are probably the first of the many filiform tentacles, sometimes referred to as the palps (Benham, *loc. cit.*), which are such a conspicuous feature of the ventral region of the head in the adult. Posterior to the mouth is the large glandular horse-shoe-shaped building organ. This is finely ciliated, especially on its anterior border and in the deep groove between it and the lateral lips. At each anterior lateral corner of this structure is a short process with sensory cilia and two fine capillary bristles, the rudimentary parapodia of the first thoracic segment. A short distance behind these a second similar pair of projections with one fine capillary bristle each represent the second thoracic segment. Then follow the three parathoracic segments with four bristles, two prominent and two inconspicuous (Plate IX, Figs. 16 and 17) in each dorsal bundle, and with two fine capillary bristles in each ventral bundle. The first three pairs of uncinigerous dorsal processes are prominent. The first pair are considerably broader in a dorso-ventral direction than the posterior two pairs, and they have about ten to twelve uncini (Plate IX, Fig. 18) each. The second pair possess five or six uncini each and the third pair four or five. The numbers of uncini vary considerably. In the drawing the ligaments attached to the uncini are indicated. Ventral to each uncinigerous process is a single long fine bristle representing the ventral bundle of the parapodium. Behind the third pair of processes two slight swellings will probably develop into the fourth pair. Posteriorly the body curves forwards ventrally and is continued as the caudal appendage, on the extremity of which the anus opens. Close to the base of the caudal appendage and on the inner surface of the bend there is a small swelling which contains a mass of dark brown pigment. This is the shrunken remains of the telotrochal swelling.

A certain amount of black pigment—really composed of dark brown granules—still remains, especially on the dorsal surface. The worm on the whole is rather opaque, and the segment limits, particularly those of the abdominal segments, are not very visible. Nototrochs are present close to the posterior borders of the segments, and also on the head, the arrangement being the same as that shown for a more advanced individual of *S. spinulosa* in Fig. 1, Plate VIII. There is also a neurotroch in a shallow ventral groove.

The gut is divided into several regions. In the parathoracic segments the rather thick wall contains a fair number of small oily globules. On either side is a large gland, probably the thoracic gland shown in the figure of a young individual in McIntosh (**16**), p. 28, Fig. 139. A clear portion with only very few small globules in the walls follows, and this portion close to the posterior end of the first abdominal segment leads into a part where the walls are crowded with many closely packed large oily globules, in which condition the gut continues to the anus. This latter portion is indicated in Plate IV. It is a very conspicuous feature of the young worm and indeed of the later larval stages where it is situated further forward and may be present as early as the larva shown in Fig. 10, Plate I. This characteristic appearance has been omitted in the earlier drawings for the sake of clearness.

During the later stages much individual variation respecting the relative times of appearance of the different organs occurs. This is well seen in the development of the caudal appendage, for while in some individuals (as in Fig. 1, Plate III) it is quite large before the crown paleæ have been directed forwards, in others it does not develop until some time after the head region has fully metamorphosed. In such cases the telotroch persists although the worm is living in a tube. Again, the palps or tentacular filaments at the anterior lateral corners of the mouth in some cases appear quite early (as in Fig. 1, Plate III), in others very much later. All grades of intermediate conditions are found. Other organs show similar variation, although perhaps in lesser degree.

(d) *The building of the first sandy tube.*

The young worms after metamorphosis were frequently, but by no means always, found to be living in tubes of mucus on the bottom of the bowl or plunger jar in which they had been reared. To the sides of these tubes debris of various sorts was attached, especially masses of living diatoms and the cast-off provisional bristles. The tubes could be detached with a pipette and then if the larvæ were supplied with fine sand they would readily build in dishes or cavity-slips, while being watched through the microscope. All larvæ with mucus tubes were able to build tubes of sand grains, the mucus tube forming a foundation. All larvæ which were without mucus tubes, either because they had been removed from them or because, apparently, they had not made them, were unable to construct sandy tubes. They would attempt to do so, but they only succeeded in cementing grains into an irregular mass, even though they were kept amid sand for several days and in some cases were supplied with pieces of sterilised oyster shell—plentifully sprinkled with sand—which might serve as an irregularly creviced substratum on which to build. Some larvæ which metamorphosed in a dish containing sand also failed to construct either a mucus or a sandy tube. The explanation of this is not apparent.

To return to the worms with mucus tubes. As soon as sand grains are supplied, some are seized by the tentacles and conveyed to the mouth. The ciliated ventral surface of a tentacle is applied to a grain and immediately it is caused to travel towards the base. The grain is moved along by the cilia, on which it appears to be balanced or held, and it probably does not come into direct contact with the surface epithelium at all. The special strong cilia arranged in pairs along each side of the tentacle appear to play an important rôle in transporting particles. A grain is not seized by a tentacle curling round it, indeed the tentacles are never sharply bent. If the worm be lying back downwards in its tube (which in these observed instances was always horizontal) the tip of a tentacle will be inserted under a particle which will then travel along with its weight supported by the cilia. This is illustrated in Fig. 2, Plate VIII. If, on the other hand, the worm be lying back upwards the tip of the tentacle will be placed on top of the particle and it will slide over the substratum. It is uncertain as to whether one tentacle alone can actually lift a particle, but the two together applied on either side can do so and are sometimes so employed, if the particle be a big one. The "palps," if long enough, also assist in the collection of building material. In one of these ways grains arrive one at a time, to be held in the mouth by the lips. The first few are cemented round the edge of the mucus tube and then others are cemented to them. While holding a grain in its mouth, the worm moves backwards in its tube so as to bring it into contact with the tube edge. It then moves forwards a little and turns the grain slightly, and then moves back once more. This backward and forward motion continues for a time, the worm continually twisting and turning the grain, trying it in different positions and at different places on the tube edge. If finally the grain more or less fits, possibly if it jams a little among those already fixed, it is cemented into place. But if after a few attempts it does not fit, it is discarded and another tried. Some worms will in this way discard several grains for every one fitted, others are more persistent in trying each particle. One larva in particular discarded very few grains; it would try each again and again all round the tube edge, turning it between every attempt, so that nearly every particle tried was finally fitted in somewhere. A particle appears to be cemented into position by the building organ, which is passed a few times over the place of contact on the inside of the tube. This rubbing of the building organ over the place of contact was seen every time a particle was fixed. Possibly the latter is also coated with some sort of cement while it is being turned about in the mouth. Fig. 2, Plate VIII, is a drawing of an actual tube. The mucus tube is covered with irregular clusters of diatoms and other debris, among which some of the larval provisional bristles are visible. The worm is shown in the act of collecting sand grains with its tentacles and one grain is held in the mouth.

The sandy tube is usually built rather slowly, the worm taking frequent rests. In one case, about thirty grains were fitted in four and a half hours, and by the next day the tube was more than twice as long. In another case—that of the particularly persistent larva mentioned above—a tube of about forty-five sand grains was constructed in two hours, while another individual during the same time fitted about thirty grains. The last tube was roughly as long as the body of the worm excluding the tentacles. On the whole, the building operation impresses the observer as a rather clumsy proceeding; certain operations are performed more or less persistently, and it appears to be a mere matter of chance as to whether any particular particle is fitted or not.

4. THE DEVELOPMENT OF *SABELLARIA SPINULOSA* LEUCKART.

(a) *The pelagic stages.*

The development of this species follows so very closely in almost all its details the development of the preceding species that a separate full description is unnecessary. Only those points, therefore, in which it differs in any way from *S. alveolata* will be dealt with in this account.

The drawings (Plates V to VIII) will serve as a further source of information.

The ova of *S. spinulosa* are on the whole slightly smaller than those of *S. alveolata*. In both species, however, variation in size occurs. They are of a pale pinkish colour, when seen in the mass by reflected light. Figs. 1 and 2, Plate V, show in dorsal and lateral views an actively swimming larva thirty-one hours old. Twenty-four hours later (Plate V, Figs. 3 and 4) the hood-fold is becoming prominent, the dorsal gap in the prototroch has formed and four provisional bristles are present in each bundle. The larva is still very granular, but the pigment is already grouping itself into chromatophores which are just like those of *S. alveolata*. The fully developed trochophore stage is represented in ventral view in Fig. 5, Plate V. It cannot be distinguished from that of the preceding species and it develops its bristles and eye-spots in just the same way. Fig. 6, Plate V, shows an early metatrochophore three weeks old. If it be compared with the corresponding stage of *S. alveolata* (Plate I, Fig. 9), a slight difference will be noticed in the form of the trunk and especially in the way in which the telotrochal swelling is marked off from the rest of the body. This difference appears, on the whole, to be constant, but considerable variation exists and it is of no practical service in separating the larvæ of a mixed culture. It is, moreover, difficult to observe in active larvæ and it disappears when the larvæ are fixed. It might be thought that the bristles would show some distinction, but none has been detected. Figs. 7 and 8, Plate V, show in lateral and ventral views a larva two months old. This stage is usually reached much earlier, but in both species the time taken by different individuals of the same culture under apparently identical conditions (i.e. in the same bowl or plunger jar) varies very greatly without any visible effect on the structure. In the lateral view the grasping cilia are represented as holding some of the bristles. The tentacles are just budding out a little posterior to the end of the anterior row of prototrochal cilia.

The larva shown in Fig. 1, Plate VI, was from the same culture and plunger jar as the one just described, but it was only one day older. It was a particularly fine large specimen. At this stage it is approaching the end of its pelagic existence, and the primary chætæ of the crown are already well developed among the bases of the provisional bristles. These chætæ differ markedly from those of *S. alveolata*, and once they have appeared larvæ of the two species are separated with ease. The paleæ (Plate IX, Fig. 1) which correspond to the broad flattened forms of *S. alveolata* are here longer and narrower and are strongly toothed along the margins. They are not flattened, but are rounded into a trough-like shape. The drawing is from a rather flattened specimen. In addition to ten or eleven of these in each bundle two pointed bristles (Plate IX, Figs. 6 and 7) are also present. The parathoracic parapodia have four bristles, two prominent (Plate IX, Fig. 8) and two inconspicuous (Plate IX, Fig. 9) in each dorsal bundle, while each of the third pair have also a long barbed bristle, of similar function to that of the other species. On these segments the ventral bundles, consisting of two fine bristles each, have appeared. The abdominal parapodia consist of the dorsal uncinigerous lobes only. Each of the first pair of lobes has about eight uncini (Plate IX, Fig. 10), the second pair about four, and the third pair about three, the actual numbers varying as in *S. alveolata.*

(b) *Metamorphosis and the early bottom stages.*

Development of the larva continues a little further until it is ready to metamorphose at a stage in development closely corresponding to that at which *S. alveolata* metamorphoses. Fig. 1, Plate VII, shows the ventral aspect of a larva in which the hood is just commencing to shrink back. This and all succeeding drawings (except Fig. 2, Plate VII) are from larvæ picked out of the plankton at a late stage and which metamorphosed in finger bowls, but all (except Fig. 2, Plate VI, and Fig. 1, Plate VIII) have afterwards been carefully checked on larvæ reared from the egg. In any case, there is not the least doubt as to the species, the crown paleæ being absolutely distinctive.

Fig. 2, Plate VII, is a dorsal view of the anterior region of a metamorphosing larva reared from the egg and over four months old. The great chæta-sacs are turning forwards. This process has almost been completed in the specimen drawn in Fig. 3 on the same plate. In the latter specimen the telotrochal swelling is flexed ventrally and the anus is on the apex of a slight cone. In some individuals at this stage the caudal appendage may be quite long. The prototroch has gone, but the telotroch remains, although its cilia are disappearing. The worm had a mucus tube which was attached to the bottom of the bowl. This is the most advanced stage to which this species has been reared from the egg. The single specimen reared as far as this was nearly fifteen weeks old.

Later stages have been obtained by rearing larvæ from the plankton. Fig. 2, Plate VI, is a ventral view of the head region of such a stage. The " palps " are only just arising, but as in *S. alveolata* there is considerable variation in the time of appearance. The hood has shrunk to very small proportions and is represented by a darkly pigmented patch anterior to the mouth. Above it is the ciliated anterior conical projection or " snout."

A dorsal view of the most advanced specimen obtained is shown in Fig. 1, Plate VIII. It is especially interesting in that the primary crown paleæ have been replaced by a secondary set. The new paleæ of the outer row have the appearance shown in Fig. 2, Plate IX, and they resemble somewhat the adult paleæ of the same row. There are six of these paleæ on the left and eight on the right side, but the crown was slightly damaged by clogging masses of diatoms when the specimen was obtained, and some may have fallen out. Inside the outer row other paleæ are present. These are three in number (Plate IX, Figs. 3, 4, and 5) and they are rather like the paleæ of the inner two rows of the adult. Unfortunately, owing to the way in which the crown was damaged, their actual positions in the crown are uncertain. A curved bristle is present in the inner side of each peduncle, as in *S. alveolata*. The parathoracic parapodia contain about five bristles in each dorsal bundle. The first pair of abdominal uncinigerous processes have about twenty uncini each, the second pair about eleven each, and the third pair five or six each. The number of chætæ in the ventral bundles of all segments is doubtful, but there are most probably two or three bristles in each ventral bundle of the parathoracic segments and one bristle in each ventral abdominal bundle. A pair of small swellings (only one is visible in the drawing), just anterior to the shrinking telotrochal swelling, may possibly be the developing fourth pair of uncinigerous processes, but if so, they are in a rather different position from the similar swellings in *S. alveolata*. A nototroch is present close to the posterior border of each segment, and a short one exists between the two pairs of eye-spots. As in the allied species, after metamorphosis, the anterior pair of these are closer together and situated more ventrally than the posterior pair.

Two young worms were obtained in which each peduncle of the crown carried one or two paleæ of the secondary type (Plate IX, Fig. 2). These were situated at the dorsal end of the curved outer row, the remainder of the paleæ in the row all being of the primary type (Plate IX, Fig. 1). We may perhaps conclude from this that the primary paleæ fall out and are replaced in regular sequence starting from the dorsal end of the curved row.

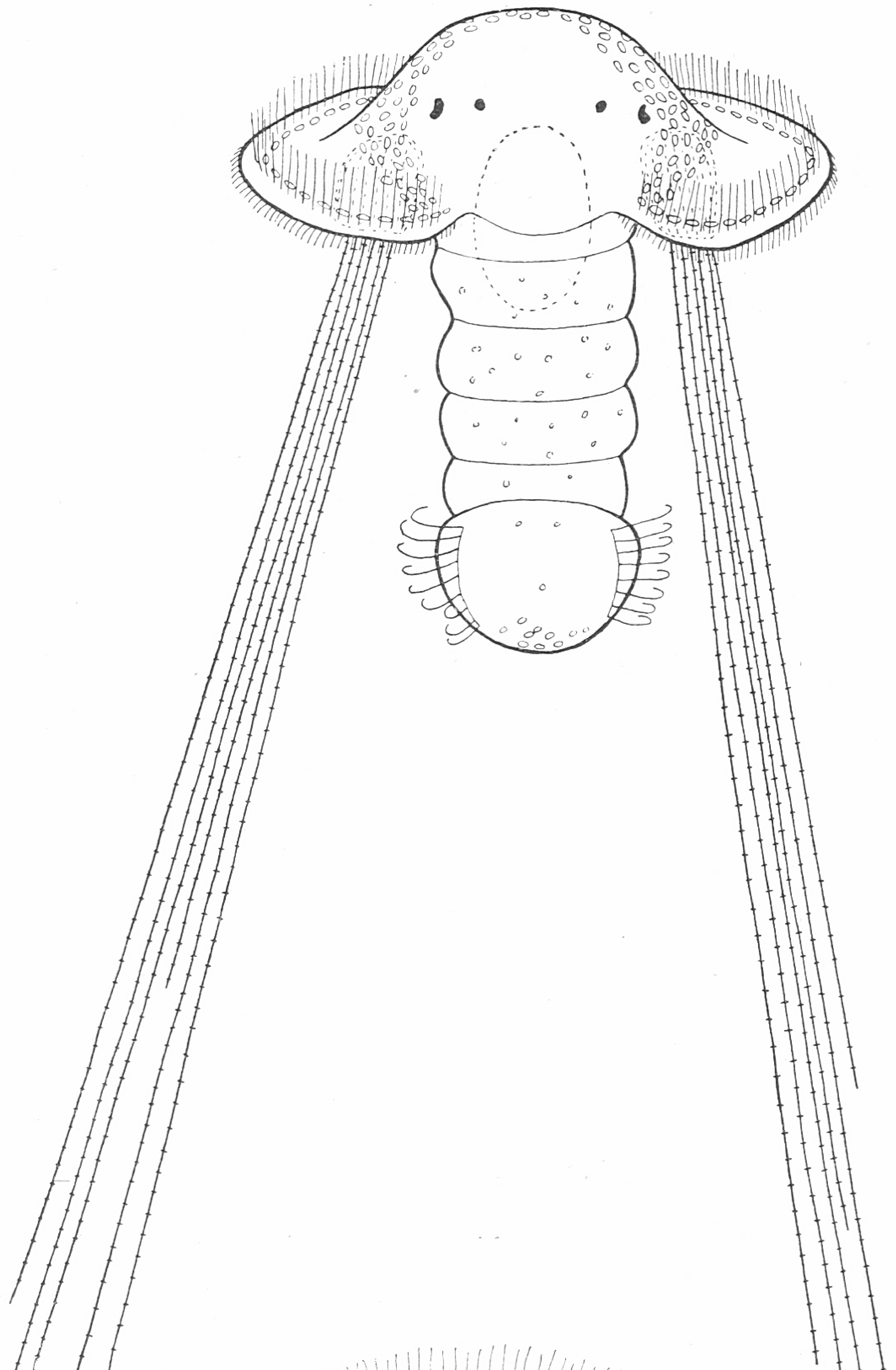
The building operations of this species have not been observed.

5. THE LARVA OF *PALLASIA MURATA* ALLEN.

Besides the two species of Sabellaria, the larvæ of which have just been described, one other Sabellarian has been recorded for the British Isles. This is the rare *Pallasia murata*, which has been described by Allen (**1**) as occurring in the neighbourhood of Plymouth, and of which only a very few specimens have been obtained, although the empty tubes are moderately common. Very little is known concerning the larval stages, but Caullery describes and figures (**3**, p. 172, and Fig. 3) a larva which he found in the plankton at Wimereux and which almost certainly belongs to this genus and most probably to the species also. It was in an advanced stage of development with primary crown chætæ at the base of the dorsal part of each bundle of provisional bristles. One of these chætæ was a strong hook resembling closely the hook present on the dorsal surface of each peduncle of the adult Pallasia. Close by each chæta-sac were about ten tentacular cirri, probably the papillæ which form a row along the external margin of each adult peduncle, and corresponding to similar papillæ in Sabellaria, in which only two are found by each chæta-sac in the later pelagic and early bottom stages. Four parathoracic segments were present, a feature in which Pallasia differs markedly from Sabellaria, where there are only three. The larva had also nine pairs of uncinigerous processes instead of only three as in Sabellaria larvæ. The anal cone, corresponding to the telotrochal swelling in Sabellaria, is of special interest in that, posterior to the telotroch, it presented fine transverse constrictions which may represent segments that will form the caudal appendage. There can be little doubt, after a consideration of these points, that this larva was indeed the larva of Pallasia, as Caullery demonstrated. It may be that his earlier larvæ also belong to the same genus, but this is at present impossible to decide. The pigment on the back, which in the Sabellaria larvæ described in this paper was very dark brown, or black in general appearance, is referred to by Caullery as " violacé " in both his early larvæ and in his Pallasia larva. This may or may not prove to be a distinction between the two genera.

Towards the end of February, 1927, at the very beginning of the present observations, and while engaged in picking out from the plankton Sabellaria larvæ which were at that time thought to be some form of Spionid, a single larva of the same type, but of a strikingly different general appearance, was obtained. Rough sketches of the dorsal aspect and of the mouth region in ventral view of this larva were made at the time and are reproduced in Text-Figs. 4 and 5. The larva was not observed in any great detail in case prolonged confinement in a cavity-slip should kill it, for it was hoped to rear it to a stage at which the genus, at least, could be determined. Unfortunately these hopes were not realised, and the larva subsequently died without further development. Since then the searching of many plankton catches has failed to yield another specimen. These rough sketches, however, have now a special interest, for it is very probable that this is the larva of *Pallasia murata* Allen. That assumption is based on the fact that *P. murata* is the only species of Sabellarian besides *S. alveolata* and *S. spinulosa* which has been recorded from anywhere reasonably close to the British Isles, and it is known to occur on grounds close to where this particular and distinctly Sabellarian larva was caught.

The larva was much bigger than the corresponding stage of Sabellaria, and the provisional bristles were longer and straighter. The hood and



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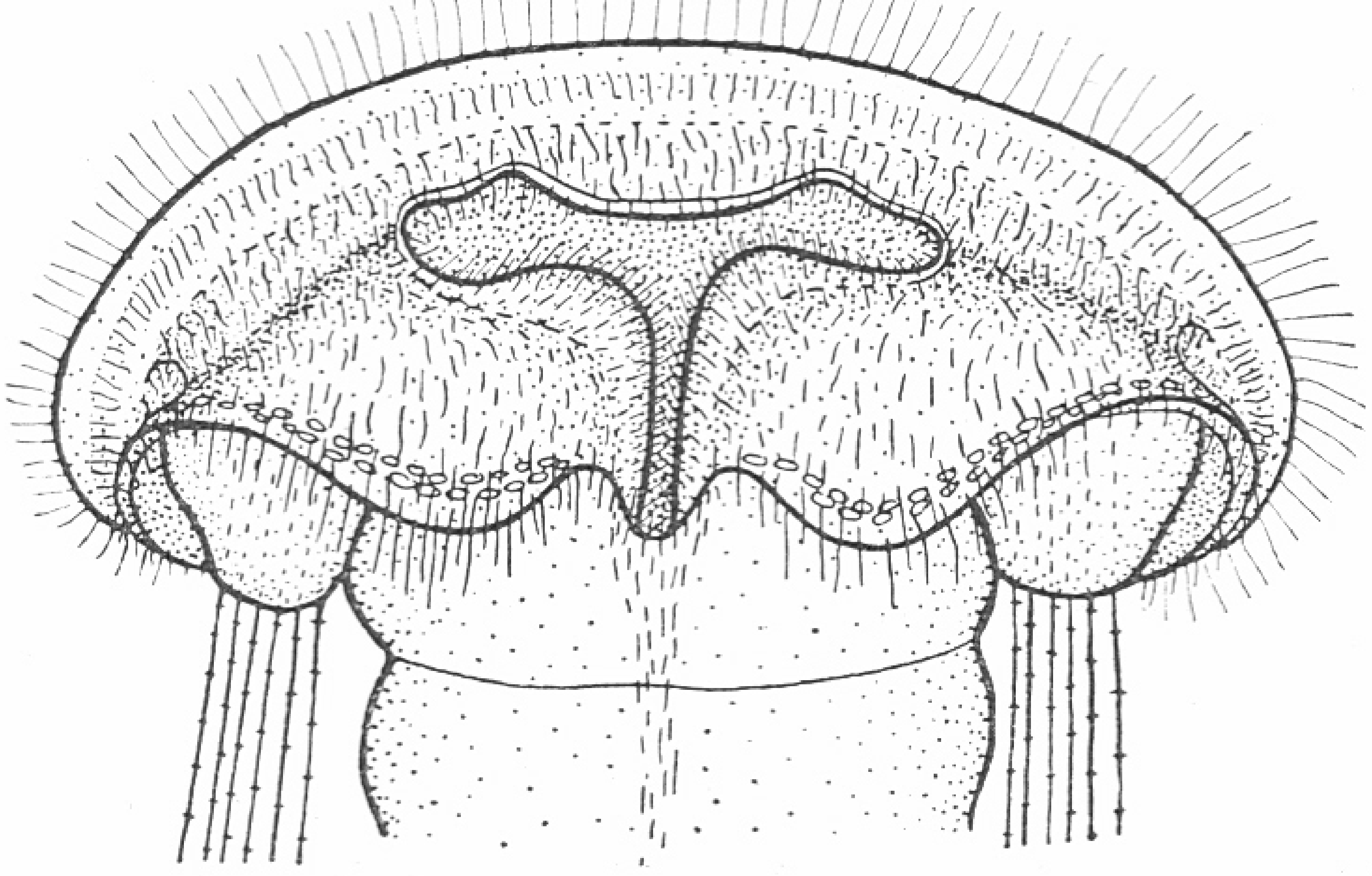

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TEXT-FIGS. 4 and 5.—Dorsal view, and ventral view of mouth region, of a Sabellarian larva which is probably the larva of *Pallasia murata* Allen. Sketch from life ×156. Actual length (excluding bristles) approx. 410μ.

lip-folds were more highly developed than they are in Sabellaria, but in their essential structure they were the same. Chromatophores of a beautiful pale green colour were scattered over certain regions of the hood and arranged in a row just anterior to the prototroch. Two pairs of eye-spots were present. The ciliation appears to have been the same as in Sabellaria. The manner in which the telotroch is drawn is interesting; the cilia shown are obviously grasping-cilia. No driving cilia are represented although it is highly probable that some were present. This drawing was made before the grasping-cilia in Sabellaria had been observed and at the time their function was certainly unsuspected.

In two points this larva can be compared with Caullery's latest stage. Thus the extra development of the hood-fold is indicated in his drawings (**3**, Fig. 3). Secondly, Caullery writes of the chromatophores as being yellow in colour, but the colour may change with age, as it does to some extent in Sabellaria, where the chromatophores gradually become darker brown when viewed as a whole.

6. KEY TO THE BRITISH SABELLARIAN LARVÆ.

It is now possible to construct a tentative key which will enable plankton workers to distinguish the later pelagic stages of the three British species of Sabellarians.

1. Provisional bristles less than 400μ long. Hood-fold fairly prominent. Chromatophores brown or yellow in general appearance..........2
   Provisional bristles approx. 760μ long. Hood-fold very prominent. Chromatophores a beautiful pale green colour or possibly yellow in the later stages..3
2. Primary crown chætæ, which appear among the bases of the provisional bristles during the later stages, very broad and flat, very slightly toothed (Plate IX, Fig. 12)..................*S. alveolata*
   Primary crown chætæ long, slightly trough-shaped, of moderate width and very strongly toothed along both edges (Plate IX, Fig. 1) *S. spinulosa.*
3. In addition, during later stages, a strong hook by the base of each bundle of provisional bristles; four parathoracic segments and more than three pairs of uncinigerous lobes.................*Pallasia murata.*

It is at present impossible to separate the early stages of the two species of Sabellaria.

7. PREVIOUS RECORDS OF SABELLARIAN LARVÆ.

De Quatrefages appears to have been the first to record the eggs and larvæ of Sabellaria. In 1847 he published a short paper (**17**) dealing mainly with fertilisation and the fertilisation membrane, followed in the next year by a longer paper (**18**) discussing those subjects in great detail, and containing also an account and figures of the segmentation and the early larvæ of a species of Sabellaria. He figures the prototroch as a wide band of cilia, which was entirely lost in his latest stage with four bristles on each side. At this stage his larvæ died. In 1850 he published another paper (**19**), describing various experiments on the artificial fertilisation of Sabellarian ova. No further work on this subject was published until 1881 when Horst (**12**) described his researches on the early development of *S. alveolata*. A short extract (**13**) of this paper was brought out about the same time. A plate of figures accompanied the longer paper, most of them concerned with the segmentation stages, in which Horst disagrees with the account given by de Quatrefages. A figure of the trochophore is also given on this plate with the chromatophores shown in colour. The colouring is quite good. He has, however, failed to distinguish the hood-fold from the lip-fold; they are shown as if they were fused into one. The strong forward arching of the prototroch over the mouth does not exist in a free-swimming larva, but might be caused by pressure beneath a cover-glass. In 1885 von Drasche (**5**) described the segmentation and early stages of *S. spinulosa*. His figure of the trochophore is also coloured, but, while he illustrates the greenish yellow ground colour of the chromatophores quite faithfully, in only two of them does he show the brown specks. A single eye-spot is shown, but is placed on the right side instead of on the left. During the present research this single eye-spot which appears first has never been seen on the right side, but always on the left. Several prototrochal rows of cilia are drawn with the cilia in the posterior rows about as long as in the anterior row. He does not seem to have realised the presence of the hood-fold, and the lip-folds are drawn to appear as though they pass below instead of above the provisional bristles. It is also interesting to note that he states that the fertilisation membrane ("Eimembran") is lost and does not form the cuticle of the larva. Nothing further was known until 1914, when Ziegler published another account (**21**) of the segmentation and early larvæ of *S. spinulosa*. He gives figures of the trochophore stage with six bristles in each bundle, in which he indicates the hood-fold. In the same year Caullery published his valuable paper (**3**), pointing out the chief characters of Sabellarian, as distinct from Spionid larvæ. This paper has already been frequently referred to. Since that time no further work on Sabellarian larvæ has been published, except that McIntosh has given some outline figures (**15**, Plate XCIV) of larvæ which probably belong to this group. Unfortunately there appears to have been some confusion in the numbering of this plate. Figs. 8 and 9 are probably Sabellarian larvæ ; the former is stated to be a Spionid larva, while Fig. 9 is not referred to. Figs. 10 and 11 are stated to be probably Sabellarian larvæ ; the former is certainly not, but the latter may be. There is no Fig. 11*a*. Some of this numbering was corrected in a later volume (**16**, p. 5).

In addition to the foregoing publications where Sabellarian larvæ are referred to as such there exist a number of papers containing figures of larvæ which almost certainly belong to the Sabellariidæ, although they are usually described as some form of Spionid. Busch, as early as 1851, figures these larvæ (**2**, Taf. VII, Figs. 5–8), which he obtained off Heligoland, the Orkneys, Cadiz, Malaga, and Trieste, but he does not name them. Fewkes (**7**) gives three figures (Plate II, Figs. 1–3), and describes them under the name of Spio sp. without giving any reasons for attributing them to that genus. He obtained his larvæ at Newport, U.S.A. Häcker also described and figured (**11**, p. 16, Taf. II, Figs. 14 and 15) similar larvæ from the west coast of Africa, and likewise called them Spio. Caullery has already suggested that the larvæ of these three authors were really Sabellarians. Both Fewkes and Häcker refer to a paper by Leuckart and Pagenstecher (**14**) who give figures of different stages of a larva which, without bringing forward any real evidence, they had referred to Spio in the following words: "Es handelt sich hier ohne Zweifel um eine *Spio*, deren Charaktere sich jedoch nicht so weit ausbildeten, dass sie eine Artunterscheidung mit Bestimmtheit gestattet hätten." They believed the species might be *Spio crenaticornis* on account of the similarity of the tentacle wrinkles of that species and those of their latest larva, and also because *S. crenaticornis* was common in Heligoland where their larvæ were obtained. Their figures (Taf. XXIII, except Fig. 1), however, show the Sabellarian characters ; even a few primary crown paleæ are indicated among the provisional bristles of their oldest stage. In the latter, it is true that five pairs of parathoracic parapodial bristle bundles are shown and no abdominal uncinigerous lobes, but the other characters, including the general shape, are so certainly Sabellarian that this can be regarded as an error of observation. Thus the responsibility of being the first to attribute Sabellaria larvæ caught in the tow-net to the genus Spio appears to rest with these joint authors and their identification was later accepted by both Fewkes and Häcker.

Claparède's early Leucodora (Polydora) larvæ (**4**, Taf. VII, Figs. 4–5) were also very probably trochophores of Sabellaria, at a stage when they had got nine or ten bristles in each bundle and before the trunk region had begun to be definitely segmented. As was pointed out in a previous paper (Wilson, **20**) Gravely (**9**, p. 46), accepting these figures and also Fig. 6 on the same plate as the larvæ of Polydora, described as metatrochophores of that genus some larvæ which he had found on several occasions in the July plankton at Port Erin. His description of these metatrochophores (which were only examined in the fixed contracted condition), so far as it goes, corresponds very well, except for one point, with Sabellaria larvæ, and not at all to Claparède's Fig. 6, Taf. VII, as Gravely himself seems to have realised. The point in which the description does not correspond is in the length of the provisional bristles, which are stated to be 850μ long, which would make them longer than the bristles of Pallasia. These bristles are described as ringed, but it is not stated that the rings (collars) were toothed. In another paper Gravely repeats Claparède's figure (**10**, Text-Fig. 3a), and uses it in a discussion on the probable mode of development of the vestibule in Polydora. If, as is highly probable, this larva is really Sabellaria, then the notch shown in the prototrochal rim in the neighbourhood of the mouth would indicate the lip-folds. The ciliated œsophagus is represented as running in an anterior direction just as it does in Sabellaria larvæ. In any case this larva and Gravely's metatrochophores are certainly not Polydora. The same remark applies to the metatrochophore figured by Flattely (**8**, Fig. 1) who, following Gravely's description, called it Polydora. The figure shows the Sabellarian characters.

8. NOTE ON THE CAUDAL APPENDAGE OF SABELLARIA.

Comparatively little appears to be known of the internal structure of the caudal appendage. This smooth achætous posterior region is usually stated to be "unsegmented." Externally at all events that does, indeed, appear to be the case, but sections reveal the presence of a number of transverse septa, fifty or sixty in number, in the adult *S. alveolata*. The gut is fused to the dorsal and lateral body-walls of the appendage, but on the ventral side the two are separated by a space. The septa cross this space at regular intervals. The space is further divided by a median longitudinal mesentery which runs down the whole length of the appendage. These septa, the well-developed blood vessels associated with them, and the caudal appendage generally, were observed by the late Mr. Arnold T. Watson, whose original notes of an extensive series of observations, spread over many years, on the anatomy of the British species of this genus, I have been privileged to consult through the kindness of Mrs. Watson and Professor Fauvel. If these septa delimit true segments, and there appears to be no reason to suppose that they do not, then the caudal appendage is really a segmented structure composed of fifty or sixty segments. In development it arises from the posterior part of what has been termed the telotrochal swelling. It appears that it is from the region immediately anterior to this swelling that new chætigerous segments are produced, and that the greater part of the swelling shrinks away when the pelagic life is over. The telotrochal swelling, as a whole, cannot therefore be properly termed a pygidium, and it is for this reason that the former term has been used here.

Sections have been cut of the caudal appendage at the stage when it was growing out during metamorphosis, but the scarcity of material has rendered it impossible to give an account of the development of the internal structures.

9. SUMMARY.

1. *Sabellaria alveolata* Linnæus has been reared for the first time from the egg through the pelagic stages and metamorphosis to early bottom stages. The chief features in the development of the external characters are described and special attention is drawn to the existence of peculiar grasping-cilia on the telotroch. The manner in which the young worm builds its first tube of sand grains is also described.

2. *Sabellaria spinulosa* Leuckart has similarly been reared for the first time from the egg to early bottom stages. Its development is very similar to that of the preceding species, but during the later pelagic life the two can easily be separated, as the primary paleæ of the crown, which appear among the long provisional bristles of the first pair of parapodia, show a marked specific difference. The early stages cannot be distinguished.

3. A larva which is probably that of the rare *Pallasia murata* Allen is described.

4. A tentative key to the British Sabellarian Larvæ is drawn up.

5. The observations of previous workers are discussed. It is shown that Sabellarian larvæ have frequently been described as the larvæ of Spio or of Polydora, in spite of the fact that the early stages of Sabellaria had been obtained more than once from artificial fertilisations. Caullery was the first to point out the error, and he is fully confirmed in this paper.

6. It is shown that the caudal appendage of a full-grown *Sabellaria alveolata* possesses internally a series of fifty or sixty transverse septa.

10. APPENDIX.

The following is an original note, by the late Mr. Arnold T. Watson, which is of special interest in that it describes early bottom stages of *Sabellaria alveolata* only a little more advanced than the latest stage to which I have been able to rear my worms. The note is dated October 16th, 1915, and apparently refers to a mass of tubes and living worms of this species which were received at Sheffield from Seascale on October 7th.

" The mass received is in a very healthy condition and in parts was encrusted with numerous very young specimens—some slightly older than others. In all young specimens a median ciliated process arises between the two opercular lobes. In the youngest it was clearly seen arising separately a short distance behind the upper lip, and the membrane joining the lobes was further still from the back of the upper lip. In older ones the ciliated process seems adhering to the membrane. There is at this stage (when the worm would be about 1·1 mm. long and have three tentacles at each side in addition to the two central tentacles) an " eye-spot " at each side of the central ciliated process and through the dorsal face two other larger eye-spots—situated nearer the mouth—can be clearly seen. When the worm bends its peristomial lobes to form a right-angle with its body both sets of eye-spots can be seen in top view forming a square. The papillæ external to the paleæ (about three or four on each side) are much longer in proportion than in the adults, and some of them (possibly all) are tipped with " tactile (?) hairs." The young Sabellarians in situ are difficult to see ; as in this specimen the lobes look like black specks and correspond closely with adjoining black sand-grains.

" A young specimen about 1·1 mm. long when extended alive has two tentacles on each side of the peristomial lobes (in addition to the two long median tentacles) and three cirri just below the paleæ, viz. : one long one at the dorsal edge and one at the ventral end of the crescent and one intermediate between the two— each with ' tactile hairs.' Two dorsal eye-spots about the level of start of long tentacles. The median ciliated process is very evident but difficult to tell whether it was above or under the membrane."

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PLATE I.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life × 156. All measurements exclude apical cilia and bristles.

FIG. 1.—Free-swimming embryo 27 hours after fertilisation. Actual length approx. 95μ (see page 223).

FIG. 2.—Embryo 46 hours after fertilisation. Actual length approx. 95μ (see page 224).

FIG. 3.—Embryo 61 hours after fertilisation. Actual length approx. 100μ (see page 224).

FIG. 4.—View of right side of the same larva as shown in Fig. 3.

FIG. 5.—Larva 91 hours old. View of left side. Actual length approx. 100μ (see page 225).

FIG. 6.—Ventral view of the same larva as shown in Fig. 5.

FIG. 7.—Larva about five and a half days old. View of left side from a slightly ventral position. Actual length approx. 100μ (see page 225).

FIG. 8.—Larva about twenty days old. View of right side. Actual length approx. 165μ (see page 228).

FIG. 9.—Ventral view of the same larva as shown in Fig. 8.

FIG. 10.—Larva about six weeks old. Dorsal view. Actual length approx. 310μ (see page 223).

FIG. 11.—Ventral view of the same larva as shown in Fig. 10.

PLATE I.


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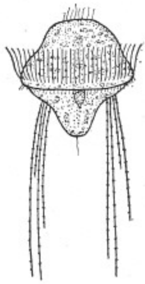
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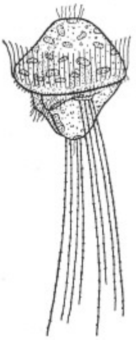
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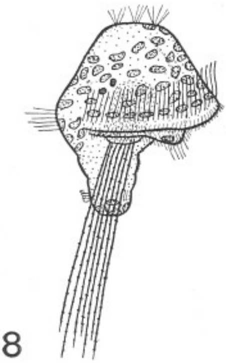
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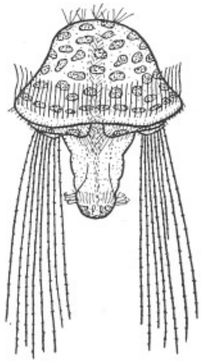
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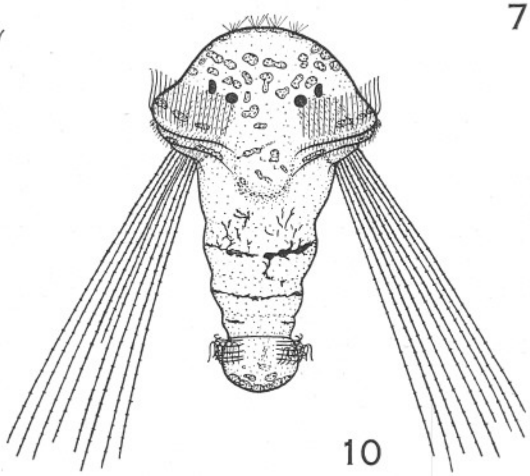
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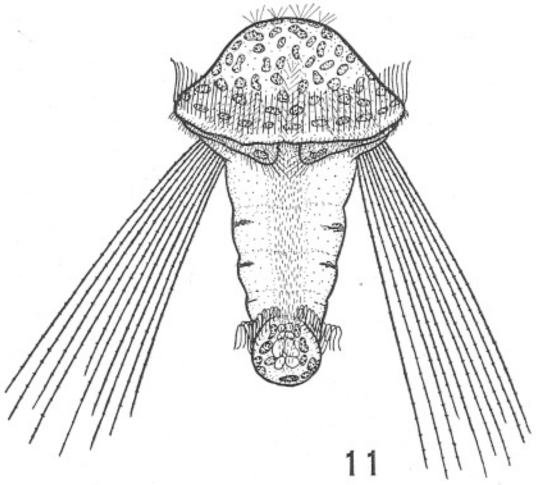
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PLATE II.

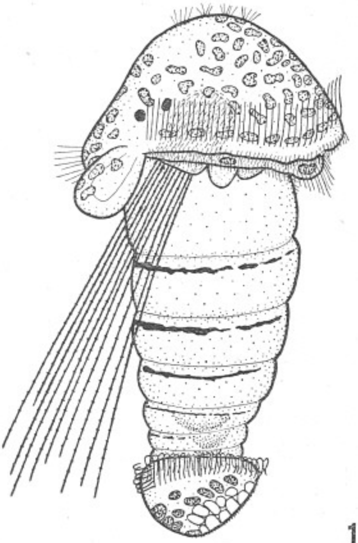
Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life × 156. All measurements exclude apical cilia and bristles.

FIG. 1.—Larva just over six weeks old. View of right side. Actual length approx. 435μ (see page 229).

FIG. 2.—Larva just over seven weeks old. View of right side. Actual length approx. 435μ (see page 229).

FIG. 3.—Larva about seven and a half weeks old. Dorsal view. Actual length approx. 500μ (see page 230).

PLATE II.



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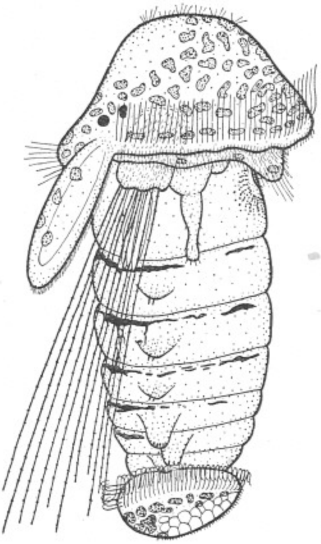

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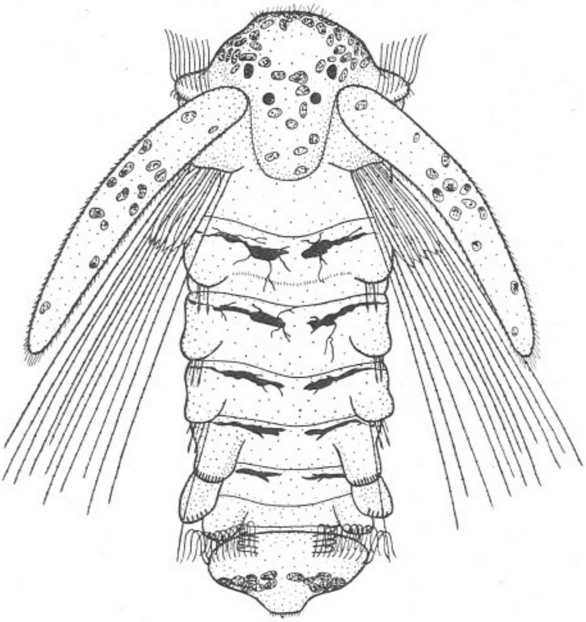

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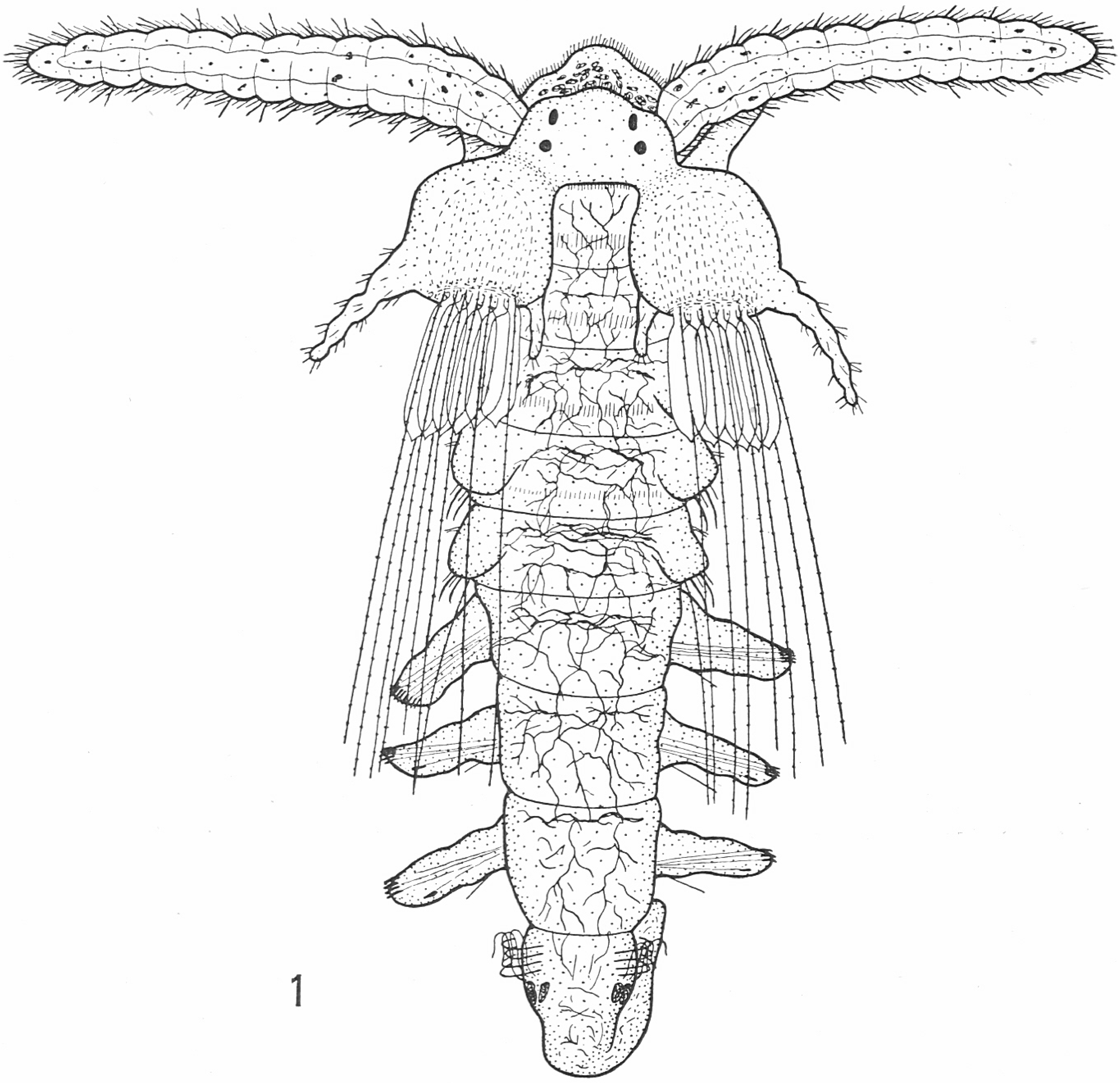
PLATE III.

Larvæ of *Sabellaria alveolata* Linnæus. All drawings from life × 156.

FIG. 1.—Dorsal view of metamorphosing larva about six and a half weeks old. Actual length, from anterior extremity of head to posterior bend, approx. 665μ (see page 234).

FIG. 2.—Ventral view of head region of larva just commencing to metamorphose. Stage earlier than that shown in Fig. 1 (see page 233).



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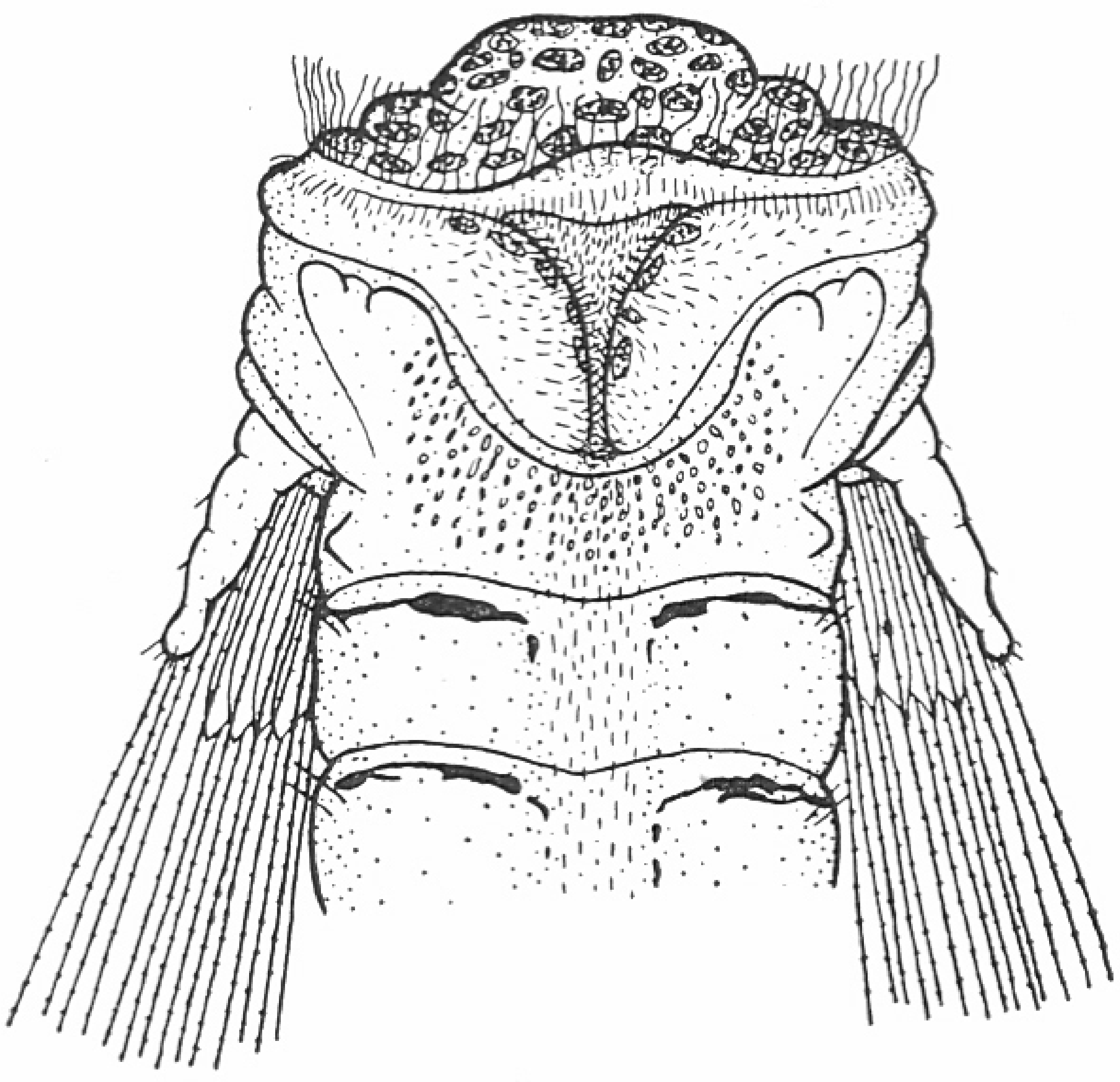

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PLATE IV.

Ventral view of early bottom stage of *Sabellaria alveolata* Linnæus. Drawn from life × 156. Age just over seven weeks after fertilisation. Actual length, from tip of snout (seen between the peduncles) to posterior flexure, approx. 780μ (see page 234).

PLATE IV.

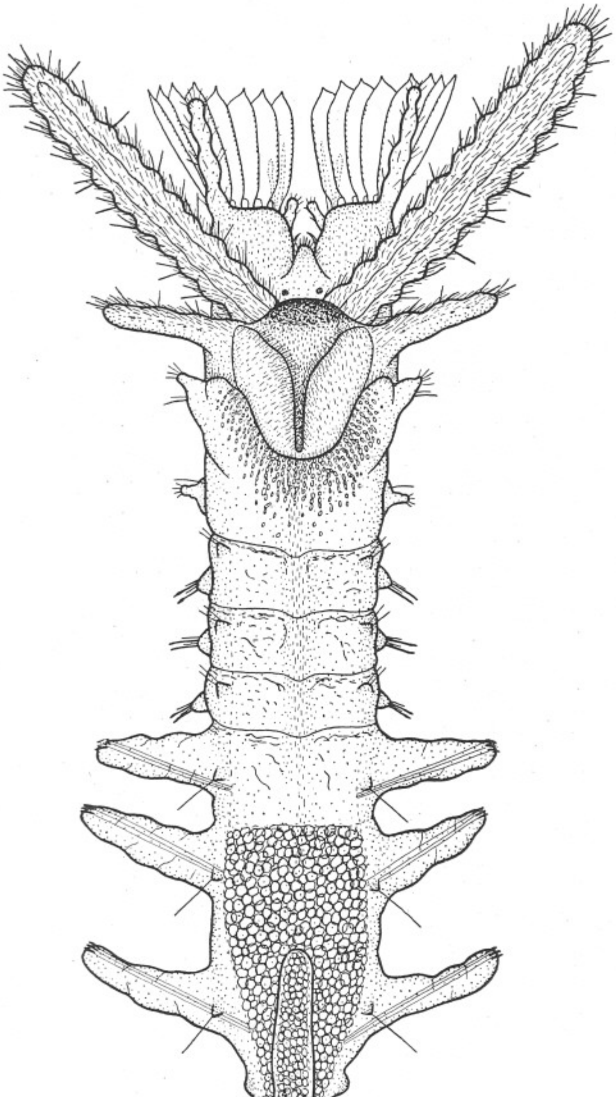

PLATE V.

Larvæ of *Sabellaria spinulosa* Leuckart. All drawings from life × 156. All measurements exclude apical cilia and bristles.

FIG. 1.—Free-swimming embryo 31 hours after fertilisation. Dorsal view. Actual length approx. 90μ (see page 239).

FIG. 2.—View of left side of the same embryo as shown in Fig. 1.

FIG. 3.—Embryo 55 hours after fertilisation. View of right side. Actual length approx. 90μ (see page 239).

FIG. 4.—Ventral view of the same embryo as shown in Fig. 3.

FIG. 5.—Larva just over four days old. Ventral view. Actual length approx. 90μ (see page 239).

FIG. 6.—Larva about three weeks old. Ventral view. Actual length approx. 180μ (see page 239).

FIG. 7.—Larva about two months old. View of right side. Actual length approx. 370μ (see page 239).

FIG. 8.—Ventral view of the same larva as shown in Fig. 7.

PLATE V.


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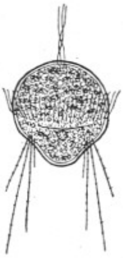
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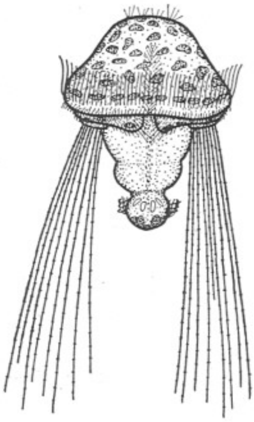
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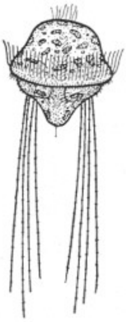
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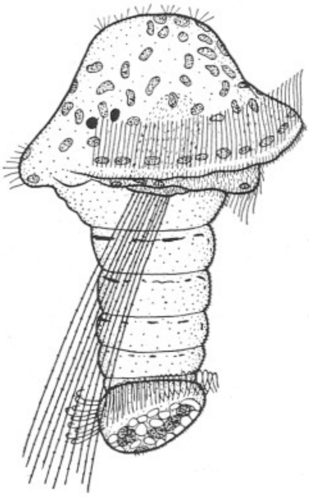
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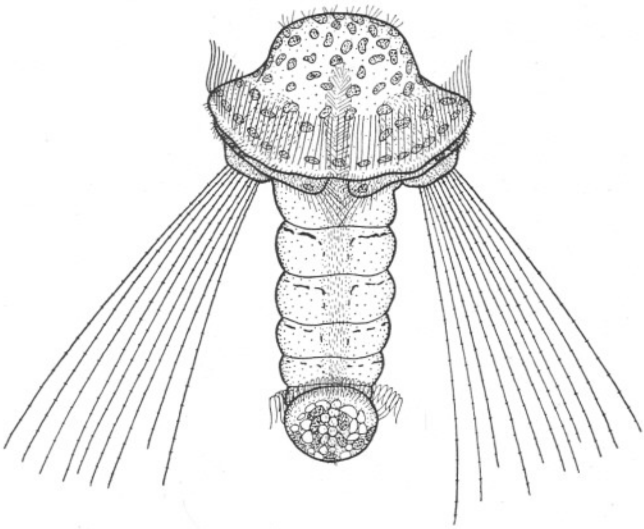
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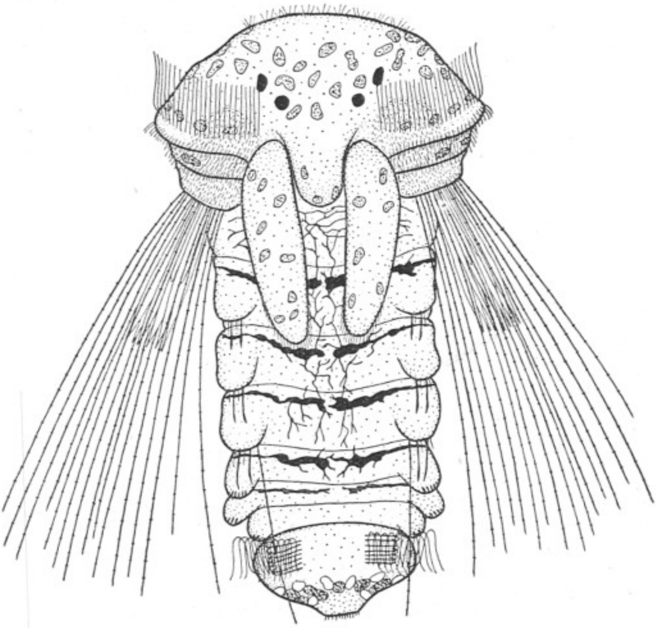
PLATE VI.

Larvæ of *Sabellaria spinulosa* Leuckart. Drawings from life × 156.

FIG. 1.—Larva about two months old. Dorsal view. Actual length approx. 500μ (see page 239).

FIG. 2.—Ventral view of head region of a metamorphosed early bottom stage (see page 240).



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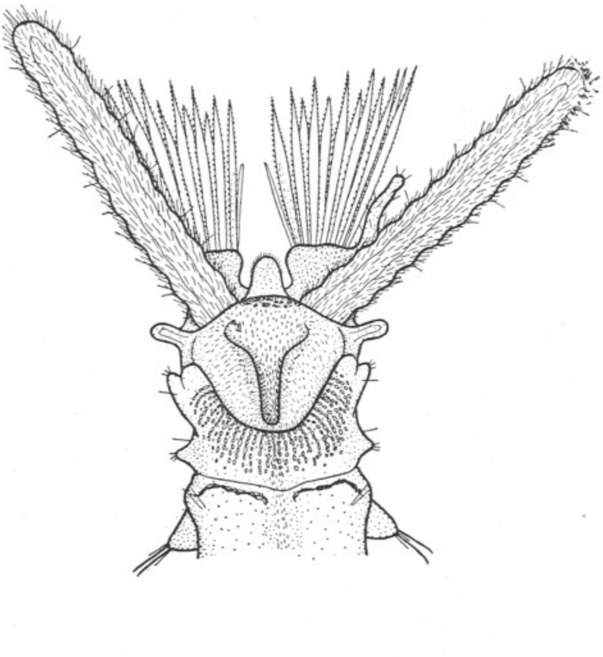

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PLATE VII.

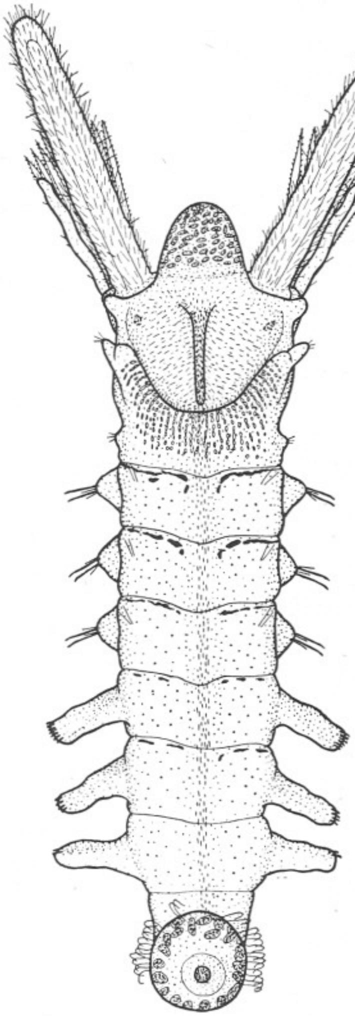
Larvæ of *Sabellaria spinulosa* Leuckart. Drawings from life × 156.

FIG. 1.—Ventral view of anterior end of a larva just commencing to metamorphose (see page 240).

FIG. 2.—Dorsal view of anterior end of metamorphosing larva about four months old (see page 240).

FIG. 3.—Ventral view of metamorphosing early bottom stage. The drawing is from a specimen picked out from the plankton before it was ready to metamorphose. A single specimen has been reared from the artificially fertilised egg as far as this stage with which it corresponded in every important particular. It was then nearly three and a half months old. Actual length (excluding tentacles) approx. 670μ (see page 240).

PLATE VII.



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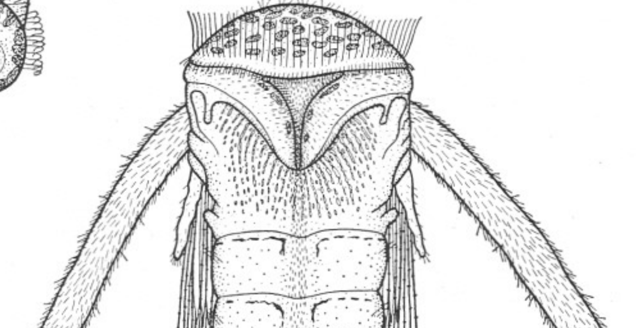

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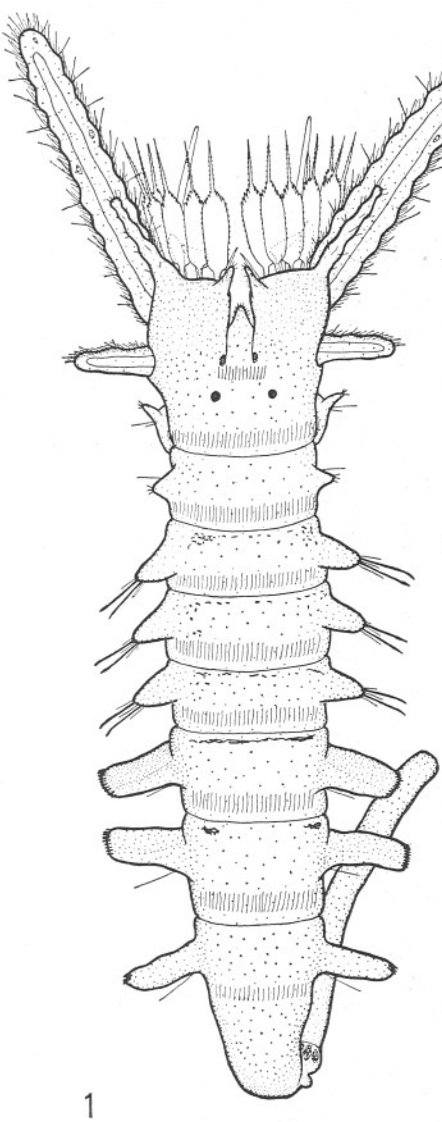
PLATE VIII.

Fig. 1.—Early bottom stage of *Sabellaria spinulosa* Leuckart. Dorsal view from life ×156. Actual length, from tip of snout (seen between the peduncles) to posterior flexure, approx. 665μ (see page 240).

Fig. 2.—Mucus and first sandy tube of early bottom stage of *Sabellaria alveolata* Linnæus ×39. Actual length of sandy portion about 1·9 mm. (see page 238).

PLATE VIII.



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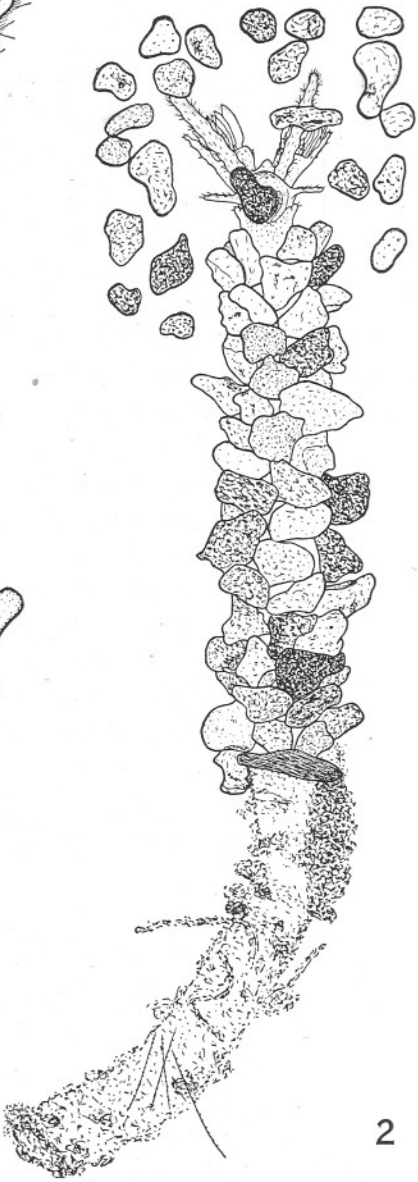

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PLATE IX.

All drawings, except Fig. 19, × 620.

A. Chætæ from larvæ and early bottom stages of *Sabellaria spinulosa* Leuckart.

Fig. 1.—One of the primary crown paleæ.

Fig. 2.—One of the secondary crown paleæ.

Figs. 3, 4 and 5.—Paleæ from one crown of the individual drawn in Fig. 1, Plate VIII.

Fig. 6.—Bristle from crown.

Fig. 7.—Bristle from crown.

Fig. 8.—Spear-shaped bristle from a parathoracic segment.

Fig. 9.—Slender bristle from a parathoracic segment.

Fig. 10.—Uncinus.

B. Chætæ from larvæ and early bottom stages of *Sabellaria alveolata* Linnæus.

Fig. 11.—Portion of ringed provisional bristle.

Fig. 12.—One of the primary crown paleæ.

Fig. 13.—Bristle from crown.

Fig. 14.—Bristle from crown.

Fig. 15.—Bristle from inner side of peduncle.

Fig. 16.—Spear-shaped bristle from a parathoracic segment.

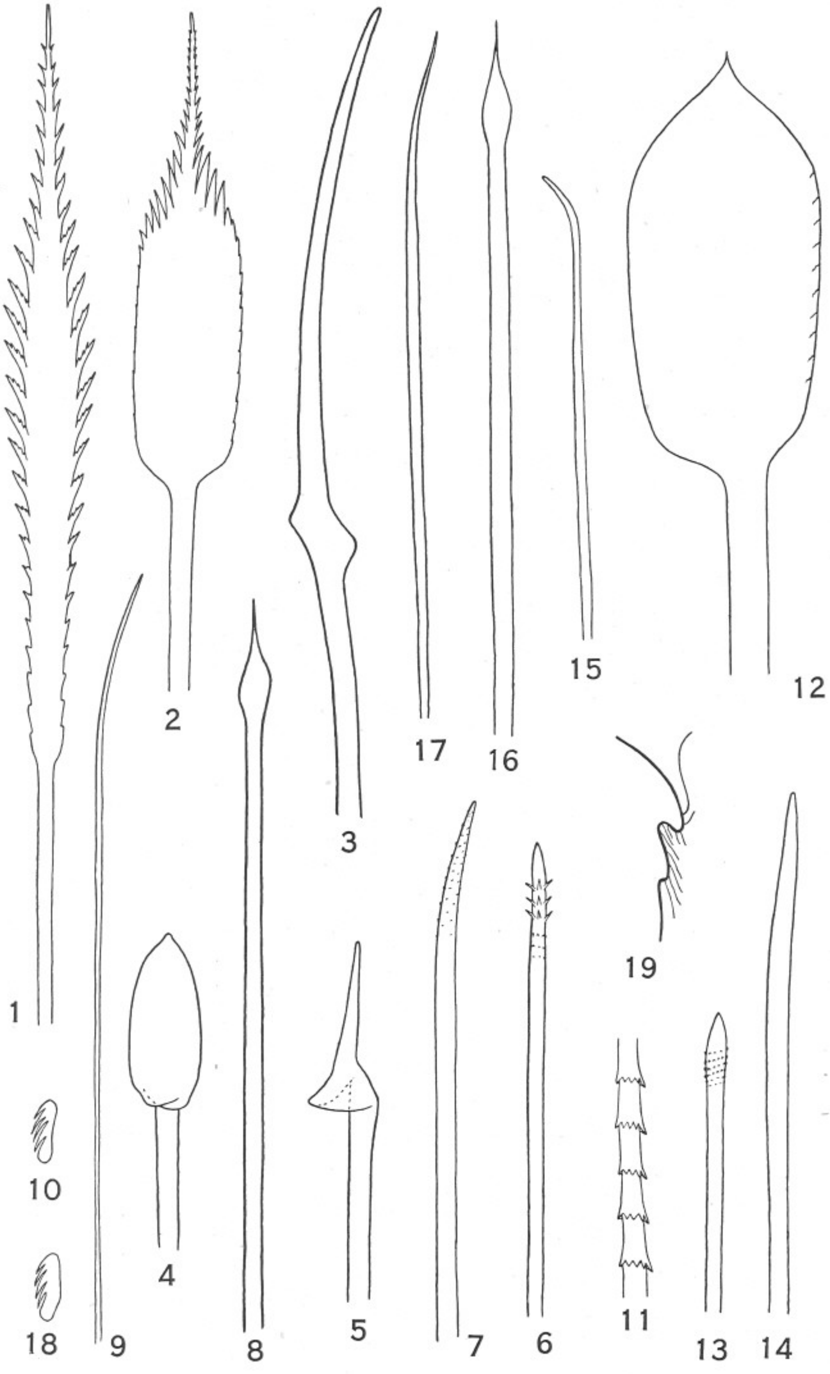
Fig. 17.—Slender bristle from a parathoracic segment.

Fig. 18.—Uncinus.

C. Hood and lip-fold of *Sabellaria alveolata* Linnæus.

Fig. 19.—Diagrammatic section through prototroch of an early larva to show roughly the extent of folding at the sides of the body.

PLATE IX.



On the Cœlomic Cilia and Circulation of the Body-Fluid in *Tomopteris helgolandica.*

By

Dr. Anton Meyer.

With 1 Figure in the Text.

A. INTRODUCTION.

THE œcological significance of cilia and ciliary currents has been studied hitherto mainly so far as they are connected either with the epidermis or with the intestine. Epidermal cilia produce currents by which either the animal itself is moved or the surrounding medium is carried over the surface of the unmoved animal. In the latter case the ciliary currents serve for collecting substances, ordinary food and oxygen. It may be said, that the degree of specialisation of epidermal cilia generally indicates the degree of intimate dependence of the animal on its outside conditions (natural surroundings). (The cases where epidermal cilia are connected with sense organs are comparatively few.)

Intestinal cilia have a more limited significance : they never serve for movement of the animal nor for sensory functions, but are probably restricted to aiding the absorption of chymus and of oxygen by moving the content of the intestine. Since the ciliated intestinal surfaces are neither fully exposed to the outside conditions nor completely closed from the latter, we may express their position as semi-inside or internal.

Besides the epidermal and entodermal layers there is a third layer which builds up the architecture of many classes of animals and which resembles the first two layers in its epithelial character and in the possession of an extensive free surface ; it is the cœlomic epithelium which surrounds the body cavity and is well developed in the Echinoderms, Chætognatha, Brachiopoda, Phoronidea, Bryozoa ectoprocta, Sipunculoidea, and Annelids. The cœlomic cavity indeed is thus the innermost part of these animals ; it is the place of sexual reproduction, and holding an intermediate position between the nutritive organs on the one side and the muscular body wall which produces waste products, it becomes connected with both nutrition and excretion. The sexual products and excretory matters are carried out through the segmental organs ; they represent a cœlomic derivative, the covering with cilia of which is well known. The remaining parts of the cœlomic epithelium, however, show, in many cases, also a covering with cilia, which may be called cœlomic cilia in the strict sense.

The cœlomic cilia have escaped observation for a long time, and with exception of the Brachiopoda (Morse, 1901[*]) they have in no case been made the subject of closer examination. As will be seen from the following, the cœlomic cilia may attain a high level of physiological differentiation which is expressed in the regular arrangement and distribution, in the constancy of the direction of the effective stroke of all cilia in a given area, and in the co-ordination of the directions in neighbouring areas. The result of these is a circulation of the cœlomic body fluid which includes more or less the complete body cavity.

Before describing the cœlomic cilia and circulatory currents in a special case, it may be well to establish the positions of cœlomic cilia in relation to the epidermal and intestinal cilia and their œcological significance in the following scheme :—

CILIATED EPITHELIA.

Position in the general architecture of lower animals.	Œcological significance.
I. Outside (external)	Moving the animal (locomotion). Moving the surrounding medium and collecting :— 1. Food (nutrition). 2. Oxygen (respiration).
II. Semi-inside (internal)	Moving the content of the intestine (nutrition, respiration).
III. Fully-inside (inside)	Moving and circulating the cœlomic body fluid (circulation, etc.).

Cœlomic cilia in the Annelids were first specially examined by myself in *Tomopteris helgolandica* (*catharina*) in 1926 and later in full detail in another species from the Mediterranean (*T. elegans*), and also in various other classes (Bryozoa ectoprocta, Chætognatha, Polynoids) 1927.[†] The species common in the North Sea and the Channel, *T. helgolandica*, is somewhat different from the Mediterranean species ; therefore a special examination of *T. helgolandica* seemed necessary.

A few words on the general structure may be in place.

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[*] Morse, E. S., 1901 : "Observations on Living Brachiopoda." Memoirs Boston Soc. of Nat. Hist., Vol. V.

[†] Die Segmentalorgane von *Tomopteris catharina* . . . ein Beitrag zur Theorie d. Segmentalorgane, Zeitschr. f. wiss. Zool., 1926.

Über Cölombewimperung u. cölomatische Kreislaufsysteme bei Wirbellosen, *ibid.*, 1927.

B. GENERAL REMARKS ON THE STRUCTURE OF TOMOPTERIS.

The Tomopterids are a family which is entirely restricted to pure planktonic life. Among the Annelid families they are a somewhat outstanding type ; in external appearance they are noteworthy for the elongated shape of the parapodia, the fin-shape and purely glandular character of the cirri, the absence of bristles in the segments behind the mouth, also for the great length of a pair of tentacular cirri, for their transparency, and in some cases for the presence of a caudal region (Fig. 1, A). The transparency is due to the entire absence of pigment cells and to the thinness of the muscular layer and absence of connective tissues. The caudal region is a body region which does not reach full development ; undoubtedly it is becoming vestigial and is in some species, e.g. *T. elegans*, fully suppressed and has phylogenetically disappeared.

The internal structure is noteworthy owing to the complete absence of transverse dissepiments. Another peculiarity is the absence of blood-vessels, which is connected with the reduced condition of retroperitoneal connective tissue and the conditions of planktonic life.

C. THE CŒLOMIC SYSTEM.

The cœlomic system includes the properties of the cœlom and the segmental organs.

The *cœlomic cavity* forms a continuous space on each side, both sides being separated by the dorsal and ventral mesentery of the gut ; the cavity of the trunk region communicates widely with the cavities of the parapodia and so it shows parapodial and interparapodial sections. The mesenteries are wanting in the pharyngeal region, and the cœlomic cavity extends here forwards into the basal region of the head tentacles.

The content of the cœlomic cavity consists mainly of the sexual products, which are easily seen floating after separation from the gonads ; the latter are situated in the cavities of the ventral and dorsal cirri of all segments behind the mouth. In the females a great number of oocytes become abortive and finally changed into numerous small plasmatic corpuscles. Those oocytes which develop into eggs are noteworthy through their considerable increase in size. True cœlomic corpuscles I have been unable to observe in *T. helgolandica* (but they are present in *T. planktonis* and *T. elegans*, although very rare). Statements of other authors, that there were a great number of true cœlomic corpuscles are wrong and are due to confusion with abortive oocytes or with spermatocytes.

It is also noteworthy that the secretion of the rosette-like organs (of both categories) is discharged into the cœlomic cavity and is phosphorescent there. The rosette-like organs (rosettes and hyaline glands) are of mesodermal origin. Those of the second category (=rosettes) are, in young stages, situated in the basal region of the first and second parapodium (only) and are metamorphosed cœlomostomes, still showing in one species, *T. mariana*, their connection with solenocytes and retaining their original position in the basal region, where in the posterior segments (from the 6th onwards) the typical cœlomostomes and solenocytes are situated.

The connection of the cœlomic cavity with the exterior is established through the segmental organs, consisting of a spherical group of solenocytes, a small cœlomostome and a "nephridial" canal; the lumen of the latter can be expanded and contracted. In the females two pairs of large cœlomostomes are developed in the 4th and 5th segments; they are situated in a position which is not homologous with that of the ordinary cœlomostomes and represent a second set of cœlomostomes which is developed *later* in ontogeny as well as in phylogeny; they represent therefore secondary gonoducts.

The *cœlomic cilia* (Fig. 1, A, B) are represented as long ciliary rows; they occur in the trunk and in the parapodial cavities and also in the cavities of the cirri and of the head tentacles. The cœlomic epithelial layer is so thin that no cell boundaries are present, the nuclei are rare. There is generally one nucleus in the neighbourhood of each ciliary row.* The ciliary rows are arranged transverse to the longitudinal axis of the trunk and of the parapodia respectively. In the parapodia they occur on the opposite sides ventral and dorsal, but the first a little approximated to the posterior wall and the second to the anterior wall. The number of both sets is almost equal and mostly 4 to 6. In the trunk region the ciliary rows are more numerous on the ventral side; they are restricted to the interparapodial regions of the trunk and their number is usually 4 to 6. In the caudal region they are much more numerous, about 6 to 10, and are situated closely one behind the other.

The direction of the effective beat is the same in all the cilia of one row and it is also the same in all rows of one side. On the opposite sides (ventral and dorsal) the direction is opposite. The result of this antagonism is that the current of the cœlomic fluid is of a circulatory nature.

The *current* of the cœlomic fluid (Fig. 1, C) runs forward on the ventral side of the trunk, on the dorsal side backwards; in the parapodia it runs on the dorsal side outwards, on the ventral side inwards. The circulation of the parapodia is not confined to the same segment, but the greater part of the fluid which arrives ventrally in the base of the parapodium *enters*

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* This can be made out with Fischer's solution of tannin-ferrous sulphate-alcohol fuchsin; it is necessary to let it act directly on the free cœlomic surface.

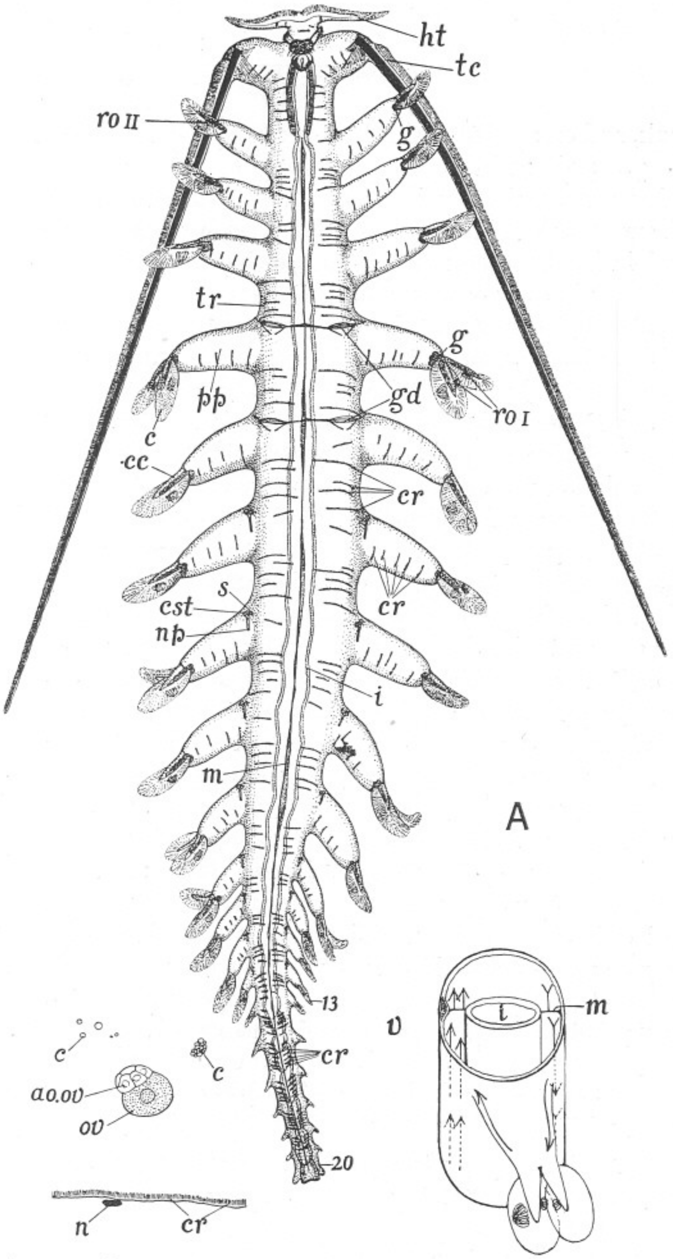

FIG. 1.—*Tomopteris helgolandica* ♀. (Watson Obj. 1, Oc. 2, working table. Reduced to one-half.) ht, head tentacles. tc, tentacular cirri (with a bristle). roI, rosette-like organs (phosphorescent) of first category (hyalin glands). roII, rosette-like organs (phosphorescent) of second category (rosettes). g, gonad. c, cirrus (=fin). cc, cirrus cavity. s, solenocytes. cst, cœlomostome. np, nephridiopore. gd, secondary gonoducts. cr, ciliary rows. i, intestine. m, mesentery. tr, trunk. pp, parapodium.

B, Content of the cœlomic fluid and ciliary row of *T. helgolandica* (Watson Obj. 3, Oc. 2, working table. Reduced to one-half.) c, corpuscles resulting from the abortive oocytes and also from the secretion of the rosette-like organs. ao. ov, abortive oocytes. ov, growing oocyte. cr, ciliary row with nucleus n.

C, scheme of the currents of the cœlomic fluid in *T. helgolandica* indicated by arrows. v, ventral. i, intestine. m, mesentery.

the trunk, and on the dorsal side fluid becomes drawn out from the trunk into the parapodium.

The directions of the circulation are more clear immediately above the ciliated surfaces than in the intermediate region, where the movement is slow and in its direction not constant, owing to the distance from the cilia and the viscosity of the fluid.

The cœlomic cilia in *T. helgolandica* are already present in young stages of nine parapodial segments* and the number of ciliary rows is almost fully established; but there also exists a small increase in the number during the progress of development and sexual maturity.

If we try to judge the general biological significance of cœlomic cilia and of the circulation produced by them we arrive at the following conclusions: (1) the cœlomic epithelium is phylogenetically of entero-cœlic (gono-cœlic) nature and therefore contains the possibility of development of cilia by inheritance from the cœlenteric ancestors; (2) cœlomic cilia are of œcological value especially in those animals where the blood-vessels are wanting and their functions are replaced by the cœlom; (3) the appearance of cœlomic cilia during individual life is not without connection with the development of the sexual products, and there exists also a relation of cœlomic cilia to the system of segmental organs which is clearly expressed in the addition of secondary components (secondary cœlomostomes and gonoducts) to the segmental organs; (4) the question whether in the primitive Annelid-ancestor circulation was carried out by cœlomic cilia or by true blood-vessels is not decided; until this question is solved from other arguments it remains undecided whether the occurrence of cœlomic cilia in the Annelids is a primitive (palingenetic) character or cenogenetic. From the physiological point of view it seems rather clear, that the occurrence of circulation by means of cœlomic cilia is more " primitive " than by means of contractile blood-vessels.

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* These stages are still provided with a pair of bristle-bearing appendages (in front of the tentacular cirri) which are usually lost later.

Observations on *Patella vulgata*. Part III. Habitat and Habits.

By

J. H. Orton, D.Sc.
(*Chief Naturalist at the Plymouth Laboratory*).

With 2 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE present contribution continues the account of studies on the common limpet, *Patella vulgata* (**1**, **2**), and forms an introduction to investigations on facts and causes of variation in shell-height, which are being continued and will be published later, and not as Part III of the series as originally intended. The cause of the variation in the shape of the shell in *P. vulgata* (**3**, **6**) has been—and continues to be—a subject of much interest to naturalists. There can be little doubt that the height of the shell varies at least roughly—but not in any simple manner—in correlation with the habitat (**5**), and that as the individual limpet rarely moves many feet away from its point of fixation (**6**, **7**, **8**, **9**) there must presumably be a close relation between certain factors in the habitat and the coexisting shape of the shell. It is therefore important in this regard to review the habits and to note and define carefully the habitats of this animal on the shore.

P. vulgata occurs on the Atlantic shores of Europe (**10**) between tide-marks. On the coasts of Devon and Cornwall the species (excluding for the present the doubtful species or variety, *athletica*) occurs mainly between a level about mean low water and one a little below the high-water spring-tide mark in the habitats and with the congeners shown in Table I, page 278.

TABLE I.

INTER-TIDAL HABITATS OF *PATELLA VULGATA* L., AND OF SOME ASSOCIATED ORGANISMS IN THE PLYMOUTH DISTRICT.

Splash-lines.	Height of tide in feet above or below Datum.		Patella habitats.	Littorina habitats.	Barnacle habitats.	Some Algal habitats.
	17—					
∿∿	16—15·7	M.H-W.S.	Patella rare	*Littorina neritoides* *L. rudis* rare		(A sp. of Lichen) Enteromorpha[1]
	15—					Enteromorpha[1]
∿∿	14—14·1	M.H-W.	Patella	*L. rudis*	Chthamalus rare	*Pelvetia canaliculata*
∿∿	13—				*Chthamalus stellatus*	*Fucus platycarpus*
	12—12·25	M.H-W.N.	Patella	*L. rudis*	*B. balanoides* rare	Enteromorpha
			Patella	*L. obtusata*	*B. balanoides*	Ascophyllum *F. vesiculosus*
	11—					
	10—		*athletica* form in pools	*L. littorea*		*F. serratus* Porphyra
	9—					
∿∿	8—8·15	M.T.L.	Patella	*L. littorea*	*B. balanoides*	*F. serratus*
	7—		*athletica* form in pools			
	6—					
∿∿	5—4·6	M.L-W.N.	Patella	*L. littorea*	*B. balanoides*	*F. serratus*
	4—				*B. perforatus*	
	3—					
∿∿	2—2·39	M.L-W.	Patella	*L. littorea*	*B. perforatus*	*F. serratus*
			Patella rare *athletica* form on rocks		*Verruca strœmia*	Gigartina Chondrus Himanthalia
	1—					
∿∿	0—0·18	M.L-W.S.	*Helcion pellucida* rare	*L. littorea* less common	*V. strœmia*	Laminaria, spp.
	-1—					
	-2—		*H. pellucida*			Laminaria, spp.

Notes to Table I.—The levels of the organisms associated with Patella are liable to vary, especially with the local splash-line, and in localities exposed to strong wave-action and strong sunshine. The data regarding tidal levels are for Devonport (see **11**, p. 370) :—

M.H-W.S. = mean high water spring tides.
M.H-W. = mean high water.
M.H-W.N. = mean high-water neap tides.
M.T.L. = mean tide level.
M.L-W.N. = mean low-water neap tides.
M.L-W. = mean low water.
M.L-W.S. = mean low-water spring tides.

[1] Where fresh water occurs.

THE DISTRIBUTION OF *PATELLA VULGATA* ON A CLIFF-BOUND, SUN-BAKED SHORE.

In studying the distribution of *P. vulgata* on the shore, it was found that at levels above high-water neaps, exposure to direct sunlight is a very important limiting factor. This effect of sunlight is easily observed by taking a rowing-boat at about the time of high water on a neap tide along a rocky or cliff-bound shore which faces mostly, or in parts, in a southerly direction. On the parts of the cliff exposed directly to the sun's rays it is seen that the limpets are distributed along and below the line *and splash-line* of high-water neaps. Where the water at H.W. neaps runs up angular depressions in the face of the rocks, limpets may be so thick as to outline the splash of the waves (herein denoted as the splash-line*) above the general mean high-water neap level, whereas elsewhere on the dry sun-baked area above this level limpets are absent or rare. Where the cliffs jut out so as to produce shade, or in caves, or on the shaded sides of rocks, limpets will be found above the level of H.W. neaps; that is, in most places where continuous direct sunlight can be avoided. Such is the distribution of limpets on the Wembury shore at the mouth of the River Yealm, near Plymouth, as seen in a calm sea on July 11th, 1928, at high water at 12.40 p.m. (S.T.), when the height of the predicted tide (**11**, p. 3) was 12 feet 7 inches above datum (mean high-water neaps at Devonport being 12·25 feet above datum, **11**, Part I, p. 344). The distribution of limpets on the cliffs near Perranporth, on the North Cornwall coast, shows similar limitations. The cliffs to the south of Perran sands face north to north-west and are sheltered from the sun during the greater part of the day, and are also in many places damp even on a summer day. On these cliffs limpets occur abundantly in most situations above high-water neaps, but on the northern part of the sands the cliffs face westerly and in 1928 were devoid of limpets above high-water neaps except for occasional small individuals hiding under the high-level seaweeds, Pelvetia, and a species of Fucus, probably *platycarpus*, which was zoning above *Ascophyllum nodosum*. On rocky shores which do not face south and yet receive a moderate amount of direct sunlight limpets may extend above high-water neaps, but in such cases they do not usually attain a large size unless they are living in a situation which is in some way maintained in a damp condition, e.g. proximity to a seepage of water. On most north-facing rocky shores—like that of Perranporth—it would appear that limpets are seldom absent above high-water neaps unless the shore be liable to be pounded with gravel or sand, or there is some other obvious deterrent.

Thus the distribution of the limpet on the shore indicates that although this animal can exist in localities which receive a certain amount of direct insolation, there is a limit beyond which existence cannot be maintained, whether the limiting cause be absence of food or direct insolation.

In the south-west of England where the low water of spring tides occurs round about midday (and midnight) (see Fig. 1, p. 281) limpets do not occur in dry places above high-water neaps which are exposed to direct sunlight during the whole, or a large portion, of the daily period

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* The splash-line is important at all tidal levels on sloping rocks or sloping beaches in apparently raising the level of a zone. I have seen Patella at least 6 feet above the general high-water spring-tide level in a cave at New Train Bay, N. Cornwall, where existence was made possible by the splash of the waves.

of duration of sunlight; but in more northern latitudes and other localities limpets may be able to exist on the southern faces of cliffs to a greater extent, especially in those situations where the *high water* of the spring tides occurs (see Fig. 2, p. 281) round about midday, e.g. south-east of England and neighbouring Continental coast, parts of northern Scotland, as at Invergordon (see Admiralty Tide-Tables, **11**, *passim*). In considering the habitats and habits of the common limpet, it is certain that the geographical orientation of the rocks comprising the habitat, the latitude of the locality, and the epoch of the day when the limpets are exposed during the spring tides, are all important factors, which if not considered might give rise to great confusion, but which when carefully noted may render concordant many apparent inconsistencies and many apparently opposed statements.

Fig. 1. Conspectus of the tidal changes in the Devon and Cornwall area, shown by a semi-diagrammatic chart of the semi-diurnal tides during a semi-lunar cycle. The time and duration of the exposure of the foreshore at different levels is also shown approximately.

(Data from Admiralty Tide-Tables, Part 1, 1929, from which are plotted the predicted times and heights (in feet) for high and low water for the tides at Devonport from April 7th to April 22nd).

Each small circle denotes the height and time of the tide at low or high water on the date given by the small figure adjacent to the circle. The courses of representative tides only are plotted: (after **11**, II, Table 4), e.g.:—the spring tide on April 12th (thick-line curve); the neap tide on April 18th (thin-line curve), and two intermediate tides on April 8th and 15th respectively (broken-line curves). The large circles give the seasonal maximum and minimum possible daily range of sunshine. The references to different tidal levels, M.H-W.S., etc. have the same meaning as in Table I, p. 278.

M.H-W. (=mean high water) and M.L-W. (=mean low water) occur midway between M.H-W.S. and M.H-W.N., and M.L-W.N. and M.L-W.S. respectively. These are important biological levels, but are not given in Admiralty Tide-Tables.

The heights of high or low water—with reference to the chart datum (which is only 0·18 foot above mean low-water springs)—are plotted as ordinates in feet, while times of day (G.M.T.) at which high or low water occurs are plotted as abscissæ. The cycle of tides shown in the diagram is repeated at essentially the same times and with slight modification in height throughout the year. Around the period of the equinoxes, March and September, the rise of tide during spring tides is higher and the fall lower than at other times: in winter, the morning high spring tides are higher and the succeeding low tides lower than the night tides, whilst the contrary is the case in summer. In the lunar cycle the greater spring tides occur after full moon in winter, but after new moon in summer. With reference to mean tide-level, in this district neap tides rise on the average higher than they fall, but spring tides fall lower than they rise on the average.

The time of high water on the same day varies slightly in Devon and Cornwall, being about one hour earlier in the extreme west (Land's End) than at Devonport, decreasing along the south coast to Devonport,

FIG. 1. DEVONPORT

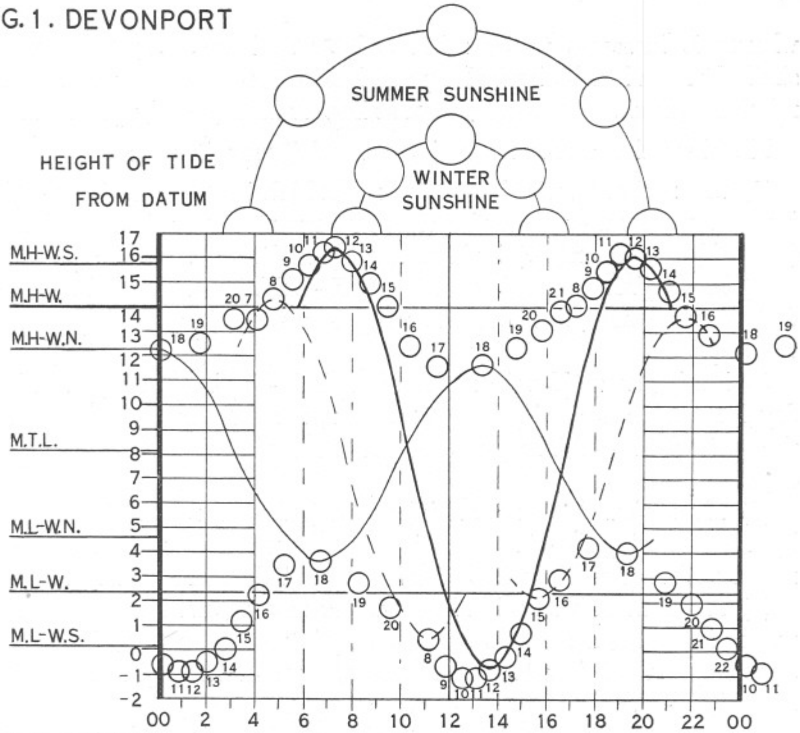
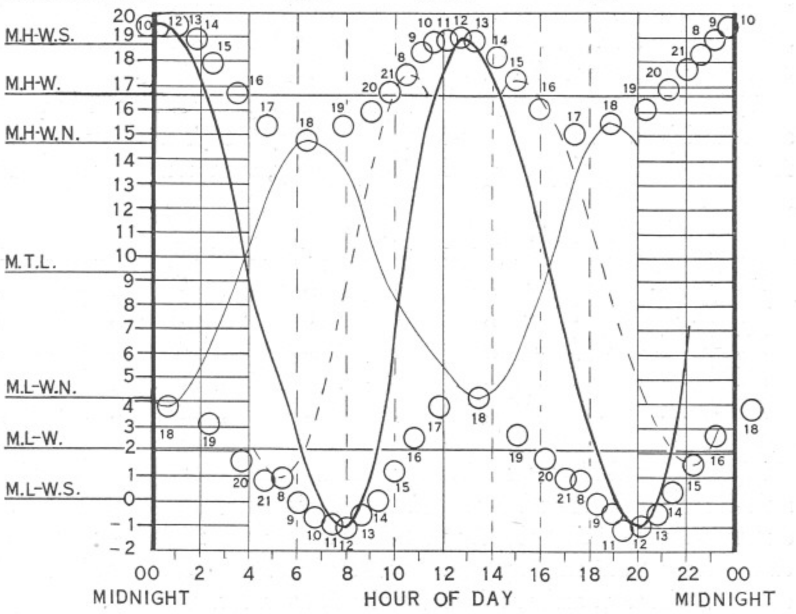


FIG. 2. DOVER



NOTE.—Height of tide from datum is given in feet.

whence it increases to 35 minutes later at Exmouth; it decreases similarly from Land's End along the North Cornwall coast to about 2 minutes earlier at Ilfracombe than at Devonport. (**11**, II, pp. 32 and 54.)

The chart shows that in the Devon and Cornwall area :—

(1) The region on the shore *above* mean high-water neaps (M.H-W.N.) is uncovered by the tide during the greater part of the middle of the day (and middle of the night) during *every* day of the year.

(2) The region on the shore below M.H-W.N. is uncovered by the sea during spring tides, but covered during neap tides, in the *middle* part of the day.

(3) During neap tides the region above M.H-W.N. may remain entirely dry for one or more tides, or in summer, for one or more days, while that below M.L-W.N. may remain covered during one or more tides or days.

(4) The region above mean high water (M.H-W.) may not be covered by the sea during about 7 days and that below mean low water (M. L-W.) may remain covered by the sea during about 7 days in a semi-lunar cycle.

(5) The time of immersion in sea-water of a region above mean high water varies from about 3 hours at spring tides to a slight wetting according to the height of the tide on any day and the height of the region above M.H-W.

(6) The time of exposure of a region of the shore below mean low water (M.L-W.) varies from about 3 hours to momentary exposure according to the height of the tide (above or below datum) and the level of the region below M.L-W.

(7) During the period of the higher tides (i.e., those rising to and above M.H-W. and including the spring tides) the different levels on the foreshore are exposed in the middle of the day, approximately and on the average, as follows :—

M.H-W.	11 to $9\frac{1}{2}$	hours	ranging	between	about	5	and	20·30	hrs.
M.H-W.N.	$9\frac{1}{2}$ to $8\frac{1}{4}$	,,	,,	,,	,,	6	,,	19·30	,,
M.T.L.	ca $6\frac{3}{4}$ to $6\frac{1}{2}$	,,	,,	,,	,,	7·30	,,	18·30	,,
M.L-W.N.	ca $4\frac{3}{4}$ to 4	,,	,,	,,	,,	8·30	,,	17·15	,,
M.L-W.	$3\frac{1}{2}$ to 1	,,	,,	,,	,,	9·30	,,	16·0	,,
M.L-W.S.	2 to 0	,,	,,	,,	,,	11·30	,,	15·0	,,

Fig. 2. Semi-diagrammatic chart of the semi-diurnal tides during a semi-lunar cycle showing the times of exposure of the foreshore at different levels during the daytime in localities where high-water spring tides occur about midday, e.g. south-east of England and neighbouring continental coast, and northern Scotland, as at Invergordon.

(From Admiralty Tide Tables, Part I, 1929, from which are plotted the predicted times and heights of high and low water at Dover from April 8th to April 21st.)

Fig. 2 shows that in any locality where high-water spring tides occur at about midday the high-water foreshore is necessarily protected during the period of the higher tides from direct exposure to air and sunshine during the hottest part of the day. In the period of neap tides the foreshore down to M.L-W.N. is exposed during the middle of the day. The region about mean low-water springs is only exposed to air and sunshine about 6 to 9 a.m. and 6 to 9 p.m., and in general the exposure conditions to extremes of temperature and insolation are much less severe than in such a region as is shown in Fig. 1.

In Fig. 1, page 281, it is shown that in the area of Devon and Cornwall (and similar tidal localities) the region above high-water neap-tide level is always exposed in the middle of the day to the air, and therefore also in certain situations also to the sun's rays. Thus, where limpets are present on the shore below and up to the level of high-water neaps, and also present in shaded places immediately above this level, while at the same time they are absent in the same locality from intermediate areas above high-water neaps which are exposed to direct sunlight, it is manifest that direct sunlight in these situations is in some manner a limiting factor in the distribution. Since, however, the limpet can exist above high-water neaps in places subject to a certain amount of direct insolation, it is also clear that this animal may be able to exist above high-water neaps at different levels on different shores, according to the duration and intensity of the incident direct insolation in different areas.

The distribution of limpets above high-water neaps indeed shows that individuals can withstand strong direct insolation for a short period, and a less strong direct insolation for a longer period, and also that resistance varies to some extent with the size of the animal (when thickness of the shell is doubtless an important factor). The absence of limpets from strongly insolated areas above high-water neaps may, however, be due either to absence of encrusting (e.g. algal) food, or to the direct effect on the animal of the sun's rays, or both of these factors. In this regard the occurrence of abundance of limpets on the high-water neap-tide line and their absence above this level in a strongly insolated area indicates that the higher level is untenable as a habitat, and that prolonged direct insolation may be as effective a limiting cause as absence of encrusting algal food. Such food is, however, apparently absent from many (shaded) situations at high water where limpets are abundant and apparently flourishing (**8**, **10**, and self), and apart from the possibility of the limpets making long feeding excursions when covered by the tide the mode of feeding in such habitats is not known. There are indeed grounds for suspecting that Patella may obtain food in other ways than in browsing on rocks. This animal will eat calcareous sand and detritus (H.-W. Looe Is.), and in aquaria I have known it eat putty and red lead, as shown by the fæces, but I have not yet detected any method of feeding whereby plankton is utilised as food. Thus the absence of encrusting algal food in any area cannot at present be regarded in itself as a certain limitation of such a habitat for the limpet.

The spat of limpets—ranging in length from 2 to 8 mm.—have been specially searched for above and below high-water neaps, but even in the latter zone tiny individuals of this size are rarely found except in very damp places, e.g. crevices or small pools. If therefore such spat settled in very dry sunny places, it is fairly certain that they would die from desiccation before succumbing to starvation. Thus, in accounting for the absence of adult limpets in strongly insolated areas of the shore above high-water neaps, it is necessary to allow some value to the fact of relative scarcity of encrusting food, though the direct effect on the animal of the actual intensity and duration of direct sunlight would appear to be the main limiting factor.

The Movements of Patella in Relation to Habitat and Climatic Conditions.

Russell (**5**, p. 856) has shown that there is no agreement among the many observers on the time that the limpet leaves its home in search of food; for example, "Lukis, Jeffreys, and Robertson state that the limpet wanders when covered by the tide; Davis and Fischer that it wanders while uncovered, and Fischer that young ones wander only when covered; Bouchard-Chanteraux that it makes excursions just after the tide goes out; Lloyd Morgan that it wanders chiefly as the tide leaves it and as the tide returns; Lloyd Morgan and Roberts are of the opinion that it does not move about when submerged." Loppens (**9**) found exposed limpets on the move between Ladram Bay and Sidmouth, but never on the beaches near Exmouth. Russell found in his experiments that limpets above 20 mm. or so in length did not wander when uncovered by the tide, but that smaller ones may wander at any time, and concluded that a habit of fixity becomes established only when the shell has attained a length of 10–15 mm., and that they wander chiefly when covered by the tide. The present writer has seen limpets of all sizes on the move away from their "homes" at high and low-tide levels at some time or other. At high water in damp situations or in situations not exposed to direct sunlight some individuals can usually be found creeping and feeding away from the home, but in dry situations at high water which are exposed to sunlight the animals are rarely seen on the move except in damp or wet weather. Small to medium-sized individuals may be seen moving on the shaded side of rocks at various tidal levels even in warm sunny weather, as may also large individuals under seaweeds near low-water mark, but limpets are very rarely seen moving when exposed to direct sunlight, while probably everyone can form a mental picture of immobile Patella at or near high-water mark in sunny warm weather.

Thus the factors controlling the feeding movements of the limpet when uncovered by sea-water appear to be mainly those which contribute to the risk or absence of risk of desiccation, and there can be no doubt that the main feeding excursions are made in all habitats when the animals are covered by water. By rowing alongside rocks covered with limpets, especially when the tide is rising at about the time of high-water neaps, it is easy in calm weather to see that the animals begin to move away from their scars very soon after immersion, just as Wells found for Acmæa and Lottia (**13**).

It is now a well-established fact that a majority of the medium to large-sized individuals return to a definite position in space after undertaking feeding excursions (see Russell, **5**; Pieron, **7**; Loppens, **9**, and Orton **8**, and **2**); but this general statement requires qualification. I agree with Loppens (**9**) that sometimes individuals do not return to the same place, and that evidence of this can sometimes be found in the lines of growth on the shell. Loppens states : " En effet, si la place ne convient plus, soit que la nourriture y manque, soit que la roche s'est trop effritée, ou pour n'importe laquelle raison, le mollusque cherche une autre résidence et ne revient plus à la première. On remarque cependant que beaucoup d'individus résident longtemps à la même place si elle est convenable. Patella peut, en effet, circuler dans un rayon de 2 mètres pour chercher la nourriture et retrouver aisément sa place sur les rochers." It is probable that Patella changes its " home " more often on a smooth and wet surface than on an uneven surface, while at the same time it is undoubtedly true that the bulk of the individuals retain the same scar for long periods in most habitats where the surface of attachment is uneven. On Padstow Dock vertical walls, which have a somewhat rough though uniformly plane surface, I found one limpet six feet above high-water neaps, carrying empty barnacle shells, which had undoubtedly grown below high-water neaps. On such a uniform surface it is probable that a limpet shell will fit fairly well at many places, and the necessity for homing is not so imperative as on more uneven surfaces. Lloyd Morgan's experiments (**12**) also show that a change of site is possible under natural conditions.

In some high-water situations adult individuals occur where younger ones could apparently not exist ; for in such situations small individuals (less than 25 mm.) can only be found in crevices or under weeds (*Pelvetia canaliculata* and *Fucus platycarpus*) where some protection from direct solar rays and drought is obtained. In these habitats, therefore, the older individuals must have moved into their final positions after attaining a medium size. In a broad consideration of the movements of Patella, it is manifest that the bulk of the larger individuals retain a definite position or home for long periods, and that the changing of the site is unusual for medium to large individuals in most habitats, but may occur more frequently in others, e.g., on smooth and wet surfaces.

The foregoing studies have therefore shown that the period of exposure of the foreshore to direct solar rays, and other conditions conducive to desiccation, as well as relative dampness of a locality, are all very important factors in determining the viable habitats and habits of the common limpet.

REMARKS ON THE FORM *Patella athletica* F. and H., or *P. vulgata*, var. *depressa* Jeffreys.

The experienced conchologists Forbes and Hanley (**10**) arrived at the conclusion, apparently however with some doubt, that the form *athletica* is sufficiently distinct from other varieties of limpets to be entitled to specific distinction. A little later Jeffreys (**3**), also an experienced conchologist, reduced the status of this form to that of a variety of the common limpet, *Patella vulgata* L., as var. 4, *depressa*. In referring to this form, Jeffreys states : " I once considered myself an adept at picking out the variety *depressa* (or ' China limpet,' as it has been called), by merely seeing the outside ; but I have since failed, and a recent examination and comparison of a great many living individuals of each form has quite convinced me that they are not separate species." In most accounts of the habitat it is stated that the form *athletica* occurs at low water ; for example, Clark, quoted in Forbes and Hanley, states : " They inhabit different levels, the *vulgata* being always in the higher zone." This latter statement is not quite accurate, the form *athletica* occurs in permanent pools (**1**, p. 860) at all levels up to high-water neaps, but also out of pools at low-water mark in some localities on the Devon and Cornwall coast and elsewhere. It has also been shown that the proportion of females with green gonads in this form was greater (in one sample) than in adjacent typical *vulgata*, nevertheless brown and green gonads occur among the females in both types (*loc. cit.*). The range of variation in all the characters of *P. vulgata* is, however, very great ; Jeffreys records that Spence Bate found the lingual ribbon broader and shorter, and the teeth perhaps somewhat larger in *athletica* (≡*depressa*) than in the common type, but the main differences so far found between these forms occur (1) in the habitat, and (2) the nature of the internal calcareous lining of the shell. With regard to habitat the form *athletica* is continuously or almost continuously immersed in water in contrast with *vulgata*, which experiences in most situations relatively long periods of exposure to the air. The lining of the shell in the former is white and entirely porcellanous, with often an orange coloration in the spatula or apical region, while *vulgata* has a greyish brown nacreous lining with a chalky-white or vitreous greyish white spatula, which may attain a great thickness (e.g., 10·1 mm.) in some high-water habitats.

The correlation between habitat and the quality of the lining of the shell suggests that the shell-differences observed may be physiological, that is, due to the nature of the environment, and therefore not genetic, i.e., specific. Thus it is possible that young limpets developing entirely in pools, or under water, may deposit porcellanous nacreous material on the inside of the shell, while others *of the same brood* developing on rocks exposed to air and light may deposit greyish brown nacreous material and a chalky or vitreous thickening at the apex of the shell. Until this problem is solved, or until some other distinct differential specific character is found in *athletica*, it would seem that there is insufficient ground for regarding the form *athletica* other than a variety of *P. vulgata* L.

At a recent meeting of the Challenger Society with Representatives of British Marine Laboratories, G. C. Robson, who has paid much attention to *P. athletica* F. and H., suggested that this form in its relation to types of *P. vulgata* would provide excellent material for a study in evolution. It is hoped that the foregoing observations may form a nucleus in the development of such a study.

SUMMARY.

The inter-tidal habitats of the common limpet, *Patella vulgata* L., have been investigated in relation to constant lunar tidal levels and tidal zones. The habitats of some common shore organisms which occur at approximately definite tidal levels or zones—and can therefore be used with discretion for zoning the habitats of Patella—are shown in a chart.

A study of the distribution of the common limpet on the shores of Devon and Cornwall has shown that limpets are absent or rare on those parts of the foreshore above high-water neaps which are subjected to prolonged periods of direct insolation. In the same locality limpets may be totally absent from the high-water region on cliff-faces or rocks facing southerly, but present on adjacent ones facing northerly or north-westerly. Strongly insolated habitats appear to be unviable as a result of the direct effect of the insolation on the animal, but the apparent deficiency of food in such habitats is probably also a limiting factor of importance.

The importance of the *splash-line* of any tidal level is emphasised. It is shown that in Devon and Cornwall the occurrence of *low-water* spring tides at about midday (and midnight) results in exposing to strong sunshine (and correlated factors) those regions of the shore above high-water

neaps which face in a southerly direction. In other localities where *high-water* spring tides occur about midday, equivalent regions of the foreshore are not so strongly nor so persistently insolated as in the former.

Viable habitats may therefore occur in different regions on the shore in different localities or at different latitudes according to the local orientation of the substratum and local tidal phenomena.

The tendency of the common limpet to wander when uncovered by the tide was found to be greatly influenced by those factors in the environment which do or do not incur risk of the animal being dried up. Wandering may occur at any level of the exposed shore in damp or shaded environments, but rarely at any level in the absence of protection from strong sunshine, hence many apparently conflicting statements on this subject may be reconciled. It is considered that the main feeding excursions or operations occur in all habitats when the animal is covered by the tide. It is shown that the habits and viable habitats of the common limpet are determined in a significant manner by factors representing the period of exposure of the foreshore to direct solar rays, other conditions conducive to desiccation, and the relative dampness to the environment. The characters of the doubtful species, *P. athletica* F. and H., are discussed briefly. It is noticed that this form differs from *vulgata* mainly in habitat and the quality of the lining of the shell, and it is suggested that the shell-quality may be a particular physiological product resulting from the special environment, and not to a genetic—and specific—factor.

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On the Occurrence of *Echinus esculentus* on the Foreshore in the British Isles.

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CONTENTS.

RECORDS AND SIGNIFICANCE OF OCCURRENCE ON THE FORESHORE.

ECHINUS ESCULENTUS, the larger common sea-urchin, occurs in the British Isles between tide-marks on rocky shores at about low-water spring-tide level in the localities given in Table I, page 292. It is, however, absent from apparently suitable foreshores in the Plymouth district, for reasons which are discussed in the present paper. Chadwick (**1**) states that " In Port Erin Bay it may be collected by hand on the beach, and on the ruined breakwater at low water of spring tides." Elmhirst (**2**) records that " In this district (Millport) *E. esculentus* occurs abundantly between tide-marks in spring and early summer on rocky coasts ; a few may be found at almost any other season. About February or early March a shoreward migration seems to set in, so that in suitable weather conditions some hundreds may be collected at springs between April and June. Then their abundance decreases until about November, from when until January it is at a minimum."

Storrow (**3**) reports that these " sea-urchins were plentiful on the local rocks (at Cullercoats, Northumberland) during July of last year (1920)," and it is known that *E. esculentus* is collected at low water by the Leeds University Biology Classes at Robin Hood's Bay, Yorkshire. Miss Trewavas (**4**) collected 5 specimens of *E. esculentus* near low-water mark during two equinoctial spring tides at Mousehole and an adjacent island on the south Cornwall coast, and states that " It should be mentioned that both these shores are sheltered on the west by the mainland, while the island acts as a breakwater on the east. This sheltered position may be connected with the occurrence of *E. esculentus* above low-tide mark in this locality," and further suggests that "either the climatic conditions of Cornwall or the Cornish seas, as contrasted with those of the Isle of Man, are unsuitable to the occurrence of 'zarts' (*E. esculentus*) in the tidal zone; or the general climatic conditions are suitable and, except in the case of Mousehole, local conditions are unfavourable." In this locality the fishermen report that "zarts" are often found exposed at low water, but elsewhere in Devon and Cornwall no records of the occurrence of the larger common sea-urchin on the foreshore are known, except a reference by Cocks (**5**) in 1849 to the finding of a young specimen of *E. sphæra* (almost certainly=*E. esculentus*) attached to stones at low-water mark in the Falmouth locality.

E. esculentus does not occur on the well-known rocky foreshores in the Plymouth district (**6**), and I have not seen it on rocky shores at low-water spring tides in frequent visits to Looe mainland and Island at all times of the year; in occasional visits to the Falmouth district (July); to Gribben Head (Sept.); to Widemouth Bay, Bude (April and Sept.); to Crackington Haven (Sept.); to Croyde Bay (Oct.); to Morwenstow (Marsland, Sept.). Nor did I find it at Sennen Cove (April), where the fishermen report that large "sea-eggs" (*E. esculentus*) may sometimes be obtained from a boat at low-water spring tides. At all these localities, however, *Parechinus miliaris* (=*Echinus*) were discovered hiding under stones or in crevices.

E. esculentus probably occurs on rocky foreshores in other less well-known localities, especially in Scotland and Ireland, and Dr. Marie V. Lebour informs me that she collected when a schoolgirl large sea-urchins —almost certainly *E. esculentus*—at Kyle Akin, in the Isle of Skye, Scotland. The absence of the species from apparently suitable and much-worked rocky shores in the Plymouth district, and in Devon and Cornwall generally, is noteworthy, and challenges explanation.

Offshore it is known (**7**) that *E. esculentus* occurs all around the British Isles down to depths of about 50 fathoms usually, but sometimes also in deeper water.

The fact that *E. esculentus* occurs off the coast all around the British Isles renders it virtually certain that the post-larval stages will be washed on to most shores from off-shore situations at some time, and would establish themselves in any localities where conditions were favourable. In the Plymouth district this species occurs in 5 to 10 fathoms close in-shore (e.g. off the Mewstone and Revelstoke Point) and has never been recorded (except as flotsam) on the adjacent rocky collecting-grounds in this locality. The existence of adult individuals so close to the shore on this part of the Devon coast makes it highly probable that the post-larvæ will be fairly frequently cast on the shore, as indeed are those of *P. miliaris.*

It is therefore a reasonable inference that the post-larvæ and the young of *E. esculentus* cannot exist on the foreshore in this locality. In a similar way it may be deduced that the general conditions are unfavourable on other rocky shores, which are apparently suitable habitats, but are constantly devoid of this sea-urchin. The general distribution of *E. esculentus*, however, indicates that this Echinoid is essentially a demersal form. Its occurrence on the foreshore may be regarded, therefore, as due either to highly favourable local conditions, which may produce a habitat suitable for both adults and young during the greater part of the year, or the habitat may only be suitable for a temporary shoreward migration at a certain part of the year. The sporadic occurrence of *E. esculentus* on the shore on some parts of the coast (**3**) indicates that this species tends to migrate shorewards, as Elmhirst noticed at Millport (**2**), at certain seasons.

Discussion on some Factors Determining Foreshore Distribution.

In reviewing the localities where *E. esculentus* occurs on the shore it would appear that some fundamental difference occurs in the general environmental conditions at Plymouth in comparison with those especially at Millport and Port Erin, for in the former locality occur protected rocky shores apparently suitable for but devoid of *E. esculentus*, and in the two latter *E. esculentus* thrives in the region of ordinary low-water springs.

In a comparison of the general conditions in the localities in the British Isles where this sea-urchin does and does not occur in apparently suitable habitats above low-water springs, one broad correlation of importance may be discerned, namely, connected with the time of day of low-water spring tides, but this requires to be considered in relation to other factors.

The chief factors contributing to the presence or absence of *E. esculentus* on the shore appear to be :—

1. The periods of the day when low-water spring tides occur.
2. The latitude of the locality.
3. The nature of the foreshore and its degree of exposure to wave-action.
4. The general seasonal hydrographic conditions in the locality.
5. The nature of the substratal approach to the foreshore from deeper water.

Time of Low-water Spring Tides.

It has been shown in a preceding paper in this *Journal* (**8**, p. 277, herein) that low-water spring tides occur on the Devon and Cornish coasts at about and just after 1 a.m. and 1 p.m. (**8**, Fig. 1, p. 281). As a result of this local tidal phenomenon the region about low-water spring-tide level is exposed to air and sunshine in nearly the hottest part of the day, and to air in a very cold part of the night. On the other hand, at Millport and Port Erin, low waters in the spring tides occur in the early morning and in the late afternoon or early evening at about the same times as at Dover (see **8**, Fig. 2, p. 281). There is thus a marked difference in the temperature conditions on the shore at the time of low water at Plymouth as against those either at Millport or Port Erin, and these differences will be accentuated by the difference in latitude.

The variation in the time of high-water spring tides on the coasts of the British Isles is especially well shown in a figure by Jenkins (**9**, Fig. 21, p. 126), while the actual (predicted) times of high and low water in particular localities are given in Admiralty Tide Tables (**10**), Parts I and II. The standard high and low tides in any locality are those which occur immediately after the moon, at full or at the change (i.e. new), has crossed the meridian (H.W. F. and C. and L.W. F. and C.), but these are not the highest or the lowest tides. The highest and lowest tides occur one to two hours later in the day than those immediately following the full and the change of the moon (see **11**, Figs. 41–43, and **8**, Figs. 1 and 2). Thus at Devonport the time of H.W. F. and C. is 5.32 (**10**, II, p. 32), but the highest tides occur about, i.e., before and after, 7 a.m. and 7 p.m. (or 19 hours), and the lowest round about 1 hour and 13 hours (see **8**, Fig. 1, p. 281).

The epochs of the day and night, before and after which high- and low-water spring tides occur in the various localities where *E. esculentus* is found on the foreshore—including Kyle Akin—are shown approximately in the following table :—

TABLE I.

CORRELATION OF THE MEAN TIME OF LOW-WATER SPRING TIDES AND THE OCCURRENCE OF *E. ESCULENTUS* ON THE FORESHORE.

No.	Locality.	H.W. F. & C.	Approx. mean time of day of H.W. springs.		Approx. mean time of day of L.W. springs.		Lat. N. ° ′	Occurrence of *E. esculentus* on the foreshore.
1.	Plymouth District and N. Cornish Coast (Devonport)	5.32	7.0	19.0	1.15	13.15	50 22	Absent.
2.	Mousehole (Penzance)	4.35	6.0	18.0	0.15	12.15	50 07	Occasional at L.W. equin. springs.
3.	Robin Hood's Bay (and Cullercoats) (Whitby)	3.45	5.15	17.15	11.30	23.30	54 29	Present ca. L.W. equin. springs.
4.	Isle of Man (S.) (Port St. Mary)	11.10	0.40	12.40	7.0	19.0	54 04	Present L.W. ord. springs.
5.	Millport, Scotland	11.50	1.20	13.20	6.30*	18.30	55 45	Ditto.
6.	Kyle Akin, Isle of Skye	6.16	7.45	19.45	2.0	14.0	57 16	Ditto.†

* The interval between H.W. and L.W. springs varies from 5¼ to 5½ hours at the Standard port, Greenock.

† Dr. Lebour's record from memory, see p. 290.

A review of Table I shows that where *E. esculentus* is easily obtained at low water on ordinary spring tides, localities 4 and 5, the time of low water falls in the early morning and late afternoon. If, however, Kyle Akin proves to be a locality where the sea-urchins are also normally easily obtained, it is seen that the time of low water in this locality is, on the contrary, in the hottest part of the day, and approaching the coldest part of the night. In locality 3, where *E. esculentus* occurs low in the zone, the time of low water is very nearly midday and midnight, while in locality 2, where sea-urchins only occur at dead low-water springs, and not in abundance, the time of low-water springs is just after midday and midnight. At Plymouth, and in North Cornwall, where *E. esculentus* is absent, low-water falls about 1.15 in the night time and 1.15 in the early afternoon.

There is thus a broad correlation at the lower latitudes between the occurrence of low-water spring tides in the morning and evening and the presence of *E. esculentus* on the shore at the level of low-water ordinary spring tides; and the absence of the sea-urchin—or its occurrence at a very low level on the foreshore—when low-water spring tides fall about midday and midnight. It would appear that at the lower latitudes at Mousehole and Robin Hood's Bay tidal and climatic conditions are just sufficiently favourable to permit the existence of *E. esculentus* at extreme low-water mark, but that at the higher latitude at Kyle Akin conditions may be sufficiently favourable to permit the existence of *E. esculentus* when low tides occur at the hottest part of the day.

NATURE AND EXPOSURE OF THE FORESHORE.

It is a fundamental fact that life on a rocky foreshore is inversely proportional in amount to the degree of exposure of the foreshore to wave-action. Very few freely moving animals can live above low-water mark on a wave-swept beach unless protection can be found under stones or in crevices. Thus even *P. miliaris* is absent or rare on heavily swept beaches where crevices and stones are rare, and it may be assumed that *E. esculentus* would require greater protection on the shore than its smaller ally. To avoid exposure to air and sunshine, the smaller sea-urchin, *P. miliaris*, hides at the time of low water under stones and in remote crevices, but the larger size of *E. esculentus* would only permit this habit on foreshores where large rocks occur, or where gulleys are common. *P. miliaris* has also the habit of covering itself with shells, stones or bits of seaweed, and such a habit undoubtedly gives additional protection from desiccation and extremes of temperature during the time of low water. *E. esculentus* does not adopt this habit in 5 to 10 fathoms of water, and it would be interesting to know whether such a habit is acquired anywhere on the foreshore.

There can be no doubt, therefore, that the large size of *E. esculentus* is an important factor in rendering this species unsuitable for life above low-water mark on any foreshore, and particularly on those where very high or very low temperatures prevail at low water, and where protection is obtained with difficulty from exposure to air, sunshine, and direct wave-action. Most of the localities given in Table I, page 292, are protected in some measure from exposure to heavy seas. Robin Hood's Bay, Cullercoats, and some places on the north Cornish coast, are relatively exposed, but on the exposed coast at Robin Hood's Bay it would appear that the existence of gulleys at about low-water level afford a sufficient measure of protection from wave-action. It is again of interest to note, however, that sheltered localities in the Plymouth district yield no populations of *E. esculentus.*

HYDROGRAPHIC AND OTHER FACTORS.

If the shoreward movement of *E. esculentus* is a spawning migration, as suggested by Elmhirst (**2**), it is probable that the animals are seeking a region of higher temperatures, such as exists on the shore in spring and summer (**12**). In this event the need for migration may vary in different localities. It is possible, for instance, that sufficiently high temperatures for spawning may occur during a great part of the year below low water in the South of England (as, in fact, is the case), whereas in higher latitudes the required degree of temperature may not occur off-shore until summer-time, but may easily occur over a greater range of—or earlier in—the year in an inshore habitat.

E. esculentus spawns naturally at Plymouth during the period April–June (ripe individuals regularly give successful fertilisations in March in the Plymouth Easter Class), and April–June is the period Elmhirst gives (*loc. cit.*) for the inshore spawning migration at Millport. The sea-temperature off Plymouth rises in this period from about 9·0° to about 13° C. (**12**, Table I), and at Millport, in shallow water, from about 45° to 52° F. (7·22 to 11·11° C.) (**13**). Thus, if a temperature of 10° to 11° C. be required for spawning, it is clear that *E. esculentus* would need to migrate shorewards at Millport in order to obtain the required temperature in spring or early summer. On the exposed foreshore the Echini would be subject to sea and air-temperatures, which in the daytime in spring and early summer would be higher on the average than those of the sea off-shore (**12**, p. 249, with bibliography).

These considerations tend to confirm the observation by Elmhirst that the appearance of numbers of *E. esculentus* on the foreshore at Millport is a result of a spawning migration, on the assumption that the optimum temperature for spawning is a specific character. As a consequence it would appear that in low latitudes (with higher mean sea-temperatures) there is less reason than in higher ones for *E. esculentus* to migrate to the foreshore for the purpose of spawning.

The general distribution of *E. esculentus* indicates that at moderate depths (15–30 fathoms) this animal does not frequent fine sandy grounds (**14**). Thus the occurrence of a belt of sandy ground between a rocky foreshore and rough ground off-shore might act as a deterrent to migrating *E. esculentus*, for this large short-spined Echinoid would no doubt be subject to the danger of rolling by wave-action when passing over sandy ground in shallow water.

CONCLUSIONS.

It would appear that the presence of *E. esculentus* on a foreshore is dependent upon the following combination of factors :—

1. The necessity for finding a spawning-ground where temperature (or correlated factors) is greater (or have higher value) than in the deeper off-shore water at a certain season of the year, which is usually the hydrographic spring.
2. A suitable rocky ground protected from excessive wave-action.
3. A foreshore habitat where exposure at low spring tides does not occur in the hottest part of the day at relatively low latitudes (e.g. 50–51°), and
4. An approach to the shore from off-shore without an intervening belt of fine sand.

There can be little doubt that the incidence of the mean time of day at which high- and low-water spring tides occur has an important bearing on the constitution, distribution, and abundance of the fauna and flora in any particular locality. Therefore the absence of *E. esculentus* from the protected foreshores in the neighbourhood of Plymouth would appear to be due primarily to the absence of any necessity for a spawning migration shorewards at this latitude ; and secondarily to the fact that low-water spring tides occur in this locality round about the hottest part of the day and near the coldest part of the night, thus rendering the region at low-water unsuitable for this large Echinoid.

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Photo-electric Measurements of Submarine Illumination throughout the Year.

By

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With 1 Figure in the Text.

ACCOUNTS have been given in previous papers (**1**, **2**, and **3**) of measurements of submarine illumination carried out near Plymouth by means of photo-electric cells. The present paper records the results so obtained during 1928, together with a description of such modifications of the apparatus as further experience had shown to be desirable.

USE OF OPAL GLASS DIFFUSING WINDOWS

In view of the troublesome and uncertain nature of the obliquity and azimuth corrections for photometers with ground-glass windows (**3**, p. 463), diffusing windows were fitted to all the photometers used on, or after, March 6th, 1928 (Series 24 *et seq.*). These windows consist of thin glass, opalized on both surfaces, supplied by Messrs. James Hetley & Co., 35 Soho Square, London. This is the best material that we have found yet for the purpose, since it is permanent, and does not cut off an undue proportion of the light. Its diffusing properties were found to be so good that the only obliquity factor required is that for reflection losses at the front surface of the glass (**2**, p. 184). Thus, the effect of azimuth may be entirely disregarded, and the same small obliquity correction applied to any photometer when used in air. As will be seen later, the average illumination in the sea seems to be at a rather low angle, about the same as that from a uniform grey sky. The obliquity factor for the water-glass surface at this angle would about compensate for the factor allowing for the reduced reflection loss at a water-glass surface as compared with an air-glass surface. Thus, when the submarine photometer is being standardised by comparison with the deck photometer the readings of both photometers are multiplied by the same obliquity factor (**2**, p. 184) corresponding to the conditions at the time, but when the submarine photometer is submerged the corresponding factor is taken as unity.

The use of this glass reduced the sensitivity of photometer G to direct light to 47·5% of its former value. Photometer L, being, originally, relatively much less sensitive to oblique light, had its direct light sensitivity reduced to 32·5%. As, however, the opal glass had also the effect of reducing the obliquity factors for low-angle light, slightly for G, and considerably for L, the effect of the glass on either photometer when illuminated by ordinary daylight, was to reduce the reading to about one-half. The advantages of the diffusing surface far outweigh this loss of sensitivity.

The opal glasses were placed in front of the existing photometer windows, the apertures of which they covered with considerable overlap. The opals on the submarine photometers K and L fitted inside the metal rims surrounding the windows, and were attached with a little "Sirs" wax. The large window of photometer G was reduced to 5 cm. aperture by a thin metal diaphragm, on the top of which the opal was placed.

With the opal in position and an anode potential of 60 volts, G required 167 metre-candles of perpendicular illumination to pass a current of 10^{-9} ampere.

Preliminary tests on the effect of this opal glass on the colour-sensitivity of the photometers shows that it is not important.

New Photometers.

In September, 1928, the Kunz cell in photometer K was replaced by another potassium hydride argon-filled cell made by the General Electric Co. This is considerably more sensitive than the older type of cell. Moreover, as it was felt that a quite unnecessary factor of safety had been used in designing the windows of the submarine photometers (**1**, p. 104, or **2**, p. 181), the aperture in this photometer was bored out from about 3 to about 5 cm. in diameter, the metal surrounding it being enamelled white.

This photometer is designated J. Its sensitivity on October 12th was 10^{-9} ampere for 0·6 m.c. with anode potential 88 volts. For bright light it is generally used at 3 volts, when its sensitivity, which, like most gas-filled cells is not constant, has been known to vary between 3 and 6 m.c. per 10^{-9} ampere. It is proposed to try a method which has been suggested by the makers for improving the constancy of this cell, by passing a sufficient current through it to cause a glow discharge just before use.

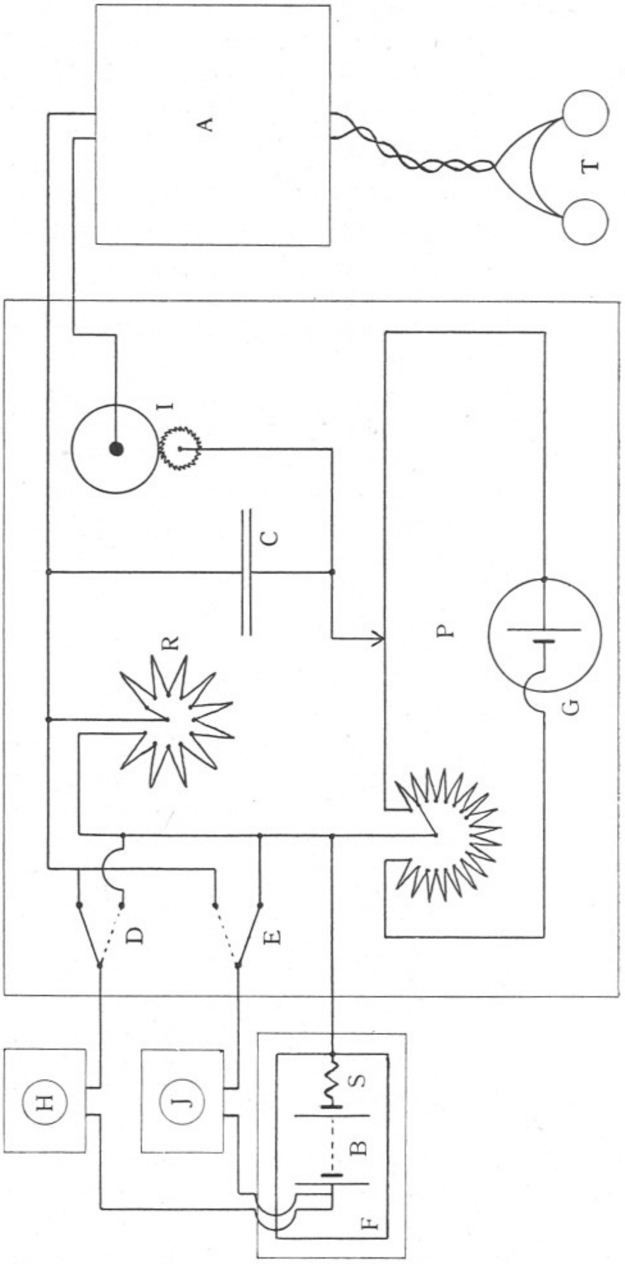
About the same date the deck photometer G was replaced by a photometer, H, containing another vacuum potassium cell which had been in use for some years on shore. This cell had been remounted, and fitted with an opal window instead of the original ground-glass one. It is more than four times as sensitive as G and only requires 40 m.c. to give 10^{-9} ampere with anode potential 60 volts.

Modifications in the Electrical Apparatus.

It was found that, for work in bad weather, the original apparatus suffered from certain grave defects. In the first place, the collection of so many circuits in a single box, which had been arranged to secure compactness, rendered satisfactory insulation more difficult, so that on very damp days "dark currents" became extremely troublesome. Secondly, this box was very heavy, which made the task of landing it from a small boat on the rocks below the Laboratory at Plymouth a difficult and dangerous one if any sea were running. Embarking it was equally difficult, and the use of any other landing-place involved its carriage over a considerable distance. Thirdly, the sound of the telephone was scarcely loud enough for comfort amid the numerous sounds which occur in a small vessel rolling heavily in a seaway, and, finally, the system of connecting the photometer cables alternately to the high-tension battery by means of wander-plugs was unsatisfactory for several reasons.

Accordingly, in October, 1928, the amplifier with its high- and low-tension batteries and also the main high-tension battery were removed from the box. This lightened the latter considerably, and allowed the apparatus remaining in it to be more conveniently arranged. Space was only provided in which one or two aluminium hot-water bottles could be placed if necessary to help in keeping the insulating surfaces dry in damp weather. This is necessary, as leakage currents over the surface of the ebonite potentiometer panel will cause "dark currents" even if the effects of extraneous leakage currents are eliminated by means of guard sheets. The design of the potentiometer is such that it would be very difficult to eliminate these internal leakage currents. For this reason it is better to disconnect the standard cell (which is not shown in the figure) from the potentiometer when taking readings under bad conditions.

The figure shows the general lay-out of the apparatus, as modified. A is the two-valve amplifier, which is of a more powerful type than that previously used. The input terminals are protected from the possibility of surface leakage from the batteries by guard rings of tin-foil gummed to the ebonite panel. It is most important that the telephones, T, should be connected on the negative side of the high-tension battery,


A
T
I
C
R
P
G
D
E
H
J
S
B
F

as otherwise a comparatively large P.D. may occur between the observer and the potentiometer, causing very serious " dark currents."

B is the anode battery, consisting of two 60-volt H.T. dry batteries. This is mounted on rubber insulators inside a metal box, F, which, in turn, is similarly insulated from the wooden box which surrounds and protects the whole. F is connected to the negative pole of the battery through a safety resistance, S, which consists of a bobbin resistance of 9,995 ohms made for a Crompton " All Test " voltmeter. F also carries two insulated terminals, to which the anode cables of the photometers, H and J, are connected. Either of these terminals can be connected by means of a wander-plug to any suitable tapping on B. This arrangement is mechanically much more satisfactory than the direct attachment of the heavy cables to the battery by means of wander-plugs. The effects of leakage currents along the surfaces of the cables are eliminated, as before, by guard wires twisted tightly round the cables and connected to F. These are not shown in the figure.

D and E are two 2-way switches to which the negative leads from H and J are connected. With these in the positions shown in the figure the current through H passes through the 100,000 ohm resistance R, and is measured by the potentiometer P, while that through J flows directly back to F and the negative terminal of B. To measure the current through J it is only necessary to reverse the switches. This arrangement enables successive readings to be taken very quickly, and ensures that the potential is applied to the photometers and cables the whole time, so that soakage effects are eliminated. When readings of a gas-filled photometer have to be taken at two different anode potentials at a given depth, it is better to compare the reading with one potential with the reading of the deck photometer, and then repeat the comparison with the new potential, sufficient time—say, several minutes—having elapsed to prevent errors due to soakage. Well-insulated electric light " corridor " switches are very suitable for use at D and E. They are mounted on an ebonite panel which also carries the terminals to which the cables are connected.

R is generally used at 100,000 ohms, but can be set to any lower multiple of 10,000 ohms which may be convenient for measuring larger currents. The capacity of the mica-insulated condenser C is 1 μF. The interrupter I has already been described (**3**, p. 458).

As the terminals of R are connected to points near the positive end of the potentiometer, the possibility of external leakage from the negative end of the potentiometer battery was eliminated by mounting it on an insulated guard plate G connected to its positive terminal. The standard cell and the amplifier also stand on guard plates (not shown in the figure) which are connected to G.

RESULTS.

The results obtained are shown in Table I, which is a continuation of Table II of our 1928 paper, the various symbols having the same significance. The work was mostly carried out at International Hydrographic Station E1, which is about 10 miles S.W. of the Eddystone lighthouse and about 20 miles from the Plymouth Sound breakwater. As before, the values of the vertical absorption coefficient, λ, for the layer between 0 and 10 m., which are printed opposite the mean depth, 5 m., are marked with an asterisk to show that a surface loss of light of 15% has been assumed. The other values of λ are obtained from the values of the percentage illumination, p, for the levels immediately above and below, respectively. In a few cases the mean of these depths differs somewhat from that opposite to which λ is printed. The vertical illumination is tabulated in thousands of metre candles (k.m.c.).

Series 25 resembles Series 15 in that the photometer window was vertical, so as to measure horizontal light. They differ in the fact that in Series 25 opal glass was used. The effect of this is seen when we compare p_h of Series 25 with the corresponding value of p in Series 24. The ratio p_h/p is given in the last column of Series 25, where it will be seen that its mean value is as high as 0·54, as compared with 0·14 in Series 15–16. The latter value is known to be too low, owing to the small sensitivity of the photometer to oblique light, but the intensity of the horizontal illumination in Series 25 is rather surprising. Too much stress must not be laid on this result, as more than two hours elapsed between the two series, and the water may have been clearer in the later one, although the approximate uniformity of the ratio p_h/p at different depths may be taken as evidence against this.

It is obvious that in air, under a perfectly uniform, sunless sky, the value of H/V would be 0·5, the vertical photometer only receiving light from half a hemisphere. Thus, the results of Series 24 and 25 indicate that the average obliquity of submarine illumination is about the same as that of diffuse daylight in air. The previous results corresponded more closely with the same light after refraction in a smooth-water surface, which would considerably increase its average altitude (**2**, p. 184, table). The average altitude of the submarine light has very little effect on the sensitivity to vertical light of a photometer with a diffusing window, as the effect of obliquity on the small reflection loss at the water-glass surface is negligible. Thus, the values given for V are not affected. On the other hand, the ratio of the total illumination, I, to V would be 2·0 for light of the distribution suggested by Series 24 and 25, as compared with 1·19 for that assumed from the results of Series 15 and 16 (**2**, *loc. cit.*). As the rate of photosynthesis depends on the total illumination, the average altitude of the light is of importance, and further measurements are desirable.

TABLE I.

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
Series 23. 1.3.'28. K Photometer. At El. Wind S.W., light. Long swell, small surface ripples. Clear sky. Approx. depth 70 m. (Chart). High water 12.59 p.m. Secchi disc 14 m. in shadow of ship at 4.30 p.m.	1.26 p.m.	31	Bright Sun	4	r	66.5	66.5	100	—
	1.34 ,,	,,	,,	,,	5	66·5	26·1	39·4	0·127*
	1.39 ,,	,,	,,	,,	10	66·5	15·7	23·7	0·103
	1.44 ,,	,,	,,	,,	15	66·5	9·6	14·4	0·099
	1.48 ,,	30	,,	,,	20	65	5·75	8·85	0·103
	1.56 ,,	,,	,,	,,	25	64·5	3·34	5·15	0·101
	2.1 ,,	29	,,	3·5	30	65	2·09	3·22	0·094
	2.6 ,,	,,	,,	,,	35	65·5	1·30	2·00	0·101
	2.13 ,,	28	,,	,,	40	64	0·75	1·17	0·109
	2.22 ,,	,,	,,	,,	45	62·5	0·42	0·67	0·127
	2.53 ,,	25	,,	,,	50	61·5	0·200	0·326	0·138
	3.3 ,,	24	,,	,,	55	54	0·090	0·167	0·156
	3.11 ,,	23	,,	3	60	52·5	0·036	0·068	0·198
	3.17 ,,	22	,,	,,	65	50	0·011	0·023	0·144
	3.26 ,,	21	,,	,,	70	48·5	0·008	0·016	—
	3.33 ,,	,,	,,	,,	45	47·5	0·175	0·357	—
	3.57 ,,	19	,,	,,	20	40·5	2·52	6·2	—
	4.8 ,,	17	,,	2·5	5	38·3	10·1	26·4	—
	4.15 ,,	15	,,	2	r	33·8	33·8	100	—
Series 24. 6.3.'28. L Photometer. About 1·5 miles N.W. of Eddystone, drifting slowly S.W. Depth 51 m. (Sounding). Wind N.W., light. Very little swell, surface ripples. Sky clear. High water 6.20 p.m. Secchi disc 13·5 m. in shadow of ship at 2.40 p.m., 11·5 m. at 2.50 in sun.	12.34 p.m.	34	Bright Sun	3	5	75	30·9	41	0·152*
	12.39 ,,	,,	,,	,,	10	73·5	13·7	18·6	0·155
	12.44 ,,	,,	,,	,,	15	73	6·35	8·7	0·151
	12.50 ,,	,,	,,	,,	20	73·5	3·03	4·1	0·147
	12.57 ,,	,,	,,	,,	25	72·5	1·47	2·0	0·155
	1.1 ,,	,,	,,	,,	30	72	0·63	0·87	0·152
	1.5 ,,	,,	,,	,,	35	71·5	0·31	0·435	—
							H	p_h	$\frac{p_h}{p}$
Series 25. 6.3.'28. L Photometer with window vertical so as to measure horizontal light. Sun through light clouds. Other conditions as in Series 24.	3.12 p.m.	24	Weak Sun	1·5	5	18·5	4·65	25·1	0·61
	3.17 ,,	23	,,	,,	10	18·35	1·90	10·3	0·555
	3.20 ,,	,,	,,	,,	15	19·7	0·90	4·55	0·525
	3.31 ,,	22	Brighter	2	20	29·6	0·57	1·92	0·47
	3.35 ,,	21	,,	,,	25	29·6	0·33	1·11	0·555
							V	p	λ
Series 26. 27.3.'28. K Photometer. At El. Wind N.W., light. Considerable swell. Overcast, grey sky. High water 9.59 p.m.	1.33 p.m.	—	Cloudy	1	r	39·3	39·3	100	—
	1.52 ,,	—	Bright	,,	5	52·5	18·0	34·3	0·172
	2.11 ,,	—	,,	,,	10	44	6·65	15·1	0·126
	2.57 ,,	32	Weak Sun	1·5	15	65·5	6·25	9·5	0·117
	3.0 ,,	,,	,,	,,	20	64·5	3·02	4·7	0·145
	3·3 ,,	31	,,	,,	25	64	1·42	2·22	0·162
	3.6 ,,	,,	,,	,,	30	66·5	0·615	0·925	0·160
	3.30 ,,	28	,,	,,	35	64	0·288	0·45	0·127
	3.42 ,,	26	,,	,,	45	44·5	0·060	0·137	—
Series 27. 5.4.'28. K Photometer. At El. Light breeze S.W. Very heavy roll at times. Blue sky to E. Heavy clouds to W. Light variable. High water 6.9 p.m. Secchi disc 10 m. in shadow of ship at 4.15 p.m.	1.2 p.m.	44	Sun	2	r	67	67	100	—
	1.13 ,,	,,	Weak Sun	1·5	5	52	21·4	41	0·139*
	1.20 ,,	,,	,,	,,	10	48	10·2	21·2	0·128
	1.32 ,,	43	,,	,,	15	41	4·65	11·3	0·129
	1.38 ,,	,,	Cloudy	1	20	28·9	1·68	5·8	0·144
	1.56 ,,	42	,,	,,	25	28·5	0·76	2·66	0·132
	2.3 ,,	41	,,	,,	30	32·7	0·505	1·54	0·092
	2.11 ,,	,,	Rain	,,	35	32·6	0·345	1·06	0·103
	2.16 ,,	40	Fine, Cloudy	,,	40	37·5	0·206	0·55	0·115
	2.23 ,,	39	,, ,,	,,	45	40	0·134	0·335	0·108
	2.34 ,,	38	Weak Sun	1·75	50	54	0·104	0·192	0·135
	3.7 ,,	33	Sun	2·5	50	86	0·149	0·173	,,
	3.13 ,,	32	,,	2	55	74·5	0·065	0·087	0·129
	3.19 ,,	,,	,,	,,	60	71	0·036	0·051	—
	3.47 ,,	29	,,	,,	20	66·5	2·83	4·25	—
	3.57 ,,	27	,,	,,	10	60	8·9	14·8	—
	4·5 ,,	26	,	,,	r	58	58	100	—

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 28. 19.4.'28. K Photometer. At El. Wind N.W., light. Slight swell from N.W. Clear sky with clouds. High water 5.23 p.m. Secchi disc 18 m. at 4.18 p.m.	11.58 a.m.	51	Bright Sun	4	r	109	109	100	—
	12.8 p.m.	,,	,,	4	a	114	109	95·5	—
	12.21 ,,	,,	Light Cloud	2	5	45·5	22·7	50	0·090*
	12.31 ,,	,,	,,	,,	10	49	17·2	35·1	0·077
	12.40 ,,	,,	Sun	3·5	,,	81	26·7	33·0	0·077
	12.50 ,,	,,	Bright Sun	4	,,	121	41	33·8	0·077
	12.56 ,,	,,	,,	,,	15	134	29·6	22·1	0·078
	1.49 ,,	48	,,	,,	,,	102	24·6	24·0	0·078
	1.54 ,,	47	,,	,,	20	100	15·6	15·6	0·079
	1.58 ,,	,,	,,	,,	25	100	10·4	10·4	0·075
	2.3 ,,	46	,,	,,	30	99	7·35	7·4	0·088
	2.11 ,,	45	,,	,,	35	97	4·15	4·25	0·119
	2.23 ,,	43	,,	,,	40	94	2·12	2·25	0·121
	2.30 ,,	42	,,	,,	45	94	1·20	1·28	0·114
	2.45 ,,	40	,,	,,	50	89	0·65	0·725	0·115
	3.0 ,,	38	,,	,,	55	84	0·342	0·405	0·109
	3.11 ,,	37	,,	,,	60	79·5	0·192	0·242	0·100
	3.15 ,,	36	,,	,,	65	78·5	0·116	0·148	0·090
	3.19 ,,	35	,,	,,	70	77·5	0·076	0·098	—
	3.35 ,,	34	,,	3·5	45	74	0·73	0·985	—
	3.53 ,,	31	,,	,,	25	73·5	5·8	7·9	—
	3.58 ,,	30	Cloudy	1	,,	25·3	1·77	7·0	—
	4.1 ,,	29	Bright Sun	3	,,	69·5	5·55	8·0	—
	4.8 ,,	28	,,	,,	r	68	68	100	—
SERIES 29. 7.5.'28. K Photometer. At El. Very light air from N. Scarcely any swell, sea glassy. Sky hazy with light clouds and hot sun. High water 7.13 p.m. Secchi disc 17 m. in shadow on weather side of ship at 2.58 p.m., 19 m. in sun on lee side of ship at 3.4 p.m. (V_a=71,000 m.c.), 14 m. to windward at 4.0 p.m. and 22 m. to leeward at 4.5 p.m. with overcast sky (V_a=18,700 m.c.).	11.13 a.m.	55	Sun	2	r	77	77	100	—
	11.29 ,,	56	,,	,,	a	84·5	76·5	90·5	—
	11.32 ,,	,,	,,	,,	b	86·5	64·5	74·5	—
	11.46 ,,	57	,,	,,	5	85·5	40·5	47·5	0·097*
	11.52 ,,	,,	,,	,,	10	85·5	27·6	32·3	0·070
	11.56 ,,	,,	,,	,,	15	84	19·5	23·2	0·083
	12.2 p.m.	,,	,,	,,	20	84·5	12·0	14·2	0·099
	12.14 ,,	,,	,,	,,	25	84·5	7·3	8·65	0·101
	12.25 ,,	,,	,,	,,	30	83	4·25	5·15	0·099
	12.29 ,,	,,	,,	,,	35	84·5	2·72	3·22	0·104
	12.35 ,,	,,	,,	,,	40	84	1·53	1·82	0·122
	12.56 ,,	56	,,	,,	45	84	0·80	0·955	0·100
	12.59 ,,	,,	,,	,,	50	82·5	0·55	0·67	0·091
	1.13 ,,	55	,,	,,	55	85	0·327	0·385	0·111
	1.21 ,,	,,	,,	,,	60	84	0·185	0·220	0·085
	1.28 ,,	54	,,	,,	65	85	0·139	0·164	0·060
	1.34 ,,	,,	,,	,,	70	84·5	0·102	0·121	—
	1.41 ,,	53	,,	,,	55	81·5	0·277	0·340	—
	1.46 ,,	,,	,,	,,	50	82	0·445	0·54	—
	1.55 ,,	52	,,	,,	40	82	1·42	1·73	—
	2.34 ,,	47	,,	1·5	20	76	10·45	13·8	—
	2.49 ,,	45	Cloudy	1	r	53·5	53·5	100	—
SERIES 30. 13.6.'28. L Photometer. At El. Wind S.E., light. Sea smooth with slight swell. Sky overcast. High water 1.23 p.m.	12.26 p.m.	—	Bright, no Sun	1	r	69·5	69·5	100	—
	12.33 ,,	—	,,	,,	a	61	48·5	79·5	—
	12.40 ,,	—	,,	,,	5	56·5	20·4	36·1	0·133*
	12.45 ,,	—	,,	,,	10	52	11·7	22·5	0·106
	12.49 ,,	—	,,	,,	15	52·5	6·55	12·5	0·116
	12.53 ,,	—	,,	,,	20	53	3·73	7·05	0·114
	12.58 ,,	—	,,	,,	25	46	1·84	4·00	0·141
	1.2 ,,	—	,,	,,	30	41·5	0·71	1·71	0·141
	1.6 ,,	—	,,	,,	35	47	0·46	0·98	0·166
	1.11 ,,	—	,,	,,	37	48·5	0·26	0·535	—
SERIES 31. 13.6.'28. K Photometer. Other conditions as in Series 30. Secchi disc 14 m. at 3.17 p.m. in lee of ship, 11 m. at 3.22 p.m. to windward of ship.	1.32 p.m.	—	Variable	1	r	34·4	34·4	100	—
	1.40 ,,	—	no Sun	,,	5	46	19·9	43·5	0·105*
	1.47 ,,	—	,,	,,	10	40	11·9	29·7	—
	2.9 ,,	—	,,	,,	30	48·5	1·77	3·65	0·106
	2·20 ,,	—	,,	,,	40	40	0·495	1·24	0·122
	2.29 ,,	—	,,	,,	50	33·3	0·106	0·32	0·115
	2.36 ,,	—	,,	,,	60	30·2	0·038	0·125	—
	2.52 ,,	—	,,	,,	25	28·7	1·87	6·5	—
	3·3 ,,	—	,,	,,	10	25·6	10·3	40·0	—
	3.11 ,,	—	,,	,,	r	48·5	48·5	100	—

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 32. 4.7.'28. L Photometer. At El. Wind S.W., freshening. Moderate swell, surface waves breaking. Bright sun with a few low clouds. High water 6.36 p.m. Secchi disc 11 m. at 12.8 p.m. in shadow of ship, 11·5 m. at 12.14 p.m. in sun (V_a=128,000 m.c.).	12.52 p.m.	62	Bright Sun	6	r	126	126	100	—
	1.2 ,,	61	,,	,,	5	123	43·8	35·6	0·156*
	1.12 ,,	,,	,,	,,	10	122·5	21·8	17·8	0·148
	1.19 ,,	60	,,	,,	15	122	9·9	8·1	0·143
	1.24 ,,	59	,,	,,	20	122·5	5·2	4·25	—
SERIES 33. 11.7.'28. L Photometer. At El. Very little wind. Light variable, owing to passage of light clouds across sun. High water 11.40 a.m.	11.55 a.m.	62	Bright Sun.	3	r	130·5	130·5	100	—
	12.13 p.m.	,,	Light clouds	,,	5	126·5	53	42	0·123*
	12.20 ,,	,,	at times	2	10	95·5	23·7	24·8	0·108
	12.28 ,,	,,	,,	2·5	15	113	16·0	14·2	0·137
	12.39 ,,	,,	,,	3	20	139·5	8·7	6·25	0·164
	12.47 ,,	,,	,,	2·5	25	105·5	2·90	2·75	0·107
	12.54 ,,	61	,,	,,	30	104·5	2·24	2·14	0·081
	12.59 ,,	,,	,,	,,	35	108·5	1·32	1·22	—
SERIES 34. 11.7.'28. K Photometer. Other conditions as in Series 33. Water surface glassy at end of series. Secchi disc 18·5 m. at 3.28 p.m. in shadow of ship, 16 m. at 3.33 p.m. in sun (V_a=76,000 m.c.).	1.19 p.m.	59	Bright Sun.	2·5	r	99	99	100	—
	1.29 ,,	58	Light clouds	,,	5	109·5	52·5	48	0·080*
	1.46 ,,	57	at times	,,	10	114	43·2	37·9	0·092
	1.52 ,,	56	,,	3	20	115·5	14·5	12·0	0·125
	1.59 ,,	,,	,,	,,	25	115	6·85	5·95	0·129
	2.6 ,,	55	,,	2·5	30	111	3·66	3·30	0·129
	2.18 ,,	54	,,	,,	35	107·5	1·76	1·64	0·126
	2.30 ,,	52	,,	,,	45	109·5	0·55	0·50	0·110
	2.38 ,,	51	,,	,,	55	108	0·194	0·180	0·117
	2.47 ,,	50	,,	,,	65	95	0·046	0·048	—
	2.58 ,,	49	,,	,,	35	94·5	1·09	1·15	—
	3.12 ,,	47	,,	2	25	82	4·1	5·0	—
	3.23 ,,	45	,,	,,	r	87	87	100	—
SERIES 35. 23.7.'28. L Photometer. At El. Wind W., light. Sea calm. Sky clear with light clouds low on the horizon. High water 9.52 a.m.	11.36 a.m.	58	Bright Sun	4·5	r	118	118	100	—
	11.52 ,,	59	,,	,,	a	121	118·5	98	—
	12.4 p.m.	,,	,,	,,	5	121	60·5	50	0·092*
	12.8 ,,	,,	,,	,,	10	119	40·2	33·7	0·081
	12.16 ,,	,,	,,	,,	15	120	26·6	22·2	0·117
	12.20 ,,	,,	,,	,,	20	120·5	12·6	10·45	0·179
	12.29 ,,	,,	,,	,,	25	120·5	4·45	3·69	0·228
	12.34 ,,	,,	,,	,,	30	118	1·26	1·07	0·196
	12.37 ,,	,,	,,	,,	35	121·5	0·63	0·52	—
SERIES 36. 23.7.'28. K Photometer. Other conditions as in Series 35. Secchi disc 17·5 m. in shadow and lee of ship at 3.26 p.m., 14 m. in sun to windward.	12.52 p.m.	59	Bright Sun	4	r	119·5	119·5	100	—
	12.57 ,,	58	,,	,,	a	120	121	101	—
	1.9 ,,	,,	,,	,,	5	119·5	68·5	57·5	0·059*
	1.24 ,,	57	,,	,,	10	117	55	47	0·086
	1.30 ,,	,,	,,	,,	20	116·5	18·4	15·8	0·117
	1·40 ,,	56	,,	3·5	25	114	9·3	8·15	0·182
	2.0 ,,	54	,,	,,	35	110	1·12	1·02	0·196
	2.17 ,,	52	,,	,,	45	107	0·174	0·162	0·163
	2.24 ,,	51	,,	,,	50	108	0·096	0·089	0·142
	2.28 ,,	50	,,	,,	55	107	0·042	0·039	0·155
	2.34 ,,	49	,,	,,	60	106	0·020	0·019	—
	2.46 ,,	47	,,	,,	35	105·5	1·03	0·98	—
	2.58 ,,	45	,,	3	25	103	4·25	4·1	—
	3.19 ,,	43	,,	,,	r	103·5	103·5	100	—
SERIES 37. 9.8.'28. L Photometer. At El. Sun and light clouds. Dark currents rather troublesome. High water 10.57 a.m.	11.36 a.m.	55	Weak Sun	1·5	r	56	56	100	—
	11.45 ,,	,,	,,	,,	5	53·5	16·0	29·9	0·196
	11.51 ,,	56	,,	,,	10	52	6·2	11·9	0·168
	11.55 ,,	,,	,,	,,	15	52·5	2·92	5·55	0·206
	11.57 ,,	,,	,,	,,	20	55	0·83	1·51	—

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 38. 9.8.'28. K Photometer. Other conditions as in Series 37. Secchi disc 10 m. in shadow of ship and 9 m. in sun at 3.30 p.m. (V_a about 50,000 m.c.).	12.51 p.m.	55	Weak Sun	1·5	r	47	47	100	—
	12.58 ,,	,,	,,	,,	5	53	18·1	34·2	0·170*
	1.4 ,,	,,	,,	,,	10	43	6·7	15·5	0·194
	1.14 ,,	54	Cloudy	1	20	28·0	0·525	1·87	0·178
	1.29 ,,	53	,,	,,	25	33·2	0·357	1·07	0·065
	1.58 ,,	50	Weak Sun	1·5	30	42	0·41	0·975	0·054
	2.10 ,,	49	,,	,,	35	41·5	0·259	0·625	0·098
	2.32 ,,	47	Cloudy	1	40	28·8	0·105	0·365	0·112
	2.36 ,,	46	,,	,,	45	27·1	0·054	0·199	0·129
	2.40 ,,	45	,,	,,	50	27·6	0·028	0·100	—
	2.54 ,,	43	Weak Sun	1·5	20	38·5	1·42	3·70	—
	3.12 ,,	41	,,	,,	10	39·2	7·65	19·6	—
	3.22 ,,	40	,,	,,	r	52·5	52·5	100	—
SERIES 39. 29.8.'28. L Photometer. At E1. Wind S.W., light. Considerable swell, some waves breaking. Clear sky with light clouds. High water 4.38 p.m.	12.4 p.m.	49	Bright Sun	4	r	108·5	108·5	100	—
	12.10 ,,	,,	,,	,,	5	109·5	52·5	48	0·126*
	12.17 ,,	,,	,,	,,	10	109·5	26·3	24·0	0·119
	12.22 ,,	,,	,,	,,	15	108	15·8	14·6	0·104
	12.26 ,,	,,	,,	,,	20	109	9·2	8·45	0·164
	12.32 ,,	,,	,,	,,	25	108	3·04	2·82	0·127
	12.44 ,,	,,	,,	,,	30	111·5	2·64	2·36	0·068
	12.50 ,,	,,	,,	,,	35	109·5	1·56	1·42	—
SERIES 40. 29.8.'28. K Photometer. Other conditions as in Series 39. Secchi disc 15 m. on lee and shadow side of ship, but illuminated by sunlight passing under the keel, at 3.28 p.m., 14 m. on weather side (V about 80,000 m.c.).	1.5 p.m.	48	Bright Sun	4	r	110	110	100	—
	1.10 ,,	47	,,	,,	5	97	46·5	48	0·100*
	1.13 ,,	,,	,,	,,	15	97·5	21·1	21·6	0·090
	1.33 ,,	46	,,	,,	20	106·5	13·15	12·3	0·134
	1.44 ,,	,,	,,	,,	30	104·5	3·03	2·90	0·138
	1.56 ,,	45	,,	,,	40	101	0·775	0·765	0·103
	2.0 ,,	44	Light Cloud	2	40	55·5	0·435	0·785	,,
	2.4 ,,	43	,,	,,	50	56	0·204	0·365	0·108
	2.24 ,,	41	Bright Sun	4	50	94	0·306	0·326	,,
	2.31 ,,	40	,,	,,	60	92·5	0·082	0·088	—
	2.53 ,,	38	,,	3·5	30	85·5	2·42	2·83	—
	3.8 ,,	37	,,	,,	r	83·5	83·5	100	—
SERIES 41. 18.9.'28. K Photometer. At E1. Calm. Sky clear after thick fog in morning, light very steady. High water 8.6 p.m. Secchi disc 16·5 m. in shadow of ship and 14 m. in sun at 4.30 p.m. (V about 25,000 m.c.).	1.45 p.m.	38	Sun	2·5	r	78·5	78·5	100	—
	1.51 ,,	37	,,	,,	5	77·5	41·5	53·5	0·086*
	1.55 ,,	,,	,,	,,	10	77	27·7	36·0	0·076
	1.59 ,,	36	,,	,,	15	77	19·2	25·0	0·084
	2.25 ,,	35	,,	2	20	72	11·2	15·6	0·092
	2.28 ,,	34	,,	,,	25	70·5	7·05	10·0	0·092
	2.32 ,,	33	,,	,,	30	69	4·3	6·25	0·100
	2.35 ,,	,,	Light Cloud	1·5	35	50	1·84	3·68	0·112
	2.42 ,,	32	Sun	2	40	68	1·38	2·03	0·117
	2.46 ,,	,,	,,	,,	45	69	0·78	1·13	—
	3.0 ,,	30	Variable	,,	25	67	4·8	7·15	—
	3.16 ,,	29	Light Cloud	1·5	25	35·8	2·79	7·8	—
	3.24 ,,	28	,,	,,	45	34·9	0·435	1·24	—
	3.29 ,,	27	,,	,,	55	32·5	0·116	0·357	0·096
	3.35 ,,	26	,,	,,	60	38·8	0·114	0·294	—
	3.45 ,,	25	,,	,,	25	32·8	3·25	9·9	—
	3.54 ,,	23	,,	,,	r	29·2	29·2	100	—
SERIES 42. 2.10.'28. L Photometer. At E1. Very faint air from N.W. Very slight roll. Sun shining through high hazy clouds. High water 7.34 p.m. Flat calm with glassy water surface later.	1.10 p.m.	35	Sun	2·5	38	65	0·365	0·56	—
	1.14 ,,	,,	,,	,,	35	65·5	0·445	0·68	0·106
	1.19 ,,	34	,,	,,	30	60	0·785	1·31	0·126
	1·36 ,,	33	,,	2	25	61	1·46	2·39	0·123
	1.39 ,,	,,	,,	,,	20	59	2·66	4·5	0·131
	1.46 ,,	32	,,	,,	15	59	5·25	8·9	0·128
	1.57 ,,	31	,,	,,	10	57	9·2	16·1	0·129
	2·3 ,,	30	,,	,,	5	55	17·7	32·2	0·166*
	2.11 ,,	29	,,	,,	r	54	54	100	—
SERIES 43. 12.10.'28. J Photometer. About 3 m. S.W. of Mewstone. Wind N.E. Considerable swell. White clouds moving rapidly across the sky. High water 5.5 p.m. Secchi disc 6·5 m. on either side of ship at 1.40 p.m.	12.30 p.m.	32	Sun	2	r	62	62	100	—
	12.48 ,,	,,	,,	,,	20	62	0·93	1·50	0·202*
	1.3 ,,	31	Light Cloud	1·5	40	49·5	0·013	0·026	—
	1·18 ,,	30	Variable	,,	20	47·5	0·675	1·42	0·202*
	1.30 ,,	29	Cloudy	1	r	30·6	30·6	100	—

Date, Remarks, etc.	T G.M.T.	α	Light.	β	d metres	V_a k.m.c.	V k.m.c.	p %	λ
SERIES 44. 30.11.'28. J Photometer. At El. Wind N.W., fresh. Waves breaking. Moderate short swell. Sky completely overcast. High water 7.51 p.m. Secchi disc 11 m. to windward, 9 m. to leeward at 3 p.m.	12.37 p.m.	—	Cloudy	1	r	15·35	15·35	100	—
	12.52 ,,	—	,,	,,	5	8·9	3·04	34·2	0·156
	12.56 ,,	—	,,	,,	10	7·8	1·38	17·7	0·125
	12.58 ,,	—	,,	,,	15	8·45	0·83	9·8	0·117
	1.1 ,,	—	,,	,,	20	7·05	0·387	5·5	0·103
	1.4 ,,	—	,,	,,	25	6·5	0·226	3·48	0·100
	1·8 ,,	—	,,	,,	30	7·25	0·146	2·01	0·117
	1.11 ,,	—	,,	,,	35	7·45	0·080	1·07	—
	1.22 ,,	—	,,	,,	15	6·4	0·43	6·7	—
	1.40 ,,	—	,,	,,	35	6·3	0·53	0·84	—
	1.50 ,,	—	,,	,,	40	7·6	0·030	0·395	0·141
	1.56 ,,	—	,,	,,	45	6·4	0·013	0·205	0·123
	2.1 ,,	—	,,	,,	50	5·3	0·006	0·115	0·082
	2.14 ,,	—	,,	,,	55	5·75	0·005	0·085	—
	2.34 ,,	—	,,	,,	25	6·65	0·170	2·56	—
	2.48 ,,	—	,,	,,	r	5·1	5·1	100	—
SERIES 45. 2.1.'29. L Photometer. At El. Strong N.E. wind. Waves breaking everywhere. Very heavy swell. Cloudy sky. Light very variable. High water 11.5 p.m.	12.35 p.m.	—	Cloudy	1	5	15·0	6·3	42	0·127*
	12.45 ,,	—	,,	,,	10	12·45	2·98	23·9	0·101
	12.52 ,,	—	,,	,,	15	13·7	2·10	15·3	0·097
	12.59 ,,	—	,,	,,	20	15·25	1·39	9·1	—
SERIES 46. 2.1.'29. J Photometer. Other conditions as in Series 45.	1.27 p.m.	—	Cloudy	1	r	7·15	7·15	100	—
	1.34 ,,	—	,,	,,	5	7·65	2·66	34·8	0·138*
	1.47 ,,	—	,,	,,	15	9·4	1·01	10·7	0·106
	1.52 ,,	—	,,	,,	25	7·45	0·315	4·25	0·082
	1.54 ,,	—	,,	,,	35	7·5	0·156	2·08	—

Series 28, obtained on April 19th, is remarkable for the high value of V_a, i.e. 134,000 m.c., obtained at 12.56 p.m. with a solar altitude of 51°. This value was the highest but one obtained during the year, and is probably attributable to the combination of clear sun and white clouds close to it. The value found for β at 12.4 p.m. was 3·75. We may compare this with the vertical illumination, 126,000 m.c., found in Series 32 on July 4th at 12.52 p.m. with $\alpha=62°$. The only clouds in the sky on this occasion were low down, and the diffuse light was remarkably low, the value found for β being over 6, which is quite exceptional. This would give 105,000 m.c. as the pure sunlight in V_a on July 4th, as compared with 98,000 m.c. on April 19th.

The highest value recorded for V_a during the year was 139,500 m.c. at 12.39 p.m. on July 11th, α being 62° (Series 33). On this occasion, also, the diffuse light was increased by the reflection from white clouds, as is shown by the fact that a measurement of β at 12.36 p.m. gave a value as low as 3·14 with $V_a=137,000$ m.c. This would mean that at 12.39 p.m. the direct sunlight amounted to about 95,000 m.c., and the diffuse light to about 44,500 m.c.

Series 28 is also interesting as showing the small effect of sudden changes of surface light on the percentage illumination at any depth. An examination of the readings from 12.31 to 12.50 p.m. and from 3.53 to 4.1 p.m. shows that the passage of a cloud across the sun reduces the aerial and submarine illuminations in about the same ratio. This accords with all our previous experience that the vertical absorption coefficient of the sea is but little affected by the obliquity of the incident light. It would seem, as already suggested, that the surface and surface layers generally have sufficient diffusing properties to control the average obliquity of the light in the deeper layers.

TABLE II.

STATION E1, COLLECTED RESULTS.

Series.	Date.	p_{20}	p_{40}	p_{60}	λ_{0-20}	λ_{20-40}	λ_{40-60}
6	1.10.'25	5·86	0·25	—	0·134	0·157	—
9 & 10	5.9.'27	0·394	—	—	0·268	—	—
11	7.9.'27	0·398	0·013	0·002	0·268	0·170	0·086
12	,,	0·126	—	—	0·325	—	—
18	3.10.'27	4·74	0·665	0·088	0·144	0·098	0·101
23	1.3.'28	8·0	1·20	0·063	0·118	0·095	0·147
26	27.3.'28	4·6	0·248	—	0·145	0·146	—
27	5.4.'28	5·2	0·58	0·057	0·139	0·110	0·116
28	19.4.'28	14·6	2·11	0·244	0·088	0·096	0·108
29	7.5.'28	14·1	1·76	0·240	0·090	0·104	0·100
30 & 31	13.6.'28	8·6	0·73	0·125	0·115	0·123	0·088
32	4.7.'28	3·96	—	—	0·153	—	—
33 & 34	11.7.'28	8·0	0·765	—	0·118	0·117	—
35 & 36	23.7.'28	10·5	0·393	0·019	0·104	0·164	0·151
37 & 38	9.8.'28	2·28	0·356	—	0·181	0·093	—
39 & 40	29.8.'28	9·0	0·78	0·088	0·112	0·122	0·109
41	18.9.'28	14·4	2·02	0·254	0·089	0·098	0·104
42	2.10.'28	4·4	0·382	—	0·148	0·122	—
44	30.11.'28	5·6	0·445	0·046	0·136	0·126	0·114
45 & 46	2.1.'29	7·7	1·22	—	0·120	0·092	—
Mean		6·62	0·72	0·085	0·150	0·120	0·111

Table II shows the percentage illuminations at 20, 40, and 60 metres, respectively, for all the series obtained so far at E1, and also the values of the mean absorption coefficients for the intervals 0 to 20, 20 to 40, and 40 to 60 metres. All series obtained closer in-shore have been omitted from this table, which is an attempt to show the seasonal changes in opacity.

When two series were taken on one day their results have been combined in the table, except in the case of Series 11 and 12. These were obtained in the autumn of 1927, when the water was very opaque, and such a large increase occurred in the opacity of the surface layers between the two series that the results differed entirely, and are shown separately. The percentage recorded at any depth is the mean of all values obtained at that depth or calculated for it from values obtained for levels within 5 m. above or below. In the single case of Series 30 and 31, as no readings were taken in Series 31 between 10 m. and 30 m., the geometric mean of the percentages at these levels was used, and combined with the 20 m. percentage of Series 30 to obtain the value given.

The values of λ, which measures the opacity of the water, are calculated from the mean percentages. A mean surface loss of 15% is assumed in finding λ_{0-20}.

Hence, since $\frac{\log_e 10}{20} = 0{\cdot}115$, $\lambda_{0-20} = 0{\cdot}115\ (\log 85 - \log p_{20})$, $\lambda_{20-40} = 0{\cdot}115\ (\log p_{20} - \log p_{40})$, and $\lambda_{40-60} = 0{\cdot}115\ (\log p_{40} - \log p_{60})$.

In finding the mean values of p given in the last line allowance has been made for the fact that occasionally, when the surface water was rather opaque, so that p_{20} was low, there was not sufficient light to measure at 60 m. and p_{60} is missing. Sometimes even p_{40} is absent. Thus, the simple averages of the figures given would exaggerate the percentages for the lower levels by eliminating the values corresponding to high opacity.

Accordingly, the average values of p_{20} were found, (a) for all the series, (b) for series containing values of p_{40}, and (c) for series containing values of p_{60}. The three means were 6·62, 7·53, and 8·65, respectively. The average of the values of p_{40} was, accordingly, multiplied by 6·62/7·53, and that for p_{60} by 6·62/8·65. This will give a fair representation of the mean percentages if the average opacity of the lower layers is independent of that of the surface layer. This assumption seems to be borne out by the readings, as we sometimes find very clear water underlying very opaque water (Series 11), while occasionally the effect is reversed (Series 35 and 36).

The mean values of the absorption coefficients are the simple averages of the figures in the columns, since, as we have seen above, there is no reason to suppose that a high opacity in the upper layer would correspond to a high opacity lower down. It must be noted that the mean opacities found in this way, though shown in the same line as the mean values of p, differ appreciably from the opacities that would be found by calculation from the mean percentages, since the latter are the arithmetic, and not the geometric means of the individual values.

Visibility of the Secchi Disc.

Table III shows a comparison of the maximum depth of visibility of the Secchi disc with other data from Series 23 to 44. The values of V_a are, in some cases, estimates from photometer readings taken a little time before or after. D is the maximum depth of visibility on whichever side of the ship gave the greatest value. The percentage illumination P at the depth D is found from the value of the product $D\lambda_{0-20}$ assuming a surface loss of 15%.

It will be seen that Dλ_{0-20} varies less than either D or λ_{0-20}, its mean value being 1·70. Hence, a very rough rule for finding the opacity is $\lambda_{0-20}=1{\cdot}7/D$. Another way of expressing the same statement is that the percentage illumination at the limit of visibility is about 16%.

There seems to be no relation between D and either β or V_a. V, the illumination at the limit of visibility, varies between 800 and 18,700 m.c. This is entirely in accord with some previous observations, which showed that the visibility of the disc was not affected by the approach of nightfall until the light became so poor that the adaptive power of the eye could no longer compensate for the reduction.

TABLE III.

VISIBILITY OF THE SECCHI DISC.

Series.	Date 1928	Time G.M.T. p.m.	β	V_a k.m.c.	D m.	λ_{0-20}	D× λ_{0-20}	P	V k.m.c.
23	1, 3	4.30	2	25	14	0·118	1·65	16·2	4·0
24	6, 3	2.40	2·5	60	13·5	0·151	2·04	11·0	6·6
27	5, 4	4.15	2	55	10	0·139	1·39	21·2	11·6
28	19, 4	4.18	3	65	18	0·088	1·58	17·4	11·3
29	7, 5	4.5	1	18·7	22	0·090	1·98	11·7	2·2
30 & 31	13, 6	3.17	1	40	14	0·115	1·61	15·9	6·4
32	4, 7	12.14	6	128	11·5	0·153	1·76	14·6	18·7
33 & 34	11, 7	3.28	2	87	18·5	0·118	2·18	9·6	8·4
35 & 36	23, 7	3·26	3	100	17·5	0·104	1·82	13·7	13·7
37 & 38	9, 8	3·30	1·5	50	10	0·181	1·81	13·9	7·0
39 & 40	29, 8	3·28	3	80	15	0·112	1·68	15·8	12·6
41	18, 9	4.30	1·5	25	16·5	0·089	1·47	19·5	4·9
43	12, 10	1.40	1	30	6·5	0·203	1·32	22·6	6·8
44	30, 11	3.0	1	4·5	11	0·136	1·50	18·8	0·8
					Mean		1·70	15·8	

It would seem, then, that we may use the Secchi disc to estimate the opacity of the water without paying any attention to even comparatively large variations in the brightness of the daylight. On the other hand, the large variations recorded in the penultimate column of Table III show that other sources of error, which must always be large where a visual estimate has to be made under very varying conditions, prevent the method from being anything more than a rough approximation.

In the 1928 paper we mentioned the desirability of trying a water telescope through which to view the Secchi disc. With any form of rigid tube it would be quite impossible to keep the disc in view when the ship was rolling more or less heavily, as was almost always the case. Accordingly attempts were made to use a wide cloth tube, about 0·3 metre in diameter and 2 m. in length. The attempts were, however, quite unsuccessful. Trials were also made with a Nicol prism, which under certain conditions extinguishes reflections from water, but with the very broken water surfaces usually encountered there was a positive disadvantage in its use. We were no more successful with various colour screens, though certain of these were often of use in picking up objects on the shore in hazy weather. The depths recorded for the visibility limit of the disc are those obtained by the youngest of the deck hands, who has remarkably good sight and could often see the disc half a metre or a metre further down than we could.

Reliability of Data.

Before discussing the interpretation of the results, it is necessary to consider what differences in the value of λ are significant. It was concluded in the previous work (1928) that the two photometers, L (vacuum) and K (gas-filled) gave results which were generally in agreement. In the course of the present work, K and L were compared very thoroughly, and were found to be in close agreement at times, so that one can rely on the differences, when found, as being of definite significance. Table IV contains data from Series 21 (see **3**, p. 474), obtained with photometer K, and shows the consistency of the results obtained under certain conditions. Furthermore, the altitude of the sun appears to have but little influence upon the value of λ though a slight rise occurred as the morning advanced and the altitude increased. On this occasion β was approximately 2, so that about half of the total light was direct sunlight.

TABLE IV.

From Series 21, Photometer K.

Hour.	α	d	λ
11.22	24°	0–10	0·160
9.36	26°	0–20	0·130
10.21	30°	0–20	0·134
11.50	35°	0–20	0·137
9.22	24°	0–40	0·121
10.28	31°	0–40	0·121
12.6	35°	0–40	0·124

Table V records values of λ obtained with the two photometers. The results agree closely at 10, 15, and 20 metres. There is an indication that the more opaque layers are found at lesser depths as the day goes on. The differences in the values of λ are quite unconnected with any slight differences in salinity, nor does there appear to be any relation between the value of λ and the temperature of the water. This point will be mentioned again later.

The values of λ for the layer next the surface is affected by the surface loss which is somewhat variable. The unsteadiness of the light just below the surface renders any method of measurement involving a telephone balance unsuitable for measuring this loss accurately, save under exceptionally favourable conditions. Moreover, a diffusing window is absolutely essential for this purpose, as the obliquity correction for the different conditions above and below the surface with the ground-glass window used in Series 7 to 23, inclusive, was too uncertain to justify any importance being attached to measurements of surface loss.

TABLE V.

Station E1, Series 9, 12.14–1.13 G.M.T. downwards.
,, 10, 2.0 –2.18 ,, downwards.
,, 10, 2.32–2.48 ,, upwards.
,, 11, 1.22–2.23 ,, downwards.
,, 12, 3.12–3.28 ,, downwards.
Series 9 and 10, $\beta=1$. Series 11, $\beta=4$. Series 12, $\beta=3$.
Series 9 and 10 on 5.9.'27. Series 11 and 12 on 7.9.'27.

d	λ (K)	λ (L)	λ (L)	t°	S $^{\circ}/_{\circ\circ}$	λ (K)	λ (L)
0	—	—	—	16·1	35·13	—	—
2·5	—	0·349*	0·356*	—	—	0·318*	0·523*
5	0·350*	0·318	0·294	—	—	0·308*	0·387
10	0·268	0·266	0·232	15·82	35·16	0·293	0·306
15	0·215	0·212	0·217	15·76	35·12	0·267	0·208
20	0·151	0·168	0·170	15·10	35·17	0·206	0·175
25	0·106	—	—	13·80	35·19	0·179	—
30	—	—	—	—	—	0·148	—
35	—	—	—	—	—	0·128	—
40	—	—	—	—	—	0·128	—
45	—	—	—	—	—	0·082	—
50	—	—	—	13·36	35·20	0·051	—
55	—	—	—	—	—	0·061	—
70	—	—	—	13·36	35·20	—	—

The temperature and salinity measurements refer to September 7th, but must be close approximations for September 5th also. The letters in brackets indicate the photometer, K or L, used.

Pending the results of further measurements of surface loss, which we hope to make by means of the time-integrating Neon Lamp Photometer devised by Dr. J. H. J. Poole (**4**), we have, throughout, assumed a surface loss of 15% as the mean of the results obtained with a diffusing window in Series 1 to 6. The largest surface loss recorded in these series was 31% (Series 4) and the smallest 5% (Series 6).

It is evident that this assumption of a uniform loss will give us too small values of λ for the upper layer when the surface is smooth and the surface loss small, and too high values for rough conditions, when the surface loss is large. The differences, however, are not very important. Remembering that $\lambda=\frac{2\cdot3}{10}(\log p_0-\log p_{10})$, where λ refers to a layer 10 metres thick, p_0 and p_{10} being the percentage illuminations just below the surface and at a depth of 10 metres, respectively, we readily find that the use of 85% instead of 95%, as the value of p_0 on a very calm day, would reduce λ by 0·011. Similarly if the surface loss were as high as 31% λ, as calculated, would be 0·021 too high.

These errors would not be of very great importance compared with the variations observed for λ. Moreover, for the values of λ given in Table II for layers 20 m. thick the errors for the upper layer would be only 0·005 and 0·010, respectively.

It is probable that errors due to the shadow of the ship are at least as important as those due to variations in the surface conditions.

Again, in deep water, the readings, though usually very steady, are small, and, consequently, even minute dark currents become highly important. Their presence, however, was carefully checked by closing the photometer window at each depth. The earlier series were also subject to a small error from soakage effects. These were eliminated by leaving the high tension plugged in continuously, and in the new arrangement, shown in the figure, this permanent connection of the high tension has been protected from any accidental displacement.

Bearing in mind these possible sources of error, one may arrive at an idea of the reliability of the various measurements, yet it is scarcely possible to assign a definite percentage value to the error, as the external conditions vary so much when the sea is rough. In particular, an error may arise through a small wave increasing the height of the column of water above the photometer, though unable to raise the ship bodily or, alternatively, the motion of the ship may raise or lower the photometer, thus rendering the light unsteady and hard to measure accurately. With the photometer at 10 metres, namely, in determining the value of λ for 5 metres, it is unlikely that the depth error ever exceeds 1 metre; 0·5 metre seems, however, quite a possible value. Again, the shading due to the ship becomes relatively more important on a dull day than on a sunny day, when the greater proportion of the illumination is due to direct sunlight if due care is taken to keep the photometer out of the direct shadow.

The error due to the cable suspending the photometer not being perpendicular when the ship is drifting, has already been shown to be negligible (1926, p. 189).

To sum up, it is probably safe to conclude that with photometers K and J between 10 and 30 metres or with photometer L between 10 and

25 metres, a 10% error in λ is unlikely, a 5% error is unusual, and the results are often considerably more accurate.

CAUSES OF THE OBSERVED SIGNIFICANT DIFFERENCES IN THE VALUES OF THE ABSORPTION COEFFICIENT.

In our 1928 paper, we suggested that the variation in the values of λ was due to the different horizontal distribution of the phytoplankton and to the zooplankton ascending or descending according to the position of the optimum light intensity for each species. We attributed the much greater clearness of the water in winter as compared with September to the fact that the sea is far poorer in plankton in mid-winter than in autumn. The high opacity of the surface layers which occurred in the autumn of 1927, and declined with the approach of winter, was not repeated in 1928, nor was it found off-shore in 1925, so the conditions in 1927 appear to have been somewhat abnormal. There is, of course, a certain absorption of light, due to inorganic matter in suspension, at all times of the year, for the whole of the English Channel is subject to detrital sedimentation. The present paper contains the results of an examination of the water throughout an entire year. We have, in addition, the data from September to December, 1927. It may be said at once that no single factor appears to be responsible for the variation in the values of λ throughout the year and throughout the day. As possible causes, we have to consider the inorganic material in suspension, the phytoplankton, the zooplankton, and the organic *débris* resulting from the living organisms or derived from the land or the bottom. Since the phytoplankton are developed near the surface in those layers in which the illumination is adequate, and since in summer the upper 15 to 25 metres is also warmer, one might expect to find some correlation between the temperature of the water and the value of λ. Table VI shows the temperatures and the values of λ obtained with the different photometers at Station E1. It should be added that Series 22 of December 14th, 1927, relates to a position near the Eddystone Lighthouse, which is 10 miles nearer shore than is Station E1. It has been inserted on account of its being the only measurement available for that winter, and the water further out to sea must have been at least as clear as at the Eddystone. Inspection of the data in Table VI reveals no such supposed correlation between high values of λ and the warm surface layer, save in September, 1927. In July, 1928, however, the clearest water was found near the surface, consequently, the view that the phytoplankton is a really important factor in causing the absorption of light in the sea must be ruled out, though it would be premature to conclude that it is of no importance.

TABLE VI.

Ser.		6	9	10		11	12		18		22		23		26
	1/10/'25		5/9/'27		7/9/'27			3/10/'27		14/12/'27		1/3/'28		27/3/'28	
m.	t° C.	λ (K)	λ (K)	λ (L)	t° C.	λ (K)	λ (L)	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (K)
0	14·9	—	—	—	16·1	—	—	13·9	—	11·8	—	9·7	—	9·6	
2·5	—	—	—	0·349*	—	0·318*	0·523*	—	—	—	—	—	—		
5	14·50	0·134	0·350*	0·318*	—	0·308*	0·387	13·80	0·166*	11·8	0·128	9·45	0·127*	9·62	0·172*
10	14·00	—	0·268	0·266	15·82	0·293	0·306	—	0·099	—	0·110	9·32	0·103	—	0·126
15	13·83	0·143	0·215	0·212	15·76	0·267	0·208	13·80	0·115	—	—	—	0·099	—	0·117
20	13·70	—	0·151	0·168	15·10	0·206	0·175	—	0·149	11·8	0·093	—	0·103	9·60	0·145
25	—	0·162	0·106	—	13·83	0·179	—	13·76	0·121	—	—	9·32	0·101	—	0·162
30	13·60	—	—	—	—	0·148	—	—	0·063	—	0·077	—	0·094	—	0·160
35	—	—	—	—	—	0·128	—	—	0·080	—	—	—	0·101	—	0·127
40	13·58	—	—	—	—	0·128	—	—	0·089	—	—	—	0·109	—	—
45	—	—	—	—	—	0·082	—	—	0·127	11·8	—	—	0·127	—	—
50	13·59	—	—	—	13·36	0·051	—	13·71	0·108	—	—	—	0·138	—	—
55	—	—	—	—	—	0·061	—	—	0·068	—	—	—	0·156	—	—
60	—	—	—	—	—	—	—	—	0·129	—	—	—	0·198	—	—
65	—	—	—	—	—	—	—	—		—	—	—	0·144	—	—
70	13·57	—	—	—	13·36	—	—	13·70		—	—	9·19	—	9·60	—

TABLE VI—(*continued*).

Ser.	27		28		29		30		31	32		33		34	35		36
	5/4/'28		19/4/'28		7/5/'28		13/6/'28			4/7/'28		11/7/'28			23/7/'28		
m.	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (K)	t° C.	λ (L)	λ (K)	t° C.	λ (L)	t° C.	λ (L)	λ (K)	t° C.	λ (L)	λ (K)
0	—	—	10·1	—	12·5	—	13·1	—	—	14·1		16·1	—	—	18·3	—	—
2·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—
5	9·80	0·139*	10·10	0·090*	12·20	0·097*	13·10	0·133*	0·105*	13·85	0·156*	14·79	0·123*	0·080*	18·06	0·092*	0·059*
10	—	0·128	—	0·077	10·96	0·070	12·71	0·106	—	13·61	0·148	14·11	0·108	0·092	17·41	0·081	0·086
15	—	0·129	10·04	0·078	10·32	0·083	—	0·116	—	13·43	0·143	13·71	0·137	—	15·13	0·117	—
20	—	0·144	—	0·079	10·30	0·099	12·42	0·114	—	13·41	—	13·21	0·164	0·125	12·76	0·179	0·117
25	9·70	0·132	—	0·075	—	0·101	—	0·141	—	13·25	—	12·35	0·107	0·129	12·62	0·228	0·182
30	—	0·092	9·98	0·088	10·25	0·099	12·35	0·141	0·106	11·82	—	11·85	0·081	0·129	12·60	0·196	—
35	—	0·103	—	0·119	—	0·104	12·26	0·166	—	—	—	—	—	0·126	—	—	0·196
40	—	0·115	—	0·121	—	0·122	11·83	—	0·122	11·72	—	11·82	—	—	12·54	—	—
45	—	0·108	—	0·114	—	0·100	—	—	—	—	—	—	—	0·110	—	—	0·163
50	—	0·135	—	0·115	—	0·091	11·24	—	0·115	11·72	—	—	—	—	12·46†	—	0·142
55	—	0·129	—	0·109	—	0·111	—	—	—	—	—	—	—	0·117	—	—	0·155
60	—	—	—	0·100	—	0·085	—	—	—	—	—	—	—	—	—	—	—
65	—	—	—	0·090	—	0·060	—	—	—	—	—	—	—	—	—	—	—
70	—	—	9·95	—	10·25	—	11·24	—	—	11·72	—	11·78	—	—	12·92†	—	—

† A second bottle gave 12·65 for 50 m. and 12·87 for 70 m.; 90 min. later 70 m. gave 12·76.

Ser.		37	38		39	40		41		42		44		45	46
		9/8/'28			29/8/'28		18/9/'28		2/10/'28		30/11/'28			2/1/'29	
m.	t° C.	λ (L)	λ (K)	t° C.	λ (L)	λ (K)	t° C.	λ (K)	t° C.	λ (L)	t° C.	λ (J)	t° C.	λ (L)	λ (J)
0	16·7	—	—	15·9	—	—	16·8	—	14·95	—	12·2	—	10·5	—	—
2·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	16·54	0·196*	0·170*	15·68	0·126*	0·100*	16·62	0·086*	14·73	0·166*	12·17	0·156*	10·70	0·127*	0·138*
10	16·45	0·168	0·194	15·68	0·119	—	16·46	0·076	14·73	0·129	—	0·125	—	0·101	—
15	16·31	0·206	—	15·09	0·104	0·090	16·32	0·084	14·71	0·128	—	0·117	10·72	0·097	0·106
20	15·91	—	0·178	13·61	0·164	0·134	15·55	0·092	—	0·131	—	0·103	—	—	—
25	13·41	—	0·065	13·58	0·127	—	13·76	0·092	14·72	0·123	12·17	0·100	—	—	0·082
30	12·96	—	0·054	13·41	0·068	0·138	13·68	0·100	—	0·126	—	0·117	—	—	—
35	—	—	0·098	—	—	—	—	0·112	—	0·106	—	—	—	—	—
40	12·92	—	0·112	12·92	—	0·103	13·55	0·117	—	—	—	0·141	10·72	—	—
45	—	—	0·129	—	—	—	—	—	—	—	—	0·123	—	—	—
50	12·92	—	—	12·78	—	0·108	—	—	14·72	—	12·17	0·082	—	—	—
55	—	—	—	—	—	—	—	0·096	—	—	—	—	—	—	—
60	—	—	—	—	—	—	13·51	—	—	—	—	—	—	—	—
65	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
70	12·92	—	—	12·76	—	—	13·53	—	14·71	—	12·17	—	10·72	—	—

Previous work on the phosphate content of sea-water has shown that at some time during each spring there is a very rapid diminution, indicating that the multiplication of the diatoms has used up the phosphate. Accordingly, one might expect that the upper layers of the sea would offer greater obstruction to the passage of light immediately after this outburst of diatoms than they did before it. Table VII shows that in 1928 the outburst occurred between April 19th and May 2nd, but the values of λ in Table VI prove that the very clear water present on April 19th persisted through early May. Again, on July 11th and 23rd, the first 15 metres was clear water, whereas on August 9th the clear water was deeper. The phosphate content was, however, closely the same on these three dates.

TABLE VII.

Phosphate in Sea-water, as mg. P_2O_5 per m^3, at Station E1, 1928.

m.	Mar. 27	April 5	April 19	May 2	May 7	July 11	July 23	Aug. 9
0	28	24	24	10	9	8·5	0	0·5
5	25	25	23	10	9	1·5	0	0
10	—	—	—	—	10	2	1·5	0
15	25	—	—	10	22	2	1·5	0·5
20	—	—	—	17	18	4	10·5	1
25	26	—	—	18	18	8·5	15	10
30	—	—	—	—	19	20	13	13
40	—	—	—	—	—	19	13	—
50	—	26	—	—	—	—	14	12
70	—	27	23	20	19	24	14	19

In the course of the study of the seasonal changes in phosphate at Station E1, extending from 1923 onwards, the conclusion has been reached that the water in this region is but little subject to influx of water from other sources, or, to be more precise, that the water which reached this position had been subjected to similar changes in its phosphate condition. The possibility, however, that some of the changes in the values of λ may be occasioned by the influx of water of different origin must be considered. Table VIII records the salinity at Stations E1, E2, mid-Channel, and E3, off Ushant, from June, 1927, to January, 1929. As a rule the water is of greater salinity at E3 than it is at E2, and the salt content of E2 is usually greater than that of E1. The analyses given were carried out at the Government Chemist's Laboratory, London. It may be concluded that from June up to November, 1927, there was no appreciable movement of water. On December 9th, however, the rather higher salinity indicates movement of water from near E2 towards E1, and this coincides with a clearing of the water. In February, 1928, an abnormal condition obtained, inasmuch as the salinity of the water decreased from E1 to E3. Such a condition was only observed once

TABLE VIII.

SALINITY AT STATIONS E1, 10 MILES S.W. OF THE EDDYSTONE, E2, MID-CHANNEL, AND E3, OFF USHANT, IN PARTS PER 1000; AVERAGED FOR THE WATER COLUMN TO INDICATE MOVEMENT OF WATER TOWARDS E1.

	1927 June 27	Aug. 2	Sept. 7	Oct. 3	Nov. 4	1927 Dec. 9	1928 Jan. 31	Feb. 21	Mar. 27	Apl. 19	1928 May 2
E1	35·21	35·22	35·17	35·16	35·14	35·23	35·17	35·18	35·12	34·98	34·98
E2	—	35·23	—	—	35·30	—	—	35·09	—	—	—
E3	—	35·30	—	—	—	—	—	35·05	—	—	—

	1928 May 8	June 4	July 4	July 23	Aug. 16	Aug. 29	Sept. 18	Oct. 2	Nov. 30	1929 Jan. 2	Jan. 7
E1	34·95	34·90	34·93	34·92	34·90	34·91	35·07	35·02	35·32	35·35	35·39
E2	34·90	—	—	—	35·29	—	—	—	—	—	35·36
E3	34·80	—	—	—	35·36	—	—	—	—	—	—

TABLE IX.

RAINFALL FOR FIVE STATIONS IN BASIN OF R. SEINE AND FOR SIX IN BASIN OF R. LOIRE, GIVEN AS mm. PER MONTH.

	Normal.			1923			1928		
	Jan.	Feb.	Mar.	Jan.	Feb.	Mar.	Jan.	Feb.	Mar.
SEINE									
Chaumont	66	55	65	45	92	64	66	96	68
Chaumont-en-Verin	50	38	44	53	88	69	69	63	55
Paris (Parc St. Maur)	39	31	41	40	64	55	61	56	49
Chartres	40	32	42	34	51	57	95	59	79
Rouen	53	41	48	71	86	65	83	94	39
Total	250	197	240	243	381	310	374	368	290
Gross total	—	—	687	—	—	934	—	—	1032
LOIRE									
Tours	56	48	59	62	111	89	77	85	67
Orleans (École)	43	33	45	61	69	79	45	55	54
Chateauroux	51	41	46	62	69	66	68	62	94
Poitiers	51	39	48	45	74	88	87	90	103
Le Mans (École)	54	39	45	46	92	125	89	61	62
Nantes	71	52	55	38	106	109	96	54	106
Total	326	252	298	314	521	556	462	407	486
Gross total	—	—	876	—	—	1391	—	—	1355
Percentages of normal.									
Seine Total	—	—	—	98	193	129	150	187	121
Gross total	—	—	—	—	—	136	—	—	150
Loire Total	—	—	—	96	207	187	142	162	163
Gross total	—	—	—	—	—	159	—	—	155

before since 1921, namely, in 1923, and the rainfall for that area of France drained by the rivers Seine and Loire was abnormally high during the first three months of that year, and for 1928, as shown in Table IX. Accordingly, we may suppose that the water of the rivers opening on to the Atlantic coast of France was responsible for the abnormal salinity conditions found. The high salinity water persisted around E1, up to March 27th, but on April 19th and early in May less saline water was found at E1. To this influx of mid-Channel water, deduced from the data of Table VIII and the known water movements of the Channel, we must attribute the exceptionally great clearness found from April 19th onwards.

It might be thought that the change in the phosphate content, attributed previously to the diatom outburst, was in reality due to this influx of water from near mid-Channel. There are good reasons, however, for rejecting this view. Firstly, the fact that the change in salinity had already taken place by April 19th, whereas the drop in phosphate content did not take place until after that, and, secondly, that, as shown in Table X, the phosphate content from February to May was very similar at all three stations.

TABLE X.

PHOSPHATE IN SEA-WATER, AS mg. P_2O_5 PER m.^{3}, AT STATIONS E1, E2, AND E3, YEAR 1928.

Large asterisk indicates that bottom has been reached before the depth indicated.

Date	February 21	21	22	May 7	8	9
m.	E1	E2	E3	E1	E2	E3
0	27	11	23	9	7	10
5	27	24	—	9	7	—
10	—	—	—	10	8	13
15	—	—	—	22	17	18
20	—	—	—	18	20	25
25	—	—	—	18	—	26
30	—	—	—	19	19	—
70	28	—	—	19	—	—
80	*	25	—	*	21	—
105		*	25		*	28

This definite connection between the sudden clearing of the water in the spring of 1928 and the variation in salinity will not, however, explain all the variations of λ. It does, however, appear to be the cause of the unusual clearness of the water found at E1 on September 18th, as shown by the sudden rise in salinity, denoting inflow from near mid-Channel. We are, therefore, faced with the necessity of accounting for the existence of layers of relatively great opacity at different levels, even on the same day and within short periods of time, during which there are no indications of any water movements. For these we may tentatively suggest the vertical movements of the zooplankton as a cause. It is true that zooplankton are fewer in numbers and individually larger than the phytoplankton; they are, however, far more capable of aggregation. Russell (**5**, **6**) has shown in a series of papers that the various members of the zooplankton are distributed at depths depending upon the intensity of the illumination at the time, and upon the duration of that illumination. At dusk the animals tend to be found near the surface. During the night they become more uniformly distributed, and at dawn they are again attracted towards the surface. With the increasing light intensity they move downwards, so that the depth at which they are found depends, not only upon the species and the degree to which they are positively or negatively phototropic, but also upon the time at their disposal for travelling under the influence of the stimulus. It becomes of interest, therefore, to see whether any relation exists between the actual intensity of the light, and the depth at which the maximum value of λ occurs in each series. Table XI contains the relevant data. Values for β have also been included as indicating whether the day as a whole was dull or of moderate or intense sunshine. It may be seen that the values of the vertical illumination V vary fairly widely, but are, as a rule, to be reckoned in thousands of metre candles, and it is remarkable that, whereas in the winter, autumn, and early spring the maximum value of λ is usually found at about 5 metres, yet in late spring and summer it may be found at from 15 to 40 metres. In this connection the results obtained in July and August, 1928, are especially significant. The maximum value of λ was found at 10 and 15 metres on August 9th, a dull day, whereas on July 11th it was found between 20 and 30 metres, on July 23rd, between 25 and 35 metres, and on August 29th, from 20 to 30 metres. These were bright sunny days. There appears, therefore, to be some evidence for considering that the layers in which light absorption is a maximum are those in which the photic stimulus has resulted in an aggregation of the zooplankton. This possibly can, of course, be tested by direct experiment, and it is hoped to do this.

In conclusion, we desire to express our thanks to Captain V. Lord and the crew of the *Salpa* for their great assistance in the transport and handling of the instruments, often under conditions of considerable difficulty, the lowering of the photometers in rough water being no easy matter. Though in use since 1924, none of the apparatus has ever been

TABLE XI.

The values of λ shown are maxima or specially high values for the various series and occurred at the depth, in metres, shown. V denotes the vertical illumination, in thousands of metre candles, at depth tabulated.

Date.	5/9/'27	5/9	5/9	7/9	7/9	7/9	7/9	3/10	14/12	1/3/'28	1/3	27/3	5/4
Ser.	9	10	10	11	11	12	12	18	22	23	23	26	27
d	5	1·2	5	1·2	5	1·2	5	5	5	5	60	5	5
λ	0·350	0·349	0·318	0·318	0·308	0·523	0·387	0·166	0·128	0·127	0·198	0·172	0·139
V	5·69	15·4	4·24	54·5	17·3	22·0	4·10	18·2	6·4	26·1	0·036	18·0	21·4
β	1	1	1	4	4	3	3	3·5	1	4	3	1	1·5

Date.	19/4	19/4	7/5	13/6	13/6	13/6	11/7	11/7	11/7	23/7	23/7	23/7
Ser.	28	28	29	30	30	31	33	34	34	35	36	36
d	40	35	40	5	25	40	20	25	30	25	25	35
λ	0·121	0·119	0·122	0·133	0·114	0·122	0·164	0·129	0·129	0·228	0·182	0·196
V	2·12	4·15	1·53	20·4	1·84	0·495	8·7	6·85	3·66	4·45	9·3	1·12
β	4	4	2	1	1	1	3	3	2·5	4·5	3·5	3·5

Date.	9/8	9/8	29/8	29/8	29/8	18/9	18/9	2/10	2/10	30/11	2/1/'29	2/1/'29
Ser.	37	38	39	40	40	41	41	42	42	44	45	46
d	15	10	20	20	30	35	40	5	20	5	5	5
λ	0·206	0·194	0·164	0·134	0·138	0·112	0·117	0·166	0·131	0·156	0·127	0·138
V	2·92	6·7	9·2	13·1	3·03	1·84	1·38	17·7	2·66	3·04	6·3	2·66
β	1·5	1·5	4	4	4	2	2	2	2	1	1	1

broken or damaged at sea. We desire also to record our indebtedness to the Royal Dublin Society for facilities connected with the construction and standardising of the photometers and to the Marine Biological Association for the major part of the apparatus and for laboratory and sea-going facilities. Our thanks are also due to the Director and Staff of the Research Laboratories of the General Electric Company for their valuable advice, and to Mr. S. G. Monk for assisting in testing for troubles associated with damp weather.

SUMMARY.

Measurements were made, throughout the year 1928, of the penetration of daylight into sea-water in the English Channel. One vacuum and two gas-filled potassium photo-electric cells were used below water. In all save the first series an efficient diffusing surface was used with the photometers so that the corrections for obliquity of illumination, necessary in our earlier work, were rendered almost negligible. From October onwards a more sensitive gas-filled cell was available for use, together with a more powerful amplifier and a more efficient insulation of the high-tension batteries; improvements in the switching of the photometers on and off were also incorporated.

The following conclusions have been reached :—

1. The conclusions put forward tentatively in 1928, concerning the agreement between the vacuum and gas-filled cells, have been substantiated in the main, although the vacuum photometer, which is relatively more sensitive to the blue end of the spectrum, generally indicated rather higher opacities.

2. There are no regular seasonal changes in the opacity of the water. A very high opacity occurred in the autumn of 1927, but this was not repeated in 1928.

3. On one occasion, in April 1928, an unusual degree of clearness of the water has been shown to have been associated with the influx of water of lesser salinity, from further out in the Channel. The clearness of the water at E1 in December, 1927, and September, 1928, is probably due to an influx of clearer water, though the salinity changes indicating this are not so well marked.

4. The main spring diatom outburst in 1928 took place when the water at E1 was exceptionally clear and failed to produce any very noticeable obscuring effect.

5. Changes in the level at which the maximum values of λ occur may be observed in the course of a day and are well marked within the

fortnightly periods of observation. Further evidence has been accumulated in favour of the view, put forward tentatively in 1928, that these changes are due to alterations in the level at which the zooplankton has become aggregated during the execution of phototropic movements. Direct evidence is lacking on this point, but it is hoped that it may be obtained this year.

6. For Station E1 the mean values of the percentages of the light in air reaching 20, 40, and 60 metres were 6·62, 0·72, and 0·085 respectively; for depths of 0–20, 20–40, 40–60 metres the mean values of λ were 0·150, 0·120, and 0·111. The most turbid water was found at 25 m. on July 23rd, λ being 0·228, with very clear water above, λ 0·081 at 10 m. The clearest water column was on April 19th, λ 0·077–0·121, though on August 9th at 25 and 30 m. values of λ 0·065 and 0·054 respectively were obtained.

7. Measurements down to 25 m. showed that the horizontal light (viz. that falling on a vertical surface) was from 0·61 to 0·47, mean 0·54 of the vertical light. The value is higher than that formerly obtained without an efficient diffusing surface on the photometer.

8. The illumination at the depth (D) at which the Secchi disc is just visible is around 16% of that in air. Very roughly the opacity may be found thus, $\lambda_{0-20}=1{\cdot}7/D$. The visibility of the disc is independent of the illumination in air, within wide limits.

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Sacconereis of Procerastea.

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With 1 Figure in the Text.

A Sacconereis "captured by the tow-net in the Firth of Clyde," according to W. C. McIntosh (1908, p. 223, Fig. 5 f.), differs from any described female bud of Autolytus, or of its allied genera such as Myrianida or Proceræa of Ehlers, especially in respect to the shape and number of ovigerous sacs, which the animal carries on its ventral side. "It appears to be fully a quarter of an inch in length, and is readily discriminated by the absence of the single ventral egg-capsule, the ova being borne in eight conspicuous globular or pear-shaped sacs."

There is no second record of the particular Sacconereis since then, and the parent stock to which the bud belongs remains, of course, unknown. Very fortunately a similar or perhaps the same type of Sacconereis was captured here in the Plymouth district, two miles east of the Eddystone, by the bottom plankton net, October 4th, 1927, and I am greatly indebted to Mr. F. S. Russell of this Laboratory for bringing it to my notice.

As will be seen in the accompanying figure, the specimen resembles very closely the female bud of Procerastea (compare with Allen's Pl. 12, Fig. 5, 1921), instead of Autolytus. The large red eyes with distinct lenses, the anterior pair being very large and ventral in aspect, are nothing more than a common character of the sexual individuals of the Autolytinæ to which the present stolon must also belong, but the appendages connected with the head are rather short and appear thicker than those of Autolytus or Myrianida. The arrangement of these tentacles and tentacular cirri exactly corresponds to that of Procerastea. The head itself seems to be composed of three segments, but separation into prostomium, buccal segment and first setigerous segment is obscure. The three prostomial appendages are all represented as smooth, tapering tentacles. Behind the dorsal eyes there is on each side a pair of rather slender tentacular cirri, and these are followed by a single dorsal tentacular cirrus, which is well in front of the first setigerous segment. The tentacular cirri are directed forwards over the head, and are smooth and tapering like the tentacles. There are, thus, roughly speaking, nine appendages on the head. The three prostomial appendages are comparatively thick, the median one being nearly as long as the two laterals. The dorsal tentacular cirrus of the buccal segment is slightly longer than the ventral and is almost as long as the similar appendage of the first setigerous segment.

McIntosh has figured a long tentacular cirrus on each side of the succeeding setigerous segments, but in my specimen the 2nd, 3rd, 4th, and 5th segments have no such elongated cirri. The dorsal cirrus in these segments is " a large rounded lobe or swelling of somewhat transparent tissue which occupies the posterior dorso-lateral angle of the segment " (Allen, *l.c.*, p. 135), exactly as in the female bud of *Procerastea Halleziana* (see again Allen's Pl. 12, Fig. 5, 1921). In the 6th setigerous segment the dorsal cirrus is somewhat elongate and tapering toward the tip, but there is still no sign of metamorphosis in the parapodium. With the 7th setigerous segment the special modifications for swimming commence, and the number of modified segments is exactly 14, as in McIntosh's specimen, as well as in the female stolon of *P. Halleziana* in Allen's Pl. 12, Fig. 5. Behind the 20th or last modified segment the notopodia and the swimming setæ are absent, as in the part in front of the 7th setigerous segment, but the dorsal cirri still persist, at first as short tapering processes similar to those in the 6th segment. McIntosh has drawn a pair of long tentacular cirri in each of the segments back to the end of the body. The short tapering cirri in my specimen, however, gradually reduce in length as we proceed backwards, and soon become replaced by small knobs of transparent-looking tissue, like those seen in the anterior unmodified segments. In the Sacconereis in question there are 32 setigerous segments in this posterior region, while the tapering cirri are observed only in the first 4 or 5 segments. The last setigerous segment is followed by the pygidium with the anal cirri as usual.

Eight ovigerous sacs, nearly of the same size, 0·7 mm. long and 0·5 mm. wide, are all of a similar pear shape. They are fixed on the ventral surface of the modified mid-segments in such a way that 4 occur on each side, arranged alternately.

Finally, as to the genetic relationship of the stolon in question, we are almost certainly dealing with the sexual individual of Procerastea, and not with such an individual of Autolytus, Proceræa, Myrianida, or Virchowia. Moreover, the parent stock of *Procerastea Halleziana* does not seem to be rare in this part of south England (Allen, 1921). The Syllid is also described from Boulogne (Malaquin, 1892 ; Caullery, 1925) and Helgoland (Langhammer, 1928), and in these districts it is found closely associated with colonies of Tubularia. At Plymouth the animal lives upon Syncoryne as well as on Tubularia.

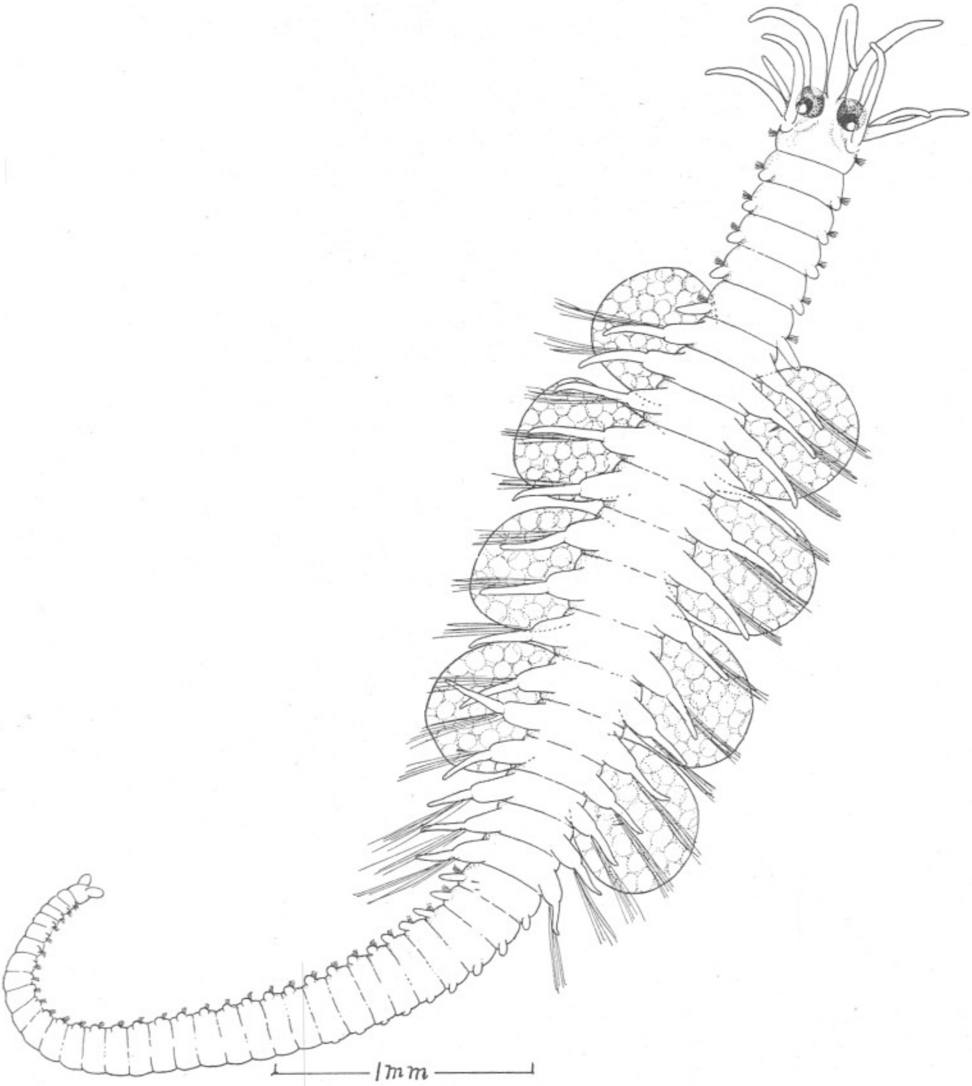

FIG. 1.—Sacconereis, probably of *Procerastea Halleziana*, captured two miles east of the Eddystone. October 4th, 1927.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Lecture Experiments on the Hydrogen Ion Concentration Changes in the Rusting of Iron.

By W. R. G. Atkins.

Nature, 1928, **121**, *p*. 615.

THE rusting of iron is ordinarily regarded as a slow process, but by adding brom thymol blue to distilled water brought to pH 6·8 by the addition of a trace of bicarbonate, the action of the iron in removing acid from the solution can be observed within two minutes. The ferrous salt thus produced is oxidised at once to ferric, with regeneration of acid. It is possible to follow each step by the use of appropriate indicators. The attack on the iron proceeds, though more slowly, in alkaline solutions in equilibrium with carbon dioxide at a very low pressure.

W. R. G. A.

The Biological Significance of the Unsaponifiable Matter of Oils.

III. Fish-Liver Oils.

By H. J. Channon.

Biochem. J., 1928, **22**, *pp*. 51–59.

1. A study has been made of the yields of unsaponifiable matter from the livers of a number of fish.

2. The liver oils of the Selachii differ from those of the Teleostei in that, in many cases, very large amounts of unsaponifiable matter occur in the former.

3. A relationship seems to exist between the percentage of unsaponifiable matter in the liver oils of the Selachii and their sterol content. The higher the percentage of unsaponifiable matter in a given oil the lower is the percentage of sterol in that fraction.

4. Squalene was not detected in the liver oils of any of the fish studied, save in those from three members of the Squalidæ family.

5. The question as to whether squalene is synthesised or is derived by the fish from its food is briefly discussed.

H. J. C.

Further Observations on Phosphagen.

By Philip Eggleton and Grace Palmer Eggleton.

J. Physiol., 1928, **65**, *pp.* 15–24.

Muscles which are capable of rapid energy output are, when resting, richer in phosphagen than muscles of slow-moving type. The muscles of such invertebrates as have been examined contain no phosphagen, or free creatine. *Amphioxus* in this respect resembles the vertebrates. The disappearance of phosphagen in a muscle resting under anaerobic conditions is not directly correlated with the lactic acid production, for the former is practically complete when the latter has only reached a quarter of the value finally attained. The disappearance of phosphagen, whether as the result of fatigue, rigor, or incubation of the minced muscle in bicarbonate buffer in the presence or absence of fluoride, results in the liberation of free creatine. In the presence of fluoride the phosphagen phosphorus becomes acid-stable, presumably being used to form hexose-esters. The reappearance of phosphagen which occurs when a fatigued muscle is allowed to recover in oxygen is very rapid in comparison with the oxidative removal of lactic acid which also occurs. The phosphagen destroyed in a muscle when resting in the absence of oxygen, or when minced and incubated in a bicarbonate buffer solution, is completely accounted for by the orthophosphoric acid produced : phosphagen destroyed during activity appears only in part as free orthophosphate, the remainder (0·40%) appearing as "lactacidogen" phosphorus—i.e. acid-stable organic phosphates rapidly hydrolysed by the muscle enzymes when the chopped muscle is incubated in a bicarbonate buffer.

Über den Auslösungsreiz des Umdrehreflexes bei Seesternen und Schlangensternen.

On the stimulus causing the righting reflex of the starfishes and ophiurians.

By Gottfried Fraenkel.

Zs. f. vergleich. Physiol., 1928, **7**, *pp.* 365–378.

The first phase of the righting movements of the starfishes consists of a dorsal bending of the arms. The latent time of this dorsal bending is exactly the same, if the dorsal sheet and the intestine of the animals are removed, also, if the animals are freely suspended in the water, in any orientation to gravity. Therefore we cannot believe the receptors for the righting reflex to be in sensitive cells of the dorsal sheet (as stated by Mangold, 1921), neither has the intestine the function of a statical organ (as Wolf [1927] has presumed). The dorsal bending of the arms takes place in all the cases in which the tube feet are not sticking on the bottom. Consequently the stimulus causing the righting movements is due to the not-touching of the tube feet on the bottom. The receptors of the stimulus are the tube feet. There is no more righting reflex, if all the tube feet are cut off.

G. F.

Brown Coloration in Interrenal Cell Tissue.

By Allan Fraser.

Nature, 1928, **122**, *p.* 206.

In a histological investigation of the interrenal tissue of the ray (*R. clavata*), it has been found that while the majority of the glands examined correspond to the usual description of an ochre-yellow body, a minority show a brown coloration apparently due to melanin pigment. In the yellow glands the lipin has been found to be confined to the cells of the lobules which compose the organ, but in the brown glands a considerable proportion of the lipin lies in the interlobular blood-spaces. The photomicrograph taken from a gland prepared by Marchis' method shows this quite clearly. The black masses of osmicated lipin obviously lie between the lobules. The appearances suggest very strongly that the brown glands when fixed were actively secreting lipin into the blood. The relation between lipin secretion and melanin formation is probably significant.

A. F.

The Effect of Electrolytes on the Muscle of the Fore-gut of *Dytiscus marginalis* with Special Reference to the Action of Potassium.

By A. D. Hobson.

Brit. J. Expt. Biol., 1928, **5**, *pp.* 385–393.

A medium of the composition NaCl 0·161M. : KCl 0·003M. : $CaCl_2$ 0·002M. : pH 7·2 will maintain rhythmic contractions of the striated muscle of the crop of Dytiscus for long periods. In the presence of normal concentrations of sodium the responses to changes of the K or Ca concentration are similar to those described by Hogben and by Wells for other invertebrate muscle preparations. If the concentrations of K and Ca are increased while the K/Ca ratio is kept constant there is decrease in the completeness of relaxation while the rhythm becomes more regular. Complete elimination of sodium from the medium is possible, and the muscle maintains its activity for a long time in presence of potassium and calcium only. Under these conditions the muscle reacts normally to changes in the K/Ca ratio. The optimum K/Ca ratio is about 0·4 which is to be compared with the optimum Na/Ca ratio of 50.

A. D. H.

The Action of Isotonic Salt Solutions on the Unfertilised Eggs of *Thalassema neptuni*.

By A. D. Hobson.

Brit. J. Expt. Biol., 1928, **6**, *pp.* 65–78.

At the pH of sea-water isotonic calcium chloride causes artificial parthenogenesis of the eggs of Thalassema. Under the same conditions the chlorides of sodium, lithium, and potassium have no activating power. KCl, in fact, inhibits maturation and quickly renders eggs incapable of being fertilised. Mixtures of $CaCl_2$ with the chloride of an alkali-metal in certain proportions cause parthenogenesis, and, in the case of potassium at least, may be more effective than pure calcium chloride. When the activating power of a series of K+Ca mixtures is tested it is found that there are two optima, one where the calcium concentration is high and one where it is low. If the calcium concentration is low, sodium and lithium seem to be much less effective in causing activation than potassium. The time factor is of great importance. For all activating solutions two optimal times of exposure were found, at 6–9 mins. and at 30 mins. It is concluded that, in Thalassema, cleavage is directly continuous with maturation, and that the difference between a stimulus causing the former and one causing the latter is merely quantitative.

A. D. H.

Observations on the Metabolism of Nervous Tissue.

By E. G. Holmes and B. E. Holmes.

Minerva Medica, 1928, **8**, No. 23 *bis*, *pp.* 1–8, *re-paged reprint.*

Previous work on the metabolism of the mammalian central nervous system is discussed. It is shown that the brain produces lactic acid from added glucose in vitro, and that under the same experimental conditions lactic acid is oxidised. The brain contains but a very small store of carbohydrate, and it is shown that during life it is dependent for lactic acid precursor on sugar supplied by the blood stream, so that the lactic acid value after death depends on the blood sugar level at the time of killing.

Observations on the peripheral nerve show that in contrast to brain this tissue has a carbohydrate reserve which, in anaerobic conditions, is connected to lactic acid. Oxidative removal of lactic acid has not been demonstrated.

Unlike both kinds of medullated mammalian nervous tissue, the non-medullated nerve ganglia of Mia contain large amounts both of glycogen and of free sugar. In vitro, this is slowly converted to lactic acid under anaerobic conditions.

E. G. H.

Entwicklungsgeschichtliche Florideenstudien.

Lunds Universitets Årsskrift, N.F. Avd. **2**, *Bd.* 24, *Nr.* 4, *pp.* 127, 64 fig.

By Harold Kylin.

The following species have been described, with illustrations : *Aghardiella tenera*, *Asparagopsis hamifera*, *Atractophora hypnoides*, *Bonnemaisonia californica*, *Calliblepharis jubata*, *Callophyllis obtusifolia*, *Callymenia reniformis*, *Catenella opuntia*, *Chantransia rhipidandra*, *Chondria dasyphylla*, *Cruoria pellita*, *Cumagloia Andersonii*, *Dudresnaya coccinea*, *Endocladia muricata*, *Epilithon membranaceum*, *Gelidium cartilagineum*, *Gigartina leptorhynchos*, *Halarachnion ligulatum*, *Helminthora divaricata*, *Iridaea cordata*, *Laurencia pinnatifida*, *Naccaria Wigghii*, *Peyssonnelia Dubyi*, *Phyllophora membranifolia*, *Ptilothamnion pluma*, *Rhodoglossum affine*, *Ricardia saccata*, *Stenogramme interrupta*.

W. R. G. A.

The Larval Stages of the Plymouth Brachyura

By M. V. Lebour.

Proc. Zool. Soc., London, 1928, *Pt.* 2. *pp.* 473–560, *Pl.* 16, *Fig.* 5.

This is a survey of all the larval crabs which have been studied in the neighbourhood of Plymouth ; 37 species are known, 33 are described fully or partially, and the relationships of the larvæ discussed. Whenever possible the crab has been hatched from the egg and a coloured drawing made of the first zoea ; 30 zoeæ were thus drawn, 23 of which came from the pre-zoea hatched from the egg. Larvæ of the rarer crabs were obtained from the plankton, also stages of various species when not reared through the complete life-history. Three species have been reared from egg to crab, many others through several stages. Larvæ from the plankton were kept until they became crabs. In this way it has been found possible to distinguish the larvæ of nearly all the Plymouth crabs. Accounts have been given of each species, with reference to the previous work of other authors and keys formed for use of plankton workers. It was found that there were distinct differences between the larvæ of the Oxyrhyncha and the Brachyrhyncha, and in most cases between the genera in both groups. It should now be possible to place any British larval crab in its proper genus if not species. A note on further work on the larval stages of foreign crabs is added. The paper is illustrated by 16 plates, 3 of which are coloured.

M. V. L.

The Food of *Sardina pilchardus* (Walbaum).

By M. V. Lebour.

Bull. Soc. d. Sci. Nat. du Maroc, 1927, **7**, *pp.* 220–223.

This is a very brief account of the food of the sardine from Casablanca, Morocco, from slides of the stomach contents, sent by Monsieur R. Ph. Dollfus. The most frequent food was *Peridinium depressum*, and secondly, the silicoflagellate *Dictyocha fibula*. These were mixed with a variety of diatoms, dinoflagellates and other protista, besides copepods and numerous larval metazoa.

M. V. L.

Brachiella obesa, a Parasitic Copepod of *Trigla Cuculus*, with a Description of the Male.

By W. H. Leigh-Sharpe.

Parasitology, 1928, **20**, *pp.* 25–31.

Brachiella obesa is not uncommon on *Trigla cuculus* at Plymouth in the neighbourhood of the Eddystone. Early in June one fish in ten harboured the parasite (5 : 50), and two of the females bore males. The appendages of the female are described; attention is called to the postero-lateral lobes of the trunk from which issue the egg-sacs, the pateriform bulla, and the striking resemblance of the maxillipedes to those of Ommatokoita. The male with its appendages is described for the first time, and while not resembling in form the more typical males, e.g. *B. thynni*, it bears a close resemblance to the American species *B. gulosa* Wilson. Some remarks on the relationship of Brachiella to other genera are added.

W. H. L.-S.

Note on the Tail-organs of Acetes.

By Yô K. Okada.

Ann. Mag. Nat. Hist., 1928, ser. 10, **1**, *pp.* 308–310.

There are two enigmatic organs in the uropod of *Acetes japonicus*, one in the basal segment and the other in its endopodite. They are visible in the fresh condition as red spots.

The structure is the same in all four; a mass of large plump cells having round nuclei forming the centre of the organ, which is limited by a thin layer of circular fibres and externally is clothed by a thick investment of radial fibres. The colour of the spots is due to the presence of red pigment granules in the outer investment.

The function is unknown, but may be photogenic. Both outer and inner investments are pierced here and there by a number of what are probably blood-capillaries, and the centre of the organ seems to receive an abundant supply of blood.

Y. K. O.

Feeding Organs and Feeding Habits of *Autolytus Edwarsi* St. Joseph.

By Yô K. Okada.

Q.J. Microscop. Sci., 1928, **72**, *pp.* 219–245.

At Plymouth *Autolytus Edwarsi* is always associated with Obelia. The meaning of this association is easily understood as the former lives upon the latter. The Syllid deprives the hydroid of the hydranths and eats them.

The worm cuts off the tentacles from the hydranth with the toothed crown of the chitinous tube, and sucks them up through the protruded pharynx by establishing in the front of the alimentary tract, by the activity of the proventriculus, a continuous water-column, which is drawn back into the intestine.

The pumping action of the proventriculus is particularly strong and distinctly visible at the outset of feeding. After a short time it dies away and the action is followed by peristalsis in the intestine.

The entire organisation in the front part of the alimentary tract, which is the feeding apparatus of the animal, suggests the system of a suction pump, the pharynx representing the pipe, the proventriculus the pump itself with a valve at each entrance, and the ventriculus the regulator of the water-column.

Y. K. O.

The Biology of Shell-fish in Relation to Public Health.

By J. H. Orton.

J. Roy. Sanitary Inst., 1928, **49**, (5), *pp.* 263–274.

In this communication is reproduced an address given to Section E, Hygiene of Food, at the Congress of the Royal Sanitary Institute at Plymouth, July, 1928.

The general structure of bivalves was illustrated by a wooden model, shown in the drawing in Fig. 1, and habits, habitats, modes of feeding, breathing and reproducing along with the incidence of disease and death were reviewed in relation to the production of pure and polluted animals.

Pollution and purification were discussed briefly, and it was shown that

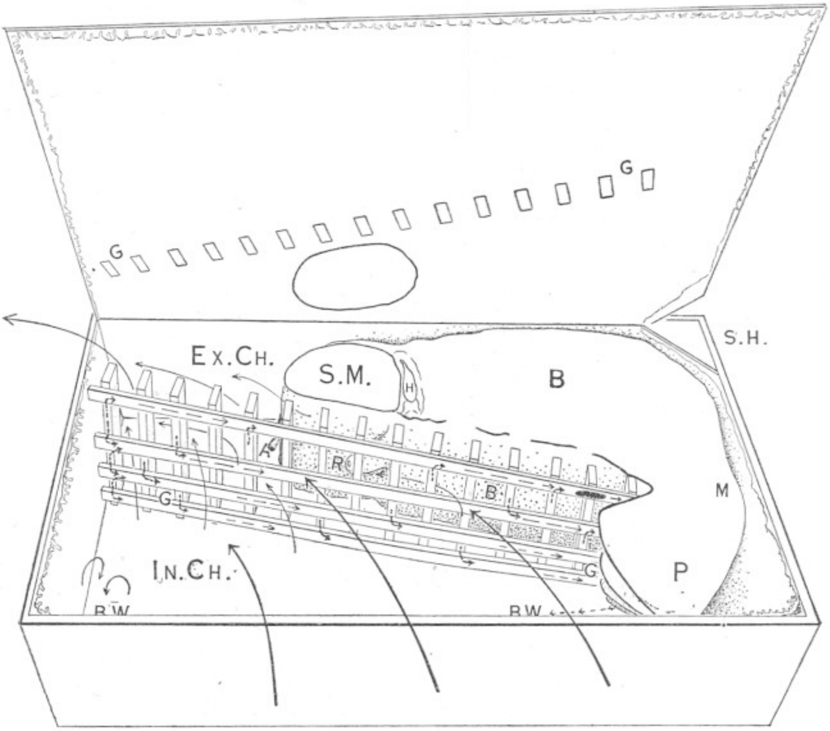

Fig. 1.—A box model of the generalised construction of a bivalve shell-fish to show essentially the division of the shell-space into two main compartments by the gill (G.G.), which is in principle a grid-like sieve. The cut edges of the vertical gill-bars and the shell-closing muscle are shown both in the lower and upper valves, which are represented by the box and its lid. One main compartment contains the body (B), the shell-closing muscle (S.M.), and the exhalent chamber (Ex.Ch.), while the other, lower compartment is composed entirely of the inhalent chamber (In.Ch.) and also contains the lip-folds or palps (P.).

G.G. The grid-like gill consists essentially of numerous vertical gill-bars and four horizontal main food channels, and hangs like a curtain between the inhalent and exhalent chambers. Sets of cilia on the gill both maintain the current of water through the gill-spaces and the shell-chambers, and sieve off the food-particles brought into the shell in this current of water. Food-particles are collected on the front faces of the vertical gill-bars and transported thence (as shown by the small broken-line arrows) into the main horizontal food channels. In these latter channels food masses or particles are carried along towards the mouth (as indicated by the larger broken-line arrows). One food-mass is shown approaching the palps in the uppermost food channel.

A. Anus and rectum in the exhalent chamber.

R. Combined renal and reproductive aperture (of the right side), which also opens into the exhalent chamber.

B.W. Back-waters in the inhalent chamber in which rejected food or other unwanted material is collected and from which such material is periodically expelled.

a consideration of the biology of bivalves leads to a recognition of the following cardinal facts :—

a. Any solid impurities which may occur in the water must necessarily be taken from the water and at least arrested on the body of the animal.

b. Bivalves are in the best condition as a food product in the fattening and pre-spawning periods of their life-history ; and in the worst condition in the spawning and post-spawning periods.

Therefore from the point of view of Public Health the following conclusions may be drawn :—

1. The indiscriminate consumption (especially in the uncooked state) during summer of those bivalves, whose spawning or post-spawning periods occur in summer, is in most cases inadvisable, if such shell-fish originate from estuarine beds.
2. There is a need for a clearly defined and recognised standard of purity in bivalves, or alternatively, the beds or other situation from which the bivalves are taken for consumption.
3. Existing beds of bivalves should be reclassified under recognised standards of purity.

J. H. O.

Contributions to the Cytology of Tetrasporic Plants of *Rhodymenia palmata* (L.) Grev., and some other Florideæ.

By M. A. Westbrook.

Ann. Bot., 1928, 42, *pp.* 149–172, Pls. II and 8 figs.

Somatic division is illustrated and described in detail for tetrasporic plants of *Laurencia pinnatifida* (Gmel.) Lamour., *Chondria dasyphylla* (Woodw.) C. Ag., and *Rhodymenia palmata* (L.) Grev., and compared with that in others of the Florideæ. Common features are the small nuclei, the large number of small chromosomes, and the absence of a spireme stage.

Stages in the prophase of the first division of the tetrasporangium are described for *Laurencia pinnatifida*, *L. hybrida* (D.C.) Lenorm., *Chondria dasyphylla*, *Stenogramme interrupta* (Ag.) Mont., and *Rhodymenia palmata*. For all but *Stenogramme* spireme stages are figured and evidence adduced for the occurrence of meiosis. In the tetrasporangia of *R. palmata* a peculiar stage is described and compared with the " growth period " of some animal oocytes, where the nucleus, after developing a spireme, returns to an apparently resting stage. A process of regeneration of the tetrasporangium is reported for *R. palmata*.

Attention is drawn to the anomalous life-history of the latter. Up to the present only male and tetrasporic plants have been found, but the cytological results here recorded are taken to indicate that there is a nuclear fusion in the life-cycle. The possible occurrence of as yet unidentified female plants is suggested.

M. A. W.

Note on a Method of Obtaining Long Working Distances with Low-power Objectives.

By Douglas P. Wilson.

J. Roy. Microscop. Soc., 1927, **47**, *pp.* 335–337.

A 2-in. or $1\frac{1}{2}$-in. objective screwed on to the nosepiece of the microscope in the usual way is used in conjunction with a $\frac{2}{3}$-in. objective which is screwed on to the lower end of the draw-tube. An eyepiece is in the usual place. By sliding the draw-tube in and out and so varying the distance between the two objectives it is possible to focus and considerably magnify small objects at a fair distance from the microscope. The same combination can also be used as a telescope.

D. P. W.

Notices of Books.

Biological Chemistry and Physics of Sea-Water. By H. W. Harvey, M.A., Hydrographer at the Laboratory of the Marine Biological Association, Plymouth. Cambridge University Press, pp. 194, 1928, 10s. 6d. net.

Of biological chemistry, as ordinarily understood, the book is quite innocent, but it does give a very readable account of the biological relations of the chemistry and physics of sea-water. There is no padding, and the pages are packed with relevant quantitative data, including many culled from the author's own researches—from which one may correctly infer that it is no mere compilation.

It contains the author's simplified presentation of Bjerknes' circulation theory, here published for the first time, so that the non-mathematical can comprehend it. The book should have many readers outside the narrow circle of marine biologists.

W. R. G. A.

Birds of the Ocean. A Handbook for Voyagers, containing descriptions of all the sea-birds of the world, with notes on their habits and guides to their identification. By W. B. Alexander, M.A. G. P. Putnam's Sons, The Knickerbocker Press, pp. 428, 1928, 15s. net.

In this handy-sized volume Mr. Alexander has produced a work from which it should be possible for any ocean voyager to identify sea-birds that may be seen from the deck of a ship. The book is copiously illustrated with excellent photographs of many of the birds, with an additional series of half-tone illustrations from drawings made by the author to illustrate the main features for identification of birds while on the wing, or, in the case of Penguins, Auks and Phalaropes, on the water. The birds are treated in their families, with a short general description of the habits of each family; the families have been subdivided into groups based on size and colouring, with keys by which the birds observed may be readily narrowed down to the groups in which they occur, the identification being then possible from the individual descriptions of each species within the group.

The book should be helpful in affording an interest to vary the monotony of sea voyages, and should be no less useful for the identification of the many birds to be seen by shore ramblers in various parts of the world.

F. S. R.

Life in Inland Waters, with especial reference to Animals. By Kathleen E. Carpenter. Sidgwick & Jackson, Ltd., 267 pp. 1928.

This work constitutes a further addition to the list of text-books of animal biology edited by Professor Julian S. Huxley.

No British book has yet appeared dealing with the subject of freshwater biology as a whole, and Miss Carpenter has therefore filled a long-felt need. The book covers a wide field, dealing first with the general characteristics and habits of the freshwater fauna and the medium in which they live ; and in the latter half of the work with the ecology of freshwater life, devoting a chapter to each of the various types of environment, such as head-streams, rivers, lakes and small water bodies.

The attention of British workers has largely been turned to Marine Biology owing to the greater wealth of animal types in the sea and its larger economic importance. Nevertheless, fresh-water biology has its economic view-points, notably in the problem of pollution and its effect on the fisheries and the water supply for our great cities.

With its helpful list of references at the end of each chapter, this book should stimulate students to further research, and, not the least important, as pointed out both by the author and editor, should help to foster that love of nature which should be inherent in all engaged in biological research.

F. S. R.

Queer Fish : Essays on Marine Science and other Aspects of Biology. By C. M. Yonge, D.Sc., Ph.D. George Routledge & Sons, Ltd., pp. 193. 1928.

In this book, in the " Science for You " series, Dr. Yonge has collected together a number of articles, most of which have already appeared in print in various periodicals. Two-thirds of the book are devoted to marine biology and our sea fisheries, stressing the importance of the resources available for mankind and the consequent need for research. Necessarily from the nature of the book the subject is not treated exhaustively, being merely a collection of essays treating marine biology and interesting items of research in an easy and popular manner.

The remaining pages comprise a set of articles on various aspects of biology, such as heredity, tissue culture and ecology.

The book can be thoroughly recommended as containing a number of interesting essays, each one of which supplies accurate information that makes light reading, but should not be regarded as producing a consecutive whole.

F. S. R.

Science of the Sea: an Elementary Handbook of Practical Oceanography for Travellers, Sailors and Yachtsmen. Prepared by The Challenger Society for the Promotion of the Study of Oceanography. Originally edited by G. Herbert Fowler, B.A. Ph.D. Second edition, edited by E. J. Allen, D.Sc., F.R.S. Oxford University Press, 1928. 15s. net.

The Challenger Society have prepared a second edition of their handbook *The Science of the Sea*, originally published in 1912, which has been re-edited by Dr. Allen. The work has been very largely revised, many of the chapters having been entirely rewritten. Of new authors who took no part in the original edition are Mr. D. Brunt and Commander Garbett, who have written the chapter on the air; Dr. W. R. G. Atkins, who contributes an article on the alkalinity of sea-water; and Dr. M. V. Lebour, who deals with the floating plants. Most of the original illustrations are reproduced with the addition of a few new ones, while the general format of the book is a vast improvement on that of the first edition.

This book should be in the library of all interested in the science of the sea, and especially of naval officers and the owners of yachts, who wish, while enjoying the pleasures of sea voyaging, to contribute something, however small, to our knowledge of life in the sea. The criticism may be made that in such a volume the study of marine life appears too formidable for a leisure hour, but really in its comprehensive nature lies its advantage, for a taste in any individual direction is catered for, and with a wise use of the book much can be achieved in the study of some special problem or group of organisms in out-of-the-way parts of the world.

F. S. R.

The Seas, our Knowledge of Life in the Sea and how it is Gained. By F. S. Russell, D.S.C., B.A. (Cantab.), Assistant Naturalist to the Marine Biological Association, Plymouth, and C. M. Yonge, D.Sc., Ph.D., Leader of the Great Barrier Reef Expedition, 1928–9. 379 pp., with 384 illustrations, 167 of which are in full colour. Frederick Warne & Co., London, 1928. 12s. 6d. net.

This book is beautifully illustrated, and the text contains accurate information on many of the main lines along which marine research is progressing. The subject is so wide that even those who are specialists in one or more of its branches are likely to find material that is new to them; this is served up in a palatable form with little or no loss in exactness. This characteristic differentiates the book from many others of a popular type—yet as a popular exposition of the subject it appears to have very considerable merit.

W. R. G. A.

Marine Biological Association of the United Kingdom.

Report of the Council, 1928.

The Council and Officers.

Four meetings of the Council have been held, at which the average attendance has been seventeen. These meetings were held in the Rooms of the Royal Society, and the thanks of the Council are due to the President and Council of the Society for this hospitality.

A Committee of nine members of the Council visited and inspected the Plymouth Laboratory, and the scientific work which was being carried on.

The Council has to report with regret the death of Mr. W. T. Brand, who had been a Governor of the Association, representing the Fishmongers' Company, for a number of years.

The Plymouth Laboratory.

The Laboratory buildings have been maintained in good condition. New ventilators of the Boyle type have been fixed above the main Laboratory, the outside painting of the old building has been carried out, and a certain amount of distempering and painting has been done inside. The cement work of the new building has been coated with a special preparation to keep out damp.

The equipment for biological and chemical work is good, save as regards the supply of some of the more costly instruments, such as polarimeter, refractometer, spectrophotometer and binocular dissecting microscopes, which are necessary for certain types of work. The supply of physical apparatus is being increased as funds permit, and it is of interest to note that various instruments, purchased as being of general utility, have all been used within the year.

The engines and pumps, circulating sea-water through the Aquarium and Laboratory tanks, have run without requiring heavy repairs. A small independent circulation, worked by an electric motor and centrifugal pump, has been installed in the new building, and has proved a valuable addition to the equipment.

A new electrical air-blower has been bought, which gives an independent supply of compressed air to the Aquarium and laboratories.

At Pier Cellars, Cawsand Bay, a sea-wall of reinforced concrete has been built across the mouth of the cove, so as to enclose a sea-water pond. This work has been done, with a special grant from the Ministry of Fisheries, for the purpose of carrying out certain experiments on the growth of Plaice, which are required by the Ministry in connection with their own work.

The Ship and Motor Boat.

The steam drifter *Salpa* and the 25 ft. motor boat have worked continuously throughout the year, in both cases at a low cost of maintenance. The ordinary surveys and refits have been carried out, and both vessels are in good order.

The Staff.

Mr. C. F. A. Pantin was again given leave of absence for some weeks in the early part of the year to enable him to repeat his course of lectures and practical work on Comparative Physiology at University College, London.

Mr. F. S. Russell, who has been lent for nine months to the Great Barrier Reef Expedition, left the Laboratory for Australia at the end of May. Early reports of the work of this expedition, which is under the leadership of Dr. C. M. Yonge, a former member of our staff, are very satisfactory.

Mr. E. Percival, Lecturer on Zoology in the University of Leeds, was appointed a temporary naturalist on the staff of the Laboratory, to take Mr. Russell's place whilst he was away. The Council desire to acknowledge their very great indebtedness to the University of Leeds for allowing Mr. Percival the leave of absence necessary for him to take up work at Plymouth. As will be described later, Mr. Percival has undertaken a special investigation of the fauna of the estuaries in the Plymouth district. The Council wish to congratulate him on his appointment to the Zoology Professorship at Christchurch, New Zealand.

Mr. D. P. Wilson, after holding a student-probationership at the Laboratory for six months, was appointed in April an Assistant Naturalist on the staff.

Mr. H. O. Bull, who for two years was a student-probationer, was appointed a research assistant to conduct the Plaice experiments at Cawsand Bay. After organising the work there he received an appointment as Naturalist at the Dove Marine Laboratory, Cullercoats. Mr. B. Dawes, of the Imperial College of Science, was appointed to take charge at Cawsand, and commenced work there in August.

Mr. V. C. Wynne-Edwards, of Oxford, and Mr. G. A. Steven, of Edinburgh, have been appointed student-probationers.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :—

Dr. W. R. Amberson, London and Philadelphia (General Physiology).
C. Amirthalingam, London and Ceylon (*Pecten opercularis*).
Miss D. Atkins, London (Pinnotheres and Loxosoma).
W. A. Bain, Edinburgh (Physiology of the Crustacean heart).
L. E. Bayliss, London (Pecten muscle).
N. J. Berrill, Leeds (Hatching enzymes in Ascidians).
Miss A. Bidder, Cambridge (Regeneration of Sponges. Digestion in Loligo).
Dr. H. Boschma, Utrecht (Oceanography).
Prof. J. P. Bouckaert, Louvain (Crustacean nerve).
E. Boyland, Manchester (Physiology of Pecten muscle).
Dr. E. Bozler, Munich (Physiology of the adductor muscle of Pecten).
Miss G. T. Brock, Oxford and Cape Town (Abnormal tails in young herring).
Miss E. M. Brown, London (Physical and chemical effects on Sea Urchins. Development of Sagartia).
F. S. Callow, London (Heterogonic growth in Eupagurus).
Dr. J. D. S. Cameron, Edinburgh (Renal excretion of urea).
A. Candeias, Lisbon (Oceanography).
Prof. H. Graham Cannon, Sheffield (Crustacean feeding mechanisms).
Mrs. H. Graham Cannon, Sheffield (Anatomy of *Amphitrite Johnstoni*).
Dr. H. H. Darby, New York (H ion concentration in relation to protozoan development).
Mrs. H. H. Darby, New York (Chemistry of Sea-water).
A. C. Downing, London (Adjusting Downing Galvanometer).
Prof. H. Dryerre, Edinburgh (The cardio-inhibitory fibres of Dogfish).
P. Eggleton, London (Chemistry of muscles of *Raia clavata*).
Mrs. P. Eggleton, London (Chemistry of muscles of *Raia clavata*).
Miss G. H. Faulkner, London (Chromosomes of Obelia. Heteronereis of Leptonereis).
A. Fraser, Aberdeen (Inter-renal cell tissue of Elasmobranchs).
K. Furusawa, London and Japan (Non-medullated nerve).
P. A. Gorer, London (Crustacean inhibitory nerves).
A. Graham, Edinburgh (Digestion in Solen and Holothuria).
Miss A. Hastings, London (Polyzoan larvæ).
H. R. Hewer, London (Colour patterns of Pleuronectidæ).
Prof. A. V. Hill, F.R.S., London (Muscle physiology).
A. D. Hobson, Edinburgh (Artificial parthenogenesis in Echinoderms and Annelids).
Dr. R. Izumi, Japan (Herring larvæ).
P. Kirtisinghe, London and Ceylon (Enteric plexus in fish).
Miss F. M. C. Leak, Sheffield (Antennal gland of Decapods. Euphausids).

M. W. De Laubenfels, California (Cellular behaviour, using Sponges).
Dr. A. Meyer, Prag (1. Cœlomic ciliary circulation in Vermes. 2. Nephridia and genital ducts in Polychæta).
Miss G. L. Naylor, Plymouth (Marsh Fucoids).
Miss E. A. Nicol, Edinburgh (Physiology of digestion in Sabella).
Dr. Yô K. Okada, Tokio (Regeneration in Autolytus and other Polychætes).
G. W. Otter, Cambridge (General Zoology).
R. Palmer, London (Effect of fixatives on the isoelectric point of basichromatin).
E. Percival, Leeds (Estuarine fauna of Rivers Tamar and Lynher).
Sister Philippa and Sister Rose Julie, Liverpool (General).
Mrs. K. F. Pinhey, Montreal (Hæmocyanin. Tyrosinase in Crustacea).
Dr. H. H. Poole, Dublin (Penetration of Light into Sea-water).
Miss R. Renton, London (Physical and chemical effects on Sea Urchins. Development of Sagartia).
H. Roy, London and Calcutta (Protozoology).
S. B. Setna, Cambridge and Madras (Histology of Lamellibranch gill).
Miss E. M. Singer, London (Physiology).
H. S. Soliman, London and Cairo (General Zoology).
Dr. K. M. Ström, Oslo (Estimation of phosphates, silicates and nitrates in sea-water).
Miss W. J. Wadge, Leeds (Effect of alterations in ionic concentration on muscular contraction).
Prof. D. M. S. Watson, F.R.S., London (General Zoology).
Miss K. Weeks, Southampton (Water vascular system of Holothuria).
S. M. White, Manchester (Nerves of fishes).
Dr. C. M. Yonge, Cambridge (Absorption in Lamellibranchs).
Dr. J. M. Yoffey, Manchester (Investigation of hæmoporesis in fishes, and the fundamentals of the splenic circulation).

The usual Easter Vacation Course in Marine Zoology was conducted by Dr. J. H. Orton, and was attended by forty-one students from Oxford, Cambridge, London, Edinburgh, Birmingham, Sheffield, Reading, and Holt.

An advanced Course in Comparative Physiology and Experimental Biology, conducted by Mr. C. F. A. Pantin, was held during the Summer Vacation and attended by twelve students.

During the Easter Vacation Dr. E. W. Shann brought a class of five boys from Rugby, Mr. J. M. Branfoot a class of six from Oundle, Mr. D. M. Reid one boy from Harrow, Mr. A. S. Gillespie a class of five from Monkton Combe School (Bath), and one boy from Caterham.

During Whitsuntide Mr. W. H. Leigh-Sharpe brought a class of five students from Chelsea Polytechnic.

General Work at the Plymouth Laboratory.

The study of the herring and its fisheries in the English Channel and off the south-east of Ireland has been continued by Mr. Ford, and four papers have been published dealing with different parts of the work, which are either completed or still in hand. Special attention has been devoted to the collection and examination of young herrings, in their first year of life, from several localities. As stated in last year's Report, sampling with a small-meshed seine in the rivers Tamar and Lynher was commenced on May 26th, 1927. As the result of this somewhat late start, the main period of metamorphosis was missed in that year. The sampling thus commenced was, however, continued regularly until July, 1928, and the highly important events occurring annually in the spring months were observed with precision in the spring of 1928. It is now possible to give an account of the general features of the growth of young herrings in these rivers from the transparent pre-metamorphosis stage, until they are fully scaled fishes one year old.

The small-meshed seine has also been successfully used in the rivers Dart and Fal, as well as off the beach at Pentewan on the Cornish coast, and excellent hauls of young herrings, sprats and pilchards obtained. It was a matter of some surprise to find that "whitebait" herrings caught off Pentewan on July 25th, 1928, where the water was made "milky" and opaque with an outflow of freshened water carrying china-clay waste, were literally gorged with the larvæ and pupæ of Chironomid flies.

The progress of the Plymouth winter fishery for herrings during the season 1927–28 was watched and samples of the fishes landed were examined for length, age and sexual condition. The total quantity of fish landed constituted a record for the port, in spite of a marked reduction in the number of vessels participating in the fishery. The average price per 1 cwt. realised on the market, on the other hand, fell to pre-war level. The records of age of the herrings, as indicated by the scales, gave evidence that "3 zoned 3 ringed" fishes were relatively much more heavily represented than in preceding seasons; in other words, fishes of the year-class 1925, which had become large enough to be caught in appreciable numbers probably for the first time during the season 1927–28, were unusually numerous. It would seem, therefore, that this year-class is destined to become an important constituent of the landings during seasons of the near future.

In accordance with the programme of work outlined in the last Report, Dr. Orton has given as much time as possible to preparing earlier work for publication. Attempts were made to examine samples of oysters at times critical for shell-growth (shell-shoots), but he finds it now difficult to obtain material regularly from the beds formerly studied, owing largely to their depleted state. A few observations were made on rapidly induced summer shell-growth (shell-shoots), in a pond at the River Yealm.

Some observations on growth, breeding, sex, and shell-shape in Patella have been prepared for publication. Parts I and II of this work are published in Vol. XV, 3, of the Journal; Part III, concerning shell-shape, called for further field-work, and is approaching completion. The variation in shell-shape in Patella, in relation to environmental conditions, is a subject of much interest, as the animal is semi-sedentary and periodically visible, while there is great diversity of statement in the literature as to the distribution, cause, and the extent of this variation. An attempt is being made to express the variations numerically, and to discover the underlying cause or causes of the variations observed. It has been found that Limpets which are covered at neap tides have low and light shells, while those growing above high-water neaps have relatively high and heavy shells, which are higher and heavier (thicker) in the drier than in the damper localities. At least two different growth-forms occur at successive ages in some—and probably all—environments, and these are somewhat different in different environments; therefore differential growth-rates are themselves subject to variation. There is a definite relation between the mean axis of the shell and weight.

In this work it has been found that the habits imposed upon the animal by environmental conditions offer a simple explanation, which can be tested experimentally, of the variation in shell-shape. A similar deduction was made regarding shell-shape in the oyster, and Dr. Orton considers that there is ground for applying the simple relation between habit and variation in shape in different types of animals. In Patella and the oyster, the thickness—and some other characters—of the shell would appear to be more directly related than shell-shape to natural environmental conditions, i.e., they are physiological effects independent of habits. A correlation between intensity of light or radiant heat and thickness of shell is suspected.

In continuing his experiments on whelk-tingles, Dr. Orton, with Mr. Winckworth, has found that on the Blackwater oyster beds, in addition to *Purpura lapillus* and *Ocenebra erinacea* (=Murex), there also occurs *Urosalpinx cinerea*. The latter is the American oyster-drill pest, which has undoubtedly been introduced into English waters, in the same way as *Crepidula fornicata*, on American oysters, and has previously escaped notice. Among 1672 tingles dredged in autumn only 5·4% were Urosalpinx, whereas in summer almost pure catches of this pest can be taken on oyster layings at low water, where these animals congregate to spawn and feed. Long-standing experiments with rather small Plymouth-born Ocenebra have so far failed to show that individuals of this species, which have never seen oysters, can recognise them as prey, although large Fal Ocenebra rapidly devour oysters from the Blackwater, but also eat barnacles.

Dr. Orton read a paper before the Royal Sanitary Congress at Plymouth on "The Biology of Shell-fish in relation to Public Health" (published in the Journal of that body, November, 1928), and one before the Challenger Society at Conway on "The Oyster as a Biological Subject."

The continuous record of hydrographic data between Plymouth and Ushant, commenced in April, 1921, has been maintained, the observations having been made by Dr. Atkins and Mr. Harvey, the data being sent to the French Fishery Department for publication in the Rapport Atlantique of the International Council. Mr. Harvey has continued investigations on the technique of determination of nitrates in the sea, with the aim of further developing and simplifying the method, so that it can be carried out on board ship with maximum accuracy. There is a demand by workers in other countries for a source of supply of the necessary reagent, the manufacture of which presents difficulties, and research in connection with this is in progress. An attempt was also made to develop a method of colour comparison, in order that the determination of small quantities of phosphate and of silicate in sea-water may be carried out with less eye-strain, with less delicate colour perception on the part of the observer, and if necessary in artificial light. A communication on these subjects and demonstrations were given at the Scientific Meeting of the International Council at Copenhagen in June. Mr. Harvey was then asked to spend October at Professor Hjort's laboratory at Oslo to collaborate with delegates from Norway, Germany and Finland in investigating the possibilities of simplifying the methods and the limitations of their application, and in drawing up recommendations for the technique of carrying out the estimations of nutrient salts in sea-water. These recommendations are being published as an appendix to the Rapports et Procès Verbaux of the Scientific Meeting of the International Council and are being communicated to the American, Danish and Dutch Expeditions, which are now at sea or shortly leaving, and include a survey of the available nutrient salts in the oceans in their scientific programmes. The development and provision for manufacture of an apparatus for colour comparison in the estimation of phosphates, embodying the principles of the apparatus evolved in the Plymouth Laboratory and used at Oslo, is being undertaken by Dr. H. Wattenburg of the *Meteor* expedition.

In view of the increasing number of workers who are employing the methods evolved at Plymouth for estimating the available nutrient salts in the sea and mapping their distribution over wide areas, it is advisable that the methods be reduced to as simple a technique as possible, and that the personal equation in colour comparison be reduced to a minimum. Much work remains to be done on the rate of re-formation of nitrate from dead organisms, on the possible direct utilisation of ammonia by phytoplankton and on the rate of diffusion upwards of nutrient salts into the depleted upper layers.

Mr. Harvey has also been engaged upon a simple method for calculating those currents which give rise to, or are maintained by, an unequal distribution of density in the sea. A communication on the hydrodynamics of the waters south-east of Ireland, embodying this method, will shortly be published.

Dr. Lebour has finished her account of the larvæ of the crabs of the Plymouth area (with the exception of a few rare forms). This has now been published in the Proceedings of the Zoological Society (July, 1928), in a paper entitled, "The Larval Stages of the Plymouth Brachyura." She has also completed her book on "The Planktonic Diatoms of Northern Seas," on the same lines as her "Dinoflagellates of Northern Seas." The Royal Society has granted £75 towards the expenses of its publication, and the Ray Society has accepted it to issue to its subscribers for 1929. She is also studying various planktonic larvæ and has distinguished those of the two species of Alpheus, *Alpheus macrocheles* having been hatched from the egg.

Dr. Lebour is now engaged upon a revision of the account of the Plymouth Marine Fauna, which has been out of print for several years. This account contains records of the positions in which each species has been found in the local area, as well as the available information as to breeding seasons.

During the early part of the year, before his departure for Australia, Mr. F. S. Russell continued his studies on the vertical distribution of young fishes and other plankton organisms. Papers have been published in the Journal dealing with the rise and fall in the water of the Copepod, *Calanus finmarchicus*, and with similar movements of young fishes. These movements have been analysed and discussed in connection with variations of the different physical conditions in which the animals live.

Mr. E. Percival spent the six months, June to November, in making and examining collections from the fauna of the River Tamar and the St. Germans River (Lynher). The regions above the junction of the two rivers were studied chiefly, but St. John's Lake, nearer the sea, was also visited. The salinity of water samples from various places was determined and an attempt made to correlate salinity and faunistic changes. It was noticed that a relatively sudden reduction in number of marine species, especially of the plankton, took place where the salinity began rapidly to fall, that some of the marine littoral species can withstand a much greater range of salinity variation than can others, and that brackish-water species also do not appear all to have the same ability to suffer similar salinity changes.

Neomysis vulgaris, *Gobius microps* and *Eurytemora affinis* were found to have the greatest ranges, persisting almost into fresh-water. An interesting succession of species was observed, in which a group of forms was succeeded, in the less saline region, by a group of closely related brackish-water species.

The brackish-water possesses a very much less varied fauna than the estuarine or harbour waters, and the apparently fresh-water region at the upper end of the tidal area has a scanty population in which figure fresh and brackish-water species. The most numerous organisms were found to be three Mysids, two Calanids, *Nereis diversicolor*, four *Polyzoa* and *Gobius microps*. The fauna is very dense in some places, especially at the edge of the tide. Over 160 species have been recorded, some being additions to the list of the Plymouth area.

Mrs. E. W. Sexton's investigations on Mendelian inheritance in *Gammarus chevreuxi*, in which she has been assisted by Miss A. R. Clark, have made progress, more especially in connection with the study of a mutation of eye-colour, which has been named "purple-white." In connection with this work, a series of experiments on the effect of temperature on the rate of development of the eggs has been completed, and the results are to be published in the immediate future. A paper by Mrs. Sexton, giving a general account of the rearing and breeding of Gammarus in Laboratory conditions, was published in the Journal during the year.

Mr. H. O. Bull's work on the formation of conditioned "responses" in fishes was described in last year's Report. The detailed paper dealing with it was published in the Journal of the Association in April, and both its scientific value and its general interest have been recognised. After completing this paper Mr. Bull became responsible for organising experiments on the growth of plaice in the sea-pond, which had been constructed at Pier Cellars, Cawsand Bay. The object of these experiments is to ascertain the relation between growth and the amount of food taken by the fishes under investigation, and particularly to determine what proportion is used for maintenance and what for growth, as measured by increase of weight. The preliminary experiments have given interesting results, and have furnished indications as to the lines upon which the work must be continued.

Mr. B. Dawes now has charge of these investigations, which it is hoped to continue during the coming year.

Mr. D. P. Wilson has been continuing his studies on larval Polychætes, and after several attempts, has this year been successful in rearing both *Sabellaria alveolata* and *S. spinulosa* from the fertilised egg right through the metamorphosis, and in the case of the former species has watched the building of the first sandy tube. Many attempts have been made to obtain artificial fertilisations of a number of Polychætes whose larvæ have not yet been described, but only in the case of *Audouinia tentaculata* and *Notomastus latericeus* was success obtained. In both these cases the pelagic life is comparatively short and the larvæ soon lose their cilia and take to creeping on the bottom.

A study of the development of the Mitraria larva of *Owenia fusiformis* has also been commenced, and this promises to be of special interest. Artificial fertilisations have been made, and twice, out of many attempts, the larvæ have been reared through their metamorphosis and have made tubes in which they have lived and grown for some considerable time. The fully developed Mitraria larva is in many ways a remarkable creature, which at the right time suddenly undergoes a cataclysmic metamorphosis, which may take no more than a few seconds to turn it into a tiny worm, busily engaged in swallowing its cast-off prototroch and other larval structures. There is a great deal in the development, however, which is still obscure and which will necessitate a considerable amount of future work to elucidate.

Mr. V. C. Wynne-Edwards has commenced a study, which is really a continuation of earlier work done at the Laboratory, on the distribution of young fishes in the western end of the Channel. He is making special attempts to follow the growth of young mackerel.

Mr. G. A. Steven is making a detailed study of the fauna of certain definite fishing areas, and is attempting to correlate the results with observations on the food actually eaten by the fishes caught in these areas. Varied methods of collecting are being used, with a view to making the records as complete as possible, and, wherever possible, quantitative estimations are undertaken.

Department of General Physiology.

Dr. Atkins and Dr. H. H. Poole have continued their collaboration on photo-electric photometers, which have been used on the *Salpa* throughout the year; the initial testing and standardisation was carried out in the laboratories of the Royal Dublin Society. Use was made of the more frequent visits to Station E 1, necessitated by the photo-electric work, to prosecute the investigations of the minor constituents of sea-water at shorter intervals, for it has now been recognised that at certain seasons the changes may proceed with great rapidity. It has become impossible, however, for Dr. Atkins to keep pace with the analytical work involved, if this is to be done on water samples not vitiated by storage. Each new constituent studied means the abandonment of the study of the seasonal changes in another one, and so the whole picture cannot be obtained simultaneously.

Work on the preservations of fishing-nets was also continued upon the samples already treated, but it was not possible to devote any additional attention to the subject. The routine tensile tests were faithfully carried out by the Laboratory assistant, Albert Ford, whose untimely and sudden death in September, at the age of twenty, was much deplored by the Laboratory.

Mr. Pantin has completed an investigation of the rôle of oxidation in amœboid movement. Under truly anaerobic conditions movement gradually falls in value, until ultimately it ceases abruptly. Oxygen is then required for recovery. Amœboid movement therefore resembles muscle in that the primary process of contraction is anaerobic, oxygen being required only for recovery. Extensive quantitative experiments have been performed on the relation of the velocity to duration of anaerobiosis. Analysis of these results in terms of various hypotheses shows that the experimental facts are in close agreement with only one hypothesis; that the controlling factor in the mechanism of movement is the rate of change of sol$\rightleftarrows$gel in the protoplasm, and that the anaerobic decay of movement is due to the accumulation of some reaction product (such as lactic acid), which progressively alters the physical state of the protoplasm. The relation of this to muscle physiology is therefore exceedingly close.

Recovery from anaerobiosis is rapid. The relation between the time required for recovery and the period of anaerobiosis indicates that a considerable oxygen debt may be accumulated by the anaerobic amœba. Important conclusions can be drawn from this and are discussed in a forthcoming paper.

In a second series of researches the relation of the velocity of movement to the external oxygen pressure has been investigated. A critical pressure of about 30 mm. of oxygen exists, above which the amœbæ remain normal indefinitely; below this increasing effects are observed, gradually approaching those of anaerobiosis.

Analysis of these results suggests that there exists a *dynamically* dissociable oxidation system in the protoplasm. Reasons are given for supposing this to be connected with the oxidase-cytochrome system of Keilin.

A third series of experiments was carried out to investigate this. The action of cyanide, sulphuretted hydrogen, alcohols and anæsthetics was studied. The results leave every reason to suppose that the oxidative recovery mechanism involves a mechanism similar to or identical with the oxidase-cytochrome system.

The Library.

A special Committee was appointed in March to consider the Library. This Committee reported that the available space for shelves had become very restricted, and that the construction of a further Library building would be imperative within the next few years. They also pointed out that the cost of the necessary scientific journals now taken was increasing rapidly, and that other very desirable new journals were being published, which could not be purchased out of the funds at present allotted for Library expenditure.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad, for copies of books and current numbers of periodicals presented to the Library or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers.

Published Memoirs.

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

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EGGLETON, P., AND EGGLETON, G. P. *Further Observations on Phosphagen.* Journ. Phys., Vol. LXV, 1928, pp. 15–24.

FRAENKEL, G. *Über den Auslösungsreiz des Umdrehreflexes bei Seesternen und Schlangensternen.* Zeitschr. f. vergl. Phys., Bd. VII, 1928, pp. 365–378.

FRASER, A. *Brown Coloration in Interrenal Cell Tissue.* "Nature," Vol. CXXII, 1928, p. 206.

GARSTANG, S. L., AND GARSTANG, W. *On the Development of Botrylloides.* Quart. Journ. Micr. Sci., Vol. LXXII, 1928, pp. 1–50.

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HOBSON, A. D. *The Effect of Electrolytes on the Muscle of the Fore-gut of Dytiscus marginalis, with Special Reference to the Action of Potassium.* Brit. Journ. Exp. Biol., Vol. V, 1928, pp. 385–393.

HOBSON, A. D. *The Action of Isotonic Salt Solutions on the Unfertilised Eggs of Thalassema neptuni.* Brit. Journ. Exp. Biol., Vol. VI, 1928, pp. 65–78.

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KYLIN, H. *Entwicklungsgeschichtliche Florideen-studien.* Lunds Univ., Arrskr. N.F. Avd. 2, Bd. XXIV, Nr. 4, 1928.

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LEIGH-SHARPE, W. H. *Brachiella obesa, a parasitic Copepod of Trigla cuculus, with a Description of the Male.* Parasitology, Vol. XX, 1928, pp. 25–31.

LEIGH-SHARPE, W. H. *Thalassema neptuni Gaertner—a British Echiuroid.* Ann. & Mag. Nat. Hist., Ser. 10, Vol. II, 1928, pp. 499–504.

LEVIN, A. *Fatigue retention of Action Current and Recovery in Crustacean Nerve.* Journ. Physiol., Vol. LXIII, 1927, pp. 113–129.

OKADA, Yô K. *Note on the Tail-organs of Acetes.* Ann. & Mag. Nat. Hist., Ser. X, Vol. I, 1928, p. 308.

OKADA, Yô K. *Feeding Organs and Feeding Habits of Autolytus Edwarsi St. Joseph.* (*Studies on the Syllidæ, I.*) Quart. Journ. Micr. Sci., Vol. LXXII, 1928, pp. 219–245.

ORTON, J. H. *The so-called Viscid Secretion in Spawning Oysters.* "Nature," Vol. CXX, 1927, p. 843.

ORTON, J. H. *The Dominant Species of Ostrea.* "Nature," Vol. CXXI, 1928, pp. 320–321.

ORTON, J. H. *The Trail of the Germ Plasm.* "Nature," Vol. CXXI, 1928, pp. 352–353.

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ORTON, J. H. *On Co-ordinated Biological Research.* "Nature," Vol. CXXII, 1928, p. 311.

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ORTON, J. H., AND WINCKWORTH, R. *The Occurrence of the American Oyster Pest, Urosalpinx cinerea (Say), on English Oyster Beds.* "Nature," Vol. CXXII, 1928, p. 241.

PORTMANN, AD., AND BIDDER, A. M. *Yolk-Absorption in Loligo and the function of the embryonic liver and pancreas.* Quart. Journ. Micr. Sci., Vol. LXXII, 1928, pp. 301–324.

RUSSELL, F. S., AND YONGE, C. M. *The Seas.* London, 1928.

WELLS, G. P. *The Action of Potassium on Muscle Preparations from Invertebrates.* Brit. Journ. Exp. Biol., Vol. V, 1928, pp. 258–282.

WESTBROOK, M. A. *Contributions to the Cytology of Tetrasporic Plants of Rhodymenia palmata (L.), Grev., and some other Florideæ.* Ann. Bot., Vol. XLII, 1928, pp. 149–172.

WILSON, D. P. *Note on a Method of Obtaining Long Working Distances with Low Power Objectives.* Journ. Roy. Micr. Soc., Vol. XLVII, 1927, pp. 335–337.

YONGE, C. M. *Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, Cuspidaria and Poromya.* Phil. Trans. Roy. Soc., Vol. CCXVI, 1928, pp. 221–263.

YONGE, C. M. *Feeding Mechanisms in the Invertebrates.* Biol. Reviews, Vol. III, 1928, pp. 21–76.

YONGE, C. M. *Queer Fish.* London, 1928.

Finance.

The Council wish to express their gratitude to the Development Commissioners for their continued support of the work of the Association. They have to thank, also, for generous grants the Fishmongers' Company (£600), the British Association (£50), the Royal Society (£30), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Oxford (£52 10s.), Cambridge (£105), London (£52 10s.), Bristol, Birmingham, Leeds, Manchester, Sheffield and the Imperial College of Science.

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The following is the list of gentlemen proposed by the Council for election for the year 1929–30 :—

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List of Annual Subscriptions

Paid during the Year, 1st April, 1928, to 31st March, 1929.

	£	*s.*	*d.*
Dr. W. M. Aders	1	1	0
E. J. Allen, Esq., D.Sc., F.R.S.	1	1	0
G. L. Alward, Esq. (1927 and 1928)	2	2	0
Dr. Ikusaku Amemiya (1928 and 1929)	2	2	0
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Miss D. Atkins	1	1	0
G. R. de Beer, Esq.	1	1	0
J. Bělehrádek, Esq., M.D. (1928 and 1929)	2	2	0
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Prof. O. V. Darbishire	1	1	0
Dr. Hugh H. Darby	1	1	0
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C. C. Dobell, Esq., F.R.S.	1	1	0
Carried forward	48	6	0

	£	s.	d.
Brought forward	48	6	0
H. V. Dobson, Esq., J.P.	1	1	0
Prof. J. S. Dunkerly, D.Sc., PH.D.	1	1	0
Prof. C. Lovatt Evans, F.R.S.	1	1	0
George Evans, Esq.	1	1	0
A. R. Fee, Esq.	1	1	0
E. Ford, Esq.	1	1	0
Miss E. A. Fraser, D.Sc.	1	1	0
K. Furusawa, Esq.	1	1	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
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Prof. D. L. Mackinnon	1	1	0
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Milford Haven Trawler Owners and Fish Salesmen's Association, Ltd.	1	1	0
Carried forward	96	12	0

	£	s.	d.
Brought forward	96	12	0
W. S. Millard, Esq.	1	1	0
P. Chalmers Mitchell, Esq., C.B.E., D.Sc., F.R.S.	1	1	0
C. C. Morley, Esq.	1	1	0
Miss Gladys L. Nayler	1	1	0
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G. W. Otter, Esq.	1	1	0
R. Palmer, Esq.	1	1	0
The Hon. John H. Parker	1	1	0
C. W. Parsons, Esq.	1	1	0
Pawlyn Bros.	1	1	0
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F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
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H. H. Sturch, Esq.	1	1	0
Prof. W. M. Tattersall	1	1	0
Sir Herbert F. Thompson	1	1	0
Carried forward	139	13	0

	£	s.	d.
Brought forward	£139	13	0
Major Nigel O. Walker, O.B.E. (1926 and 1927)	2	2	0
Arthur Walton, Esq.	1	1	0
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Prof. D. M. S. Watson, F.R.S.	1	1	0
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D. P. Wilson, Esq.	1	1	0
Ronald Winckworth, Esq.	1	1	0
V. C. Wynne-Edwards, Esq. (1928 and 1929)	2	2	0
C. M. Yonge, Esq., D.Sc., PH.D.	1	1	0
Total	£155	8	0

List of Composition Fees

Paid during the Year, 1st April, 1928, to 31st March, 1929.

	£	s.	d.
L. E. Bayliss, Esq.	15	15	0
Prof. R. R. Gates	15	15	0
E. R. Gunther, Esq.	15	15	0
Miss S. M. Manton	15	15	0
G. W. Otter, Esq.	15	15	0
Total	£78	15	0

List of Donations to the General Fund

For the Year, 1st April, 1928, to 31st March, 1929.

	£	s.	d.
L. E. Bayliss, Esq.	10	0	0
New Era Productions Ltd.	5	5	0
Oyster Merchants and Planters' Association	5	5	0
Total	£20	10	0

THE MARINE BIOLOGICAL ASSOCIATION

Dr. *Statement of Receipts and Payments for the*

GENERAL

	£	s.	d.	£	s.	d.
To Balance from 31st March, 1928:—						
Cash in hand	21	12	1			
Cash at Bank	156	11	1	178	3	2
,, Grants:—						
Ministry of Agriculture and Fisheries Grant from Development Fund	11,240	15	0			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	30	0	0			
Physiological Society	30	0	0	11,950	15	0
,, Subscriptions				155	8	0
,, Composition Fees				78	15	0
,, Donations				20	10	0
,, Sale of Specimens (*less* Purchases)				888	8	11
,, ,, Fish (*less* Expenses)				36	1	3
,, ,, Nets, Gear, and Hydrographical Apparatus				417	13	10
,, Table Rent (including Cambridge University, £105; Oxford University, £52 10s.; London University, £52 10s.; Bristol University, £25; Birmingham University, £15 15s.; Leeds University, £10 10s.; Manchester University, £10 10s.; Sheffield University, £10; Imperial College of Science and Technology, £10; Trustees of the Ray Lankester Fund, £20)				426	5	6
,, Tank Room Receipts				449	8	7
,, Interest on Investments:—						
4% War Stock	3	2	8			
4% New Zealand Stock	13	2	10			
Deposit Account	7	10	9	23	16	3
,, Sale of Dr. M. V. Lebour's Book				4	11	8
				£14,629	17	2

The Association's Bankers held on its behalf:—
£51 National Savings Certificates.
£78 9s. 4d. 4% War Stock, 1929–42 (Deed Stock).
£410 14s. 8d. New Zealand 4%, 1943–63.

PLAICE EXPERIMENTS

	£	s.	d.
To Grant from Ministry of Agriculture and Fisheries	300	0	0
,, General Fund	55	6	10
	£355	6	10

OF THE UNITED KINGDOM.

Year 1*st April*, 1928, *to* 31*st March*, 1929. Cr.

FUND.

	£	*s.*	*d.*	£	*s.*	*d.*
By Salaries :—						
Director	1,162	10	0			
Physiologist	910	0	0			
Naturalists	3,570	8	8			
Hydrographer	578	6	8	6,221	5	4
,, Laboratory Wages (including National Insurances)				1,952	5	2
,, Annual Upkeep of Library				446	5	6
,, Scientific Publications :—						
Journal, Vol. XV, Nos. 2 and 3	539	13	7			
Less Sales	100	5	1	439	8	6
,, Annual Upkeep of Laboratories and Tank Rooms :—						
Building and Machinery	523	6	0			
Electricity, Gas, Coal, and Water	280	16	3			
Chemicals and Apparatus	524	4	8			
Rates, Taxes, and Insurance	107	9	3			
Travelling	149	18	11			
,, "Challenger" Society Meetings	28	17	10			
Stationery, Postages, Telephone, Carriage, and Sundries	381	18	8	1,996	11	7
,, Annual Maintenance and Hire of Boats :—						
Wages (including Diet Allowance, National Insurance, and Casual Labour)	1,621	0	10			
Coal and Water	465	2	0			
Maintenance and Repairs, with Nets, Gear, and Apparatus	1,002	3	0			
Boat Hire and Collecting Expeditions	21	5	1			
Insurance	343	2	6	3,452	13	5
,, Interest on Bank Loans				1	12	11
,, Plaice Experiments Account :—						
Expenditure in Excess of Grant from Ministry of Agriculture and Fisheries				55	6	10
,, Balance, 31st March, 1929 :—						
Cash in hand	16	11	3			
Cash at Lloyds Bank £178 1 3						
Less Coutts & Co.—Overdraft 130 4 7	47	16	8	64	7	11
				£14,629	17	2

AT CAWSAND.

	£	*s.*	*d.*
By Expenditure on Building Fishpond and Raft Boxes	197	1	7
,, Half-Salary of Mr. Bull and Mr. Dawes	113	10	10
,, Incidental Expenses	44	14	5
	£355	6	10

Examined and found correct,

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
23rd *April* 1929.

(Signed) N. E. Waterhouse, *Auditor.*
W. T. Calman } *Members of*
Jos. M. Tabor } *Council.*

THE

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OF

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