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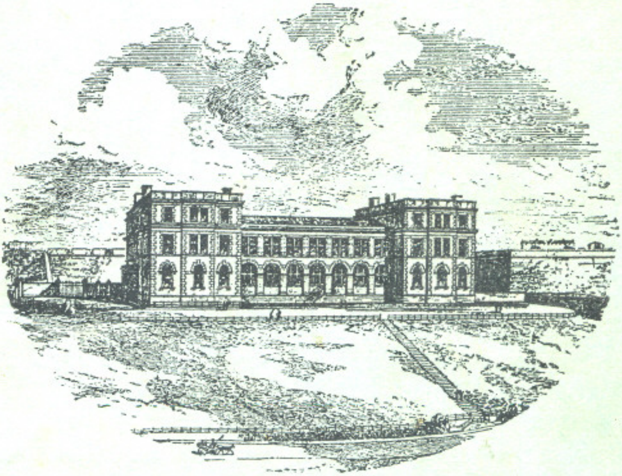

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Notes on the Biology of Certain Lamellibranchs on the Scottish Coast.

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With 15 Figures in the Text.

CONTENTS.

1. INTRODUCTION.

CASUAL observations on Cardium at Millport not agreeing closely with Orton's account of his work at Plymouth (**2**), it was felt that there might be important differences between the two areas which would make an investigation in the Millport area of interest and importance. Further, Millport is very favourably situated for such observations since the rich, extensive and little disturbed cockle-beds on the Hunterston Sands are of easy access from the Laboratory. The growth and spatting of the species have been studied for a year, from the autumn of 1929 until the autumn of 1930. The results so far obtained seem of sufficient importance to warrant a preliminary account, and it is hoped later to deal with several other points in the biology of Cardium which at present are not sufficiently clear.

The observations on *Tellina tenuis* at Stn. 5 in Kames Bay, Cumbrae, are summarised.

An attempt has also been made to carry out similar work with *Macoma baltica* in the Firth of Forth. It is unfortunate that this species is not present in the necessary quantity at Millport to give results comparable with those for Cardium and Tellina.

The methods used throughout have been those originally adopted for studying *Tellina tenuis*. Unless otherwise stated collections have been made with a 2-mm. sieve, and from an area of ¼ sq. m. dug to a depth of 15 cm. The " length " of the shell, or annual ring, has been taken as the measurement in a straight line of the greatest antero-posterior diameter. All measurements have been taken to the nearest mm. above, e.g. all specimens from 4·1 to 5·0 mm. have been counted as 5 mm. The total length of the shell has been measured on a measuring board, and the measurements of the annual rings have been made with a pair of fine dividers.

For part of the material and for the facilities which I have enjoyed at the Millport Marine Station, I am indebted to the superintendent, Mr. Elmhirst, without whose ungrudging assistance the work could not have been accomplished.

2. CARDIUM EDULE.

(a) *Introductory.*

Johnstone (**1**) states that *Cardium edule* breeds during spring and summer, this conclusion having evidently been reached from an examination of the reproductive organs. As we now know, however, this is not always a safe guide since many species carry apparently ripe reproductive products for a considerable time before spawning. Orton (**2**) largely accepts his conclusion and considers that all specimens without a well-defined ring on the shell are spatted in the same year. He also concludes that the first of the several conspicuous rings usually seen on a large shell represents the *first* winter ring. While this may be the case at Plymouth it is not borne out by the observations at Millport. As will be shown later, however, the evidence on which Orton based his conclusions is open to an alternative interpretation. The conclusions reached regarding the time of spatting at Millport have been drawn, not from the doubtful evidence of the state of the reproductive organs, but from the time of appearance of very small cockles at various stations. The evidence drawn from the observations made at Millport during 1929 and 1930 seems to point conclusively to (*a*) a summer breeding period and (*b*) to the ring laid down in the first winter being faint and easily overlooked, the first conspicuous ring being the *second*, not the *first*, winter ring.

The observations were carried out on the Hunterston Sands, which lie on the Ayrshire coast opposite the Cumbrae, and have a length of about three miles and a maximum width of about a mile at low tide. Previous to the main experiment a general survey was undertaken in the autumn of 1929 during which 26 stations, equally spaced over the sands, were examined. At each station the sand, or muddy sand, was dug out to a depth of 15 cm. from an area of ¼ sq. m. and run through a 1-mm. sieve. From the results of this survey four stations, representing the chief types of the Cardium ground, were selected for further work. These stations were as follows :—

Stn. 8.	North-east part of the sands, about half-tide, in the middle of a rich cockle bed.
Stn. 13.	Near H.W.M. at the upper edge of this bed close to the Black Rocks.
Stn. 18.	In the middle of the sands north of Poteath, about half-tide, where the Tellina and Cardium grounds overlap.
Stn. 21.	South-west end of the sands about half-tide, in the middle of a rich cockle bed.

(*b*) TIME OF SPAT-FALL.

Of the four stations No. 21 was most intensively worked and may conveniently be discussed separately.

TABLE I.*

TABLE SHOWING THE RATE OF GROWTH OF THE 1929 SPAT DURING 1930, AND THE TIME OF APPEARANCE OF THE 1930 SPAT AT STN. 21.

	Size in mm.																		Aver. size 1929	Aver. size 1930
Date.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	spat.	spat.
13.9.29	1	7	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4·4	.
18.4.30	2	17	9	6	2	2	1	1	.	.	.	.	.	.	.	.	.	.	5·1	.
1.7.30	.	.	.	.	.	3	6	13	20	19	16	8	5	5	2	1	.	.	12·1	.
24.7.30	.	.	.	1	.	.	3	1	2	2	5	5	5	2	1	.	1	.	13·1	.
6.8.30	28	4	.	.	.	.	.	.	.	.	1	2	1	7	1	1	1	.	15·9	3·1
4.10.30	18	28	21	6	1	1	.	.	.	.	.	.	.	.	1	1	1	.	18·0	4·3

* Since the older individuals do not come under review in this paragraph, the table is confined to specimens under 21 mm. in length, the rest of the collections being dealt with later.

In September, 1929, a group of very small cockles, ranging from 3 to 6 m.m., was found, but from 7 to 21 mm. there was a hiatus. Growth starts early in spring, but collecting was delayed until April so that the new year's growth should have had time to show, and the nature of the winter ring laid down by these fragile spat could be seen. In passing it may be remarked that in most of the specimens this ring was narrow and insignificant, but the original small shell could usually be distinguished by its darker colour.

In the April collection, while some shells had reached a length of 10 mm., the majority were still from 4 to 6 mm. in length, with an average size of 5·1 mm.; that is practically the same as in autumn. From April onwards growth was rapid, and in the beginning of July the young cockles ranged from 8 to 18 mm. with an average size of 12·1 mm. No specimens under 7 mm. were taken. Three weeks later the range was from 9 to 19 mm., with the exception of one specimen at 6 mm., and the average size was 13·1 mm.

By the beginning of August a great change had taken pace. The spat of 1929 now ranged from 13 to 19 mm. with an average size of 15·9 mm.; and a new group of small individuals ranging up to 4 mm. in length—the 1930 spat—had appeared. The figures, so far, all refer to the collections made with the 2-mm. sieve, but, in addition small samples of sand were run through a 1-mm. sieve as a check on new spat. Until August this procedure had shown that all the young cockles were being retained by the 2-mm. sieve, but in August it was evident that the numbers of cockles retained by the 2-mm. sieve represented only a small fraction of the spat, since from an area of $\frac{1}{4}$ sq. m. 51 cockles passed the 2-mm. sieve and were retained by the 1-mm. sieve.

By the beginning of October the 1929 spat was very much reduced in numbers, and only three specimens, ranging from 17 to 19 mm., were taken. The 1930 spat then ranged up to 8 mm. with an average size of 4·3 mm., and both its size-frequency and average size were similar to those of the 1929 spat.

Similar remarks apply to the other stations. At Stn. 8, for example (Table II), in September, 1929, there was a group of small individuals ranging from 3 mm. to 5 mm. By the end of May, 1930, the range was from 4 mm. to 13 mm. and the average size was 8·6 mm. A month later the range was from 7 mm. to 16 mm. and the average size 10·7 mm. No further collection was made until October, when only four specimens of the 1929 brood, 15 mm. to 19 mm., and only two specimens of the 1930 brood were taken. The collection taken in the beginning of December contained only seven specimens of the 1930 spat and none of the 1929 spat.

At Stn. 13 also a group of small individuals ranging from 3–7 mm. was present in September, 1929. By the end of May the range was from

5 mm. to 14 mm. and the average size was 8·1 mm. A month later the range was from 6 mm. to 15 mm. and the average size was 10·9 mm. In the beginning of October only one specimen of the 1929 spat was taken, but the new 1930 spat was present as a group of small individuals from 3 mm. to 5 mm. In the collection taken in the beginning of December the 1929 spat was found to range from 15 mm. to 19 mm. The range of the 1930 spat had increased and was from 3 mm. to 8 mm., but most of the specimens were under 7 mm. in length.

Stn. 18 was only sampled in the autumns of 1929 and 1930. Both in range and average size the spats of the two years were very similar, that of 1930 being, on the whole, rather more numerous.

TABLE II.

STN. 8.

								Length in mm.										Aver. size 1929	Aver. size 1930
Date.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	spat.	spat.
9.29	2	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3·8	.
26.5.30	.	1	4	10	18	21	20	23	10	4	2	.	.	.	.	.	.	8·6	.
29.6.30	.	.	.	.	2	1	2	7	5	6	2	.	.	1	.	.	.	10·7	.
4.10.30	1	.	1	.	.	.	.	.	.	.	.	.	1	1	.	1	1	.	.
12.12.30	6	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3·1

STN. 13.

								Length in mm.										Aver. size 1929	Aver. size 1930
Date.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	spat.	spat.
9.29	4	5	4	1	1	.	.	.	.	.	.	.	.	.	.	.	.	4·3	.
26.5.30	.	.	2	5	3	9	3	.	2	2	.	1	.	.	.	.	.	8·1	.
29.6.30	.	.	.	2	1	1	1	1	1	2	2	3	1	.	.	.	.	10·9	.
4.10.30	4	4	3	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3·9
12.12.30	6	33	17	17	2	1	.	.	.	.	.	.	2	2	2	.	1	.	4·7

STN. 18.

								Length in mm.										Aver. size 1929	Aver. size 1930
Date.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	spat.	spat.
12.9.29	28	8	3	1	2	1	.	.	.	.	.	.	.	.	.	.	.	3·7	.
4.10.30	25	59	23	9	2	.	.	.	.	.	.	.	1	1	.	.	.	.	4·2

These results indicate that at Millport the cockle breeds in summer and that the spat is to be found on the ground towards the end of August. Of the spat some few individuals may reach a size of 10 mm. before winter, but most are under 6 mm. The winter ring laid down by these small shells is usually visible if looked for carefully. It is easily seen in young specimens up to one or two years of age, but in older shells, especially if there has been any erosion, the ring is often quite obliterated.

Further evidence confirming the time of spatting has been got from the state of the reproductive organs which, at Millport, seem to be ripe from about the end of July. Spawning has only once been observed. Some cockles taken on the 1st July, 1930, were put in a jar and next day, on being given fresh water, proceeded to emit clouds of eggs and sperms. The sperms were active and clustered round each egg, but further development did not take place.

Reference has already been made to Orton's paper (**2**). Much of what he says is applicable to the Millport cockles, the great point of divergence is in the estimate of what constitutes the first winter ring. Orton in his figure (**2**, p. 251) undoubtedly calls the *first distinct ring* on the shell, apart from marking rings, the first winter ring, whereas in the Millport specimens this is the *second* winter ring. His experiment, however, while suitable for studying the growth of Cardium was not suitable for studying its spat fall. The experiment was conducted by placing marked cockles of varying size in a box moored in the river, and, to allow fresh water to flow through, the sides were covered with material having perforations 6 mm. in diameter. The box was opened periodically and the cockles examined. During spring and summer, in addition to the original large cockles, Orton found a number of small ones. These he assumed were spat carried in by the currents. While there is a possibility that this may have been the case, the more probable explanation is that these small cockles were some of the previous autumn brood which had either been washed into the box or had climbed in. The box was near the bottom of the river and it was quite possible for material from the bottom to be washed in as Orton admits (**2**, p. 253). The possibility that the small cockles may have climbed in is not at all improbable as the following observation shows. A number of small cockles about 4 mm. in length, were placed in a dish containing sea-water. One of these climbed up the side of the vessel to a height of about 2 cm. above the water, and repeated this twice when pushed back. The perforations in Orton's box were 6 mm. in diameter and, at Millport at least, even in early summer it is possible to find cockles of the previous autumn spat at this size. The smallness of the immigrating cockles, therefore, does not necessarily point to their being new spat. The question of time of spat fall is important, since on it depends the correct reading of the rings, and it would be of great value to have the question reinvestigated at Plymouth to decide if the breeding period of cockles in the two areas is really so different.

(*c*) DISTURBANCE RINGS.

Orton found that a ring was formed on the shell whenever the cockles were taken out and marked. These "false" or "disturbance rings" were similar in appearance to the true winter rings, and would have been read as such by anyone unacquainted with the history of the particular specimen. Practically all the cockles taken at Millport were of the same type, that is, they had the first two or three obvious rings on the shell separated by fairly large intervals. Only some half-dozen specimens departed from this type in that instead of one ring there were two very close together. These are similar to the disturbance rings figured by Orton. In the cockle beds from which the collections were taken it would appear that disturbance rings are only found in a small percentage of the shells.

(*d*) AGE-COMPOSITION OF THE CARDIUM ON THE HUNTERSTON SANDS.

The material on which this and the subsequent paragraph are based consists of the quantitative collections from the regular stations, supplemented by three large collections from an unmeasured area of shore at Stns. 8 and 21. In addition, two other collections from the Hunterston Sands and one from Kilchattan Bay in Bute are included since they throw light on some particular point. The numbers are not sufficient to allow of any estimate of the rate of mortality or of the proportions of the various year-groups in the population before and after spatting. The collections from each station have been considered as a whole. Some few of the specimens in which the number of rings was not clear, e.g. those showing disturbance rings, have been left out of consideration.

TABLE III.

SHOWING THE PROPORTION OF EACH YEAR'S SPAT IN THE COLLECTIONS FROM EACH STATION CONSIDERED AS A WHOLE.

Stn.	1920.	1921.	1922.	1923.	1924.	1925.	1926.	1927.	1928.
8	.	.	.	.	7	17	189	19	24
13	.	.	2	1	6	15	26	10	17
18	.	1	.	1	1	10	18	5	4
21	1	4	8	8	14	21	279	57	40

Specimens spatted in all years from 1920 were taken and the numbers belonging to each year-group are set out in Table III, the spat of the years 1929 and 1930 excepted since they have been fully dealt with already.

The group spatted in 1926 was the dominant group at all stations, especially at Stns. 21 and 8 in the middle of the beds where density is greatest. At Stns. 13 and 18, at the landward and seaward edges of the beds, it was almost rivalled in numbers by the survivors of the 1925 spat. A supplementary collection from a position 100 yards landwards from Stn. 21 yielded 27 cockles from $\frac{1}{4}$ sq. m. of ground, and of these 21 were spatted in 1926.

This preponderance of the 1926 spat is significant when compared with the similar predominance of the 1926 spat of Tellina in Kames Bay. The observations on Tellina were made in a very small area, but the figures for Cardium are drawn from stations about a mile apart and on the other side of the channel from Kames Bay. Taking the two sets of results into consideration the summer of 1926 seems to have been unusually favourable for the spatting of both Cardium and Tellina, and possibly other species as well. The causes of these variations have not yet been determined.

The predominance of the cockles spatted in 1926 over the other year-groups during the period 1926–1930, seems to have extended beyond the comparatively small area on the east side of the Cumbrae covered by these experiments. On the opposite side of the Cumbrae, and separated from it by about 3 miles of sea, lies Kilchattan Bay in Bute. A collection of cockles from near H.W.M. in the spring of 1929 gave the following distribution of year-groups :—

1924 spat . . .	11
1925 ,, . . .	3
1926 ,, . . .	15
1927 ,, . . .	2
1928 ,, . . .	0

This would point to the survival of the 1926 spat in unusual quantities over a fairly wide area. It is not possible at present to say just how far that area extended.

(*e*) SIZE AT EACH WINTER RING.

The size of each winter ring in the survivors of the successive broods has been calculated, but, except in the case of the 1926 spat, the numbers are so small that only a general summary has been given.

1930 *Spat.* (Tables I and II.)

In the beginning of August this was found at Stn. 21. The other stations were not examined at this time, but this spat would certainly have been found at them also. By the beginning of October at Stn. 21 the range extended up to 8 mm., but most of the specimens were not over 5 mm. in length. At Stn. 18 the range in October extended up to 7 mm., as at Stn. 21, however, most of the specimens were under 5 mm. At Stn. 13 only a few specimens ranging up to 5 mm. were taken. At Stn. 8 the October collection yielded only a few spat, and its scarceness at this station was emphasised by the December collection, when only 7 specimens were taken from $\frac{1}{4}$ sq. m. of ground. On the other hand, a collection taken at Stn. 13 in December gave 76 specimens per $\frac{1}{4}$ sq. m. These ranged up to 8 mm. in length, but the majority were below 6 mm.

1929 *Spat.* (Tables I and II.)

The individuals belonging to this group, like those spatted in 1930, showed no well-marked ring, only the faint first winter ring being visible. The first clear ring would be laid down in the winter 1930–31. Briefly summarised—this group spatted in the late summer of 1929 was found at all stations in September of that year, ranging up to 8 mm. in length. During the following year it gradually decreased in abundance and was comparatively scarce by the end of 1930, the survivors then being between 15 and 19 mm. in length.

There is naturally a certain amount of variation from sample to sample, but during the year the numbers steadily declined and this was confirmed by an examination of the shore in October when the empty shells were lying everywhere. This raises the question as to whether the modes and means at various periods of the year, e.g. Tables I and II, represent the actual rate of growth of the survivors. I think they do not and that they are consistently too low. Some individuals of a group grow quickly from the start, others slowly, and it seems to be amongst the slower growing members that mortality is greatest.

1928 *Spat.* (Table IV.)

The cockles spatted in 1928 and taken during 1930 had only one well-defined ring on the shell, namely, the 1929–30 winter ring. They were not very plentiful. At Stn. 18 only four specimens were taken, and need not be considered. Those taken at Stns. 21 and 8 were alike, in that the range was large, 15–25 mm. and 14–26 mm. respectively, and the means much the same, 20·6 mm. and 20·3 mm., but differed from those taken at Stn. 13 where it was small, 15–20 mm., and the mean low, 17·4 mm.

TABLE IV.

SHOWING THE SIZE-FREQUENCY IN MM. OF THE 1929–30 WINTER RING IN THE 1928 SPAT.

Stn.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25.	26.	Mean.
21	.	1	1	.	2	10	4	7	7	4	3	1	.	20·6
18	.	.	1	.	1	.	.	.	.	.	2	.	.	.
13	.	5	1	2	2	5	2	.	.	.	.	.	.	17·4
8	1	.	2	1	4	3	3	2	.	3	2	2	1	20·3

1927 *Spat.* (Table V.)

The individuals derived from this spat and taken in September, 1929, had only one well-marked ring, the 1928–29 winter ring, while those taken during 1930 had two, the 1928–29 and 1929–30 winter rings. This was the scarcest of all the recent year-groups and, except at Stn. 21, only a few were taken.

1928–29 *Winter Ring.*

At Stn. 21 the range was from 14 mm. to 27 mm. and the mean was 20·8 mm. At Stn. 8 the range was rather narrower, but the mean was about the same. At Stn. 13 the range was narrower and the mean less than at either of these two stations.

1929–30 *Ring.*

At Stn. 21 the range was from 22 mm. to 37 mm. and the mean was at 29·8 mm. At Stn. 13 the range was narrower, 24–28 mm., and the mean less, 26·4 mm.

TABLE V.

Showing the Size-Frequency of the 1928–29 and 1929–30 Winter Rings in the 1927 Spat.

1928–1929 Ring.

Stn.	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	Mean.
8	.	.	.	1	1	.	2	6	3	1	1	.	.	.	.	.	20·9
13	.	.	1	.	1	2	1	4	1	.	.	.	.	.	.	.	19·6
18	.	.	.	.	.	.	.	2	1	.	.	1	1	.	.	.	.
21	2	.	1	4	4	9	7	6	9	7	4	1	2	1	.	.	20·8

1929–1930 Ring.

Stn.	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Mean.
8	.	.	.	.	.	1	1	2	5	2	1	.	1	1	.	.	30·4
13	.	.	1	2	1	4	2	.	.	.	.	.	.	.	.	.	26·4
18	.	.	.	.	.	.	1	2	.	.	.	1	1	.	.	.	.
21	1	.	1	2	7	6	6	9	4	3	2	6	1	3	2	3	29·8

TABLE VI.

Showing the Size-Frequencies of the Winter Rings for the 1926 Spat.

1927–28 Ring.

Stn.	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Mean.
8	1	.	.	3	5	5	16	21	33	22	23	11	26	8	11	1	2	1	22·3
13	1	.	.	1	1	5	5	7	3	1	1	1	.	.	.	.	.	.	19·3
18	.	.	.	.	.	.	.	3	2	3	2	6	1	1	.	.	.	.	22·7
21	.	2	.	1	5	7	18	38	30	54	53	28	24	13	4	2	.	.	22·4

1928–29 Ring.

Stn.	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	Mean.
8	.	.	1	2	3	7	17	17	26	25	26	18	14	16	11	3	2	1	31·2
13	1	4	1	6	4	2	4	2	2	.	.	.	.	.	.	.	.	.	25·2
18	.	.	.	.	.	1	2	4	4	3	1	.	.	2	.	1	.	.	30·6
21	1	.	2	3	6	8	27	43	50	57	40	20	15	5	2	.	.	.	30·4

1929–30 Ring.

Stn.	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	Mean.
8	.	.	.	.	.	1	8	11	14	21	31	26	23	20	9	17	3	3	.	2	36·0
13	1	3	2	5	4	2	2	4	2	1	.	.	.	.	.	.	.	.	.	.	29·3
18	.	.	.	.	.	1	1	4	5	1	1	2	.	2	.	1	.	.	.	.	33·9
21	.	.	.	1	.	7	21	31	40	46	52	41	27	5	5	2	1	.	.	.	34·2

1930–31 Ring.

Stn.	33	34	35	36	37	38	39	40	41	42	Mean.
8	3	3	3	3	5	3	3	1	.	1	36·5
18	1	1	.	3	1	2	.	.	.	.	36·0

1926 *Spat.* (Table VI.)

The specimens taken during September, 1929, had two well-marked rings, and those taken during 1930 had three well-marked rings. The length of specimens taken October and December, 1930, may be taken as the equivalent of the 1930–31 winter ring, which would just be beginning to be laid down. The size-frequencies and means of the various winter rings are set out in Table VI.

1927–28 *Winter Ring.*

At Stn. 8 the range was from 13 to 30 mm., but in most of the specimens was between 19 and 27 mm., and the mean size was 22·3 mm. At Stns. 13 and 18 comparatively few specimens were taken and on these the range was from 13 to 24 mm. with the mean at 19·3 mm. in the first case, and from 20 to 26 mm. with the mean at 22·7 mm. in the second case. At Stn. 21 the range was from 14 to 28 mm., but in most of the specimens was between 18 and 27 mm., and the mean was at 22·4 mm. The means at Stns. 8, 18, and 21 were all very nearly the same, but the mean at Stn. 13 was considerably lower.

1928–29 *Winter Ring.*

At Stn. 8 the range was from 24 to 39 mm., but as before most of the measurements were confined within narrower limits, namely, 28 to 36 mm. The mean was at 31·2 mm. At Stn. 13 the range was from 22 to 30 mm. and the mean was at 25·2 mm. At Stn. 18 the range was from 27 to 37 mm. and the mean was 30·6 mm. At Stn. 21 the range was again large, being from 22 to 36 mm.; as before the majority of the rings were confined within narrower limits, namely, 28 mm. to 34 mm. The mean was at 30·4 mm. As before the mean at Stn. 13 was considerably below the means of the other stations.

1929–30 *Winter Ring.*

At Stn. 8 the range was from 30 to 44 mm., but most of the figures lay between 32 and 40 mm., with the mean at 36·0 mm. At Stn. 13 the range was from 25 to 34 mm. and the mean was at 29·3 mm. At Stn. 18 the range was from 30 to 40 mm. and the mean was at 33·9 mm. At Stn. 21 the range was from 28 to 41 mm., but most of the figures lay between 30 and 38 mm., with the mean at 34·2 mm.

1930–31 *Winter Ring.*

The October and December measurements of the lengths of the shell may be taken as representing approximately the size of this ring. Since only very few specimens were taken at Stns. 13 and 21 these stations have not been included in Table VI.

At Stn. 8 the range was from 33 to 42 mm. and the mean was at 36·5 mm. At Stn. 18 the range was from 33 to 38 mm. with the mean at 36·0 mm.

Spat of 1925 *and Previous Years.* (Table VII.)

Very few of the cockles spatted in these years were found in the collections, and no useful purpose would be served by considering the size-frequencies of the various winter rings in detail, but for comparison the means of the various winter rings have been calculated. Table VII.

TABLE VII.

Table Showing the Mean Size of the successive Distinct Rings on each Year's Spat at the various Stations. Where only one or two Specimens were present the Average has not been calculated. At Stns. 8 and 13 the presumed Length of the 1930–31 Ring is included. The Material was Collected during 1929 and 1930.

stn. 21.

1921	20·5	30·2	35·8	39·2	42·0	44·5	46·0	47·2	.
1922	22·4	32·4	37·0	40·1	42·9	44·9	46·2	.	.
1923	22·2	32·1	37·2	40·3	42·8	44·1	.	.	.
1924	22·7	32·5	37·2	39·3	40·6	.	.	.	.
1925	23·0	33·0	35·6	39·2	.	.	.	.	.
1926	22·4	30·4	34·2	.	.	.	.	.	.
1927	20·8	29·8	.	.	.	.	.	.	.
1928	20·6	.	.	.	.	.	.	.	.

stn. 18.

1925	23·6	33·2	35·9	38·1	.	.	.	.	.
1926	22·7	30·6	33·9	.	.	.	.	.	.

stn. 13.

1924	22·8	28·7	31·7	33·8	35·7	38·0	.	.	.
1925	19·8	25·5	28·7	31·1	.	.	.	.	.
1926	19·3	25·2	29·3	.	.	.	.	.	.
1927	19·6	26·4	.	.	.	.	.	.	.
1928	17·4	.	.	.	.	.	.	.	.

stn. 8.

1924	25·9	35·6	39·3	41·3	42·6	.	.	.	.
1925	21·1	28·2	33·1	35·4	37·8	.	.	.	.
1926	22·3	31·2	36·0	36·5	.	.	.	.	.
1927	20·9	30·4	.	.	.	.	.	.	.
1928	20·3	.	.	.	.	.	.	.	.

In all but the 1926 year-group the numbers are too few to allow of much reliance being placed on the means, especially considering the wide range of the size-frequency figures for any one ring, e.g. Tables I, II, and IV, but the figures are fairly consistent. For any one station the means of the older groups are distinctly higher than those of the younger groups, and this would point to the suggestion already made that mortality tends to be heaviest at the lower end of the size-frequency scale.

It is interesting to compare this table with Orton **2**, p. 250, Table II, showing the rate of growth of his marked cockles. Their rate of growth corresponds fairly well with that at Stn. 21, i.e. an average section from a natural bed and, except for the difference in the estimation of what constitutes the first winter ring, the two investigations are confirmatory.

In addition to the collections from the regular stations two others from these sands may be mentioned. One sample taken on the 16.8.30, from a position 100 yards landwards from Stn. 21, contained 27 cockles per $\frac{1}{4}$ sq. m. This position was roughly intermediate between Stns. 21 and 13 as regards level and, as was to be expected, both the range and means were intermediate between those of these two stations, e.g.

1927–28 Ring.	1928–29 Ring.	1929–30 Ring.
Range 17–24 mm.	Range 23–31 mm.	Range 27–33 mm.
Mean 20·5 mm.	Mean 27·8 mm.	Mean 30·5 mm.

Another collection was taken in July at some distance to the seaward of Stn. 21 beyond the cockle beds proper, and in the Tellina ground where only few and large cockles occur. (Stn. 16.) A $\frac{1}{4}$ sq. m. sample yielded 7 cockles which were remarkable for their large growth, e.g. Table VIII.

TABLE VIII.

1925–6 Ring.	1926–7 Ring.	1927–8 Ring.	1928–9 Ring.	1929–30 Ring.	Total length 1.7.30.	Spatted in autumn of
33	44	52	53	54	54	1924
.	.	.	27	38	44	1927
.	.	.	24	35	39	,,
.	.	.	.	27	37	1928
.	.	.	.	29	35	,,
.	.	.	.	27	34	,,
.	.	.	.	26	33	,,

1928 Spat.
1929–30 Ring.
Mean 27·3 mm.

Kilchattan Bay, Bute.

This collection, already referred to on p. 284, was taken close to H.W.M., 29.3.29, and the means would be expected to compare with those of Stn. 13. This is actually the case, as may be seen by comparing with Stn. 13 the specimens spatted in 1924 and 1926, of which 11 and 15 specimens, respectively, were taken.

	1925–26 Ring.	1926–27 Ring.	1927–28 Ring.	1928–29 Ring.
Stn. 13. Hunterston 1926 spat	.	.	19·3	25·2
Kilchattan Bay 1926 spat	.	.	17·9	25·7
,, ,, 1924 spat	20·0	25·8	28·8	31·5

(*f*) DIFFERENCES IN THE RATE OF GROWTH BETWEEN H.W.M. AND L.W.M.

It has already been shown (Stephen, **5**) that the cockle gets smaller from L.W.M. to H.W.M. This could come about in two ways, either by the rate of growth being different at various levels, or by the spat falling in greatest quantity on the upper part of the beach and gradually migrating seawards. The first explanation seems to be the correct one if the means are compared. If migration took place the means of the rings formed in the earlier years of life should be very much the same for all specimens and at all levels, actually the means increase from H.W.M. to L.W.M. Although the following four stations do not lie in a straight line their means may be used to illustrate this difference of growth. The means for the first three stations are those of the 1926 spat and for Stn. 16 that of the 1928 spat. Table IX.

TABLE IX.

	1st Clear Ring.	2nd Clear Ring.	3rd Clear Ring.
Stn. 13. Near H.W.M.	19·3	25·2	29·3
100 yards up from Stn. 21. $\frac{3}{4}$ tide .	20·5	27·8	30·5
Stn. 21, half-tide	22·4	30·4	34·2
Stn. 16, near L.W.M.	27·3	.	.

The cockle therefore increases regularly in size from H.W.M. to L.W.M. In this it resembles *Arenicola marina* and differs from *Tellina tenuis* and *Donax vittatus*.

So far as could be seen almost all the cockles at any station were of the same type, but occasionally at the lower stations a cockle was found which had obviously been washed down from higher up. At Stn. 21, for example, only three of the cockles taken were exceptional in that they had the annual rings much closer together than the rest of the specimens, and corresponded to the type found at the station 100 yards further up the beach.

This summary deals only with some of the more important points in the biology of the cockle, but others are being investigated, and it is hoped at a later date to deal with the species in greater detail.

3. TELLINA TENUIS.

Observations in Kames Bay have been carried out regularly during the period middle of September, 1926, to end of August, 1930, and while there is little to add to the accounts already published of the rate of growth and time of spat-fall (Stephen, **3** and **4**), new facts have been gathered regarding (*a*) the variations in the quantity of spat and in the total population from year to year, and (*b*) the growth and final disappearance of the generation spatted in the autumn of 1926.

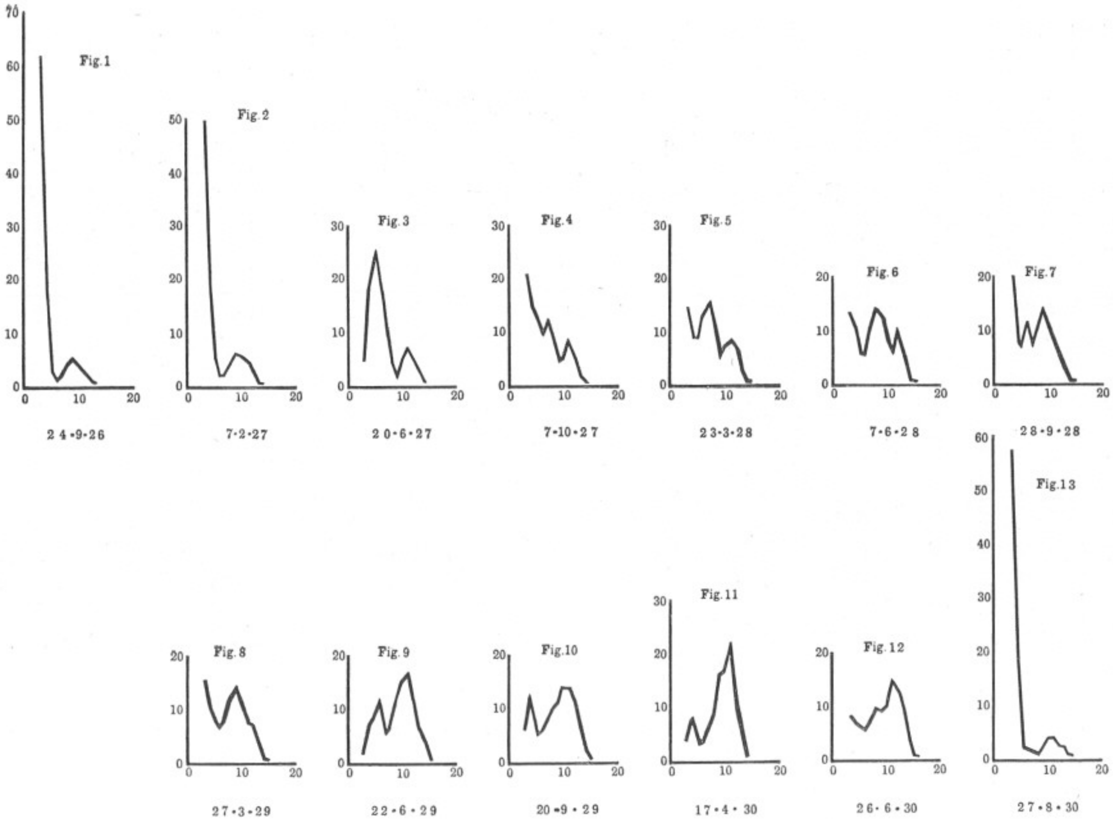
(*a*) VARIATIONS IN THE QUANTITY OF SPAT AND IN THE TOTAL POPULATION.

In the earlier part of the investigation on *Tellina tenuis* in Kames Bay, collections were made at several stations, which were later reduced to two, namely, Stn. 2 near H.W.M. neaps and Stn. 5 at L.W.M. springs. Early in 1930 heavy storms completely altered and destroyed much of the upper part of the beach. The continuity of the experiment at Stn. 2 was therefore broken, but fortunately Stn. 5 was not affected, and a complete record of the size-frequencies of the population from September, 1926, to the end of August, 1930, has been obtained. Regular collections were made in spring, summer, and autumn, and in all but two cases these were quantitative. On the two occasions the station was not completely uncovered by the tide and qualitative collections only were obtained. A few supplementary collections were taken from time to time.

The amount of " spat " per unit area in Kames Bay in the autumn of each year is given in Table X A, all specimens 3 and 4 mm. in length being counted as " spat." These figures are probably a slight underestimate.

Spat was not laid down in equal amounts each year. In the autumn of 1926 it was very abundant and formed about 80% of the population. In 1927 it was also abundant, but the amount was only about half that of the previous year. Owing to the high rate of survival of the 1926 spat, however, it only formed 36% of the population. In 1928 spat was fairly plentiful, but again owing to the large number of older individuals on the ground formed only 28% of the population. Spat was very scarce in 1929, reaching the comparatively low figure of about 230 per sq. m.; 1930 was once more a year of abundance, although the number of spat was below that of 1926. The older individuals seem to have died out very largely after spatting, and the percentage of spat to total population once more rose nearly to the 1926 figure of 80%. These changes are shown in Figures 1 to 13.

There are two seasons when mortality might be expected to be high, (*a*) in winter amongst the spat and (*b*) in summer after spatting, amongst the older specimens. Winter mortality amongst the spat seems to be comparatively slight. In Table X B the percentage of spat to total population



Figs. 1–13.—Showing the size-frequency of the *Tellina tenuis* population at Kames Bay, Millport, from 1926–30. The Ordinates represent the percentage of the catch and the abscissæ the sizes in mm.

has been tabulated for autumn and spring. In each case the spring percentage is only a little less than the autumn one, and it is evident that the death-rate has been low. In the second case mortality after spatting is often very heavy, and a whole year-group may die off within a short period (pp. 294, 297).

TABLE X.

SHOWING THE PERCENTAGE OF SPAT TO TOTAL POPULATION IN AUTUMN AND SPRING AT STN. 5, KAMES BAY, MILLPORT.

A. AUTUMN.

Date.	No. of Spat per sq. m.	Total Tellina Population per sq. m.	% of Spat.
24.9.26	2620	3288	80
7.10.27	1088	3056	36
28.9.28	854	3038	28
20.9.29	232	1348	17
27.8.30	1628	2136	76

B. SPRING.

Date.	No. of Spat per sq. m.	Total Tellina Population per sq. m.	% of Spat.
13.4.27	2664	3595	74
23.3.28	716	2912	25
27.3.29	508	2004	25
17.4.30	156	1480	11

(*b*) VARIATION IN DENSITY OF POPULATION.

In accordance with the variation in recruitment from unequal spattings coupled with the rise and decline of the 1926 spat, the density of population at Stn. 5 has fluctuated considerably during the period, as may be seen from Table XI.

TABLE XI

SHOWING THE VARIATION IN DENSITY OF POPULATION PER SQ. M. AT STN. 5. (Owing to the great similarity of the figures for each of the collections during 1927 and 1928 the table has been shortened by giving the average for these years.)

24.9.26	3288 per sq. m.
1927 (average)	3403 ,, ,,
1928 ,,	2883 ,, ,,
27.3.29	2004 ,, ,,
20.9.29	1348 ,, ,,
17.4.30	1480 ,, ,,
26.6.30	1094 ,, ,,
27.8.30	2136 ,, ,,

In the autumn of 1926 the density of population was over 3000 per sq. m. During 1927 the figure was very much the same and dropped only slightly during 1928. From the autumn of 1928 onwards the fall was rapid, till by the middle of 1930 the density was just over 1000 per sq. m. In August the appearance of the new 1930 spat in large quantities almost doubled the density.

(*c*) RISE AND DECLINE OF THE 1926 SPAT.

As already stated, spat appeared in abundance in the autumn of 1926 and the survivors continued to be the dominant year-group until the summer of 1930, when, after spatting, they largely died out. This has been illustrated graphically in Figs.. 1–13. The figures from which these curves are drawn are given in Stephen, **3**, for 1926–27, Stephen, **4**, for 1928, and in Table XIII for 1929–30.

Judging by the modes, Table XII, this group seems to have reached its maximum size by the summer of 1929.

TABLE XII.

Showing the Modes of the 1926 Spat at Stn. 5 for each time of Collection, 1926–1930.

24.9.26	3 mm.	27.3.29	9 mm.
13.4.27	3 mm.	22.6.29	11 mm.
20.6.27	5 mm.	20.9.29	11 mm.
7.10.27	7 mm.	17.4.30	11 mm.
23.3.28	7 mm.	26.6.30	11 mm.
7.6.28	8 mm.	27.8.30	11 mm.
28.9.28	9 mm.		

The story of the 1926 spat may therefore be summarised as follows :—Spatted in the late summer of 1926, it was found in quantity at Stn. 5 in September, forming a well-defined peak on the size-frequency curve and comprising about 80% of the population. The modal size in September, 1926, was 3 mm., and by the autumn of 1927 this had increased to 7 mm. By the autumn of 1928 it had reached 9 mm., and by June, 1929, 11 mm., at which figure it remained until the following year. In the first half of 1930 the ground was very largely populated by the 1926 spat, but by August the character of the population was completely changed. The individuals spatted in 1926 had largely died out and the 1930 spat had appeared in quantity. The percentage of spat to total population was 76%, that is, approximately, the 1926 figure, after an interval of four years.

The fate of the spat of the intervening years 1927–29 is of interest since the curves (Figs. 1–13) are largely bimodal and give the false impression that there are only two year-groups on the ground.

In the autumn of 1927 spat came down in fair abundance and showed on the curves for the whole of the next year. The mode was at 3 mm. in October, 1927 (Fig. 4), and March, 1928 (Fig. 5) ; 3 mm. in June (Fig. 6) ; and 6 mm. in September (Fig. 7). From then onwards it seems to have disappeared entirely from the curves, having apparently failed to survive the winter.

In 1928 spat was also found in fair abundance. In September, 1928, it showed as a group with the mode at 3 mm. (Fig. 7). The mode was at the same figure in March, 1929 (Fig. 8). In June the mode was at 6 mm. (Fig. 9), and by September this spat had apparently overtaken the slowest growing individuals of the 1926 spat and the two curves merge into one, forming a composite group, the mode showing as an irregularity on the curve about 8–9 mm. (Fig. 10). This irregularity continued to show on the curves until June, 1930 (Figs. 11 and 12), and it is presumed that the 1928 spat continued to survive until then. The spat in 1929 was very scarce and could not be traced on the curves for 1930.

Rich spat-falls apparently occur only at intervals, and may produce a year-group which remains dominant on the ground for some years. Two factors probably combine to produce this result. There must, of course, be a specially abundant spat-fall, but the spat must also get a good start, for a poor start is apparently a handicap which is never overcome. For example, the spat of 1927 was more abundant than that of 1928, yet the spat of 1927 soon disappeared from the curves while the 1928 spat could be traced until June, 1930. A possible reason for this difference appears if the early history of each year-group is compared. Both ceased to grow during the winter and both started off with a mode of 3 mm. in spring, but whereas the mode of the 1927 spat was still at 3 mm. in June (1928) the mode of the 1928 spat was at 6 mm. in June (1929). By the end of 1928 the mode of the 1927 spat had only reached 6 mm. (equivalent to the June mode of the 1928 spat), while by the end of 1929 the 1928 spat had reached 8–9 mm. Apparently the adverse spring of 1928 had been a handicap to the 1927 spat from which it had never recovered. These interesting problems will be the subject of further investigation.

TABLE XIII.

SHOWING PERCENTAGE AT EACH MM. SIZE FOR TELLINA TENUIS AT STN. 5, KAMES BAY, 1929–1930.

Date.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total No. of specimens.
27.3.29	15·3	10·1	8·0	6·3	7·5	11·5	13·4	10·1	7·1	6·8	3·3	0·5	0·2	.	0·1	1002
22.6.29	1·8	6·7	8·0	10·6	5·0	6·2	10·6	14·1	15·9	11·8	5·9	3·8	0·3	.	.	341
20.9.29	5·8	11·3	4·6	5·3	7·6	9·6	10·3	13·5	13·4	11·1	5·5	1·7	0·4	.	.	1012
17.4.30	3·5	7·3	3·0	3·2	6·0	8·4	15·9	16·1	20·8	10·5	5·1	0·8	.	.	.	370
26.6.30	8·0	6·7	6·0	5·1	6·7	9·0	8·8	9·9	14·0	12·6	8·9	3·1	0·6	0·2	.	547
27.8.30	57·7	18·4	2·2	2·0	1·8	0·9	2·9	4·0	4·1	2·4	2·3	0·9	0·3	.	.	1068

4. MACOMA BALTICA.

RATE OF GROWTH AND TIME OF SPAT-FALL (FIGS. 14 AND 15).

An attempt has been made to estimate the rate of growth and time of spat-fall for this species. It is not very abundant in the Cumbrae area, but is plentiful in certain parts of the Firth of Forth. In Aberlady Bay, for example, where the species is relatively abundant, the density reaches about 150 to 200 per sq. m. in places. This bay was therefore chosen as a suitable locality for study, and collections were made during 1929 and 1930 at one station about 100 yards from H.W.M.

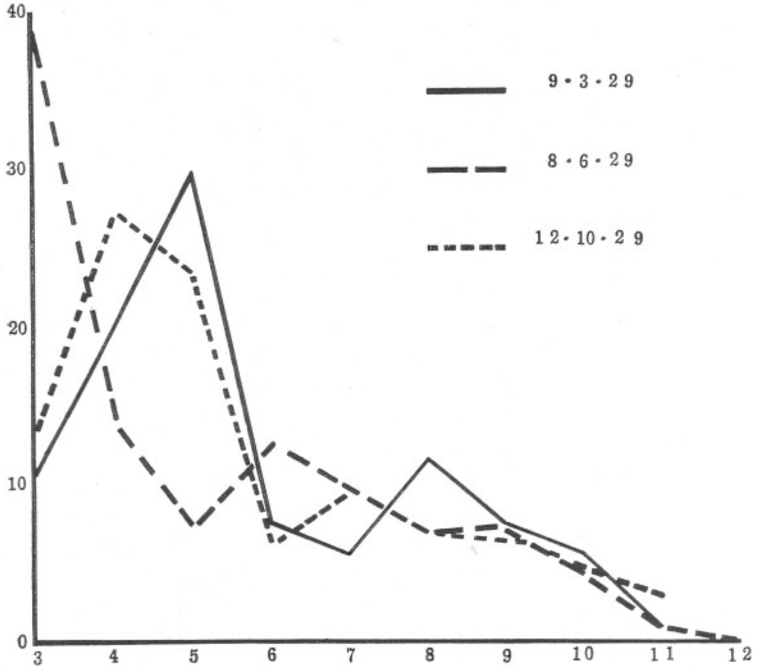


FIG. 14.—Showing the size-frequency curves for the collections of *Macoma baltica* taken in Aberlady Bay during 1929.

Ordinate percentage of the total catch.
Abscissa size in mm.

In the spring of 1929 there were modes at 5 mm. and 8 mm. on the curve, representing, it may be assumed in the light of later knowledge, the 1928 and 1927 spat respectively. In the beginning of June the modes were at 3 mm. and 6 mm. with a hint of a third at 9 mm. The mode at 3 mm. represents the new 1929 spat, that at 6 mm. the 1928 spat, and the mode at 9 mm. the 1927 spat. The latter seemed to be dying off after the breeding season. In October the modes were at 4 mm. and 7 mm., the 927 group having apparently entirely disappeared.

Compared with the spring modes of 1929, which may be taken as the equivalent of the October, 1928, modes, since growth ceases during the winter, the position of the modes in October, 1929, would point to growth having been slower than in the previous year, probably on account of the heavier spat-fall and therefore greater competition for food.

In 1930 growth among the smaller individuals had begun before the spring samples were taken, since the first mode had moved from 4 mm. to 5 mm. The second mode remained unaltered. On the June curve, as in the previous year, there were three modes at 3 mm., 5 mm., and 9 mm., representing the new 1930 spat, the 1929 spat, and the 1928 spat respectively. Sampling was repeated on two occasions in October, but for several reasons the collections were unsatisfactory. The size-frequency curve for these small collections gave a hint of modes at 5 mm. and 7 mm., but it was impossible to judge if the oldest group had survived.

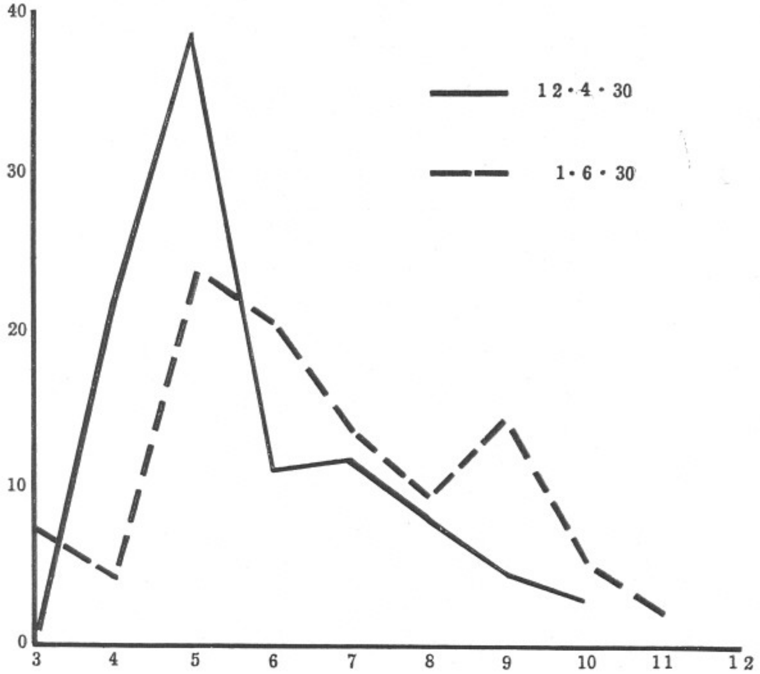


Fig. 15.—Showing the size-frequency curves for the collections of *Macoma baltica* taken in Aberlady Bay in 1930.

Ordinate percentage of the total catch.
Abscissa size in mm.

Judging by the analogy of the previous year it had probably died out more or less completely after the breeding season.

To summarise. *Macoma baltica* apparently breeds in spring, and since spat was found in June of both the years 1929, 1930, the period April to May is suggested as the possible breeding period. The spat is well-grown before winter sets in. Judging by the modes the size at the end of the first autumn is about 5 mm. and at the end of the second about 7–8 mm. at this particular station. It would seem from the 1929 figures that mortality is heavy after spatting in the third summer. Breeding probably occurs earlier in life, but it is after this time that the large individuals tend to disappear in greatest numbers.

The year 1929 seems to have been a very favourable one for spat, since the average density of spat in June was about 150 per sq. m. On the other hand, the year 1930 seems to have been very poor, since the density in June of that year was only about 30 per sq. m. The term "spat" in the above paragraph has been restricted to individuals up to 3 mm. in length. The size-frequencies of the specimens taken in 1929 and 1930 are set out in Table XIV.

TABLE XIV.

SHOWING THE FREQUENCY AT EACH MM. SIZE FOR *M. baltica* IN ABERLADY BAY, FIRTH OF FORTH, DURING 1929 AND 1930.

Date.	3	4	5	6	7	8	9	10	11	12	Total No. of specimens.
9.3.29	11·0	20·3	30·0	7·4	5·5	11·5	7·4	5·5	0·9	.	216
8.6.29	37·9	14·0	7·2	12·4	9·7	7·0	7·2	4·3	0·8	0·2	518
12.10.29	13·6	27·2	23·2	6·3	9·4	7·4	6·3	4·2	2·6	.	191
12.4.30	0·6	21·5	38·4	11·0	12·8	8·1	4·7	2·9	.	.	172
1.6.30	7·2	4·1	23·7	20·6	13·4	9·2	14·4	5·2	2·1	.	97

5. SUMMARY.

(*a*) CARDIUM EDULE OR COCKLE.

1. The observations were made on the Hunterston Sands, Ayrshire, opposite the Cumbrae.

2. Small cockles appear on the ground about the beginning of August. This points to the breeding season being in *summer* and not spring, as is usually stated.

3. By the end of the first autumn some few of the spat are as much as 10 mm. in length, but most are under 6 mm. The winter ring is faint and easily overlooked.

4. The first of the several well-defined rings is therefore not the *first* but the *second* winter ring.

5. Certain year-groups predominate. The specimens taken during 1929 and 1930 were largely the survivors of the 1926 spat.

6. The mean length of each of the winter rings has been tabulated for each year-group. These means tend to be higher in the older groups, pointing to mortality being heaviest amongst the slower growing individuals.

7. The size increases regularly from H.W.M. to L.W.M., due to an increased rate of growth. Growth is very fast amongst the scattered individuals living in the Tellina ground, that is, seawards of the cockle beds proper.

TELLINA TENUIS.

1. The variations in the annual spat-fall at Stn. 5 in Kames Bay from 1926–30 are traced. Some years give a rich spat, others only a poor spat, but the final contribution to the population may depend on other factors as well, e.g. a good growing start.

2. Mortality is comparatively light amongst the spat during winter, but may be exceedingly heavy after spatting amongst the adult population.

3. At Stn. 5 the group spatted in the autumn of 1926 remained the dominant year-group until the summer of 1930.

4. The spat of 1930 was abundant and, owing to the heavy mortality amongst the adults after spatting, the type of size-frequency curve seen in September, 1926, was repeated, after an interval of four years.

MACOMA BALTICA.

1. The species was observed in Aberlady Bay, Firth of Forth.

2. Small individuals appear in June and the breeding period is probably April to May.

3. By the end of the first year the average size is about 5 mm., and by the end of the second 8 to 9 mm. The end of the breeding season in the third summer seems to mark the termination of the life of the average individual.

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On the Effect of the severe Winter of 1928–1929 on the Oyster Drills (with a record of five years' observations on sea-temperature on the oyster-beds) of the Blackwater Estuary.

By

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With 2 Figures in the Text.

During the year 1928 the writer was engaged in a study of the bionomics of the oyster drills on the oyster beds in the region of the River Blackwater, Essex. At this time the presence of a foreign species was detected (**1**) and definite records were made of the relative abundance of the three following drills or tingles :—*Murex erinaceus* (=Ocinebra), *Purpura lapillus* (=Nucella), and *Urosalpinx cinerea*. It so happened that the winter of 1928–29 was unusually cold ; the temperature of the water over the oyster beds was unusually low in January and February, 1929, ranging about the freezing-point of fresh water (see Table II and Fig. 1). The oyster-cultivators in this locality had many years previously stated that during severe winters many marine animals, such as the oyster drills or tingles and the burr *Echinus miliaris*, are killed in such great numbers as sometimes to exterminate the species. The observations made by the writer in 1928 offered an opportunity to test these statements, and of estimating the effect of the extreme cold in early 1929 on the animals mentioned above.

Three of the four species studied, namely, Murex, Purpura, and Echinus, are rarely found—in the district of the River Blackwater—above low-water mark ; Urosalpinx may be taken by hand in fair numbers especially in the warmer months of the year on or about oysters at extreme low-water springs. (Such a habitat is noteworthy in the case of *Purpura lapillus*, which is abundant on the foreshore in the *Balanus balanoides* zone on the coasts of Devon and Cornwall, and in some other localities.)

The constant immersion during the winter period of the four species noted eliminates any direct effect of air temperature, and confines the influence of temperature to that of the water. Temperature readings at and about high and low water have been recorded almost daily for the writer by Mr. Laban Pearce (see **2**) over a period of five years, and are recorded in Tables VII, p. 313, I and II, and Fig. 1, p. 304, being reduced to mean monthly figures. These readings prove that the mean monthly temperature of the water over the oyster beds in the River Blackwater was 4° to 10° F. below normal during most of January and February and the first week in March in 1929. The two-day means of readings (usually four) during January and February are also plotted in Fig. 1, p. 304, from the daily readings given in Table II.

TABLE I.

MEAN MONTHLY TEMPERATURE OF SEA AND AIR OF THE BLACKWATER ESTUARY (IN DEGREES FAHRENHEIT).

	Air* (1876–1910) Blackwater.	Sea‡ (1926–8, 1930) Blackwater.				Air† (1928–9) Clacton-on-Sea.	Sea (1928–9) Blackwater.
		H.W.	L.W.	Mean °F.	Mean °C.		
Jan.	37·9	38·9	38·7	38·8	3·7	34·9	34·2
Feb.	39·3	40·6	40·3	40·4	4·6	31·9	32·5
March	41·7	43·6	43·9	43·7	6·5	41·1	38·9
April	47·0	48·5	48·8	48·8	9·2	43·5	45·1
May	52·4	54·9	55·5	55·2	12·9		
June	58·4	61·5	62·0	61·7	16·5		
July	62·1	65·8	65·8	65·8	18·7		
Aug.	62·4	64·3	64·2	64·3	17·9		
Sept.	58·0	61·8	61·3	61·6	16·4		
Oct.	51·1	53·2	52·5	52·8	12·6		
Nov.	44·4	46·0	45·3	45·6	7·5	1928	
Dec.	40·0	39·9	39·0	39·5	4·1	39·7	39·4

The effect of this extreme cold is well shown in the analyses of catches of oyster drills made in 1928, 1929, and 1930, as given in Table III. Of the 10,852 living drills examined during the three years the percentages there shown were obtained. But, owing to the fact that the drills have different habits, it is necessary to discuss the relative abundance of the

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* Mean of the monthly means of maximal and minimal readings at Clacton-on-Sea and Southend combined (see **8** M.O. 214a, App. IV).

† Means are only available for Clacton-on-Sea: temperatures at the more insular situations on the Blackwater are slightly lower in cold and higher in warm periods (see **7**, p. 213).

‡ Means of daily readings at about high and low water except Sundays. About 50 readings per month were made in most months. For a discussion on the significance of the readings see **2**, p. 387, and legend to Fig. 1, p. 305, herein.

animals on different types of grounds, in order to assess the significance of the figures obtained.

The environs of the mouth of the Blackwater River and the site of the oyster beds are shown in Fig. 2, p. 306. It was found in 1929 and 1930 that the grounds A_1, A_2, A_3, and A, which are headwaters or creeks, yielded only Urosalpinx. As these grounds had not previously been carefully surveyed, it is probable that Murex, and possible that Purpura, did

TABLE II.

Daily Sea-temperature readings at Thornfleet* on the Blackwater Estuary during the cold period December 1928–March 1929 (to nearest degree Fahrenheit).

	L.W.	H.W.		L.W.	H.W.		L.W.	H.W.
Dec. 17	37	39	Jan. 18	32	33	Feb. 19	29	30
,, 18	37	38	,, 19	33	32	,, 20	29	30
,, 19	36	37	,, 21	32	33	,, 21	31	32
,, 20	37	36	,, 22	33	33	,, 22	31	32
,, 21	37	37	,, 23	34	34	,, 23	—	33
,, 22	38	37	,, 24	34	34	,, 25	31	32
,, 24	37	38	,, 25	34	34	,, 26	31	32
,, 25	—	39	,, 26	34	34	,, 27	30	31
,, 27	39	40	,, 28	32	34	,, 28	30	32
,, 28	40	40	,, 29	32	34	Mar. 1	30	32
,, 29	39	—	,, 30	34	34	,, 2	31	—
,, 31	37	37	,, 31	36	35	,, 4	33	32
Jan. 1	37	37	Feb. 1	37	35	,, 5	33	32
,, 2	36	37	,, 2	36	38	,, 6	35	34
,, 3	36	36	,, 4	35	36	,, 7	37	36
,, 4	35	35	,, 5	35	35	,, 8	38	36
,, 5	35	35	,, 6	36	35	,, 9	37	36
,, 7	33	34	,, 7	36	36	,, 11	37	36
,, 8	34	34	,, 8	37	36	,, 12	39	37
,, 9	36	35	,, 9	36	37	,, 13	40	37
,, 10	35	35	,, 11	34	33	,, 14	39	37
,, 11	35	35	,, 12	29	32	,, 15	38	37
,, 12	33	34	,, 13	29	31	,, 16	38	—
,, 14	38	35	,, 14	29	31	,, 18	38	38
,, 15	34	35	,, 15	28	30	,, 20	41	39
,, 16	33	35	,, 16	ice		,, 23	42	41
,, 17	33	34	,, 18	29	29			

TABLE III.

	Urosalpinx.	Murex.	Purpura.	No. Total.
1928	7·8%	41·2%	51·0%	1,739
1929	83·4%	0·1%	16·6%	1,184
1930	84·5%	0·1%	15·4%	7,927

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* Occasional readings, which were of the same order as those obtained at Thornfleet, were also made at the following stations:—Off Tollesbury Pier, West Boundary, South Shore. Readings made from Calderara thermometer with N.P.L. certificate and read to nearest degree.

not formerly occur there, except as occasional introductions. On the other hand, Urosalpinx had—for at least a few years before 1928—been taken there in abundance. The captures for these " A " grounds are therefore listed separately in Table VI, p. 312, in order to permit of a direct comparison of the captures during the three years on those beds where both Murex and Purpura were known to occur in abundance in 1928. Thus, omitting the " A " grounds or creeks, the following percentages of the living tingles are obtained :—

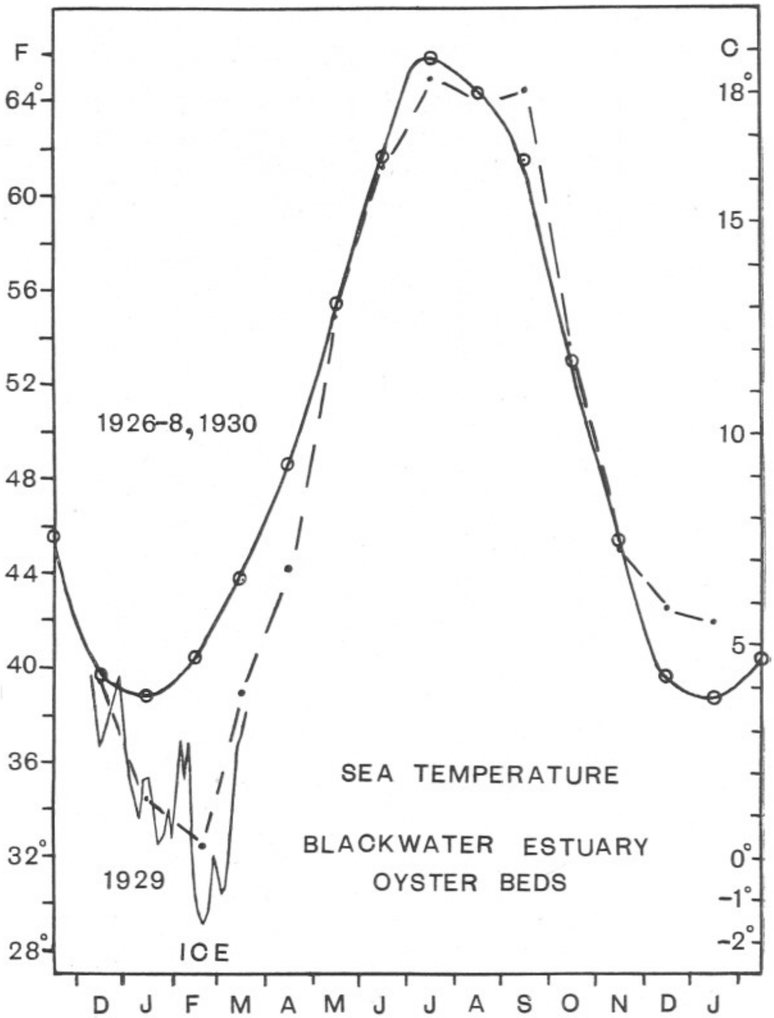

Fig. 1. (See foot of page 305.)

TABLE IV.

	Urosalpinx.	Murex.	Purpura.	No. Total.
1928	7·8%	41·2%	51·0%	1,739
1929	71·2%	0·2%*	28·6%	584
1930	77·9%	0·11%*	22·0%	5,467

In this Table the yields of tingle in the three years are directly comparable and were all obtained by dredging. There can be no doubt, therefore, that after the winter of 1928–29 (*a*) Murex was almost eliminated from the beds, and (*b*) that Purpura most probably also became far less abundant, (*c*) that apparently Urosalpinx increased in abundance. The absence of any increase in the proportion of Murex and Purpura in 1930 virtually proves that these tingle were not driven into deeper water in the winter of 1928–29. There can be no doubt, therefore, that Murex did in fact suffer almost complete annihilation, and that serious mortality occurred among the Purpura. Since quantitative hauls were not made it is impossible to state that Urosalpinx actually increased in numbers, although it is probable that an increase occurred. The fishermen report that tingle as a whole were less abundant in 1930 than formerly.

FIG. 1.—Mean monthly temperature of the sea over the oyster beds in the Blackwater Estuary compiled from daily readings at a depth of about one metre (surface) at about high and low water (Sundays excepted) for the five years 1926–1930.

The means of the four years, 1926–28, 1930, are averaged to give the continuous thick-lined curve. The means for the year 1929 are shown by the discontinuous thick-lined graph; the means of readings (usually four) for each two days in the cold period, December to the middle of March, are shown in the continuous thin-lined graph.

The readings were taken at the temperature stations shown in circles Fig. 2, p. 306, and mainly at the Thornfleet Station. The number of readings at each station is as follows:—

		Depth in fathoms at low water.	No. of readings.
A_1	Thornfleet	2	2185
C_1	Tollesbury Pier=Mell Pier	3	325
E.B.	East Boundary	3	223
W.B.	West Boundary	3	197
M.	Marfleet	5	15
E.	South Shore	2	24
S.H.	Shingle Head	3	3
C_3	Nass End	2	27
B.	Deeps	2	67
A_4	*Dan's* Moorings	1	192
	Other stations.	–	6

Readings below the surface rarely differ from bottom temperatures (as determined by a Nansen-Pettersen water-bottle) by more than a fraction of a degree F., at the shallower stations, i.e. where the depth of water is about 2–3 fathoms at low water. Slightly greater differences may occur between surface and bottom when the depth is greater, i.e. 5 to 10 fathoms (see **6**, *loc. cit.*, p. 6).

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* All individuals small to medium in size. See Table VI, p. 312.

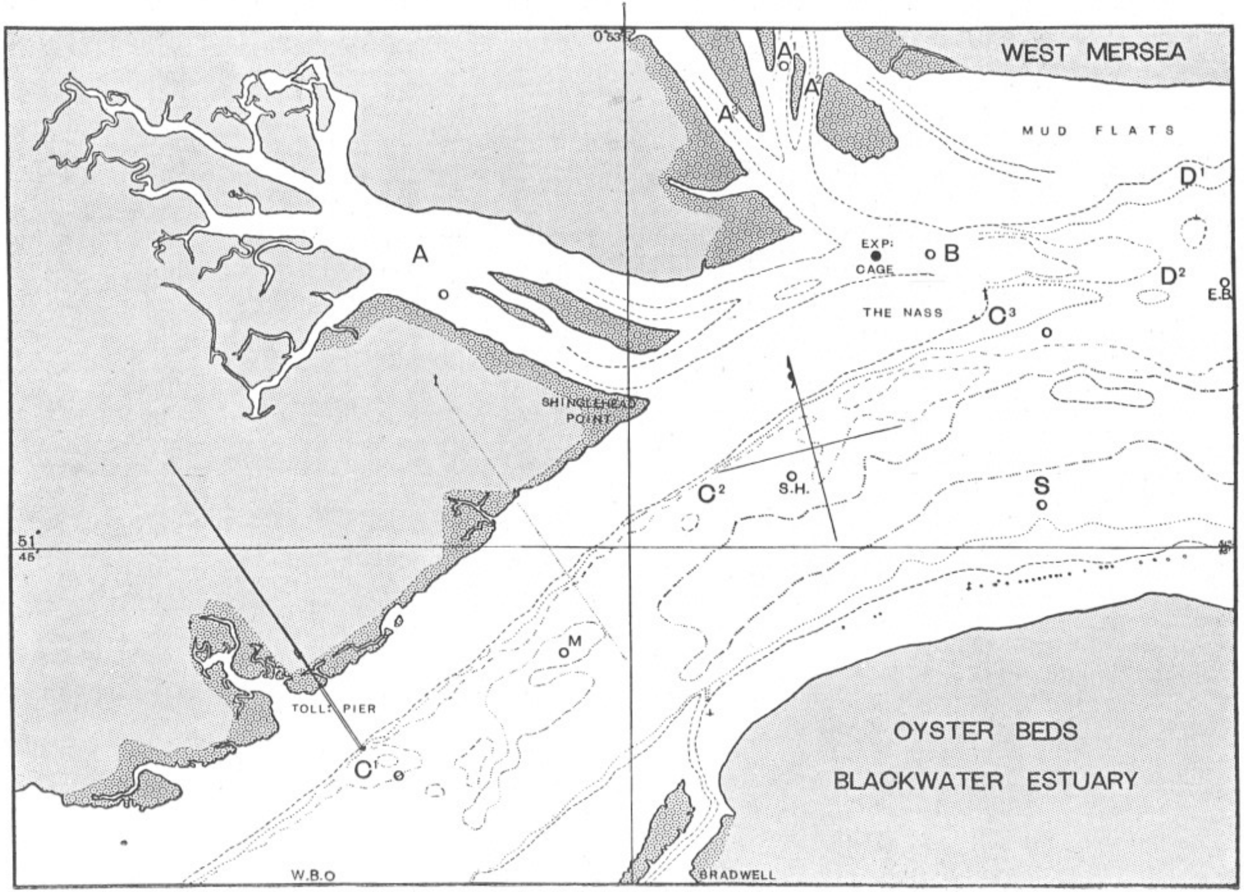

FIG. 2 (see foot of page 307).

Contributory evidence to these conclusions is offered by the figures of the dead tingle obtained with the living ones. In 1929 and 1930 the dead individuals were carefully separated from the living and counted. (To prove death it was necessary to break open the doubtful shells. It was then observed that Purpura can retract itself much further into the shell than Urosalpinx, and that very badly worn and apparently empty shells of Purpura may contain an exceedingly emaciated living animal.) The proportions of dead and living shells in the catches made in 1929 and 1930 are shown in Table VI, p. 312, and summarised below in Table V. The dead shells caught in 1928 were not recorded.

TABLE V.

Grounds.	Urosalpinx.		Murex.		Purpura.		Total dead.		Total living.
B, C, D.	No.	%	No.	%	No.	%	No.	%	
1929	16	3·7	25	96·2	17	9·2	58	9·0	584
1930	41	0·9	126	95·5	110	8·4	277	4·8	5,467

The " A " grounds may be excluded from consideration, as it is probable that they do not constitute a natural habitat of Murex and Purpura. On the remaining grounds the total number of each species taken dead in 1929 and 1930 is shown above, along with the percentage of dead shells calculated on the total number of living and dead shells of each species. The total number of dead shells of *all* species is also shown, as well as the total percentage dead of the total living and dead. The very high percentages of 96·2 and 95·5 Murex dead, and the greater actual number of Murex dead in comparison with the total dead of Urosalpinx and Purpura, both offer additional evidence of the virtual annihilation of the rough English tingle on the Blackwater oyster beds in the winter of 1928–29.

The great increase in the percentage of living Urosalpinx on grounds C, D, and E in 1929 and 1930, as shown in Tables II and III, is undoubtedly an indication of the greater capacity of this species to resist extreme cold.

FIG. 2.—Chart of the West Mersea oyster beds and temperature stations in the Blackwater Estuary. (From Admiralty Chart 3740, 1918.)

A_1	Thornfleet beds.
A_2	Mersea Fleet beds.
A_3	Salcott Fleet beds.
A	Tollesbury Fleet and M.V. *Dan's* Moorings.
B	Deeps.
Exp. cage	Site of experimental oyster cage.
C_1	Grounds off Tollesbury Pier (=Toll. Pier).
C_2	Grounds below Marfleet (M.) and off Shingle Head.
C_3	Grounds off the Nass End.
D_1	North shore ground near East Boundary (E.B.).
D_2	Offshore northern grounds (Flat Ground).
S.	South shore beds near watch boat.

Thirslet Creek lies a little above Tollesbury Pier and is not shown. The temperature stations (shown in circles) are denoted in the legend to Fig. 1, p. 305.

The virtual absence of Murex in the catches is at the same time an indication of the susceptibility of this species to low temperatures or conditions associated with low temperatures of the kind and duration shown in Table I; on the figures shown it is highly probable that Purpura also succumbed in considerable numbers under these unusual conditions.

Reviewing the oyster fishery as a whole it is clear that the American oyster tingle has now spread to all the grounds and has replaced the English tingles to a great extent; inasmuch as among nearly 8,000 individuals of all kinds captured in 1930, Urosalpinx occurred in percentages varying from 43 to 100 on the different beds and constituted 84% of the total captures. As Urosalpinx is known to be a voracious feeder on young oysters (**1**), the economic difficulties of prosecuting oyster culture on the Blackwater beds—already made difficult by the multiplication of the American slipper-limpet, *Crepidula fornicata* (**3**)—have been seriously increased. There is no evidence of unusual mortality among Crepidula on these beds as a result of the cold conditions noted, but as this species is exceedingly abundant, it is probable that a slight increase in mortality would pass unnoticed. Individuals were, however, observed to be weak and easily detachable from their chains.

The differential resistance of the specific protoplasms of (certain organs of ?) these species of Urosalpinx, Purpura, and Murex in the natural habitat to the low temperatures observed and recorded herein is apparently the cause of the selective mortality observed. It would seem that such a fundamental property of specific protoplasms is worthy of further experimental investigation on the lines of Huntsman and Sparks (**4**) and Battle (**5**).

The result of the study has proved that the observations of local naturalist-fishermen are correct as regards *Murex erinaceus* and (as will be shown later) *Echinus miliaris*, but incorrect concerning *Purpura lapillus* and *Urosalpinx cinerea;* but as the latter is not an English form and the actual date of its introduction into English waters is doubtful, it is certain that the American tingle has not been included in the consciousness of the local fishermen in the last 20 to 30 years. It is probable that *Murex erinaceus* was the dominant tingle on the Blackwater oyster beds until 20 to 30 years ago.

ECHINUS MILIARIS.

Echinus miliaris was abundant about and in the creek (Thirslet Creek) immediately above Ground C_1 (Fig. 2, p. 306) in 1913, but rarely occurred on any of the Blackwater beds in the post-war years. It is probable that this species was exterminated from these habitats in the cold winter of 1916–17, though it survived in smaller numbers on some deeper offshore beds. During the years 1920–28 it is known that this species occurred in abundance on the oyster beds off Whitstable (**6**), and samples up to 500 or more have been utilised at intervals at Plymouth for transplantation, experimental work, and artificial fertilisations. In the spring of 1929, however, it was found impossible to obtain samples ; it was reported that all the *Echinus miliaris* had been killed off during the winter on the shallower inshore grounds, but could still be obtained in small numbers in the deeper offshore waters, which are rarely worked.

The variation in the sea-temperature over the Whitstable oyster beds is comparable with that on the Blackwater beds, except that temperatures range somewhat higher in the summer and lower in the winter on the latter (**8**). There can be no doubt, therefore, that *Echinus miliaris* was exterminated as a result of the low temperatures of the winter of 1928–29 on the Whitstable oyster beds in the same way as Murex on the Blackwater beds.

It is impossible to state in what precise way the unusual reduction in temperature causes death in such instances as are noted above without experimental observations. The probable factors are :—the change in absolute temperature, the rate and period of fall or rise of temperature, and the correlated degree of salinity at different phases of change. No observations on salinity were made during the cold period, but information can be culled from data on the concomitant precipitations as compared with the normal. The monthly weather reports for the period, December 1928 to April 1929, show that the variations from monthly normals (**8**) in total rainfall (in mm.) were respectively December +39, January +6, February −19, March −32, and April +9. There was therefore an exceptional rainfall only in December (17 mm. on the 29th), some six to seven weeks before the water was reduced to freezing-point, and exceptional dryness in March. In the coldest period there was very little dilution of the sea-water by precipitation, and no heavy rains followed in March and April during the period of rapid rise in temperature. It would seem, therefore, that the mortality observed was due mainly either to the fall in absolute temperature or the rate of change of temperature at a low level, but that the reduction in salinity at the onset of the cold period may have predisposed the animals in some degree to a lethal effect of low temperature.

On Natural Selection.

It is interesting to note that the foregoing events comprise a minor cataclasm of the kind envisaged by Bidder (**9**). Among the three species studied, Urosalpinx and—to a less extent—Purpura survived the (locally) unusual environmental phases. Within the species of *Murex erinaceus* a high degree of mortality occurred, but a small proportion of individuals survived, and may be stated to have been naturally selected.

The surviving individuals which were captured, it is of great interest to note, were all either of small or medium size, that is, lengths in mm., 15.6.29, ca. 25; 19.5.30, 25·3; 23.4.30, 29·0, 20·8; 24.5.30, 32·2, 29·0, 25·3; giving an average length of about 27·0 mm. In 1928 a common size among the larger individuals was 40 to 45 mm. (See **11**.) It is permissible to speculate whether the surviving individuals avoided death by some peculiarity of their own or of their parents, and if so, whether that peculiarity might be heritable. There is, however, no critical evidence available on the subject in this instance, which may be regarded as typical of a series of phenomena in which Darwin considered (**10**) that natural selection might operate.

ACKNOWLEDGMENTS.

During the course of many years from 1913 to the present I have been assisted in the present studies (1) on the River Blackwater beds by Dr. J. H. Salter, Messrs. L. French, H. Mole, L. Pearce, J. Pearce, G. French, and Mr. C. Springett; and (2) on the Whitstable beds by Major A. Gardiner and Mr. E. Luckhurst. The valuable series of temperature observations was obtained in co-operation with the writer by Mr. Laban Pearce from the motor boat *Dan* in all kinds of weather, and by the courtesy of the Tollesbury and Mersea Native Oyster Company. The writer has spent many pleasant days afloat with Mr. Laban Pearce, who has shown special interest and care in obtaining the series of records extending over more than five years. All the work herein recorded prior to September, 1929, was accomplished while the writer was a Naturalist on the staff of the Marine Biological Association, Plymouth; the work on the River Blackwater was partly subsidised by a Government grant from the Royal Society.

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TABLE VI.

ANALYSIS OF CAPTURES OF OYSTER DRILLS ON THE OYSTER BEDS IN THE BLACKWATER ESTUARY, 1928–30.*

		1928				1929				1930			
Chart reference.	Designation of bed.	Date.	Uro-salpinx.	Murex.	Pur-pura.	Date.	Uro-salpinx.	Murex.	Pur-pura.	Date.	Uro-salpinx.	Murex.	Pur-pura.
B	Deeps	31/8	44	31	0		N.R.†				N.R.†		
B–A$_1$	Thornfleet and Deeps			N.R.		15/6	313+*14*	1+*16*	96+*11*		do.		
C$_1$, D, E	T. Pier, S. Shore, Flat Ground	17/10	46	262	325			N.R.		C$_1$ 23/4	445+*3*	2+*19*	589+*16*
C$_1$	T. Pier–Nass End	26/10	45	423	563			do.					
C$_2$–D	Back of Nass and Flat Ground			N.R.		2/6	88+*0*	0+*0*	3+*0*	13/5	692+*8*	0+*20*	192+*27*
C$_{2\text{-}3}$	Back of Nass			do.		6/7	15+*2*	0+*9*	68+*6*				
D	Flat Ground, N. Shore			N.R.				N.R.		29/4	361+*3*	0+*7*	41+*13*
D	N.E. Ground near E. Boundary			do.				do.		19/5	885+*12*	1+*33*	123+*23*
D	Flat Ground, do.			do.				do.		24/5	1875+*15*	3+*47*	258+*31*
	Totals		135	716	888		416+*16*	1+*25*	167+17		4258+*41*	6‡+*126*	1203+*110*
	% living		**7·8**	**41·2**	**51·0**		**71·2**	**0·2**	**28·6**		**77·9**	**0·1**	**22·0**
	Gross total for year			1739				584+*58*				5467+*277*	
A$_1$	Thornfleet			N.R.		2/7	135+*4*	0+*1*	11+*0*	28/3	15+*0*	0+*0*	0+*0*
A$_1$	do.			do.		9/7	214+*6*	0+*4*	12+*2*	4/5	30+*0*	0+*0*	0+*0*
A$_1$	do.			do.						16/6	100+*0*	0+*0*	1+*1*
A$_1$	do.			do.						19/6	290+*3*	0+*3*	3+*2*
A$_2$	Mersea Fleet			do.		7/6	115+*0*	0+*0*	0+*0*	20/2	20+*0*	0+*0*	1+*0*
A$_2$	do.			do.		7/11	107+*1*	0+*0*	6+*0*	20/5	386+*2*	0+*0*	1+*0*
A$_3$	Salcott Fleet			do.				N.R.		23/5	101+*0*	0+*0*	0+*0*
A$_3$	do.			do.				do.		13/5	160+*1*	0+*0*	0+*0*
A$_4$	Tollesbury Fleet			do.				do.		20/2	81+*0*	0+*0*	0+*0*
	do.			do.				do.		13/5	310+*3*	0+*0*	4+*0*
	do.			do.				do.		22/5	424+*0*	0+*0*	4+*0*
	do.			do.				do.		30/5	208+*0*	0+*0*	1+*0*
	do.			do.				do.		6/6	319+*0*	0+*0*	1+*0*
	Totals " A " Grounds			N.R.			571+*11*	0+*5*	29+*2*		2444+*9*	0+*3*	16+*3*
	Totals all Grounds		135	716	888		987+*27*	1+*30*	196+*19*		6702+*50*	6+*129*	1219+*113*
	Gross yearly total			1739				1184+*76*				7927+*292*	

* The numbers in italics refer to dead animals. † N.R. No record. ‡ Individuals of small or medium size.

TABLE VII.

Mean Monthly Temperature of the Sea over the Oyster Beds in the Blackwater Estuary for the period October 1925 to December 1930. (From daily observations at about High and Low water (except Sunday), mainly at Thornfleet and Tollesbury Pier Stations (see Fig. 1 and description, p. 305).

	H.W.	No. of Obs.	L.W.	No. of Obs.	Mean of all Obs.	No. of Obs.	H.W.	No. of Obs.	L.W.	No. of Obs.	Mean of all Obs.	No. of Obs.
			1925						1926			
Jan.							38·5	26	37·7	26	38·1	52
Feb.							43·1	24	43·3	24	43·2	48
Mar.							44·6	26	44·5	27	44·5	53
April							49·0	24	49·4	25	49·2	49
May							53·2	24	54·0	24	53·6	48
June							61·2	26	61·7	26	61·5	52
July							66·2	28	65·9	28	66·0	56
Aug.							65·5	26	65·5	27	65·5	53
Sept.							63·8	24	63·8	25	63·8	49
Oct.	52·3	28	51·6	28	52·0	56	52·4	25	51·7	24	52·0	49
Nov.	39·7	23	38·3	23	39·0	46	44·9	26	44·4	26	44·7	52
Dec.	36·6	25	35·4	26	36·0	51	40·0	24	39·0	24	39·5	48
			1927						1928			
Jan.	37·8	24	37·3	23	37·6	47	37·6	25	37·9	26	37·8	52
Feb.	38·8	23	38·5	23	38·6	46	41·8	23	41·3	24	41·5	47
Mar.	44·8	26	45·4	27	45·1	53	42·8	26	43·4	25	43·1	51
April	49·5	25	49·8	26	49·6	51	47·9	24	48·1	25	48·0	49
May	56·9	27	57·0	26	57·0	53	54·3	27	54·6	27	54·5	54
June	59·8	27	59·7	24	59·6	68	60·8	26	61·1	26	60·9	52
July	63·7	24	63·7	25	63·7	79	67·6	25	68·1	26	67·8	55
Aug.	64·6	25	64·6	26	64·8	62	64·4	25	64·0	26	64·2	51
Sept.	59·8	26	59·2	25	59·5	51	61·6	25	60·9	25	61·3	50
Oct.	53·5	24	53·0	24	53·2	48	53·5	26	52·5	26	53·0	52
Nov.	46·3	26	45·9	26	46·1	53	47·5	25	46·1	25	46·8	50
Dec.	37·9	25	36·8	25	37·4	25	39·9	23	38·9	23	39·4	46
			1929						1930			
Jan.	34·4	27	34·0	27	34·2	54	42·0	25	41·9	25	42·0	50
Feb.	32·9	23	32·1	22	32·5	45	38·7	24	38·2	24	38·5	48
Mar.	38·1	23	39·7	26	38·9	49	42·3	25	42·4	25	42·3	50
April	45·4	25	44·7	24	45·1	49	47·8	25	48·1	25	47·9	50
May	54·7	26	55·5	26	55·1	52	55·5	25	56·6	26	56·1	51
June	61·4	25	61·4	25	61·4	50	64·4	25	65·6	24	65·0	49
July	64·8	27	65·2	27	65·0	54	65·2	27	64·9	27	65·0	54
Aug.	64·2	26	63·7	26	64·0	52	62·9	25	63·0	26	62·9	51
Sept.	64·4	23	64·3	23	64·4	46	62·3	24	61·4	25	61·8	49
Oct.	54·4	27	53·2	27	53·8	54	53·5	27	52·8	27	53·2	54
Nov.	45·4	24	44·7	26	45·0	50	45·4	25	44·7	25	45·0	50
Dec.	42·9	23	42·1	22	42·5	45	42·0	23	41·4	22	41·9	45

Observations and Experiments on Sex-Change in the European Oyster (*O. edulis*). Part II. On the Gonad of Egg-Spawning Individuals.

By

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and

C. Amirthalingam, B.Sc., Ph.D.,

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With 12 Figures in the Text.

IN an earlier publication (**1**, 1927) it has been shown that female-functioning oysters (*O. edulis*) normally begin to develop spermatozoa with great rapidity immediately after extruding a batch of eggs. Thus, while the extruded eggs are developing in the mantle cavity of the oyster, spermatozoa are developing at the same time within the body of the oyster. In these circumstances sperm develop so quickly that a few hours after the extrusion of eggs small clumps of characteristic spermatocytes can be detected in the gonad either in the fresh material or in microscopic sections. Within about 14 hours from the extrusion of ova, relatively large clumps of spermatocytes are easily recognisable in preparations of the fresh gonad ; while within about 45 hours the gonadial tubes become filled with maturing sperm, and in some cases sperm-morulæ may already occur. After 3½ days from egg-spawning the percentage of gonads containing ripe sperm rapidly increases, until at about 8½ days after the extrusion of ova—when the larvæ which the oyster is carrying have become fully developed veligers ready to be extruded—sperm development may have proceeded so far that the gonadial ducts themselves become filled with ripe sperm-morulæ as shown in Figure 1, p. 316. The rates of development quoted above are averages for those occurring in English oyster beds ; but are with little doubt mainly dependent on the prevailing temperature.

After an oyster has extruded its larvæ sperm-production continues for a few weeks, but begins to wane about one month after egg-spawning (see **1**, Table XII, p. 1035, 1927). Two months after the last egg-spawning (if this has occurred in early- or mid-summer) sperm-production has usually ceased ; the gonad passes into a quiescent condition (in British waters and under normal conditions) and a period of "fattening," or the accumulation of reserves, usually follows. If egg-spawning occurs late in the summer, the sperm subsequently developed may be retained over the winter period. A full discussion of such cases will, however, be given later when data can be presented.

In this paper figures are given to illustrate successive stages of the gonad after egg-spawning, and also the state of the ripe female gonad in the spawning condition. As the condition of the gonad can usually be easily and quickly ascertained by an examination of a fresh preparation of the gonad, figures of the microscopic fields obtained from fresh preparations are given as well as those of microscopic sections. In order to obtain a fresh preparation of the gonad of the oyster a cut may be made in the visceral mass near the pericardium or dorsally near the loop of the intestine which encircles the stomach (see **2**, Plate XII). In this way is avoided a possible incision of the main gonoducts which lie mostly superficially. When it is obvious that the gonoducts are empty, the visceral mass may be cut across entirely. When the cut is made a microscope slide is pressed gently against the cut in order to collect a little of the fluid which is exuded. This drop of fluid is examined at once under the microscope without a cover-slip, and without adding sea-water; it is advisable to try several samples until familiarity with the method is obtained. To test the ripeness of the sperm, sea-water may afterwards be added, when—if the preparation has not been allowed to dry—it will be found that ripe sperm-morulæ break up into separate active sperm on the slide.

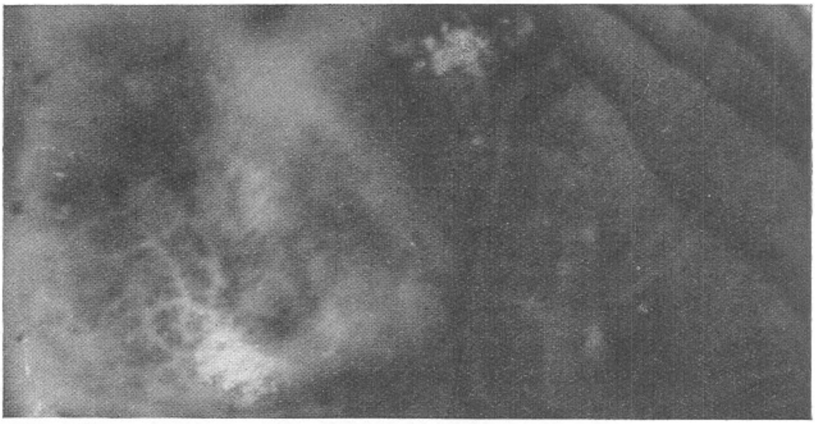


Photo. A.J.S.

FIG. 1.—View of the visceral mass of a recently black-sick oyster with gonoducts already filled with ripe sperm-morulæ.

(Photo of the living animal by Mr. A. J. Smith.)

In Table I, p. 318, are given full details of the series of figures shown herein with the correlated states of development of both the embryos (or larvæ) carried by an oyster, and the sperm-morulæ within the body of the same individual.

The arbitrary periods, A, B, C–F, are defined in **1**, p. 983, and the arbitrary categories I, III–X, are shown in **1**, Table II, p. 981 ; arbitrary periods G to J are defined *loc. cit.* on p. 1022. The significance of the correlation between the arbitrary period and the arbitrary categories associated in Table I herein can be seen at a glance in **1**, Table XII, p. 1035.

ACKNOWLEDGMENTS.

One of us (C. A.) takes this opportunity to thank the Council of the Marine Biological Association for the kind hospitality extended to him to work in its laboratory ; and to express his gratitude to Dr. E. J. Allen and Professor D. M. S. Watson for their encouragement and help.

Our thanks are due to Mr. A. J. Smith for the photograph for Fig. 1.

SUMMARY.

Illustrations are given of successive stages of the gonadial products of the European oyster (*O. edulis*) after the act of egg-spawning. Both microscopic and fresh preparations are figured.

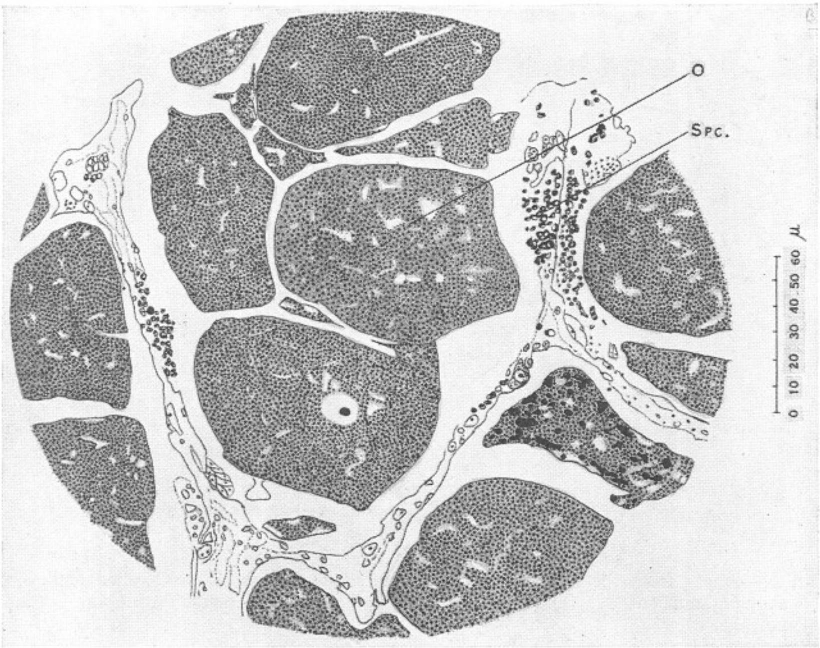
REFERENCES.

1. ORTON, J. H. 1927. Observations and Experiments on Sex-Change in the European Oyster (*O. edulis*). Part I. The Change from Female to Male. Journ. Mar. Biol. Assoc., N.S., Vol. XIV, No. 4, pp. 967–1045.
2. ORTON, J. H. 1924. An Account of Investigations into the Cause or Causes of the Unusual Mortality among Oysters in English Oyster Beds during 1920 and 1921. Part I. Fish. Invest., London, Ser. II, Vol. VI, No. 3, 1923 (1924).

TABLE I.

CORRELATED STATES OF DEVELOPMENT OF SPERM AND EMBRYO IN INDIVIDUALS OF *O. EDULIS*, ILLUSTRATED HEREIN.

	Condition of eggs, embryos or larvæ.	Approx. age of embryos or larvæ.	Date and locality.	Arbitrary period.	Sex-cells in gonad.			Arbitrary category.	Description of illustration.
					sperm-morulæ ripe.	sperm-morulæ unripe.	ripe ova.		
Fig. 2	Ripe eggs; from female in act of spawning.	0 hours	22 June, 1926 Truro beds	A	none	none	∞	I	Section of gonad.
Fig. 3	1 and 2-celled embryos	2 ,,	31 May, 1927 West Mersea	A	none	fair no. very young	few spots	III	Section of gonad microscopic field.
Fig. 4	1 and 2-celled with 2 to 5 nuclei	2½ ,,	30 Aug., 1929 R. Yealm	A	none	few up to 40μ	∞ in patches	III	From living gonad microscopic field.
Fig. 5	10% in 32-celled stages	20 ,,	14 Oct., 1927 Truro beds	B	none	fair no. up to 60μ	f. ∞ in spots	IV	From living gonad.
Fig. 6	about 64-celled stages	46 ,,	16 Sept., 1929 R. Yealm	C	none	∞ ca. $60\ \mu$	none	IV	Microscopic field from living gonad.
Fig. 7	Ciliated embryos with trace of shell	3 days	1 June, 1927 West Mersea	D	none	∞ large nearly ripe	rare	IV	Section of gonad.
Fig. 8	White-sick; larval shell about 100μ	4½ ,,	31 July, 1930 R. Yealm	E	few to fair no.	∞	rare	V	Microscopic field from living gonad.
Fig. 9	Black-sick; fully shelled larvæ	6–8 days	8 Oct., 1926 Truro beds	F	∞	∞	none	VI	Section of gonad.
Fig. 10	Black-sick; larval shell 200μ	,,	25 July, 1929 R. Yealm	F	∞	∞	none	VI	Microscopic field from living gonad.
Fig. 11	Post-sick oyster	estimated 1–2 months	16 Sept., 1929 R. Yealm	H or I	∞	none	none	VIII	Microscopic field from living gonad.
Fig. 12	Post-sick oyster	ca. 50 days	10 Sept., 1930 R. Yealm Spawned 31.7.30	H	few or fair no.	none	none	IX	Microscopic field from living gonad.



Del. C.A.

Fig. 2.—Microscopic section of the gonad of an individual of *O. edulis* caught in the act of spawning, 22 June, 1926. O. mature ova filling the gonadial tubules. Spc. gametogonia destined to become spermatocytes.

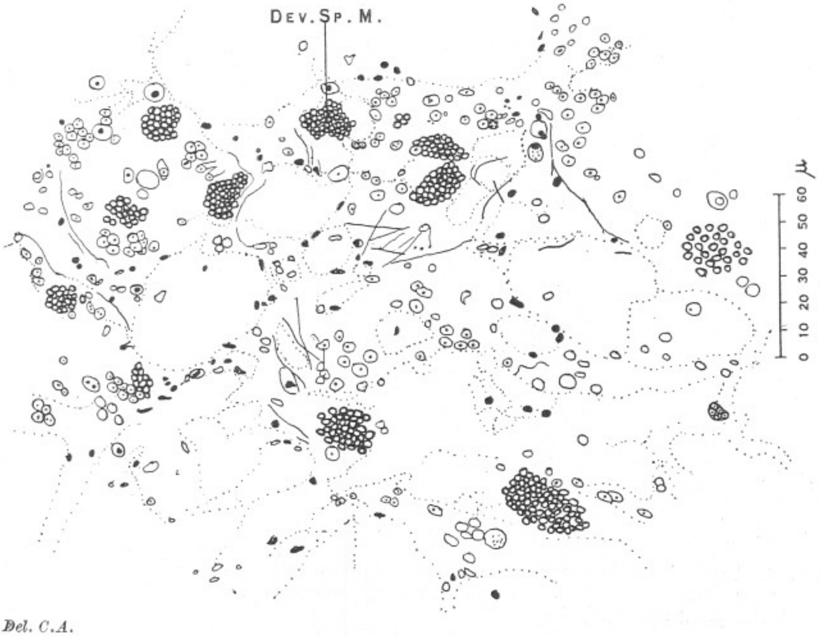


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Fig. 3.—Microscopic section of gonadial tubules of *O. edulis* carrying 1 to 2-celled embryos showing very young developing sperm-morulæ. (Dev. Sp. M.)

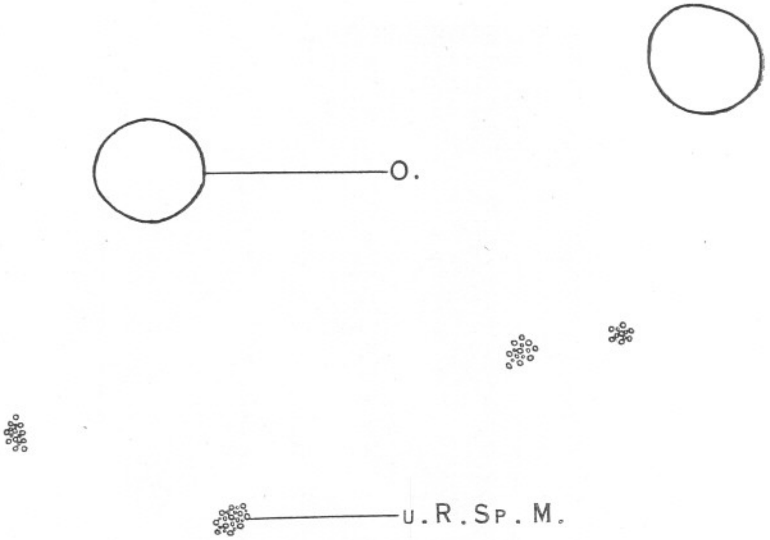

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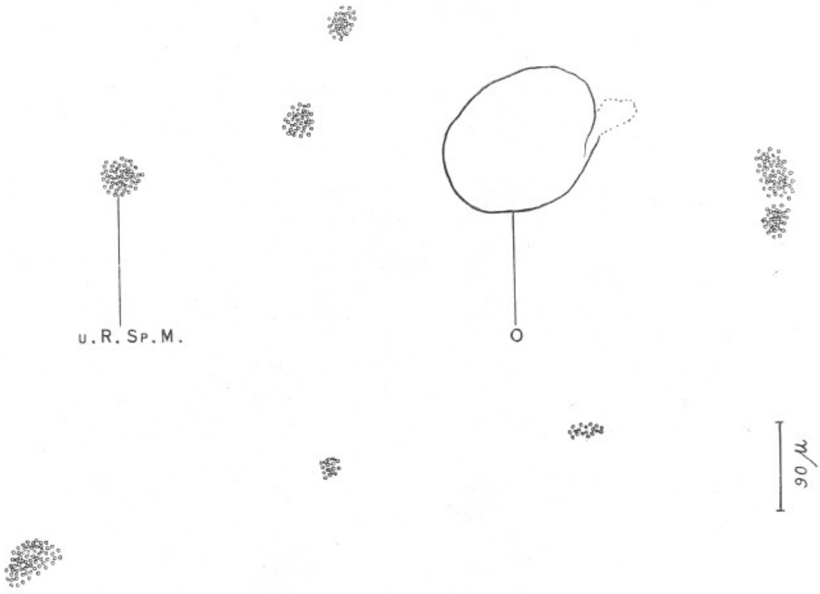
Fig. 4.—Smear from the living gonad of an *O. edulis* carrying 1 to 2-celled embryos, showing unspent ova, O (about 150μ in diameter), and small developing sperm-morulæ.



Del. C.A.

Fig. 5.—Smear from the living gonad of an *O. edulis* carrying embryos in about 32-celled stages, showing unspent ova, O, and fairly numerous developing sperm-morulæ (u.R.Sp.M.) about 60μ long.

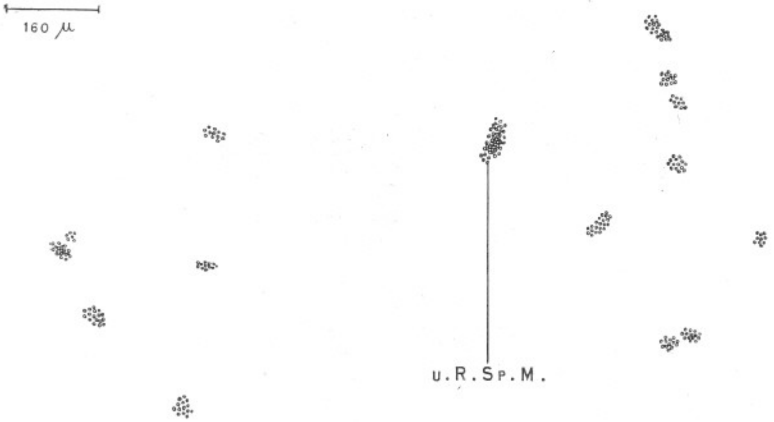


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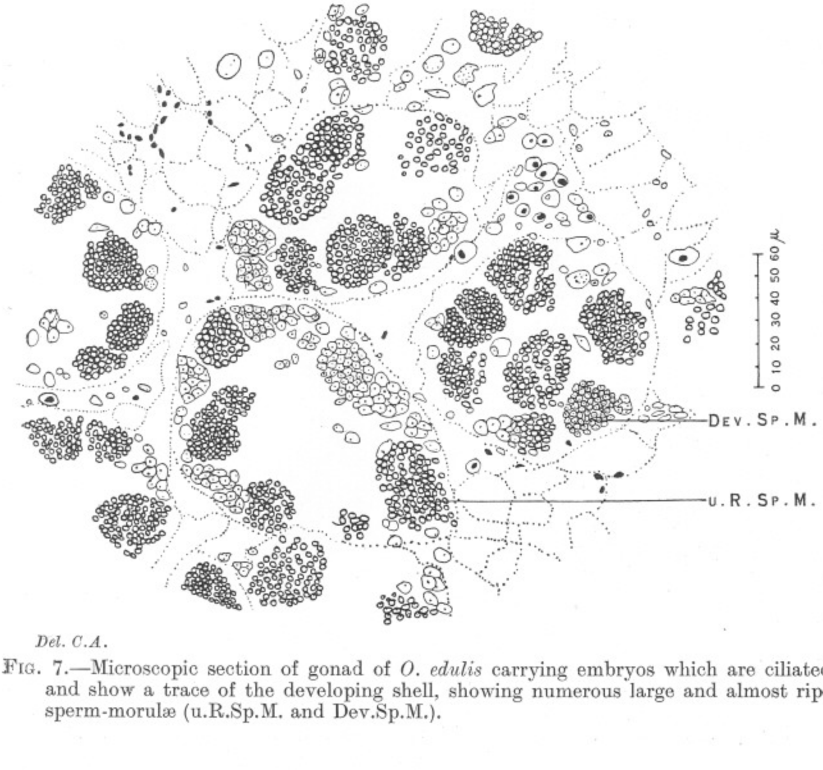
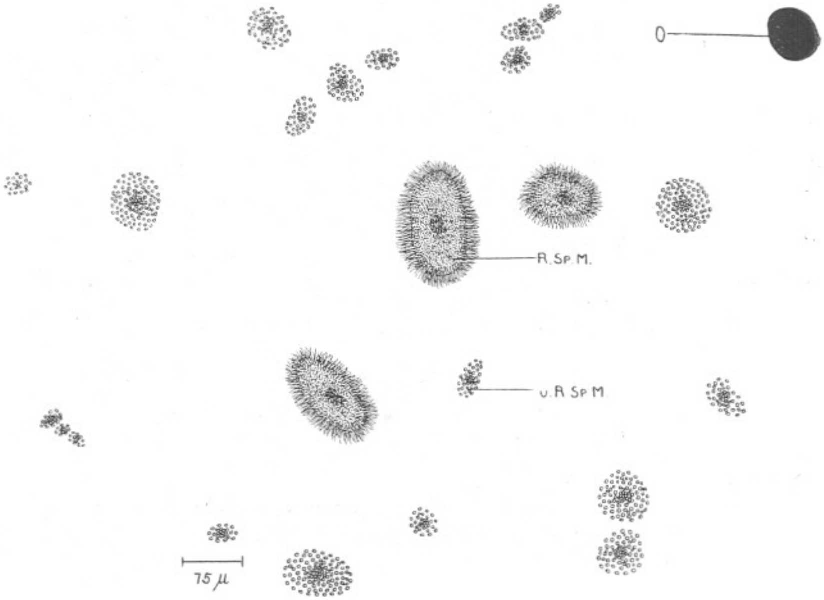
Fig. 6.—Smear from the living gonad of an *O. edulis* carrying 64-celled embryos, showing numerous large developing sperm-morulæ (u.R.Sp.M.) about 60μ long.



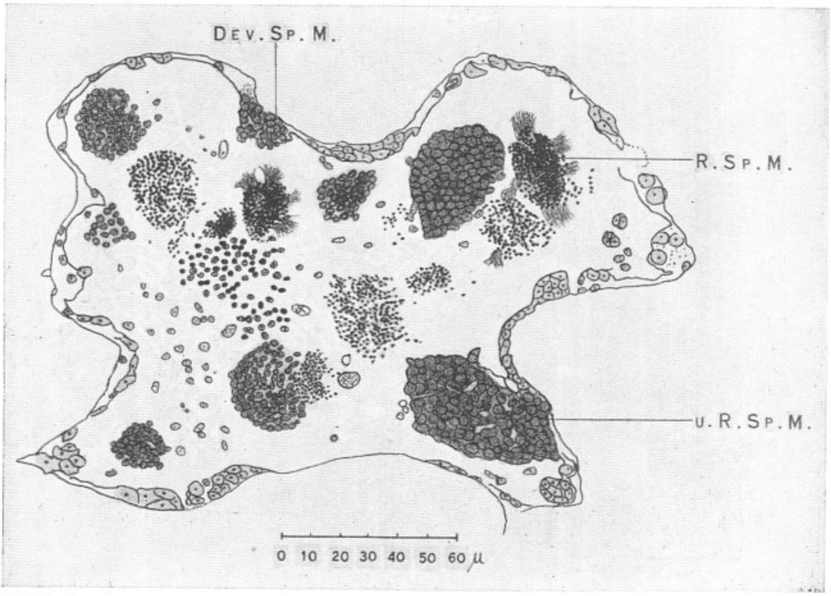
Del. C.A.

Fig. 7.—Microscopic section of gonad of *O. edulis* carrying embryos which are ciliated and show a trace of the developing shell, showing numerous large and almost ripe sperm-morulæ (u.R.Sp.M. and Dev.Sp.M.).



Del. C.A.

FIG. 8.—Smear from the living gonad of a grey-sick *O. edulis*, i.e. carrying embryos with half-developed shells and no pigment in the digestive organ, showing numerous large developing sperm-morulæ (u.R.Sp.M.), a fair number of ripe sperm-morulæ (R.Sp.M.), and a degenerating ovum, O.



Del. C.A.

FIG. 9.—Microscopic section of gonadial tubule of a black-sick oyster carrying fully-developed larvæ (i.e. shells 200μ long) and showing ripe (R.Sp.M.) and large developing sperm-morulæ (u.R.Sp.M.), and also younger masses (Dev.Sp.M.) *in situ*.

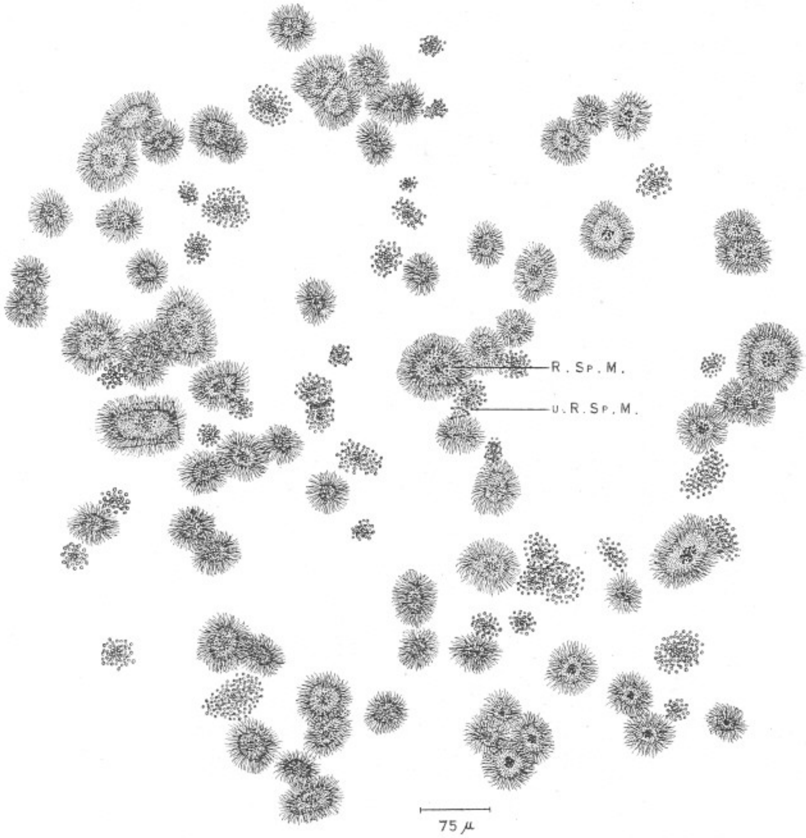


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Fig. 10.—Smear from the living gonad of a black-sick oyster, showing numerous ripe (R.Sp.M.) and numerous large unripe sperm-morulæ (u.R.Sp.M.) in a small portion of the microscopic field.

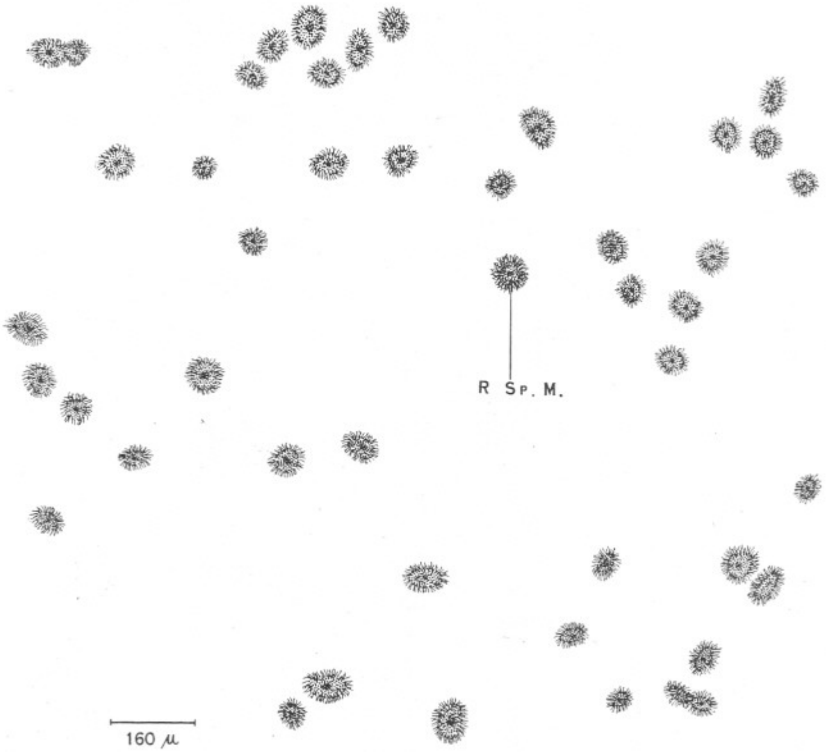

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FIG. 11.—Smear from the living gonad of a post-sick *O. edulis* (identified from seasonal studies in sex-change) showing numerous ripe sperm-morulæ only.

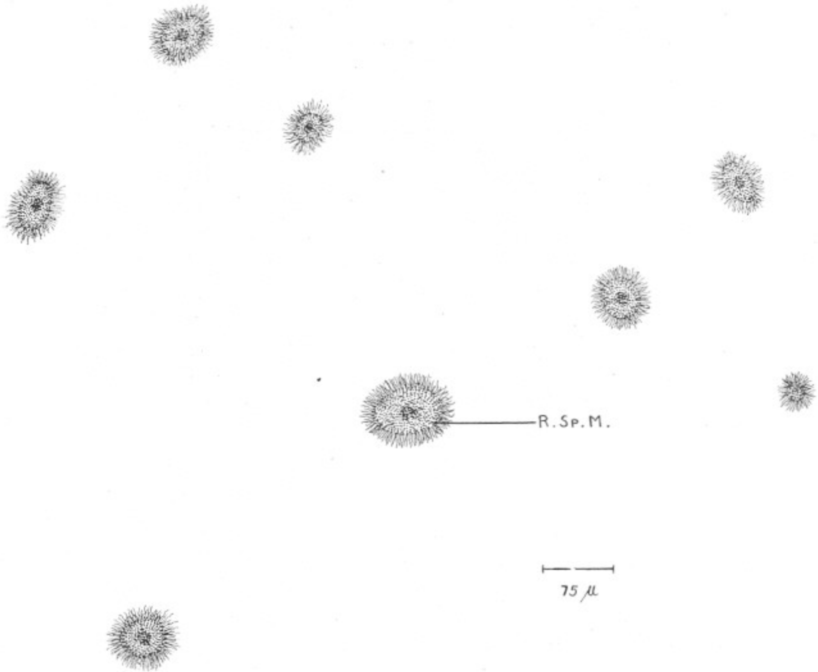

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FIG. 12.—Smear from the living gonad of a post-sick *O. edulis*, showing a fair number of ripe sperm-morulæ only. (White-sick 31 July, 1930 ; kept in tanks afterwards at Plymouth until 10 September, 1930.)

The Muds of the Clyde Sea Area.
III. Chemical and Physical Conditions; Rate and Nature of Sedimentation; and Fauna.

By

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Assistant Naturalist at the Marine Station, Millport.

With 11 Figures in the Text.

A PRELIMINARY survey of the area with regard to the distribution of the total nitrogen and phosphate content of the muds was described in a previous paper (Moore, **5**). A number of stations were worked, and these were further examined for nature and distribution of particles, water content, and density, and as a result of this survey certain stations were chosen as suitable for more extensive work. At the same time it became evident that the layers in which the greatest and most important changes were taking place were those within a few centimetres of the surface, and these were therefore studied most intensively.

Among these stations many show very irregular deposition, owing to tidal currents or other causes. At some, conditions appear to be comparatively stable, and a series of these was chosen to illustrate the four chief types of mud found in this area, which are as follows :—

Deep Water Type. This is found in the deepest channels where there is little or no tidal action, a slow rate of sedimentation and very little influence from the land, e.g. Station 7, 110 metres ; St. 7b, 166 metres ; St. 23, 73 metres.

Mid-Loch Type. This is a shallower water type than the preceding, usually in a depth of 45 to 75 metres. There is little tidal action and the small amount of matter received from streams is of very fine grade. Deposition is more rapid, and the mud tends to be softer than in the previous type, e.g. Station 8b, 37 m. ; St. 9, 37 m., Kyles of Bute ; St. 11, 73 m., Loch Striven ; St. 13, 73 m., Loch Goil ; St. 13a, 82 m. ; St. 15, 58 m. ; St. 15a, 64 m., Loch Long ; St. 16a, 26 m., Holy Loch.

Loch Head Type. Here there is practically no tidal action ; the depth is from 20 to 25 metres, with the exception of Loch Goil Head where it is deeper. Only small streams enter the lochs, but their influence is most marked on these loch-head stations. The mud is of a more open composition, containing more numerous and larger vegetable remains and sand grains, e.g. St. 10, 24 m., Loch Striven ; St. 12, 51 m., Loch Goil ; St. 14, 22 m., Loch Long ; St. 16, 22 m., Holy Loch ; St. 18, 24 m., Gare Loch.

Sandy Mud Type. Although this work has not been extended to shore sands, some sandy muds have been examined for comparison. These occur chiefly in bays and in parts of channels where there is evidence of strong tidal action, e.g. St. 1b, 25 m., Kames Bay, Cumbrae ; St. 17a, 73 m., Dunoon Basin ; St. 25, 46 m., Barrier Plateau.

A number of stations not described in the previous paper have since been worked and their positions are defined in Table I.

TABLE I.

POSITIONS OF NEW STATIONS.*

St. 1b.	Kames Bay, Cumbrae, 25 m.
St. 1c.	100 yards North of Hunterston Perch, Fairlie Sands, 22 m.
St. 7b.	3·5 miles West of Garroch Head, 166 m.
St. 17d.	Kilchattan Bay, 22 m.
St. 23.	South of Little Cumbrae light, West of Ardrossan, 73 m.
St. 25.	Midway between Ailsa Craig and Campbelton, 46 m.

METHOD OF SAMPLING.

The samples consisted of undisturbed cores of mud 3·2 cm. in diameter and up to 40 cm. in length. The sampler (Moore and Neill, **6**) collects the cores in glass tubes which are then corked at both ends and taken to the laboratory for examination.

SOLUBLE SALTS.

Under natural conditions the soluble salts leave the mud partly by diffusion into the overlying water via the interstitial water of the mud itself, and partly also by the expression of this interstitial water during the packing of the mud. In these estimations, therefore, wet mud was shaken up with a large amount of sea-water, and the increase in concentration of the various salts in this determined ; in the case of phosphate, it being undesirable to extract with a citric acid solution, a sample of the mud which when dry would weigh about 100 gm. was rubbed down in a little sea-water until no lumps remained, and was then shaken with 2200 c.c. of sea-water for two hours in an end-over-end shaker. This was then allowed to stand for 24 hours in the dark, and the supernatant water siphoned off for analysis. Shaking for this period was found to remove all the soluble phosphate. The results for the other soluble salts are not yet completed.

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* The localities of all other stations referred to are given in Journ. Mar. Biol. Assoc., N.S., Vol. XVI, No. 2, 1930, p. 597.

For the estimation of soluble phosphates, Atkins' modification of Denigès method (Atkins, **1**) was used, the water being passed through a washed Whatman No. 3 filter paper before the estimation. This was found to give identical results with samples cleared by centrifuging.

The results for soluble phosphates are given in Table II, and graphically in Figure 1. St. 11 is in most respects normal, so that the curve shown is probably typical for a mid-loch station. It agrees in shape with that for St. 13, except that the latter is much richer in soluble phosphate as it is in other salts including total phosphate. In both, the values are high at the surface of the mud but decrease rapidly to a depth of 6 cm., and then much more slowly. The very low values at St. 1b are to be expected in a sandy mud, but the even lower values at St. 10, at Loch Striven Head, are unexpected as the total phosphate there is almost as high as that at St. 11. The more open condition of the mud may allow more rapid loss

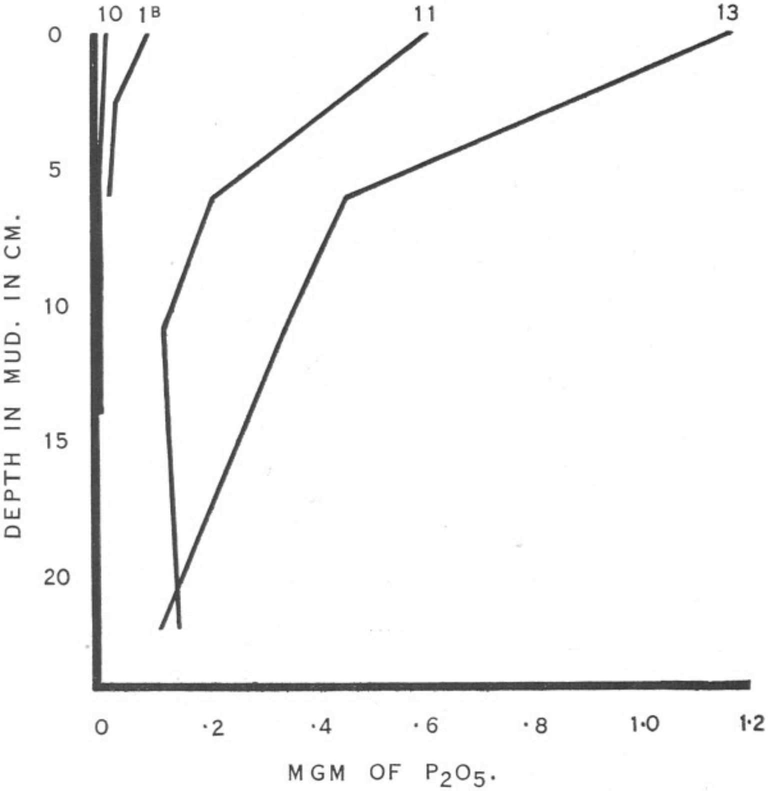

FIG. 1.—Distribution of Soluble Phosphate with depth in the mud.

by diffusion, but this does not seem to be sufficient to account for the great difference between the two stations.

It is significant that the greatest loss of soluble phosphate occurs in the same layer as that from which the greatest amount of interstitial water is being expressed by packing, that is the upper 6 cm.

OXYGEN ABSORPTION BY MUD.

The condition of the mud with regard to oxygen was estimated by shaking samples of the mud with sea-water of known oxygen content, and measuring the decrease in the latter by Winkler's method. From the amount taken up in this way it is clear that not only can there be no dissolved oxygen in the interstitial water even at the extreme surface in any mud examined, but also that any oxygen diffusing in from the overlying water will be rapidly absorbed. The general results for all types of station show an increase in the amount of the immediate chemical absorption, as distinct from the slower biological oxygen absorption down to a depth of about 5 cm., below which it becomes more or less constant at about 0·3 to 0·5 mg. of oxygen absorbed per gm. of mud (dry weight). In the mid-loch stations where there is a rain of rich organic matter on the surface, the amount of oxygen absorbed by this surface

TABLE II.

SOLUBLE P_2O_5 IN MG. PER 100 GM. OF MUD.

Station.	Depth.	Sol. P_2O_5.
1b	0–1 cm.	0·08
	2–3	0·03
	5–6	0·02
10	0–2 cm.	0·01
	4–6	0·004
	8–10	0·006
	12–14	0·006
11	0–2 cm.	0·54
	5–7	0·21
	10–12	0·12
	20–22	0·14
13	0–2 cm.	1·05
	5–7	0·46
	10–12	0·34
	20–22	0·13

layer is correspondingly high, but in the loch head and sandy types the mud is of a more open consistency, allowing deeper diffusion of the overlying water, and this phenomenon is not shown.

REACTION.

The estimation of the pH of the interstitial water of the mud presents certain difficulties ; it is not usually possible to withdraw such water except in small quantities and only by the use of reduced pressure on a filter, which would affect the CO_2 content and hence the pH. Also turbid solutions may be obtained, so that a colorimetric method of estimation is not reliable.

For the latter reason a quinhydrone electrode was used, with a calomel half-cell as standard (Clark, **2**). The soil analysis method of shaking the dried soil with distilled water, is not applicable here, and even shaking the fresh wet mud with distilled water yields erratic results, and always of a low value. On the other hand, if the mud is shaken with sea-water, or with saline solution, regular values are obtained, and these are in agreement with the values obtained from the interstitial water itself in those cases where the mud is of such consistency as to allow of the easy withdrawal of the latter. In practice a tube of mud was cut up into one-centimetre layers, and each of these immediately shaken up with about 20 c.c. of sea-water, the buffering power of the mud being sufficient to overcome that of the water. Quinhydrone was then added to this and the pH read as quickly as possible. The method is in agreement with that recommended by the International Society of Soil Science (**3**) with the exception that their suggestion is the use of a solution of KCl where we have used NaCl. The use of quinhydrone in the presence of a reducing medium such as a mud extract necessarily introduces an error, but the rate of potential drift suggests that this should be small if the estimation is made quickly after the addition of the quinhydrone.

The results for the four types of station are shown in Figure 2. In general, with increasing depth in the mud there is a steady rise in pH followed by a less rapid fall again, the depth at which the maximum occurs varying from one station to another. The overlying water has a higher pH than the mud, and its influence seems to affect the top centimetre layer of the mud whose pH is usually distinctly higher than that of the succeeding centimetre. In the case of the more open sandy and loch-head types, this influence is also felt in the second centimetre. The absence of the rise in the mud from St. 13 is probably due to experimental error, it being very difficult to isolate the semi-fluid surface layer in this case. The drop at 5 to 6 cm. at St. 11 in Loch Striven is a peculiarity of that loch [*vide* distribution of total P_2O_5 (Moore, **5**)], as it occurs in most parts of the channel but not in other lochs.

Considering the high organic content of these muds it is surprising that the pH values are so high, the lowest recorded being only 7·45. Curiously, too, a mud as rich as that at St. 13 may have as high a pH as 7·84 well below the surface. The higher surface values are probably to be explained by the influence of the sea-water which has always a higher value than that of the mud. The rise in pH from 2 cm. downwards may be due to the decreasing amount of organic matter with depth, but this gives no account

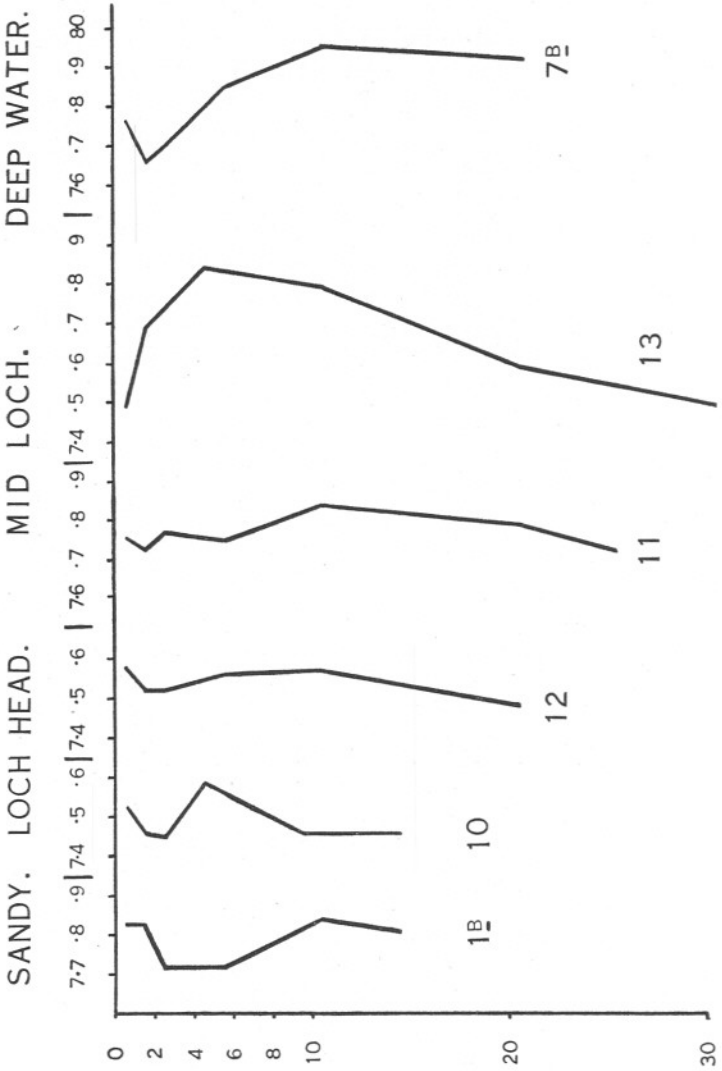

FIG. 2.—Distribution of pH with depth in mud (ordinate) in cm., for the four types of station.

of the succeeding drop which is so marked in the deepest samples taken, i.e. St. 11 and 13. From a biological aspect, however, the outstanding point is the absence of any extremes of pH even in very different types of mud. The actual values obtained are shown in Table III.

TABLE III.

DISTRIBUTION OF pH WITH DEPTH IN MUD.

Depth in. Mud in cm.	Stations.					
	1b.	10.	12.	11.	13.	7b.
0–1	7·83	7·53	7·58	7·76	7·49	7·76
1–2	7·83	7·46	7·52	7·73	7·69	7·66
2–3	7·72	7·45	7·52	7·77	—	7·70
4–5	—	7·59	—	—	7·84	—
5–6	7·72	—	7·56	7·75	—	7·85
9–10	—	7·46	—	—	—	—
10–11	7·84	—	7·57	7·84	7·79	7·95
14–15	7·81	7·46	—	—	—	—
20–21	—	—	7·48	7·79	7·59	7·92
25–26	—	—	—	7·72	—	—
30–31	—	—	—	—	7·49	—

WATER CONTENT.

The distribution of density and water content with depth in the mud was estimated simultaneously in a number of muds. The method found to be most applicable was that of weighing about 10 gm. of the wet mud, on a tared watch-glass, then reweighing immersed in sea-water, and finally tipping off the free water from the glass, drying in a water oven at 100° C., and weighing again. From these results the density of the wet and of the dried mud, and the percentage by volume of water in the wet mud can be calculated. The chief error introduced is that of the salt content of the interstitial water, and of such water as clings to the mud and the watch-glass on drying. This will cause the figures for density to be about 5% too high, but since the water content does not vary sufficiently to affect this appreciably, the error has been assumed to be constant, and no correction has been made for it. Similarly, the figure for the percentage of contained water will be about 2% too low and will also have an almost constant error. The error due to weighing in sea-water instead of fresh is allowed for.

The values obtained for the various stations, which are expressed as percentages by volume of water in the wet mud, are given in Table IV. It must be understood that these figures do not refer to the amount of true free interstitial water, but to the total loss on drying at 100° C., some of

TABLE IV.

Distribution of Water Content with Depth in Mud.

Values expressed as percentage of water, by volume, in the wet mud.

	Depth in mud in cm.												
Station.	0–2·5.	2·5–5.	5–7·5.	7·5–10.	10–12·5.	12·5–15.	15–17·5.	17·5–20.	20–22·5.	22·5–25.	25–27·5.	27·5–30.	30–32·5.
1 . .	74·4	69·4	70·9	70·2	67·7	66·6							
11 . .	84·6	81·0	78·3	78·8	77·7		77·5	78·6	77·9	76·8	77·6	76·0	
11b . .	80·8	80·1	78·6	78·4	77·3	77·3	77·8	76·6	74·9	72·9	72·9	72·1	68·4
12 . .	81·0	81·7	78·9	79·1	77·6	77·7		74·0	72·8	75·7	75·7		
13 . .	86·7	87·1	85·0	85·2	81·7	81·2	83·5		80·2	80·1	80·8	79·0	81·0
13a . .	80·4	81·7	80·7	79·7	78·2	79·1	77·9	79·1	79·1	74·7			
14 . .	82·4	78·9	78·8	78·3	77·4	77·6	77·7	76·9	77·8	75·2		76·3	
15a . .	81·4	79·6	79·8	78·5	76·1	74·3	76·2	76·1	75·6	76·2	74·4	74·6	
16 . .	79·3	77·2	75·1	74·0	72·5	71·4	68·3	71·3	72·2				
16a . .	77·7	73·8	73·0	73·7	72·2	71·2	71·1	70·1	70·2	69·1	65·6	64·9	
17 . .	81·5	79·8	77·3	77·7	76·8	74·8	76·0	77·2	73·5	75·3			
17a . .	59·6	60·8	58·1	60·4	54·4	48·0							
17b . .	80·9	77·5	77·5	76·3	77·1	76·3	80·7	77·3	76·7	75·0	74·8		75·4
17c . .	74·5	72·6	75·2		71·5	73·4	72·6	70·7	71·5	68·6	68·5		
19 . .	81·2		77·4		75·5		74·3		74·2				
20a . .	50·7	56·6	68·1	71·2	71·3	71·4	66·9	71·5	55·5				
23 . .	80·1		74·7		76·2		73·9		73·9		71·9		
24 . .	82·8	80·3	78·7	77·7	76·7	73·6	76·1	74·3	74·2	72·4	72·9	68·6	
26 . .	71·7	68·9	68·1	66·8	64·5	62·8	58·8	59·4	56·3				

which may be due to water contained in the form of gels or otherwise fixed.

Figure 3 shows the distribution of the water content with depth in the mud for St. 11, a mid-loch type. Here there is a rapid fall in the quantity of water from 85% at the surface to 79% at about 6 cm. Below this depth the fall is very much slower. Though the slope of the curve varies at different stations, there occurs typically a rapid fall in water content near the surface followed at a varying depth by a more slowly decreasing or constant amount. The depth at which this constant amount is attained varies, and in some cases, i.e. St. 26, the sampling seems not to have been taken deep enough to reach this level, though it would probably be reached with a longer sample. Certain stations are very erratic, notably those in the Dunoon Basin, and of these St. 20a is of interest since a sample there shows at the surface a layer of sand, superimposed at a depth of about 10 cm. on a layer of mud and this again at about 20 cm. on another layer of sand. The water content shows corresponding changes being lower in the sandy layers than in the mud. Since this station must be largely influenced by the river, it would appear that the nature of the material deposited had changed considerably from time to time.

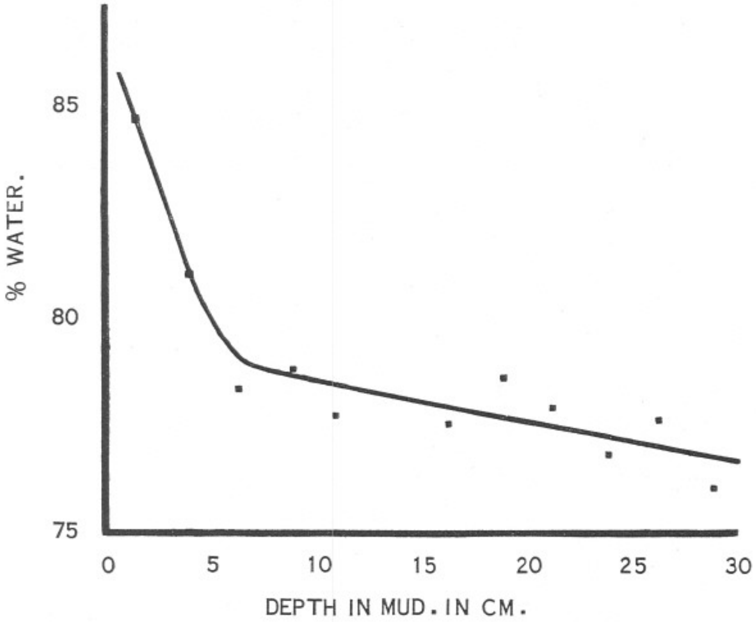

FIG. 3.—Variation of water content with depth in mud at St. 11—mid-loch type.

There does not appear to be any correlation between the shape of the curve and the type of station, with the exception of the sandy type which has a very much lower water content than the softer muds. In the other types the surface values are remarkably high, frequently lying between 80% and 85%. The constant value attained usually lies between 70% and 80%, though in the case of St. 26 the value has fallen from 72% to 56% without becoming constant. This station, however, is far from land and of a different type from that of the lochs.

In a later section it is shown that the mud is laid down on the surface

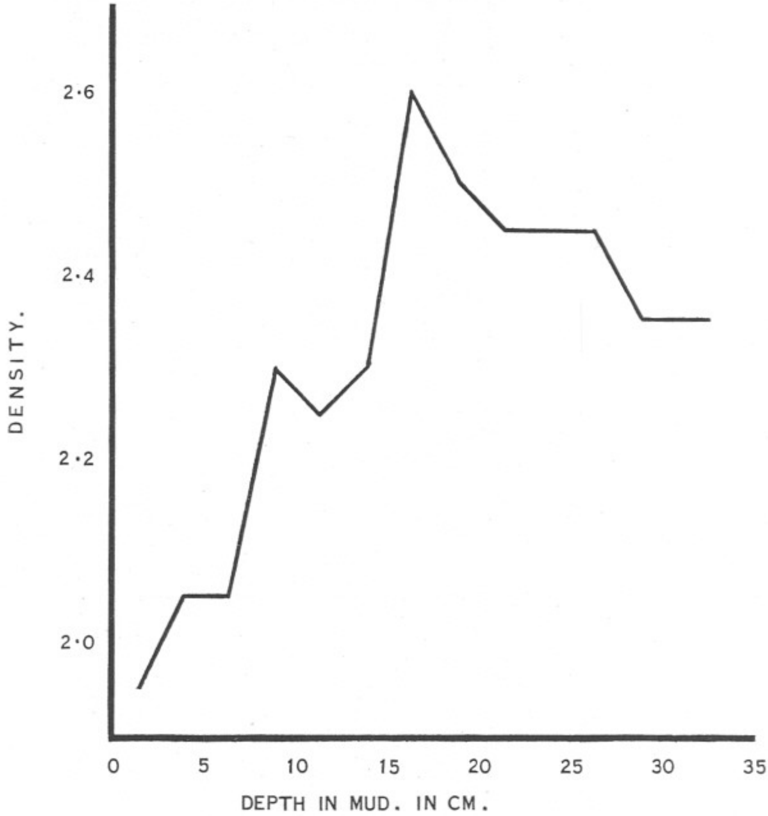

FIG. 4.—Distribution of density with depth in the mud for St. 13—mid-loch type.

in a very fine and loose condition ; and an examination of a tube sample shows that it becomes steadily harder and more like a clay with increasing depth. The above figures show that this is due to packing accompanied by expression of water. The interesting point, however, is that this packing continues for such a long time ; in the case of St. 11, as shown later, the chief packing being completed at the end of about ten years, and at a depth of about 5 cm., while in cases such as St. 26 packing probably continues for a very much longer period.

Finally, the cause of the packing may be assigned to several factors. Primarily, no doubt, it is due to the weight of the superimposed mud, but another factor of importance will be the packing effect of the small organisms, such as worms, moving about in the mud ; while yet another factor of great importance is the consolidation of the fine mud particles into firm pellets in the guts of animals which eat them. This question of pellet formation, which is of tremendous importance in some muds, is discussed more fully later. Finally, there is the possibility of packing accompanying chemical change in the break down of organic matter in the mud.

DENSITY.

The distribution of the density of the dried mud throughout the area is given in Table V, while that for St. 13 is shown graphically in Figure 4, this being fairly typical for the area. Of the nineteen stations worked there was a rise in density below the surface in twelve, followed by a fall in density in half of these. While the density of individual particles may vary much more widely, that of the mud *en masse* lies usually between 2·0 and 2·5. These values, together with an increasing density at greater depths, are to be expected in a mud consisting chiefly of a mixture of quartz and calcareous particles with a varying amount of lighter organic matter, the quantity of the latter decreasing with depth.

The subsequent fall at some stations is less clear, especially as it occurs only in the mid-loch type of station where conditions are stable. Of the loch-head type, three stations show a rise but no fall, possibly because the sampling has not been deep enough, the rate of deposition being greater in these. The stations in the Dunoon Basin—Stations 20a, 17, 17a, 17b, 17c—are usually erratic in every way, St. 20a reflecting its alternate layers of mud and sand in its density. In the sandy type of station there is very little variation, the density being that of the quartz of which it is almost entirely composed.

NATURE AND DISTRIBUTION OF PARTICLES.

The abundance of fæcal pellets and the large quantity of organic matter present render sieving an unsuitable method of grading ; for the same reason the standard method of grading by rate of settling in distilled water after first drying, treating with H_2O_2 and washing with distilled water, would completely alter the nature of the mud from a biological standpoint. An attempt to estimate particle size from rate of settling of fresh mud in sea-water would also yield erroneous results, since the coarser grades may consist of a mixture of quartz grains with pellets of twice their size, while in the finer grades it has been shown that the density of the particles may vary in extreme cases from 1·2 to over 4·0.

TABLE V.

Distribution of Density with Depth in Mud.

Depth in mud in cm.

Station	0–2·5.	2·5–5.	5–7·5.	7·5–10.	10–12·5.	12·5–15.	15–17·5.	17·5–20.	20–22·5.	22·5–25.	25–27·5.	27·5–30.	30–32·5.
1	2·60	2·60	2·60	2·60	2·60	2·65	—	—	—	—	—	—	—
11	2·30	2·35	2·35	2·40	2·30	2·35	2·40	2·50	2·35	2·30	2·35	2·30	—
11b	2·35	2·45	2·50	2·50	2·45	2·45	2·60	2·60	2·65	2·55	2·55	2·50	2·40
12	2·00	2·20	2·25	2·30	2·30	2·35	—	2·20	2·25	2·30	2·25	—	—
13	1·95	2·05	2·05	2·30	2·25	2·30	2·60	2·50	2·45	2·45	2·45	2·35	2·35
13a	2·30	2·20	2·40	2·45	2·45	2·45	2·40	2·50	2·50	2·25	—	—	—
14	2·25	2·35	2·35	2·55	2·30	2·35	2·40	2·40	2·45	2·35	2·30	2·40	—
15a	2·40	2·45	2·50	2·45	2·45	2·50	2·55	2·60	2·50	2·55	2·60	2·55	—
16	2·35	2·40	2·45	2·40	2·45	2·40	2·35	2·50	2·55	—	—	—	—
16a	2·40	2·45	2·45	2·50	2·50	2·55	2·55	2·55	2·55	2·55	2·60	2·60	—
17	2·50	2·45	2·40	2·45	2·40	2·50	2·40	2·45	2·45	2·45	—	—	—
17a	2·65	2·60	2·65	2·65	2·65	2·65	—	—	—	—	—	—	—
17b	2·50	2·50	2·50	2·45	2·45	2·50	2·65	2·60	2·70	2·55	2·55	2·55	2·60
17c	2·40	2·35	2·45	2·35	2·40	2·40	2·45	2·35	2·45	2·45	2·45	—	—
19	2·30		2·35		2·35		2·40		2·30				
20a	2·50	2·40	2·45	2·40	2·40	2·40	2·40	2·45	2·55	—	—	—	—
23	2·35		2·45		2·45		2·45		2·50		2·50		
24	2·40	2·35	2·35	2·45	2·45	2·45	2·50	2·55	2·50	2·45	2·50	2·55	—
26	2·40	2·45	2·50	2·45	2·50	2·55	2·55	2·60	2·55	2·60	—	—	—

One of the most significant factors in these muds is the conversion into fæcal pellets of the very fine material falling on the surface. In extreme cases the whole of the mud may consist of pellets with no admixture of fine material at all, and it is normal for them to form up to 40% of the total. For these reasons a simple type of elutriator has been used which differentiates the mud into four grades of fairly definite constitution, and gives an idea of the distribution of the pellets and their relation to the fine material. The elutriation is carried out with sea-water, in four upright conical glass vessels connected in series, the vertical rate of flow at the widest part in each being as follows :—

Grade.	Rate of flow in cm. per minute.
G. 1	10·0
G. 2	2·5
G. 3	1·5
G. 4	1·0

The constitution of these grades is fairly constant and the following description of the grades from a bucket sample from St. 10 may be generally applied. Where there are many fragments of plant origin they are distributed in all grades according to size. Occasionally also in the surface layers Grade I may contain numerous very small worm tubes.

Grade I. Chiefly pellets of large Maldanid worms (length 0·2 to 1·0 mm.) and of *Syndosmya alba* (length ca. 0·5 mm.) ; also some large masses of organic detritus, and sand grains of about 0·1 mm. long. In deep-water stations there are very few large sand grains.

Grade II. Almost entirely pellets of Maldanids (length up to 0·2 mm.), and some small sand grains.

Grade III. Chiefly small mineral fragments, with masses of fine detritus, some recognisably of organic origin, up to 0·1 mm. long, and a few small Maldanid pellets of the same length or less.

Grade IV. Similar to Grade III only of smaller size and with no pellets.

The small amount of material passing Grade IV has been neglected.

Before elutriation it is necessary to rub the mud in some sea-water into a fluid condition. This causes an appreciable amount of break down of the large pellets in Grade I. The surface mud is soft and needs very little rubbing, so that in it there will be little break down, but in the deeper and harder muds more rubbing is necessary, and hence more break down takes place. The pellets in Grade II are smaller, and unless the mud is so stiff as to necessitate considerable rubbing they will be little subject to break down. This is borne out by the fact that in the case of softer muds, such as those from Stations 14 and 16a, the sums of Grades III and IV, into which the pellets would break down, show no steady rise with increasing depth. They do, however, show such a rise in St. 11 which is more clayey.

TABLE

ELUTRIATION GRADE

Expressed as percentage

Station.	Grade.	0–2·5.	2·5–5.	5–7·5.	7·5–10.	10–12·5.	12·5–15.	15–17·5	17·5–20.	20–22·5.	22·5–25.	25–27·5.	27·5–30.	30–32·5.
1.	1.	9·2	1·1	4·5	2·0	1·0	0·9							
	2.	67·2	72·5	26·9	69·8	64·8	65·2							
	3.	0·5	0·6	30·8	0·6	14·8	16·4							
	4.	23·1	25·7	37·8	27·6	19·4	17·2							
6a.	1.	11·7		2·4		12·1		2·7						
	2.	32·1		36·6		15·0		31·4						
	3.	27·9		0·7		43·5		35·2						
	4.	28·3		60·3		29·4		30·8						
8.	1.	8·9		0·9		5·9		2·5		2·2				
	2.	43·2		34·1		45·1		62·6		37·9				
	3.	5·7		28·1		1·0		25·9		0·1				
	4.	42·2		36·9		48·0		9·1		59·8				
8b.	1.	10·6				11·3		9·4		0·9				
	2.	33·0				38·6		19·9		16·2				
	3.	25·8				36·9		49·1		1·9				
	4.	30·6				13·2		21·6		81·0				
9.	1.	16·5		14·0		2·7		1·5						
	2.	33·7		23·3		33·8		29·9						
	3.	19·6		27·2		0·6		1·7						
	4.	30·2		35·5		62·9		66·9						
11.	1.	13·0	25·9	14·5	7·0		8·1	3·2	4·2	2·1	2·2	3·7	1·9	
	2.	41·5	33·1	41·5	46·5		29·1	24·4	13·4	18·4	27·4	24·2	15·9	
	3.	1·7	20·7	17·1	16·5		47·1	57·5	69·0	59·0	50·7	52·7	10·0	
	4.	43·8	20·3	26·9	30·0		15·7	14·9	13·4	20·5	19·7	19·4	73·2	
11b.	1.	9·0	4·9	1·9	13·0	2·4	3·0	3·4	13·3	1·2		2·3	5·0	24·3
	2.	44·6	44·7	42·5	30·1	22·7	37·1	33·2	26·6	25·8		32·1	39·8	23·5
	3.	12·5	18·6	23·8	24·2	44·2	36·2	11·6	30·7	42·1		2·1	3·0	1·8
	4.	33·9	31·8	31·8	32·7	30·7	23·7	52·0	29·4	30·9		63·5	52·2	50·4
12.	1.	3·6		3·7	3·8	2·0	2·0	0·9	0·7	2·7	6·9	4·6		
	2.	32·6		43·7	62·4	50·2	50·3	40·3	20·5	55·3	56·0	78·7		
	3.	0·7		0·6	1·8	1·0	1·5	2·0	65·2	1·4	0·7	0·7		
	4.	63·1		52·0	32·0	46·8	46·2	56·8	13·6	40·6	36·4	16·0		
13.	1.	12·2	2·9	3·7	3·8	3·9	1·3	2·1	3·6	1·7	1·5	1·7	7·4	8·9
	2.	52·1	57·8	53·7	68·2	59·7	54·1	49·5	60·2	46·6	47·7	50·1	48·3	38·2
	3.	3·4	3·2	3·4	2·2	15·2	2·0	21·8	3·8	26·5	20·6	3·4	1·4	1·8
	4.	32·3	36·1	39·2	25·8	21·2	42·6	26·6	32·4	25·2	30·2	44·8	42·9	51·1
13a.	1.	15·2	6·3	2·2	9·7	1·9	0·9	1·6	1·5	1·9				
	2.	71·3	57·7	72·4	56·8	41·3	38·7	33·9	39·9	40·0				
	3.	1·6	1·2	1·3	2·8	29·2	17·7	38·9	25·3	9·7				
	4.	11·9	34·8	24·1	30·7	27·6	42·7	25·6	33·3	48·4				
14.	1.	6·1	11·3		3·7	7·2	3·1	10·0	10·6	6·4	2·1	3·5	6·2	
	2.	52·3	47·8		56·0	53·4	64·4	53·2	56·8	43·6	53·3	50·5	51·9	
	3.	1·4	14·0		16·8	1·3	6·1	1·5	1·9	1·9	1·3	2·6	1·2	
	4.	40·3	26·9		23·5	38·1	26·4	35·3	30·7	48·1	43·3	43·4	40·7	
15.	1.	0·6	6·2	13·7	12·5	12·8		2·5	2·5	3·8	2·2	1·4	7·3	
	2.	65·7	58·6	83·0	55·3	47·7		52·8	44·2	46·3	29·3	20·4	16·0	
	3.	0·9	3·4	0·4	0·9	0·8		0·6	0·5	0·7	0·4	60·8	70·0	
	4.	32·8	31·8	2·9	31·3	38·7		44·1	52·8	49·2	68·1	17·4	6·7	
15a.	1.	29·8	21·9		2·3	2·4	6·4	3·6	3·7	5·6	8·3	5·7	11·7	
	2.	33·4	61·2		34·9	30·1	34·5	35·8	38·8	31·3	26·8	23·7	15·8	
	3.	1·2	1·2		1·0	30·3	9·5	2·3	1·0	28·0	29·6	28·0	38·9	
	4.	35·6	15·7		61·8	37·2	49·6	58·3	56·5	35·1	35·3	42·6	33·6	

VI.

PERCENTAGES.

dry weight.

Station.	Grade.	0–2·5.	2·5–5.	5–7·5.	7·5–10.	10–12·5.	12·5–15.	15–17·5.	17·5–20.	20–22·5.	22·5–25.	25–27·5.	27·5–30.	30–32·5.
16.	1.	3·6	4·9	4·2	5·6	5·3	6·8	4·7	2·4	2·1	2·4			
	2.	45·7	34·8	32·9	31·1	36·9	39·5	41·5	42·2	43·8	37·7			
	3.	1·3	0·3	2·3	1·9	37·4	30·8	27·1	20·3	5·2	14·2			
	4.	49·4	60·0	60·6	61·4	20·4	22·9	26·7	35·1	48·9	45·7			
16a.	1.	4·6	13·6	6·2	2·1	1·1		1·0	1·0	0·7	1·3	1·2	0·5	
	2.	45·6	44·2	37·9	47·5	46·6		48·7	45·6	43·8	50·6	42·0	46·1	
	3.	1·6	18·7	30·6	24·2	28·0		26·1	30·3	32·7	22·6	1·3	1·3	
	4.	48·2	23·5	25·3	26·2	24·3		24·2	23·1	22·8	25·5	55·5	52·1	
17.	1.	23·9	5·5	2·9	3·7	1·3	9·9	14·3	7·8	1·6	0·8			
	2.	1·7	3·7	48·7	35·1	43·8	28·8	0·8	26·5	15·8	19·5			
	3.	8·3	48·0	1·0	0·7	0·6	0·4	46·4	18·3	56·4	53·5			
	4.	66·1	41·9	47·4	60·5	54·3	60·9	38·5	47·4	26·2	26·2			
17a.	1.	83·1	84·4	83·9	76·2	80·6	86·9	89·5						
	2.	8·1	7·5	7·9	9·5	8·3	8·1	7·5						
	3.	6·5	4·5	0·1	5·5	0·1	0·2	0·2						
	4.	2·3	3·6	8·1	8·8	11·0	4·8	2·8						
17b.	1.	11·6	26·3	21·1	22·2	16·8	2·5	3·6	2·1	1·5	0·5	1·0	1·3	1·4
	2.	19·3	2·0	21·6	25·1	42·1	57·7	9·4	19·5	7·8	13·7	9·8	1·7	24·5
	3.	2·2	14·2	0·8	0·9	26·1	1·2	32·4	32·2	39·5	1·1	38·2	60·4	1·4
	4.	66·9	57·5	56·5	51·8	15·0	38·6	54·6	46·2	51·2	84·7	51·0	36·6	72·7
17c.	1.	22·9	18·9	20·1	14·1	13·0	14·4	2·3	0·9	1·8	22·3	15·3		
	2.	3·2	29·0	37·0	32·3	31·2	31·6	10·0	25·1	23·0	24·0	27·4		
	3.	14·4	0·6	0·5	1·0	0·7	1·1	61·7	0·9	17·3	16·9	2·3		
	4.	59·5	51·5	42·4	52·6	55·1	52·9	26·0	73·1	57·9	36·8	55·0		
18.	1.	19·4		8·5		7·8		14·5		10·7				
	2.	30·0		24·5		50·2		25·7		24·1				
	3.	30·4		35·0		5·1		46·6		48·6				
	4.	20·2		32·0		36·9		13·2		16·6				
19.	1.	3·6		5·3		10·2		1·7		1·1		3·8		
	2.	3·4		32·4		22·1		19·4		4·6		21·2		
	3.	37·9		39·3		51·2		44·3		61·5		48·2		
	4.	55·1		23·0		16·5		34·6		32·8		26·8		
20.	1.	86·3	34·4	18·9	1·2	12·2	9·1	15·5	18·2	41·1				
	2.	0·4	9·8	1·2	0·6	0·7	11·9	12·0	0·6	1·9				
	3.	10·2	23·1	46·2	56·9	47·7	34·3	48·9	65·4	32·8				
	4.	3·1	32·7	33·7	31·3	39·4	44·7	23·6	15·8	24·2				
23.	1.	5·0		2·1		1·6		3·1		2·2				
	2.	1·2		2·6		5·9		2·7		4·2				
	3.	23·3		41·8		61·5		75·4		71·8				
	4.	70·5		53·5		31·0		18·8		21·8				
24.	1	8·9	8·8	5·7	3·8	2·7	2·4	2·7	2·6	1·7	3·9	1·8	12·7	
	2.	37·4	22·1	26·8	10·9	13·7	7·0	11·8	0·2	3·8	6·3	1·9	1·7	
	3.	7·0	5·8	4·9	25·0	2·0	34·6	47·1	52·6	70·2	7·5	19·5	5·5	
	4.	46·7	63·3	62·6	60·3	81·6	56·0	38·4	44·6	24·3	82·3	76·8	80·1	
25.	1.	60·0				51·9		59·2						
	2.	27·9				29·5		27·8						
	3.	0·2				0·4		0·4						
	4.	11·9				18·2		12·6						
26.	1.	3·0	1·7	2·1	1·0	1·8	1·3	0·6	0·5	0·5	0·6			
	2.	51·4	42·4	47·4	48·6	41·6	41·4	53·9	47·4	45·5	56·2			
	3	1·9	1·4	33·3	37·5	1·0	1·1	26·0	3·0	0·7	1·7			
	4.	43·7	54·7	17·2	12·9	55·6	56·2	19·5	49·1	53·3	41·5			

Pellets such as those of Calanus which fall in large quantities on the mud surface, but are more friable than those of Maldanids, are broken down in the course of the elutriation.

Figure 5 shows the distribution of these four grades for St. 16a in the Holy Loch as an example of the mid-loch type; while the figures for all the stations are given in Table VI. The material falling on the mud surface is largely fine detritus with some larger particles of organic origin: this is reflected in the high value of Grade IV at the surface. Much of this fine detritus is eaten by animals living near the surface of the mud, and is converted by them into pellets. The effect of this is a rapid drop in the amount of Grade IV in the first 2 to 5 cm. and a corresponding increase in Grade I. Grade II is more erratic, and shows no clear general rise to correspond with this, though such frequently takes place a few centimetres deeper. Below this depth the mud is packed to a much harder consistency with the result that it needs more rubbing down, and Grade I decreases rapidly. This fall then is assumed to be largely artificial. At the same time natural break down of the organic particles causes a rise in the amount of Grade III in the first 5 to 10 cm. With the decrease in life

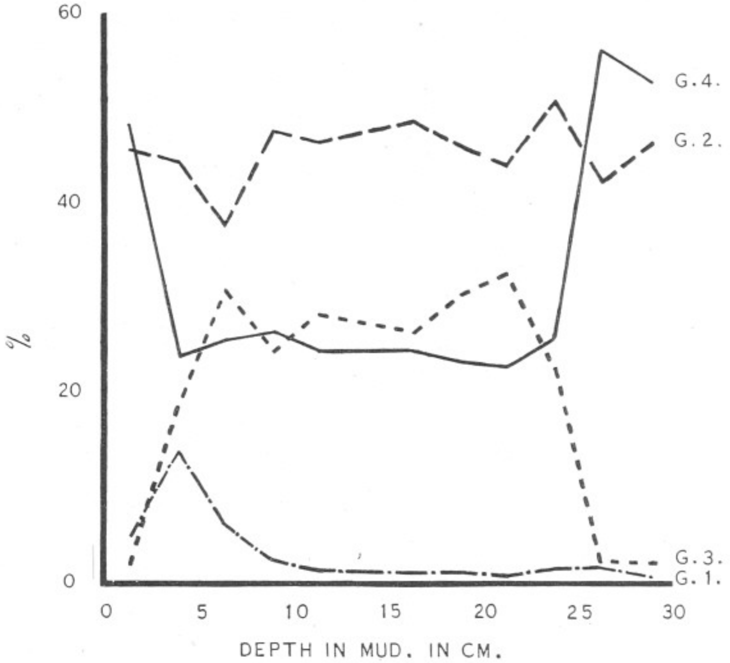

FIG. 5.—Distribution of particle grades with depth in the mud for St. 16a. G. 1 is the coarsest and G. 4 the finest.

deep in the mud, there is little further pellet formation, and Grade II remains more or less constant. But the break down of the organic particles is still continuing, and at a depth of about 25 cm. Grade III suddenly drops to about 2% with a corresponding rise in the amount of Grade IV. The magnitude of this change may appear exaggerated since the difference in particle size in Grades III and IV is less than that between any other two grades. It points, however, to a steady slow break down of these organic particles.

As would be expected, at many stations conditions of deposition and change are not sufficiently regular to give as simple a curve as the one described. The type is best illustrated in the mid-loch stations, though the transitions in Grades III and IV usually take place more gradually than at St. 16a; Stations 8b, 11, 16a, and 23 show the type fairly well, and Stations 9, 13, and 13a less clearly. The loch-head type of station shows much more erratic results, though St. 14 suggests this type. The stations in the Dunoon Basin are, as in other characters, very erratic, and the sandy stations are of course of quite a different nature. Station 20a shows a high proportion of Grade I in the two sandy layers, with a low Grade I and a high Grade III and IV in the intermediate mud layers.

There are then two distinct processes taking place in the mud. Firstly, the fine material which falls on the surface of the mud is being eaten and converted into larger aggregates in the form of pellets which form quite the most outstanding feature of the muds; and secondly, there is a steady break down of the larger organic particles which fall on to the mud surface into finer material, many of these large particles being pellets, such as those of Calanus, but of a very much more friable nature than those formed in the mud. The pellet formation takes place only at the levels at which animal life exists, and chiefly close to the surface. Dr. Lloyd (**4**) has shown that bacteria are present in numbers in these muds in the deepest samples which have been taken, and perhaps due to them the break down of the organic particles continues to a greater depth.

NATURE AND RATE OF SEDIMENTATION.

With a view to determining the nature and origin of the sediments falling on the mud surface, and whether these showed variation in relation to any factors such as rainfall or plankton, collections have been made at various stations by means of two types of sediment pots.

The Type "A" pots are glass preserving jars, 32 cm. high, with an internal diameter of 9 cm. at the mouth. These were attached in string nets to a rope, buoyed at the surface. At the bottom of the rope was a lead weight, hanging just clear of the bottom at low water, and beyond this about 10 metres of slack rope attached to a heavy stone as an anchor.

The pots thus moved vertically with the tide, but hung more or less upright.

Another type of pot, " B," was used later in order to ascertain whether there was any lifting of bottom material once it had settled on the mud. The gear consisted of a series of seven smaller pots attached at 30 cm. intervals to a vertical iron rod, and this connected by a ring to a concrete block. A rope was attached to the top of the rod, and a set of submerged glass floats twenty metres above the rod kept the latter upright as well as keeping any slack rope clear of the pots ; the floats were connected by a slack rope to a buoy at the surface. The pots used here were preserving jars, 17 cm. high, with an internal diameter at the mouth of 5·5 cm.

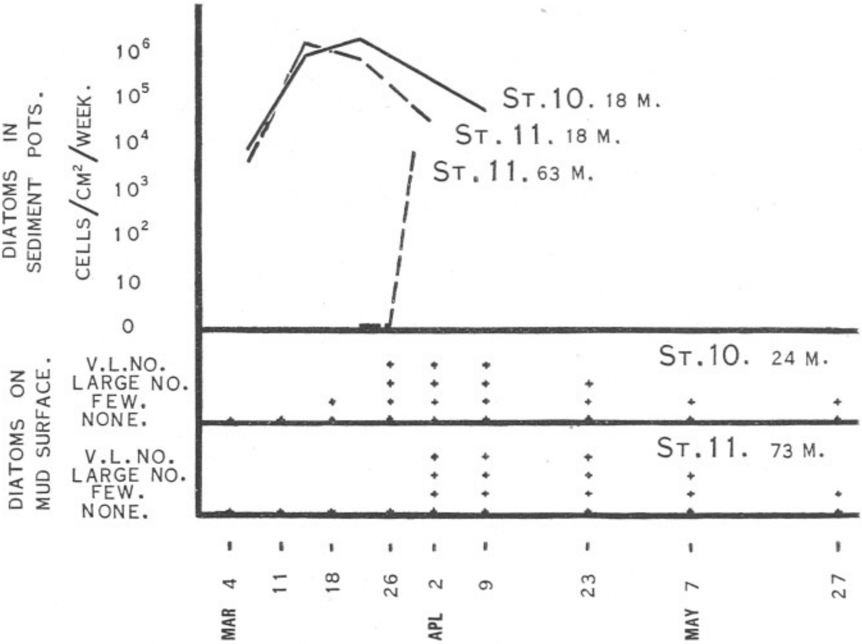

FIG. 6.—Occurrence of diatoms in the sediment pots (upper part of figure) and on the mud surface (lower part of figure) ; showing their appearance in sequence at the upper pots, the lower pots and the mud surface.

Type " A " pots were put out first at Stations 10 and 11. At St. 10, at Loch Striven Head, where the depth of water is 24 metres, only one pot was attached at a depth of 18 metres. At St. 11, at the middle of the same loch, one pot was attached at 18 metres, and one just clear of the bottom at 68 metres, the depth of water being 73 metres.

The gear was first put out on February 25th, 1930, and the pots were replaced at first weekly, and later fortnightly. At the same time vertical hauls were made for plankton and tube samples of the bottom were taken for examination of the mud surface. Where possible diatom counts were made in the sediments by stirring up the latter with sea-water, and counting aliquot samples of it. The sediments were then washed, dried at 100° C. and weighed. Some difficulty was experienced with the bottom pot at St. 11 touching the bottom, so that records for this pot were not obtained until March 18th. Also diatom counts in this pot later became impossible owing to the large numbers of fæcal pellets of Calanus which were present. Both the diatom numbers and the sediment weights are expressed as the amount falling on one square centimetre in one week. Since *Skeletonema costatum* formed 95% of the diatom population at this time, other forms were neglected in the counts.

At St. 11 the diatoms reached a maximum at the surface of the water on March 25th and about three days later at the 10 and 20-metre levels. In the sediments from St. 10 and the top pot of St. 11 the diatom numbers run a very similar course (Fig. 6), reaching maxima of two million at St. 10 and one million at St. 11 in the weeks March 11th–18th and 18th–25th respectively, and then decreasing again. At the same time a count in the bottom pot at St. 11 showed no diatoms for the week March 18th–25th, but 3,800 the following week. Although no actual count of the numbers of diatoms on the mud surface was possible, it was clear that they appeared there quite suddenly and were present for a time in enormous quantities. At St. 10 they appeared first on the mud surface in small numbers on March 18th, and were present in very great numbers the following week. At St. 11, in much deeper water, they were not found on the mud until April 2nd, when, as at St. 10, they were present in great quantity. They continued very numerous at St. 10 up to April 9th ; on the 23rd they were definitely less, and on May 7th there were few left. In the same way, on St. 11, they were still numerous up to April 23rd ; on May 7th they were decreasing in numbers, and by the 27th there were few left, though,

TABLE VII.

NUMBERS OF SKELETONEMA CELLS IN SEDIMENT POTS DURING 1930.

Expressed as number of cells per sq. cm. per week.

Date.	St. 10.	St. 11. Top Pot.	St. 11. Bottom Pot.
March 4th–11th	13,700	11,500	—
,, 11th–18th	987,000	1,040,000	—
,, 18–26th	2,000,000	669,000	0
,, 26th–April 2nd	—	84,000	3,800
April 2nd–9th	103,000	—	—

of course, some are to be found on both stations all through the summer. The results are shown graphically in Figure 6 and the actual numbers in Table VII.

TABLE VIII.

WEIGHTS OF SEDIMENTS IN SEDIMENT POTS DURING 1930.

Expressed as mg. per sq. cm. per week.

Date.	St. 10.	St. 11. Top Pot.	St. 11. Bottom Pot.
February 25th–March 4th	6·9	0·54	—
March 4th–11th . .	4·0	0·79	—
,, 11th–18th . .	9·4	0·71	—
,, 18th–26th . .	9·2	2·5	24·7
,, 26th–April 2nd .	4·2	3·4	33·4
April 2nd–9th . .	7·8	4·3	25·9
,, 9th–23rd . .	—	1·0	7·4
,, 23rd–May 7th . .	7·1	1·8	9·8
May 7th–27th . .	—	1·1	3·3
,, 27th–June 14th .	—	0·24	0·27

The weekly weights of sediments for the three pots are shown in Figure 7, and the actual quantities in Table VIII. Those for the top pot at St. 11 show a strong peak following the diatom increase in the water, but about three weeks later ; and the weight is greatly in excess of that which could be due alone to the diatoms in the pot. This excess is due to the presence of the pellets of *Calanus finmarchicus* of which the sediment was just then almost entirely composed. The vertical tow-nettings showed that these copepods began to appear in large numbers just after the spring diatom increase ; and at the same time their pellets first occurred in the pots. The suddenness of the drop in sediment weight after April 9th suggests that the Calanus shoals were no longer to any great extent feeding—or at any rate shedding their pellets—at this level in this particular area. The weights of sediment for the bottom pot at this station follow a similar course, with a peak following the spring diatom increase maximum, though for no obvious reason the peak comes a week earlier in the case of the bottom pot. During the " Peak," the actual weight of the sediment is considerably greater at the bottom than in the upper pot, but later in the season they show little difference, i.e. 0·24 mg. in the upper pot, and 0·27 mg. in the lower. The pellets in the pots show that the difference is due, at any rate largely, to swarms of Calanus and Euphausids.

The constitution of the sediment is very similar in the two pots. In both there is a considerable amount of fine detritus of unrecognisable origin, although much of it clearly comes from the plankton ; a few quartz grains up to 0·2 mm. in length, though usually smaller, may be present. The main bulk of the material in both pots during the summer is pellets, those of Calanus being predominant in the top pot and mixed with the larger pellets of Mysids and Euphausids in the lower pot. There are always a certain number of dead animals from the plankton, i.e.

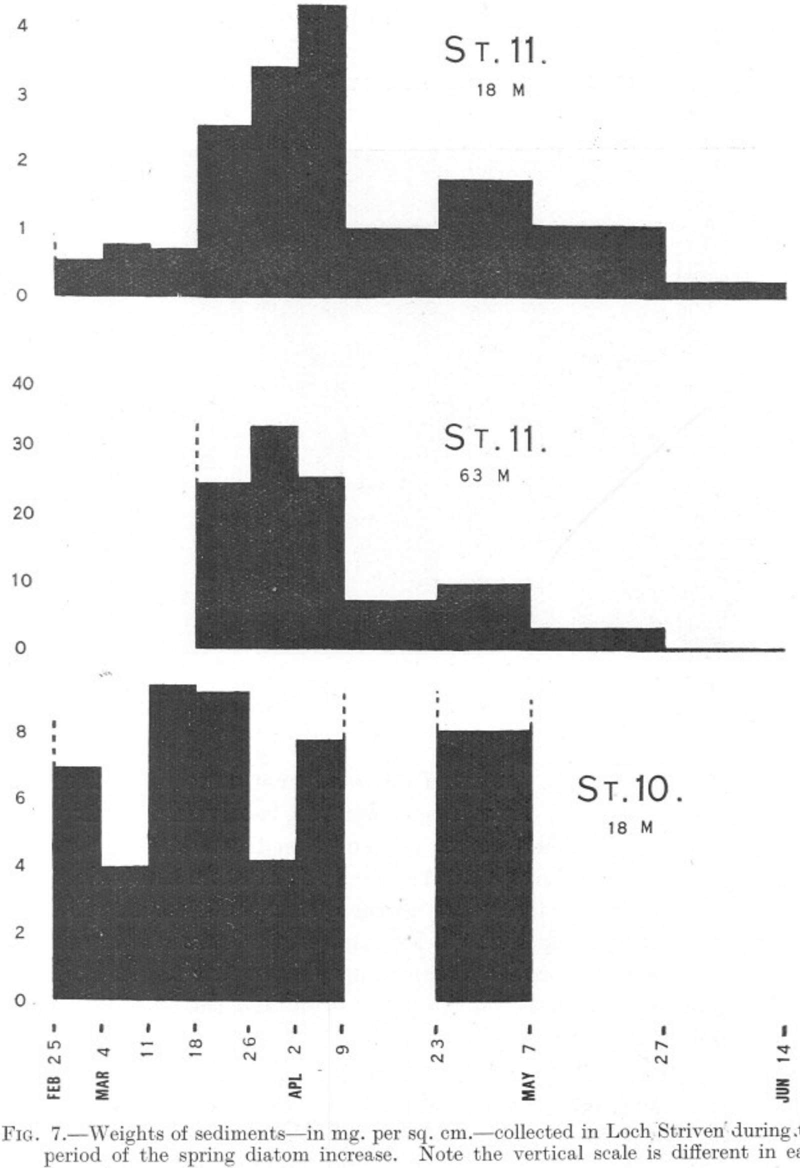

FIG. 7.—Weights of sediments—in mg. per sq. cm.—collected in Loch Striven during the period of the spring diatom increase. Note the vertical scale is different in each example.

copepods, rotifers, etc., as well as diatoms, the latter sometimes in very great quantity. At certain seasons, too, young lamellibranchs and polychætes are very common in the pots.

The sediment weights from the pot at St. 10 are very much more erratic than those from the other station, and show no " Peak " correlated with the spring diatom increase. In general the weight is considerably higher than that for the pot at the same depth at St. 11, and the sediment generally contains much more sand. Since we know that the contribution to it from the plankton, as reflected by the numbers of diatoms, is very similar on both stations, the extra material must come either from the land or from the beach. If the former were the case we should expect to find some correlation between the amount of sediment and the rainfall and this has been found not to be the case. At the same time it does bear some relation to the strength of the northerly component of the wind, and it appears that this wind tends to lift sand off the banks at the sides of the loch in this region, and to carry it into deeper water. On St. 11 no such relation is found between rainfall or wind and the amount of sediment or the occurrence of sand grains in it.

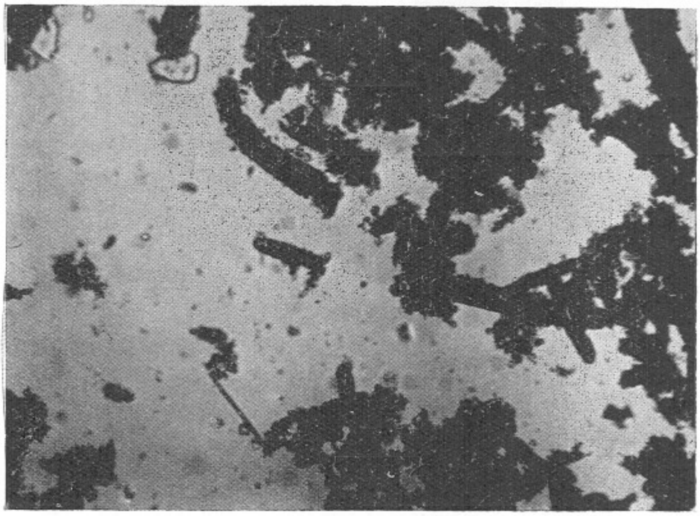

FIG. 8.—Sediment from St. 17d, showing Calanus fæces, diatoms and sand grains.

In order to compare these results with those for less sheltered positions, two other stations were chosen, and pots put out at each of these for two periods of over a week. The first position chosen was St. 17d in Kilchattan Bay. The depth here is 22 metres, and the bottom sandy and steeply shelving, and the bay itself fairly sheltered. One pot was placed as before at a depth of 18 metres. The weights of sediment per cm.^{2} per week were as follows :—

May 22nd to June 5th . . .	3·42 mg.
June 5th to June 14th . . .	5·37 mg.

The nature of the sediment was very similar to that obtained at this time in the lochs, i.e. mainly Calanus pellets together with some Euphausid pellets, and a few diatom chains. There was also a small amount of fine detritus and some sand grains up to 0·5 mm. in length, these being more abundant during the second period : one of these sediments is shown in Figure 8. The greater amount of sediment in this second period was due to the drifting of sand particles offshore, the wind being almost continuously from the east for the first period, and from the north-west for the second.

The pots were then put down at the same depth at St. 1c off Fairlie sands. The bottom here is sandy and exposed to a strong tide, and inshore there are extensive beds of Zostera. The first time there was a small whiting in the pot, so that the results may be too low. The material was almost entirely sand, together with some Calanus pellets. Some fragments of decayed Zostera were present, but these were very few considering the extent of the Zostera beds close to the pots, and as in the case of the Danish waters the weed is no doubt being carried in large masses into deeper and quieter water before it settles (Ostenfeld, **8**). The weight of sediment per cm.^{2} per week was 20·3 mg. The following week the Type " B " pots were used, and showed very similar results, with evidence that much of the material was being swept from the inshore sandbanks, there being pellets of Nucula in the pot 90 cm. above the bottom, and much sand in all pots. The average weight of sediment for the pots was 33·3 mg.

The Type " B " pots were also used on St. 11 in Loch Striven to ascertain whether there was any lifting of bottom material once it had been deposited. Their evidence is not conclusive, but it may be inferred from it, together with the presence of undisturbed diatoms on the extreme surface after the spring increase and also from the evidence of layering which is discussed later, that no such lifting takes place in these sheltered waters.

The results from these pots for a typical period are given below ; the top of No. 1 pot lying about 20 cm. above the mud surface, and that of No. 7 pot about 230 cm. above it.

Wt. of Sediment in mg.	1.	2.	3.	4.	5.	6.	7.
per cm.^{2} per week .	0·72	0·66	0·65	0·59	0·54	0·52	0·44

In the bottom pot—No. 1—there were a few Maldanid pellets indicating slight disturbance of the bottom in lowering the gear, but this did not affect any of the higher pots. The material in the latter was partly fine detritus, but chiefly pellets ; these were mostly from Calanus in the top pot—No. 7—but with a great many large Euphausid pellets in the lower pots. Although no count was possible, the number of these seemed sufficient to account for the increase in weight near the bottom, where the Euphausids are most abundant. If any lifting of bottom material had taken place, recognisable, small bottom pellets would have been expected at any rate in No. 2 pot and none were found.

It is interesting to compare these results with those given by Petersen for Thirsted Bredning in 1910 (Petersen, **9**). These give an average of 6 mg. of sediment per sq. cm. per week ; and if we neglect the fourth, which was taken in much shallower water than the others, they give a striking suggestion of a spring maximum similar to that found in Loch Striven. Petersen states, however, that the sediment collected consisted almost entirely of fine detritus of unrecognisable origin, and that the plankton contributed little to it.

No.	Date.	Depth in m.	Sediment weight in mg. per sq. cm. per week.
1.	April 1st to April 15th . . .	12	1·36
2.	April 15th to April 22nd . .	12	3·51
3.	April 25th to May 21st . . .	14	15·68
4.	June 4th to July 5th . . .	7	(0·49)
5.	July 6th to August 10th . .	10·5	8·96

Estimation of Rate of Deposition of Sediments.

If a tube sample of mud from a suitable locality is allowed to stand in a bright light or even in direct sunlight, it begins after a few weeks to develop alternate bands respectively lighter and darker than the original colour of the sample, and these may continue to intensify for from one to eighteen months. No such bands are visible in the fresh sample. While the light bands vary from 3 to 7 mm. in depth, the dark bands are narrow and not more than 1 or 2 mm. deep, and the pigmentation appears to be due to the formation of peat (see below). From a series of samples from St. 11, of which three, taken in February, early June, and July, are shown in Figure 9, it is clear that the dark band represents the sediment laid down at about the period of the spring diatom increase, and it is most probable that the colouration is due to the diatoms. At any rate it was shown in the previous section that there is a rich layer of diatoms on the surface of the mud on this station during the whole of April, and it is about this time that a new dark band appears.

No trace of diatom skeletons can be found in the layers, but they are probably an unstable form of silica which quickly disappears. The peat formation is probably associated with the very large numbers of bacteria found by Lloyd (**4**) on the mud surface during the period of this rain of diatoms.

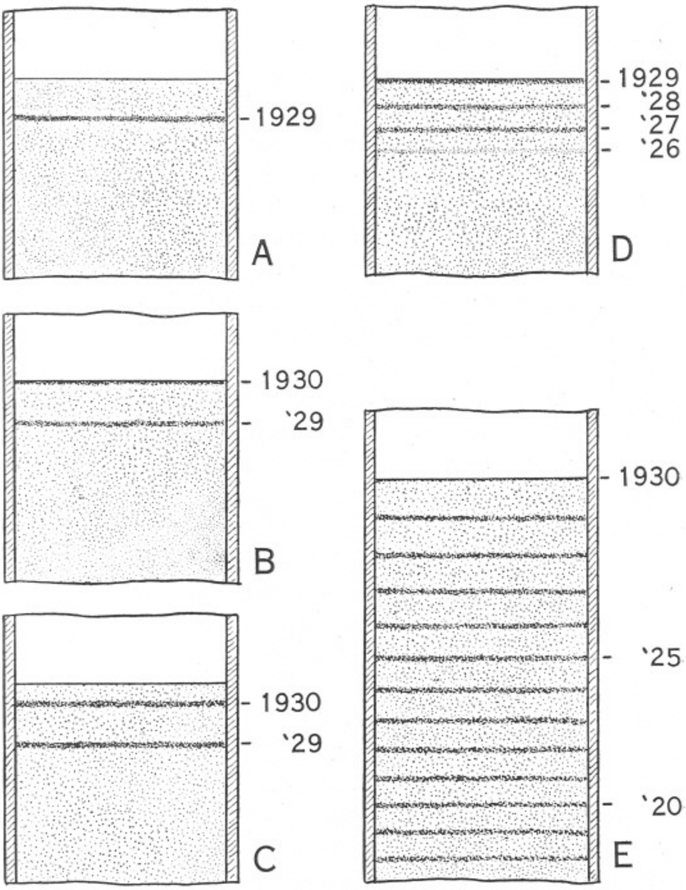

Fig. 9.—Annual layers as seen in tube samples of mud. The dark layers correspond to the spring diatom increase.

A. St. 11. 11th February, 1930.
B. St. 11. 5th June, 1930.
C. St. 11. 18th July, 1930.
D. St. 7. May, 1929.
E. Theoretical spacing of undisturbed bands for St. 11; packing practically ceases after ten years.

These bands are only found on stations where there is very fine sediment falling, and where there are no currents to disturb this once it has settled.

They are, therefore, not to be seen in the coarse mud of the Loch Head stations, nor those in the region of the Dunoon Basin where there are strong tidal currents, but they are well seen in the deeper ones at Stations 11, 7a, and 7b. On St. 11 the maximum number of bands which has been found is two, but on St. 7 four have been seen, the deepest rather faint. The non-appearance of bands below this is in all probability due to the mixing of the mud by the fauna, and this is in accord with the fact that on both stations the dominant forms, i.e. nematodes, are most abundant in the 1 to 2 cm. layer, while the layering is best seen in the top centimetre.

From the distance between the layers, it is possible to calculate the rate at which mud is being laid down at any station. For St. 11, the density and water content of the mud, being known, a graph can be obtained, giving the rate of packing of the mud with depth; and from this, the theoretical spacing of the layers shown in Figure 8, E. At the surface the layers are 6 mm. thick, at about 5 cm. they have packed to 4 mm. thick, and beyond this depth there is little further packing. The top 5 cm. then corresponds to 9½ years' sedimentation, and below this 40 cm. corresponds to about 100 years. At St. 7 the layers are 3·5 mm. apart at the surface so the rate of sedimentation is a little more than half that at St. 11.

The evidence that these are annual layers seems sufficient, but their spacing may be checked by comparison with the results from the sediment pots. If the water content at the surface of St. 11 is 85% and the density 2·3, the amount of material between the first two layers corresponds to 207 mg. per sq. cm. or a weekly average of about 4 mg. This is in agreement with the results from the bottom pot at the same place, which collected 100 mg. of sediment per sq. cm. during the 12 weeks which included the spring increase, or a weekly average of 8·3 mg. Considering the abnormally high values obtaining at the time, this is quite reasonable.

A similar type of stratification is found in the muds on the bottom of the Black Sea, although the conditions of deposition there are very different. The following is an extract (translated) from a paper by Schokalsky (**10**) in which he shows that the layers are probably the result of an alternation of a winter terrigenous deposit with a spring and summer planktonic deposit. Also, in the Black Sea muds, the sediment is undisturbed from the time that it is deposited, so that it is possible to trace layers layed down seven thousand years ago in the very long cores which he has taken.

"The fine stratification gives ten to twelve layers per millimetre; it shows them best in samples taken near the coast. Each of the fine layers is composed of two, one black and organic in nature, the other grey and inorganic; and we have likened each layer to an annual deposit. The black is the product of the plankton dying in winter, while the grey is the accumulation of debris carried down by rivers and coastal waters in the spring. If we accept this hypothesis we arrive at the following results : a thickness of one centimetre is laid down in 50 years. In the layers of calcareous mud a similar stratification is observed, each layer again being double, one formed of calcium carbonate and the other of dead organic matter. From this we conclude that in any case the deposition of a column of mud of one metre will take about 4000 years."

I am indebted to Mr. A. Halimond for the following report on the geological nature of the layered Clyde Muds.

"Sections prepared by infiltration with artificial resin show a typical fine grained mud with small angular quartz grains and flakes of mica in a clayey ground mass. Small brown pellets are common, and there are also larger circular and elliptic areas containing in the centre the same minerals as the mud, but richer towards the margin in an isotropic brownish material, probably phosphate. A section through the top centimetre of the mud (E. 27845) shows a clear mud next to the surface, while at a depth of about half a centimetre there occurs a layer containing particles of brown amorphous ground mass which are probably either peaty or phosphatic matter.

At a depth of nine centimetres (E. 27844) the mud is generally similar to the lower layers of the surface."

The circular and elliptical bodies referred to above are, of course, the fæcal pellets of Maldanid worms.

DISTRIBUTION OF FAUNA.

Although the sea bottom of the Clyde Sea Area has been very thoroughly worked from a faunistic point of view, such quantitative work as has been done has all been restricted to the shore and immediately below low-tide mark, and even here only horizontal and not vertical distribution in the substratum has been described in detail. In the deep water, the fauna may be divided into two main groups. The first comprises the large forms which either live at the surface of the mud, or can come up to it at intervals to breathe, and also the burrowing and tubicolous forms which, while penetrating to a considerable depth, maintain an open connexion with the overlying water. Of this type we have taken *Calocaris macandreæ* in its burrow at a depth of 20 cm., and tubes of Sabellid worms extending to a depth of over 30 cm. To take these in quantity, however, an instrument holding a large amount of mud would be necessary, and this has not been available.

The second group comprises those forms sufficiently small to be contained in a layer of mud not more than about a centimetre thick, and whose environment is determined by the nature of this layer. Since the nature of the mud may change very considerably within a vertical space of two centimetres, it is necessary to examine only forms of less than about five millimetres long, if they are to be correlated with the nature of the mud in particular layers.

Several tube samples were taken from each station, and the mud cut up into one-centimetre layers as soon as possible. This was then passed successively through sieves of 10 and 120 meshes to the inch, and any polychætes retained in the former were neglected; small nematodes were also retained sometimes, entangled in masses of detritus, and these were removed and counted. The whole of the material left in the 120-mesh sieve was examined under a binocular microscope, and the various living animals picked out. The results of counts on a Loch Head, a Mid-Loch, and a Deep Water Station are given in Table IX, and the distribution of the two commonest forms, namely nematodes and copepods, is shown in Figure 10. Except in the surface layer, only very few ostracods and copepods were found, and these few individuals may either have straggled down from the upper layers, or else have been carried down into a deeper layer by the rim of the sampler. At any rate, they occur too rarely in the deeper layers to show definitely that they live there, and for this reason they have been neglected in Figure 10. The polychætes taken were mostly immature forms, and from their patchy distribution are not suitable for comparison.

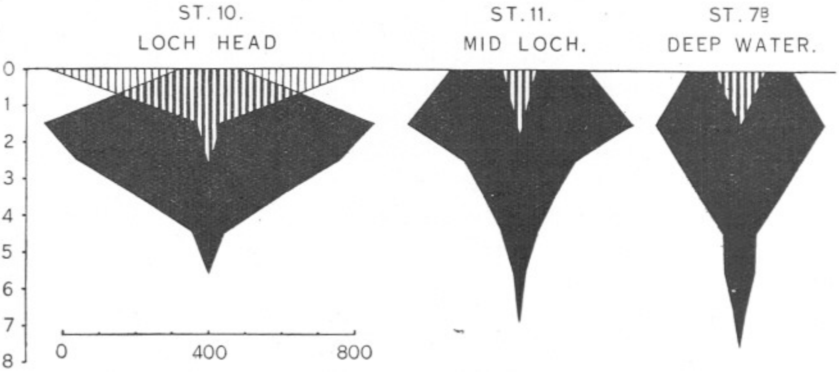

FIG. 10.—Distribution of the smaller fauna with depth in the mud on three types of stations: numbers of individuals—nematodes (black) and copepods (shaded)—in each one-cm. layer in a column of mud of 100 cm.^{2} surface area.

All the copepods taken were Harpacticids, and they were limited almost entirely to the surface centimetre of the mud. Mr. Elmhirst examined a sample of these and found them to consist chiefly of *Danielssenia typica* Boek. and *Cletodes longicaudatas* Boek., with a few *Harpacticus uniremis* Kroyer. They are also very much more abundant in the Loch Head type of station than in either of those in deeper water, the former showing a total density of 697 copepods per 100 sq. cm. while the other two show only 106 and 136. Ostracods show a very similar range, being also restricted chiefly to the top centimetre, and decreasing in abundance in the deeper stations, the total numbers per hundred square centimetres being respectively 125, 86, and 12.

The nematodes, on the other hand, show an entirely different type of distribution. Their maximum numbers in each station are attained in the 1–2-cm. layer and they are still found in quantity two centimetres deeper. While, as in the case of the copepods, the total densities decrease with increasing depth of water—namely, 2515, 1704, and 1570 respectively per hundred square centimetres—the depth in the mud to which they are taken increases in the deeper stations, the limits for the three stations being 6, 7, and 8 cm.

TABLE IX.

Fauna Densities.

Numbers per 100 sq. cm. in each 1-cm. layer.

	Loch Head Type St. 10.				Mid-Loch Type St. 11.				Deep Water Type St. 7B.			
Depth in mud in cm.	*Nematodes.*	*Polychætes.*	*Ostracods.*	*Copepods.*	*Nematodes.*	*Polychætes.*	*Ostracods.*	*Copepods.*	*Nematodes.*	*Polychætes.*	*Ostracods.*	*Copepods.*
0–1	402	25	106	607	452	21	58	62	341	19	12	93
1–2	900	3	16	68	615	25	12	12	459	0	0	6
2–3	728	3	3	16	302	29	4	0	341	12	0	(19)
3–4	395	3	0	6	195	4	4	(4)	218	12	0	(6)
4–5	84	0	0	0	95	8	4	(12)	87	0	0	(12)
5–6	6	0	0	0	33	0	0	(8)	81	6	0	0
6–7	0	0	0	0	12	0	4	(8)	37	0	0	0
7–8	—	—	—	—	—	—	—	—	6	0	0	0
8–9	—	—	—	—	—	—	—	—	0	0	0	0
9–10	—	—	—	—	—	—	—	—	—	—	—	—
10–11	—	—	—	—	0	0	0	0	—	—	—	—
Total	2515	34	125	697	1704	87	86	106	1570	49	12	136

From the general similarity of the three types of station, together with the decrease in total densities of all forms in the deeper water stations, it would appear that either there is less available food in the deeper water or else other conditions are generally less favourable there. The chief differences between the three stations are the steadily decreasing rates of sedimentation with increasing depth of water, and hence a decrease in available food, and the much smaller oxygen avidity at the surface in St. 10. Now in all the muds, even at the surface, the oxygen content is zero, and for forms needing free oxygen this must necessarily be a limiting factor. In view then of the experiments described below it is clear that the copepods cannot live for long in the absence of oxygen, and hence must live within easy reach of the oxygenated overlying water. The nematodes on the other hand are able to live in the absence of oxygen, at any rate for a longer period, so that the deeper layers, where they will have little competition, are available to them. Another factor, however, which must not be forgotten is the consistency of the mud, for it is clear that a copepod will find it difficult to move in a clayey mud, though able to do so easily in the loose surface mud, while a nematode from its shape and size is well adapted for movement even in the stiffer clays.

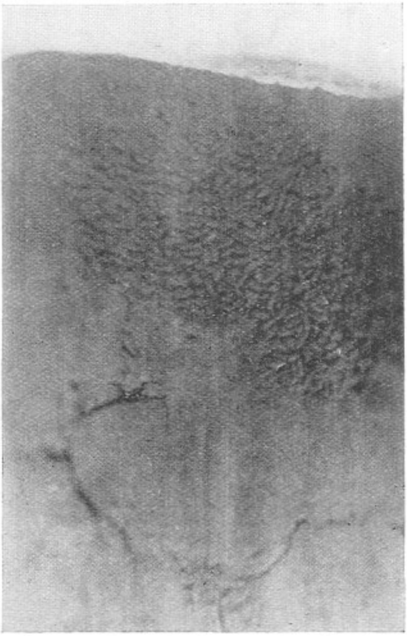

FIG. 11.—Photograph showing mud converted into pellets by a Maldanid worm.

The reaction of the mud cannot be to any extent a limiting factor, since the differences found are so small, and also the differences between two stations in which the same species may occur are greater than those occurring within any one of the stations.

The larger forms are not taken in the sampler in sufficient numbers to allow any quantitative estimate of their importance. But they have a very great effect on the structure of the mud, since most of them feed on the finer particles either in the mud itself or falling from the water, and convert them in their guts into firm pellets. That this process is of extreme importance in the muds is shown by the large numbers of pellets present. At St. 11, for example, 30% to 50% of the mud is converted into these pellets, and the average of a series of counts shows about 3400 pellets per cubic centimetre of mud. The effect of this aggregation on the effective particle size of the mud is obvious. In the first place, the liability of the mud to be carried by currents is greatly decreased, and in the second place, the mud is kept very much more open so that water can more readily diffuse into it. This will be clearly seen from an examination of Figure 11, although this certainly represents an abnormal sample in which practically the whole of the mud had been converted by a Maldanid worm into pellets. From a biological aspect also the process is important, since mud which has once passed through an alimentary canal and presumably lost much of its available nutrient material, instead of being set free to be re-eaten by some other animal is bound up in a distinctive form which will be refused by another selective feeder meeting it. This can be clearly seen in the case of a form like *Syndosmya alba* which lies buried, while its extended siphons feed indiscriminately from the surface of the mud. Periodically it blows out rejected material through one siphon, and this is found on examination to be largely composed of the pellets of other molluscs, worms, etc. The method of identification of these pellets, with special reference to those occurring on St. 11, is given in another paper (Moore, **7**). While accurate counts of the numbers of pellets are difficult, the following very approximate figures show the dominant form on St. 11.

Maldanids	3400 per c.c.
Nucula spp.	24 ,,
Syndosmya alba	12 ,,

These results also demonstrate the value of pellet determinations compared with sampling of the actual animal by a " mud bucket " since the latter takes the two molluscs readily, but only occasional fragments of the deeper burrowing Maldanids.

RESISTANCE TO ANÆROBIC CONDITIONS.

In order to determine the ability of various of the mud-dwelling forms to exist in water containing no oxygen, the following tests were made. Animals were kept in the dark in stoppered bottles, in water from which as much oxygen as possible had been removed. This was done by alternately removing dissolved gas with a pump, and then saturating with washed hydrogen, and the oxygen content as determined by Winkler's method was reduced to less than 0·2 mg. per litre. In some cases this residue of oxygen also was removed by shaking with a small quantity of mud, but with no difference in results.

Syndosmya alba.

None lived for more than three and a half days, even in large vessels which were stirred twice a day with a stream of hydrogen. This is to be expected, since they normally keep a continuous connection with the overlying water by means of their siphons.

Nucula tenuis.

These lived and remained active for periods of from five to seventeen days, and death then may have been due to poisoning of the water by the animals' own excreta. The results are in agreement with the fact that Nucula is not provided with siphons like Syndosmya, and yet is found feeding at a depth of several inches below the surface of the mud.

Copepods.

Seventy-five per cent were dead at the end of 7 hours, and 90% at the end of 14 hours. A tube full of copepods in which all were apparently dead was opened at the end of 12 hours, and on exposure to the air, about two-thirds of them recovered, but after a longer period without oxygen there was no recovery.

Nematodes.

At the end of nine days 75% were dead and 90% at the end of a fortnight, while all the controls in oxygenated water were alive.

In these experiments the animals are undoubtedly in an environment very different from that of the mud, so that it is not legitimate to infer from them more than the fact that Syndosmya and copepods cannot live long in the absence of oxygen, but Nucula and the nematodes in question may be able to withstand it for comparatively long periods. In the case of the latter it would seem possible that they might live permanently without free oxygen. In an attempt more closely to reproduce natural conditions in the mud, the water in the tubes above a fresh sample of mud was replaced by deoxygenated water. The tube was then sealed at the bottom with paraffin wax, and the water covered with a layer of liquid paraffin. The tube was stored in the dark, and opened after thirty-five days. At the end of this time all the copepods were dead, but the nematodes were normal and active.

SUMMARY OF GENERAL CONDITIONS IN THE MUD.

The deep channels throughout the area have in general a bottom composed of mud. Where the bottom is sandy this is usually found to be associated with strong currents. The typical muds show a gradation from the type found at the heads of the lochs where streams enter, and the water is shallow, to those found in deeper water.

In all there is a steady deposition of fine material, the source of a large proportion of which being referable to the plankton in the overlying water. The chief differences in the material of the muds lie in the finer sediments in deeper water, and the coarser ones near the loch-heads, where large particles are contributed both by streams and by the beds of littoral and sublittoral algæ. The particles other than these vegetable remains reach the bottom in the form of fine detritus, diatoms, etc., and the fæcal pellets of forms like Calanus and various Euphausids ; and at different seasons the proportions of these vary, giving rise to very different types of sediment.

In these sheltered channels the surface of the mud appears to be sharply marked off from the overlying water, there being normally no mixing of the mud into the water. But the mud near the surface is in a very soft condition with a high water content of 80% to 85%. This soft condition may extend to a depth of 5 centimetres or more, representing about ten years' deposition, but by various agencies water is being pressed out of the mud, bringing it to a more clayey constitution, and at a depth of 20 centimetres it is usually stiff and comparatively hard. The mid-loch and deep-water types of station are alike in this, but the loch-head ones differ in that the mud is of a more open nature owing to the large organic particles present, and often also to an admixture of sand grains.

The nature of the mud changes considerably with increasing depth. The particles themselves are no longer the same. The friable pellets of the planktonic organisms are no longer recognisable and have probably broken down. At the same time much of the fine material has been aggregated by the various mud-dwelling forms into firm pellets which may last at any rate for a hundred years and probably for much longer. The chemical nature of the mud is also changing ; the total nitrogen and phosphate decreasing as well as the soluble phosphate, the latter decreasing most rapidly in the top five centimetres where most water is being expressed. Of special biological importance is the complete absence of oxygen even in the surface layers of the mud. The variation of pH is not great and has not been correlated with any other factors.

The relation of these factors has been studied chiefly with regard to the smaller organisms of which Copepods and Ostracods especially, and also Nematodes, are more abundant on the shallower stations. The distribution of all forms with depth in the mud seems to be regulated chiefly by their need for free oxygen and their mechanism for obtaining it. Syndosmya can burrow to the depth of its siphons, but dies quickly in the absence of oxygen. Nucula has no such siphons, but on the other hand is able to resist anærobic conditions of much longer periods, and can burrow to a considerable depth. Of the smaller forms with no such mechanism as that of Syndosmya, the various nematodes found are able, like Nucula, to resist anærobic conditions for some time if not permanently, while the small crustacea, of which Harpacticids are the most abundant, have no such resistance, and are therefore confined to the extreme surface layers. Dr. Lloyd (**4**) has shown that bacterial life is abundant deep in the muds, but with the exception of tubicolous or burrowing forms nearly all animal life ceases at about ten centimetres.

Finally, I wish to express my thanks to the members of the staff at Millport who have assisted in the work.

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The Specific Identification of Fæcal Pellets.

By

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With 6 Figures in the Text.

In fine muds such as those covering most of the bottom in the deeper parts of the Clyde Sea Area the formation of fæcal pellets is a factor of great biological importance. In these muds up to 40 per cent of the fine material is often consolidated into fæcal masses, and in extreme cases even the whole of the mud may be in the form of pellets. The significance of this process is clear. In the first place, the effective particle size of a large proportion of the mud is very greatly increased, and this in turn affects such characters as the porosity of the bottom, and the liability of the material to be transported by currents. In the second place, among selective feeders such as *Syndosmya alba*, which feed on the mud, there is an economy of labour, in that food which has once passed through the gut is set aside in a form in which it will be refused if again taken in by the siphons. This latter process can readily be seen in the example cited whose rejecta on examination prove to be almost entirely composed of pellets of its own and other species.

The object of the present paper is to show the possibility of distinguishing between the various types of pellet occurring on any given ground. While it would be impossible to give a key distinguishing between all the types of pellets occurring in nature, it is probable that this may be done for any individual locality where the number of dominant species present is not too great. The locality chosen—St. 11—lies in a depth of 73 metres in Loch Striven, and is a very sheltered area with a soft mud bottom. The general nature of the mud here, as well as the fauna, is discussed in other papers (Moore, **4** and **5**).

Many mud-dwelling species, such as *Syndosmya alba* (Fig. 1), Nucula spp. and various polychætes, form pellets of very precise and unvarying shape. Others like *Syndosmya nitida* (Fig. 2) show much less regularity, while a few such as *Axinus flexuosus* void their fæces with no definite form. The majority of the important mud-dwelling species, however, form pellets, and these are surprisingly solid and resistant ; they will stand fairly rough handling, and can even be boiled with sulphuric acid

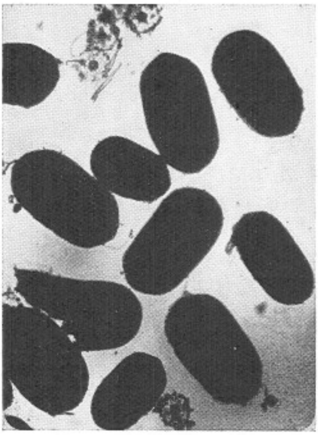

FIG. 1.—Pellets of *Syndosmya alba*, ×60.

FIG. 2.—Pellets of *Syndosmya nitida*, ×36.

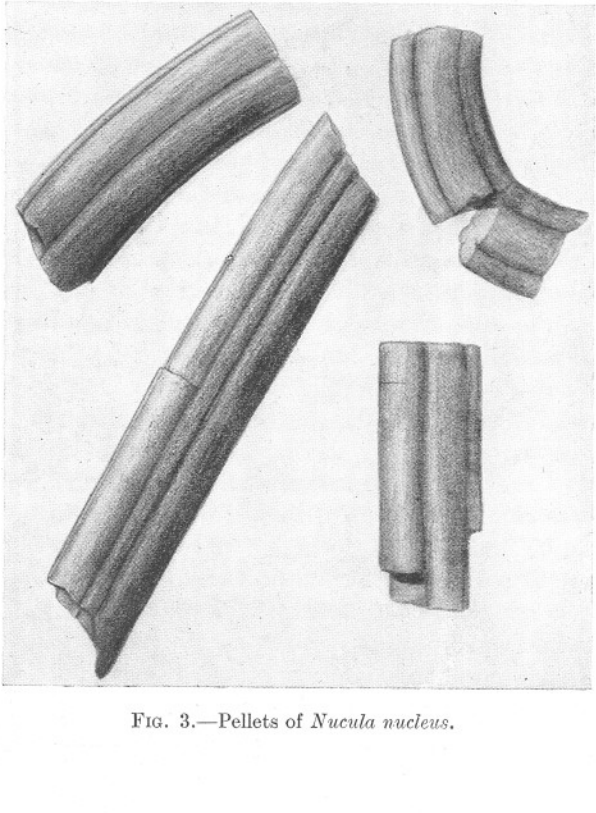

FIG. 3.—Pellets of *Nucula nucleus*.

or strong caustic soda without breaking down. On the other hand, the pellets of some of the planktonic forms such as Calanus, though quite definite in form, are much more easily destroyed, and are consequently not often identified except on the extreme surface of the mud.

The pellets have been examined both by collecting those shed by animals while under observation, and also by clearing the rectum in oil, or—as in the case of Nucula—by embedding the rectum in paraffin wax, and sectioning it. Except where stated, the following descriptions are the result of the examination of a number of specimens. There is a suggestion in the case of forms such as Calanus and Euphausids that the nature of the pellets may depend to some extent on the type of food which has been eaten. Dodgson (**1**) has found variation in the colour of the fæces of *Mytilus edulis* according to the nature of the food. The following are the chief types distinguishable on this station.

Nucula. The pellets of Nucula are voided in the form of a long rod of compact mud which breaks into lengths of 0·2 to 1·0 mm. or more, the breadth being about 0·15 mm. in pellets from an individual 1 cm. long. The intestine of Nucula shows thickened longitudinal ridges with long cilia, and these form grooves in the smooth surface of the pellet, whose number and position vary according to the species (Fig. 3). These pellets are sufficiently firm to allow identification in muds laid down on the bottom for over fifty years (Moore, **5**).

Nucula tenuis. Fig. 4, A.

Five very prominent equal longitudinal ridges; all the grooves are deeply cut, and the ventral pair are the most open.

Nucula nitida. Fig. 4, B.

Seven longitudinal ridges, the ventral one being smaller and sunk between the two on either side; none of the grooves are deeply cut, and in a rubbed or dirty pellet they may appear to be absent.

*Nucula nitida**—radiate form. Fig. 4, C.

Only five longitudinal ridges, but they are of the nitida type, with the lateral and ventro-lateral ridges fused to form one broad ridge; the grooves are shallow and the ventral ridge slightly sunk as in *N. nitida.*

Nucula nucleus and N. radiata. Fig. 4, D and F; and Fig. 3.

Seven longitudinal ridges as in *N. nitida,* but more prominent and with the grooves more deeply cut—sometimes more deeply than shown in the figure and even so much so as to allow the ridges to be split off separately.

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* This form is distinct from *N. radiata*, but also according to its pellets distinct from *N. nitida*. I am indebted to Mr. R. Winkworth for its identification.

Fig. 4, F, shows diagrammatically the position of the grooves as seen in surface view, but identification of all these forms is easier by examination of the ends.

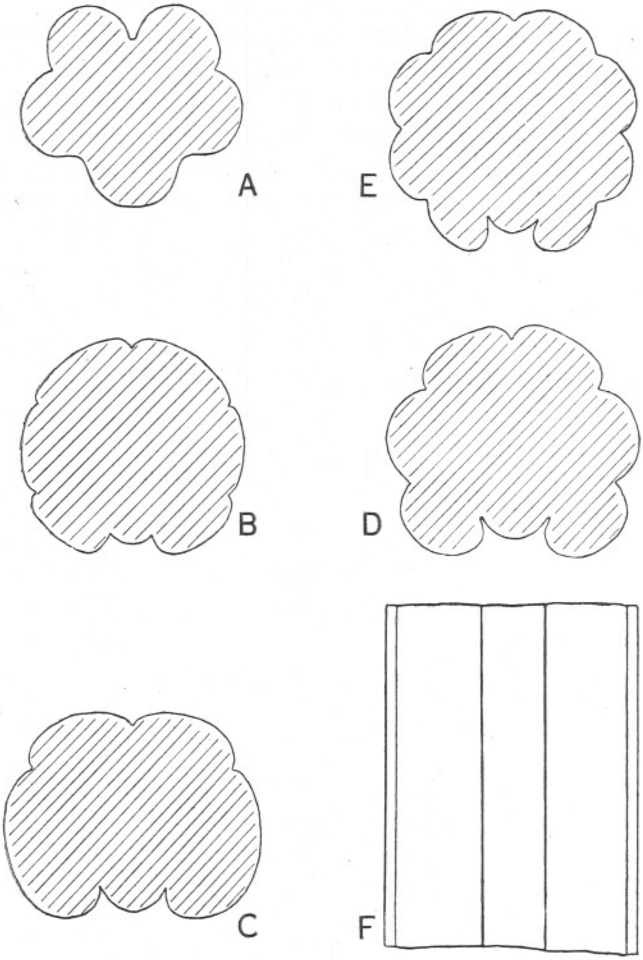

FIG. 4.—All ×200. A, Pellet of *Nucula tenuis*, end view: B, Pellet of *Nucula nitida*, end view: C, Pellet of *Nucula nitida*, radiate form, end view: D, Pellet of *Nucula nucleus*, end view: E, Pellet of *Nucula sulcata*, end view: F, Pellet of *Nucula nucleus*, plan of lower surface.

Nucula sulcata.* Fig. 4, E.

Nine longitudinal ridges, separated by grooves of medium depth ; the ventral ridge deeply sunk as in *Nucula nucleus*.

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* Although occurring on this ground, no fresh specimens were available, and the above description and figure are from a single specimen supplied by Mr. A. C. Stephen from the east coast of Scotland.

Pecten septemradiatus. Fig. 5, A.

This also voids its pellets in the form of a long rod, but the surface is less smooth than in Nucula, and frequently marked by transverse clefts so that the pellet breaks into short lengths. In section the pellet is triangular with rounded corners, one being usually sharper than the other two, and with slightly concave sides. From a specimen 3·5 cm. across the shell the pellets are about 0·6 mm. broad and in lengths of one to three millimetres or more.

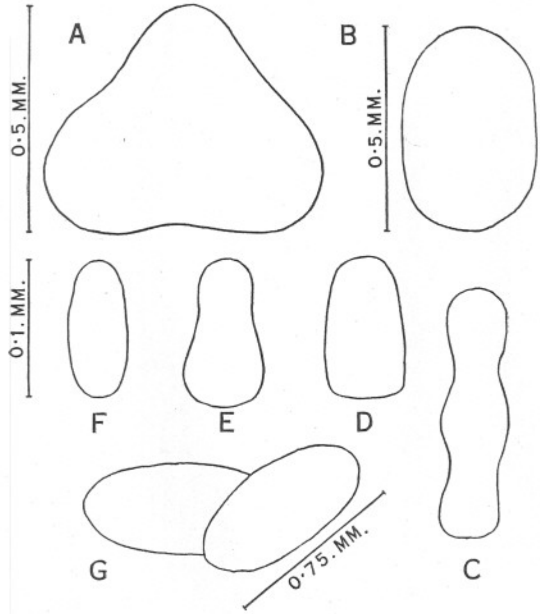

FIG. 5.—A, Pellet of *Pecten septemradiatus*, end view: B, Pellet of *Syndosmya alba*, seen from above: C, D, and E, Pellets of *Syndosmya nitida*, to same scale as B: F, Pellet of young Maldanid worm: G, Pellets of Maldanid–Rhodine sp.

Syndosmya alba. Fig. 5, B; and Fig. 1.

The pellets are extremely uniform in shape, parallel-sided with rounded ends and circular in section; the surface is smooth and regular; the usual breadth is 0·25 to 0·3 mm., and the ratio of length to breadth about 1·75.

Syndosmya nitida. Fig. 5, C, D, and E; and Fig. 2.

Much less regular in form than *S. alba*, and frequently either tapered at one end or constricted at one or more points; surface smooth; narrower than *S. alba*, breadth 0·2 to 0·25 mm.

Maldanids, various. Fig. 5, F and G.

There is a type of pellet very common in the mud, and not referable to any one species ; this is an elongated, oval pellet quite distinct in shape from that of *S. alba*, and of from 0·1 mm. to 2·0 mm. in length. Two examples are shown in Fig. 5, F, being that of a young unidentified Maldanid about 4 mm. long common in the mud, and Fig. 5, G, a pellet 0·85 mm. long from the gut of a specimen of *Rhodine* sp. about 10 cm. long.

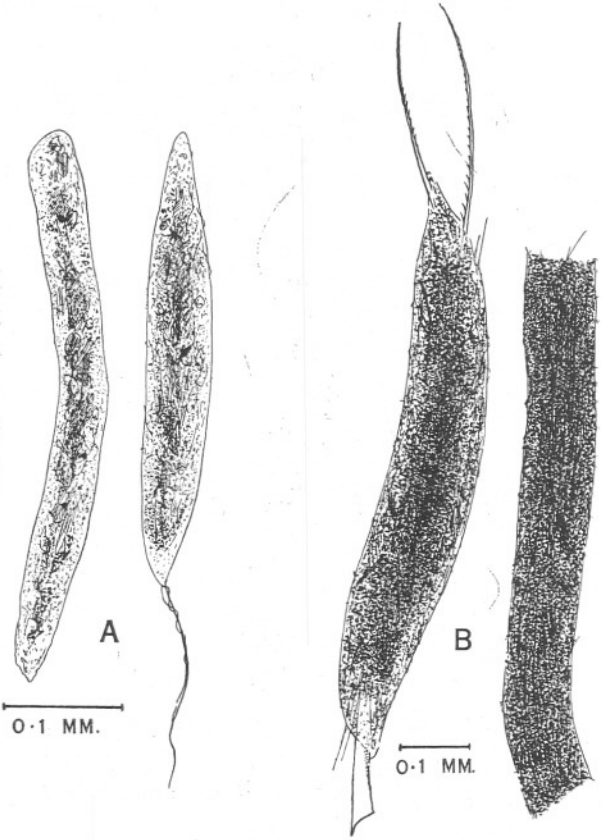

FIG. 6.—A, Pellets of *Calanus finmarchicus* : B, Pellets of *Meganyctiphanes norvegica*.

Of the planktonic forms whose pellets may be found on the mud, Calanus is the most abundant ; Sagitta, though very abundant, appears not to form a solid pellet. Euphausids, and to a lesser extent Mysids and Crangonids, are common near the bottom, but it is only possible to describe a single type of pellet common to all three.

Calanus finmarchicus. Fig. 6, A.

This has a rather transparent pellet usually 0·05 to 0·1 mm. in breadth and 0·2 to 0·4 mm. long. They vary considerably in shape, but are always elongate. The ends may be broken off, but one or both is often rounded or pointed, and one often drawn out into a long clear " tail " (Fig. 6, A). The constitution of the pellets has been described by Marshall (**3**) who shows that it is largely composed of diatoms and other plankton organisms, including a certain amount of crustacean fragments. The pellet is usually most transparent towards either end.

Euphausids. Fig. 6, B—i.e. *Meganyctiphanes norvegica*, *Nyctiphanes couchii*, and *Thysanoessa raschii*.

These have pellets somewhat similar to those of Calanus, but larger and more opaque ; the ends are sometimes rounded, but they are generally broken off and frayed ; crustacean remains are frequent (Macdonald, **2**), and large crustacean spines often project from either end of the pellet. They vary greatly in size, those of a 30 mm. Meganyctiphanes being about 0·1 to 0·15 mm. broad and up to 4 mm. long, though pellets collected on the bottom have always been found to be shorter than those shed in captivity. The above description applies also to the pellets of those Mysids and Crangonids occurring on this ground.

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Rays and Skates of Devon and Cornwall. Methods of Rapid Identification on the Fishmarket.

By

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With 10 Figures in the Text.

In carrying out detailed investigations into the life-histories and distribution of the Rays and Skates around the extreme south-west of England, large numbers of commercial landings have had to be examined. On account of their size and cost, regular and adequate samples of Rays and Skates cannot be delivered at the laboratory, as is possible with such a small and inexpensive fish as the Herring, for example. It therefore has been essential to learn rapidly to distinguish the different species as they lie exposed for sale on the fishmarkets. This has been necessary not only to promote rapidity of work, but also to obviate all unnecessary handling of the fish, too much interference with which is apt greatly to annoy fishermen, salesmen, and buyers alike.

As Rays and Skates are laid out for sale in lots often of one hundred or more all with their lower surfaces upwards, the task of identifying the species without raising each fish to examine its upper side was found at first to be one of extreme difficulty, and accurate determinations were not possible. But gradually, as the result of concentration and much practice, it became possible to identify—simply from the characters discernible on their under surfaces—the eleven species of Raia landed at the various ports of Devon and Cornwall. Only when this facility has been acquired is it possible to make a general survey of the stocks present on the various fishing grounds by dealing rapidly, amidst the bustle and confusion of a busy market, with large numbers of fish in commercial catches.

In this paper, therefore, an attempt is made to enumerate and describe as clearly as possible the distinguishing features which have been found most useful for rapid identification of the species landed in this area. The descriptions are applicable to fishes of marketable size, and must not be expected to apply to stages less than about 30 cm. across the disc which do not ordinarily find a place in commercial landings. It will readily be understood, too, that minute details of obscure features, no matter how diagnostic they may be, will receive no mention.*

By careful observation of the characters here described any worker, even without previous experience of the family, should be able to distinguish with certainty and ease at least seven of the eleven species of Raia likely to be seen on the fishmarkets of Devon and Cornwall. The four others are less easily recognised, but a little patient practice should render possible the identification of them also from the characters normally visible on the under side. Nevertheless, even the experienced worker will encounter, from time to time, a fish which will require at least a glance at the upper surface to establish its identity. Occasionally, too, a specimen may occur which will be at once recognisable as either *Raia brachyura* or *R. montagui*—two short-nosed Rays often very similar in appearance—but cannot readily be assigned to its correct species even on careful examination of both sides. In such circumstances the easiest and most certain method of deciding the point, if several other undoubted examples of both species be available, is as follows :—

Lay out, back upwards, two separate lots of fish, one lot consisting of *R. brachyura* alone and the other of *R. montagui* alone. This done, place the doubtful specimen in the middle first of the one lot and then of the other ; it will then at once be obvious to which lot—and therefore to which species—it rightly belongs.

As indicated above, eleven species of Raia are landed more or less regularly at the various fishing ports of Devon and Cornwall. These are *R. montagui*, *R. brachyura*, *R. undulata*, *R. microcellata*, *R. clavata*, *R. naevus*, *R. circularis*, *R. fullonica*, *R. marginata*, *R. batis*, and *R. oxyrhynchus*.† These eleven species fall naturally into two main divisions :—

I. those whose under sides are of a decidedly dark ground-colour richly studded with black spots and which, for our present purpose, may be called " Black-bellied Species."

II. " White-bellied Species."

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* For such detailed descriptions reference should be made to Clark's admirable monograph on the European species of Raia (**1**).

† Nomenclature according to Clark's monograph (**1**).

I. Black-bellied Species (Skates).

Only two species—*R. batis* Linn., and *R. oxyrhynchus* Linn.—are included in this division. They are separately distinguished as follows :—

RAIA OXYRHYNCHUS.	*RAIA BATIS.*
Long-nosed Skate. Bottle-nosed Skate.	Common Skate. Blue Skate.

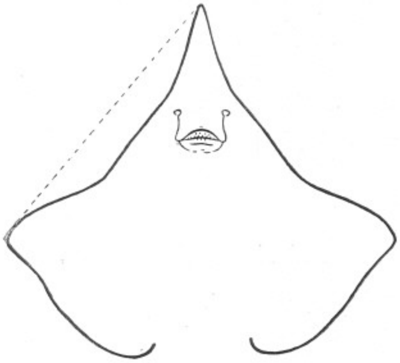

Fig. 1a.—*Raia oxyrhynchus*—outline of disc.

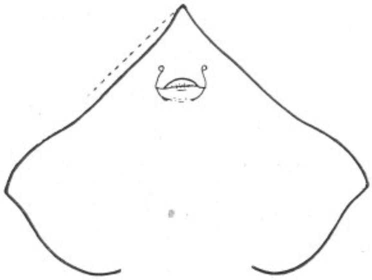

Fig. 1b.—*Raia batis*—outline of disc.

(Fig. 1a.)	(Fig. 1b.)
Snout very long, narrow, and pointed.	Snout relatively much shorter, broader, and less pointed than in *R. oxyrhynchus.*
Outline of anterior margin of disc strongly concave.	Outline of anterior margin of disc only slightly concave, often nearly straight.
Rarely reaches a width of 100 cm. across the disc.	Grows to a very large size, specimens of 150 cm. in width being not uncommon.

Large Skates are generally picked out by the fishermen and spread separately on the fishmarket. The smaller sizes, up to about 50 cm. across the disc, are laid out with the Rays interspersed indiscriminately among them.

II. WHITE-BELLIED SPECIES (RAYS).

These fall into three distinct groups, according to the shape of the disc.

1. LONG-NOSED RAYS . .	*R. fullonica* Linnæus. *R. marginata* Lacépède.
2. CIRCULAR RAYS . .	*R. undulata* Lacépède. *R. naevus* Müller and Henle. *R. circularis* Couch.
3. SHORT-NOSED RAYS . .	*R. clavata* Linnæus. *R. brachyura* Lafont. *R. montagui* Fowler. *R. microcellata* Montagu.

1. LONG-NOSED RAYS.

The two species included in this group both have long and pointed snouts which mark them out at once from all the others.

RAIA FULLONICA.

Shagreen Ray.

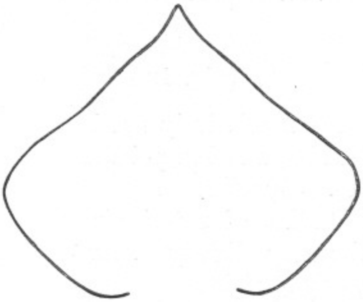

FIG. 2A.—*Raia fullonica*—outline of disc.

(Figs. 2A and 3.)

There is a well-marked groove (Fig. 3, G) in the middle of the upper jaw and a corresponding

RAIA MARGINATA.

Bordered Ray (Young).
White-bellied Skate* (Adult).

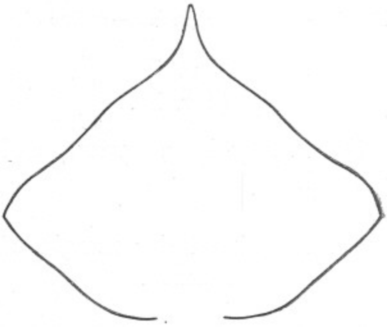

FIG. 2B.—*Raia marginata*—outline of disc.

(Figs. 2B and 4.)

Curve of mouth cleft quite regular.

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* The large adults of this species are known to fishermen as "White-bellied Skates" and are laid out apart from the Rays, either by themselves or along with the large Blue and Bottle-nosed Skates. They are then very conspicuous because of the clear whiteness of their under sides, sharp snouts, and strongly undulated anterior disc margins.

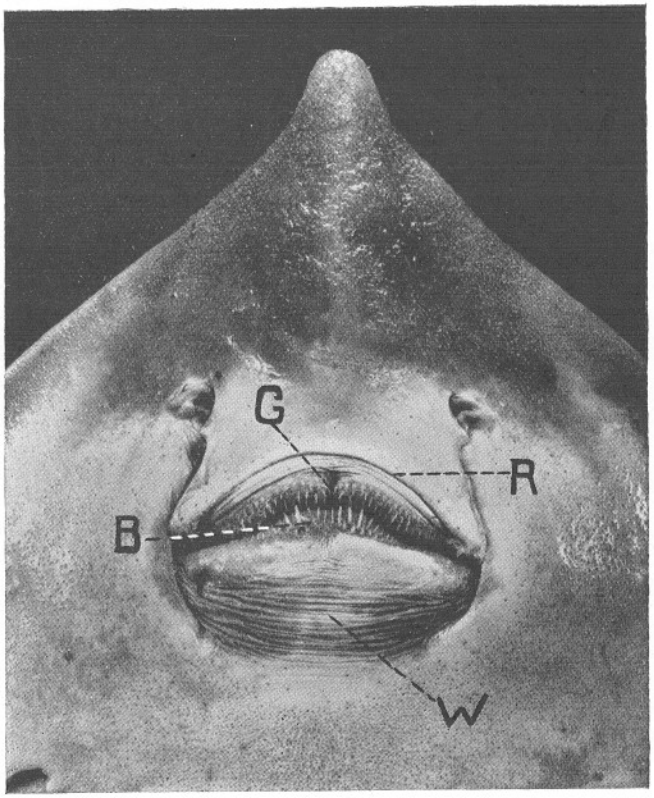

Fig. 3.—*Raia fullonica*—mouth and nasal regions.

R—pre-oral recess.
G—groove in middle of upper jaw.
B—" boss " in middle of lower jaw,
W—post-oral wrinkled region,

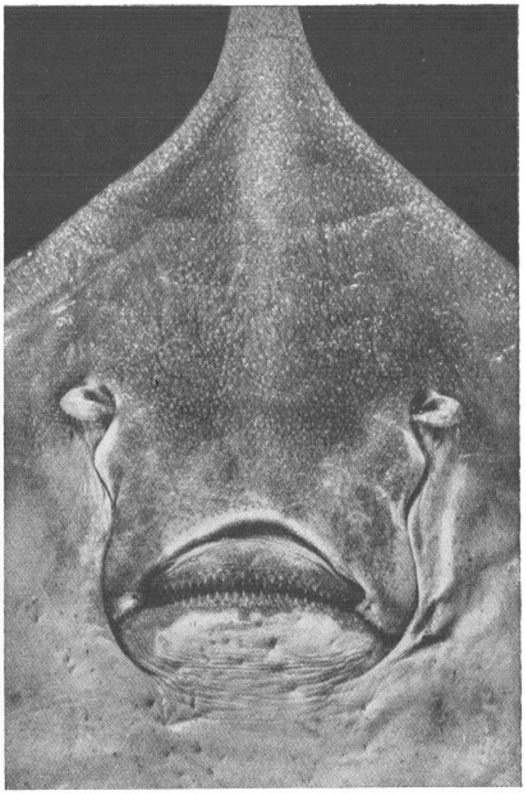

Fig. 4.—*Raia marginata*—mouth and nasal regions.

"boss" (Fig. 3, B) in the middle of the lower jaw which give the mouth cleft a very irregular outline.	
Internasal distance appreciably less than width of mouth.	Internasal distance about equal to, or slightly greater than, width of mouth.
Anterior margin of disc not strongly undulated.	Anterior margin of disc strongly undulated.
Ventral surface of tail white.	Ventral surface of tail dark-coloured, sometimes nearly black.*
Seldom grows beyond 70 cm. in width of disc.	Adults very large, up to 150 cm. across the disc.

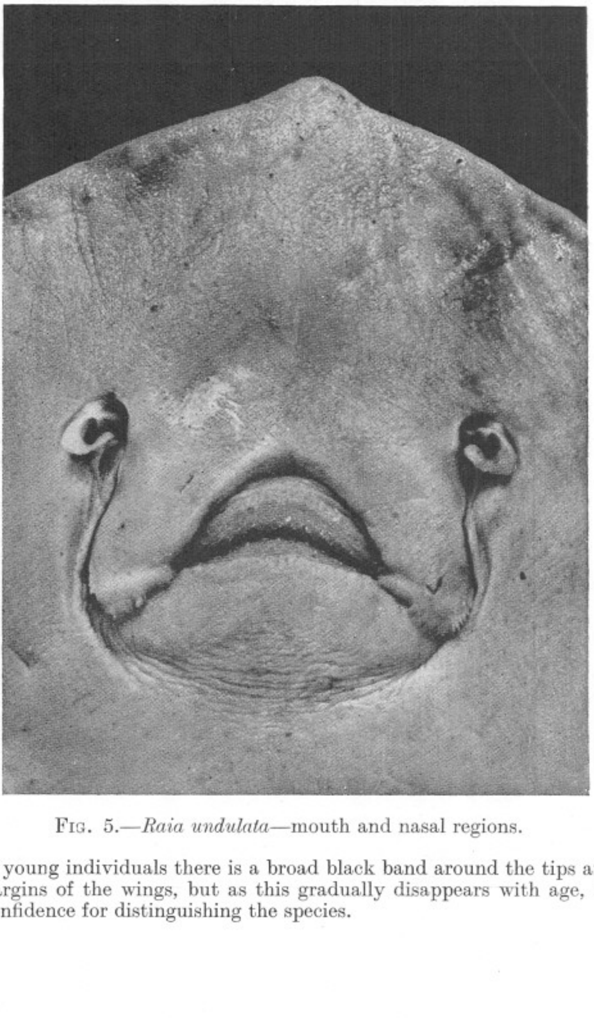

FIG. 5.—*Raia undulata*—mouth and nasal regions.

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* In very young individuals there is a broad black band around the tips and along the posterior margins of the wings, but as this gradually disappears with age, it cannot be used with confidence for distinguishing the species.

2. CIRCULAR RAYS.

The three species which fall into this group all have the tips of their wings decidedly rounded and their snouts scarcely project in front of the main contour of the disc—characters which give them a typically "circular" appearance.

RAIA UNDULATA.

Marbled Ray.

(Fig. 5).

Arch of pre-oral recess high and acute.

Teeth flattened and close set, so that the separate rows are not discernible.

"Groove and boss" absent.

RAIA NAEVUS.

Cuckoo Ray.

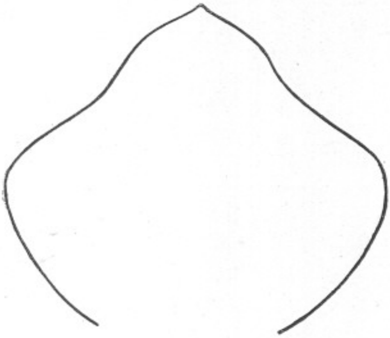

FIG. 6A.—*Raia naevus*—outline of disc.

(Fig. 6a.)

RAIA CIRCULARIS.

Sand Ray.

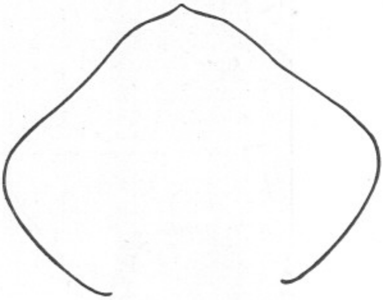

FIG. 6B.—*Raia circularis*—outline of disc.

(Fig. 6b.)

Arch of pre-oral recess low and obtuse.

Teeth long, pointed, and in widely separated rows which show up clearly.

"Groove and boss" generally discernible.

Anterior margin of disc strongly undulated.	Anterior margin of disc not strongly undulated.
Fish very thick and fleshy.	Fish always appreciably thinner than a specimen of *R. naevus* of the same width across the disc.
The smallest of the Devon and Cornwall Rays, seldom exceeding 40 cm. across the disc.	Adults commonly as much as 70–75 cm. across the disc.

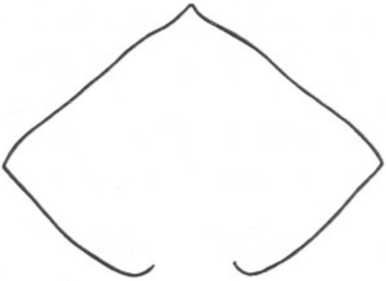

Fig. 7.—*Raia clavata*—outline of disc.

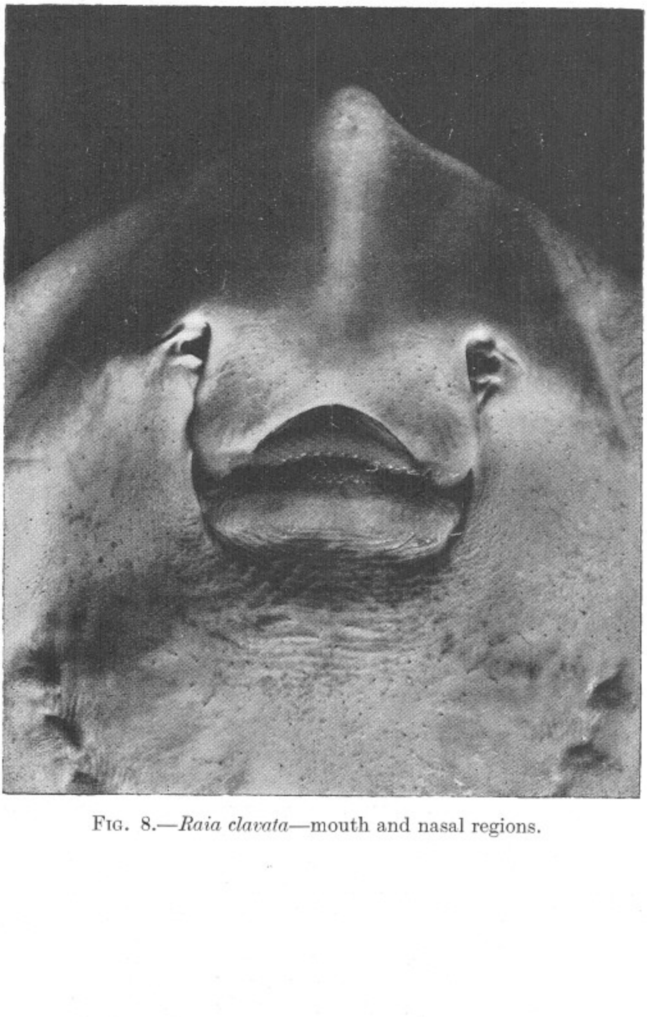

Fig. 8.—*Raia clavata*—mouth and nasal regions.

3. SHORT-NOSED RAYS.

In each of the four species included in this group, the general outline of the disc is typically diamond-shaped, due to the sharpness of the wing-tips and the presence of a short but well-defined snout (see Fig. 7).

RAIA CLAVATA.

Thornback Ray.

(Figs. 7 and 8.)

Arch of pre-oral recess high and acute.

Teeth large and distinct, markedly tessellated in adult females and in immature specimens of both sexes ; more pointed in adult males.

Internasal width about equal to width of mouth.

Lower surface with large spines and/or rough patches.

RAIA BRACHYURA.	*RAIA MONTAGUI.*
Blonde Ray.	Spotted Ray. Homelyn Ray.
(Fig. 9.)	(Fig. 10.)

Arch of pre-oral recess low and obtuse (except in adult males).

Internasal distance always less than width of mouth.

Large spines never present on lower surface.

Outline described by oro-nasal canals and hinder margin of post-oral wrinkled area (see Fig. 3, W) forming a wide  with nearly straight or even concave base.	Outline described by oro-nasal canals and hinder margin of post-oral wrinkled area forming a more rounded  with convex base.
Surface smooth all over except in large adults which may show some rough patches.	Surface smooth at all ages.
Often grows to 80 cm. in width of disc.	Seldom grows beyond 50 cm. across the disc.

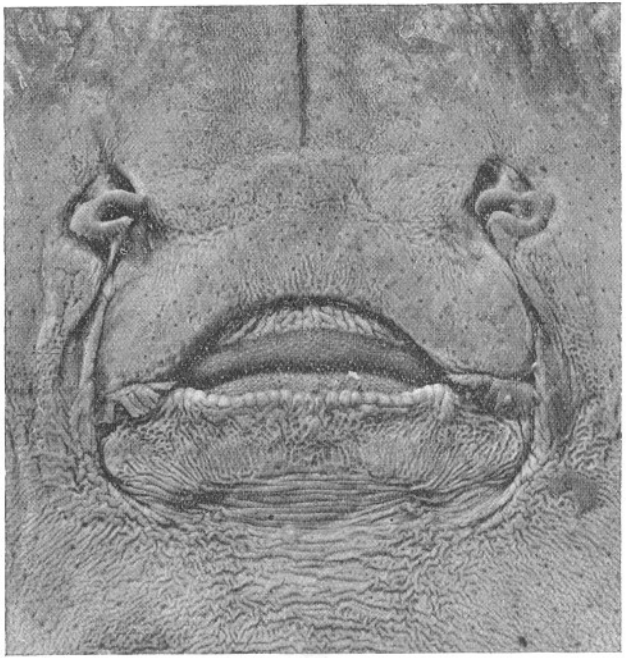

FIG. 9.—*Raia brachyura*—mouth and nasal regions.

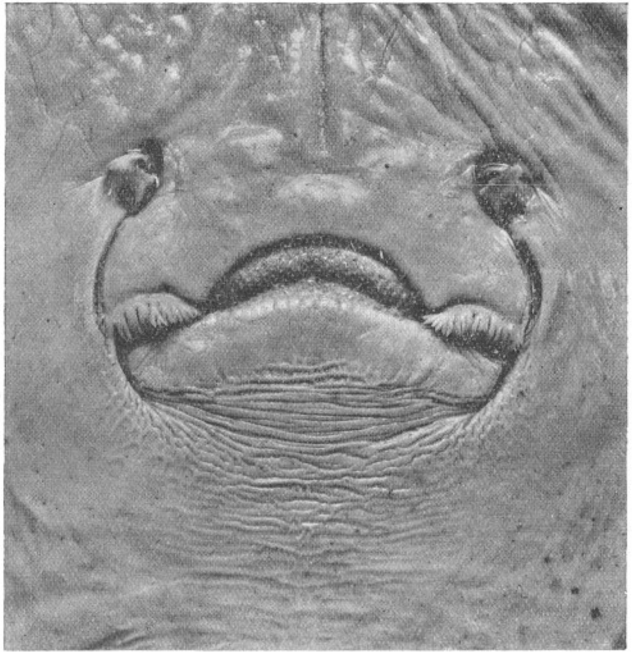

FIG. 10.—*Raia montagui*—mouth and nasal regions.

RAIA MICROCELLATA.

Painted Ray.

Resembles *R. montagui* in the characters of the mouth and nasal regions, but the pre-nasal area is covered with small spinulæ. In large specimens these are easily seen, but in smaller individuals it sometimes is necessary to touch the surface with the fingers in order definitely to establish their presence or absence.

Adults often grow to 70 cm. across the disc.

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Tube Formation in *Pomatoceros triqueter* L.

By

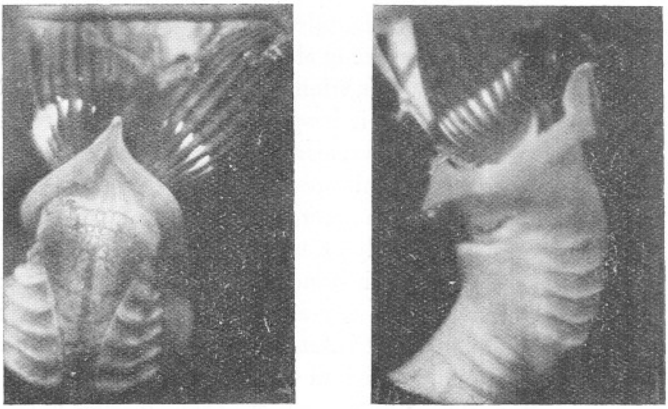
Dr. H. Faouzi.

With 3 Figures in the Text.

As a serpulid, *Pomatoceros triqueter* L. realises to the highest degree the adaptation to a sedentary life. The calcareous tube in which this annelid lives is characterised by a keel running along its upper surface. It is rather misleading to say that this tube is triangular in section. Figure 2 shows a newly formed calcareous rod ; it is spur-shaped ; the two rami of the spur might approach each other so nearly as to simulate an almost complete tube. The substratum in this species not only serves as a support, but completes the tube. This is in accordance with the fact that the tubes of Pomatoceros never extend freely off the support as happens with tubes of other serpulids—Protula, for instance. The aim of this paper is to record some observations on the way an adult Pomatoceros endeavours to build a new calcareous tube if it is artificially removed from its old one. I undertook this observation as original work at Roscoff, where a complete literature was not available. I discovered later that Harms, in the course of his research on regeneration in *Hydroides pectinata*, arrived at identical results. My paper cannot therefore pretend to more than a confirmation of previous results.

The Pomatoceros is removed from its tube, and placed carefully in a flat-bottomed dish full of sea-water. The worm lies on its side, its abdomen curved in a dorsal direction, performing a forward and backward undulation. If the individual happens to be sexually mature, its first preoccupation is to throw off its sexual elements—pink eggs or whitish spermatozoa—in such a quantity that one can notice with the naked eye floculent material streaming out from among the gills, and colouring the water. Through the binocular it can easily be seen that these elements stream through the fæcal groove, from its posterior end, follow its bend at the thorax, until they leave the head on its dorsal surface, to pass freely into the sea-water. Once the annelid has exhausted its sexually-mature contents, nothing more notable is to be observed for some hours (usually 6 to 10). Then a certain turbidity begins to show in the fold of the collar, just in the middle third of each side of this organ. Figure 1 shows how in the natural disposition of the collar there is a crest in the middle which divides it, so to speak, into two parts. This crest is orange-coloured normally and by the time the fold shows the white turbidity, this crest begins to whiten. A little later the turbidity definitely forms two white rods, occupying always the middle-third of both sides of the fold; the crest follows by forming in its fold another rod. These white rods were proved to be calcareous, and the process itself showed subsequently how we were in presence of a newly forming tube.

Active secretion of the collar adds to the substance of the laterally-placed calcareous rods, and they lengthen in this way until they attain a position vertically above the calcareous crest already mentioned, in which they fuse, and we have at last a spur-shaped piece reproducing exactly the space in the fold of the collar, with its ventrally situated crest. Figure 2 shows a piece of this type formed by one of the worms and thrown accidentally off the worm. As a matter of fact, the least shock at this moment is sufficient to provoke this accident.



Ventral view. Lateral view.

Fig. 1.—Microphotograph of the anterior half of a Pomatoceros deprived of its tube, to show the folded collar with a crest in the middle.

The next step is the lengthening of the spur-rami dorsally; the free ventral extremities of the collar come nearer to each other but never to such an extent as to join the rami together. Here lies the explanation of the incomplete tube of the Pomatoceros of which mention was made above. This does not mean that where a complete tube is found in the serpulid a complete collar is to be expected. I have examined a Protula—a species with a complete tube—which has none the less an incomplete collar. The collar is so flabby in Protula, compared with that of Pomatoceros, so easily pliable as to be able to surround completely the dorsal side of the thorax, a fact which facilitates the joining of both rami in this species and the formation of a complete tube.

Calcareous secretion goes on as described, but this time increasing the surface of the rod ; one should imagine a long series of spur-shaped pieces formed continuously and as a whole until a definitely-formed Pomatoceros tube is produced. The keel is due to the calcareous crest formed in the ventrally situated collar-fold. To come back again to Protula—a species with a completely round tube—one notes the absence of this particular fold characteristic of serpulids with keeled tubes.

Pomatoceros is then capable of reconstituting its tube. This notion is rather theoretical, and practically these worms are unable to resist the all-powerful circumstances that surround them, once they lose their shell. I have succeeded in keeping alive a single Pomatoceros for forty days ; I had to protect it and, so to speak, help it to live. One of the reasons for this difficulty must first be excluded, as it is the condition *sine qua non* of any calcareous formation whatsoever : the calcareous reserve once exhausted, the animal is unable to form a new tube. It thus happened at Roscoff that I found worms that either did not form calcareous rods at all, or, once these rods formed, secretion did not go on any further. These cases were rather rare at Roscoff between August and September. At Plymouth I tried to repeat the experiment with a view to procuring material for cytological examination ; on twenty worms removed by the method I described, not a single one gave evidence of regenerative activities. This happened in April, and points perhaps to some relation with sexual activity which did not manifest itself in April at Plymouth, while sexually mature Pomatoceros were the rule at Roscoff in August and September.

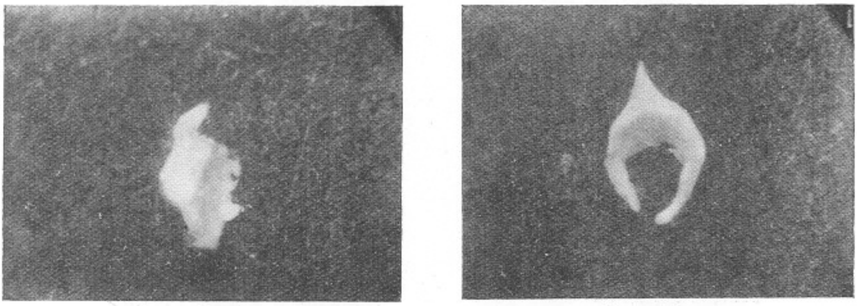
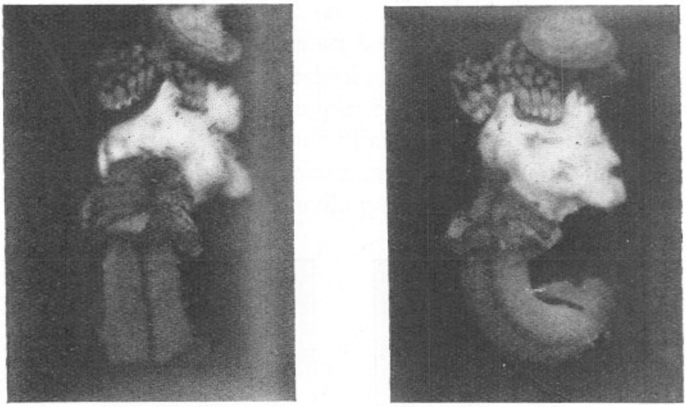

Lateral view. Face view.

FIG. 2.—Microphotograph of a spur-shaped calcareous piece, formed in the fold of the collar and removed accidentally. The point of the spur is the origin of the keel to be seen on the upper surface of tubes of Pomatoceros.

Then comes the absolute absence of defence on the part of the worm deprived of its tube. Active planktonic fauna, floating in the aquarium tank, crustaceans and small annelids, surround the naked worm, in search of the least breach in the surface of its body to start their work of destruction.

As regards the Pomatoceros that I succeeded in keeping for forty days (Fig. 3) I had to take many precautions : cleaning vessels daily, managing to get rather clean sea-water by passing it through a series of siphons, taking off particles of excreta and foreign matter from the body of the worm. The Pomatoceros went on forming a tube, but did not succeed in



Ventral view

Ventro-lateral.

Left-lateral.

Right-lateral.

FIG. 3.—Pomatoceros which continued forming a tube for forty days ; the various views of the worm show the irregular tube, formed as usual but displaced from time to time owing to the continued movement of the naked serpulid ; the spur points do not correspond as they should do under normal conditions to form a single continuous keel.

fixing that tube. This is due to the continual movement of the abdomen. The ventro-dorsal movement proves very deleterious to the fine calcareous rods, lying loose in the fold of the collar ; the least shock is sufficient to displace these rods, or even the well-formed spur. It was by mere chance that one Pomatoceros out of many was able to go on secreting a continuous piece for forty days, and even in this case the calcareous ring was displaced, not enough to leave the worm entirely, but to turn in a circular direction, the keel coming to a lateral position. A study of the accompanying figures shows how irregular this tube is ; it presents as many keels as there were displacements : after each turning of the calcareous ring, the worm proceeded with its new tube formation, and thus the new keel did not come in line with the old one and so on. I saw later how Harms succeeded in helping a *Hydroides pectinata* to fix its tube to the substratum by ablation of the abdomen. I wonder if the Pomatoceros could have resisted this drastic measure ?

However this may be, it is seen how the conditions described contribute to the failure of real tube regeneration ; by real is meant a tube that covers completely the worm and allows it to continue living. Observation of the larvæ might reveal in this connexion very interesting details.

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The Larvæ of the Plymouth Galatheidæ.
II. *Galathea squamifera* and *Galathea intermedia*.

By

Marie V. Lebour, D.Sc.,
Naturalist at the Plymouth Laboratory.

With one Figure in the Text and Plate I.

IN a previous paper (Lebour, 1930) the general characters of the larvæ of Galathea were described and the various stages of *Galathea strigosa* and *Galathea dispersa* identified. The present paper deals with the larvæ of *Galathea squamifera* and *Galathea intermedia* which have also been followed through their life histories. This completes the larvæ of the Galatheidæ from Plymouth with the exception of *Galathea nexa*, the larvæ of which have not been seen. As is noted in the previous paper this Galathea is regarded as a separate species from *G. dispersa*.

The four Galathea larvæ now known are quite easily distinguishable from one another; firstly, by their size, *G. strigosa* being the largest, *G. dispersa* next, *G. squamifera* smaller still, and *G. intermedia* the smallest of all; secondly, by their colour, notes of which are given below for the two last, those of the two first having already been described; thirdly, by their abdominal spines, *G. squamifera* having them on the fourth and fifth segments, but much smaller than in *G. strigosa*, and *G. intermedia* having them on the fifth segment only as in *G. dispersa*, but the size and colour of the little larva make it unmistakable.

The two larvæ dealt with in this paper have already been partly described by Sars (1900) who takes all the species together, figuring certain stages, but it is not easy to distinguish the two from his figures. Webb (1921) also figures the first larva of *G. squamifera*.

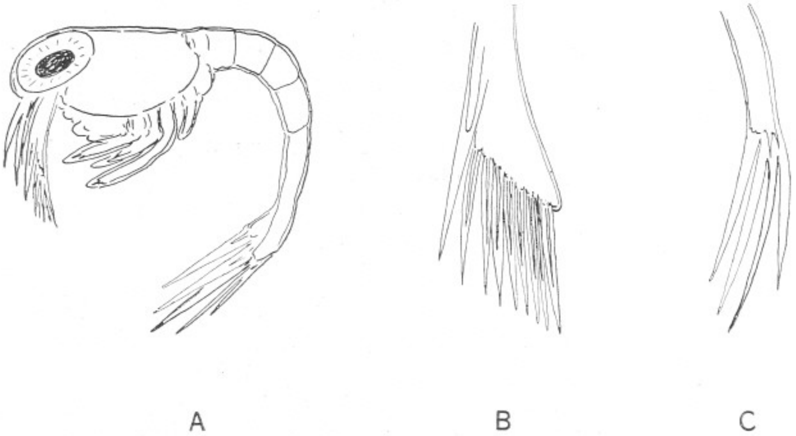
Galathea squamifera is the common inshore form and is usually to be found between tide marks under stones. The larvæ are common inshore, sometimes but rarely, outside, in spring and summer and less commonly in autumn and winter. Females in berry from February onwards. *Galathea intermedia* is not so common, occurring in the Sound and outside on the Mewstone and Eddystone grounds. Larvæ both inside and outside, not so common as *G. squamifera*, chiefly in spring and summer and usually outside the Sound.

Galathea squamifera Leach.

(Plate I, Figs. A–E.)

Four larval stages (no fifth seen), the fourth changing to a young Galathea. First larva from egg, second from first, third from second from plankton, fourth from third from plankton, young Galathea from fourth from plankton. Eggs 0·52 mm. by 0·48 mm. when about half-way to hatching, 0·56 mm. by 0·64 mm. when ready to hatch. At first orange-red, then brownish. Embryonic cuticle like that of Munida with seven long spines on the telson, the antenna with eight spines, the antennule with four (Text-fig. 1, A–C).

Larvæ very transparent, but with much orange-red on the thorax, first and fifth abdominal segments (sometimes on the second), on the maxillipedes, antennular peduncle (sometimes absent), in front of the eyes (sometimes absent) and at the base of the telson (later this colour is at the hind end of the sixth abdominal segment). Usually, but not always, there is dark brown pigment in three masses at the base of the telson ; in later stages these are on the sixth abdominal segment, above the red. The brown is in the form of three chromatophores which may be contracted or spread out into masses, one behind the other, two of which are on a level in front of it. These brown chromatophores are usually found in the young stages as well as in the later stages, but cases have been seen when they were absent. In the later stages there is more brown, especially above the thorax, and the fourth spine on the telson (the longest) usually has brown pigment at the base. This is the only species at



Text-Fig. 1.—A, prezoea of *Galathea squamifera*.
B, antenna of same.
C, antennule of same.

Plymouth which has the brown pigment to any extent. The red on the fifth and sixth abdominal segments tends to be crimson. There may be yellow in the thoracic region in the later stages. Length of first larva *ca.* 2·2 to 2·5 mm., second larva *ca.* 3·2 mm., third larva *ca.* 4 mm., fourth larva *ca.* 4·8 mm. The rostrum is moderately long with spicules, but not so long as in *G. strigosa*. The carapace spines and spines on the antennal scales are also shorter. The fourth abdominal segment has a pair of very short lateral spines and the fifth a pair of short spines rather longer than those on the fourth. In both they are much smaller than in *G. strigosa*. Denticulations occur on the hind margin of the second to the fifth abdominal segments, becoming smaller in the later stages. The telson is not so wide as in *G. strigosa*. In the last (fourth) stage there are five or six spines on the inner uropods. The young Galathea which emerged from the fourth larva was very like that of *G. strigosa* and *G. dispersa*, with long rostrum armed with five teeth each side and five principal teeth on the side of the carapace with additional smaller teeth between or behind. The colour of the first young stage is reddish, but with the casting of its skin it is brownish with a distinct white mark on the first legs.

Galathea intermedia Lilljeborg.

(Plate I, Figs. F–J.)

Larvæ partly described by Sars (1900) who figures the last stage and the first young stage. This is much the smallest of all the Galathea larvæ and also the brightest coloured.

Four larval stages (no fifth seen), the fourth changing to a young Galathea. First larva from egg, second not seen, third from plankton, fourth (last) from third from plankton, young stage from fourth from plankton. Eggs 0·4 mm. by 0·32 mm. when about three-parts towards hatching, 0·48 mm. by 0·4 mm. when ready to hatch. At first orange-red, then brownish.

Larvæ very transparent, but very brightly coloured. The only Galathea larva known to have orange-red pigment at the outer corners of the telson. Orange-red on the thorax with bright yellow, orange-red on the antennular base, on the second and fourth abdominal segments (on the fourth turning to crimson) and crimson-red at the base of the telson (in later stages on the sixth abdominal segment. An orange-red chromatophore at each corner of the telson at its outer angles. Yellow on the thorax and over the eyes.

Length of first larva *ca.* 2 mm. or less, second not seen, third *ca.* 2·8 to 3·6 mm. (varying in size considerably), fourth *ca.* 3·8 mm. The rostral spine is comparatively short, not always pronouncedly prickly, the carapace spines and spines on the antennal scales and uropods are also short. Usually there are no lateral spines on the fourth abdominal segment but traces of them may sometimes be seen in the first stage. A pair of short lateral spines on the fifth segment. The outer uropods in the last stage with 7 spines. The first young stage is much like those of the other three species but slightly smaller. It has a fairly long rostrum with three principal teeth and two smaller each side and five lateral teeth on the carapace with one or two smaller intermediate teeth. Behind the rostrum are the characteristic two spines of the adult. The young Galathea is a brilliantly speckled orange-red with bright blue lines in the second stage.

It is now possible to make a key of the larvæ of the Plymouth Galatheidæ :—

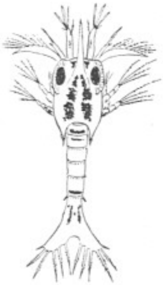
I. Antennal scale aciculate: two dorsal spines on the abdominal segments 3, 4, and 5—(Munida).

II. Antennal scale fairly broad, small denticulations on the abdominal segments 3, 4, and 5—(Galathea).

- A. Spines on fourth and fifth abdominal segments.
    - a. larvæ large, first larva *ca.* 3·5 mm., rostrum long, smooth, abdominal spines large—*Galathea strigosa.*
    - b. larvæ of moderate size, first larva *ca.* 2·2–2·5 mm., rostrum fairly long, prickly, abdominal spines of moderate size—*Galathea squamifera.*
- B. Spines on fifth abdominal segment only.
    - a. larvæ of moderate size, first larva *ca.* 2·6 mm., last larva *ca.* 5 to 6·5 mm. (fourth and fifth). No pigment on angles of telson—*Galathea dispersa.*
    - b. larvæ small, first larva *ca.* 2 mm. or less, last larva *ca.* 3·8 mm. Orange-red pigment on angles of telson—*Galathea intermedia.*

PLATE I.

FIG. A. *Galathea squamifera* from egg, 2·2 mm. long.
B. ,, ,, second larva from first from plankton, 3·2 mm. long.
C. ,, ,, third larva from second from plankton, 4 mm. long.
D. ,, ,, fourth larva from third from plankton, 4·8 mm. long.
E. ,, ,, carapace of first juv. from fourth larva.
F. *Galathea intermedia* from egg, 2 mm. long.
G. ,, ,, third larva from plankton, 2·8 mm. long.
H. ,, ,, fourth larva from third from plankton, 3·8 mm. long.
J. ,, ,, carapace of first juv. from fourth larva.



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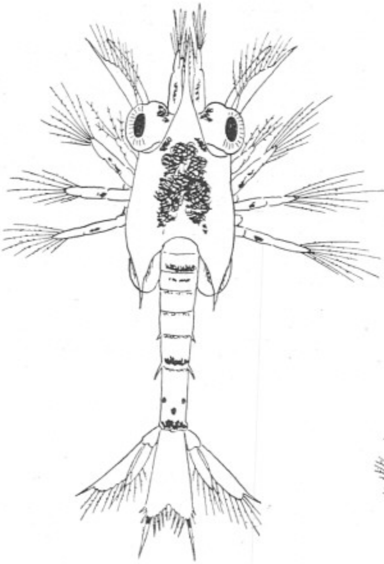

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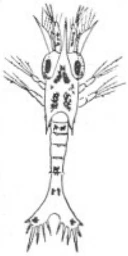

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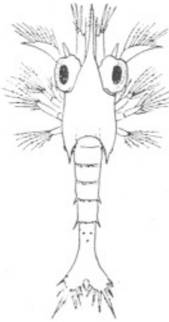

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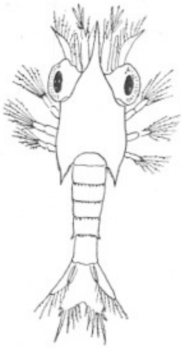

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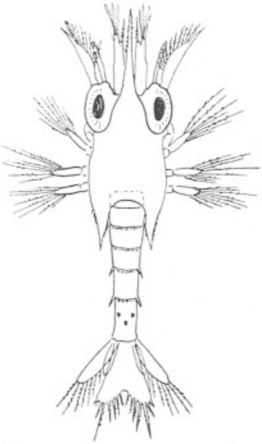

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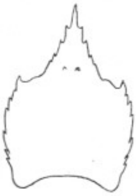

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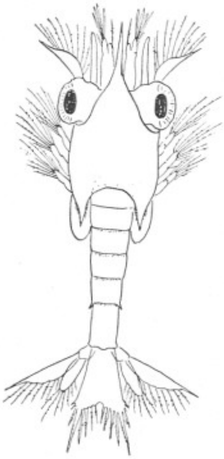

H

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The Vertical Distribution of Marine Macroplankton. X. Notes on the Behaviour of Sagitta in the Plymouth Area.

By

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

With 8 Figures in the Text.

THE researches on the vertical distribution of plankton in the sea in the Plymouth area are tending to indicate that light is a controlling factor of great importance in the behaviour of the larger plankton animals (**13** and **16**). It appears probable that for some species there are certain conditions of light that members of that species tend to collect in during the daytime, and owing to the absorption of light penetrating from above the animals move vertically upwards or downwards towards their light optimum. But in the sea we do not find that *all* the members of the species are concentrated at the level at which apparently the optimum conditions occur ; rather is it that only the greatest number are found at that level, the remainder being at varying distances above and below and decreasing in number with distance apparently as modified by the rate of light absorption. In other words, the animals appear to be distributed around the optimum on a probability curve.

Now in speaking of the members of a species above, it is assumed that we are referring to a population of animals all of the same sex and age. It is well known that animals of different ages seem to prefer different depths (**16**, p. 239) ; therefore in attempting to unravel the leading principles in the behaviour of plankton animals by means of field collections it is essential that we should be careful to base our conclusions on populations of a species all as nearly as possible of the same age. From this standpoint the Crustacea are probably the best group to work on, as the successive stages are well marked and easily recognisable on account of the habit of moulting. It is probably for this reason that of all the animals studied in our previous researches on vertical distribution the copepod *Calanus finmarchicus* has given us the picture of a typical daytime distribution most nearly corresponding to that we should expect if the animals are distributed round an optimum light condition with upper and lower limits within which the population lives, as in the theory previously outlined (**13**,

p. 419); for we have known that we were dealing with animals of the same sex and of as nearly as possible the same age.

With the majority of other animals, however, the vertical distributions given in the previous publications have been, for each species, those of populations of a heterogeneous mixture of ages and perhaps of sex. It is not legitimate therefore to attempt to draw fundamental conclusions from such results; they have merely provided us with a knowledge of the depths at which the majority of any one species live and the range within which a mixed population of that species remains. This important point is well brought out in the following pages in which the behaviour of a Sagitta population is dealt with.

General Results.

The details given here represent the results of collections made with the 2-metre stramin ring-trawl during 24 hours on two different occasions, the first on July 15–16th, 1924, and the second on June 3–4th, 1926.

A careful examination of the Sagitta occurring on these occasions has shown that there are in the Plymouth area two common species, *Sagitta elegans* Verrill, and what is probably *Sagitta setosa* J. Müller. These two species have in previous records been included under one name, *Sagitta bipunctata* Quoy and Gaimard, a name now used for a warm-water species apparently not occurring in this area (**17**, pp. 7–16, and **18**, p. 19). The results for the Sagitta population as a whole on June 15–16th, 1924, have already been published (**11**, p. 792)—under the name of *Sagitta bipunctata;* the original material has since been re-examined and studied in more detail and the results are given in the following pages. Fortunately it was found that on that date almost the entire catches were made up of *S. elegans*, and that *S. setosa* was either absent or only present in such small numbers as not to affect the general picture given in **11**, page 792 and Figure 3, which must now be regarded as referring to *S. elegans*.

On June 3–4th, 1926, *S. setosa* was much more common, and it is probable that its abundance varies from year to year. An examination of the Sagitta populations throughout the year 1930 has shown that *S. setosa* was almost absent in June and July. Meek (**8**, p. 743) has found in the North Sea off the Northumberland coast that the two species, *S. elegans* and *S. setosa,* vary much in their relative abundance, the years in which one species was common apparently showing a rarity of the other species and vice versa.

The collections described in this paper were both made with the 2-metre stramin ring-trawl and the full conditions at the time of collecting have already been published (**11** and **15**). On each date five series of collections were made at definite times during the 24 hours, the net being towed horizontally for periods of ten minutes each at different depths in each

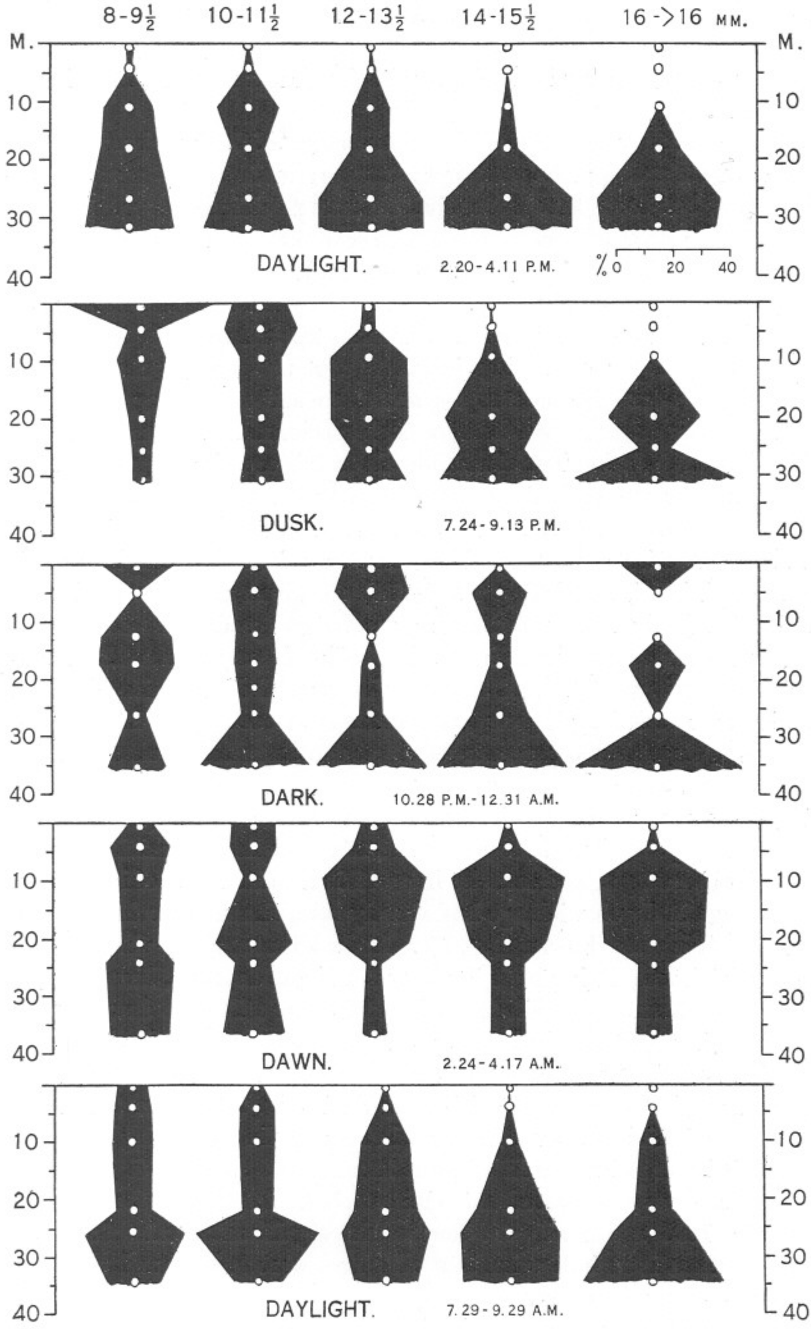

FIG. 1.—The percentage vertical distribution of *Sagitta elegans* at the times shown on June 3rd–4th, 1926. For each period—" daylight," " dusk," " dark," " dawn," and " daylight "—the Sagitta are divided into 8–9½, 10–11½, 12–13½, 14–15½, and 16–>16 millimetre groups. The white spots and black circles indicate the average depths at which hauls were taken. Bottom was at 54 metres.

series, the depths being indicated by the depth-recorder (**11**, Fig. 1, and **15**, Fig. 1).

Measurements were made of the total lengths of Sagitta from samples from each collection ; the measurements were made to the nearest half-millimetre, but have here been divided into 2-millimetre groups. The numbers in each 2-millimetre group of those measured have been given in Tables IV, V, and VI on pages 409–411 ; unfortunately in the June, 1926, collections the numbers measured are on some occasions rather low. The collections had been previously worked up and samples only of the whole catches kept ; on finding that there were two species present it was necessary to re-examine the samples, and as a result of dividing the Sagitta into the two species the numbers for each species measured are low. The indications of the behaviour of the animals on this occasion appear however to be quite definite and are confirmed by the July, 1924, collections for which larger numbers of animals were available for measurement.

Tables IV–VI show the numbers measured in each sample, and in Tables VII, VIII, and IX (pp. 412–414) are given the calculated total numbers of Sagitta in each 2-millimetre length group for each collection. These results, given in Tables VII–IX, are expressed diagramatically in Figures 1, 2, and 3, where the vertical distribution diagrams are given for each length group, the numbers at each depth in each diagram being expressed as percentages of the total number at all depths for that diagram.

These diagrams show that in the daylight the younger stages of *Sagitta elegans* are apparently able to withstand much higher intensities of light than the older stages, and can also live within a wider range of intensities. This change in depth with age has already been shown for other species, e.g. *Krohnia hamata* (Fowler, **4**, p. 76). At dusk it seems that the youngest stages, which were living high in the water in the daytime, have reached the surface in numbers while the older stages are still deep down. This behaviour is most clearly brought out in Figure 1, which shows the behaviour of *S. elegans* on June 3–4th, 1926. A very similar type of behaviour was shown on July 15–16th, 1924 (Fig. 2), but in this figure there are no individuals over 13½ mm. in length. In comparing Figures 1 and 2 this latter point should be borne in mind and only the diagrams for similar size groups compared one with another. After dark the numbers caught in 1926 were really too low to give significant results ; in 1924, however, there is an indication that all stages were to be found unevenly mixed from top to bottom.

In the dawn a process of resorting is taking place, and on both occasions it is very evident that the older stages started to leave the surface first ; this is clearly shown in both Figures 1 and 2, while in Figure 1 the stages from 12 mm. and upwards in length appear already to be massing in an

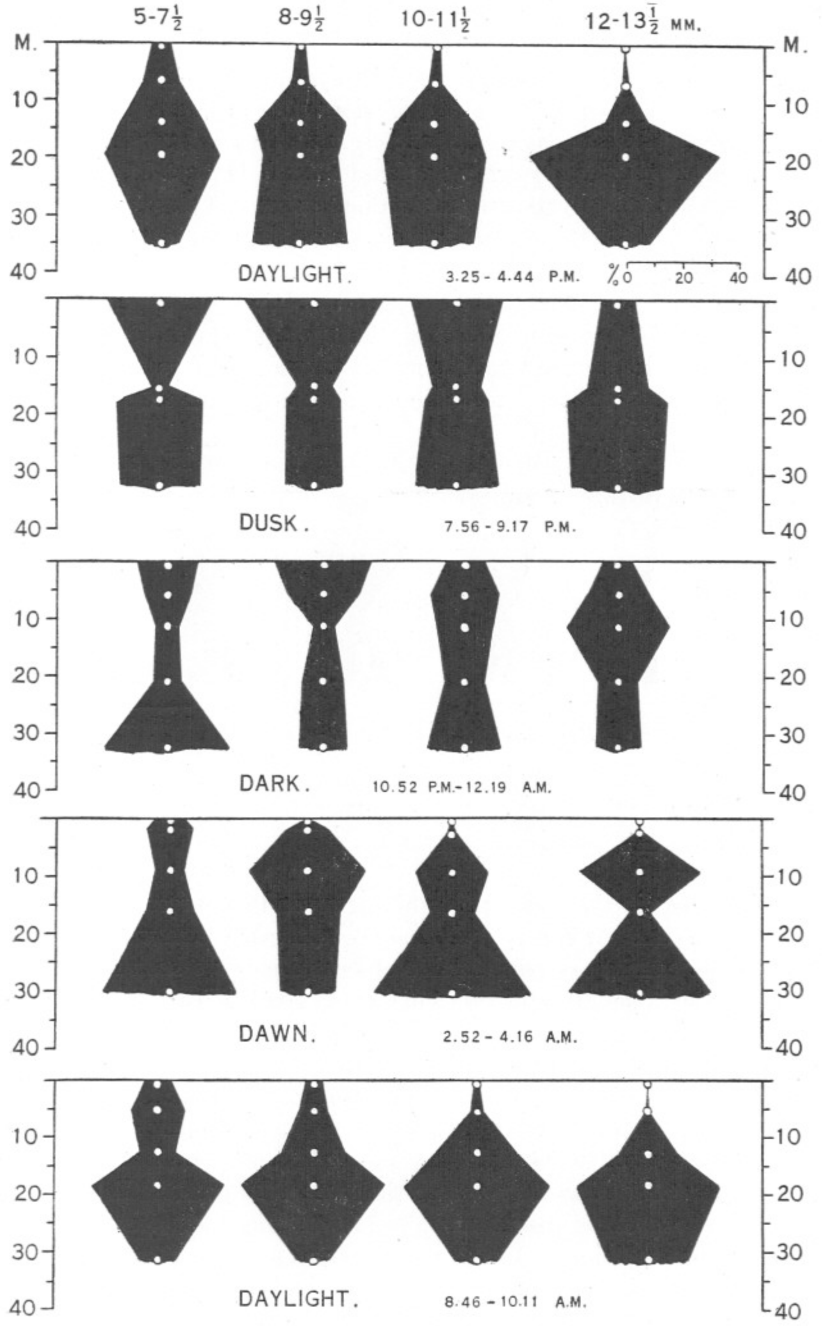

FIG. 2.—The percentage vertical distribution of *Sagitta elegans* at the times shown on July 15th–16th, 1924. For each period—" daylight," " dusk," " dark," " dawn," and " daylight "—the Sagitta are divided in 5–7½, 8–9½, 10–11½, and 12–13½ millimetre groups. The white spots and black circles indicate the average depths at which hauls were taken. Bottom was at 54 metres.

optimum region. The following day the vertical distribution has assumed a picture very similar to that of the previous afternoon, except that there is a tendency for the Sagitta to stretch more into the upper layers—a phenomenon exhibited by other plankton animals on that day and probably due to clouding of the water by a thick swarm of Calanus.

On June 3–4th, 1926, *Sagitta setosa* were on the whole not sufficiently abundant to give a picture of their behaviour ; at dusk, however, when they were most abundant in the catches, their behaviour appears to have been very similar to that of *S. elegans*. The younger stages have migrated to the surface before the larger forms, as shown in Figure 3. It is to be noticed also that on the whole there is a tendency for all stages to be slightly higher in the water than the corresponding stages of *S. elegans* at the same time (cf. Fig. 1) : whether this difference is shown also in the daytime we cannot say until further observations have been made.

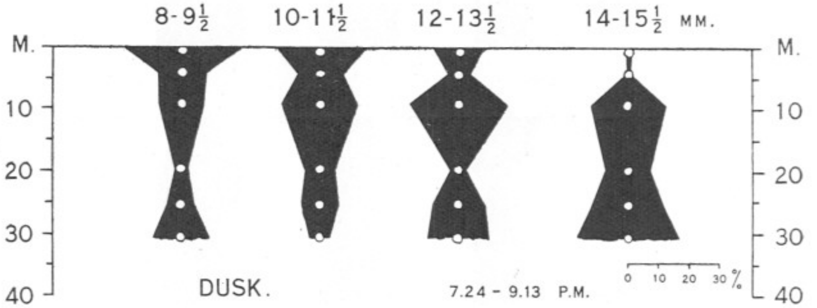

FIG. 3.—The percentage vertical distribution of *Sagitta setosa* at "dusk" on June 3rd, 1926. The Sagitta have been divided into 8–9½, 10–11½, 12–13½, and 14–15½ millimetre groups. The white spots and black circles indicate the average depths at which hauls were taken. Bottom was at 54 metres.

Huntsman in the Atlantic waters of Canada gives indications of a similar type of behaviour with *Sagitta elegans*. For instance (**5**, p. 465), he divided the Sagitta into two groups, those under and those over 20 mm. in length. Of the larger group specimens were only obtained at the surface at 6 p.m., 9 p.m., and 12 midnight ; while those under 20 mm. were present at the surface at all hours of the day and night, and there is an indication that the smallest sizes stay nearer the surface longest in the daytime, e.g. 9 a.m., occasional specimens up to 10 mm. long ; 12 noon, occasional specimens up to 9 mm. ; 3 p.m., many specimens up to 13 mm. ; 6 p.m., very many specimens up to 16 mm. ; 12 midnight, many specimens up to 20 mm. ; 3 a.m., several specimens up to 18 mm. ; and 6 a.m., occasional specimens up to 11 mm. He says further, "inside the Gulf in June larger individuals came to the surface than came above 30 metres in August, for 9 a.m., 12 m., 9 p.m., 12 midnight and 6 a.m. This decrease in the daily vertical migration is doubtless due to the warming of the surface water."

He sums up, "The facts point to the following conclusions: *Sagitta elegans* is confined to water of comparatively low salinity, being stopped in its migration into the depths by water of high salinity. It is affected by light, coming nearer the surface at night. It is affected by temperature, keeping to the colder water. The young behave differently from the adults, living in the lighter, warmer surface water. With increasing age it becomes gradually restricted to the darker, colder water, which is deeper." These results are confirmed by Bigelow (**2**, p. 316) in his survey of the plankton of the Gulf of Maine, and Huntsman and Reid (**6**) give further data on increase of size with depth.

A COMPARISON OF THE BEHAVIOUR OF SAGITTA WITH THE LIGHT INTENSITY CONDITIONS.

In a previous publication I illustrated in outline the theory of the vertical movements of plankton animals on the basis that they were distributed in a chance distribution around an optimum condition of light in the daytime. It was suggested that they followed this optimum condition towards the surface at dusk, and that at night the light stimulus was removed and they became free to move anywhere.* The following day those near the surface pick up their optimum condition again and follow it downwards as the light increases in strength, picking up recruits from deeper layers as they come into the influence of the stimulus of the increasing light. "It seems most probable that the types of distribution shown by the different species are due to a combination of the speed of upward movement of which they are capable and the time at their disposal for such upward migration" (**16**, p. 236).

This theory appears essentially to be borne out by the results here given for *Sagitta elegans*; we see very clearly how at dusk the younger stages only have had time to reach the surface *en masse* before the light fades away, but the older stages coming from deeper layers never have time to reach the surface in quantity until after dark when they are free to roam anywhere.

An attempt has been made to compare these results with the actual variations of the light intensity beneath the surface of the sea. Throughout the year 1930 continuous records of light intensity have been made from a photometer on the parapet of the flat roof of the Laboratory. The photometer contained a Burt vacuum sodium photo-electric cell sensitive mainly to blue light, and the intensities were recorded on a thread recorder

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* It must be understood that this behaviour would be modified under extreme conditions of other factors, such as temperature, as would the vertical movements (Russell **13**, p. 435, and Nikitine **9**).

in the Laboratory (**1**). It so happened that on June 4th, 1930, the weather was cloudless and clear, and the light conditions must have approximated very closely to those on June 3rd and 4th, 1926, when the collections of Sagitta were made (for weather conditions see **15**, p. 830). The actual light intensities throughout June 4th, 1930, have been recorded on the above instrument, and I am able here to publish the curve (Fig. 4) through the kind permission of Dr. W. R. G. Atkins by whom the researches on light intensity are being carried out. In Figure 4 the actual intensities are given as thousands of metre candles, based upon a standardization of a vacuum potassium cell against a carbon arc; the sodium cell was then standardized in daylight against the potassium cell.

Unfortunately, however, we do not know the transparency of the water on June 3rd, 1926, except that the Secchi disc disappeared at a depth of 10 metres, and we are therefore unable to estimate for certain the intensities at different depths beneath the surface. Animal plankton on that day was very abundant, and it is possible that the coefficient of absorption may have been in the region of 0·200; it seems almost certain to have been considerably more than 0·100. Poole and Atkins (**10**, p. 308) give as a mean coefficient of absorption for Station E1 for a number of readings throughout the year 0·150 for the upper 20 metres, 0·120 for 20 to 40 metres, and 0·111 for 40 to 60 metres. Moreover, their work has shown that there is considerable variation to be found in the opacity of the water at different depths on any one day, due possibly to the aggregation of plankton animals into definite zones. One cannot therefore hope to estimate with any accuracy the light conditions beneath the surface unless actual light measurements have been made, at any rate at a few depths.

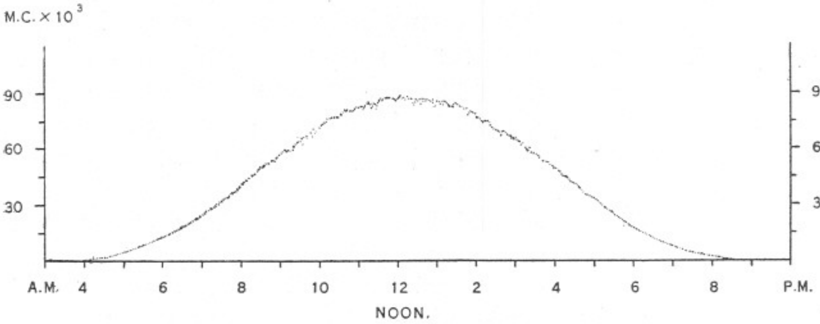

Fig. 4.—Curve of light intensity obtained on roof of Plymouth Laboratory with vacuum photo-electric cell and thread-recorder (**1**) on June 4th, 1930: a clear cloudless day. (By courtesy of Dr. W. R. G. Atkins.) The intensities are given as thousands of metre-candles.

Taking a coefficient of absorption of 0·200 for all depths with a surface loss of illumination of 15% by reflection (**10**, p. 309) and using the air

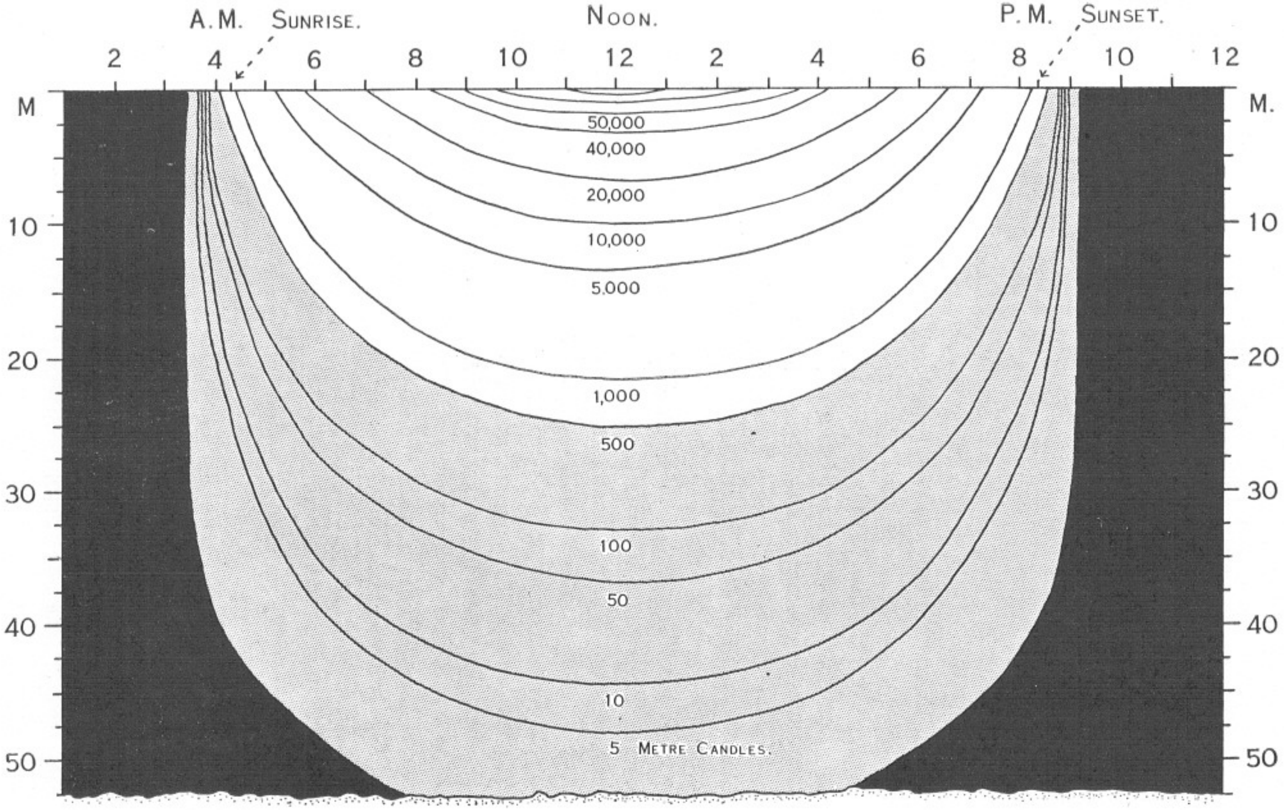

FIG. 5.—Curves of equal light intensities beneath the sea surface throughout the 24 hours, calculated from the air intensities obtained on June 5th, 1930, taking the coefficient of absorption of the water as being 0·200 at all depths and allowing for a reflection loss of 15%. The blackened area corresponds to the zone of "darkness" (see text) and the stippled area to the region in which "twilight" intensities would be experienced. The intensities are given in metre-candles and the depths in metres.

illumination figures obtained for June 4th, 1930 (Fig. 4), I have calculated the intensities beneath the sea surface at all times of the day.* By means of these results I have drawn in Figure 5 the lines of equal light intensities beneath the sea surface throughout the day. As I have already said, this picture can have no real significance and must be hypothetical only, but it is instructive as giving an idea of the conditions beneath the sea surface and as we shall see later it will serve a purpose. In Figure 7, p. 403, I have also given the lines of equal intensities for the same conditions, save that in this case the coefficient of absorption has been taken as being 0·100 at all depths. It is probably somewhere between the conditions figured in Figures 5 and 7 that the conditions beneath the surface on June 3rd and 4th, 1926, lay. In both these figures I have marked in black the area in which the conditions are those of "darkness" in the accepted meaning of the word, that is where the light intensity is such as we experience well after sunset when the stars are shining brightly, or less. The shaded area represents intensities of light lying between darkness and the illumination almost immediately after sunset on a clear evening, conditions which would be covered by the term "twilight." We thus can see at a glance at what times and depths darkness or twilight conditions would be experienced.

Let us study first Figure 5. It shows that between the hours of 7 a.m. and 5 p.m. the lines of equal intensities do not vary greatly in depth, but that before and after these times their slopes become very steep until eventually the light fades out almost abruptly. From this figure we could easily understand how animals living around an optimum of, say, 5000 m.c. at midday will have time to mass at the surface in the evening if they follow their optimum upwards; but animals which live at 50 m.c. at midday will be unable to keep pace with the suddenly disappearing light at evening and will never reach the surface in great numbers as the light stimulus is removed too soon.

But if we compare this figure with the behaviour of Sagitta given in Figures 1 and 2 an interesting point arises. In Figure 6 I have plotted the depths at which *Sagitta elegans*, 12 to 13½ mm. in length, first appear beneath the surface in abundance equivalent to 30% on the scale given in Figures 1 and 2, in the morning and afternoon of the two days in question.

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* I am indebted to Dr. W. R. G. Atkins for the light intensities after sunset. It is probable that actually at sunset the usual illumination is in the neighbourhood of 1000 metre candles: the figures given me by Dr. Atkins were measured on October 3rd, 1927, and were as follows: sun just down, 620 m.c.; 15 minutes after, 530 m.c.; 20 minutes after, 178 m.c.; 26 minutes after, 73 m.c.; 30 minutes after, 35 m.c. (small print readable); 34 minutes after, 19 m.c. (small print readable with difficulty); 39 minutes after, 9·5 m.c.; 41 minutes after, 2·5 m.c. (Jupiter and first magnitude stars visible). The lag between sunset and 15 minutes after was probably due to cloud reflection; it has been smoothed out in Figures 5 and 7. The intensities before sunrise are taken as being the same as those after sunset.

It will be seen that on June 3rd–4th, 1926, the two points lie very close to 25 metres, and on July 15th–16th, 1924, they again appear very nearly at the same depth, namely, in this case 15 metres. From the curves of equal intensities given in Figure 5 it appears that in 1924 the Sagitta were therefore becoming abundant at somewhere between 2000 and 3000 metre-candles in both the morning and the afternoon, and similarly that in 1926 these points lay somewhere between 300 and 400 m.c. If now we plot the similar points for the dawn distribution we find that in 1924 it lies not on the 2000–3000 m.c. curve, but only at 50–100 m.c., at about 7·5 metres. A similar state of affairs is shown for 1926, where the 30% point lies at about 8·5 metres at an intensity of below 5 m.c. Now the close agreement in the intensities at which the Sagitta are living in the morning and afternoon may be mere coincidence and have no significance, since we cannot say for certain what the intensities were on the days in question. But the difference between the intensities to which the Sagitta were reacting at dawn and those which they experienced in the daytime must be significant. Examination of Figures 1 and 2 shows clearly that the Sagitta of 12 mm. and over had started to leave the surface even before sunrise,

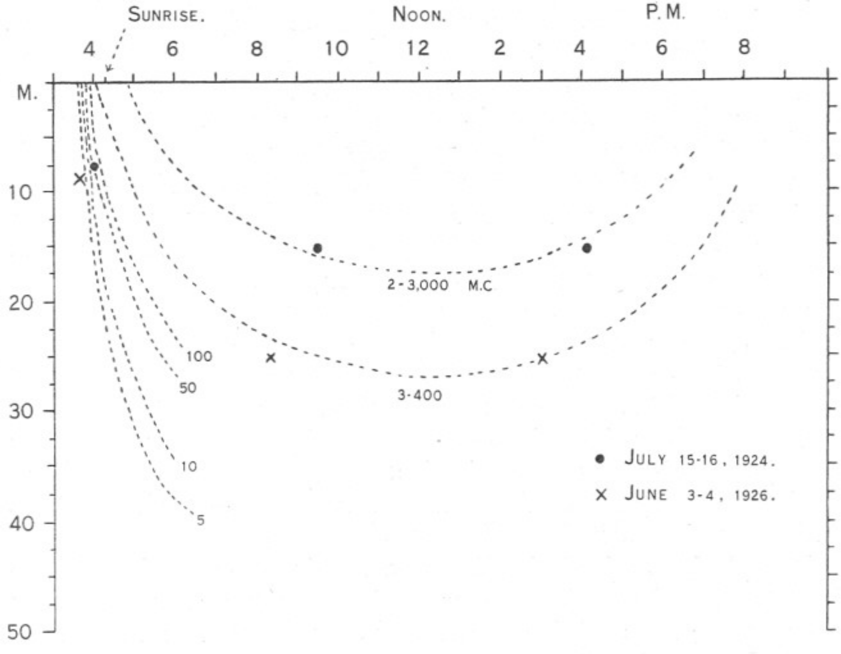

FIG. 6.—Depths at which *Sagitta elegans* of 12 to 13½ mm. in length first appear beneath the surface in an abundance equalling 30% on the scale in Figures 1 and 2 on June 3rd–4th, 1926, and July 15th–16th, 1924, in the morning, afternoon, and at "dawn." The dotted curves are the lines of equal light intensities taken from Figure 5.

For instance, on June 4th, 1926, Sagitta 12–13½ mm. long were already showing signs of leaving the surface, and those of 14–15½ mm. in length and longer had already left the surface layers down to 4 metres when the haul at that depth was made at 3.49–3.59 a.m. : this is well before sunrise, which occurred at 4.17 a.m.,* and the air illumination must probably have been less than 300 m.c. at any rate. Similarly, on July 16th, 1924, Sagitta 12–13½ mm. long had already left the surface layers by 3.51–4.1 a.m., when sunrise should be at 4.24 a.m. (sunrise not recorded in log).

It seems from these data that the Sagitta must have started to leave the surface before the illumination reached that at which many are found to be living in the daytime. This would appear to indicate that the Sagitta are more sensitive to light immediately after the darkness of the night than they are later in the daytime. Thus is would seem that they can become adapted to light conditions of higher intensity as the morning goes on.

Indications that this may be so with some fresh-water plankton animals is given by Worthington, who says (**19**, p. 2) as a result of observations made during 26 hours in Lake Lucerne, " Most species start their descent at dawn and reach their lowest level before the sun attains its zenith. Then a slow upward movement starts, accelerates at dusk, and continues for two or three hours after complete darkness."

Clarke, experimenting with the fresh-water Daphnia, has recently produced evidence that this crustacean can become adapted to light of various intensities. He suggests that (**3**, p. 120) " There is, then, no ' absolute optimum ' light intensity for these *Daphnia.* They do not seek any particular intensity of illumination. The animals become adapted to the light intensity which exists at that time and place—this is for them a ' relative optimum.' "

That plankton animals should show a certain power of adaptation to light conditions is probably to be expected, and it would seem that possibly they live around a shifting optimum during the course of the day. It should be borne in mind, however, that probably they are only capable of adaptation within limits, and that outside these limits definite avoiding reactions set in. Until observations in the field are made synchronously with accurate light-intensity measurements at all depths it is premature to discuss the matter further.

Figure 7 has been inserted to draw attention to the very great effect that the transparency of the water has upon the intensity of the illumination beneath the surface. In this figure the coefficient of absorption of the water has been taken as 0·100 at all depths, and it can be seen that each iso-intensity line has been pushed down exactly twice as deep as in Figure 5,

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* This is the sunrise time recorded in the log : theoretically it should have been 4.11 a.m. : the discrepancy is probably due to " sunrise " being the appearance of the sun above the hills of Dartmoor.

where the coefficient of absorption was taken as being 0·200 at all depths. This will mean that animals living in the "twilight" zone with an upper limit of about 500 m.c. will be abundant nearly up to 25 metres at midday under the conditions of Figure 5, while under the conditions of Figure 7 they will be forced right to the bottom.

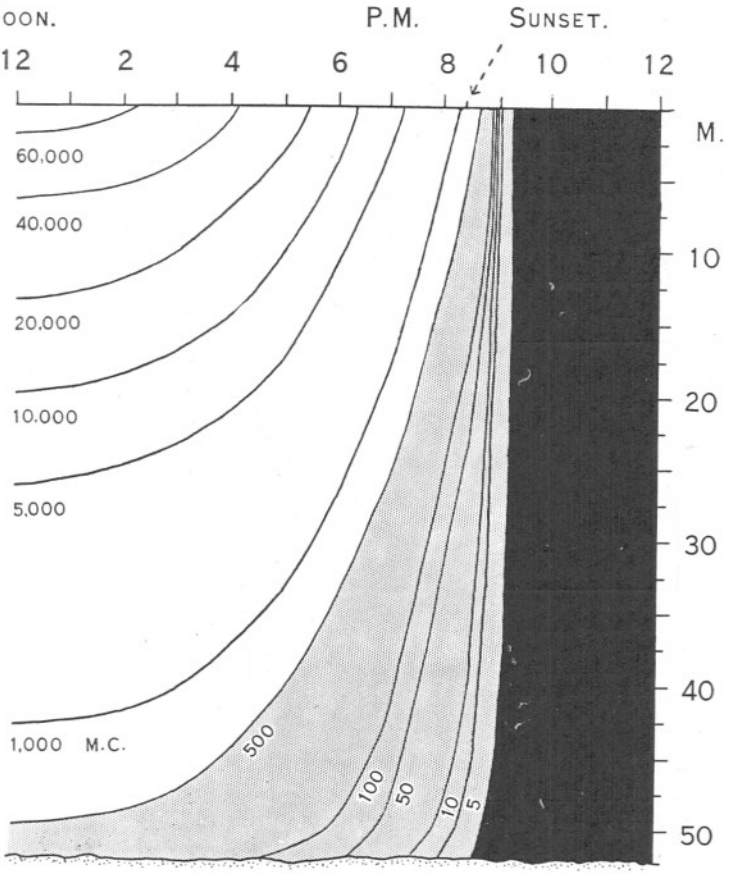

FIG. 7.—Curves of equal light intensities beneath the sea surface from noon to midnight, calculated from the air intensities obtained on June 5th, 1930, taking the coefficient of absorption of the water as being 0·100 at all depths and allowing for a reflection loss of 15%. The blackened area corresponds to the zone of "darkness," and the stippled area to the region in which "twilight" intensities would be experienced. The intensities are given in metre-candles and the depths in metres.

In view of the above I have reproduced here Figure 8 which gives the behaviour of Sagitta on two successive days, June 16th, 17th, and 18th, 1925. This figure has already been published as for *S. bipunctata* (**13**, p. 88); unfortunately the material is no longer available, so that it is not possible to say whether *S. elegans* or *S. setosa* predominated. It can be seen that the behaviour here shown differs very markedly from that on the other two dates given in Figures 1 and 2 in this present publication. On June 16th–18th, 1925, the Sagittas became very abundant at night, but in the daytime they were very scarce, and the impression gained is that they must have retreated to very near the bottom (54 m.) in the daytime. It may well have been that on these two days in June, 1925, the water was far more transparent than on the two occasions in 1924 and 1926; certainly the animal plankton was very much less abundant, on the two days in 1925, than it was on either of the days in 1924 or 1926, and this alone would probably have an appreciable effect on the transparency of the water. But why the Sagitta should have left the surface so suddenly in the early mornings of June 18th and 19th, 1925, is hard to explain. Inspection of Figure 8 shows that apparently the majority of the Sagitta had already left the upper 30 metres by 2.36 a.m. and 2.28 a.m., about an hour and a half before sunrise. At this time the light intensity must have been almost negligible and some other factor was perhaps operating.

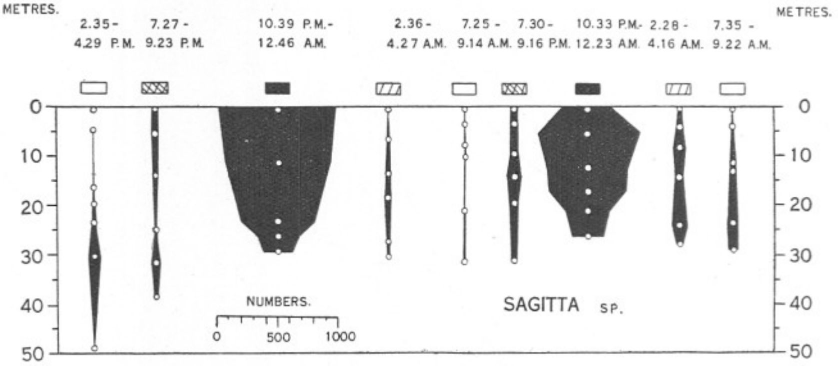

FIG. 8.—The vertical distribution of Sagitta sp. at the times shown, on June 17–18–19th, 1925. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

It should be realised that on days of intermittent sunshine the light intensity beneath the sea surface is changing to an enormous degree. Under such conditions it is natural to suppose that the animals take up an average position in the water, being constantly stimulated to move upwards or downwards. On clear bright days, however, the position in the water appears to be very constant, but presumably it must take a little time for a population of animals to settle around their optimum conditions.

This leads one to wonder whether in nature there are not perhaps two separable types of behaviour, namely the picking up of optimum conditions by means of random movements under fairly constant intensities, and the stimulation of active responses by sudden changes in intensity. This latter would operate at dusk and dawn; that such a behaviour is possible is perhaps indicated by the work of Kikuchi (**7**) who has shown an apparent double migration to the surface in the evening, first on the sun striking behind a mountain and secondly at the time of true sunset. This might possibly account for the sudden disappearance of Sagitta so early before sunrise.

SUMMARY.

1. The diurnal behaviour of Sagitta of different sizes is shown as a result of collections made with the 2-metre stramin ring-trawl throughout 24 hours on July 15th–16th, 1924, and on June 3rd–4th, 1926.

2. The younger stages of *Sagitta elegans* appear to withstand higher intensities of light in the daytime than do the older stages, and they migrate first to the surface at dusk, as do those of *Sagitta setosa*. The older stages leave the surface first at dawn.

3. Diagrams are given showing the curves of equal intensities of light beneath the sea surface throughout 24 hours as calculated from air intensities obtained in June, with a reflection loss of 15%; (*a*) assuming a coefficient of absorption of 0·200 at all depths, and (*b*) assuming a coefficient of absorption of 0·100 at all depths.

4. It appears, from a comparison of the behaviour of *Sagitta elegans* with the calculated light conditions beneath the surface, that the older Sagitta at any rate are more sensitive to light in the early morning after the darkness of the night and can become adapted to light of higher intensities later in the day.

5. Previously published observations on the behaviour of Sagitta sp. on June 17th–18th–19th, 1925, show quite a different type of behaviour from the above, possibly due to more transparent water, the Sagitta only appearing abundantly above 30 metres in the dark. They had again migrated to below 30 m. before there was any appreciable light.

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TABLE I.

Total numbers of Sagitta elegans caught in 10-minute hauls of the 2-metre Ring-trawl at each depth on June 3rd–4th, 1926.

	Daylight. 2.20– 4.11 p.m.	Dusk. 7.24– 9.13 p.m.	Dark. 10.28 p.m.– 12.31 a.m.	Dawn. 2.24– 4.17 a.m.	Daylight. 7.29– 9.29 a.m.
S.	40	513	143	257	117
II.	92	392	188	454	347
III.	1028	755	108	1152	852
IV.	1117	1318	156	993	1426
V.	3784	766	124	388	2428
VI.	4090	1530	456	507	2112

TABLE II.

Total numbers of Sagitta setosa caught in 10-minute hauls of the 2-meter Ring-trawl at each depth on June 3rd–4th, 1926.

	Daylight. 2.20– 4.11 p.m.	Dusk. 7.24– 9.13 p.m.	Dark. 10.28 p.m.– 12.31 a.m.	Dawn. 2.24– 4.17 a.m.	Daylight. 7.29– 9.29 a.m.
S.	13	677	287	93	13
II.	49	288	452	116	244
III.	92	745	412	338	107
IV.	83	252	264	207	194
V.	167	464	317	172	272
VI.	120	550	604	72	808

TABLE III.

Total numbers of Sagitta elegans caught in 10-minute hauls of the 2-metre Ring-trawl at each depth on July 15–16th, 1924.

	Daylight. 3.25– 4.45 p.m.	Dusk. 7.55– 9.17 p.m.	Dark. 10.50 p.m.– 12.20 a.m.	Dawn. 2.50– 4.16 a.m.	Daylight. 8.45– 10.11 a.m.
S.	98	2060	1040	66	355
II.	196	1230	1600	203	760
III.	1195	1460	1760	1010	3400
IV.	2925	2290	990	490	7130
V.	1190	2400	1573	1510	2710

TABLE IV.

ACTUAL NUMBERS OF SAGITTA ELEGANS MEASURED FROM CATCHES ON JUNE 3RD–4TH, 1926.

DAYLIGHT. 2.20–4.11 p.m.

Depth in metres.	Length in millimetres.						Total.
	<7½	8–9½	10–11½	12–13½	14–15½	>16	
S.	1	11	10	14	2	–	38
4·3	–	2	15	10	2	1	30
10·8	1	7	33	45	14	–	100
18	3	7	15	42	24	9	100
26·6	–	3	10	35	44	8	100
31·5	1	3	16	32	41	7	100
DUSK. 7.24–9.13 p.m.							
S.	4	16	15	5	–	–	40
4·4	1	4	25	7	2	–	39
9·3	2	6	12	35	9	–	64
19·7	–	3	11	33	36	17	100
25·3	1	3	10	19	28	7	68
30·3	–	2	10	26	36	26	100
DARK. 10.28 p.m.–12.31 a.m.							
S.	1	4	2	5	–	1	13
4·6	–	–	3	4	3	–	10
12·3	–	4	4	–	2	–	10
17·2	1	5	5	2	2	1	16
25·9	–	1	3	2	5	–	11
35	2	3	10	9	10	2	36
DAWN. 2.24–4.17 a.m.							
S.	–	1	6	5	1	–	13
4	–	4	10	13	8	2	37
9·5	1	3	6	36	48	20	114
20·5	1	3	20	24	30	17	95
24·4	–	5	8	5	11	4	33
36·3	–	4	14	7	12	5	42
DAYLIGHT. 7.29–9.29 a.m.							
S.	–	5	6	2	3	–	16
4	–	4	11	12	3	1	31
10	1	2	5	15	7	4	34
21·8	–	2	5	22	28	6	63
25·7	1	5	19	30	38	14	107
34·3	1	3	8	23	40	26	101

TABLE V.

ACTUAL NUMBERS OF SAGITTA SETOSA MEASURED FROM CATCHES ON JUNE 3RD–4TH, 1926.

Depth in metres.	<7½	8–9½	10–11½	12–13½	14–15½	>16	Total.
DAYLIGHT. 2.20–4.11 p.m.							
S.	–	2	3	2	3	2	12
4·3	–	5	6	1	4	–	16
10·8	2	2	3	1	1	–	9
18	1	1	3	3	–	–	8
26·6	1	2	5	6	1	1	16
31·5	–	1	5	1	1	1	9
DUSK. 7.24–9.13 p.m.							
S.	1	22	26	15	1	1	66
4·4	1	8	13	6	1	–	29
9·3	1	8	20	24	11	1	65
19·7	–	2	7	4	6	1	20
25·3	–	5	10	13	11	3	42
30·3	–	10	6	16	16	3	51
DARK. 10.28 p.m.–12.31 a.m.							
S.	–	2	7	7	5	5	26
4·6	1	1	2	4	16	–	24
12·3	–	5	8	4	14	7	38
17·2	–	4	3	4	12	3	26
25·9	–	2	4	8	9	5	28
35	2	3	3	12	21	7	48
DAWN. 2.24–4.17 a.m.							
S.	–	1	3	4	–	–	8
4	–	3	1	6	1	–	11
9·5	1	4	5	10	9	4	33
20·5	2	2	4	4	5	3	20
24·4	1	4	5	2	3	1	16
36·3	–	1	–	1	3	–	5
DAYLIGHT. 7.29–9.29 a.m.							
S.	1	–	–	–	1	–	2
4	2	14	5	1	1	–	23
10	–	1	–	2	3	–	6
21·8	–	1	3	2	3	–	9
25·7	–	2	–	5	6	–	13
34·3	–	3	8	8	12	8	39

TABLE VI.

ACTUAL NUMBERS OF SAGITTA ELEGANS MEASURED FROM CATCHES ON JULY 16–17TH, 1924.

Depth in metres.	<7½	8–9½	10–11½	12–13½	>14	Total.
			DAYLIGHT. 3.25–4.45 p.m.			
S.	4	7	16	6	–	33
6·6	12	17	43	29	–	101
13·6	10	34	94	79	7	224
19·5	5	10	44	127	14	200
34·5	2	18	49	43	3	115
			DUSK. 7.55–9.17 p.m.			
S.	12	67	123	55	1	258
7	–	–	–	–	–	–*
15·1	1	9	32	47	3	92
17·1	6	16	50	93	8	173
32·3	6	18	73	89	6	192
			DARK. 10.50 p.m.–12.20 a.m.			
S.	5	17	23	19	–	64
5·8	4	12	37	39	1	93
11·2	2	4	31	63	2	102
20·7	3	10	31	36	2	82
32·2	11	9	44	34	2	100
			DAWN. 2.50–4.16 a.m.			
S.	23	9	7	–	–	39
1·9	37	51	28	5	–	121
9	3	15	26	22	1	67
16	5	9	18	4	–	36
30·1	13	8	62	30	–	113
			DAYLIGHT. 8.45–10.11 a.m.			
S.	38	62	34	1	–	135
5·3	12	15	15	3	–	45
12·5	6	23	69	42	1	141
18·3	16	38	90	78	–	222
31·1	7	16	49	81	2	155

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* The tube containing these specimens had dried up.

TABLE VII.

Total numbers of Sagitta elegans at 2-millimetre intervals occurring at each depth; on June 3rd–4th, 1926, in 10-minute hauls with the 2-metre Ring-trawl.

Depth in metres.	Time.	Length in millimetres.						
		<8	**8–9½**	**10–11½**	**12–13½**	**14–15½**	**>15½**	Total.
			Daylight.					
S.	4.1 p.m.	1	12	10	15	2	–	40
4·3	3.44 ,,	–	6	46	31	6	3	92
10·8	3.25 ,,	10	71	340	463	144	–	1028
18	3.3 ,,	33	78	168	469	268	101	1117
26·6	2.42 ,,	–	113	378	1325	1665	303	3784
31·5	2.20 ,,	41	123	655	1308	1677	286	4090
			Dusk.					
S.	9.3 p.m.	51	205	195	62	–	–	513
4·4	8.46 ,,	12	39	251	71	19	–	392
9·3	8.26 ,,	23	68	143	415	106	–	755
19·7	8.9 ,,	–	39	145	435	475	224	1318
25·3	7.48 ,,	15	31	115	215	314	76	766
30·3	7.24 ,,	–	31	153	397	552	398	1530
			Dark.					
S.	12.21 a.m.	11	45	22	54	–	11	143
4·6	12.1 ,,	–	–	56	76	56	–	188
12·3	11.36 p.m.	–	43	43	–	22	–	108
17·2	11.13 ,,	9	48	48	21	21	9	156
25·9	10.51 ,,	–	11	33	23	57	–	124
35	10.28 ,,	27	37	128	109	128	27	456
			Dawn.					
S.	4.7 a.m.	–	21	117	98	21	–	257
4	3.49 ,,	–	50	123	159	99	23	454
9·5	3.29 ,,	12	35	57	369	484	196	1152
20·5	3.8 ,,	10	30	209	247	318	179	993
24·4	2.47 ,,	–	58	93	58	128	51	388
36·3	2.24 ,,	–	50	167	86	143	61	507
			Daylight.					
S.	9.19 a.m.	–	36	45	15	21	–	117
4	8.59 ,,	–	45	121	135	35	11	347
10	8.38 ,,	26	51	128	375	170	102	852
21·8	8.17 ,,	–	43	114	499	627	143	1426
25·7	7.52 ,,	24	121	437	680	850	316	2428
34·3	7.29 ,,	21	63	169	486	824	549	2112

TABLE VIII.

TOTAL NUMBERS OF SAGITTA SETOSA AT 2-MILLIMETRE INTERVALS OCCURRING AT EACH DEPTH ON JUNE 3RD–4TH, 1926, IN 10-MINUTE HAULS WITH THE 2-METRE RING-TRAWL.

Depth in metres.	Time.	Length in millimetres.						
		<8	**8–9½**	**10–11½**	**12–13½**	**14–15½**	**>15½**	Total.
			DAYLIGHT.					
S.	4.1 p.m.	–	2	3	2	4	2	13
4·3	3.44 ,,	–	15	19	3	12	–	49
10·8	3.25 ,,	21	21	30	10	10	–	92
18	3.2 ,,	11	11	30	31	–	–	83
26·6	2.41 ,,	10	22	52	63	10	10	167
31·5	2.20 ,,	–	13	68	13	13	13	120
			DUSK.					
S.	9.3 p.m.	14	224	264	149	13	13	677
4·4	8.46 ,,	8	81	130	61	8	–	288
9·3	8.28 ,,	15	89	224	275	127	15	745
19·7	8.9 ,,	–	25	88	50	76	13	252
25·3	7.48 ,,	–	56	111	144	121	32	464
30·3	7.24 ,,	–	110	66	171	171	33	550
			DARK.					
S.	12.21 a.m.	–	23	78	78	54	54	287
4·6	12.1 ,,	18	18	36	77	303	–	452
12·3	11.36 p.m.	–	54	87	45	152	74	412
17·2	11.13 ,,	–	40	32	40	120	32	264
25·9	10.51 ,	–	22	44	92	102	57	317
35	10.28		36	36	151	266	91	604
			DAWN.					
S.	4.7 a.m.	–	11	35	47	–	–	93
4	3.49 ,,	–	32	10	64	10	–	116
9·5	3.29 ,,	10	41	51	105	90	41	338
20·5	3.8 ,,	21	21	41	41	52	31	207
24·4	2.47 ,,	10	43	53	23	33	10	172
36·3	2.24 ,,	–	14	–	14	44	–	72
			DAYLIGHT.					
S.	9.19 a.m.	7	–	–	–	6	–	13
4	8.59 ,,	22	148	54	10	10	–	244
10	8.38 ,,	–	18	–	35	54	–	107
21·8	8.17 ,,	–	21	64	45	64	–	194
25·7	7.52 ,,	–	41	–	106	125	–	272
34·3	7.29 ,,	–	65	161	170	251	161	808

TABLE IX.

Total numbers of Sagitta elegans at 2-millimetre intervals occurring at each depth on July 16–17th, 1924, in 10-minute hauls with the 2-metre Ring-trawl.

Depth in metres.	Time.	Length in millimetres.					Total.
		<8	8–9½	10–11½	12–13½	>13½	
			Daylight.				
S.	4.34 p.m.	12	21	47	18	–	98
6·6	4.18 ,,	23	33	84	56	–	196
13·6	4.1 ,,	54	180	502	422	37	1195
19·5	3.44 ,,	73	146	644	1857	205	2925
34·5	3.25 ,,	20	187	507	445	31	1190
			Dusk.				
S.	9.7 p.m.	97	534	983	438	8	2060
7	8.49 ,,	–	–	–	–	–*	1230
15·1	8.32 ,,	16	143	508	745	48	1460
17·1	8.15 ,,	80	211	662	1232	105	2290
32·3	7.56 ,,	74	225	913	1114	74	2400
			Dark.				
S.	12.9 a.m.	83	281	364	312	–	1040
5·8	11.52 p.m.	64	208	640	672	16	1600
11·2	11.34 ,,	35	70	528	1092	35	1760
20·7	11.16 ,,	40	118	376	436	20	990
32·2	10.52 ,,	173	142	692	535	31	1573
			Dawn.				
S.	4.6 a.m.	39	15	12	–	–	66
1·9	3·51 ,,	63	85	47	8	–	203
9	3.34 ,,	40	222	394	334	20	1010
16	3.14 ,,	69	122	245	54	–	490
30·1	2.52 ,,	181	105	831	393	–	1510
			Daylight.				
S.	10 a.m.	99	163	89	4	–	355
5·3	9.43 ,,	205	251	251	53	–	760
12·5	9.26 ,,	136	543	1667	1020	34	3400
18·3	9.8 ,,	500	1211	2924	2495	–	7130
31·1	8.46 ,,	136	271	866	1410	27	2710

* The tube containing these specimens had dried up.

The Lower Limits of Perception of Electrical Currents by Fish.

By

H. C. Regnart, M.Sc., F.Z.S.

In recent years attention has been given to the influence of electrical currents as fish deflectors or screens, and experiments have been made to determine the magnitude of the currents which are sufficient to paralyse or act as deterrents to fish which may enter the electrical field,* but in such strong fields the perception of the mechanism by which fish respond to electric currents is masked by the paralysis produced. It seemed possible that experiments with very weak currents might give fuller information concerning the mechanism by which fish respond to electrical stimulus than those made in strong fields. There is also the possibility that weak electric currents may occur in nature to which fish respond, but before exploring that field of phenomena it is necessary to observe the behaviour of fish under the influence of very weak fields. McMillan found that the field (volts per inch) required to paralyse young salmon varied with the resistivity of the water; thus when the latter was 10,000 ohms per inch cube the paralysing voltage was about 1·5, so that a current density of $\frac{1{\cdot}5}{10^4}=0{\cdot}00015$ ampere per square inch was sufficient to cause paralysis, whereas when the resistivity was twelve ohms per inch cube the current required was ·03 ampere. In the former case the conductivity of the fish was greater than that of the water, in the latter case less.

In the experiments to be described to determine the lower limit a preliminary investigation was made by applying a current field to freely-swimming fish. When a fish is subjected to such a stimulus it is desirable to measure the current in terms of its density, e.g. amperes per square centimetre, otherwise there can be no adequate standard of comparison of the results of different experiments.

Some initial tests were made, using goldfish (*Carassius auratus*) maintained in a wooden tank 12 ft. long containing fresh water. Into this were fitted vertically two rustless steel plates measuring 30×32 cm. wide which exactly fitted the cross section. The tank was placed in a

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* F. O. McMillan, "Electric Fish Screen," Bulletin of U.S. Bureau of Fisheries in Washington, 1929, Vol. XLIV, 1928, p. 97, with current alternating at 60 periods a second.

separate darkened room free from all forms of vibration and other disturbances. The plates were arranged at a distance of 100 cm. apart, and using these as electrodes the effect of various intensities of direct currents on small fish about 6 cm. long was investigated. The tank was provided with a glass window and the fish were observed from a distance by means of a large periscope. The water was kept at a constant depth of 20 cm. Responses were obtained on completing the circuit, and occasionally again in a weaker form on breaking the circuit, the latter being a response to the removal of the current stimulus. The nature of the responses varied according to the position of the fish. When orientated so that the anterior end was facing the positive or higher potential plate, completing the circuit caused a rapid convulsion and generally an immediate retreat. When, on the other hand, the anterior end of the fish was facing the negative plate, there was often no response or sometimes a slight twitch although the current was the same as before. The field was unidirectional.

When the fish swam transversely across the field responses were slight and infrequent. Repeated application of the current every few seconds caused the responses of the fish to become weaker and finally to cease altogether. These responses were very definite with a total current of 100 milliamperes (and a potential difference of 15 volts across the plates) which corresponds to a current density of 0·00016 amperes per sq. cm.

When the circuit was completed and then broken rapidly, sharper responses were obtained. While the current was passing steadily for a short time, the fish were not affected. Similar, but definite though weaker, responses were observed on completing the circuit carrying a current of 10 milliamperes (and a potential difference across the plates of 1·5 volts) for which the density was 16 microamperes per sq. cm.

There appeared to be no sharply defined lower limit at which the fish became sensitive, and they were shown to respond to still lower current densities than the above by the following experiment. The tank was brightly illuminated and a narrow band of shadow, about 4 inches wide, cast transversely across the middle. The fish at first sheltered in the shaded area, but presently began to emerge and swim into the lighted region ; but on making and breaking several times a current of 3 milliamperes (current density=5 microamperes per sq. cm.), the fish could all be caused to retreat and assemble again in the shaded area, but not to exhibit the characteristic sudden responses.

The next experiments were performed in sea-water on marine fish, and the same plates as before were lowered into a large floor pool in the Dove Marine Laboratory at Cullercoats, at a distance of 8 feet apart. The length of this pool was 17 feet, its width 10 feet, and its depth 1½ feet. Three codling (*Gadus callarias*), each about a foot long, were limited to swim up and down between the plates by means of string netting, so that the available cross section of movement was the same as the area of the plates. With direct current varying between 0·2 and 0·6 amperes (and 2–4 volts potential difference on the circuit including the adjustable resistance, this giving some measure of the initial shock) definite responses were obtained with a pendulum switch set for 0·5 sec. contact, but much better results followed when the current was made by a quick action switch; the pendulum contacts were probably too light. After the response at the make of the current, the fish were not affected while it flowed continuously. The effect was mainly at the make of the current, but occasionally in a weaker form at the break. This indicated that a stabbing switch set to work at short intervals, e.g. half a second, would be more effective as a fish screen than a steady current. As before, the most marked results were obtained when the fish were so orientated that the anterior end was facing the positive plate, with occasionally a slight twitch when facing the negative plate. As in the case of the fish tested in fresh water, the responses to repeated stimulus grew less vigorous until finally no effect was obtained at the make and break of the current. Stronger currents caused more vigorous responses and more tests could be made before the fish ceased to respond. Continued trials carried out over several days adversely affected the fish and made them sluggish and unsuitable for further experiment until they had been rested for some days.

In order to place the fish under more natural conditions the nets were removed. The fish then swam freely about, and when facing the positive plate gave better responses with these currents (0·2–0·6 amps. at from 2–4 volts). A disadvantage of these experiments was that after a few responses the fish avoided the region between the two plates. All these trials were made under suitable conditions with freedom from ground vibrations and other disturbances, and in a weak light. The responses were recorded with the help of three additional observers and no observations accepted unless agreed to by all. Owing to the fact that in this case when working in the floor pool the current between the plates spread out, the actual current densities were from 15 to 45 microamperes per sq. cm.* Similar experiments were made with alternating currents, using the same fish. Under these circumstances the fish gave a slight response when facing the earth plate, but a more vigorous response was observed when facing the high-tension plate. As before, the best results were obtained at the

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* Note by Professor W. M. Thornton:

If the current i is taken as spreading out from small cylindrical electrodes the density midway between them is approximately $i/\pi Dt$, where D is their distance apart and t the depth of the liquid. With $i=0{\cdot}2$ ampere, $D=250$ cm., $t=44$ cm., this is equal to 5·8 microamperes. If the current is taken as spreading from strip elements of two flat plates 30 cm. wide and the effect is integrated over their width, the density midway is 19 microamperes. A more complete treatment, assuming the electrodes cylindrical and relatively large (see Pidduck, "Electricity and Magnetism," §46. See also F. O. McMillan, "Electric Fish Screen," Bulletin of the U.S. Bureau of Fisheries, Vol. XLIV, 1928, Fig. 12, p. 117), gives the estimated values 15 to 45 microamperes per sq. cm.

make and break of the current. With a current of 3 amperes and the plates 6 feet apart, very violent responses were obtained. Trials were made with currents over the range 0·5 to 3 amperes, corresponding to the current densities 0·000038 to 0·00022 ampere per sq. cm., at the lower of which response was just perceptible.

In order to investigate the threshold values in sea-water more definitely the following method was used. Twelve codling, about 8–10 inches long, were maintained in a healthy condition in a tank with a glass side which measured 4 feet 6 inches deep, 4 feet wide, and 4 feet long. A wooden frame covered with string netting which exactly fitted the tank was lowered into the water until it was 18 inches from the bottom, and the fish were kept confined in this space with the electrodes arranged at each end and 3 feet 4 inches apart. Under these circumstances, the fish, while swimming freely, were constrained to move more slowly and the sudden twitch due to an electric impulse could be very clearly distinguished. Tests were made at 6-minute intervals. The responses were very definite at first, but after a time became weaker and the fish finally failed altogether to respond. As the current was increased more responses were obtained before the effect ceased. The fish, after two days during which the tests were carried out, became sluggish and refused to feed, and the tests had to be made at least every other day to give them time to recover from the effects of the repeated stimuli and their confinement in a limited space. Alternating current was used over the range 0·025 to 0·65 ampere, which in this case gave the current density range of 2 to 50 microamperes per sq. cm. In these experiments the fish were tested when facing the positive plate and either in the centre of the field or nearer to it. After a time the fish avoided going near the higher tension plate, and this was proved by reversing the leads on the plates. The fish also would avoid swimming frequently between the plates. As before, three additional observers were employed and only vigorous movements regarded as positive; doubtful cases were taken as negative. These responses were quite distinct from the slower movements made when the current was not passing. They consisted of two movements, (1) a sudden twitch, (2) an immediate change of direction in swimming. A larger number of consecutive readings could not be obtained, as after carrying on the experiments for several weeks the fish as before became sluggish and refused to feed.

Experiments were next undertaken to ascertain if possible the regions which function as receptors of the stimulus of the current field; and as a first attempt the lateral canals with their sense organs were considered. As before codling about 15 inches long were used. Three fish were anæsthetized by the addition of some chloroform to the water and cuts made on both sides of each fish, which severed the supra-opthalmic, suborbital, and hyomandibular branches of the facial nerve, the lateralis nerve, and the ventral ramus of the lateralis nerve. These operations eliminated the organs of the lateral canals (and also the skin of the anterior part of the head, since cutting the supra-opthalmic branch of the facial nerve also involved cutting the corresponding associated branch of the trigeminal nerve). The fish were left for a fortnight to recover, and as they had but a few days before been obtained directly from the sea, the recoveries were very rapid. Under similar conditions to those already described, the fish were still found to respond to stimuli of the order of 15–30 microamperes per sq. cm. although they were less sensitive than in the case of unoperated fish. One of the fish with lateral organs eliminated was then subjected to section of the optic nerve on both sides and again the sensitivity to electrical stimuli was not completely eliminated. In all these operative experiments the fish were killed after experiment and the fish after being hardened in spirit dissected to verify the nerve-cutting work. These experiments made it probable that other areas of the fish such as gills were involved in the perception of these electrical stimuli, but the marked reduction in the strength of the response caused by eliminating the lateral organs made it certain that they played a large part in the response to electrical currents. This is possibly due to the relatively high electrical conductivity of the mucus in the canals, but this point requires further investigation.

As a further proof of the role played by the lateral organs as electrical receptors the following experiments were made which show that these organs may have influence in the perception of the direction of the source of an electrical current in the sea. On the application of an electric field to a normal freely swimming fish, the direction of movement of response was found to depend on the orientation of the fish with respect to the field. Thus, when swimming towards the higher tension plate and inclined to it at a slight angle, the response was generally such that it swam away from the plate in a direction either to left or right which removed it most rapidly from that region.

Two fishes were then operated on by in one cutting the supra-opthalmic branch of the facial nerve on the right side and in the other the corresponding nerve on the left side, and on recovery they behaved like normal fish in their directional movements with respect to the positive plate. Finally, two fish were each subjected to section of all the nerves to the lateral canals on the right side ; these fish were then found to give a strong twitch to the left on stimulation whatever their position in the field might be when facing the higher potential plate. These results were obtained over a range of 300 tests and the response to the left was 100 per cent. Next two fresh fish were taken and all the lateral organs on the left side eliminated in each case. These fish gave a twitch to the right over a corresponding series of tests.

These experiments indicated that the lateral canals with their mucous secretions and the organs associated with them may have considerable importance as receptors for directional purposes, and support the suggestion that the greater development of these organs in certain deep-sea fish is for this purpose.*

It should be emphasized that the above experiments were performed upon fish which were exposed to light and other unnatural environmental conditions and that due to confinement and diet they could not be comparable in vigour and sensitiveness with those in a free state; but even under such unfavourable conditions the results obtained prove that fish are extremely sensitive to electric currents.

The above results may be summarised as follows:

1. Goldfish had a lower sensitivity threshold at about 5 microamperes per sq. cm. direct current.
2. With Codling in a shallow floor pool the threshold was about 15 microamperes per sq. cm. direct current.
3. In a large wall tank their threshold value was about 2 microamperes per sq. cm. alternating current.
4. The lateral organs are proved to play a most important part in the perception of electric stimulus. Section of the nerves of those on the right-hand side caused the fish to throw to the left, and vice versa.

The early experiments were carried out in an annex of the Electrical Engineering Laboratory at Armstrong College; the experiments on sea fish were made by kind permission at the Dove Marine Laboratory, at Cullercoats.

I am greatly indebted to Professor W. M. Thornton for suggesting the research and for his constant help and advice.

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* Vide "Electrical Perception by Deep Sea Fish," W. M. Thornton. University of Durham Philosophical Society. Proc., Vol. 8, Part 4.

Some Observations on Schooling in Fish.

By

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Student Probationer at the Plymouth Laboratory.

With 12 Figures in the Text.

CONTENTS.

I. INTRODUCTION.

THE SCHOOLING HABIT.

The habit among certain kinds of fish of living in herds, or "schools," is too familiar to require much in the way of introduction. Those fish in which the habit is most strongly developed, such as members of the herring and mackerel families, though scarcely developing such organisation as can be seen in some bird flocks, clearly display a considerable degree of mutual adjustment between individuals. The term "school" or "shoal" is applied to fish herds which are not mere chance aggregates brought together by the common attraction of some external condition (e.g. collections of salmon on migration up river) but definitely involve mutual reaction of one individual to another.

Almost every stage can be found between regular school fish and those in which temporary bunching together may occur on certain occasions, as Parr (**3**) has pointed out, giving *Gobius ruthensparii* as an example of a simple case. " The adults of this species generally do not school at all, but when splashing among the algæ where they are scattered one may very commonly observe that they do not dart off in all directions, but converge to form a school of very short duration, spreading again after a short flight."* Other kinds form more stable, though not permanent, schools. As an example there is the European Stickleback (*Gasterosteus aculeatus*), " which will travel in rather perfectly formed schools but will scatter for breeding and feeding. Similar behaviour also seems to be found among the American killies (*Fundulus*) and many other fishes " (p. 29). The bass (*Morone labrax*), in its immature stages, lives in considerable schools, but as it grows older becomes increasingly less sociable. During the shoaling period, however, the habit is not so dominant as to preclude considerable independent individual action, and has its main effect in keeping the group together, rather than in co-ordinating movements.

From such cases we pass to permanent school fish, such as members of the herring and mackerel families, in which the school is extremely stable and is not broken up unless there is violent disturbance. Since these fish are continually on the move, for feeding as well as travelling, their case differs from that of *Gasterosteus aculeatus*, etc., only in degree. The behaviour of individuals of these fish leaves an impression of being extremely stereotyped, and non-variable, and specialised in the development of actions suitable for the maintainance of the school. That these actions are developed to a degree of some refinement is apparent from the regularity and co-ordination of movement so characteristic of the schools. So, when the individual is considered, it may well be asked what are the nature of its actions that result in the school apparently working as a unity. Here is a subject for enquiry.

PROBLEMS CONNECTED WITH SCHOOLING.

The phenomenon of schooling has received surprisingly little attention either from fishery investigators or from those studying animal behaviour. Parr (**3**), it would appear, has been the first to examine the subject in the light of cold reason, and to apply a form of scientific treatment to it. But the subject is here approached from a somewhat different aspect.

Setting ecological questions aside for the time being, and keeping an

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* The habit of packing together when scared is common among true schooling fish, as has been observed in the case of mackerel kept in the aquarium, and is well known to occur when sprat, pilchard, etc., are attacked by sea birds. It is possible also that it occurs among non-schooling fish such as hake (Bateson **1**, p. 249). If so this is a case of schooling in its most rudimentary form.

analytical standpoint, the problems connected with schooling, whether permanent or temporary, well developed or indefinite, may be expressed as follows :—

1. Given the phenomenon of schooling.

(*a*) What sort of actions on the part of the individual are concerned in keeping the school together, and how can various activities displayed by the school be interpreted in terms of behaviour of single fish ?

(*b*) What are the essential elements in the aspect of its surroundings to which the individual reacts, and which in general influence its behaviour ?

(*c*) From the special aspect of sense physiology, what are the senses concerned ? How refined are these senses ?

2. Given a fish liable to display schooling behaviour.

(*a*) Under what conditions will that behaviour be displayed ?

(*b*) How determinate is that behaviour—to what degree of probability can it be predicted ?

(*c*) To what degree of certainty can it be experimentally induced ?

(1) Questions 1 (*a*) and (*b*) cannot strictly be separated from each other, being really only two ways of propounding the same problem. The one focuses attention on the animal's actions, the other on the surrounding conditions. But actions cannot be described without some sort of reference to environment, and the effect of the latter can only be stated in terms of actions being performed at the moment. Only in limiting cases does a clear distinction emerge ; the first enquiry dealing with "reactions," the second with "stimuli" producing them. And as for experimental purposes it is generally convenient to deal with clear-cut reactions, these two aspects of the phenomenon may be kept separate.

(1*a*) This is largely a matter of description, but observation should be made on whether the individual behaviour is variable or rigid, complicated or consisting of a limited set of more or less cut and dried reactions. Naturally, the more stable and mechanical the movement of the school, the more automatic the actions of the individual fish are likely to be. It is of interest to know how strongly developed and how permanent are the reactions involved ; e.g. will a fish always react to a neighbour in a similar way whether forming part of a school or not ? It is further to be noted how far external conditions influence the observed behaviour. For instance, when a school is feeding there are not such rigid adjustments between individuals as when it is travelling ordinarily ; in the former case like orientation of all the members of the school may completely disappear.

(1*b*) Here one is particularly concerned with such questions as "How do the fish recognise each other ?" Or rather, "What distinctions do the fish draw between neighbouring fish and other objects ? " Or, put another way, " What are the essential elements in a situation which results in a schooling response ? " In any case, however the question is framed, it is not intended that it should convey anything beyond an objective meaning. Experimentally a fish, which reacts in a definite way when another fish comes near it, is tested under various circumstances in which some factor in the normal situation is lacking. The features shared in common by those situations which produce the normal reaction may be considered as their essential elements. By this means evidence may be procured as to the importance of movement, form, general contrast, details, spatial relations, and so on. The extent of the data obtainable depends on the strength and persistency of the original reaction.

(1*c*) By treatment of the animal as a unit, it is possible to demonstrate empirically the dominant sense involved ; and to deal with such questions as the following : " Assuming sight to be involved, at what distance (for given illumination and turbidity of water) will a fish exert attraction on another ? " " How complete an image is necessary and what are the essential elements of it ? " " What illumination is necessary ? " Further, the degree of refinement of the sense may be tested with considerable accuracy by conditioning methods. But neither these nor other exact analytical methods of sense physiology are here utilised, and so further consideration of them is unnecessary.

(2) Once observation is undertaken on fish in the above connections, this second side of the problem is bound to open up. The answers given to the questions concerned can at best be approximations, and in any case only apply to specified laboratory conditions. As for elucidation of behaviour under natural circumstances, they cannot legitimately be used except as evidence (often, however, this evidence, combined with that of what observation is possible in the field, is sufficient to give an adequate answer).

(2*a*) By this is implied not only what are the conditions under which fish maintain a school, but also what changes are necessary to convert a " non-schooling " state of the fish into a " schooling " state, and vice versa.

(2*b* and *c*) To deal with these questions fully would involve the whole subject of determinancy with respect to behaviour actions of animals. It is enough to record such observations as bear on the points. Empirical treatment is given to these questions not merely for the sake of cautious procedure, but because theoretical consideration leads round to this as the only permissible method. The questions are framed in a way which does not presuppose tropistic behaviour or indeed any causal relations whatever, but if actions exist that are sufficiently fixed to be conveniently termed "tropisms," they will appear during investigation. The habit of postulating hypothetical tropisms constant only in hypothetical ideal conditions (so that in practice they would be partially obscured by secondary influences) is considered a fallacious method of treatment.

In this paper an account is given of certain observations on the bass (*Morone labrax* L.). These are discussed in their bearing on the problems outlined above in so far as they concern that species.

Bass as a Subject for Experiments on Schooling.

Choice of schooling fish suitable for observation in captivity is limited to a very few species. Small mackerel, herring, and sprat are excluded on account of difficulties involved in keeping them in confinement. The species most readily obtainable was the bass (*Morone labrax*), a fish which, though not such a specialist as the herring or mackerel, has quite a strong tendency to form schools.

The bass is a lively, vigorous fish with a traditional reputation for capriciousness and wariness. Admittedly, when all the facts known about its habits are considered, one cannot avoid the conclusion that its behaviour is normally far less stereotyped than that of most fish, showing much diversity and adaptability. Its diet, which is principally animal, preferably alive, covers a wide range from seaweeds to sewage effluents, and various are the methods adopted by the fish in obtaining it. The bass also shows considerable powers of resistance to environmental fluctuations such as changes in salinity and lack of oxygen. It lives well in captivity, surviving conditions that would be detrimental to most fish. In captivity it is seen to be alert and quick to take alarm—in fact, gives the appearance of living in a considerable state of nervous suspense—but is capable of becoming habituated to such conditions, if constantly repeated or continually present, as at first produced fright reactions.

The schooling habit is best developed in the younger fish which invade estuaries during summer months. At this period, especially in the earlier part of the season, while feeding vigorously, they form considerable schools, and even when the larger schools disperse the fish still keep together, at least in small parties. Schooling behaviour appears to weaken as the season advances. It has been observed (**2**, p. 117) that fish of the same size school together.

Summarily compared with other schooling fish, the bass may be said to represent a type in which schooling behaviour is not developed to such a predominating extent that it is practically stereotyped into automatic action, but rather, so to speak, exists as one of several forms of behaviour which at different times are liable to emerge from the general "behaviour pattern." In other words, it is a good generalised type in which schooling behaviour is present, but not in an exaggerated form. Compared with the schooling habit of specialists like the herring, that of the bass is not so well defined, nor so deeply engrained, nor so persistent. A variable element in seasonal change has been indicated above. Observations in captivity show that there is a considerable difference in the intensity of this behaviour under different circumstances, being stronger, for instance, when the fish are alarmed, and weaker when hungry. By the comparison of the behaviour of bass kept in an aquarium tank with that of grey mullet and mackerel under similar conditions and with sprat in tidal pools, it was seen that of these four species the orientation of individuals in relation to one another is least evident in the bass. In this species also there is much scope for independent individual action. In fact, when a number are together in a moderate sized tank, there is little, if any, evidence of schooling behaviour. Yet, as is shown below, individual fish have a strong attraction for each other.

It is this attraction between individuals that was made a basis for the experiments here described.

II. DESCRIPTION OF EXPERIMENTS.

Preliminary.

Preliminary investigations were started in October, 1929, on four fish, between 6 and 7 inches long, taken from the tank in the aquarium where a considerable number had been living for some months. They were placed in a tank in the main laboratory. A view of the interior of the tank ($58\frac{1}{2}'' \times 31''$ and $18\frac{1}{2}''$ deep, holding a depth of water of 14″) was obtainable through the front which, except for the lower 6 in., consists of glass. The other walls of the tank are dark and the glass was covered with black paper, leaving only a space for a peephole in the middle. When not in use the peephole was kept covered over. Besides this, no attempt was made to exclude such disturbing influences of the surroundings as might be reflected in the behaviour of the fish.

The difference between the surroundings in the aquarium and those in the laboratory tank were considerable and it is not surprising that for some time the behaviour of the fish was dominated by "fear" or "response to disturbance" actions. At any rate, they were much inclined to keep to the far side of the tank, lying low in corners or behind a vertical outlet pipe in the centre. This, on the one hand, contrasts with the behaviour in the aquarium tank, in which the fish displayed considerable activity, swimming high in the water and attracted rather than repelled by movement outside the glass; and on the other hand is clearly related to behaviour towards a disturbance, from the side or above, when the fish, having at first darted rapidly to and fro, take up a position of rest low down in a corner or under some shelter if available, and lie quiet facing the source of disturbance.

As time went on the fish became less and less inclined to lie low at the back of the tank. Movement at the peephole had increasingly less effect. In fact, when the observer was quite still and took care that as little light as possible entered through the peephole, the fish behaved unconcernedly, so long as they did not swim up too close.

During observation on these four fish in daylight, with the aid of glass partitions set up in the tank, the following conclusions were soon reached.

(1) Fish placed in a tank, especially if disturbed, collect together and are restless when separated.

When their "attention was attracted" they bunched together orientated towards the source of disturbance. If one began to move away the others followed. But they also kept together when undisturbed. All through subsequent experiments when more than one fish was used the tendency was very evident.

(2) Fish separated by a glass partition move towards each other and school on either side of the glass.

The following tests were made :—

(*a*) Two glass plates (XY, YZ) were placed in the tank as indicated in Figure 1. The usual position of the fish (when the tank is clear) is along AB. When the plates were put in, one fish was separated from the other three which were penned in the area XYZ. When observation began the three inside fish were lying behind the vertical outlet pipe (OP), while the single fish lay up against the glass at X. The three fish moved in the direction of B ; whereupon the single fish made great efforts to follow them, persistently swimming up against the glass XY.

This was repeated on two other occasions with the same result.

The outside fish was observed attempting to pass XY when the other fish had come to rest near Z. The attraction of the one for three was always greater than that of the three for one.

A black plate, PQ (Fig. 2), was placed against XY so as to cover it for much of its length, leaving, however, QY free. Whereas (1) before this the fish had attempted to pass through region XQ, (2) when the plate was put in it kept to region QY ; and (3) when the plate was shifted to P^1Q^1 it attempted to pass XP^1.

(*b*) Three fish were penned by glass plates within area XZ (Fig. 3), one left outside.

Outside fish, previously, when entirely alone in the tank, was not observed to come forward at all from region AB.

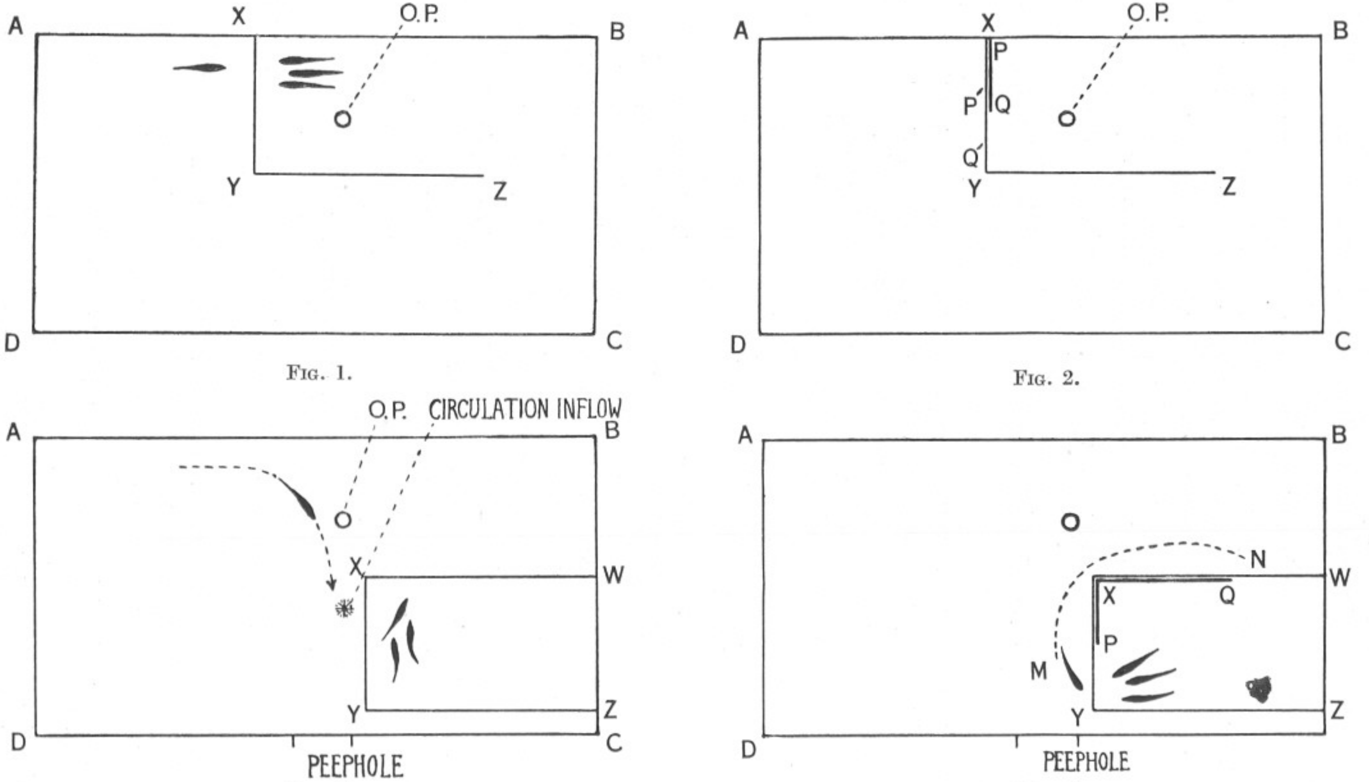

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Figs. 1–4.—Diagrams of the arrangement within the tanks on particular occasions during the course of the experiments. (See text.)

ABCD= Outlines of tank. W, X, Y, Z in all cases represent glass partitions standing vertically in the water. They were supported at their lower corners by bricks, which are not shown in the figures. O.P.= The overflow pipe standing vertically in the water.

But when the three fish are in XZ the outside fish was seen on many occasions to swim forward towards the peephole along XY.

NOTE.—The outside fish came up more readily when the circulation inflow was striking the water at the point marked with a star, close to region of XY, and breaking the surface. On one occasion the observer was looking down from on top. When the circulation inflow was turned off or diverted into XZ, so clearing the view, the fish did not come forward when the observer was looking down into the tank, but did so when the observer was keeping still at the peephole.

The outside fish now and again tried to pass into XZ between X and Y, and in one case between X and W.

Black plates were put in positions XP and XQ (Fig. 4). (i) The four fish took up position on either side of PY, thus indicating that the inside fish were affected by the other and not merely the other way round. (ii) Subsequently the inside fish took up various positions ; the outside fish spent much time moving round arc MN, now and again attempting to join the inside fish either at QW or PY.

The black plates were tried in other positions, always with the same results ; the outside fish attempted to pass through the clear glass spaces towards the inside fish.

All results were seen to be independent of the position of the circulation inflow—this did not appear to offer any attraction. It could be used with advantage as a screen.

(*c*) The tank was divided down the centre by a glass partition (Fig. 5).

Normal position of fish somewhere along AB.

Two pairs of fish are separated by the glass.

If left alone they collect on either side of XY and orientate themselves, as a rule, in the same direction. They frequently are observed attempting to pass through the glass partition, and will snap at food falling on the other side of the glass.

If a black plate is placed at XY the fish take up a position at P. If frightened back they come forward again in a short time, even though they may be moving towards a source of disturbance.

XY glass only . . .	Fish greater part of time at XY.
XY glass+black plate .	Fish for a larger part at P.

However, two pairs of fish do not exert the same mutual attraction as two single fish or as one fish towards three.

The mutual attraction that exists in these fish is best seen, then, in the case of a single fish separated off from a batch of others.

(3) The attraction of one fish for another may be strong enough to overcome what would otherwise be repelling effects.

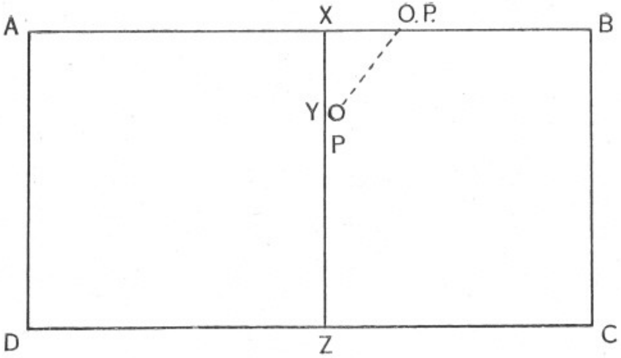

Fig. 5.

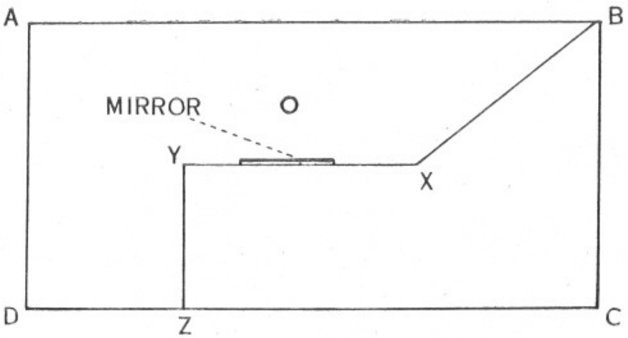

Fig. 6.

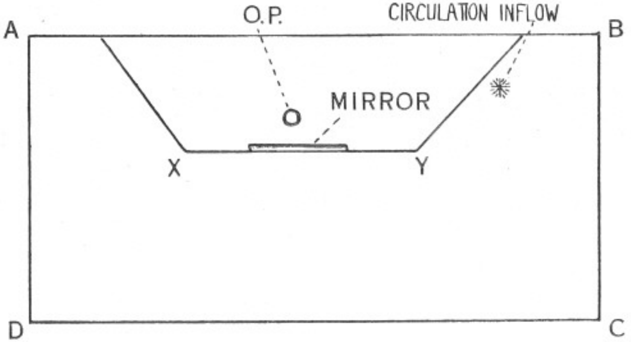

Fig. 7.

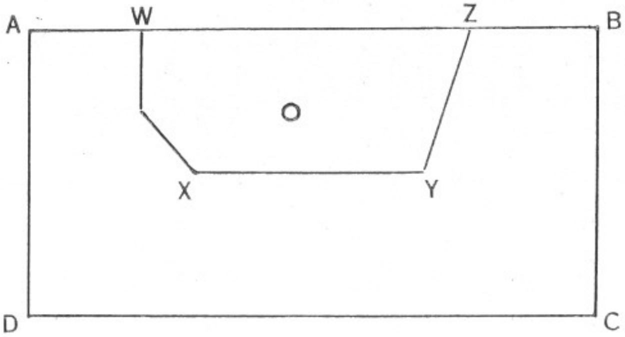

Fig. 8.

Figs. 5–8.—For description, see Fig. 1, pages 427, 428.

An instance of this has been given above. An isolated fish moves towards peephole when attracted by fish penned in glass.

In addition there was good indication that :—

(1) The fish do not readily, if at all, " sense " the glass plates. They will swim into them, and often persist for some time in swimming against them when held up.

(2) The fish behave as if reacting to each other by *sight*, the evidence being :—

(*a*) A fish separated from others by glass alone will make conspicuous efforts to pass through towards other fish. But this does not happen if they are separated by an opaque screen, although enough space is left for the passage of dissolved substances or vibrations in the water.

(*b*) There is never any reaction to the spaces or crevices on the edge of the separating plates.

(*c*) When a fish is attempting to pass through a partition which is partly opaque and partly transparent, it will only attempt to pass through the transparent parts.

Showing that Sight is Involved—Reactions of the Fish to a Mirror.

In order to test out the proposition that bass react to each other by means of sight, experiments were carried out on the behaviour of the fish in the presence of a mirror.

From this point a second tank (59″ × 30″, holding a depth of 15″ of water) was used, situated in a part of the laboratory where the light was dimmer and in general less liable to disturbing influences. In order that the fish might be observed without being disturbed at all, a hood of black cloth was hung over the side of the tank (in addition to black paper stuck on the glass), arranged over the peephole in such a way that all light from behind was cut off, and the observer's face rendered invisible.

The arrangement proved entirely satisfactory, its effectiveness being finally estimated by the influence, if any, on the behaviour of the fish. The fish frequently swam alongside the peephole showing not the least concern for any strange appearance that may have intruded upon their visual field. It was possible, however, if right up close to the glass, to produce by movement a reaction on the part of the fish.* It is beside the point to consider whether the fish detected the observer (whatever that means) or not ; what matters is whether behaviour was affected or unaffected. And as in this case there was a clear contrast between

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* For kind of movement, see below.

"behaviour affected by movement at peephole" and "behaviour unaffected," it was possible to estimate when the latter condition held.

The reactions of the fish when coming in front of a mirror are best seen in single specimens isolated from the rest. If in a moderately active state, it spends a good deal of time swimming to and fro across the mirror surface with its face close against the glass as though attempting to pass through it. It passes up and down, often making futile snaps at the surface and displaying other reactions characteristic of frustrated effort. When the head passed beyond the field of the mirror, the fish very frequently pulled up short and turned back. This action, very striking on occasions, showed clearly that the abrupt change from a visual field containing the reflection to a visual field without it may provide a sufficient stimulus to produce a sharp reaction in the fish. Since precautions were taken to have the background approximately similar in the two fields, the difference between the two fields is reduced to that between presence and absence of image, and it is safe to infer that the sudden disappearance of the mirror image in the visual field of the fish is enough to stimulate a sudden reaction.

When the fish is in a less active state it lies up against the mirror for hours at a time. If driven off it will be back again before long.

Particular cases are described below. Small specimens of 3 and 4 inches reacted in a most energetic manner.

The behaviour thus outlined suggests that the mirror image exerts an influence identical with that of the presence of another individual, evoking a schooling response. Definite proof, however, that the image itself really counts for something was furnished during the course of various experiments. One particular instance is of itself practically conclusive.

Glass plates were arranged as shown in Figure 6 (BXYZ). There is a single fish in the tank in front of the glass (area YC). Along XY is placed a mirror covered with black paper except for a rectangular patch of $1 \times 2\frac{1}{2}''$. During a period of two days the fish is observed to react to its reflection in the mirror exposure and to lie up against it for hours. After this a piece of plain glass similarly covered with black paper with a similar $1 \times 2\frac{1}{2}''$ opening was substituted for the mirror. The fish did not react to the opening in at all the same way, but still rested in the region in front of it. The mirror was then replaced, this time along YZ. The fish just afterwards reacted to its reflection and remained in the region before YZ. Mirror and glass were then interchanged and the fish returned to its former position. The interchange of mirror and glass was repeated several times and in every case the distinction in the behaviour of the fish in front of the openings was most definite, the mirror being invariably "discovered." The effects of relative position being excluded by interchange of the plates, the only difference between the two rectangular openings in the black surface was that one contained a reflection of the fish and the other not.

As might be expected, the mirror exerts less attraction on two or more fish together than on one isolated individual—progressively less as the number increases. Nevertheless the same sort of behaviour is seen and individual fish may for a time react quite intensely.

Summary of Experiments with a Plain Mirror.*

A. *Reactions of individual fish.*

1.

Eleven days after the original four fish had been placed in the first tank, they were presented with a rectangular mirror in a brown wooden frame. Being evidently "put off" by the unfamiliar appearance of the frame, none of them behaved in a way which gave much evidence of the effect of their mirror reflection. But when one of the fish (A) was moved to the second tank, the mirror being stood across one corner, a most definite reaction was seen. Since the whole situation was new for the fish, it might have been expected that the mirror and its frame would not exert the same repellent effect as when placed among already familiar surroundings. Again, whereas the fish had always been accustomed to the presence of others its own kind and size, it was now alone. Further, since it had been subjected to the shock of capture in a net and transference from the tank to another, its shoaling instinct should be strong.

It was found that in whatever part of the tank the mirror was placed, wherever the fish was driven, it always returned to the mirror after a short time. Now it swam over the surface, obliquely, with its head against the glass, as though trying to pass through to the other side of the frame; now around in the region close in front of the glass. When it passed out of the sphere of the mirror, it always turned back again, and so, even when most active, remained in one very restricted area. The turning back was most striking when the fish moved along the mirror's surface. On passing the frame (as it was constantly doing) it immediately turned back sharply and often moved in an agitated way until its reflection appeared before it once more.

When not active the fish lay alongside the mirror.

The mirror was placed in different parts of the tank; in every case the fish was attracted to it, behaving in the way described above.

This sort of behaviour has been found to be typical, though it may not always be so intense or so definite.

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* These were carried out mostly in daylight, but sometimes in the evening under artificial light. The fish behaved in the same way in either case.

2.

Another fish was then placed in the tank with the above. The hood had now been fixed over the tank so that the fish could be observed without being distracted by the observer. On the first day the reaction was weak. On the second day it was quite strong : every time the fish were observed they were in the region of the mirror, either resting by it or moving slowly round in front of it. On passing beyond the view of their reflection they turned sharply back.

The next day the mirror was removed from its frame and used from now on as a simple rectangular plate ($10'' \times 8''$). The fish were immediately attracted to it and for the rest of the day their reaction was quite strong.

The mirror was then placed in the position shown in Figure 7, the region behind the vertical outlet pipe being cut off by glass partitions with mirror lying up against the longitudinal partition XY facing the peephole. The field of the mirror differed from that of the adjoining glass in that the reflected wall stood further back than the real back wall seen through the glass.

On the first two days the fish, whether active or not, showed quite a strong reaction to the mirror. When active they swum around in the region between mirror and peephole, constantly turning abruptly towards the mirror when the reflections disappeared from the field of view ; when inactive, they lay up against it. On one occasion one of the fish got inside the partition ; it was much attracted by the outside fish which was busy reacting, in turn, to its own reflection.

Two special cases which showed the effect of the mirror image may be mentioned. On one occasion a fish moving along the line from C to D, on arriving opposite the mirror (about 14 in. away) turned at right angles so as to approach it. Another time one fish was lying against, and at an angle to, the mirror ; the reflection of the other, moving in the opposite direction, came into view ; whereupon the former turned and orientated itself accordingly.

Some tests with different models were then made, after which the mirror was again used. It was placed an inch or two behind the glass partition. This was eight days after the fish had been put in the tank. The reaction to the mirror was now distinctly weak. The fish were at first moving about actively and paying a certain amount of attention to the mirror ; but not greatly attracted to it. Occasionally they try to pass through the glass towards it. But they mostly lay quiet in the left-hand side of the tank, and returned there even if shifted toward the mirror.

The fish seemed to be developing a " depressed condition," so, as a test, the mirror was removed and another fish placed inside the glass enclosure. The original fish were not in the least attracted—hence the failure to react to the mirror was accompanied by failure to react to other fish. The mirror was replaced, but the fish gave no reaction. They were then removed.

3.

Two new fish, netted in the Tamar Estuary a week before, were tried with the mirror arranged in a similar manner as above, but now the glass partition was further forward, half-way between the front and back walls of the tank. This gave less contrast between the background of the mirror and that of the plain glass. (Fig. 8, mirror against centre of XY.)

During the two days these two fish were watched they were greatly attracted by the mirror, spending much time swimming slowly between it and the peephole and not straying from this area. They do not try to pass through the mirror, nor are much inclined to lie beside it; but then they do not closely attract one another. The reaction of these two fish is good, being much like that of the fish mentioned above.

4.

The behaviour of two small fish (K and L) of 4 in. and one (O) of 3 in. was observed on several occasions. At this size much greater activity is shown than by larger fish. The reaction to the mirror, though variable, was typically most vigorous.

On the first occasion on which the small 3-in. fish (O) was observed in front of the mirror it was alone. The mirror was put in the tank at 3 p.m. At 3.15 the fish was busily swimming before the mirror, in a state of great activity, darting to and fro in front of it and continually swimming at it as though to pass through it. On these latter occasions the dorsal fin was frequently raised, an action which is characteristic of impeded movement. Every few minutes the fish was observed and all the time, until the last observation at 5.50, it was still reacting to the mirror in an astonishingly persistent manner. The next day the tank was divided down the centre by a glass partition and a single 6-in. fish placed on the right, the small fish and the mirror being on the left. In spite of such distraction as may have been provided by the larger fish, the small fish still continued reacting strongly to the mirror, and if it moved away very soon returned.

Each of the 4-in. fish, when tested separately, behaved in a similar way, remaining for a long period in front of the mirror. At times they lay still against the mirror, but for the most part they swam actively up and down and to and fro over the surface, frequently raising their dorsal fin in agitated effort to pass through, and returning whenever they happened to move out of the range of the mirror reflection.

Fishes K and O together reacted strongly in the same way.

Four days later the three fish were put together in a clear tank. The mirror was stood up against the vertical outlet pipe for half an hour, but during this period the fish paid little attention to it. They were not attracting each other to any extent and passing the edge of the mirror was not sufficient stimulation to make them turn back to their reflections. It was noticeable that, on swimming past the mirror, they almost invariably wheeled and swam round behind the outlet pipe. Again, when, immediately after, the mirror was stood across the space behind the outlet pipe facing the side walls, the fish spent little time in front of it.

In contrast to this, three days afterwards it was observed that the three fish together reacted readily to the mirror. At first the tank was clear ; it was then partly divided down the middle by a glass partition as in Figure 10, the mirror being placed against the right side wall. At first there was only one fish in the right half, but very soon afterwards all three were on the right in front of the mirror.

These last examples provide an illustration of how behaviour is apt to vary from one occasion to another.

As a rule, however, it may be said that the small 3- and 4-in. fish react in a very decided fashion.

5.

Many further instances were obtained showing the attraction exerted by the mirror on individual fish. The behaviour exhibited by them was always essentially of the kind described above.

Tests were also made on a group of about twenty fish and the reactions of individuals were seen to be of the same definite character.

6.

In connection with the appreciation shown by the fish for their reflection, their behaviour with respect to reflecting surfaces lying on the floor of the tank has some bearing.

To a *plain mirror* reflecting light upwards the fish react in a most distinct and peculiar way. They swim over the glass, with the axis of the body tilted upwards (sometimes practically upright !) and snout close against the surface, in a rapid zigzag motion. They keep within the confines of the area of the mirror, turning inwards on reaching the edge.

To a *piece of dark glass*, lying on the floor of the tank or up against a sloping face of glass, they react in a like manner, but not so intensely. A distinct reflection is appreciable to the human eye.

To a *piece of plain glass* lying on the floor of the tank, a similar reaction is given, but it is far less decisive. There is still some sort of reflection in this case.

To a piece of plain glass tilted so that one end is raised and the other rests on the floor of the tank, there is no reaction. Reflection appears to be absent in this case.

To a piece of silver paper (which had previously been crumpled) lying under a piece of glass on the floor of the tank, there is even less reaction —when indeed there is any—than to plain glass alone.

The evidence of these facts indicates strongly that the mirror reflection is the essential element in the situation which evokes this characteristic behaviour. It is not merely the smoothness of the surface—a tilted piece of plain glass does not produce any reaction at all. The effect of dark glass shows that brightness is not essential, and of silver paper that brightness alone is ineffectual. Smoothness and brightness being thus eliminated, it must be concluded that the actual reflection of the fish, or some general characteristic of it, is concerned. The positive evidence for this is that the intensity of the fish's reaction decreases with decrease in clearness of the reflection.

7.

These, then, are examples of cases in which bass were observed to behave in a distinct manner when in the presence of a mirror. This behaviour is comparable in kind and intensity to that towards other fish behind a glass partition. This serves to show—even in the absence of other evidence—that in this species vision plays a leading rôle in schooling. The reflection calls out the same reactions as would real fish under similar circumstances. It "stimulates schooling reactions"; it creates a "schooling situation."

As far as the actions of individuals are concerned, they are nevertheless apt to vary in intensity from one occasion to another and are far from automatic. They vary even with the fish's activity. Indeed, on the whole, though the type of behaviour is characteristic enough, there is no definite cut-and-dried reaction which could be used as a basis for detailed experimentation.

B. *General power of attraction of a mirror as determined by comparison of average positions of the fish.*

1. Single fish.

For this test a fish was specially chosen which was hardly appreciably reacting to its reflection and which, to all appearances, was scarcely attracted to the mirror at all. An attempt was made to compare the frequency with which the fish was positioned in front of the mirror with that in front of a plain glass with similar background. The fish never lay for any length of time in front of the mirror; could it be shown that it was more frequently in front of the mirror than in front of a similar patch of plain glass ?

The glass plates were arranged as in Figure 8. The front 28-in. plate was covered with black paper (kept in place with elastic bands) leaving two square openings, each 14 × 13 cm. A mirror is placed behind one of these and the other space left clear. The reflected background is very similar to the actual background seen through the clear space.

The frequencies of the occurrence of the fish in front of the two spaces are compared with one another. By this means an indication may be given as to whether the presence of the mirror makes any difference.

The fish is rather sluggishly disposed and shows little definite reaction to the mirror. Hence if any results are obtained from it, other fish should give more decisive results.

During the period this fish was being observed, a note was made every time it was seen in front of one of the spaces (irrespective of the reaction to it) or in the region between, and this was indicated in the accompanying table by a +. The time is divided up into $\frac{1}{4}$-hour periods, in each of which no more than one + is available for any one column.

The results obtained were as follows :—

		Plain glass.	Region between.	Mirror.
6.viii.30	9–9.15 a.m.	–	–	+
	9.15–9.30	–	+	+
	9.30–9.45	–	+	–
	9.45–10.0	–	–	–
	10.20	–	–	–
	10.45	–	–	–
	12.0–12.15 p.m.	–	+	+
	12.30–12.45	–	–	+
	12.45–1	–	–	–
	2.45–3	–	–	–
	5.45–6	–	–	+
	6–6.15	–	–	–
7.viii.30	9.45–10.0	–	–	+
	11.15–11.30	–	–	+
	12.0–12.15	–	–	–
	3.0	–	–	–
		(Mirror changed over)		
	3.45–4.0	+	–	+
	4.0–4.15	–	+	+
	4.15–4.30	–	–	–
	4.34	–	–	–
	5.10	–	–	–
8.viii.30	8.45–9.0	–	+	+
	9.15–9.30	–	–	+
	9.30–9.45	–	+	+
	10.15–10.30	–	+	+
	10.45–11.0	–	+	+

		Plain glass.	Region between.	Mirror.
	11.0–11.15	+	+	+
	11.15–11.30	−	+	−
	11.30–11.45	+	−	−
	11.45–12.0	+	+	−
	12.0–12.15	−	+	−
	12.15–12.30	−	+	−
	12.30–12.45	−	+	−
	1.15–1.30	−	+	−
	8.30 p.m.	−	+	−
	8.45–9.0	−	+	+
	9.0–9.15	−	−	−
11.viii.30	9.30–9.45 a.m.	−	−	+
	11.15–11.30	−	−	−
	11.45–12.0	−	+	+
	12.45–1.0	−	−	−
	2.30–2.45	−	−	+
	3.0–3.15	−	−	+
	3.30–3.45	−	−	+
	(Mirror changed over)			
	4.15–4.30	−	+	+
	5.0–5.15	−	−	+
	5.15–5.30	+	−	−
	5.30–5.45	−	−	+
	8.30–8.45 p.m.	−	−	+
	9.0–9.15	−	−	+
	9.15–9.30	−	−	+
	Total	5	19	27

The figures representing Mirror : Space between : Plain glass are 27 : 19 : 5, showing a very decided balance in favour of "Mirror"—there is a greater probability that the fish will be in front of the mirror than in front of the plain glass.

2. Aggregate of fish.

With a number of fish in the tank an attempt was made to show that the presence of a mirror would affect their distribution, i.e. if the mirror were placed at one end there should be, on the average, more fish in that half of the tank than in the other.

For this purpose the tank was divided down the middle with a glass plate, leaving a gap just in front of the peephole (Fig. 10). The tank was that used in preliminary tests, with no hood or any special precautions for rendering the observer invisible.

There were 21 fish of between 6 and $7\frac{1}{2}$ in. in the tank. They moved about the tank on the whole quite actively, and when left to themselves soon equalised their numbers in the two halves. At intervals the numbers in the two sides were counted, observation being made through the peephole. Owing to the observer's presence, the fish would no longer swim to and fro in the connecting space ; so the numbers in either part of the tank could be counted at leisure. For the most part it was sufficient to count the fish in that part of the tank in which there were least.

The distribution of this group of fish in the two halves of the tank is represented graphically. Figure 11 (*a* and *b*) shows normal condition, the fish being distributed with equal probability of preponderance in either half. Figure 12 (*a* and *b*) shows the effect of a mirror standing up against one of the side walls.

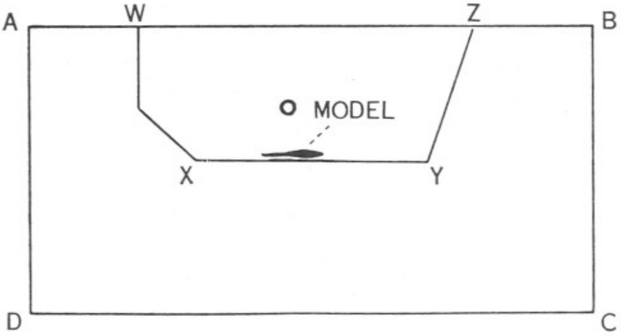


Fig. 9.

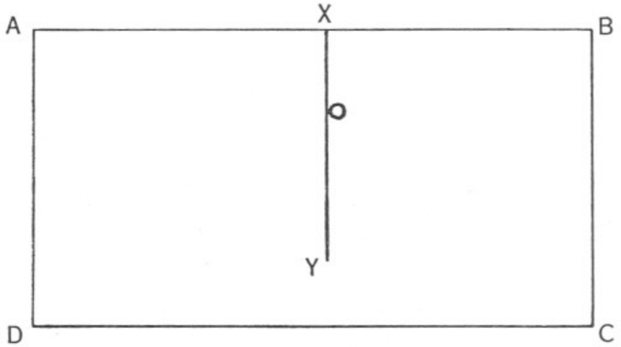
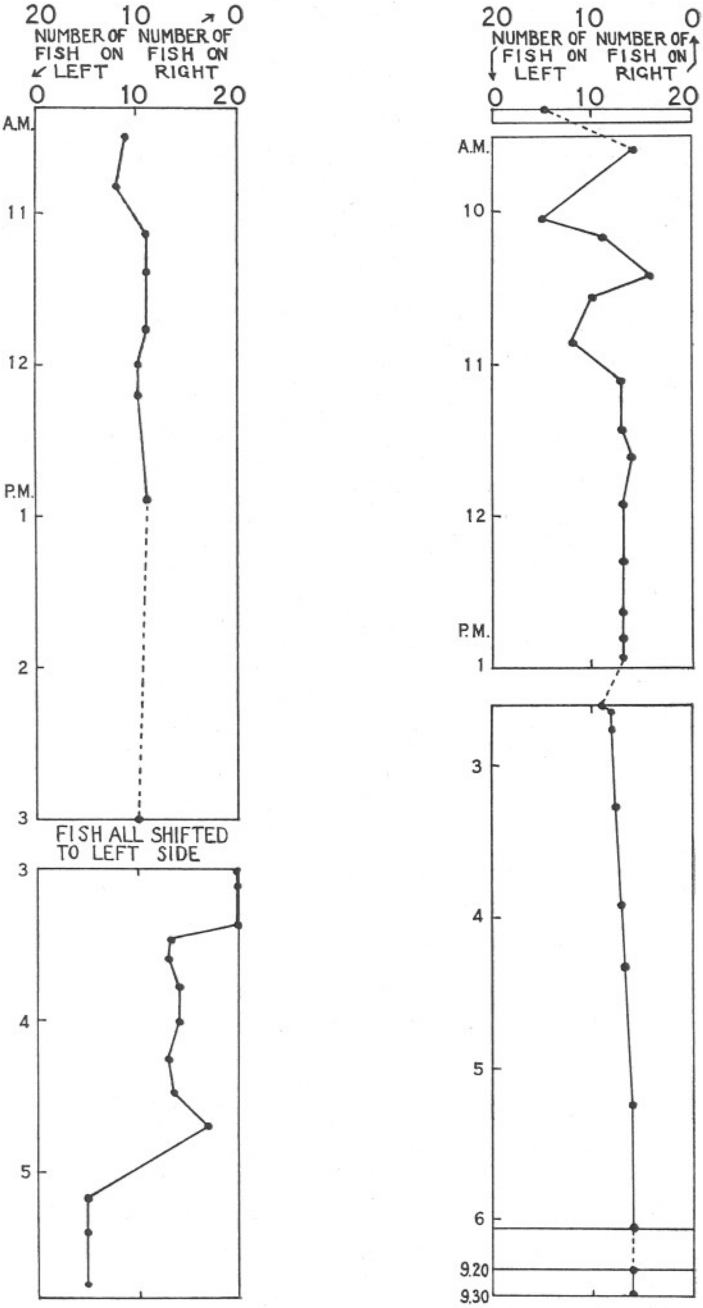


Fig. 10.

Figs. 9–10.—For description, see Fig. 1, pages 427, 428.

There is a clear distinction between the two cases. The results show : (*a*) the probability of a larger proportion of fish in that half of the tank which contains the mirror ; (*b*) the marked change in distribution following the change of the mirror from one side to the other.

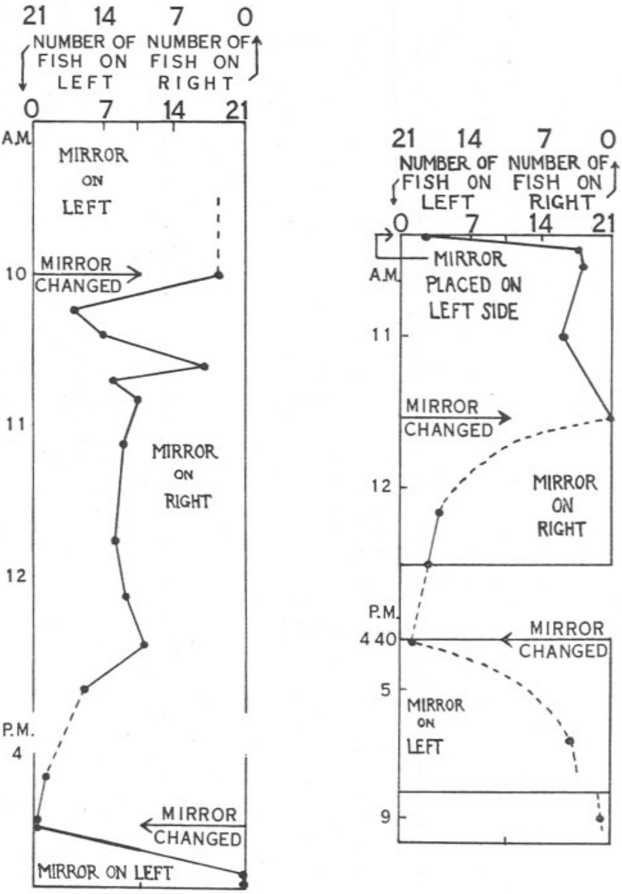


a. *b.*

Fig. 11.—Graphs showing the distribution of a party of 20 or 21 fish in the two halves of a tank arranged as in Fig. 10. Two examples of the normal type of distribution.

The Main Attributes of That which induces a Schooling Response.

A bass is attracted towards another of its kind separated by a glass partition; it is attracted by its own reflection in a mirror. It may be asked, what are the essential characters in the object of attraction as distinguished by the fish? Even granted that it is the "general appearance" as a whole which is significant, it may still be asked what are the main elements which contribute to the general resemblance—whether form, or movement, or pattern.



a. *b.*

Fig. 12.—Graphs showing the distribution of a party of 20 or 21 fish in the two halves of a tank arranged as in Fig. 10. The effect of placing a mirror on one side and periodically changing it.

It was found that the fish will be attracted to, and lie alongside, a dead fish supported by glass in the position of a resting live fish.

The tank was fitted as shown in Figure 9. Two fish were in front of the glass. A dead fish supported in a glass jar was placed in the position ("MODEL") previously occupied by a mirror to which the fish had reacted well. (The tank was subjected to considerable disturbance while the arrangement was being fitted up.)

26.x.29	Mirror in position	Fish in region before mirror.	
28.x.29 10 a.m.	Dead fish in place of mirror	Fish quiet in region of CD	? Interval while effects of disturbance wore off.
11.45	,, ,, ,, ,,	,, ,, ,, ,,	
12.20	Mirror in front of dead fish		
12.45 1.0	,, ,, ,, ,,	Fish not in front of mirror	
2.10	Mirror removed, dead fish exposed to view	Both fish by mirror, but disturbed by the removal of it.	
2.30	,, ,, ,, ,,	Fish in region of CD, not by dead fish.	
2.59	,, ,, ,, ,,	Both fish lying up against dead fish, all facing in the same direction.	
2.59 to 4.5 continuously	,, ,, ,, ,,	All this time the fish were lying up against dead fish, quiet. Sometimes orientated in some direction, sometimes in opposite, sometimes both differently.	
4.15 to 4.32	,, ,, ,, ,,	Fish away from dead fish in L. centre of the tank.	
4.43	,, ,, ,, ,,	At least one fish by dead fish.	
5.20 5.23	,, ,, ,, ,,	Both fish lying by dead fish.	
29.x.30 9.5 10.0	,, ,, ,, ,,	Through this period the fish were lying against dead fish, all orientated in the same direction.	
10.10	Dead fish removed.		

On another occasion a similar experiment was repeated with similar results.

This shows clearly enough that the fish are attracted by the form of another fish, although it is completely devoid of movement. Hence movement of fins, for instance, is not an essential item.

Following on the experiment outlined above, several kinds of rough models were tried. One type bore the exact shape of the fish and was painted green, another of plasticene with a roughened surface, another a piece of bent tinfoil shaded dark in the upper half. The fish were attracted by none; when they were too conspicuous the fish were definitely repelled. And it is scarcely surprising, for however much the models resembled fish in the air, under the water they stood out all too crudely. Little success was attained in getting a uniform lighting and still less in avoiding a harsh contrast with the background.

Still, it is at least an indication that the fish require an object that closely resembles a fish, the general shading and contrast between it and the background being important.

REACTION TO MIRRORS USED AS A BASIS FOR FURTHER EXPERIMENTS.

The fact that a fish will react, in a manner indicated above, towards other fish like itself might provide a starting-point for experiments to determine how far variation in the properties of the object to which reaction is made affects the results. For instance, what is the effect of cutting down the size of the space through which the object—whether another fish or mirror reflection—is viewed ? How much of the fish or image is necessary ?

Unfortunately the reactions of the fish to each other and to a mirror are not sufficiently cut-and-dried to provide a basis on which accurate comparisons can be drawn. It has been seen that the reaction of an individual fish to a plain mirror may vary considerably. For any given fish it is impossible to predict definitely how it will behave, but it is possible to say how it will most probably behave or the probable intensity of its reaction, especially if its condition is not abnormal. But it is not possible to measure this probability. Hence, in comparing the behaviour of an individual fish to a less efficient mirror or a less complete image, the comparison cannot be expressed at all accurately. All that can be said is that " the reaction on the whole appears less intense in this case than that " or " the probability for a certain reaction appears less in this case than that."

The nearest approach to a definite form of behaviour is seen in the case of a single fish in the presence of a mirror. It is strongly attracted to the mirror and spends much time in front of it. It is possible, therefore, to compare, as is attempted below, the behaviour of the fish towards various sizes of mirror exposure or various types of broken surface. But allowance must be made for greater variation in behaviour to less definite* situations

The method whereby the distribution of a number of fish gives statistical comparison (see pp. 441 and 442) does not lend itself for more refined application. It is adequate for showing the difference between " mirror " and " no mirror," but a glance at the figures is enough to show what little scope there is for expressing finer distinctions.

One attempt was made with the mirror covered over with black paper except for a slit $\frac{1}{2}'' \times 10''$. This had no effect on the grouping of the fish.

Consideration of such a statistical method shows that, even if the school is large enough (which it isn't) to eliminate individual variations, there is no reason why the mean value of the " state " of the fish should remain a normal constant. If the " state " of one fish changes, it is very likely that other fish for the same reasons will be changing in the same way. Hence the mean value, as it were, will shift. It must also be remembered that

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* i.e. situations in which there is less contrast.

reaction to a mirror belongs to those set of reactions which keep the school together. Hence both reactions will interfere with each other; particularly will the presence of other fish decrease intensity of reaction to the mirror.

Reaction of fish to small areas of mirror.

With a view to obtaining evidence on how complete an image is necessary to bring out the kind of behaviour described in earlier paragraphs, the fish were presented with exposures of mirror of various sizes. These were obtained by covering over a mirror with black paper out of which a piece of the required dimensions had been cut. The reflections of the fish, therefore, came to view as though through a gap in a black upright partition.

The results of observations are summarised as follows :—

	Whole Mirror.	Section ½ in. × 10 in.	Whole Mirror.	Section ¼ in. × 10 in.
Small fish K, L, & O	Reacted well.	One fish reacts strongly, but is more attracted by the other fish.	Reacted well.	No reaction at all: apart from certain slight changes in their actions which might be the result of having detected movement.

	½ in. × 10 in.		1 in × 10 in.	1 in. × 2½ in.
	Various individuals have been observed to react to this slit, but has no statistical effect on a group of fish.			
Fish M 6¼ in.	Small fish in tank as well. Reacted to reflection, but more attracted by young fish.	Alone. Reacted fairly well and lay up against it for some time.	Reacted as to full mirror.	Reacted very well. A good contrast in behaviour towards a similar exposure of plain glass.

	1 in. × 1 in. Exposure.
Fish N about 6 in.	Though watched over several days, never reacted at all.

As far as these tests go, it is clear that a complete image is not necessary, but it seems that it must be nearly complete. An eye alone or the head alone appears to exert no attraction. Furthermore, it must be remembered that the measure of the size of the exposure is no measure of the dimension of the image: when the eye is close to the aperture the field of view is extensive.

Reactions to a broken mirror surface.

One or two observations were made on the reactions of individual fish to a broken area of mirror surface. The mirror was covered with elastic bands, ¼ in. wide, spaced at definite intervals, running both across and along the surface. This gave a meshwork with small sections of mirror showing in between.

The following results were obtained from three small active fish (K, L, and O) which reacted well to a full mirror.

	Bands $\frac{3}{4}$ in. apart.	Bands $\frac{3}{8}$ in. apart.	Bands $\frac{1}{4}$ in. apart.
3 small fish, K, L, & O.	Definite reaction and fish spent some time lying against it.	Some sort of reaction but it was weak. Not attracted.	Scarcely reacted. Not attracted.

Another test showed that a number of fish will group in front of a mirror with a $\frac{3}{4}$-in. meshwork in the same way as in front of a partition of plain glass with similar meshwork through which other fish are visible beyond.

Experiments with banded mirrors were not continued because it became obvious that the results obtainable, unless possibly continued for an inordinately long time, were vague and of little value. When the bands were $\frac{1}{4}$-in. apart it could be seen that the fish on passing exhibited slight changes in their behaviour actions, and since bass are very sensitive to movement in the visual field it is not unreasonable to suppose that the movement of their reflection had effect on them. Movements of this kind are apt to attract the fish, no doubt because they are associated with "food situation." At what point is one entitled to distinguish between this type of attraction and that which produces a schooling response ? One must pay attention to those reactions which are different in the two situations, i.e. in one case there is the tendency to remain near or lie still against the source of attraction, in the other case there is none. When the whole reaction becomes so indefinite that these actions do not appear for certain, distinctions can no longer be drawn.

III. APPLICATION OF RESULTS TO THE SCHOOLING PROBLEM.

We have now to consider in what respects the data so far obtained bear on the problem of school formation for the particular case of the bass, and may therefore summarise them under the headings set down in the introduction (p. 423).

1 (*a*). With the bass, we have not been concerned with maintenance of school formation by a party of active fish moving from place to place. Within the confines of a laboratory tank schooling phenomena were limited to the grouping together of the few individuals under observation, particularly when in a resting or not very active state. The actions of individuals, however, which bring about the grouping in a tank, are at least connected, if not identical, with those which concern school formation under natural conditions.

The following are the kinds of actions which were observed. Movement towards other individuals (or one individual) up to within a certain short distance ; movement towards and stopping close besides resting individuals ; the pursuit of another individual on the move ; orientation in the same direction as other individuals, either moving or resting ; change of direction of movement following change in the course of another fish ; movement instigated at the appearance of a moving fish ; speed of movement adjusted to that of other fish.

(*b*) The aspect of the environment concerned in these actions involves some kind of visual image in which undoubtedly shading, shape, and other spatial relations are distinguished. For evoking schooling behaviour movement is not essential, and a complete image is not essential.

(*c*) Results are sufficient to show that sight is the predominant, if not the only, sense involved ; but no experiments in sense physiology have been made to find what visual distinctions are most appreciated or what degree of refinement is exhibited.

2. It has been seen how bass in a tank are prone to group together, and, if separated, to move towards each other.

(*a*) They group more readily when disturbed or alarmed, and least when hunting for food. Small 3- and 4-in. fish will group with larger 6–7-in. fish, but not the larger with the smaller.

(*b*) The behaviour is variable, particularly in intensity, and cannot be profitably expressed on the basis of a simple tropism or system of tropisms. Since it clearly varies with the state of the fish, prediction of readiness to school cannot be made unless the state of the fish can be described.

(*c*) Two fish placed in a tank by themselves will keep fairly well together, but, if moving about actively, or engaged in feeding, or when signs of depression set in, their movements may be all but independent of each other. Inducing schooling experimentally goes no further than placing a fish which has a natural tendency to school under just those conditions which are normally required for schooling behaviour !

My best thanks are due to Dr. E. J. Allen particularly for suggesting this line of work and for the readiness with which he has given his valuable help and advice during the course of it.

SUMMARY.

1. Among schooling fish, the younger stages of the bass (*Morone labrax*) provide an instance in which the schooling habit, though strong, is not stereotyped into fixed forms of behaviour.

2. Observations were made on individual fish in connection with their attraction for one another, a special point being made of observing their behaviour in front of a mirror.

3. The data so obtained are summarised in the light of their bearing on the problems of school formation.

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The Validity of Single Vertical Hauls of the International Net in the Study of the Distribution of the Plankton.

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With 2 Figures in the Text.

PLANKTON studies, to be of direct application to fishery problems, should be of such a kind as to enable comparisons to be instituted between the fluctuations in a fishery and those in the plankton itself. But the collection of data on such a scale raises a whole host of difficulties, not the least of these being the degree to which a single haul of a vertical net—a method with much to recommend it—can be considered to yield a representative sample.

In 1922 the late Sir William Herdman (**1**), using a Nansen net, showed, for the waters off the Isle of Man, that " . . . conclusions drawn from any one haul might be anything up to 50 per cent wrong in either direction."

In 1925 Gardiner and Graham (**2**) described an experiment on the same lines, but using in this case a Petersen Young Fish Trawl, which net, they found, compared favourably with the so-called quantitative net employed by Herdman. But, in both cases, the fact emerged that the catches of successive hauls in the same limited area differed considerably from one another, the spread measured by the Standard Deviation being in the nature of $\pm 50\%$ of the mean. In order to see whether this does represent a fair figure, two series of consecutive hauls made during 1926 have been examined. Both the collection of the material, and the subsequent enumeration were the work of Mr. R. E. Savage, to whom I am greatly indebted for permission to make use of them. My thanks are also due to Mr. Michael Graham and others of my colleagues at Lowestoft, and particularly to Mr. Edser of the Ministry's Statistical Section, to whom I am indebted for many helpful suggestions. The net used was the International Net (**3**), of No. 3 silk (60 meshes to the inch), fished vertically by the Wollaston method (**4**).

In the first experiment 40 hauls were made during the course of the night May 31st–June 1st, 1926, whilst drifting in an area centred on a position about 15 miles E.½N. from the Tyne (Lat., 55° 5′ N.;

Long., 1° 0′ W.). The wind was westerly and light (Force 2 on the Beaufort Scale=approx. 5 m.p.h.), and the sea smooth. Soundings varied during the experiment, the nets being fished from 62–80 metres to the surface. The first haul was made at 1755, and the last at 0951, G.M.T. The duration of each haul, in seconds, was measured by means of a stop-watch.

In the forty hauls copepoda comprised from 70–95% of the total catch, the mean being 86%. The dominant species were *Pseudocalanus elongatus* and *Paracalanus parvus*, which for our present purpose have not been separated. The next two species in order of abundance were *Temora longicornis* and *Calanus finmarchicus*. Of non-copepoda, the only species that occurred regularly in fair quantities were Oikopleura spp., but the numbers were not large.

The second experiment comprised 38 hauls of the International Net made some three weeks later during the night of June 24th–25th, 1926, in an area centred on a position about 16 miles E.½N. from the Tyne (Lat., 55° 4′ N.; Long., 0° 57′ W.). The wind was northerly and stronger than before (Force 3 on the Beaufort Scale=approx. 10 m.p.h.). The sea was "slight to moderate" (3–4). Soundings remained fairly constant, and all hauls were made from a depth of 70 metres to the surface. The first haul was made at 2023, and the last at 0750, G.M.T.

Copepods were both absolutely and relatively more abundant, comprising about 94% of the plankton captured by the net. Oikopleura spp. were no longer common. Sagitta spp. were regularly present, but the numbers again were not large.

For the enumeration of the catch in the Laboratory, a Hensen Stempel-pipette was used, and two, or more, separate samples were counted in the majority of cases, the factor being, usually, 50.

The numbers per metre depth of the selected organisms are set out in Tables I and II. The time at which each haul was made (in G.M.T.), the depth from which the net was fished, and the speed of hauling expressed as seconds per metre are included. For convenience in studying the tables, those observations lying close to one another in time are enclosed by brackets.

Before these data can be applied to the question before us, namely, to determine the reliability of a single haul of a vertical net, it is necessary to examine the conditions under which they were obtained. Both series of successive hauls were made from a drifting ship, and the time interval between the first and last haul was in one case about 16 hours, and in the other about 12 hours. There is no information as to the area of sea surface covered during the course of these experiments, but it must have been considerable. Further, owing to the wind, under the influence of which the vessel would tend to move independently of the main body of water, and to changes in level of the various species of the plankton, due

TABLE I.

First Experiment, May 31st/June 1st, 1926.

Times, Speeds, and Numbers per metre depth of Selected Organisms.

Haul No.	Time.	Depth.	Speed secs/metre.	Calanus.	Temora.	Pseudo-calanus + Para-calanus.	Total organisms.
1.	1755	80	1·3	6	21	12	50
2.	1805	80	1·1	14	37	22	80
3.	1820	80	2·0	12	29	27	80
4.	1825	80	1·9	2	9	12	46
5.	1940	80	1·8	18	26	32	93
6.		80	1·7	13	28	47	104
7.	1950	80	1·4	6	24	17	65
8.	2058	80	1·8	13	28	25	80
9.	2310	62	2·3	8	23	16	72
10.	0014	62	2·7	7	15	31	65
11.	0139	65	2·5	11	24	22	69
12.	0225	65	2·1	17	27	25	82
13.	0320	70	1·7	14	41	36	118
14.	0415	70	1·7	7	26	65	112
15.	0510	80	1·4	11	20	23	82
16.	0620	60	2·1	16	34	30	92
17.	0627	80	1·5	27	50	35	134
18.	0630	80	1·9	15	25	24	72
19.		80	1·8	20	45	29	110
20.	0647	80	2·2	32	62	61	180
21.	0650	75	2·0	38	44	42	142
22.	0655	75	1·5	5	32	27	85
23.	0700	80	1·7	28	27	51	120
24.		*80**	1·7	8	30	31	80
25.		*80*	1·7	35	38	57	168
26.		80	1·6	10	23	33	79
27.		80	1·7	7	21	16	51
28.		75	—	23	33	29	93
29.		80	1·7	13	25	24	70
30.		75	1·8	9	20	19	54
31.		*75*	—	7	29	23	65
32.		70	1·6	17	32	30	97
33.	0908	65	1·8	10	20	25	72
34.	0912	65	1·6	5	13	18	46
35.	0916	65	1·7	8	37	55	130
36.	0923	65	1·6	8	23	28	78
37.	0929	65	1·6	12	14	36	79
38.	0934	65	1·5	11	16	30	66
39.	0939	65	1·6	6	17	26	76
40.	0951	65	1·6	6	25	19	58

* Depths in italics are interpolated, the actual depths having been omitted from the records.

TABLE II.

Second Experiment, June 24th/25th, 1926.

Times, Speeds, and Numbers per metre depth of Selected Organisms.

Haul No.	Time.	Speed secs/metre.	Calanus.	Temora.	Pseudo-calanus + Para-calanus.	Total organisms.
1.	2023	1·9	56	22	47	146
2.	2200	1·6	69	13	61	174
3.	2205	1·8	46	15	55	198
4.	2220	1·8	37	8	84	141
5.	0125	2·1	36	19	47	112
6.	0130	1·9	25	15	66	122
7.	0137	1·9	98	44	159	355
8.	0145	1·9	64	38	51	219
9.	0155	2·0	58	20	112	232
10.	0245	2·0	92	15	111	261
11.	0254	2·1	139	26	132	332
12.	0305	1·9	139	28	142	359
13.	0315	2·2	95	31	193	380
14.	0323	2·0	155	50	134	379
15.	0350	2·0	95	36	169	352
16.	0355	2·0	159	61	139	444
17.	0402	2·3	156	43	206	492
18.	0408	2·3	150	49	208	496
19.	0415	2·2	166	57	237	544
20.	0420	2·1	91	46	229	406
21.	0426	2·3	116	39	—	446
22.	0433	2·3	101	43	161	367
23.	0500	2·1	89	46	73	246
24.	0507	2·0	111	59	77	275
25.	0515	2·3	72	61	102	279
26.	0520	2·1	90	30	89	265
27.	0525	2·1	108	45	154	356
28.	0532	2·3	119	47	—	308
29.	0535	2·3	151	53	132	384
30.	0645	2·3	104	44	192	394
31.	0700	2·3	101	71	154	352
32.	0708	2·4	146	84	231	539
33.	0712	2·4	113	74	199	458
34.	0720	2·4	115	62	137	365
35.	0730	2·4	111	58	234	461
36.	0736	2·4	143	44	169	404
37.	0745	2·2	114	50	151	381
38.	0750	2·4	102	47	164	391

to their own vertical migrations, it would be unwarrantable to assume that the same population has been sampled throughout the course of either experiment. Accordingly, to consider either series of experiments as a unit for subsequent statistical treatment would be to produce, in all probability, a false idea of the variation in numbers of individuals caught in successive hauls, and would tend unduly to lessen the degree upon which a single haul of a vertical net is to be relied. For this reason, then, although the full data for each experiment are given in Tables I and II, a certain proportion only has been utilised. The choice has been regulated as follows : No group of observations covers more than 1 hour ; no hourly group comprises less than 5 observations ; the observations within any group are not separated from one another by more than 12 minutes.

If Tables I and II are examined it will be seen that there are considerable variations in the catches of successive hauls, even where the time interval is short. The extent of this variation is most conveniently given by determining the mean number of individuals caught in groups of successive hauls, selected as above, and expressing the departure of each observation from this mean as a percentage deviation. These groups are shown in Tables I and II enclosed in brackets. The mean number of individuals captured in each group of observations has been called throughout the " group mean." In order readily to compare the extent of the variation within any one group with that in another, the Average Deviation within each group has been calculated.

The selected data treated in this way are set out in Tables III and IV.

It should be noted at this point that the whole of the variation between catches of successive hauls has apparently been assigned to the variability of the organisms themselves, and not to errors of the methodique. As will be seen later, this is in the main correct, the effect of such contributory errors as variations in the speed of hauling, the part played by light and darkness on the catching power of the net, and the magnitude of the enumeration error, being insufficient to account for the variation observed. The evidence in support of this is collected in an appendix, since by reason of its bulk it might otherwise appear to be the main burden of this paper.

By treating the data in such a way that the variations in the numbers of the more abundant species caught within periods of not more than one hour's duration are related to the mean of the period—the group mean—the observations are directly comparable one with another despite the fact that the density of population may be quite different. In this way, too, it may be possible to utilise observations from the two experiments as a unit for statistical treatment, if it can be shown that the degree of variation within the several groups is of about the same order of magnitude. Further, it may even be possible to consider all the species together.

TABLE III.

FIRST EXPERIMENT. PERCENTAGE DEVIATIONS OF SELECTED OBSERVATIONS FROM THE MEANS FOR THE PERIODS IN WHICH THE OBSERVATIONS WERE MADE, AND AVERAGE DEVIATION FOR THE PERIOD.

		Percentage Deviations from Group Means of :—		
Haul No.	Times.	Calanus.	Temora.	Pseudo- + Paracalanus.
16		30	15	19
17		17	25	5
18		35	38	35
19	0620	13	13	22
20	to	39	55	65
21	0700	65	10	14
22		78	20	27
23		22	33	38
Group Mean		*23*	*40*	*37*
Average Deviation		37%	26%	28%
33		25	5	17
34		38	38	40
35		0	76	83
36	0908	0	10	7
37	to	50	33	20
38	0951	38	24	0
39		25	19	13
40		25	19	37
Group Mean		*8*	*21*	*30*
Average Deviation		25%	28%	27%

N.B. The Group Mean from which the percentage deviations have been calculated is shown in italics.

TABLE IV.

SECOND EXPERIMENT. PERCENTAGE DEVIATIONS OF SELECTED OBSERVATIONS FROM THE MEANS FOR THE PERIODS IN WHICH THE OBSERVATIONS WERE MADE, AND AVERAGE DEVIATION FOR THE PERIOD.

		Percentage Deviations from Group Means of:—		
Haul No.	Times.	Calanus.	Temora.	Pseudo- + Paracalanus.
5		36	30	46
6	0125	55	44	24
7	to	75	63	83
8	0155	14	41	41
9		4	26	29
Group Mean		*56*	*27*	*87*
Average Deviation		37%	41%	45%

		Percentage Deviations from Group Means of :—		
Haul No.	Times.	Calanus.	Temora.	Pseudo- ± Paracalanus.
10		26	50	22
11	0245	12	13	7
12	to	12	7	0
13	0323	23	3	36
14		25	67	6
Group Mean		*124*	*30*	*142*
Average Deviation		20%	28%	14%
15		26	23	12
16		23	30	28
17		21	9	7
18	0350	16	4	8
19	to	29	21	23
20	0433	29	2	19
21		10	17	No observation
22		22	9	17
Group Mean		*129*	*47*	*193*
Average Deviation		22%	14%	16%
23		16	6	30
24		5	20	27
25	0500	32	24	3
26	to	15	39	15
27	0535	2	8	47
28		12	4	No observation
29		42	8	26
Group Mean		*106*	*49*	*105*
Average Deviation		18%	16%	25%
31		14	16	14
32		24	38	28
33		4	21	11
34	0700	3	2	24
35	to	6	5	30
36	0750	21	28	6
37		3	18	16
38		14	23	9
Group Mean		*118*	*61*	*180*
Average Deviation		11%	19%	17%

In order to answer these points, the averages of the deviation within each group have been collected together in Table V, and the values examined from the following points of view :

(*a*) Does any one species exhibit throughout a greater tendency to vary than any other ?
(*b*) Is the degree of variability greater during any one period ?
(*c*) Is the degree of variability more marked in either experiment ?

TABLE V.

COMPARISON OF SPREAD, EXPRESSED AS AVERAGE OF THE DEVIATIONS OF THE SELECTED OBSERVATIONS FROM THE GROUP MEANS.

Species.	Spread within each of the selected periods in the two experiments.							
Calanus	1st Experiment :			37%			25%	
	2nd Experiment :	37%	20%		22%	18%		11%
Temora	1st Experiment :			26%			28%	
	2nd Experiment :	41%	28%		14%	16%		19%
Pseudo-+ Paracalanus	1st Experiment :			28%			27%	
	2nd Experiment :	45%	14%		16%	25%		17%

It does not appear that one species exhibits greater variability than another.

During the first period of the Second Experiment, however, the Average Deviations are all bigger than obtained during the course of the remainder. They only differ, however, to a very small extent from those obtaining during the course of the First Experiment. On this account, therefore, there would seem to be no grounds on which any group of observations can legitimately be excluded. Nor does it appear to be unreasonable to treat all the observations as a unit for statistical treatment.

The problem may now be considered as follows : We have 145 attempts to obtain a measure of populations whose true values are given to us by the mean number captured in from 5–8 consecutive hauls of a vertical net. That is to say, we have sampled the population below a small area of the sea surface a number of times by a uniform method, and have determined the amounts by which any single haul differs from the mean of 5–8 hauls. This mean is taken, *faute de mieux,* to represent the actual number of organisms present, and is, in all probability, a close approximation to it. The same result would have been obtained had a special cruise been made, where, instead of the usual single haul at each station, a number of hauls at close intervals of time were taken, and the mean number of individuals used to give the density of population at each station. In view of the variability which has been shown to exist between successive hauls it would probably be desirable always to make up to 5 hauls at each station visited, but to do so would be to reduce the number of stations that could be visited in the course of a routine cruise.

If, however, the chance of a single haul giving a value within so much of the mean can be determined by some such method as that described above, we are enabled to state, with some degree of certainty, whether the resulting picture of the distribution of the plankton is more likely than not to be an accurate one.

In the two experiments under discussion we have been enabled, by the method adopted, to determine what proportion of our 145 observations lie within any desired amount of the mean. The point that arises now is to decide what latitude shall be allowed. To place the standard too low, and to say, for instance, that only those hauls lying within ±10% of the mean will be considered true values, is probably to aim at a degree of accuracy which, it is felt, is neither possible nor necessary. On the other hand, a standard placed at, say, ±50% allows, perhaps, too much latitude, and accordingly it has been placed at 33%. That is to say, any values lying within plus or minus 33% of the mean (or true) value, will be considered as near the truth as is necessary, taking into consideration their mode of collection, enumeration, and the use to which they are put.

The number of observations lying within 10%, 20%, 33% of the mean and the number above this amount are set out in Table VI.

TABLE VI.

FREQUENCY DISTRIBUTION OF PERCENTAGE DEVIATIONS (SIGNS IGNORED) OF ALL OBSERVATIONS FROM BOTH EXPERIMENTS.

Groups. %	Frequency.	Cumulative Frequency.	Percentage Cumulative Frequency.
0–9	33	33	23
10–19	33	66	46
20–33	46	112	77
34–39	13	125	86
40–49	7	132	91
50–59	4	136	94
60–69	4	140	97
70–79	3	143	99
80–89	2	145	100

It will be seen that of our 145 observations 112, that is 77 out of 100, lie within 33% plus or minus of the mean. Of the remainder, 13 out of 33 are within ±40%. Thus, in the area where the two experiments were carried out, it is to be expected that, approximately, four out of every five hauls would give a value which for all practical purposes may be considered a true one. There is, however, the chance of getting values outside 33%, which may be termed extreme values, and, further, that such extreme values as ±90% and even greater may be expected occasionally.

This result shows only limited agreement with that of Herdman (*loc. cit.*), and the question whether the degree of variability in the area where

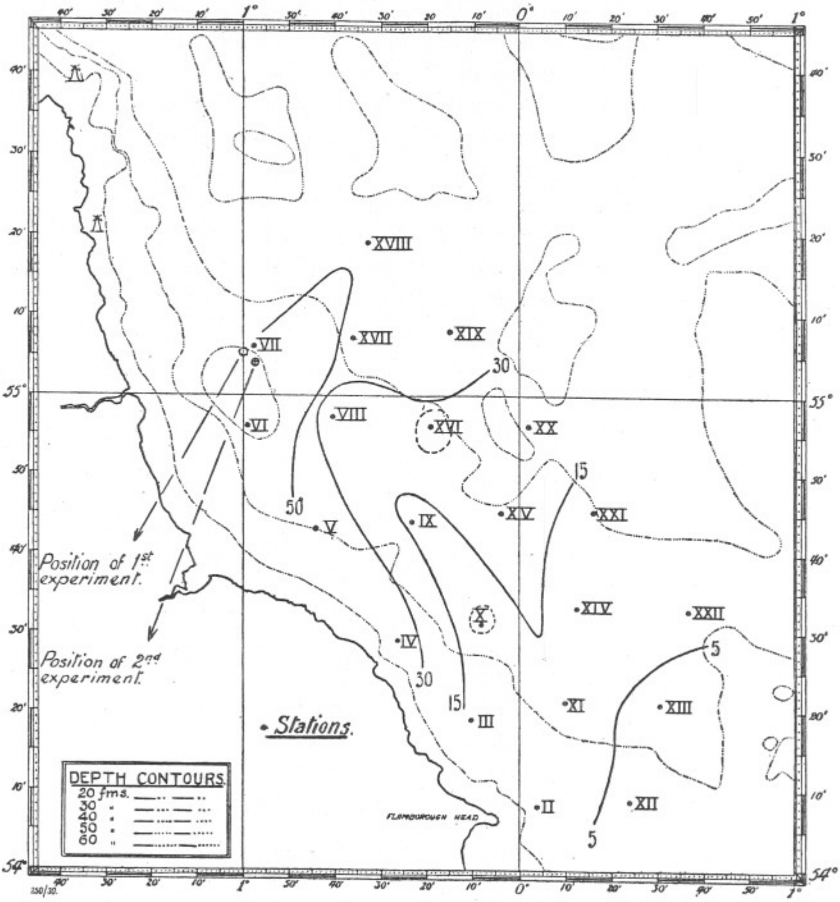

FIG. 1.—Position of Stations on Cruise 28 and Distribution of *Calanus finmarchicus*.

Roman numerals are station numbers. The distribution of Calanus is shown by contours according to the numbers per metre in a vertical haul. The observations of Stations X and XVI have been disregarded (see text, p. 461).

the experiments were performed *is peculiar to the area* must now be examined. In order to do so, the results obtained from a routine plankton cruise have been examined. The cruise selected (Number 28) was made immediately on the completion of our second series of experiments, and extended from June 26th–29th, 1926. At each of the twenty-one stations a haul was made with the International Net (No. 3 Silk), fished vertically; horizontal hauls at 10-metre intervals from the surface to the bottom, with the same net, were taken at the eleven even-numbered stations, II, IV, VI, etc., and hauls of the Petersen Young Fish Trawl, fished obliquely for 30 minutes from (near) the bottom to the surface, were taken at the ten odd-numbered stations, III, V, VII, etc.

The position of the stations worked is shown in Figure 1. It will be seen that they lie on four lines roughly parallel to the coast. The numbers of one species (*Calanus finmarchicus*) per metre depth caught in the 21 hauls of the vertical net are given in Table VII.

TABLE VII.

NUMBERS PER METRE DEPTH OF CALANUS TAKEN IN VERTICAL NETS ON THE ROUTINE CRUISE OF JUNE 26TH–29TH, 1926, AND MEAN NUMBERS AT EACH STATION OF HORIZONTAL HAULS AT 10-METRE INTERVALS.

	CALANUS.	
Station No.	Nos. per metre vertical.	No. per Haul horizontal.
II	8	715
III	13	
IV	39	7,560
V	33	
VI	72	42,484
VII	46	
VIII	24	3,167
IX	12	
X	3	4,791
XI	10	
XII	3	820
XIII	1	
XIV	8	1,100
XV	27	
XVI	2	4,675
XVII	39	
XVIII	40	9,788
XIX	38	
XX	19	3,306
XXI	8	
XXII	8	750

If this Table is studied in connection with Figure 1, it will be seen that the numbers of Calanus increase as we go from south to north, reaching a maximum at Station VI. The species remains fairly abundant at Stations VII and VIII, but declines thence as we go again to the southward. Turning now at Station XIII, and running northwards further offshore, the numbers rise with one exception till Station XVIII is reached. Going south again from here, Station XIX, the second on our last line, shows large numbers of Calanus, but further south the numbers decrease steadily. An attempt has been made to "contour" the distribution of the species (see Fig. 1), and it is obvious that Calanus is *apparently* more abundant both near the coast and in the northernmost water of the area sampled. This is shown equally clearly by Figure 2, which represents the numbers per metre of Calanus at each station, the stations being arranged in numerical order.

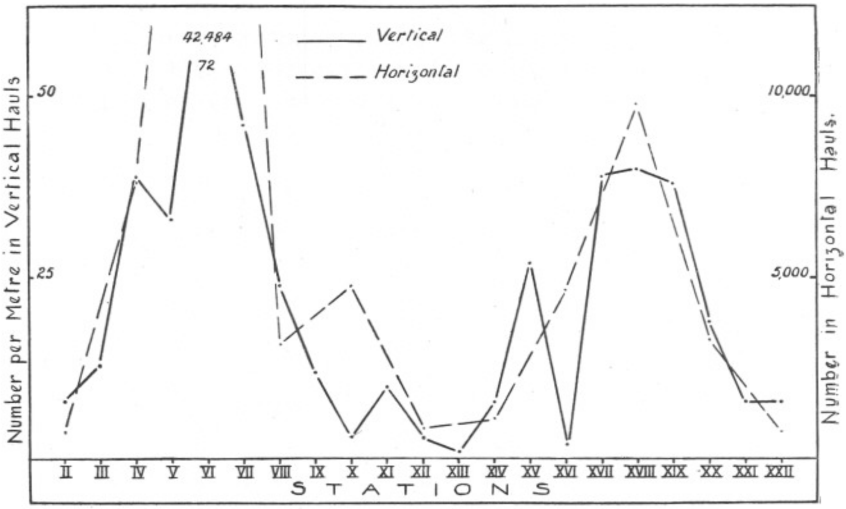

FIG. 2.—Numbers of Calanus taken in Vertical and Horizontal Hauls, Cruise 28.

The unbroken line represents the numbers of Calanus captured in 21 vertical hauls. This gives, of course, the same apparent distribution as our contour. The chance that this distribution is a true picture is considerably enhanced by the continuity, and it can scarcely be the result of sampling an approximately uniform population by an unreliable method, or due to the fortuitous operation of chance in a population with no real geographical distribution.

The dotted line in Figure 2 represents the catches of eleven series of horizontal hauls with the same net at the even-numbered stations. This curve follows that of the vertical hauls so closely as to leave very little room for doubt that the distribution is no more to be considered "apparent," but is a true picture.

Further, very slight confirmation of this is given by the 10 hauls of the Petersen Young Fish Trawl at the odd-numbered stations. The mean number of Calanus taken in the 30-minute oblique haul was only 385, whereas the mean for the horizontal hauls with a net of mouth area considerably smaller was 7196, showing that by far the greater proportion of Calanus must pass through the meshes of the fish trawl. In general, the catches of Calanus with this net are so small as to be of little value, but it is interesting to record that the biggest catch (2160) occurred at Station VII, which is in our area of greatest concentration.

It may be claimed, then, for this one cruise, that the distribution of Calanus, as given to us by single hauls of a vertical net at each station, lends support to a belief that the degree of variability in the area sampled is about the same as that in the smaller area where the two experiments were made.

The result of these two experiments, it will be recalled, was to show that only about 1/5th of the observations would give extreme values. Actually, on the cruise of 21 stations it is to be expected that 16 of the observed values would be within 33% of the truth, and that of the remaining 5 some would give values so far removed from it as completely to upset any attempt at contouring the observations. There are two such values at Stations X and XVI respectively. For both of these there is evidence from the horizontal hauls that the value is probably much too low (see Table VII), and there is, accordingly, good reason to believe that the contour should stand, approximately as drawn, the two discordantly low values being omitted. It is interesting to record that the contours were drawn in the first instance without the information which was derived later from the horizontal hauls, the two discordant values being omitted in view of the positions at which they occurred and the good continuity shown by the remainder, and because of the knowledge that such very discordant values were to be expected in, probably, not more than 2–3 cases. The evidence provided later by the horizontal hauls confirmed the omission of these two observations and tended materially to strengthen the belief in the criteria adopted.

In the course of examining the available information for this paper, the geographical distribution of Temora on this same routine cruise, and of Calanus and Temora on a preceding cruise was determined. (These data will be available shortly in a paper by Savage (**5**), and to save repetition are not reproduced here.) From a study of the contours produced, it would appear that the chance of approximately 4/5ths of the observations lying within 33% of the mean, and so providing values on which contours can be based, may be taken as a fairly safe guide.

We are now in a position to sum up both the results which have been obtained and their application to the question of the degree to which single hauls of a vertical net are reliable.

I. The distribution of the copepods Calanus, Temora, Pseudocalanus, and Paracalanus is such that consecutive vertical hauls of the International Net will not catch each time the same number of individuals. The greater proportion of any such hauls, however, will give values within ±33% of the mean (or true) value.

The actual proportion determined was 77 per 100, or approximately 4/5ths. Of the remaining 1/5th, nearly one-half will lie within ±40% of the mean, but extreme values up to ±90% and higher are to be expected.

II. The results of a routine plankton cruise during which 21 stations were worked in that part of the North Sea between 54° N. and 55° 20′ N., from near the coast to a line approximately 40 miles from it, suggest that probably no larger a proportion of extreme values obtains in this area, since the results can be contoured with the exception of 2 discordant values only.

III. The criteria which it is suggested should be adopted to enable the probability of accuracy of any distribution picture derived from the use of single hauls of a vertical net to be gauged are (*a*) the continuity of the observations themselves, by which is meant the mutual support lent to each other by the observations at adjacent stations, and (*b*) the knowledge that, probably, no less than 4/5ths of the observations will lie within ±33% of the mean.

IV. It appears that extreme values of ±50% and upwards of the mean are to be expected occasionally, but probably not more often than once in ten, and on this account a single high or low value unsupported by similar values at adjacent stations is meaningless.

V. Where there is no continuity (see III (*a*) above) it must be taken to mean that the species itself has exhibited no clearly defined area-preference.

VI. Subject to the limitations of III and IV (above), the use of single vertical hauls to study the distribution of the plankton in both space and time may be expected to give reliable results.

APPENDIX A.

SOURCES OF ERROR WHICH MAY ACCOUNT ENTIRELY, OR IN PART, FOR THE VARIATION IN THE SIZE OF CATCH OF THE SUCCESSIVE HAULS CONSIDERED IN THE FOREGOING SECTION.

In this appendix it is proposed to examine those sources of error of the methodique to which the observed variations may be due. The main sources of error will be :—

1. Variations in the speed at which the net was hauled through the water.
2. The effect of light and darkness on the catch of the net.
3. The enumeration error.

Other, minor, sources of error are :—

4. Losses due to insufficient washing of the net, accidents in bottling the sample, etc.
5. Mistakes in identification during enumeration.

The two last-named may safely be considered unimportant, but the effects of the first three may have been considerable, and it is with these that this section will deal.

1. *Speed of Hauling.*

Robert (**6**) working in fresh water with a Fuhrmann Net, No. 20 silk, showed that the numbers of certain zoo- and phyto-planktons captured were directly proportional to the speed at which the net was fished. In both our experiments the speed varied between successive hauls, and it is desirable to see the effect of this, if any, on the catches. In the second series, owing presumably to the stronger wind resulting in the vessel drifting more during the haul, the mean time the net took to pass through 1 metre of water was slightly longer than in the first (2·1 seconds per metre, and 1·8 seconds per metre respectively). This, coupled with the fact that the population had increased, does not allow us to treat the two experiments together, which would be desirable in view of the relatively small number of observations.

In the first series the time of hauling per metre varied from 1·1 to 2·7 seconds, with a Standard Deviation of $\pm 0{\cdot}306$. In the second case, the speed was more uniform, the range being from 1·6 to 2·4 seconds per metre with a sigma of $\pm 0{\cdot}187$. If a correlation exists between variations in the speed of hauling and in the numbers of individuals captured, it should appear in the first experiment, and it is this series that has been examined. The data selected for this purpose were the totals of the four dominant copepods, whose abundance in each of the 40 hauls of this series has been related to the speed (metres per second) at which each haul was made, and the coefficient of correlation (r) determined. The value of r from these data was found to be inconsiderable, namely, $-0{\cdot}13$. It is, accordingly, a legitimate conclusion that the variations in the numbers of organisms captured are due to some other cause than changes in the speed of hauling.

2. *The Effect of Light and Darkness on the Catch of the Net.*

This question arises in view of the fact that there is some evidence that certain species are taken, even in vertical hauls, in greater numbers by night than by day. Whether this is due to the animals rising from those lowest layers which the vertical net does not sample, or whether, as suggested by Southern and Gardiner (**7**), certain forms can see and avoid a net by day, is outside the scope of this paper. But there is a possibility that the night catches may have differed in amount from those by day. Had it not been necessary, for the reasons given on page 453, to consider only those differences in the size of catch of hauls closely related to one another in time, the effect of light and darkness might have been considerable. As it is, it is unlikely that great changes in level are to be expected in the course of the short intervals of time separating the hauls within each group, and for the same reason it is not to be expected that changes in light intensity would be sufficiently great to influence the reaction of the organism towards the net.

In the first experiment, the selected catches were all made in daylight (see Table I). In the second experiment (Table II) the hauls of the first three groups were made at night, and those of the remaining two by day, the mean number of the selected copepods being as follows :—

Species.	Day.		Night.	
	No. of Hauls made.	Mean No. Captured.	No. of Hauls made.	Mean No. Captured.
Calanus	15	112	18	107
Temora	15	55	18	37
Pseudo- + Paracalanus	14	148	17	147

Apart from Temora, which is nearly 50% more abundant by day, the day and night means are to all purposes the same, and it is probably safe to assume that those species are not more abundant in hauls made at night, and that the possibility of this phenomenon vitiating our conclusions may thus be ignored.

The Enumeration Error.

It has long been recognised that a single sample withdrawn by means of a Hensen Stempel-pipette, and raised by the dilution factor, will not give the actual number of organisms present in the whole catch, and Hensen adopted a method of averaging to minimise the discrepancy, *vide* Jenkins (**8**). A large enumeration error might, of course, account for a great part of the differences that have been observed in the size of catches of successive nets, and, in order to gain an idea of the magnitude of the error when a single sample only is withdrawn for enumeration a series of test "counts" was made. One cubic centimetre was withdrawn, by means of a Hensen Stempel-pipette, 25 times from a stock sample of North Sea plankton, diluted to 200 c.c. After each "count" the organisms were drained, replaced in the flask, and 1·0 c.c. of water run in from a burette. In this way the " population " was kept constant.

The results of these 25 " counts " are set out in Table VIII. To get the total number of each species actually present in the sample the counts should be multiplied by the factor 200.

TABLE VIII.

RESULTS OF 25 TEST COUNTS.

Sample.	Calanus.	Pseudo- + Paracalanus.	Temora.	Total Organisms.
1.	39	51	11	115
2.	28	59	12	123
3.	38	47	16	131
4.	49	59	8	133
5.	43	60	17	134
6.	42	49	15	122
7.	51	57	12	138
8.	39	54	10	118
9.	41	44	13	115
10.	40	37	16	108
11.	36	59	8	118
12.	49	63	9	138
13.	38	42	7	103
14.	44	52	17	127
15.	36	50	16	113
16.	38	59	16	125
17.	39	60	13	127
18.	46	58	20	146
19.	43	65	11	135
20.	43	49	9	119
21.	40	61	9	122
22.	43	56	14	129
23.	38	60	13	125
24.	53	69	9	149
25.	34	57	9	119
Total	1,030	1,377	310	3,132
Mean	41·2	55·1	12·4	125·3
Mean × 200	8,240	11,020	2,480	25,060

To get a measure of the spread of this series of counts the Standard Deviations (σ) have been calculated, after raising each count by the dilution factor of 200, for the three copepod species and for all the organisms present. These are set out in Table IX.

TABLE IX.

STANDARD DEVIATION OF 25 TEST COUNTS.

(Given in Table VIII.)

Calanus.	Temora.	Pseudo- + Paracalanus.	Total Organisms.
1,088	1,472	690	2,179

TABLE X.

COMPARISON OF 25 HAULS FROM THE SECOND EXPERIMENT, SELECTED BY CHANCE, WITH THE 25 TEST COUNTS.

Actual Hauls.			Test Counts.		
Haul No.	Total Calanus.	Percentage Deviation from Mean.	Count No.	Total Calanus.	Percentage Deviation from Mean.
29	10,575	+ 40·5	1	7,800	− 5·3
13	6,675	− 11·3	2	5,600	− 32·0
36	10,025	+ 33·2	3	7,600	− 7·8
20	6,360	− 15·5	4	9,800	+ 18·9
4	2,600	− 65·5	5	8,600	+ 4·4
23	6,225	− 17·3	6	8,400	+ 1·9
7	6,900	− 8·3	7	10,200	+ 23·8
34	8,160	+ 8·4	8	7,800	− 5·3
18	10,500	+ 39·5	9	8,200	− 0·5
2	4,845	− 35·6	10	8,000	− 2·9
25	5,400	− 28·3	11	7,200	− 12·6
9	4,050	− 46·2	12	9,800	+ 18·9
32	10,200	+ 35·5	13	7,600	− 7·8
16	11,100	+ 47·5	14	8,800	+ 6·8
35	7,800	+ 3·6	15	7,200	− 12·6
19	11,640	+ 54·6	16	7,600	− 7·8
3	3,240	− 57·0	17	7,800	− 5·3
30	7,275	− 3·3	18	9,200	+ 11·7
14	10,875	+ 44·5	19	8,600	+ 4·4
33	7,920	+ 5·2	20	8,600	+ 4·4
21	8,100	+ 7·6	21	8,000	− 2·9
5	2,520	− 66·5	22	8,600	+ 4·4
28	8,325	+ 10·6	23	7,600	− 7·8
12	9,775	+ 29·9	24	10,600	+ 28·6
31	7,080	− 5·9	25	6,800	− 17·5
Mean	7,527	28·85	Mean	8,240	10·25

The results cannot be considered altogether satisfactory, and the possibility that part, at least, of the variation in the size of catch may be due to the enumeration error cannot be ruled out. That the variation found is not due solely to this cause is demonstrated by the following table, where the variation in the numbers of Calanus captured in 25 hauls of the 38 consecutive hauls of the Second Experiment is compared with that of this series of 25 test counts. The 25 hauls in Table X, opposite, were selected from the total of 38 hauls of Table II, by dealing out the first 25 cards from a pack of 38 numbered 1–38, the choice being in this way unbiased.

It will be seen at once that the degree of variation in the numbers of Calanus caught in the 25 hauls, selected from the series of consecutive hauls of the Second Experiment, is much greater than that of the test counts. Further, it must be remembered that column 5 shows the situation at its worst, for in both the actual experiments the factor, instead of 200, was usually 50, and the enumerated totals were based on an average of 2 (and sometimes more) separate counts. Turning again to Table IX, we see that sigma for Calanus was ±1088, while $\frac{100\cdot\sigma}{\mathrm{m}}$ is ±13·2%. If now we compute sigma for the twenty-five counts taken two at a time, sigma becomes ±715, $\frac{100\cdot\sigma}{\mathrm{m}}$ becoming ±8·7%. It may fairly be claimed, therefore, that although the enumeration error may be considerable, it is not sufficient to account for the differences observed in our two series of successive hauls.

SUMMARY.

In both the series of hauls made for the purpose of estimating the reliability of a single haul of the International Vertical Net, the possibility that the variation in the size of catch of successive hauls is due to errors of the methodique has been examined.

Errors due to variations in the speed of hauling, and to the effect of light and darkness on the catch of the net can be ruled out.

The enumeration error, even where the enumerated total rests on a single count, is insufficient to account for the major part of the variations found, and, having regard to the fact that such totals were derived from two, and sometimes more, separate " counts " from each sample, there is good reason to believe that the main cause of variation in the size of catch is to be sought elsewhere, the most likely being the lack of uniformity in the distribution of the organisms themselves.

APPENDIX B.

VARIATIONS IN THE COMPOSITION OF THE PLANKTON DURING THE COURSE OF THE TWO SERIES OF CONSECUTIVE HAULS.

A STUDY of Tables I and II (pp. 451 to 452), which give the numbers per metre depth of the selected species in each haul, shows that there was considerable variation in the numbers of individuals caught, even where the time interval between the hauls was quite short. Whether this variation was ever sufficiently great to warrant the statement that the plankton was patchy, or that the individuals comprising it occurred in swarms, will depend upon the interpretation placed on these somewhat vague terms. Apstein (**9**), for instance, defines a swarm as a local assemblage of animals of one species in waters where, elsewhere, this species is absent or very sparsely distributed. It will be seen, however, that he regards a swarm as composed of one species. With this definition in mind, the data have been examined to see whether or not a population has been sampled that, whilst varying in abundance, maintained a fairly uniform specific composition. The method adopted has been to express the numbers of the dominant copepods as plus or minus percentage deviations from their own means, in which way it has then been possible to see whether the species tend to increase or decrease separately or together. The data treated in this way are set out in Tables XI and XII.

TABLE XI.

NUMBERS OF CALANUS, TEMORA AND OF PSEUDO- AND PARACALANUS PER METRE DEPTH IN 40 CONSECUTIVE HAULS FROM THE FIRST EXPERIMENT, EXPRESSED AS PERCENTAGE DEVIATIONS FROM THEIR OWN MEANS.

(Hauls in which the numbers of the three genera did *not* rise or fall together are in italics.)

Haul	Calanus.		Temora.		Pseudo- + Paracalanus.	
No.	+ %	− %	+ %	− %	+ %	− %
1.		57		25		61
2.	*0*	*0*	*32*			*29*
3.		*14*	*4*			*13*
4.		86		68		61
5.	*29*			*7*	*3*	
6.		*7*	*0*	*0*	*52*	
7.		57		14		45
8.		*7*	*0*	*0*		*19*
9.		43		18		48
10.		*50*		*46*	*0*	*0*

Haul	Calanus.		Temora.		Pseudo- + Paracalanus.	
No.	+ %	− %	+ %	− %	+ %	− %
11.		21		14		29
12.	*21*			*4*		*19*
13.	*0*	*0*	*46*		*16*	
14.		*50*		*7*	*110*	
15.		21		29		26
16.	*14*		*21*			*3*
17.	93		79		13	
18.	*7*			*11*		*23*
19.	*43*		*61*			*6*
20.	129		121		97	
21.	171		57		35	
22.		*64*	*14*			*13*
23.	*100*			*4*	*65*	
24.		*43*	*7*		*0*	*0*
25.	150		36		84	
26.		*29*		*18*	*6*	
27.		50		25		48
28.	*64*		*18*			*6*
29.		7		11		23
30.		36		29		39
31.		*50*	*4*			*26*
32.	*21*		*14*			*3*
33.		29		29		19
34.		64		54		42
35.		*43*	*32*		*77*	
36.		43		18		10
37.		*14*		*50*	*16*	
38.		21		43		3
39.		57		39		16
40.		57		11		39

TABLE XII.

NUMBERS OF CALANUS, TEMORA AND OF PSEUDO- AND PARACALANUS PER METRE DEPTH, IN 38 CONSECUTIVE HAULS, FROM THE SECOND EXPERIMENT, EXPRESSED AS PERCENTAGE DEVIATIONS FROM THEIR OWN MEANS.

(Hauls in which the numbers of the three genera did *not* rise or fall together are in italics.)

Haul	Calanus.		Temora.		Pseudo- + Paracalanus.	
No.	+ %	− %	+ %	− %	+ %	− %
1.		46		48		66
2.		34		69		56
3.		56		64		60
4.		64		81		40
5.		65		55		66
6.		76		64		53
7.		*6*	*5*		*14*	
8.		38		10		63
9.		44		52		19
10.		12		64		20
11.	*34*			*38*		*5*
12.	*34*			*33*	*2*	
13.		*9*		*26*	*39*	
14.	*49*		*19*			*4*
15.		*9*		*14*	*22*	
16.	*53*		*45*		*0*	*0*
17.	50		2		48	
18.	44		17		50	
19.	60		36		71	
20.		*12*	*10*		*65*	
21.	*12*			*7*	No observation.	
22.		*3*	*2*		*16*	
23.		*14*	*10*			*47*
24.	*7*		*40*			*45*
25.		*31*	*45*			*27*
26.		13		29		36
27.	4		7		11	
28.	*14*		*12*		No observation.	
29.	*45*		*26*			*5*
30.	*0*	*0*	*5*		*38*	

Haul	Calanus.		Temora.		Pseudo- + Paracalanus.	
No.	+ %	− %	+ %	− %	+ %	− %
31.		*3*	*69*		*11*	
32.	40		100		66	
33.	9		76		43	
34.	*11*		*48*			*1*
35.	7		38		68	
36.	37		5		22	
37.	10		19		9	
38.		*2*	*12*		*18*	

In the First Experiment (Table XI) all three of the selected species rise or fall together in 19 out of 40 cases. These are shown in ordinary type. In 15 of these cases the amounts are below the respective means, and in 4 they are above. Taken by itself, this is not perhaps very impressive, but the probability that it does indicate a tendency for the three species to behave similarly is heightened by a study of the figures themselves, which in several cases are of the same order of magnitude.

In one case, however, haul 14 (Table XI), the copepods Pseudo- and Paracalanus occurred in considerable numbers, whilst the numbers of Calanus and Temora showed a decrease, suggesting that here a definite aggregation of the species must have been sampled.

In the Second Experiment (Table XII), the three copepods rise or fall together on 19 occasions out of 36. On 10 occasions they have all fallen and on 9 they have risen together. Here again, particularly in hauls 1–6, Table XII, where the three species are all relatively scarce, the probability that the species have behaved in the same way is heightened by the similarity of the deviations.

In this series there is no evidence of a mono-specific swarm.

In conclusion, it would probably be unwise to attach too great weight to these somewhat scanty data, but it would appear that mono-specific aggregations are only exceptionally encountered, and that the population sampled has maintained a relatively constant composition.

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The Deterioration of Fabrics Exposed on a Roof after Treatment with Fishing-net Preservatives.

By

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WORK on fishing nets showed that the rapid deterioration which they undergo in water is due to bacterial action and may be greatly reduced by the use of appropriate preservatives which hinder bacterial growth. Nets are however exposed to sunlight and to diffuse light also, as well as to the action of rain and wind. It seemed desirable, therefore, to see whether the preservatives found to be of use against bacterial action were also useful in affording protection against the weather and such a degree of moisture as normally occurs in fabrics thus exposed. Instead however of using nets, fabrics were used, as they give rather more uniform results than do nets, each strip tested being made up of many strands. Furthermore, previous experience with fabrics had shown how great their rate of deterioration might be in Egypt, where there is intense sunlight. For example, the linen used on aeroplane wings, when exposed untreated, is reduced to about half its initial tensile strength in fifty days during summer, and the stout fabric of which hangars are made may be reduced to between one-fifth and one-tenth of its tensile strength in ten months—this refers to the side facing south, the north side being far less acted on.

It was found that cotton resisted weathering better than linen. Neither cuprammonium treatment (Willesden canvas), treatment with bitumen, rubber proofing nor dyes availed to lessen the rate of deterioration. Proofing with basic aluminium acetate was however definitely better than no treatment.

Conditions in Plymouth are however rather different, the sunlight is less intense, and the fabrics remain wet for longer periods, so that one might expect the deterioration due to bacteria and moulds to be relatively greater than in Egypt, in spite of the lower temperature.

There was another object in view in undertaking these tests, namely, to ascertain whether treatment with the preservatives recommended for use on nets had any injurious action on their tensile strength when exposed to sunlight, either from the properties of the preservative or of such decomposition products as might arise in the course of weathering.

EXPOSURE TESTS.

The fabrics were exposed on the flat roof of the Laboratory. This faces the sea and from it come the prevailing winds. Even with other winds the air is not polluted nearly as heavily as in industrial towns; accordingly the effect of acid fumes on the fibres may be considered as of little importance, especially as there is enough driven spray from the sea during storms to neutralize traces of acid.

The fabrics were exposed after being stretched by hand on wooden frames of the dimensions used for such tests at the National Physical Laboratory; these permit of five two-inch strips, eight inches long, being cut both to test warp and weft, leaving a good margin from the edge so as to avoid any possible effects due to the wood. The frames were exposed horizontally.

The materials used were a thick cotton, sold in yard widths at almost three shillings a yard; a lighter cotton, same width, sold at twenty-two pence per yard, and a stout linen, same width, sold at twenty-eight pence per yard. The preservatives and their method of application are as previously given in the work on net preservation (1928). The results of the exposures are shown in the three tables. The tensile tests were carried out at the Royal William Yard, Plymouth, through the courtesy of the Superintendent and Mr. R. M. Filmer, F.I.C., Chief Chemist.

The tests were carried out upon strips 2 inches wide and $6\frac{5}{8}$ inches between the grips of the Goodbrand Machine under the standard conditions for such tests. The columns show the percentage strength of the strips at breaking, the breaks being clean. The figures are the mean of the five determinations in each case and are calculated on the values for the untreated, unexposed, controls.

TABLE I.

To show deterioration in a heavy weight cotton fabric, initial tensile strength No. 1, warp 166, weft 276 lbs. per inch, No. 25, warp 165, weft 150 lbs. per inch, thickness approximately 0·8 mm., exposed horizontally on the roof, Nos. 2–4, from 10/1/'25–10/1/'27, two years, Nos. 15–19, from 12/9/'25–18/11/'26, fourteen months, and Nos. 27–31, from 25/11/'26–25/3/'29, two years and four months. No. 25 is control for above from No. 15 onwards.

No.	Treatment.	Warp.	Weft.
1	None, unexposed	100	100
2	None, exposed	66	70
3	Dried and dipped in 10% copper oleate . .	62	62
4	Dried and dipped twice in 5% mixed copper soaps .	62	63

No.	Treatment.	Warp.	Weft.
15	None, exposed	77	81
16	Dipped in 10% mixed copper soaps	70	79
17	Do. + $\frac{1}{4}$ lb. resin per gallon	73	82
18	Do. + $\frac{1}{2}$ lb. ,, ,,	68	77
19	Do. + 1 lb. ,, ,,	71	85
25	None, unexposed	100	100
27	Dipped in Cuprinol	49	59
29	Dipped in 10% mixed copper soaps	62	75
30	Do. + 2 oz. coal tar per gallon	65	77
31	Do. + 4 oz. ,, ,, ,,	64	70

TABLE II.

To show deterioration in a light weight cotton fabric, initial strength, warp 124, weft 78 lbs. per inch, approximately 0·5 mm. thick, exposed horizontally on the roof from 10/1/'25 to 10/1/'27.

No.	Treatment.	Warp.	Weft.
9	Untreated, unexposed	100	100
10	Untreated	31	31
11	Dipped in 10% copper oleate	28	30
12	Do., but dried before dip	27	28
13	Dipped in 5% mixed copper soaps, dried previously	31	30
14	Dipped twice ,, ,, ,, ,,	28	31

TABLE III.

To show deterioration in a heavy linen fabric, approximately 0·7 mm. thick, exposed horizontally on the roof, Nos. 6–8 for two years, 10/1/'25–10/1/'27, Nos. 20–24 from 12/9/'25–18/11/'26, viz. 14 months, Nos. 32–36, exposed 25/11/'26–25/3/'29, two years and four months. No. 5 is control for Nos. 6–8 and had a tensile strength of 200 lbs. per inch in the warp and 178 lbs. in the weft. No. 26 is control for Nos. 20–24 and 32–36 ; it had a tensile strength of 170 lbs. per inch in the warp and 206 lbs in the weft.

No.	Treatment.	Warp.	Weft.
5	Untreated, unexposed	100	100
6	Untreated	40	54
7	Dipped in 10% copper oleate ; previously dried	39	57
8	Dipped in 5% mixed copper soaps ; previously dried	39	67

No.	Treatment.	Warp.	Weft.
20	Untreated, exposed 12/9/'25	55	62
21	Dipped in 10% mixed copper soaps	75	72
22	Do. + $\frac{1}{4}$ lb. resin per gallon	70	85
23	Do. + $\frac{1}{2}$ lb. ,, ,,	69	83
24	Do. + 1 lb. ,, ,,	76	79
26	Untreated, unexposed	100	100
32	Cuprinol, one dip, exposed 25/11/'26	42	65
35	Mixed copper soaps, one dip	60	68
36	Do. + tar 4 oz. per gallon, one dip	54	66

DISCUSSION OF RESULTS.

In the first series of exposures, Nos. 1–14, it may be seen that the cotton (Table I) lost about one-third of its strength in the two years, the thinner cotton (Table II) over two-thirds, and the linen (Table III) 60 per cent in warp and 46 per cent in weft. In all three sets the copper oleate or mixed copper soap (oleate, stearate, palmitate) treatment gave final strengths very close to that of the untreated fabrics. It is therefore obvious that the deterioration was due to the weathering, especially the action of light, since the copper soaps protect against bacteria and moulds. Under such conditions the effect of the latter appears to be negligible. The soaps, however, have not hastened the weathering action.

In the second series, Nos. 15–26, the treated cottons (Table I) are slightly weaker in the weft, but the same as or stronger than the control in the warp. The linen (Table III) is better than the control in both warp and weft, though the difference is not large. The resin copper soap mixtures adhere better and so resist the leaching action of rain, though after 14 months the upper surfaces showed no visible effects of the treatment, though the lower surfaces did.

The third series was again a two years' exposure, like the first. The copper soap treated cotton, No. 29, was very similar in its behaviour to that in the first set, No. 4, whereas the linen behaved rather better in the third series, cp. Nos. 35 and 7. The addition of tar to the soaps was intended to improve their adherence, which it does, and to cut off the light, which it does not appear to do, as far as the surface is concerned, for any length of time, for Nos. 30 and 31 are only slightly better than Nos. 3 and 4, these being cotton. With the linen, Nos. 35 and 36, the preservation is rather better than in Nos. 7 and 8. Very strangely the Cuprinol-treated fabrics, both linen and cotton, are appreciably weaker than the fatty soap and tar mixtures. Cuprinol, which is a copper soap of a petroleum acid, gives excellent protection against bacterial action and remains on the exposed fabric well, better than the fatty soaps alone.

None of the treatments tried, therefore, are really effective in lessening the destructive weathering action. Dr. R. H. Pickard, Director of the British Cotton Industry Research Association, kindly drew the author's attention to a method of preserving fabrics used at Woolwich, by means of precipitated chromium or chromium and iron hydroxides. The value of this treatment was made clear by work of Cunliffe and Farrow (1928), though they refer to Mr. J. R. Hannay for pointing out its value to them. It will be of interest to see whether it is not possible to combine this with the copper soap treatment. Possibly the chrome-green process alone may have an appreciable antiseptic action. In any case, it ought to be of value for sails and other fabrics exposed on a sea-going craft.

SUMMARY.

(1) Cotton and linen fabrics were exposed horizontally on the Laboratory roof at Plymouth for two years. During this time the fabrics lost from one to two-thirds of their initial tensile strengths in both warp and weft.

(2) The application of copper oleate, mixed copper soaps, also of the latter with resin or tar as binding agents, had no effect or a slight effect only in lessening deterioration ; such weakening must therefore be due to weathering, chiefly the action of light, since these substances have been shown to be useful antiseptics on nets immersed in salt or fresh water.

(3) No deleterious action may be expected when nets treated with these substances are exposed to light, since the treated fabrics were no weaker than the untreated ; but where Cuprinol had been used, there appears to have been some weakening, though the antiseptic properties of Cuprinol are excellent.

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Note on the Condition of the Water in a Marine Aquarium.

By

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Somewhere about 1914 D. J. Matthews maintained the sea-water in the Plymouth aquarium tanks at a pH value close to that of the outside sea-water by the addition of suitable quantities of sodium carbonate.

In 1922 the writer found that the aquarium tanks were usually at pH 7·6, whereas the water of the Sound was at pH 8·1 on an average and the open sea between pH 8·14 and 8·28. Any lowering of the value for the tanks denotes an abnormal excess of carbon dioxide, and when pH 7·3 is reached symptoms of distress may appear among the fishes; water at pH 7·1 was found to be definitely foul and evil-smelling.

It was suggested that lime should be added to the tank water to remove the excess of carbon dioxide. This also serves to neutralise acid substances excreted by the animals. It was found that the addition of about 1·5 kg. of quicklime, mixed in a bucket of water, to the resting reservoir each week sufficed to maintain the reaction slightly over pH 8. There are two reservoirs, which are used in the circulation and allowed to sediment during alternate weeks. Though the fishes and many invertebrates throve in water at pH 7·6 the more delicate organisms did better when it was maintained at pH 8. With no addition of lime the water is oxygenated by splashing and by compressed air, and at the same time much carbon dioxide is removed. Additions of sea-water are made at infrequent irregular intervals when the Sound water is specially clear and clean. The addition of lime has now gone on since about 1923 with satisfactory results.

The method has however been criticised unfavourably by Breder and Howley (1930), who have also made statements concerning aquarium water which call for comment.

The fishes are said to produce carbon dioxide which "by hydrolysis forms carbonic acid (H_2CO_3) which tends to make the water more acid." The process is not hydrolysis nor does the water ever become acid, though its alkalinity is of course reduced somewhat.

It is further stated that "the continued excretion of acid metabolites (principally sulphates) leads on the one hand, to a reduction of the normal bicarbonate content, etc." As against this Smith's (1930) conclusion may be placed: "It is shown that the intestinal Mg and SO_4 come from ingested sea-water and that the urinary Mg and SO_4 come from the alimentary absorption of these substances" [in marine teleosts]. Furthermore, normal sulphates (M_2SO_4) are usually neutral; no acid sulphates ($MHSO_4$) are met with in urine or faeces, since acid sulphates are of high acidity, around pH 2·6 for N/100 concentration. Urine, however, is generally no more acid than pH 6, and may be alkaline. When acid, the acidity is due to weak organic acids and to phosphates. The excreted sulphates, which do arise from ingested sulphur compounds, are excreted as neutral salts of metals, as ammonium sulphate and as ethereal sulphates, together with sulphur compounds of a more complex nature in which the sulphur is less oxidised than is that of a sulphate. It is obvious therefore that to represent the sodium bicarbonate as neutralised by sulphuric acid, as is done by Breder and Howley, bears no relation to any actual process taking place in sea-water.

The method recommended by Breder and Howley is to add sodium bicarbonate to the sea-water to correct the bicarbonate balance and to rely on adequate aeration for removal of CO_2. Their 50,000-gallon tank (U.S.A. gallons) is not very different from our tank of 50,000 Imperial gallons capacity, yet it required 73 kg. of sodium bicarbonate in six months, as against about 39 kg. of quicklime. They write of the danger of lime causing "a very rapid and dangerous increase in pH easily passing out of the range it is possible for fishes to exist in." This risk can only be described as a very remote one, when it is remembered that magnesium hydroxide is precipitated from sea-water at pH 10, a figure which may be reached, or almost reached, by the removal of carbon dioxide by plants during photosynthesis. Moreover, in our practice no such figure is even approached, for the water is tested with cresol red, which should give a marked, but not intense, red as in natural sea-water. No blue should be shown with thymol blue, but only a yellow. It is not necessary to be provided with a set of buffer tubes as standards, since the correct colours are easy to distinguish.

The reason why quicklime, freshly slaked in tap water, was chosen, was that it directly removes carbon dioxide forming the almost insoluble calcium carbonate or, with excess of carbon dioxide, the bicarbonate which is only slightly soluble.

It may be concluded, therefore, that while the use of sodium bicarbonate is advantageous provided the aeration be adequate to remove the excess of carbon dioxide, yet the use of lime is to be preferred in that it removes the carbon dioxide directly. With ordinary care it need never—and has never—led to the "catastrophe" feared by Breder and Howley. Sodium carbonate too removes carbon dioxide, though not quite as efficiently, weight for weight, when in the form of crystals.

In the London Zoological Society's Aquarium, where filtration and storage in the dark are used for purification, the buffering of the water does become somewhat reduced (Stowell, 1925, 1926 ; Brown, 1929).

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On the Colorimetric Determination of pH in Sea-Water.

By

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With 2 Figures in the Text.

It is not always possible accurately to carry out pH determinations on board ship, owing to bad light or other conditions, although it may be possible to collect water samples. Hitherto it has not been considered possible to determine pH more than a few hours after collection, owing to the action of bacteria and phytoplankton and the exchange of carbon dioxide with the atmosphere.

A method has now been found whereby the water may be kept in its original condition for some considerable time after collection, enabling the actual determination to be carried out under more favourable conditions in a shore laboratory.

Colorimetric estimation is made by matching the samples under examination with buffer solutions corresponding to known pH. Accurate comparison is dependent upon the quality of the light used, since the colour exhibited by an indicator is due to the selective absorption of certain frequencies of the incident light. An estimation made with sunlight is not rigorously the same as if it is made with diffused or artificial light which is richer in yellow and poorer in blue. When working with an accuracy greater than 0·1 pH it is better to use a source of constant light, operating under special conditions.

The bactericidal action of mercuric chloride prevents the troublesome activity of micro-organisms present in the sea-water whilst its very small dissociation coefficient ($\alpha = 0{\cdot}013$) is without effect on the pH. If when the samples are collected on board about four drops of a saturated solution of mercuric chloride is added to each 100 c.c., bacterial action is stopped, and furthermore if the sample bottle is completely filled, no air-space being left over the water, evasion or invasion of carbon dioxide is inhibited or at least very greatly restricted.

The determinations of pH in sea-water samples have been carried out by means of the well-known McClendon method **(1)** in order to obviate the salt error. The buffer solutions were " boric " (18·6 gm. boric acid and

22·5 gm. sodium chloride made up to 1 litre with boiled distilled water) and " borax " (28·67 gm. sodium borate and 19·0 gm. sodium chloride made up to 1 litre with boiled distilled water) ; the total volume of each standard made by mixing these two buffers in correct proportions was 10 c.c. against 30 c.c. used by McClendon. The indicator was 0·5 c.c. of 0·02% cresol red solution prepared from a 0·2% alcoholic solution. A stock solution of this strength was made in order to avoid the addition of a very little sodium hydroxide necessary for the complete dissolution of cresol red as an 0·6% solution. The test tubes, of Monax resistance glass (12 cm. in height and 1·3 cm. in diameter), were chosen so that, when 10 c.c. of water were added to each, the columns of liquid had approximately the same height. The tubes after washing with distilled water were steamed and finally dried in the stove at 110° C. Ten c.c. of the appropriate buffer mixture, 0·5 c.c. of the indicator and two drops of toluene were placed in each tube, which was closed by a cork coated with paraffin wax. Finally an efficient seal is ensured by a second coat of wax over the cork and top of the tube, and label. The standards remain unchanged and fit for use even after many months (**2**). When not in use the tubes are kept in the dark as a precaution. The standards were at pH=8·40–7·30 with a difference of 0·05 or 0·03.

The addition of two drops of a 2·5% mercuric chloride solution to the sea-water samples in the test tubes does not interfere with the pH, and if these samples containing mercuric chloride are stored in darkness at a temperature of 12–14° C. in test tubes carefully sealed no changes in pH are noticed after some days. In water samples without mercuric chloride a much more rapid fading in the colour is observed. An unpreserved sea-water sample from one mile N.W. of the Eddystone, whose pH on the day of collection was 8·11, gave 8·06 on the following day, and 7·38 after 12 days. A sample of the same water containing mercuric chloride and also stored in darkness at 12–14° C. did not alter its pH for three weeks. Other samples also from the Eddystone, containing mercuric chloride, gave the same value of pH (8·11) for a month, after which the colour changed a little, giving the value 8·07.

The colour of certain samples, preserved and stored in the same way, changed after 5–6 days, but the tubes were found to have been imperfectly sealed. Thus the mercuric chloride stopped the activity of the micro-organisms, but the entry of atmospheric carbon dioxide modified the pH.

If the water samples are taken in ordinary bottles not completely full, to which mercuric chloride is added on collection and the addition of indicator made a few days afterwards, the pH observed is less than on the day on which they were taken. Determinations made on opening the tubes a week later, gave a result 8·05 on the water with mercuric chloride and

TABLE I.

Effect of Mercuric Chloride at 12° C.

St.	Water.	Day of collection.	One day after.	2 days after.	3 days after.	4 days after.	5 days after.	6 days after.	7 days after.	8 days after.	9 days after.	11 days after.	12 days after.	13 days after.	14 days after.	15 days after.	17 days after.	18 days after.	19 days after.	20 days after.	21 days after.	23 days after
L1	alone	8·05	8·04	7·92	7·83	7·58	7·38	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
L1	plus merc. chloride	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	8·05	7·97	7·95	7·96	7·95	7·91	7·91	7·91
L2	alone	8·07	8·05	8·03	7·88	7·73	7·68	7·53	7·38	—	—	—	—	—	—	—	—	—	—	—	—	—
L2	plus merc. chloride	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	8·07	7·95	7·94	7·91	7·91	7·90	7·90	7·90
L3	alone	8·09	8·09	8·00	7·88	7·78	7·68	7·58	7·58	7·58	7·58	7·56	7·56	7·56	7·56	7·56	7·56	7·50	—	—	—	—
L3	plus merc. chloride	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·09	8·05	8·05	8·04	8·02	8·01	8·01	8·01
L4	alone	8·10	8·10	8·05	7·93	7·75	7·63	7·63	7·58	7·53	7·48	7·38	—	—	—	—	—	—	—	—	—	—
L4	plus merc. chloride	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·10	8·02	8·02	7·99	7·96	7·96	7·96	7·96
L5	alone	8·11	8·09	8·00	7·93	7·73	7·63	7·55	7·43	—	—	—	—	—	—	—	—	—	—	—	—	—
L5	plus merc. chloride	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·10	8·11	8·11	8·11	8·11	8·09	8·06	8·06

7·93 on the water without antiseptic. These values are lower than the values found (8·10) on the day when the water was collected.

But if the samples containing mercuric chloride are drawn from bottles completely full the pH determined by adding the indicator some days afterwards is the same as the original value.

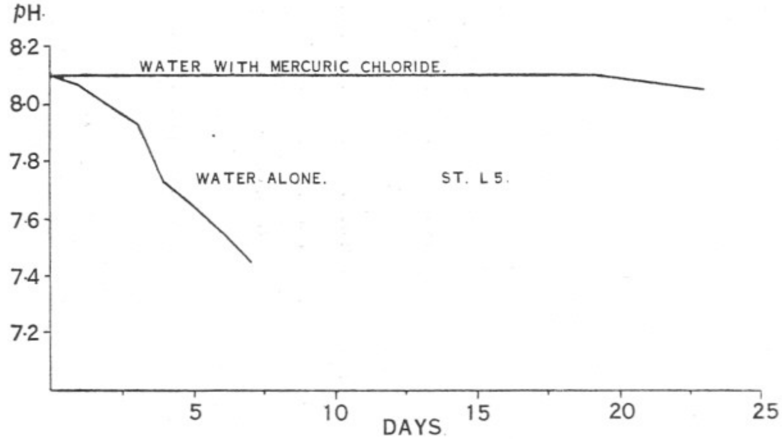

FIG. 1.

The following table contains the results obtained on sea-water samples from the International Hydrographical Stations L1, L2, L3, L4, and L5 (on Feb. 5th) with and without mercuric chloride. These were stored on the day of collection in carefully sealed test tubes and kept in darkness at 12–14° C. The data for Station L5 are shown graphically in Figure 1.

Other preservatives have been tried. Toluene was the best, but as the figures in Table II show, it is much less effective than mercuric chloride.

TABLE II.

EFFECT OF DIFFERENT PRESERVATIVES AT 12° C.

	1st day.	2nd day.	3rd day.	4th day.	6th day.	7th day.	8th day.	9th day.	10th day.
W. alone	8·11	8·11	8·06	7·91	7·78	7·73	7·63	7·53	7·48
W. + toluene	8·11	8·11	8·10	7·98	7·93	7·93	7·83	7·83	7·83
W. + mercuric chloride	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11	8·11

It is well known that temperature plays an important part in the determination of pH, because heat increases the dissociation of ions and correlatively the pH decreases. The determinations must be made with the water samples at the same temperature as the buffer mixtures.

If the test tubes containing the sea-water samples plus indicator are stored at a temperature higher than 12–14° C. the colour fades more quickly.

TABLE III.

EFFECT OF MERCURIC CHLORIDE AT 33° C.

Stn.	Water.	1st day.	2nd day.	3rd day.	4th day.	5th day.	6th day.	7th day.	8th day.	9th day.	10th day.	12th day.
L2	alone	8·07	8·00	7·80	7·43	7·20	—	—	—	—	—	—
L2	plus mercuric chloride	8·07	8·07	8·06	8·02	7·91	7·91	7·91	7·91	7·91	7·83	7·73
L5	alone	8·11	8·06	8·00	7·73	7·23	—	—	—	—	—	—
L5	plus mercuric chloride	8·11	8·11	8·10	8·05	7·88	7·88	7·88	7·88	7·88	7·88	7·88

Figure 2 shows these variations in sea-water from L2 and L5 with and without mercuric chloride kept in a thermostat at 33° C. We noticed that the pH of the sealed samples containing mercuric chloride show no change after two days, but that in unpreserved water the decrease is very rapid indeed, somewhat naturally even more rapid that at the lower temperature.

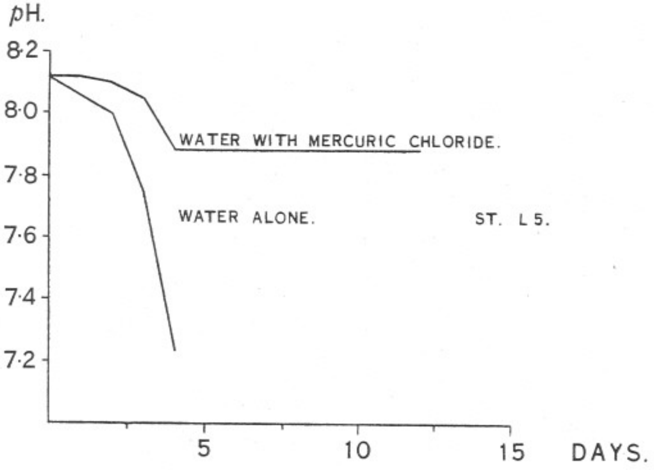

FIG. 2.

The buffer mixtures did not change at 33° C. as judged by subsequent comparison with buffers kept at 12° C.

The erratic decreases are owing to different causes. According to Legendre proteins can influence the indicators, perhaps partially absorbing them, and although the sea-water contains these nitrogenous substances in very small amount, different proportions of them may produce a variable fading in the colour.

It was stated above that to every test tube containing McClendon mixtures two drops of toluene were added, to preserve them ; but it is possible to work under the same conditions by adding two drops of a 2·5% mercuric chloride solution in place of toluene, making a correction in the value of pH. As is well known mercuric chloride gives a precipitate of basic salt with sodium borate, but in the presence of boric acid there is no precipitation since a complex is formed. The pH is therefore slightly changed. Buffer mixtures were prepared in this way and their values were 0·03 less than in the original mixtures with toluene.

The author desires to thank Mr. H. W. Harvey and Dr. L. H. N. Cooper of this Laboratory for their interest in this work.

SUMMARY.

1. It is not always feasible to determine pH on board ship, owing to bad light and other conditions, although it may be possible to collect water samples.

2. By preserving the water samples on collection with mercuric chloride solution (four drops per 100 c.c. of water) and by taking care to leave only a small air-space in the bottles it is possible to keep the water practically unchanged for many days.

3. Test tubes containing such water (10 c.c.) plus 0·02% cresol red (0·5 c.c.) have been kept unchanged for three weeks at 12–14° C. and for two days at 33° C., whereas unpreserved water showed a drop in pH of 0·05 unit in one day at 12° C.

4. McClendon buffer solutions may also be preserved by mercuric chloride, but in this case a small correction must be applied since complex formation leads to a removal of effective buffer salts from the solution and a small decrease in pH.

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On Abnormal Conditions of the Gills in *Mytilus edulis.* Part II. Structural Abnormalities, with a Note on the Method of Division of the Mantle Cavity in Normal Individuals.

By

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Amy, Lady Tate, Scholar of Bedford College.

With 27 Figures in the Text.

CONTENTS.

INTRODUCTION.

IN Part I of this paper (**2**) the presence of secondary grooves and folds on the gills of *Mytilus edulis* especially was described, together with the occurrence of permanent natural reversal of the frontal cilia on the gill filaments composing the majority of these grooves and folds. The present paper is concerned with certain, chiefly structural, abnormalities of the gills, namely: (*a*) folding over of the free ventral edge of the gill with concrescence, (*b*) fusion of the gill filaments side by side, (*c*) enlargement of the gill filaments and (*d*) concrescence of the two gills of one side. The mussels in which the first two of these conditions were observed, were almost entirely from various parts of the Fal Estuary, the average percentage with abnormal gills being 31·8% among 1398* recorded from October 28th to November 25th, 1927, and 44·4% among 162 examined in March, 1930. In no other locality from which mussels have been obtained, was anything approaching these conditions seen, though a very

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* Given in error as 1488 in (**2**) Part I, p. 919.

occasional specimen might have abnormal gills. Batches of mussels have been examined from the Estuaries of the Hamoaze, mostly from near Weir Point (1291 between October 8th, 1927, and February 17th, 1928); the Estuary of the Yealm (296 between October 10th, 1927, and August 3rd, 1928); the Estuary at Teignmouth (9262 between December 6th, 1927, and February 26th, 1929); the Estuary of the Camel, near St. Issey Cliff, Padstow (10,866 between November 8th, 1927, and August 9th, 1929); and from the Promenade Pier, Plymouth (340 December, 1927, and September, 1928).

The widespread abnormal conditions of the gills of the Fal Estuary mussels would seem to be correlated, most probably, with some factor or combination of factors in the environment and not to be due to injury, though several cases of accessory palps, divided palps, and accessory feet possibly had a traumatic origin. The percentages of pea-crabs (*Pinnotheres pisum*) in the Fal Estuary mussels of 1927 were so low (see Table I, p. 517) that their presence could have no relation to the abnormal conditions of the gills, and in the 1930 sample from that locality, mussels containing pea-crabs, of a size likely to cause injury, have been omitted from the total on which the percentage of 44·4 is based. In a certain few cases—about three in March, 1930—in which the gills were exceedingly narrow, or nearly missing, for a short distance, the injury could be almost certainly traced to an old boring by the whelk-tingles, Murex or Purpura. Apart from these few cases, it is suggested that the abnormal conditions of the gills of the Fal Estuary mussels are correlated with some peculiar factor or combination of factors in the environment, though it is by no means clear why mussels from the estuaries of the Hamoaze, Yealm, Teign, and Camel are so little affected.

A consideration of abnormality in the gills of Mytilus is of some importance in regard to the problem of purification of this mollusc for consumption (**12**).

DESCRIPTION OF STRUCTURAL ABNORMALITIES OF THE GILLS.

(*a*) Folding over of the Free Ventral Edge of the Gill, with Concrescence.

This abnormal condition of the gills was restricted to the Fal Estuary mussels, except for its occurrence, in a much modified degree, in a few mussels from other localities, which were inhabited, in practically all instances, by pea-crabs. The deep and regular folding over of all four gills,* as shown in Figure 1, has been observed to occur only in the Fal

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* As in Part I (**2**), for convenience in description the two demibranchs on each side of the body are considered as two gills.

mussels, a number of which had the gills permanently folded over lengthwise, the fold in some cases extending up to two-thirds of the length of the gill. The extreme anterior and posterior ends of the gills were very rarely involved in the fold. It is peculiar that with few exceptions (one exception only noticed) the gills were folded away from each other, the inner gill of either side being folded inwards, and the outer gill outwards (cf. the direction of upward folding of the ventral tips of the descending filaments during development). The filaments in the folded over portion tend to become fused or concresced in varying degree with those beneath them; various stages in the process were observed. In the very early stages the entire fold can be raised, though when placed in water the gill will not straighten out. Fusion first occurs near the bend of the fold and the major part can be raised; in later stages the folded over portion has become entirely fused with the lamella beneath. In the mussel sketched in Figure 1 the fold of the left inner gill alone was entirely fused, those of the other three gills could be raised almost to the bend.

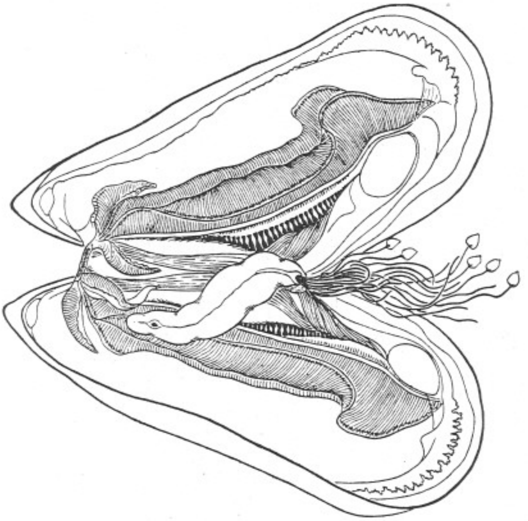

FIG. 1.—Sketch from life of a mussel from the Fal Estuary, October 28th, 1927, showing folding over of the four gills. The folded portion of the left inner gill alone was entirely fused; that of the other three gills could be raised almost to the bend. Natural size.

The appearance in surface view of a small part of a gill in which the fold had become completely fused, is shown in some detail in Figure 2 (p. 492). The main food groove now runs across the surface of the lamella (at G), and just dorsal to it there is a narrow zone in which fusion of the filaments side by side, and considerable irregular proliferation of the frontal surfaces of the filaments has occurred. Fusion of the filaments has also taken place along a narrow region ventral to the food groove, as well as near the bend of the fold, at what is now the free edge of the gill. The occurrence of fusion of the filaments laterally, added to the fact that the folding is

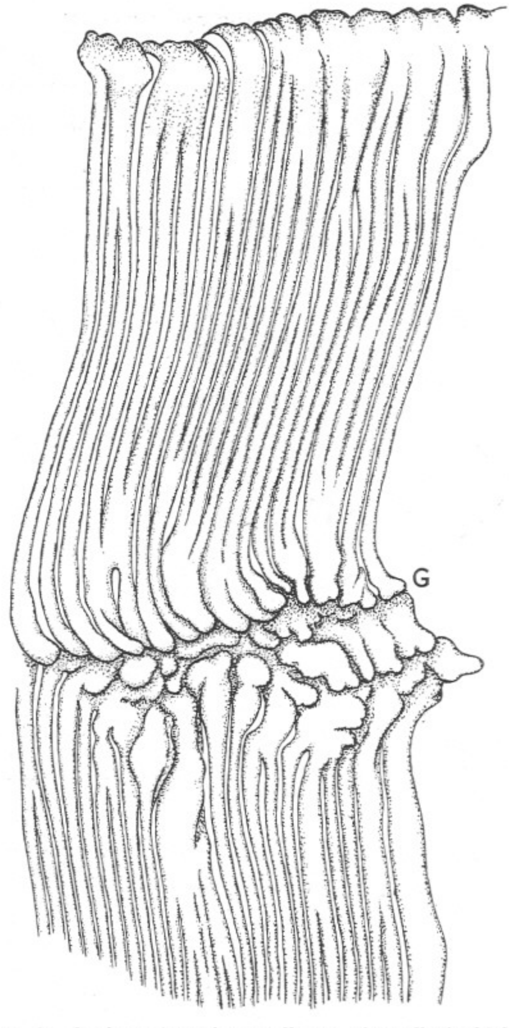

FIG. 2.—Surface view of a small area of a gill of which the folded portion had entirely fused, the main ventral food groove (G) now running across the surface of the lamella. The fusion of the gill filaments side by side is shown, and the irregular growth of the frontal epithelium in a narrow region dorsal to the fused food groove. The ventral and folded edge of the gill is at the top of the figure. From a mussel from East Bank, Fal Estuary, November 23, 1927. From preserved material. × ca. $24\frac{1}{3}$.

usually slightly oblique—a filament generally being folded over on to one posterior to it in the series—makes it difficult to separate a single filament, or even a few filaments, to examine in side view.

Figure 3 shows in side view small groups of filaments from gills

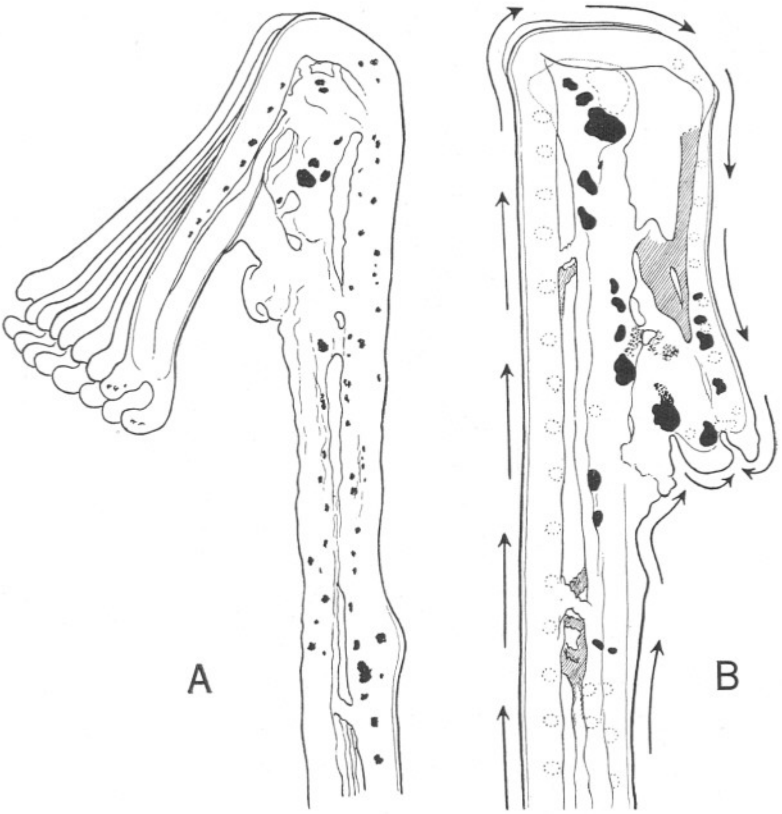

Fig. 3.

A. Side view of a small group of filaments from a gill of Mytilus in which the folded over portion had fused at the bend only. Considerable fusion of filaments side by side had occurred, and the surface sketched showed no ciliated discs, while lateral and latero-frontal cilia were absent for the most part, indicating presumably that fusion with the next filament in the series had already begun. The accumulation of brown pigment in masses is shown. From a mussel from East Bank, Fal Estuary, November, 1927.

B. Side view of a small group of filaments from the same gill as that of Fig. 2, showing complete fusion of the folded over portion of the gill with the ascending lamella. The two inner arms of the fold have apparently fused and are undergoing degeneration: masses of brown pigment are indicated. There is some fusion of the ascending filaments laterally, dorsal to the food groove, with slight enlargement of the frontal surfaces of the filaments. The arrows, showing the direction of the ciliary current on the frontal surface, have been added from a living gill, which showed a similar fold and fusion.

A–B, from preserved material. ×18$\frac{1}{4}$.

with different degrees of fusion of the folds. Figure 3, A, was from a gill where the fold had only fused at the bend. There was much fusion of the filaments side by side dorsal to the fold, and the lateral surface sketched showed no ciliated discs, and, for the most part, lateral and latero-frontal cilia were absent, indicating that fusion with the neighbouring filament had begun. As is well shown by the example in Figure 3, B, fusion and degeneration of the two inner arms of the fold take place, and pigment—no doubt liberated from degenerating cells—is generally found collected into granular masses of considerable size. Transverse sections show varying degrees of fusion in different parts, and at different levels of the same fold. In some places four lamellæ are distinct, in others three, the two inner ones having fused. In one fold sectioned the middle one of the three lamellæ was seen to be formed by the fusion of two lamellæ, that is the two inner arms of the fold, as clearly shown by the presence of two series of chitinous supports, mostly somewhat contorted (see Fig. 4, A, p. 495). In another fold sectioned, however, though four lamellæ were present in places, yet where only three were present, the chitinous supports could not be clearly distinguishable into two sets ; this perhaps may be due to the obliquity of the folding. In one example sectioned, where the apparent fold was only about 1·6 mm. deep, the middle lamella of the three present was clearly single—as shown by the distinct single set of poorly developed chitinous supports—and was the ascending lamella (Fig. 4, B). Complete fusion side by side of all the filaments in the middle lamella had not taken place, a few small ciliated spaces remaining. This case would not seem to be explicable by folding alone, but possibly also by differential growth.

Some gills which appeared in surface view to have undergone folding, showed when the filaments were examined in side view, an appearance as in Figure 5 (p. 496). The ascending filaments were only about a third the length of the descending, and in consequence the descending filaments appear to have been pulled over. It would seem that the shortness of the ascending lamella was due to injury to, or puckering of, the filaments composing it. The gills of the mussel in which this condition was noted, had, however, very few interlamellar connexions in the abnormal portion ; possibly they had snapped at some time, for there were small masses of subfilamentar tissue.

In gills where folding with concrescence has occurred, the ascending lamella is sometimes considerably shorter, dorso-ventrally, than the descending one; the question therefore arises whether gills in such a condition will be able to effect a ciliary junction with the mantle and the visceral mass (see Orton, **33**, pp. 460, 462 ; Dodgson, **12**, pp. 168, 171, and the present paper, p. 533). If they are unable to do so there would be imperfect division of the pallial cavity into supra- and infra-branchial

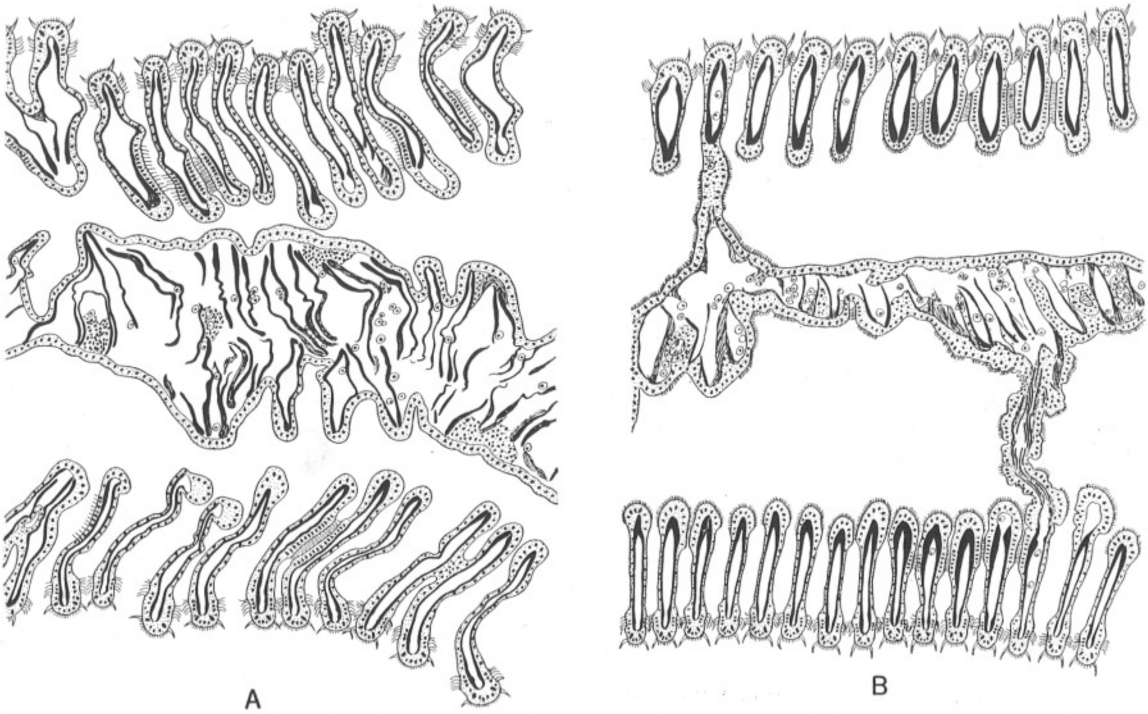

Fig. 4.

A. *M. edulis.* Transverse section through region of a fold—such as shown in Fig. 2—showing three lamellæ, the middle one formed by the fusion of the two inner arms of the fold, the two sets of chitinous supports being clearly discernible in places. The material, fixed in formalin, was badly preserved, but sufficiently to show the chitinous supports. The distribution of the nuclei and cilia is represented diagrammatically: the abfrontal cilia and the numerous gland cells, present especially in the epithelium of the middle lamella, have been omitted. Iron hæmatoxylin and acid fuchsin. ×93⅓.

B. Transverse section through folded region of a gill (fold only ca. 1·6 mm. deep) in which the middle lamella, as shown by the single series of chitinous supports, is single. Complete fusion laterally of all the filaments in the middle lamella had not occurred, a few small ciliated spaces remaining. The difference in width—from frontal to abfrontal surface—of the filaments in the two outer lamellæ is due to the section being slightly oblique. The distribution of the nuclei and cilia is represented diagrammatically. Bouin's fixative; Mann's methyl-blue-eosin. ×93⅓.

chambers; the exhalent current would, in all probability, cease or diminish in strength, and the feeding mechanism would be most probably deranged (see Dodgson, **12**, p. 171). In some mussels with abnormally short ascending lamellæ it has been noticed that such short lamellæ seem

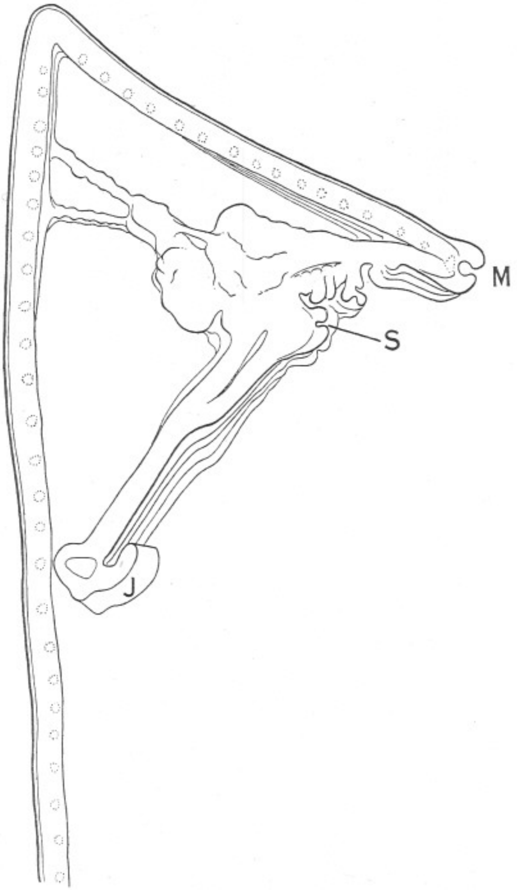

Fig. 5.—Lateral view of a small group of filaments from the gill of a mussel from East Bank, Fal Estuary, November 23, 1927, which showed an apparent fold in surface view. M, main ventral food groove; S, secondary food groove; J, junction area of interlocking cilia on outer surface of dorsal food groove. From preserved material. × ca. $12\frac{1}{8}$.

to be turned out almost at right angles, whence it is possible that the dorsal free edge of the gill, by pulling the gill over towards the side of junction, is able to touch the mantle or the visceral mass. In a few mussels with gills in this condition, a well-defined ridge in the mantle has been noticed (as in Fig. 6, B and C, p. 497), which may help to enable the

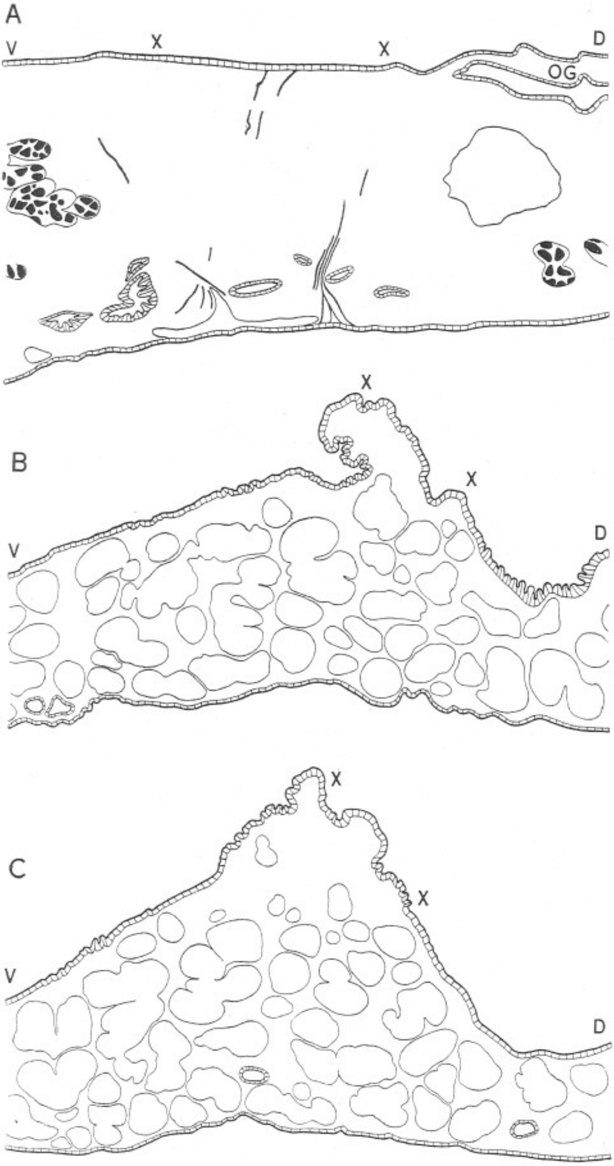

Fig. 6.

A. Transverse section of mantle of normal Mytilus, passing through the zone of interlocking cilia, X to X. OG, plicate organ; D and V, Dorsal and Ventral.

B and C. Transverse sections through different regions of a ridge present in mantle of a Mytilus, in which the gills of that side were extremely short, dorso-ventrally. X–X marks the position of the zone of interlocking cilia on the dorsal slope of the ridge.

D and V, Dorsal and Ventral.

A–C. × ca. $27\frac{1}{2}$.

outer gills to effect a ciliary junction with the mantle. The interlocking cilia (see p. 533) are present on the dorsalward slope of the ridge. Such a ridge tends to become lower some time after the mussel is opened, and also on preservation, perhaps indicating that it is partly due to turgescence.

A marked ridge in the mantle (Fig. 6, B and C) is also generally found in mussels with a gill, or gills, almost entirely absent for a short distance, as may occur through injury, in some instances by whelk-tingles. It would appear to be an effort of the mantle to effect a ciliary junction with the rudimentary or missing part of the gill. A ridge in one instance was noticed to be strongly pigmented.

Gills in which folding has taken place, occasionally have short secondary food grooves along the bend, at what is now the free edge of the gill. It is perhaps only when the filaments are split or injured at the bend that a new food groove arises in this position.

Mussels with folded gills were often in poor condition: the folding, involving considerable reduction of the gill surface and pumping power, as well as frequently disorganising the main food grooves, must necessarily reduce the quantity of food passing to the mouth. In cases, however, where the gill is folded over neatly, as in Figure 1 (p. 491), beyond causing a certain reduction in the area of the catching surface, the food paths would not seem to be greatly disorganised, as particles on the descending filaments pass round the bend and into the main food groove—though it now runs across the surface of the gill—and are carried along it towards the mouth.

Figure 7 (p. 499) shows to what an extent the normal food currents of a gill may be disorganised by irregular folding with concrescence. All four gills of this mussel were in a similar condition. When the gills were supplied with carmine particles it was evident that there was no continuous ciliary current at, or near, the ventral free edge of the gill, or in any position on the gill. Particles collected in small masses, either because of the meeting of ciliary currents, or because of the abrupt termination of short irregular food grooves. No doubt when these reached a certain size they would spill over, and coming under the influence of other currents, might in some cases travel a little further towards the mouth. As all the gills were short there was no likelihood that particles dropping from one or other of the left or right gills would be caught up by the other one of that side. In spite of the apparent impossibility of food in any quantity being able to reach the mouth, the mussel in this particular instance was in fair condition. This perhaps may be regarded as an indication that the changes in gill structure were rapid.

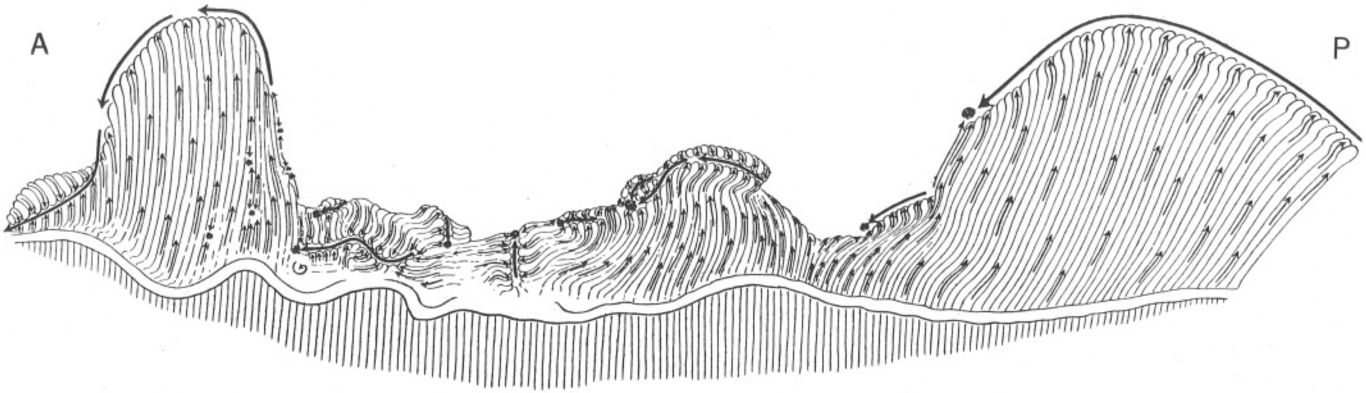

Fig. 7.—Sketch of living gill from a mussel from North Bank, Fal Estuary, 1930, showing disorganisation of food currents by what is, presumably, irregular folding of the gill with fusion. All four gills of this mussel were in a similar state. The direction of the currents along food grooves is indicated by heavy arrows; the direction of the currents caused by the frontal cilia on the filaments by fine arrows. The currents were investigated only by means of powdered carmine on the surface of the gill. A certain amount of reversal of ciliary current appeared to have occurred as indicated. Towards the anterior end of the gill reversal occurred on filaments without secondary grooves: some fusion of filaments laterally had taken place in this region. In two places the dorsal food groove on the ascending lamella was missing. The ascending lamella was considerably shorter than the descending lamella. A, anterior; P, posterior end of gill. The outline of the gill was drawn by camera lucida, but the details were filled in freehand. × ca. $4\frac{1}{2}$.

(*b*) Fusion of the Gill Filaments side by side.

Fusion and crumpling of the filaments, which was greatly developed among the mussels from the Fal Estuary, was very rarely found among mussels—other than those infected with Pinnotheres—from other localities: exceedingly few examples were detected among those from the Estuaries of the Hamoaze and from the Teign Estuary.

This condition varies greatly in extent from the fusion of two or more filaments side by side, to extensive areas of fusion scattered irregularly over the greater part of the lamella.

Some fusion is generally found where slight crumpling or puckering of the gill occurs, as in Figure 8, A (p. 501), and is probably due to crowding of the filaments. In the case of crumpling, the filaments are not only crowded together, but there is also a tendency for them to be forced on to their sides, and, as the lateral faces are of greater width than the frontal, this increases the crowding. In some instances small areas of fusion may be accompanied by a tiny food groove as in Figure 8, B.

Slight fusion of filaments has also been noticed, in some individuals, near the dorsal food groove on the ascending lamella (Fig. 8, C), and is again probably due to the same direct cause, namely crowding, occasioned by slight shortening, antero-posteriorly, of the dorsal free edge of the gill. In the example sketched, seven filaments are fused, but at the food groove the composite filament is not noticeably wider than the normal filaments (see also Rice, **41**, pp. 74, 78).

In some few cases the dorsal food groove on the ascending lamella was seen to be noticeably shortened antero-posteriorly—due apparently in the case sectioned to the presence of cysts*—so that the ascending lamella was thrown into folds parallel to the long axes of the filaments, the folds decreasing in depth ventrally; while the descending lamella was hardly affected, the folds being exceedingly slight and not sufficient to cause fusion of the filaments. Transverse sections showed much fusion of the filaments composing the deep folds of the ascending lamella (Fig. 9, p. 502); the fusion was, however, almost entirely restricted to the abfrontal ends of the filaments and would have been practically invisible in surface view.

Fusion, according to Rice, does not normally occur in filamentous gills, even where folding is extreme, as in Pecten, and he says that its absence "may be easily explained on the ground of the looser structure of the gill (as compared with the folded lamellar gills of certain Eulamellibranchs†) and the possibility of a displacement of the filaments, with consequent

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* The cyst sectioned was lined with ciliated epithelium: the contained body had a roughly concentric structure, but was evidently degenerating and could not be identified.

† The interpolation is mine.

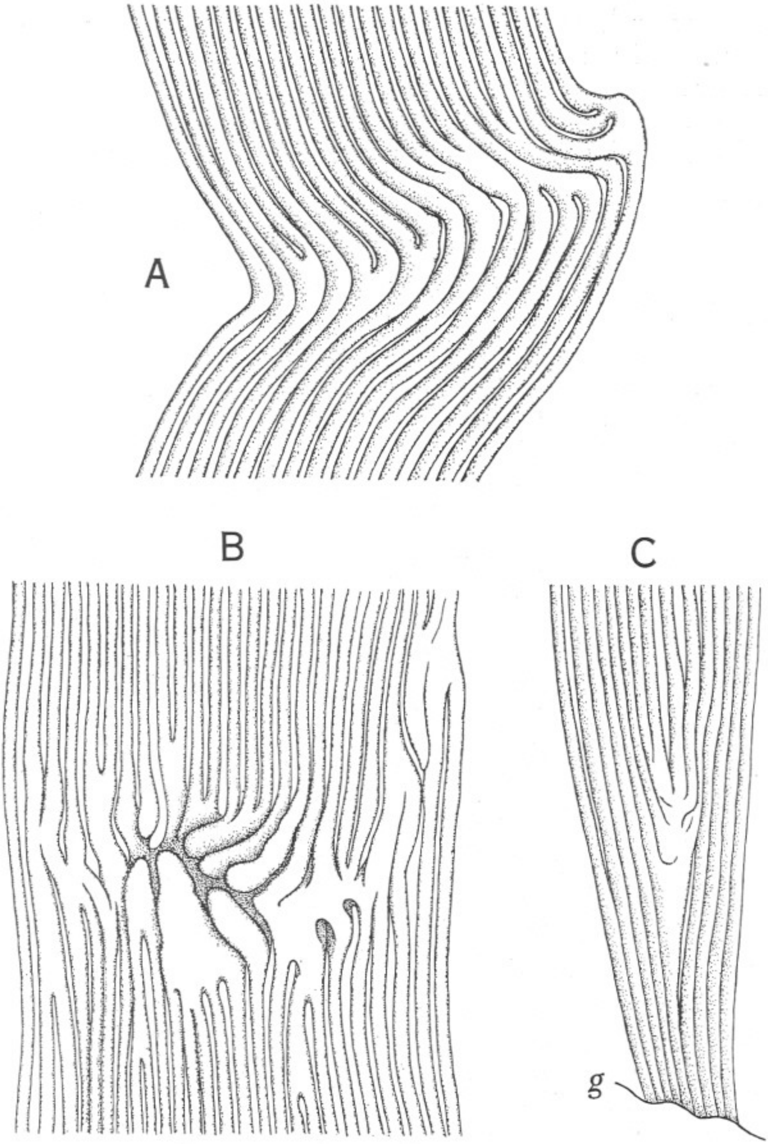

FIG. 8.—Sketches showing fusion of gill filaments on the gills of a mussel from Trelissick Reach, Fal River, November 1, 1927. From preserved material. × ca. 41½.

A. Fusion of gill filaments where crowding had occurred, owing to the filaments being bent out of their true direction. This is an enlargement of a small area, just posterior to the secondary gill or fold, on the right inner gill sketched in Fig. 1, p. 920, Part I (**2**).

B. Fusion of gill filaments, together with a tiny secondary food groove. From right outer gill. (Anterior is on the left.)

C. Fusion of seven filaments near the dorsal food groove on the ascending lamella, right inner gill. g, ventral edge of dorsal food groove.

relief of pressure" (**41**, p. 78). Its presence in Mytilus gills, which have been thrown into folds, is therefore of interest.

A section such as that of Figure 9 has a superficial resemblance to those of *Avicula argentea* (**43**, Fig. 16, p. 212) and *Margaritifera vulgaris* (**24**, Figs. 7, 12, Pl. 27), but in these two forms fusion of the actual filaments does not occur ; there is a tendency for the filaments to form interlamellar extensions, particularly in the region of the ciliated discs, which by their fusion form interfilamentar junctions ; this is clearly seen from Herdman's Figure 6, Plate 27 (**24**).

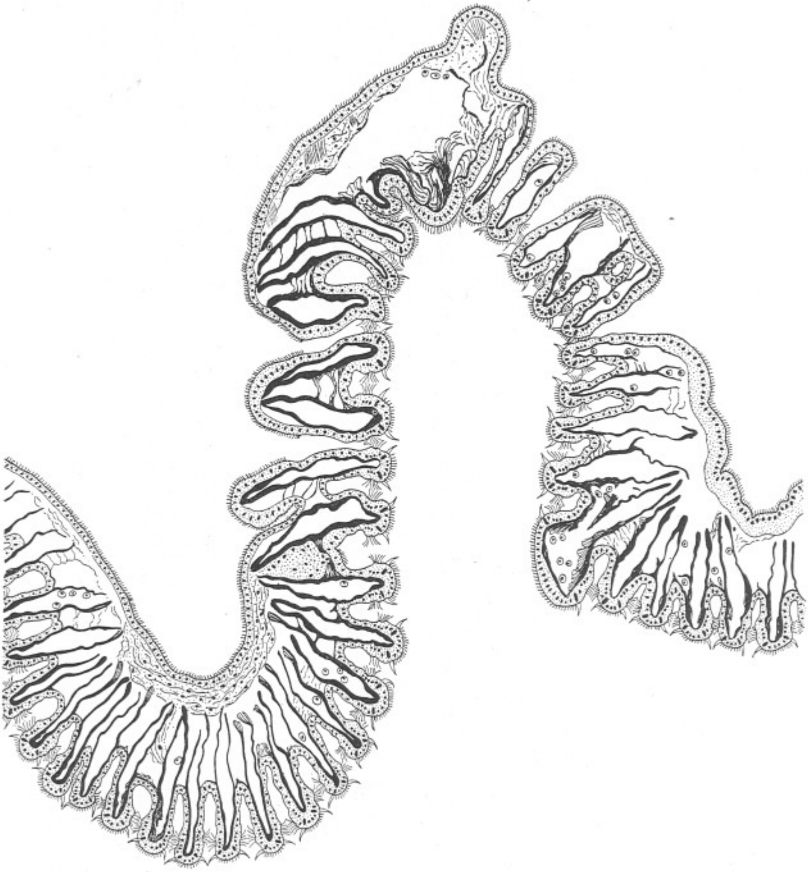

FIG. 9.—Transverse section through dorso-ventral folds in an ascending lamella, near the dorsal food groove, of a mussel from North Bank, Fal Estuary, 1930. The distribution of the cilia and nuclei is represented diagrammatically. The extensive area of ciliation on the abfrontal surface of the lamella, is, however, noteworthy. Bouin's fixative ; Mann's methyl-blue-eosin. × ca. $93\frac{1}{3}$.

The foregoing examples of fusion would appear to be due to crowding, consequent on the puckering and folding of the lamellæ—whatever may be the cause of the latter—but it is more difficult to suggest a cause for the extensive areas of fusion involving irregularly the greater part of a lamella.

A crumpled or puckered appearance of the entire surface of the lamellæ of some gills has been noticed—sometimes restricted to one lamella of a

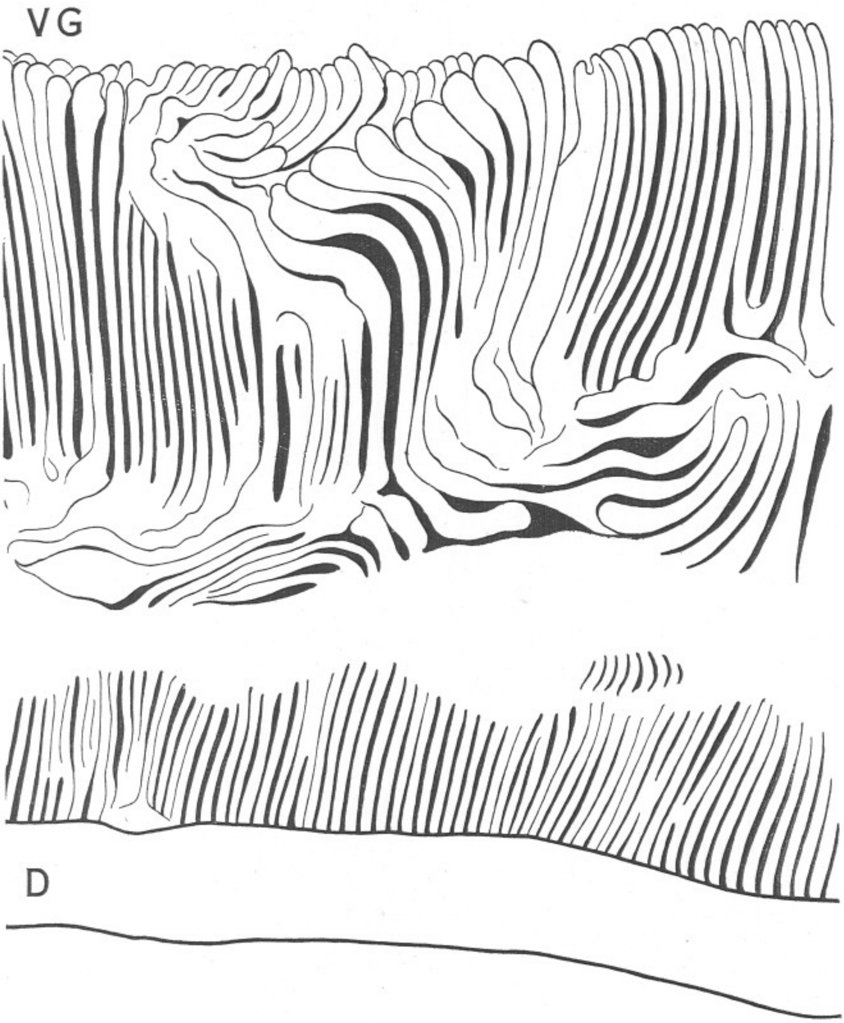

FIG. 10.—Sketch of part of ascending lamella of a gill, showing contortion and fusion of the filaments; in some places the filaments are almost at right angles to their normal direction. The ascending lamella was considerably shorter, dorso-ventrally, than the descending lamella. VG, ventral edge of gill; D, dorsal food groove. From a mussel from Mylor Bank, Fal Estuary, November 22, 1927; preserved material. × ca. $24\frac{1}{3}$.

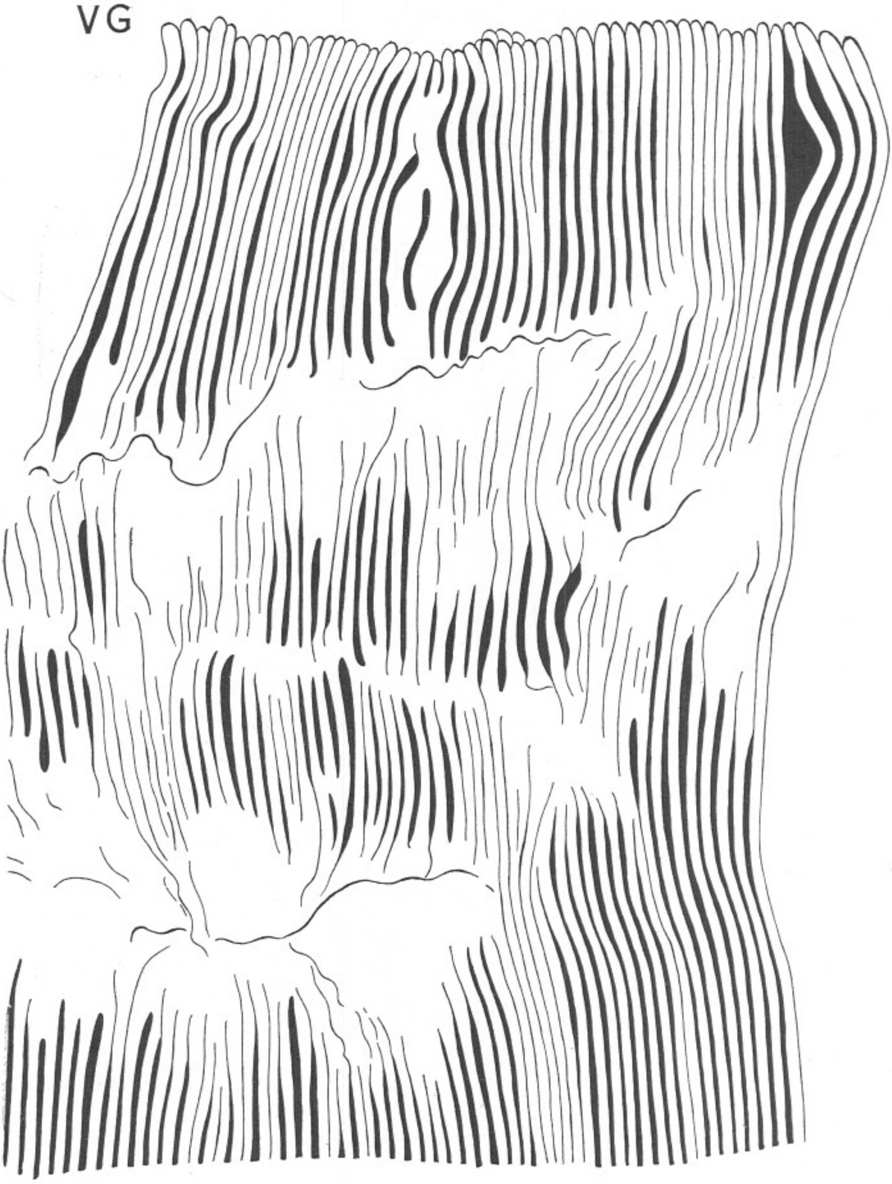

Fig. 11.—Sketch of part of ascending lamella of a gill, showing considerable areas of fusion of the filaments. The living gill showed much brown pigment, collected in masses. VG, ventral edge of gill. From a mussel from near the junction of the Tamar and Tavy (Weir Point), November 3, 1927: preserved material. × ca. 24⅓.

gill and that most usually the ascending lamella—which remains when the gill is placed in water, and this condition may possibly be the forerunner of cases of extensive fusion, where the filaments, when distinguishable, appear to have undergone a kind of puckering, some running almost at right-angles to their normal direction (Fig. 10, p. 503).

In other instances, however, the fused areas have an approximately flat surface (Fig. 11, p. 504), which has the appearance of being due to the fusion side by side of undisturbed filaments, and it is questionable whether this may not have occurred in certain circumstances, consequent on the possible swelling of filaments. It is, however, perhaps only a further stage in the process of fusion, masking the irregular surface which follows puckering. The irregular disposition of the chitinous supports, as seen in sections, suggests this possibility, though they have doubtless undergone a certain amount of distortion during embedding and sectioning.

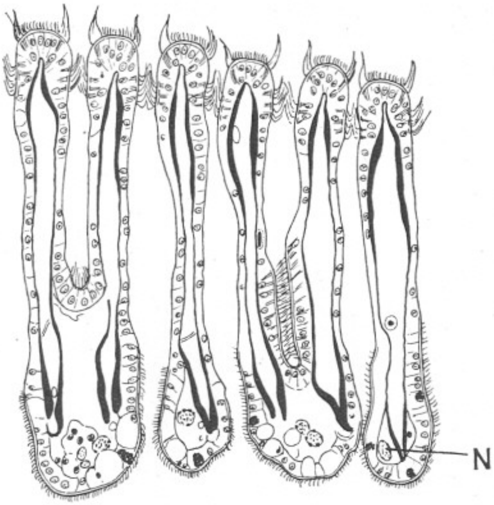

FIG. 12.—Transverse section, single gill lamella, showing fusion of the interlamellar (abfrontal) ends of filaments. N, ? nerve. Bouin's fixative; Mann's methyl-blue-eosin. × 210.

Probable stages in the process of fusion are given in Figures 12; 13, A and B; and 14. Figures 12 and 13, A and B (p. 506), are from a series from one gill of a mussel from the Fal Estuary, 1930; Figure 13, A and B, from different levels of the same lamella, and Figure 12 from the opposite lamella. Figure 14 (p. 508) is a section through part of the same lamella as that sketched in surface view in Figure 11 (p. 504), and was from a mussel from near Weir Point (Tamar Estuary). While the ascending lamella showed extensive areas of fusion, the descending one was almost

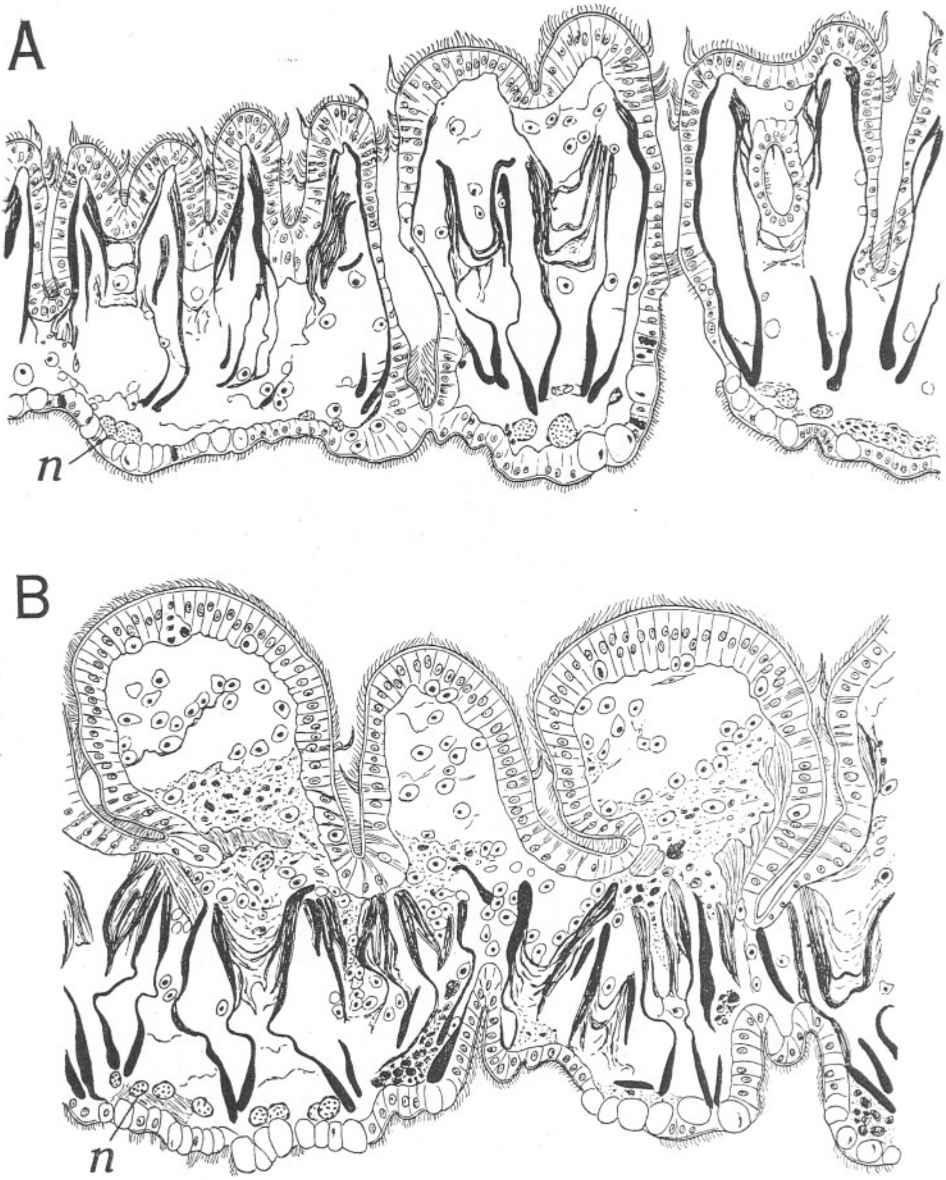

FIG. 13.

A. Transverse section of part of the opposite lamella to that of Fig. 12, showing a further stage in fusion. Towards the centre of the figure three filaments have fused—as shown by the three sets of chitinous supports—though the frontal surface has the appearance of two fused filaments. Between the three sets of chitinous supports are strands or loops of pale staining chitin. The abfrontal epithelium is continuously ciliated, except for the numerous gland cells, which are swollen and pale staining, or darkly staining and granular. n, ? nerve. Bouin's fixative; Mann's methyl-blue-eosin. × 210.

B. Transverse section, single lamella, where fusion is pronounced. Not only has fusion occurred, but also a certain amount of abnormal proliferation of the frontal surface of the lamella in the form of broad ridges and bosses. Ciliated discs persist in some of the furrows, and also latero-frontal and in some instances the lateral cilia. The frontal ends of the chitinous supports are abnormally developed, the additional chitin being pale staining. Gland cells are numerous in the abfrontal epithelium. n, ? nerve. Bouin's fixative; iron hæmatoxylin and acid fuchsin. × 210.

normal, very little fusion occurring: this restriction of fusion to one lamella while the opposite one is almost normal is a rather common feature.

The ridges and bosses caused by irregular proliferation of the frontal epithelium, as in Figure 13, B, may possibly in turn fuse to give a surface resembling that of Figure 14. This is perhaps indicated by the two enclosed spaces—one showing the remains of ciliated discs—and the deep furrow shown in that figure.

While the fused epithelial surfaces doubtless degenerate and are removed by the action of phagocytes, the chitinous supports of the filaments would appear to be very resistant. They are, therefore, in the majority of cases, clear and reliable indicators of the number of filaments which have fused to form a certain stretch of fused lamella, and would seem to offer definite evidence that it is fusion which has occurred.

It may be noted in Figure 13, A, that the central portion of the section, which from the frontal surface would appear to have been formed by the fusion of two filaments, is in reality formed by the fusion of three, as shown by the chitinous supports. In this part of the section the gradual retreat of the spaces, or the smoothing out of the furrows, separating the three filaments, is clearly shown by the successive positions of the strands or loops of pale staining chitin.

The great depth of the cells of the frontal epithelium as shown in Figure 13, A and B, especially in Figure 13, B, may be noted; it will be referred to again under the following section.

Areas of fusion are often visible at a glance owing to their heavy pigmentation, the pigment frequently occurring in dark brown or orange masses of considerable size. Mytilus gills are normally somewhat pigmented, especially along the four main food grooves at the free ventral edges of the gills. The colour is generally yellow or pale orange, though in young normal mussels from Padstow the gills were tinted, more or less entirely, a bluish purple. Following fusion, and the degeneration of a certain amount of tissue, the pigment granules are doubtless liberated and collect in masses (cf. the pigment, which following the transformation of tissue previous to regeneration in *Tubularia mesembryanthemum*, is found lying in a ball within the digestive tract of the newly formed hydranth (**30**, pp. 59, 268).

The ciliation of some areas of fusion was investigated by means of powdered carmine. The ciliary current mostly goes ventrally towards the free edge of the gill, though not always directly ventrally; it may pass somewhat diagonally across the area of fusion. In other cases investigated there were small areas of reversal—judged entirely by movement of carmine particles—and sometimes a swirl of current. Such variations

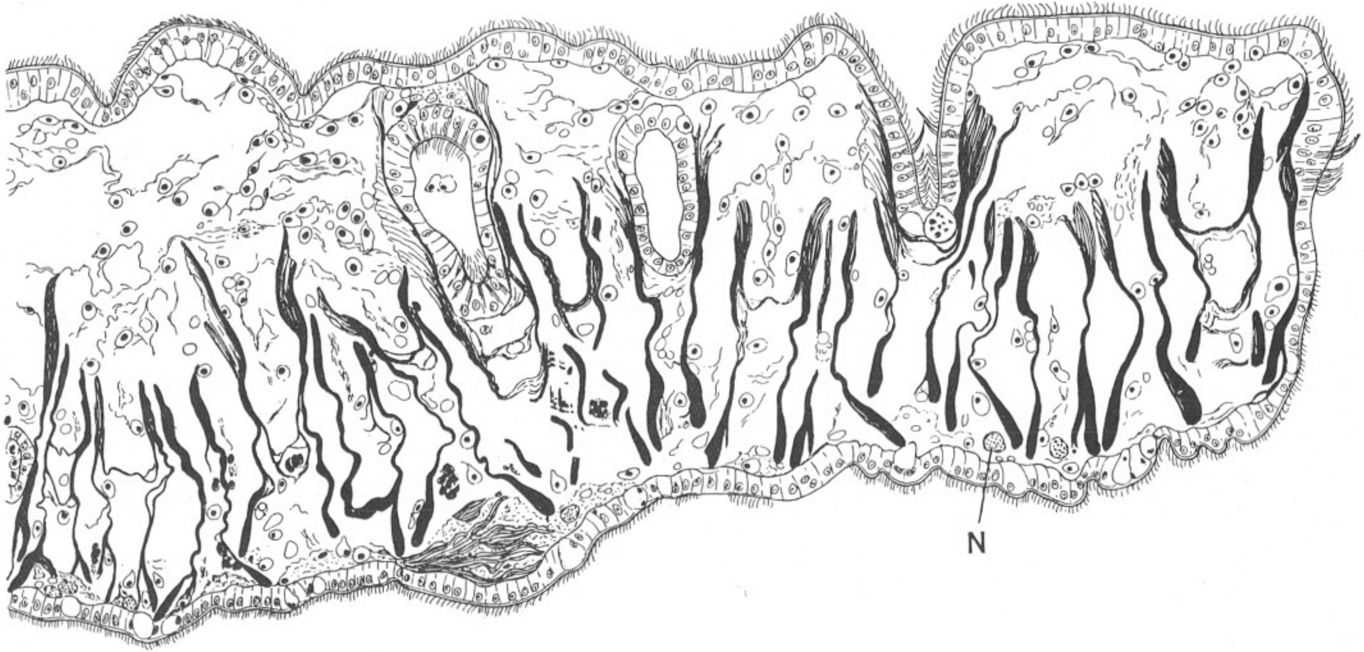

FIG. 14.—Transverse section, ascending lamella, showing extensive fusion of the filaments (17 filaments in the part sketched). This is from the lamella, part of which is shown in surface view in Fig. 11. The frontal surface is approximately flat except for a deep furrow towards the right side of the section: in the furrow latero-frontal and lateral cilia are still discernible. Two enclosed spaces, due to incomplete fusion of the filaments, are present; ciliated discs persist in one of these. The frontal half of the chitinous supports have become enlarged by the addition of layers of pale staining chitin. A certain number of gland cells are present among the ciliated cells of the abfrontal epithelium. Small masses of granular pigment occur. N, ? nerve. Bouin's fixative; iron hæmatoxylin and acid fuchsin. × 210.

may possibly depend on whether the fused filaments were straight, askew, or crumpled.

(c) Enlargement of the Gill Filaments.

The enlargement of the gill filaments was a rare occurrence: the majority of such examples—five—came from the estuary at Teignmouth, and one from the Fal Estuary in 1930. (Enlargement of an occasional filament or tiny group of filaments may be found on a gill beneath a pea-crab.) The most striking example was a mussel from Teignmouth (August 21st, 1928) which showed enlargement of the filaments, generally in small groups, in a zone about 2·0 to 3·0 mm. wide along both sides (descending and ascending lamellæ) of the free ventral edges of all four gills. The enlarged filaments had an irregularly swollen appearance, being pitted in some places with small pockets, and tended to overlie laterally the normal filaments, where these occurred (Fig. 15). While the width across the frontal surface of a normal filament is about 0·05 mm., in an enlarged filament it may reach 0·3 mm. or more. Fusion of filaments laterally, however, was of somewhat rare occurrence and where

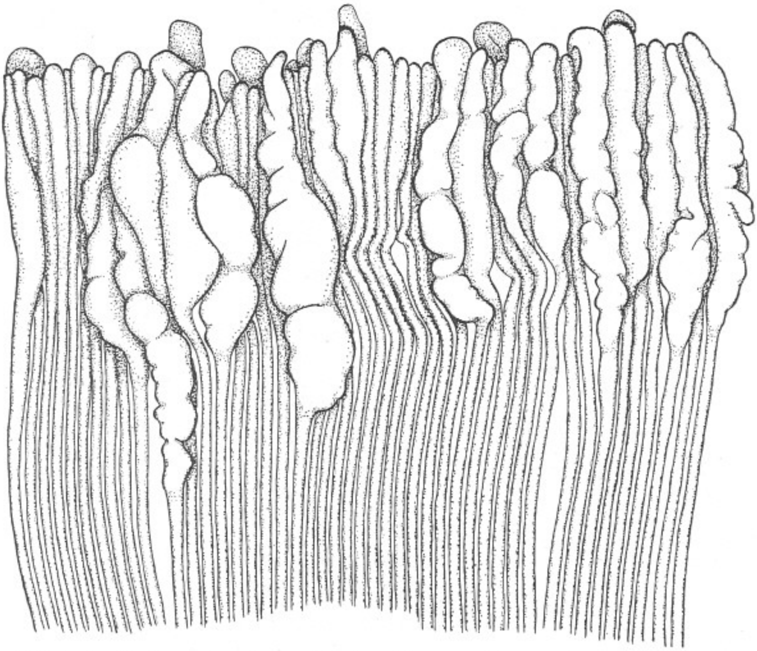

Fig. 15.—Surface view of a small region of an ascending lamella to show enlargement of the filaments in a zone 2·0 to 3·0 mm. wide at the ventral edge of the gill. The main food groove has an irregular appearance owing to the extension ventrally of some of the filaments. From a mussel from Teignmouth, August 21, 1928; preserved material. × ca. $24\frac{1}{3}$.

it had taken place was restricted to the fusion of the abfrontal ends of the filaments. A single filament in side view is shown in Figure 16, A (p. 510). Out-growth of the lobes of the ventral food grooves had occurred giving an irregular appearance to the ventral edges of the gills (Fig. 15), which appeared otherwise to be straight and uninjured.

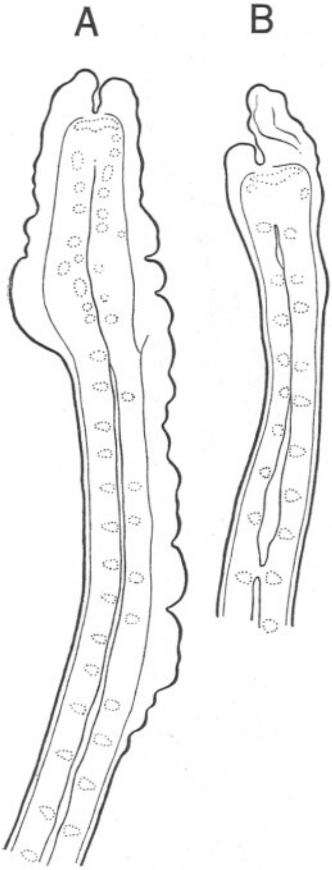

FIG. 16.—Lateral views of two filaments which have suffered enlargement of the frontal surface. B, shows extension of one side of the main ventral food groove. The fine inner line indicates the position of the lateral cilia. From preserved material. × ca. 18¼.

A mussel from the same locality on August 16th, 1928, had the gills in a similar condition, but the enlargement was restricted to a narrower zone (1·0 to 2·0 mm.) at the ventral edges.

The mussels, most unfortunately, were preserved whole in formalin, so that the fixation was poor, but transverse sections of one (Teignmouth, August 21st, 1928) showed certain points fairly clearly (Fig. 17, p. 511). The enlargement of the filament was confined mainly to the frontal face, for the position of the conspicuous lateral and latero-frontal rows of cilia was little changed; proliferation of the ciliated frontal epithelium appeared to have occurred, resulting in a much swollen frontal face with a corresponding enlargement of the internal canal (cf. the apical filaments of the two Eulamellibranchs *Pinna virgata* (**43**, Fig. 17, p. 214) and *Lima inflata* (**43**, Fig. 18, p. 216)). In the section sketched in Figure 17 there appears to be some interlamellar extension of the swollen filament, but this was not evident in all. Transverse sections of the enlarged gill filaments of this mussel showed a great irregular development of the frontal ends of the chitinous supports. While the chitinous supports of normal filaments stain quite darkly, this extra development of chitin is pale staining. Mucus cells were unusually well developed among the ciliated cells of the frontal epithelium; these were seen not only in sections (see Fig. 17) but in single filaments, stained with borax carmine and picro-nigrosin, and mounted whole.

Another mussel, also from Teignmouth (July 10th, 1928), showed slight irregular growth in the occasional extension of a filament beyond the free ventral edge of the gill (Fig. 16, B, p. 510) and in rare isolated groups of

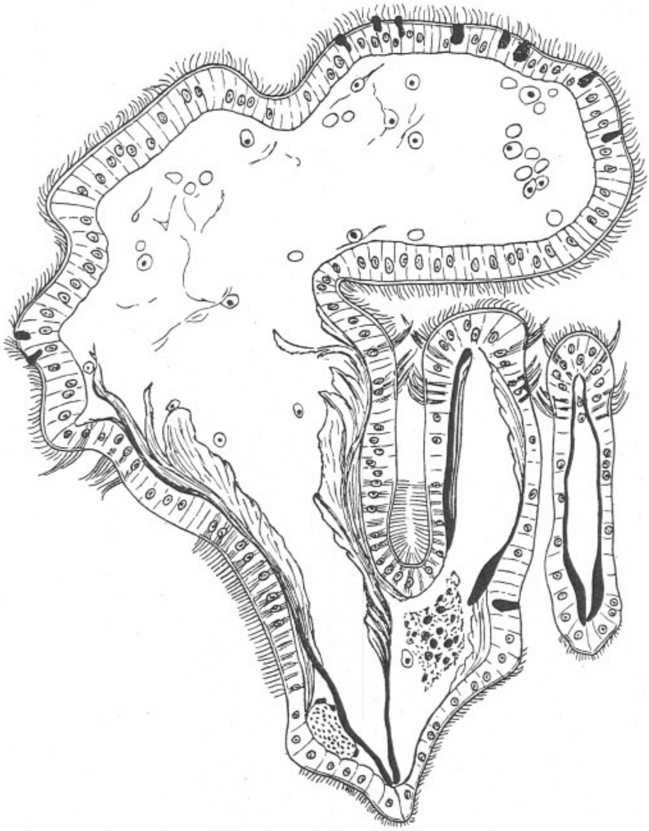

FIG. 17.—Transverse section of filaments from the gill of a mussel from Teignmouth (the same individual from which Fig. 15 was taken), showing one much enlarged filament. As shown by the position of the lateral and latero-frontal cilia, the increased size is largely, or almost entirely, due to the great increase of the frontal surface. This filament has also extended in an interlamellar direction and has partly fused with an adjacent filament, which is only slightly enlarged: a mass of granular pigment is present at the junction of the two filaments. Especially striking is the development of the chitinous support of the enlarged filament; as indicated by the light shading this additional chitin is pale staining. A normal filament is shown on the right. Gland cells are present among the ciliated cells of the frontal epithelium. Formalin; Borax carmine and picro-nigrosin. × 210.

three or four filaments on the surface of the lamellæ as in Figure 18, A (p. 512). Very occasionally a mussel may be opened, in which, following a tear, the torn ends of the filaments have swollen or proliferated in an

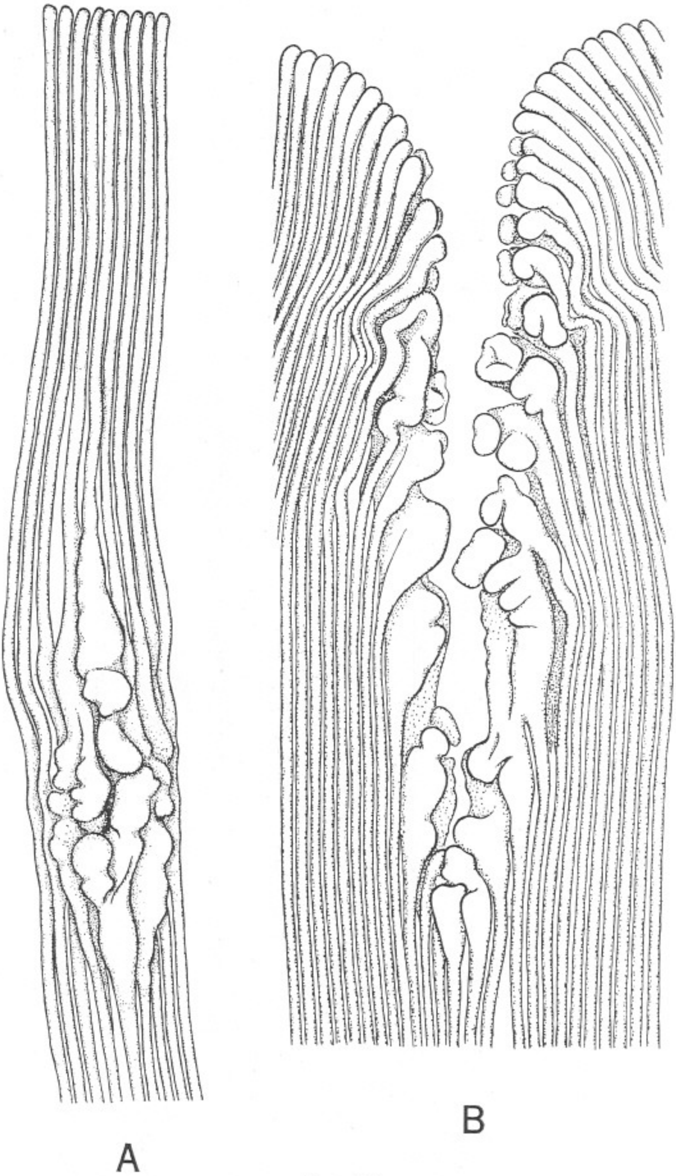

FIG. 18.

A. Sketch showing a small area of enlargement of filaments—three filaments are chiefly concerned—on the surface of a gill of a mussel from Teignmouth, July 10, 1928.

B. Enlargement of the ends of filaments, presumably following a tear, with the formation of a new but irregular food groove. From the same gill as A.

A–B. From preserved material. × ca. 24$\frac{1}{3}$.

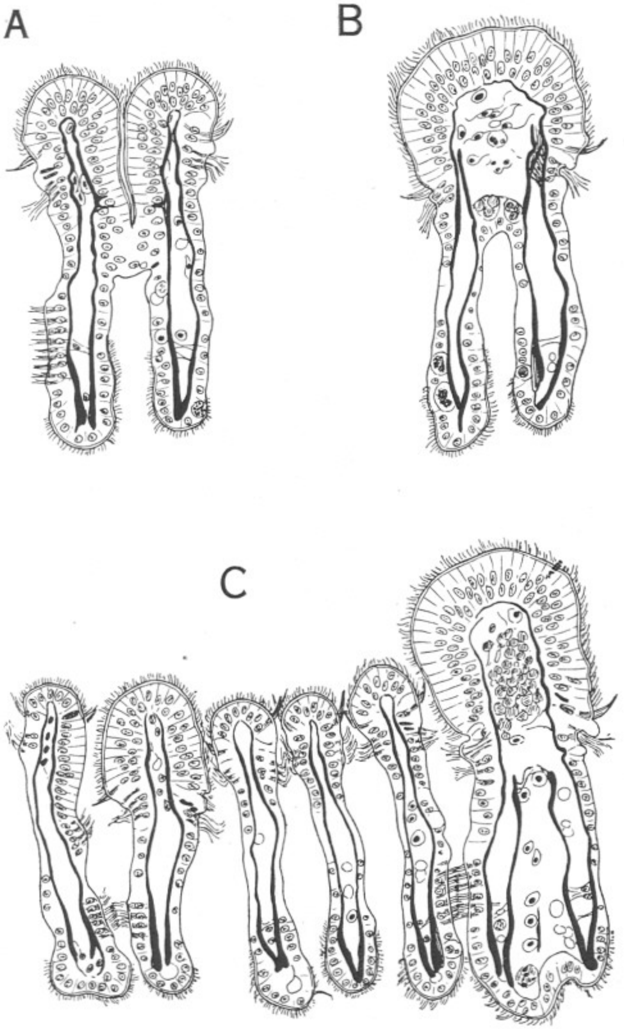

FIG. 19.—Transverse sections (from the same series as that of Fig. 20) showing filaments with abnormally deep cells towards the frontal face; one filament shows deep cells on one side only. To the right of C two fused filaments show a similar condition of the cells. A and B are sections of these same two filaments at a higher—more dorsal—level: in A the fusion is beginning, in B the frontal halves of the two filaments have fused, while in C the fusion is complete. In C a mass of granular pigment is present within the two fused filaments. From a mussel from North Bank, Fal Estuary, 1930. Bouin's fixative; Borax carmine and picro-nigrosin. × 210.

irregular manner while forming a new food groove, as had occurred on the gill of this mussel (Fig. 18, B).

Among the mussels received from the Fal Estuary in March, 1930, a single individual showed enlargement of the filaments. The ventral free edges of the gills were somewhat irregular in places, as though shallow pieces had been removed by injury, and the swollen extensions of the ventral ends of occasional filaments increased the irregular appearance. The scattered groups of swollen filaments were mostly found near the ventral margins of the gills, but rarely the swelling was continued to almost half the width of the gill; the swellings had a much pitted appearance. Some of the lamellæ, however, also showed many of the filaments slightly widened, but otherwise normal. In transverse sections of such filaments it was seen that the widening was due to the unusually great depth of the cells towards the frontal part of the filament (Fig. 19, p. 513) (cf. the condition of the frontal epithelium near the ventral food

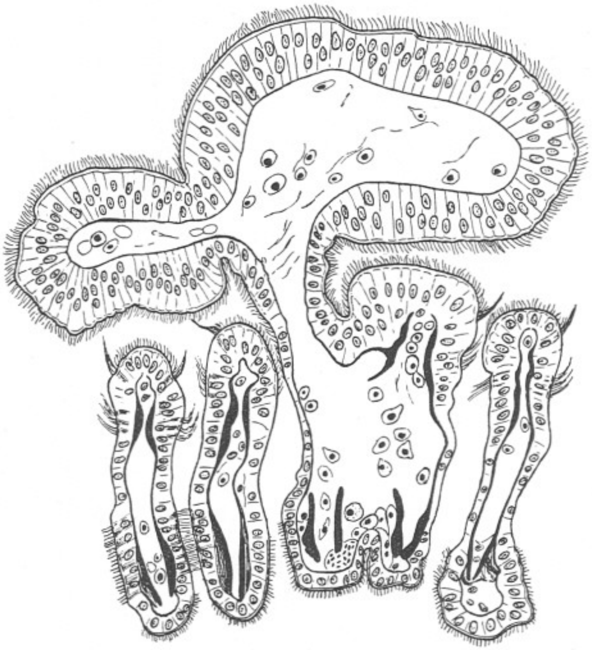

FIG. 20.—Transverse section of five filaments from the gill of a mussel from North Bank, Fal Estuary, 1930, showing a filament with greatly increased frontal surface and great depth of cells, fused with a filament on the right in which the frontal cells are also of great depth. There is no increase in the development of the chitinous supports (cf. Fig. 17). The separate filament on the right shows increased depth of the frontal cells of one side. (From the same series as that of Fig. 19.) Bouin's fixative; Borax carmine and picro-nigrosin. × 210.

grove of normal filaments). Filaments were observed with the cells of one side of normal depth, while those of the opposite side were much deeper. Figure 19, A, B and C (right-hand part of section), which are sections through the same two filaments at different levels, show three stages in the gradual fusion of two filaments with enlarged frontal cells. Transverse sections of much enlarged gill filaments showed in this case, as in those from Teignmouth, that it was mostly proliferation of the frontal cells that had produced the swelling (Fig. 20, p. 514) : these cells were of abnormal depth, in some instances almost as deep again as those of the enlarged filaments of the Teignmouth mussels of August 21st, 1928 (cf. Figs. 17 and 20). There was no increased production of chitin, as in the Teignmouth example sectioned.

The enlargement of the gill filaments in the cases given was due no doubt to increased growth of the frontal epithelium dependent on some factor in the environment, e.g. decrease in salinity with consequent increased endosmosis. The abnormally great depth of the epithelial cells of the gill filaments of some mussels (as in Figs. 19 ; 20) is strongly suggestive of growth acceleration.

In the cases cited the enlargement was mostly of the frontal surface of the filaments, and little interlamellar extension was seen ; that it may occur, however, in such a situation in Mytilus was shown by the swollen out-growths in connexion with the interlamellar junctions in the gill of a mussel from the Fal Estuary.

The cilia on the swollen frontal surfaces beat normally and in general in a ventral direction, as shown by the movement of carmine particles.

(*d*) CONCRESCENCE OF THE TWO GILLS OF ONE SIDE.

A Mytilus from Teignmouth (July 10th, 1928) showed a curious condition of the gills of the right side. Anteriorly, for about 7·0 mm., the two gills appeared to be fused side by side, and, since the outer one was somewhat shorter than the inner, the two ventral food grooves were at different levels ; immediately behind for about 7·0 mm. the two gills were fairly distinct : throughout this anterior region the gill filaments showed much crumpling. The gills then appeared to have fused again, so that in the middle region for about 18·0 mm. there was one " gill " only, but here it appeared to be formed of two lamellæ only —they could be clearly separated to within 3 mm. of the ventral edge, where they were connected by interlamellar junctions—and as both were provided with a dorsal food groove, they were presumably ascending lamellæ ; the gill was entirely free from the body. At this part the gill was about 7 mm. deep. While the gill filaments of the outer lamella appeared from surface view to be normal, those of the inner lamella were in places bent somewhat out of the true dorso-ventral direction (i.e. crumpled), with some slight fusion side by side. For the remaining posterior 20·0 mm. the gills were normal and about 11·0 mm. deep. The shell had suffered no injury, and the inner surface of the valve was perfectly smooth.

A Mytilus from North Bank, Fal Estuary (March, 1930), had the gills of the left side, for about 5·0 mm. in the middle region, exceeding narrow (ca. 1·0 to 4·0 mm. deep), fused together, and entirely free from the body. So far as could be judged, the two ascending lamellæ (see **39**, Fig. 209, p. 229) alone were present in the fused portion as there was a dorsal food groove on both lamellæ. From the gill ridge hung short ends (ca. 1·0 mm. long) of the filaments of the two descending lamellæ. The left valve was occupied by a large blister, and though no hole had been bored through the shell in the region of shortness of the gill (Cliona borings were present in the umbo region), yet this condition was possibly due to injury, for the short ends of the descending filaments appeared to have been cut across. The case previously described may possibly have arisen from a condition such as this, as it is now known that regeneration of the gill may occur (see following note in this Journal, p. 551).

Peck (**37**, p. 50) gives an instance of abnormal concrescence in the gills of Anodonta. "In this case a torn portion of the inner gill-plate of the left side beyond the posterior edge of the root of the foot had become intimately adherent by concrescence to the inner surface of the inner gill-plate of the right side of the animal."

GENERAL CONDITION OF MYTILUS FROM THE VARIOUS LOCALITIES INVESTIGATED.

FAL ESTUARY.*

The mussels obtained from the Fal Estuary in 1927 (1648 examined from October 26th to November 25th) were mostly of small or medium size, ranging, however, from about 4·0 to 10·0 cm. in length, with but few of the large size, and were on the whole in rather poor condition, though the condition varied somewhat in different parts of the Estuary (see Table I). Not only were many of them poorly fished, but a certain number (6·6%) had large blisters and flat areas of wrinkled brown skin on the inner surface of the valves (Fig. 21, p. 519). Some of the blisters were so large that they covered the greater part of the valve and in certain cases projected into the cavity of the opposite one. The covering of such blisters varied greatly : in some it was a soft dark brown skin, in some a

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* A chart of the Fal Estuary may be found in **36**, p. 3.

TABLE I.

CONDITION OF *Mytilus edulis* FROM VARIOUS LOCALITIES IN THE FAL ESTUARY.

Locality in Fal Estuary.	Date.	Number of mussels.	Number of mussels with Pinnotheres.	Number of mussels with Abnormal Gills.	Number of mussels with blisters in valves.	Remarks.
Position not definitely known.	1927 Oct. 26	250	17 (6·8%)	Numerous, but number not known.	9 (3·6%)	On the whole in rather poor condition. 4·0–9·8 cm. in length.
Position not definitely known.	Oct. 28	295	13 (4·4%)	59 (20%)	19 (6·44%)	On the whole in rather poor condition.
East Bank.	Nov. 2	279	9 (3·22%)	88 (31·54%)	23 (8·24%)	On the whole in poor condition.
Trelissick Reach.	Nov. 2	102	3 (2·94%)	19 (18·62%)	0	On the whole in good condition. Mostly about 5 or 6 cm. in length.
Turnaware Bar.	Nov. 10	9	0	2 (22·2%)	0	
Mylor Bank.	Nov. 23	195	13 (6·66%)	90 (46·15%) (*a*) 67 (*b*) 20 (*c*) 3	17 (8·72%)	Medium condition. 5·5–9·0 cm. long.
East Bank.	Nov. 24	254	10 (3·94%)	121 (47·64%) (*a*) 91 (*b*) 30 (*c*) 0	27 (10·63%)	Medium condition. 4·6–9·2 cm. long.
Parson's Bank.	Nov. 25	264	6 (2·27%)	97 (36·74%) (*a*) 74 (*b*) 23 (*c*) 0	14 (5·30%)	Well fished on the whole. Of rather larger size than those from East Bank.
North Bank, between Mylor Pt. and St. Just Pt.	1930 March 7	181	19 (10·5%)	72* (44·44%) (*a*) 22 (*b*) 44 (*c*) 6	26 (5 inhabited by Pinnotheres) (14·36%)	On the whole in fairly good condition. 5·4–12·4 cm. long.

(*a*) = Folding over of free ventral edge of the gill.
(*b*) = Fusion of filaments side by side.
(*c*) = Other abnormalities, including secondary grooves and folds, and simple narrowness of the gill.
* Out of total of 162 free from Pinnotheres.

layer of easily broken shell material, while in others it was so thick that it was difficult to pierce. The contents of those blisters examined, were in some instances almost clear liquid, in others mud, sometimes evil smelling. A certain number of the blisters were no doubt caused by the presence of *Polydora hoplura*,* which badly infested the shells. Cliona had attacked a number of the shells—generally the thicker part towards the umbo—and in a few instances apparently caused blisters.

FIG. 21.—Photographs of a selection of *Mytilus edulis* from the Estuaries of the Fal and Teign, showing blisters on the inner surface of the valves. The mantle has been entirely removed from the valves, except in E, where a triangular area of very thin mantle has been left on the blister. Various reductions.

A. Valve with round blister, which projects (about 8·0 mm.) into the opposite valve, in the posterior region, just ventral to the posterior adductor muscle. In opening the mussel the blister, which is of fairly thin shell, was cut: the dark line on the photograph, due to the cut, is on a level with the edge of the valve. Mussel 6·3 cm. long.

B. Valve with a blister of fairly thin shell material, entirely filling the anterior part of the valve in the mouth region. Mussel 7·5 cm. long.

C. Valve with blisters of fairly thin shell material almost entirely covering the surface. Antero-ventrally one of the blisters, though of shell material, has a wrinkled surface. The depth of the largest blister, measured at the spot where a small piece of the roof has been removed (small black area in photo), is about 11·5 mm. Mussel 9·2 cm. long.

D. Valve with a hard blister, convoluted in form, extending the length of the shell. Mussel 6·0 cm. long.

E. Valve with a large blister, occupying the greater portion, and projecting for about 8 mm. into the opposite valve. The shelly covering is extremely thin and in places has flaked off, exposing the brown skin beneath. The posterior adductor muscle has, to a certain extent, been encroached on by the blister. Towards the anterior and dorsal part of the shell there is a small flat area of dark brown skin. Mussel 7·1 cm. long.

F. Valve with a large smooth blister occupying much of the deeper portion, and reducing the depth of the valve in this region to about 4·0 to 6·0 mm. The blister, in this case, is covered by the shining nacreous layer and appears to be of considerable thickness, while in most other cases the shelly covering, which is somewhat thin, is of a greyish colour with a dull to rather dull surface. Mussel 7·7 cm. long.

G. Valve with almost the entire surface covered by an irregular low blister of dark brown skin. The shining spots on the surface of the blister would appear to be small areas of shell deposit. Posteriorly the blister has been removed from a round area exposing a worm aperture. Mussel 8·0 cm. long.

H. Valve with almost the entire surface covered with blisters, the covering of which is chiefly wrinkled brown skin; in places, however, the lower part of the wall is of very thin shell material. An L-shaped blister in the ventral and anterior part of the valve has had most of its roof removed. Mussel 7·1 cm. long.

I. A solid growth of shell material—judging by the weight—on the inner surface of the valve of a mussel from Teignmouth: it projects about 2·0 mm. beyond the level of the edge of the valve. The surface of the growth is of a dull dark grey colour and finely corrugated. Mussel 7·0 cm. long.

J. Occupying the middle and posterior part of the valve is a rather low irregular blister of hard shell material, with a ridged surface posteriorly. Towards the ventral edge of the valve is a blister of hard shell—except for a narrow irregular line along which it can be pierced by a needle—on a small base: it is about 9·0 mm. deep. Partly merged with the shadow cast by the latter is a small area of wrinkled dark brown skin. Mussel 8·0 cm. long.

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* Identified by Mr. D. P. Wilson.

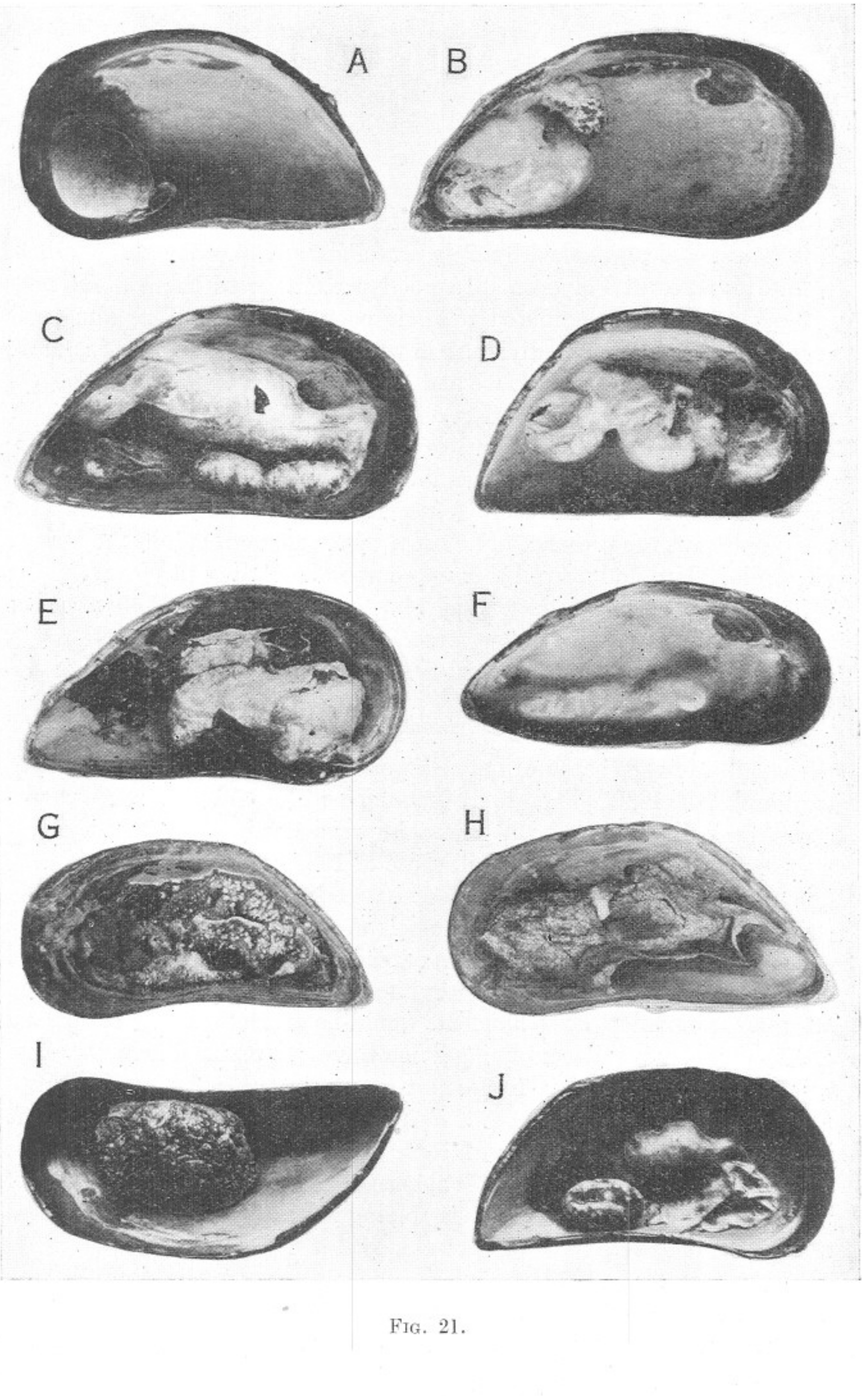

Fig. 21.

Many of the mussels attacked by Polydora showed—on the inner surface of the valves—raised but entirely closed in, tubular passages (see **28**, Fig. III, p. 41) covered with shell deposit of such a thickness that they could only be broken into with bone forceps ; in others, however, the covering was much thinner and in a few cases the tube of the worm projected through the thickness of the mantle into the mantle cavity, the apertures of the tube being entirely internal. A somewhat similar state of affairs has been described by Whitelegge in oysters of the coast of New South Wales attacked by *Polydora ciliata* (**47**, p. 48).

The presence of Polydora in a good percentage of the Fal Estuary mussels no doubt contributed to their poor condition. The abnormal condition of the gills, in individuals in which this took the form of folding, with reduction of the gill surface and disorganisation of the food grooves, no doubt also had an adverse effect on the general condition of the mussels.

In a certain number of the mussels there had been incomplete spawning, with irregular retention of the genital products in small masses projecting from the mantle surface. A peculiarity that was noticed in two specimens, was the presence of a horny, dark-coloured, ball in the byssus pit, while a third had a swollen mass, composed of many tiny, translucent balls, in the same position. It might be noted that among the batches of October 26th and 28th, a few mussels arrived with the mantle much swollen out with an accumulation of water between it and the face of the valve.

As it was desirable to know whether the abnormal conditions of the gills persisted, a further batch of mussels was obtained from the Fal Estuary on March 7th, 1930. These were examined with special reference to the state of the gills. Though the general impression gained was that the gills were not so badly abnormal as in those of 1927, yet the percentage with abnormal gills was quite high, namely, 44·4%. This may perhaps be explained by the fact that these mussels were examined especially for the state of the gills, while the previous batches obtained from the Estuary in 1927 were examined primarily for Pinnotheres : in a rapid inspection small areas of fusion of the filaments would be overlooked. In the March 1930 sample, mussels containing Pinnotheres of a size likely to cause injury have been omitted from the percentage with affected gills given above. While the percentage of mussels with abnormal gills is high, it is composed mostly of those with some degree of fusion of the filaments ; 22 only—out of a total of 72 with abnormal gills—had the ventral edge of the gill folded over, and in these the folding was not generally as extensive as in those of 1927.

The mussels of the 1930 batch varied in length between 5·4 and 12·4 cm., very few being over 9·0 cm. long. They were on the whole in fairly good condition, though a certain number, including those with highly abnormal gills—with the surface much reduced and food grooves disorganised—were in poor condition.

Blisters were present in 26 mussels out of a total of 181 (14·36%). In some specimens they occurred in both valves, varying in number from one to three in each. The blisters were broken open and the contents examined : they mostly contained liquid with a varying quantity of mud ; in an exceptional case a piece of the mantle appeared to have been included. Worms were found in nine of the blisters, and in a further six the mud was in the form of fæces, indicating the previous presence of worms. Those found in seven of the blisters were one or more individuals of *Dodecaceria concharum*,* associated in one instance with three or four individuals of *Polydora ciliata*, while in two of the blisters Polydora was present alone. Some few shells were noticed with borings of *Cliona celata* in the thicker part of the shell near the umbo. Old borings of whelk-tingles were seen in some of the shells (about nine ; in two cases, one in each valve) ; they had been covered by shell deposit or skin, and in a few instances had given rise to large blisters. Very rarely blisters so formed were occupied by Dodecaceria or coated with *Cliona celata*,† these forms, no doubt, following the whelk-tingle. In three cases it was noticed that the outer gill of one side was extremely narrow or almost missing near the position of a former Gastropod boring ; the whelk-tingle, no doubt, had partly eaten the gill before being disturbed.

ESTUARIES OF THE HAMOAZE, NEAR WEIR POINT.

Mussels from this locality—1291 were examined between October 8th, 1927, and February 17th, 1928—were of varying size, from about 4·0 cm. to 12·0 cm. long ; the batches examined were fairly well fished, though the condition varied somewhat. A number had the shells covered with Halichondria. A certain amount of infection with Polydora occurred : in three cases it was noticed that the tube of the worm passed through the mantle so that the openings were entirely internal ; two of these contained *P. hoplura*, while nothing was found in the third. Mytilus with abnormal gills, other than those inhabited by Pinnotheres, were of rare occurrence.

ESTUARY OF THE YEALM.

The samples obtained from the Yealm Estuary—296 were examined between October 10th, 1927, and August 3rd, 1928—were composed of a good percentage of large specimens (about 7·0 to 12·0 cm. long), but the shape of the shell was very different from that of the Padstow mussels, which were also of large size, being of greater breadth in relation to the height. They were generally well fished, but the flesh inclined to be

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* Identified by Mr. D. P. Wilson. † Identified by Mr. M. Burton.

yellowish. Very few mussels were noticed with abnormal gills, other than those infected with Pinnotheres, and the percentage of infected mussels was high.

ESTUARY OF THE TEIGN.

The mussels from the Teign Estuary—9262 were examined between December 6th, 1927, and February 26th, 1929—were mostly of small or medium size and on the whole rather poorly fished, though the condition varied somewhat with the different batches, roughly of about 1000 each; those on January 4th, July 10th, July 19th, and August 21st, 1928, being in fairly good condition. Many were infested with Polydora, the inner surface of the valves showing raised, but covered in, tubular passages of the worms (see **28**, Fig. 111, p. 41). A small number had blisters in the valves; one had a peculiar, large growth of shell in one valve, which, judging by the weight, was solid (Fig. 21, I, p. 519).

Two specimens, out of a total of 9262 mussels, were seen to be infested with the sporocysts and cercariæ (Bucephalus) of Gasterostomum.

About a dozen cases were noted of the presence of a horny ball in the byssus pit.

Mussels with abnormal gills were of exceptional occurrence, and in most of those noticed the abnormality consisted in enlargement of the gill filaments in certain areas.

It is of interest to note that Patella taken from mussels from this locality are a high shelled form (see also Report of the Council, Journ. Mar. Biol. Assoc., Vol. XVI (N.S.), p. 993, 1930).

THE ESTUARY OF THE CAMEL, NEAR ST. ISSEY CLIFF, PADSTOW.

The mussels from the Estuary at Padstow—10,866 were examined between November 8th, 1927, and August 9th, 1929—were fine specimens with smooth, clean shells, high and not very broad. The batches, of about 1000 each, contained a majority of medium and large specimens up to about 13·5 cm. in length. Throughout the period during which mussels were obtained, they were on the whole consistently well fished, with light-coloured flesh.

Blisters, in the valves of the Padstow mussels, were rare; infection with Polydora was slight, and it was only exceptionally that the worm was found in small heaps of mud just inside the valves at the posterior end.

Infection by a species of Trematode (probably a new species*) occurred in about 235 out of the total of 10,866 mussels examined (2·16%), and seven cases were noted of infection by the sporocysts and cercariæ of Gasterostomum.

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* The Trematode is being investigated at Leeds University.

Exceedingly few specimens—other than those infected by Pinnotheres or the Trematode—showed any abnormalities of the gills.

THE PROMENADE PIER, PLYMOUTH.

Two small batches only were examined from the Promenade Pier, one in December, 1927, of 232 mussels, and one in September, 1928, of 108 mussels, a total of 340 mussels. They were of small size: those of the former date were poorly fished, those of the latter date were well fished. A good number had the gills with jagged ventral edges, and three or so had the gills absent, or much reduced in length (dorso-ventrally), for a short distance, with a ridge in the mantle in this region. These have not been considered as abnormalities, as they were most probably due to injury by animals. A single Pinnotheres was found in each batch of mussels.

DISCUSSION.

The abnormalities of the gills of Mytilus, which have been described would appear to be correlated with some factor or combination of factors in the environment, and in the very great majority of cases not to be due to mechanical injury.

Mussels in estuarine, and especially in high estuarine situations, are subject to very fluctuating environmental conditions; great salinity variations are known to occur, the quantity of detritus carried by the water would vary greatly, and possibly also the mineral constituents of the water and of the silt on the beds, temperature and other factors. Certainly the Fal Estuary mussels would appear to have been, and perhaps are still, subject to the influence of some adverse factor or factors which have upset the physiological processes, resulting in a high percentage of mussels with badly abnormal gills; but without experimental work it is useless to attempt to attribute the abnormality of these mussels to any one factor. It is curious that mussels from other estuaries (see section, p. 516) were so little affected, and it would appear that conditions in the Fal Estuary differ markedly in some respect.

The various banks in the Fal Estuary* from which mussels were obtained are "mainly muddy, with, in places, top dressings of small shells which vary in amount in different parts"; but the North Bank and southern part of the Mylor and East Banks, however, have an admixture of calcareous algal gravel, forming "a bottom of medium nature from a slightly muddy gravel, to a slightly gravelly mud" (see Orton, **36**, p. 73).

From the work of Orton (**35**, **36**) on the Fal Estuary oyster beds, it is known that the soil of the beds is rich in certain metals, and some of these

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* A chart of the Fal Estuary may be found in **36**, p. 3.

may just possibly have an adverse effect on mussels. The soil on some of the beds, especially the Mylor Bank, contains an appreciable amount of copper (**36**, pp. 67, 70 ; **35**, p. 156), and it is noteworthy that Orton records that there was a distinct variation in the absorption of copper by oysters in March and May, 1921, and November, 1924. He suggests that this difference may mean " either that the copper in the bottom soil on Mylor Bank is becoming covered over, or is to some way losing its power to affect the oysters, or that oysters absorb copper differently at different seasons of the year " (**36**, pp. 67). Oysters apparently " can carry an unbelievable amount of copper in their tissues and still remain healthy in the sense that they are capable of reproduction " (**35**, p. 146). No mussels, however, from the Fal Estuary, or indeed from any other locality, have been noticed with any trace of greenness due to copper absorption, and it is possible that mussels are affected in a different way from oysters by the presence of copper, for Dodgson (**12**, p. 232) apparently found that copper salts had a deleterious effect on mussels, though this was probably in standing water.

Arsenic in somewhat large amounts—arsenic mines occur on the tributaries of the Fal—is also present in the silt on the banks (**35**, pp. 150, 153, 156, 159, 171). Its effect on mussels is unknown, but it may be noted that arsenic, as well as copper, mines were worked at one time also on the River Tamar, below Calstock—though they have been abandoned for some years—and mussels with abnormal gills are exceedingly rare from the beds near Weir Point, at the junction of the Tamar and Tavy.

Zinc occurs in appreciable amounts ; judging by the quantity present in oysters it would appear to be greatest in the locality of Restronguet Creek (**35**, p. 147). Zinc is apparently very toxic to mussels, at least, in standing water, for Dodgson (**12**, p. 140) found that it was impossible to use galvanised wire netting in cleansing experiments because " zinc was deleterious to the mussels, even to the extent of killing them." Under natural conditions, however, the toxicity of zinc to marine animals is probably very slight (see Orton, **35**, p. 147).

In an analysis of samples of soil from beds in the Fal Estuary, 100 to 1600 parts of arsenic, 16 to 240 parts of copper, 21 to 160 parts of zinc, and 20 to 40 parts of tin per million were found simultaneously (see Orton, **35**, p. 159).

The most comprehensive account of the physiology of the mussel is to be found in the section on " The Physiology of the Mussel with special reference to purification " in Dodgson's " Report on Mussel Purification " (**12**). He observed the conditions under which mussels will function normally, and one is impressed with their hardiness and tolerance to widely differing conditions. Their behaviour with regard to much silt in the water (**12**, p. 175), strength of tidal currents (p. 191), variations in temperature (pp. 194, 198), and in salinity (pp. 208, 209), and lack of oxygen (p. 221) is dealt with in his work. The fact that mussels may exist for as long as 40 days under anærobic conditions, whilst ciliary action may persist for at least 25 days (**12**, p. 221), is especially interesting in view of conditions—such as temporary silting up of mud on the beds, sudden decrease in salinity, etc.—which might exist on the beds causing mussels to remain closed for long periods, with a possible adverse effect on the gills. According to Gray (**21**, p. 79), however, in closed mussels (removed from sea-water) ciliary movement would most probably be inhibited in two or three hours, owing to the concentration of CO_2 in the shell water, and thus the oxygen requirements of the animal would be reduced.

That mussels are tolerant of wide variations in salinity, and may even survive in fresh water, if the dilution of the sea-water be gradual, was shown as long ago as 1816 by Beudant (see Fredericq, **20**, p. 27), but it is well known that heavy mortality may be caused among mussels (**18**, p. 241)—and oysters (**36**, p. 69 ; **8**, p. 17)—in certain situations in estuaries by excessive freshness of the water due to exceptionally heavy rainfall. It is perhaps possible that sudden variations in salinity of an order not sufficient to cause death of the mussel, might yet adversely affect the gills. In spite of the great range of tolerance of the mussel, Flattely and Walton (**19**, p. 81) consider that there is undoubtedly a mean optimum salinity, and it is when exposed to this that the animal is capable of reaching its full development.

The Fal Estuary mussels were on the whole in poor condition, but it is impossible to say whether this was originally the cause or the effect of the abnormal conditions of the gills. As previously mentioned (p. 516), the mussels were badly infested with Polydora and to a less extent with Dodecaceria and Cliona, which in some cases had apparently caused the formation of large blisters in the valves, with general weakening of the mussels ; in some instances the mantle being nothing more than a thin, transparent skin. In this connection it is noteworthy that Daniel (**11**, p. 154) found, in comparing mussels deprived of food with mussels under normal conditions, that they had lost the power to control the water content of the tissue and that " In proportion to the total weight, the loss of water from the tissues of the mussels deprived of food is greater than that which occurs in the control mussels " (**11**, p. 158).

The factor or factors acting on the Fal Estuary mussels have apparently resulted in some cases in a tendency for the gill to collapse, the middle region—the part least supported—folding over longitudinally. Once folding had occurred, fusion of the folded over portion with the surface of the lamella beneath it would appear almost inevitably to follow. In other instances crumpling or puckering had arisen, most probably resulting in the crowding together of the filaments in certain areas, which, when it became marked, would cause fusion of the filaments. It is curious that in gills which showed numerous areas of fusion it was frequently only one lamella of a gill which was affected, and that most usually the ascending lamella.

As is well known, concrescence is a common phenomenon among the Lamellibranchs, and various authors have given examples of variation—within the same species—in the concresence of gills with the visceral mass, with the mantle and between themselves (see Pelseneer, **38**, pp. 214, 215; Odhner, **32**, pp. 45, 48, 50, 53, 55, 60, 64; and Jackson, **25**, p. 326 footnote).

In certain Eulamellibranchs—such as *Cardium edule, Chama pellucida, Batissa tenebrosa, Psammobia vespertina, Donax serra*, etc.—where there is folding of the gill, Rice (**41**, p. 77) has described fusion of the gill filaments as a mechanical correlative of the folding of the lamellæ with consequent crowding of the filaments in certain regions; in this way explaining the presence of a greater number in the upper (dorsal) part of a fold than in the lower (ventral). Ridewood (**43**, p. 159) questioned whether the numerical discrepancy was not due to filamentar branching in the upper parts rather than to fusion in the lower parts of a fold. While perhaps fusion would seem more fully to satisfy the conditions, it is not apparent from Rice's sections through the gill of *Cardium edule* (**41**, Figs. 4–8, p. 79), whether it is fusion or branching. In the case of Mytilus the persistence of the separate chitinous supports, after fusion, would seem clearly to indicate that it is a case of fusion, and not of splitting or branching.

Rice (**41**, p. 78) found that in the Filibranchs—where the gill filaments are only loosely connected by ciliated discs—fusion of gill filaments side by side does not normally occur, even where the folding is extreme, the connexion being sufficiently loose to allow a considerable amount of play. In the light of Rice's findings, the widespread occurrence, among the Fal Estuary mussels, of varying degrees of fusion is of especial interest.

The enlargement of the gill filaments noted in five mussels from Teignmouth and one from North Bank, Fal Estuary, would appear to be due to some factor which has accelerated growth; the great depth of the cells in some parts is especially suggestive of this. In connexion with the abnormal growth of gill filaments in Mytilus, it is noteworthy that Ridewood (**43**, p. 174) in discussing the variation in extent of the interlamellar extensions of certain Lamellibranchs says, "Like so many features of gill structure this proneness of the filaments to extension in an interlamellar direction is of little, if any, systematic value. It is possibly related to the conditions under which the animal is living, and is the outcome of a permanently altered metabolism of the tissues of the gills. Perhaps it indicates abundant nutrition, or may be ascribable to increased temperature or diminished salinity of the water, or to the depth below the surface at which the animal lives. Since, however, there is abundant subfilamentar tissue in *Unio pictorum* and *Psammobia pallida*, but little in *Unio ambiguus* and *Psammobia ferroensis*, one hesitates to frame generalisations."

One would imagine that Mytilus would not be prone to indulge in an abnormal growth of gill tissue, for Ridewood (**43**, p. 174) notes that "It is a significant fact that interlamellar junctions having the form of rods occur only in those genera with feeble development of subfilamentar tissue, viz. certain Filibranchia and Submytilacea."

That gill filaments may swell and retain the size after fixation was shown in one case, which is of interest in comparison with the enlarged gill filaments previously described (see p. 509). A Padstow mussel containing a Pinnotheres had shortness (dorso-ventrally) of the gill beneath the crab, and also six or so small groups of enlarged filaments on the face of the gill in this region. This gill was cut out and placed in a finger-bowl of the sea-water in general circulation in the tanks. After three days there was noticeable extension of the ends of some of the filaments along the ventral food groove, as well as swelling of certain of them in a narrow zone along the ventral margin. The cut ends of the filaments, where the gill had been detached from the body, also showed much enlargement. Compared with the swellings seen on the gill when the mussel was first opened, this secondary swelling appeared rather transparent, as though distended with water. The two conspicuous lines of ciliation—the lateral and latero-frontal lines of cilia—were more or less in their normal position in relation to one another, so that it appeared to be chiefly the sides of the filaments that had been blown out. Transverse sections through the swollen filaments are sketched in Fig. 22 (p. 528), and it will be seen that they have a very different appearance from those of Figures 17 (p. 511) and 20 (p. 514). This particular gill, beyond having the filaments somewhat roughly divided in attempting to separate them for examination, was otherwise treated in the same manner as numerous gills which did not undergo swelling. It might be noted that the chitinous supports were poorly developed, and that some few of the filaments were crowded with phagocytes. Later an unsuccessful attempt was made, by pulling filaments somewhat roughly apart, to induce swelling in other gills, when cut out of the mussel and placed in finger-bowls of sea-water. (The salinity of the sea-water in circulation (ca. $36°/_{\circ\circ}$–$37°/_{\circ\circ}$) is higher than that of normal sea-water (ca. $35°/_{\circ\circ}$).)

Drew's (**14**) suggestion, that the intrafilamentar septum (in Pecten) is a brace to keep the filaments from swelling laterally owing to pressure of the blood, and in this way becoming circular and obstructing the flow of water between the filaments (see **10**, p. 44), is especially interesting in view of the swelling of the filaments of this gill. It may be noted that difference of opinion exists as to the nature of the intrafilamentar septum; various authors, including Ridewood (**43**, pp. 166, 168), holding it to be composed of chitin, while Kellog (**26**, p. 421) believes it to be endothelium (in *Pecten irradians*). Dakin (**10**, p. 43) found in *P. maximus* that it appeared to stain quite differently from the chitinous skeleton, appearing almost as if it were cellular, while nuclei, which were not adhering blood corpuscles, were seen in it. Setna (**45**, p. 376) states that in Pecten (three species), material fixed in Bouin and stained with Dobell's methyl-blue-eosin, while the chitin stains blue, the endothelial lining, as well as the intrafilamentar septum, stains red. This difference in colour staining between the chitinous supports and the intrafilamentar septum is also seen in *M. edulis* and *Modiolus modiolus* with Mann's methyl-blue-eosin and Mallory's Triple stain, after Bouin and Bouin-Dubosq fixation, but the difference is not so apparent with other stains such as borax carmine followed by picro-nigrosin (used by Ridewood). It is perhaps possible that the intrafilamentar septum may be composed of delicate muscle fibres.

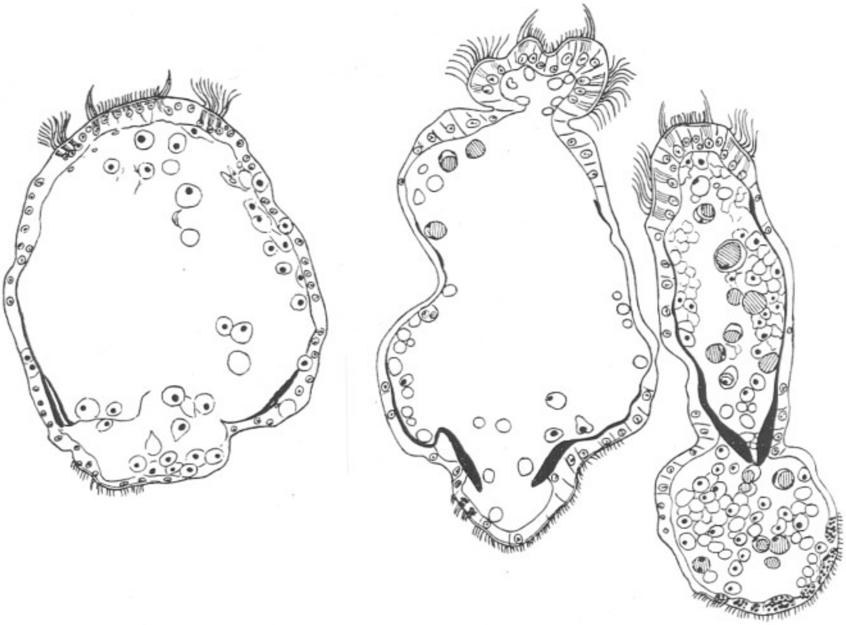

FIG. 22.—Transverse section of filaments from gill which showed increase in size of some of the filaments, after the gill had been cut from the mussel and left three days in a finger bowl of sea-water. The slight development of the chitinous supports and the numerous phagocytes in the filament on the right may be noted. The two filaments on the right are from a different part of the series. Bouin's fixative, Delafield's hæmatoxylin and eosin. × 210.

That gill filaments may be increased in size to an alarming extent without rupturing was demonstrated by the active sporocysts of a species of Trematode within the lumen of the filaments of some few mussels from Padstow, causing the temporary enlargement of the filaments as they wormed their way along (Fig. 23). The Trematode possibly spreads through the mussel by way of the blood vessels ; in some instances they are seen crowded in the pallial vessels, causing them to assume a deep orange colour against the creamy white of the mantle ; the colour of the sporocysts varies, however, from cream to orange in different mussels. In badly infested mussels, the plicate canals (*organes godronnés*) of Sabatier, **44**) are packed with them, as are the mantle and parts of the visceral mass. The dorsal food grooves on the ascending lamellæ are

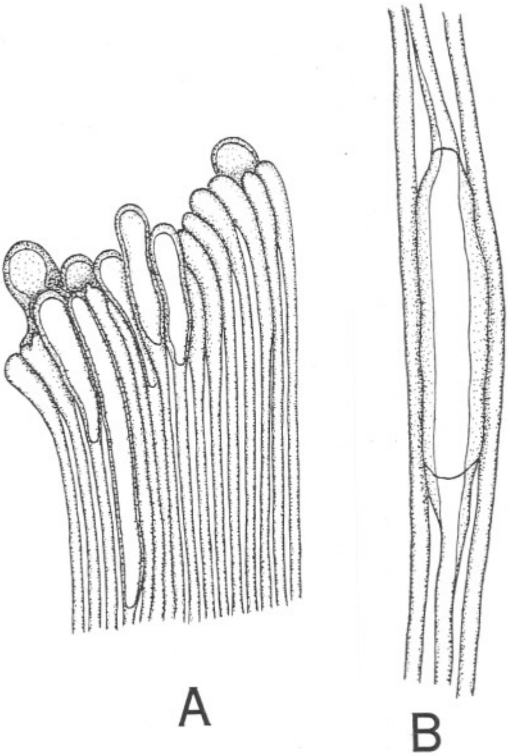

FIG. 23.—Sketches of living gill with sporocysts of a Trematode within the gill filaments. The main ventral food groove in A has an irregular appearance, due to the active sporocysts attempting to push forward. From both A and B it may be seen that the gill filaments recover their normal size after the passing of the Trematode. A, ca. 24⅓ ; B, ca. 76⅓.

occasionally crowded with the active sporocysts and cercariæ of this Trematode, but on few occasions have they been seen actually within the gill filaments, though they have at times been noticed pushing their way along the interfilamentar spaces, in which case they may have actually burst through the gill epithelium, or may possibly have been individuals liberated in opening the mussel. When inside the filaments the active sporocysts would seem to tend to work their way towards the ventral free edge of the gill, where they cause extension of the lobes of the main food groove, giving the ventral edge of the gill an irregular appearance (Fig. 23, A, p. 529); and towards the dorsal food groove on the ascending lamella. The parasites can be seen to cause such great distension of the filaments that it is surprising they do not burst through the epithelium; it is manifest that the filaments are highly elastic as these resume the normal size after the passage of the parasite. The presence of the sporocysts gives to the filaments containing them an appearance somewhat similar to that described previously (p. 509, and Fig. 15); but the swelling is smooth and also the lines of latero-frontal cilia can be seen running across the swelling (Fig. 23, B), showing that the frontal epithelium experiences no more stretching—possibly less—than the rest of the epithelium. The extreme enlargement of the filaments is strikingly shown

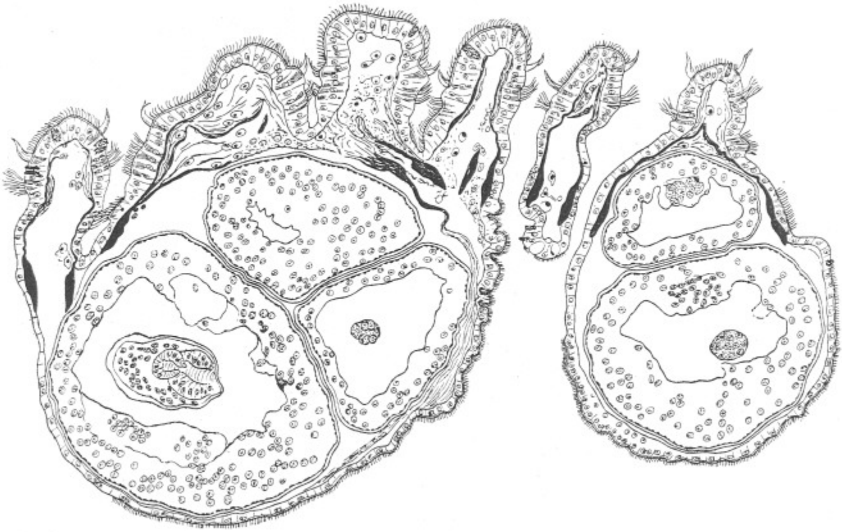

Fig. 24.—Transverse section of part of single lamella of a gill, near the dorsal food groove, showing great enlargement of the interlamellar (abfrontal) ends of the gill filaments owing to the presence of the sporocysts of a Trematode. In the filament on the right, two sporocysts are present side by side: on the left the enlargement of the gill filaments has apparently caused fusion. A cercaria is seen within one of the sporocysts. Bouin's fixative, Delafield hæmatoxylin and eosin. × 140.

in transverse sections, such as Figure 24, where there are two sporocysts side by side in the same filament. The enlargement of the area of ciliated abfrontal epithelium may be noted. This section also shows that fusion of the filaments may presumably be caused where swollen filaments are forced against each other. One would imagine that fusion from this cause is only likely to occur in areas where the active sporocysts tend to congregate for some time, e.g. near the ventral and dorsal edges of the gills. As mussels infected with the Trematode came from Padstow, where exceedingly little abnormality of the gills occurred among the mussels—apart from those infected with either Pinnotheres or the Trematode—the fusion in this case may be fairly safely attributed to the presence of the Trematode. Figure 25 shows the crowding which resulted when five out of seven filaments, in the same lamella, each contained a small sporocyst.

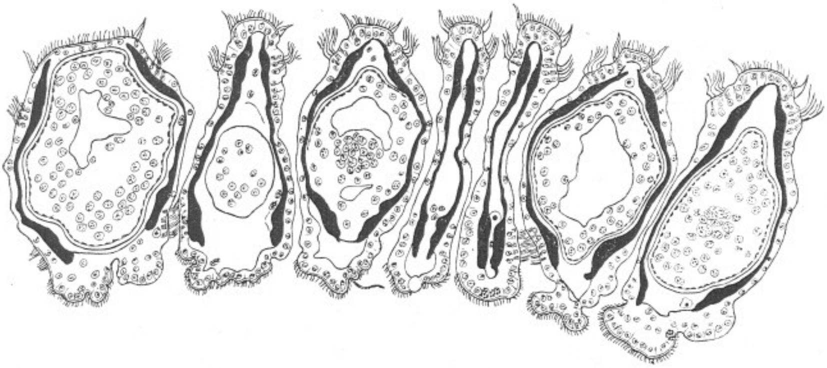

FIG. 25.—Transverse section of part of a single lamella of a gill, to show the crowding of filaments caused by the presence of sporocysts of a Trematode in five out of the seven gill filaments drawn. Bouin's fixative, Mann's methyl-blue-eosin. × ca. 171.

The various abnormalities described would appear to support Rice's contention that "the lamellibranch gill is an extremely plastic organ, and one very liable to adaptive modification" (**42**, p. 76).

SUMMARY.

In the examination of a total of about twenty-four thousand mussels from various localities in Devon and Cornwall—estuaries of the Fal, Hamoaze, Yealm, Teign and Camel, and the Promenade Pier, Plymouth—it has been observed that those from various parts of the Fal Estuary included a high percentage of specimens with the gills in an abnormal condition, whereas such abnormalities were rare or absent in other localities. The abnormalities are described from living and preserved material and consisted in the following types :

(*a*) Folding over of the free ventral edge of the gill, with concrescence.

Various stages in the degree of fusion have been observed, from slight fusion at the bend of the fold, to complete fusion of the folded over portion with the lamella beneath. Fusion and degeneration of the two inner arms of the fold, follows folding. The effect is noted of the reduction of gill surface, pumping power, and the disorganisation of the food grooves, consequent on folding, on the general condition of the mussel.

(*b*) Fusion of the gill filaments side by side.

This condition varied greatly in extent, from the fusion of two or more filaments side by side, to extensive areas of fusion scattered irregularly over the greater part of a lamella. Fusion was found to be confined almost entirely to one lamella, generally the ascending, the opposite one being little affected. It is suggested that fusion is due to crowding of the filaments, whatever may be the cause of the latter. The persistence of separate chitinous supports in the fused area, is considered as evidence that fusion has occurred, and not splitting or branching of the filaments.

(*c*) Enlargement of the gill filaments.

This rare form of abnormality was found in five mussels from the Teignmouth Estuary, and in one from the Fal Estuary. The enlargement of the filaments was mostly confined to a narrow zone at the free ventral edge of the gill, and appeared to be due to proliferation of the ciliated frontal epithelium, with a corresponding enlargement of the internal canal. In the mussel from the Fal Estuary the frontal cells of some of the gill filaments were of abnormally great depth : in the case of the gill sectioned from a Teignmouth mussel, great development of the frontal ends of the chitinous supports had occurred. It is suggested that the enlargement of the gill filaments may be due to some factor which has accelerated growth.

(*d*) Concrescence of the two gills of one side.

In two specimens of Mytilus it was noted that on one side, for a short distance in the middle region, one "gill" only was present, formed apparently of two ascending lamellæ and free from the body.

Brief notes are given of the general condition of Mytilus from the various localities investigated. The presence of blisters, in some instances of large size, in the valves of about 7% of the mussels from the Fal Estuary, and of a small number from the Teignmouth Estuary, is noted.

It is suggested that the abnormalities of the gills are correlated with some factor or combination of factors in the environment, information regarding which may be obtainable from further experimental observations.

METHOD OF DIVISION OF THE MANTLE CAVITY IN NORMAL INDIVIDUALS.

It is well known that in certain Lamellibranchs the division of the mantle cavity by the gills into supra- and infra-branchial chambers is not a morphological one, the union of the gills with the mantle, with the visceral mass, and with each other being a ciliary one. (See **39**, p. 228.) The actual method of connexion, however, has been described in but few forms. Herdman (**24**) described and figured it for *Margaritifera vulgaris*, living and well-preserved specimens of which showed apparent continuity of the walls of the supra-branchial chamber, slight pressure being needed for the separation of parts, when the ciliary nature of the junction was revealed. It might be noted that he remarks that in some, if not all, specimens, there was also some slight organic connexion between the two inner gills.

Ridewood described in *Anomia aculeata**—in which descending lamellæ alone are developed—the adhesion of the lower edges of the outer gills with the mantle, and the mutual adhesion of the lower edges of the two inner gills by means of patches of interlocking cilia (**43**, p. 194, and Fig. 8); while similar ciliary junctions have been described by Orton in Nucula (**33**, pp. 462, 463, 468, and Fig. 18) and in *Solenomya togata* (**34**, pp. 39, 41, 42, and Fig. 11), by means of which there is a complete division of the mantle cavity into supra- and infra-branchial chambers.

Dodgson (**12**, p. 171) gives diagrammatic representations of the boundaries of the supra- and infra-branchial chambers in *M. edulis* in three transverse planes.

In living Mytilus the normal ciliary junction between the gills and the mantle, and between the gills and the visceral mass, may be seen in individuals in which the posterior adductor muscle has been cut, if the two valves are separated only sufficiently for the line of junction to be seen. (The animal should be left to recover from shock.) It was found that the junction with the mantle was more likely to occur if the mantle—with the exception of the edge—were separated from the surface of the valve (this may be done by inserting the handle of a scalpel from the anterior end and carefully separating the mantle from the shell), so that it billows out somewhat, in this way compensating, in some degree, for the separation of the valves.

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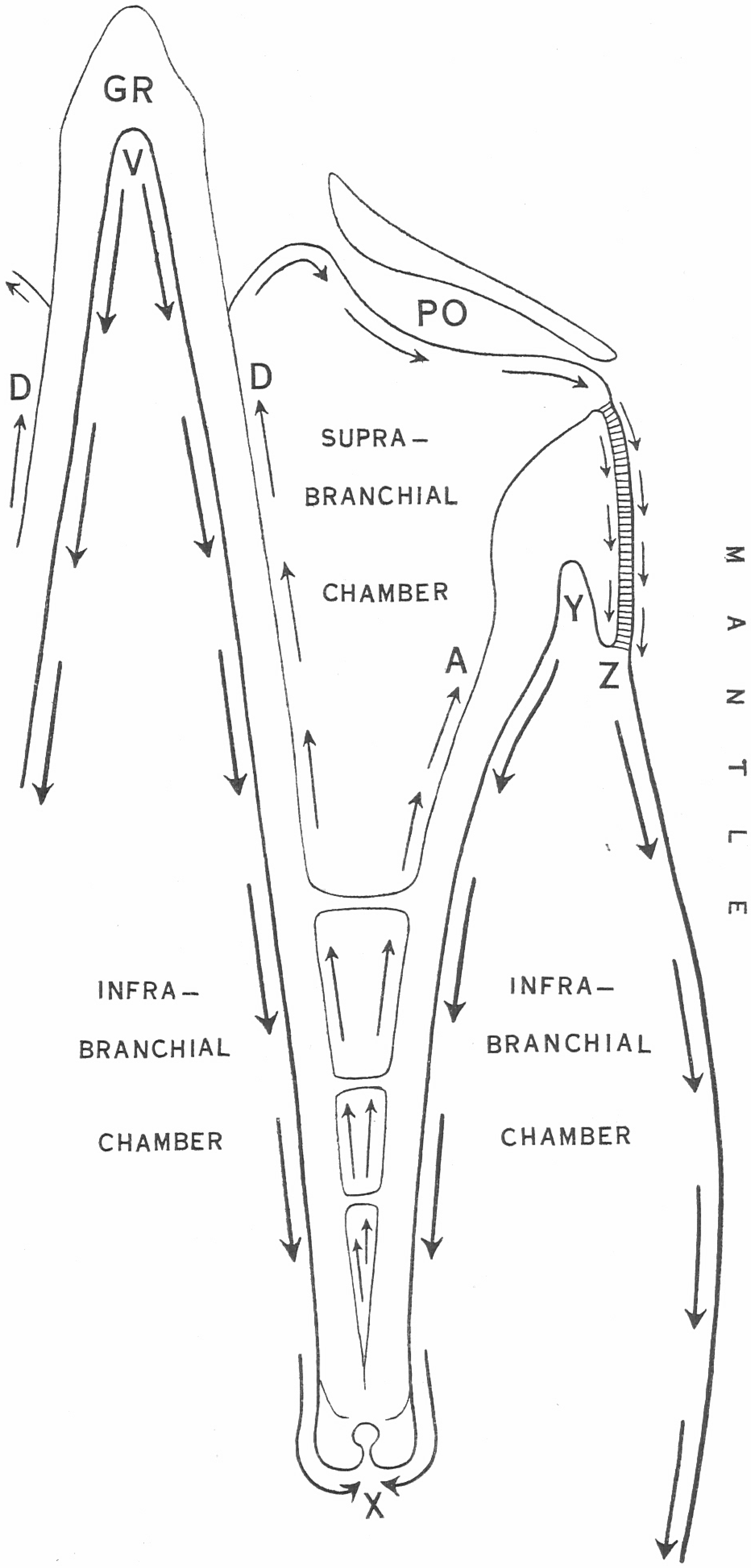
* Now *Heteranomia squamula*, see Winckworth, Proc. Malac. Soc., Vol. xv., pp. 32–4, 1922.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INFRA–
BRANCHIAL
CHAMBER
X

Fig. 26.

In two individuals, in which the outer surface of the dorsal food groove of the ascending lamella of both outer gills made almost complete junction with the mantle, it was noted that gentle pressure on the gill caused slight raising of the mantle, which in one instance was very thin. In opened mussels the ciliary junction of gill and visceral mass was only seen for short stretches, owing to the visceral mass being damaged in opening.

The line of ciliary junction of the gill with the mantle in Mytilus is just ventral to the outer ends of the external plicate canals (Fig. 26), and investigation of the surface of the mantle in this region, by means of starch grains stained with iodine, showed that there is a narrow longitudinal zone, roughly about 1·0 mm. wide, over which the movement of particles is extremely slow, to the unaided eye and even with a lens the movement being almost indistinguishable ; particles, however, do move and tend to accumulate at the ventral edge of the zone, which by this means is shown to have a sharply marked ventral boundary. This boundary is usually visible in the living animal, owing to the lesser pigmentation of the zone in comparison with the rest of the mantle. Sections show that normally this region is not a ridge (see Fig. 6, A, p. 497) and may perhaps in specimens with well-developed gonad be slightly sunk. (It was found advisable to fix the mussel in the shell, in this way serious contraction of the mantle being prevented.) As food particles accumulate along the ventral boundary of the zone they get pushed into a narrow anteriorly directed ciliary current which runs just ventral to it (Fig. 26, Z), and from which they tend to be drawn into the ventrally directed ciliary currents over

FIG. 26.—*Mytilus edulis*. Diagrammatic representation of one outer division of the supra-branchial chamber, showing the ciliary junction between the outer surface of the dorsal food groove, Y, and the mantle ; and also the currents set up by the cilia on the walls of the chamber. The ciliary currents on the abfrontal surface of the filaments are shown as being directly dorsal, but actually they are somewhat posterior in direction (see Fig. 27). The ciliary currents on the frontal face of the filament and on the mantle are indicated by heavy arrows. The short arrows alongside the junction area, denote currents which occur over the interlocking cilia when the upturned edge of the gill is not adhering to the mantle.

GR, Gill ridge. PO, Plicate organ on roof of supra-branchial chamber.

A and D. Mark the position of posteriorly directed ciliary currents across the abfrontal surface of the ascending and descending lamella respectively, in the region where the ends of the filaments become fused together.

V. Marks the position of the anteriorly directed ciliary current between the bases of contiguous gills. The strength of this current appears to vary in different individuals, which may possibly explain why Kellog (**27**, p. 653) was unable to find it, though it has been observed by Orton (**33**, p. 460).

X. Marks the position of the anteriorly directed ciliary current along the main ventral food groove.

Y. Marks the position of the anteriorly directed ciliary current along the dorsal food groove on the ascending lamella.

Z. Marks the position of the narrow anteriorly directed ciliary current on the mantle. When the dorsal edge of the gill is touching the mantle, Y and Z form one anteriorly directed current.

the mantle region (see Orton, **33**, Fig. 11, p. 459, and Kellog, **27**, Fig. 18, p. 652); this, of course, only occurring when the gill is not adhering to the mantle. It is difficult to observe the appearance of the cilia clothing this tract in the living Mytilus, except in individuals in which the mantle is exceptionally thin, but in *Modiolus modiolus* where the mantle is normally very thin—not being invaded by the gonad in this species—a piece may be cut out and folded, so that the cilia are seen in side view. They closely resemble in appearance those of the ciliated discs on the lateral faces of the gill filaments, with which they agree in their interlocking function. In the living animal, as well as in sections, they have a stiff, regular appearance, as though they do not move far from the vertical during their beat, and can be easily distinguished from those on the mantle dorsal and ventral to them.

The position of the corresponding tracts of interlocking cilia on the visceral mass, may also be demonstrated by the use of starch grains stained with iodine, a longitudinal zone over which particles move extremely slowly, being visible beyond the inner ends of the internal plicate canals.

An examination of the outer face of the dorsal food groove on the ascending lamella of living Mytilus and Modiolus shows that this surface is clothed with cilia of the same appearance as those of the specialised tract on the mantle. A rather slow, somewhat irregular movement of particles occurs over this surface in a dorso-ventral direction, particles being drawn into the anteriorly directed current along the groove (Fig. 26, Y), from which there is a tendency for them eventually to pass on to the frontal face of the gill filaments. This, again, only occurs when the gill is not adhering to the mantle.

Sections show that the ciliated cells of the outer face of the dorsal food groove of the gill, and of the specialised tract on the mantle, have a marked border (see also Herdman, **24**, p. 227), formed by the basal granules.

The slow current over these surfaces may perhaps be sufficient to keep them clean, when the gill is not touching the mantle, and may transfer particles from the supra- to the infra-branchial chamber. When the gill is closely interlocked with the mantle or with the visceral mass, however, it is unlikely that any particles would be able to penetrate the barrier of interlaced cilia.

When the gill is interlocked with the mantle, the anteriorly directed current on the mantle forms, with that along the dorsal groove of the gill (Fig. 26, Z and Y), a single anteriorly directed current. In this condition the current is more clearly defined, and there seems to be less tendency for particles to be drawn from the dorsal groove on to the frontal faces of the filaments, probably because the groove may be more widely open when gill edge and mantle are interlocked. The animal is able to alter the form of the food groove considerably, and in specimens of Modiolus killed without narcotising, the outer wall of the groove may be reflected, so that the groove is non-existent ; while in Mytilus there is much contraction.

The abfrontal surface of the dorsal groove is abundantly supplied with scattered, very large cilia, and it is possible that they may have a tactile function, giving warning when the ascending lamella falls back on the descending lamella. These large cilia, which may occur singly, or two or three together, beat slowly, passing through 90°, and occasionally less than 90°, though this may be due to abnormal conditions during observation. Similar large cilia are also present among the short cilia on the abfrontal and frontal surfaces of the gill filaments ; and in addition occur among the ciliated cells of the plicate organs, on the surface of the mantle and the body, and on the palps (see also List **29**, p. 110) ; in fact, they probably occur on most external ciliated surfaces. On fixation they separate into their constituent fibres (see also List **29**, p. 110), and in sections, therefore, have the appearance of a tuft of cilia. These large cilia vary considerably in size, as may be seen on examining those on the abfrontal surface of a living gill-filament of Mytilus or Modiolus. In *Modiolus modiolus* they attain a great length, some times reaching 120μ. Gray, in a recent paper (**22**), has analysed the movement of these large cilia on the abfrontal surface of the gill filaments of Mytilus.

Contraction and expansion of the interlamellar junctions, which are first present some short distance ventral to the dorsal groove, along with the muscles of the dorsal groove itself, would most probably be sufficient to pull the gills away from the mantle, from the visceral mass, and from each other, causing temporary separation and approximation such as Dodgson (**12**, p. 170) described between the free dorsal edges of the ascending lamellæ of the inner gills in certain more or less moribund mussels. In this way the supra- and infra-branchial chambers may become continuous. As previously mentioned the dorsal grooves of the gills are provided with muscle-fibres, as seen in sections and shown by the curling up of pieces of dorsal groove cut from the gill.

In animals, which have been opened by cutting the posterior adductor muscle, movement of the gills is observable ; slight in the case of Mytilus (see also Pelseneer in **12**, p. 172), more evident in Modiolus. In the latter, the gills, from a position in which the ventral edges of the two gills of one side are touching, may separate until the angle between the descending lamellæ is 90° or more. Movements of separation and approximation of the gills, may be elicited, at least in Modiolus, by touching the frontal or abfrontal surface of the lamella with a needle. This movement may be compared with the concertina movement of the gills of Pecten, described by Setna (**45**, p. 370), but in Modiolus, while the whole gill is generally involved in the movement, the response is slower and not as certain, and the movement slower than in Pecten. In Mytilus, the response to the touching of the gills is uncertain and the movement feeble. Such movements of separation and approximation of the gills, however, may also possibly contribute to the application of the dorsal free edges of the gills to the mantle, to the visceral mass, and to each other.

There is little difference in width between the outer surface of the dorsal groove of the gills (about 0·6 to 0·9 mm. wide, varying slightly in different regions and in different individuals) and the longitudinal tract of interlocking cilia on the mantle (about 1·0 mm. wide), so that practically no play of the dorsal free edge of the gill, in a dorso-ventral direction, is allowed for.

Although the junction of the gills with the mantle and the visceral mass in Mytilus and Modiolus would appear to be somewhat easily broken, it is probably of a less temporary nature than in the active Pecten. An opened mussel in which one of the outer gills had made complete junction with the mantle, was kept under observation for three hours, and throughout that time the junction remained unbroken, and was left in that condition when the watching ceased. In fact, observations point to the conclusion that, in mussels which have been opened, once the connection is made it tends to persist while the animal remains healthy, that is up to at least four days. It may be noted that Dodgson (**12**, p. 170) records that in a healthy mussel, under normal conditions, the free edges of the ascending inner lamellæ (in the posterior region) have always been seen to be in close apposition.

During the time the gill is connected with the mantle slight separation and approximation of the descending and ascending lamellæ occur, and, if the mantle has been freed from the shell, these movements may be sufficient to raise the mantle, exceedingly slightly.

In Pecten the temporary nature of the division of the mantle cavity has been observed by Orton (**33**, p. 461), who says " the upturned edges of the outer gill filaments touch the mantle during feeding, and in this way form at this point a temporary food groove." It may be noted that preparatory to the clapping of the valves the free posterior ends of the gills swing forward by contraction of the ctenidial muscles (see also **45**) and any connection between the gills and the mantle is broken.

Currents on the walls of the supra-branchial chamber.—In the supra-branchial chamber of Mytilus the main water current is posterior in direction (see Orton, **33**, Fig. 11, p. 459), and most of the surface currents on the walls of the chamber have also a posterior tendency, but have not previously been described.

The plicate canals are found on the roof of the supra-branchial chamber, the width of each division of the chamber being roughly the length of these organs. The external surfaces of the canals are highly ciliated, rapid currents passing over them, in the main, in a dorso-ventral direction (see Fig. 26). These canals, to which Sabatier gave the name of *organes godronnés* (**44**, p. 56), have a respiratory function.

In Mytilus the cilia on the abfrontal faces of the filaments beat chiefly in a dorsal direction, but actually obliquely across the filaments, so that particles pass across the abfrontal surfaces of the lamellæ in a direction which is anterior-ventral to posterior-dorsal (Fig. 27). Across the dorsal ends of the gill filaments—in the region where they become fused together—of both descending and ascending lamellæ, the cilia maintain a posteriorly directed current (Figs. 26, D and A; 27). In most of the individuals which were examined the epithelium covering the fused ends of the filaments was either feebly ciliated, or destitute of cilia with the exception of scattered very large cilia (see p. 537), and there

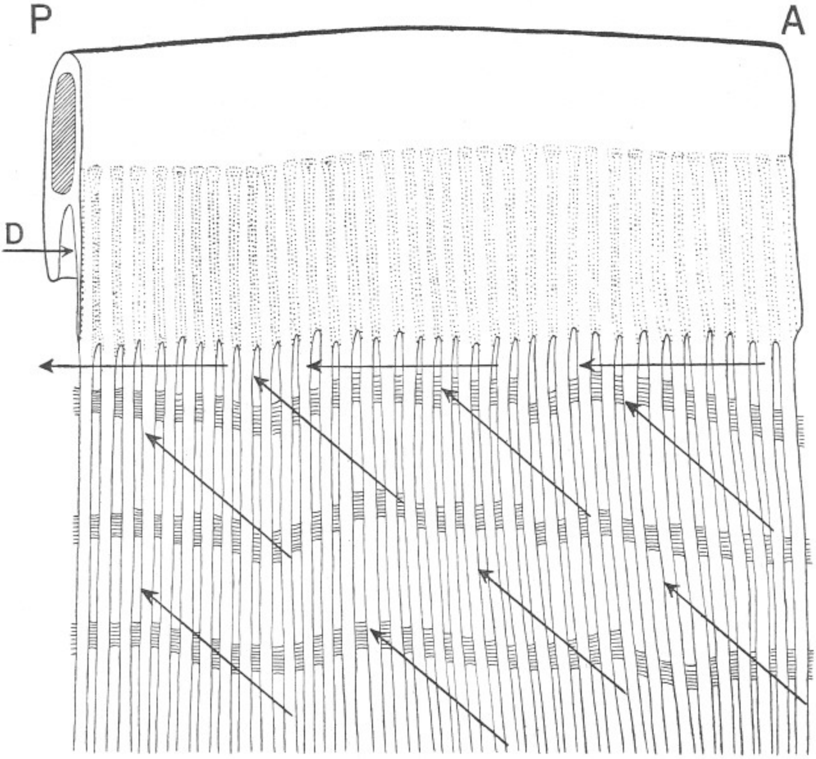

FIG. 27.—Mytilus. View of the abfrontal surface of an ascending lamella in the region of the dorsal food groove, to show the ciliary currents.

A and P. Anterior and posterior.

D. Arrow showing the direction of the current along the dorsal food groove. The narrow stippled areas indicate the chitinous supports in the region where the ends of the filaments are fused together. × ca. 41½.

was only occasional slight movement dorsalwards of particles jerked forward by the latter: in such individuals the posterior ciliary current across the base of the filaments was very clear. Very rarely individuals were seen in which the abfrontal cilia were continued on to the epithelium covering the fused ends of the filaments; there was in consequence a ciliary current across this surface, in a postero-dorsal direction, and the purely posteriorly directed ciliary current was not then as clear.

In the few specimens of *Modiolus modiolus* examined, the abfrontal cilia of the gill filaments were very poorly developed or absent, except for large scattered cilia, and the ciliary currents on the abfrontal surfaces of the lamellæ were therefore weak or absent.

The greater part of the material for the work recorded in this paper was obtained during the tenure of a research studentship of Bedford College, University of London. I wish again to express my gratitude to the Director and Council of the Marine Biological Association for allowing me to work at their Laboratory at Plymouth, and to the London University for granting me the use of their table. For the composite photograph of Figure 21 I am indebted to Mr. A. J. Smith. My sincere thanks are due to Prof. J. H. Orton for reading the manuscript, and for helpful criticism and advice.

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Note on Some Abnormalities of Labial Palps and Foot of *Mytilus edulis.*

By

D. Atkins, B.Sc.

With 7 Figures in the Text.

In view of Pelseneer's work on "Les Variations et leur Hérédité chez les Mollusques,"* it seems worth while to record briefly certain observed abnormalities of the labial palps and the foot of *Mytilus edulis*. Among some thousands of specimens examined, however, such conditions were rare, and it is probable that at least some of them arose through injury.

LABIAL PALPS.

The abnormality of the palps most generally met with is evidently the result of natural regeneration, following injury to the tips of the palps. From the injured surface tiny outgrowths arise, usually three in number, two of which appear to have a common base. Figures 1, A–C, shew different degrees of regeneration; two examples have been seen in approximately similar conditions. (The normal tip of the palp may be seen at P in Figure 2.)

Pelseneer (p. 181) records the finding by Sykes of a specimen of *Tellina incarnata* in which the palps were missing, but gives no further examples of variation in palps. However, his Figure 121 (p. 204) of a gill of *Boreochiton marginatus* with trifurcated tip shows a similar state of affairs to that recorded in this note for the palps of *M. edulis*.

Bifurcation of the tip of the palp has been observed in one or two instances.

The right inner palp of a Mytilus from Padstow showed two small accessory palps near the base (Figure 2); these had a common base, only the tips, which pointed in opposite directions, being free. In preservation the tips have become curled, and that of the more proximal secondary palp is hidden beneath that of the more distal one. A second example of this type of accessory palps was noted on the right inner palp of another Mytilus from the same locality, but in this instance they originated about

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* P. Pelseneer, Les Variations et leur Hérédité chez les Mollusques. Acad. Roy. Bel. Mém., 2nd sér., Tome V, 1920.

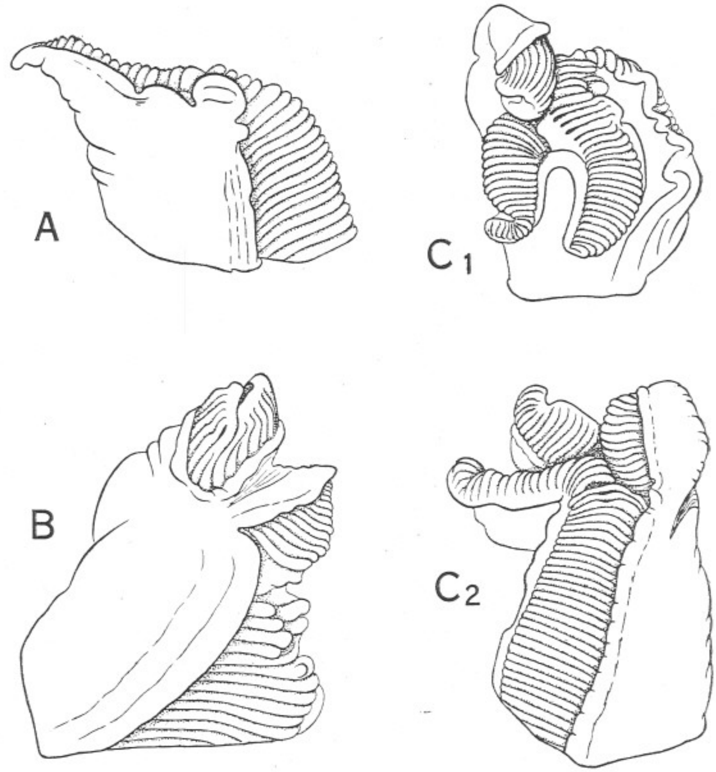

Fig. 1, A–C.—*Mytilus edulis.* Sketches showing stages in the formation of outgrowths from the tips of three palps, A, being the youngest and C, the oldest stage. In C1, the trifurcated tip of the palp has become folded back on to the smooth outer surface during fixation; in C2, it has been forcibly flattened out. × ca. 6¼.

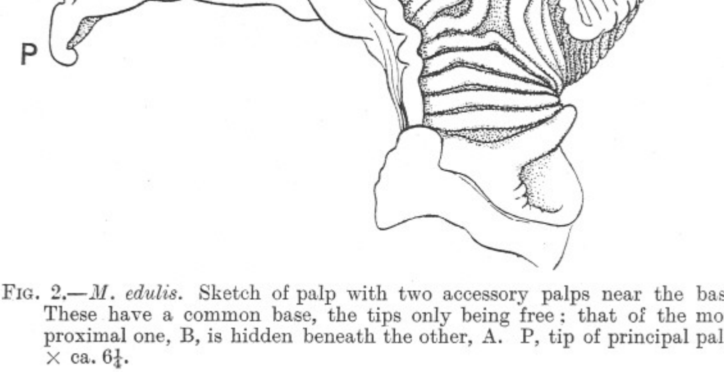

Fig. 2.—*M. edulis.* Sketch of palp with two accessory palps near the base. These have a common base, the tips only being free; that of the more proximal one, B, is hidden beneath the other, A. P, tip of principal palp. × ca. 6¼.

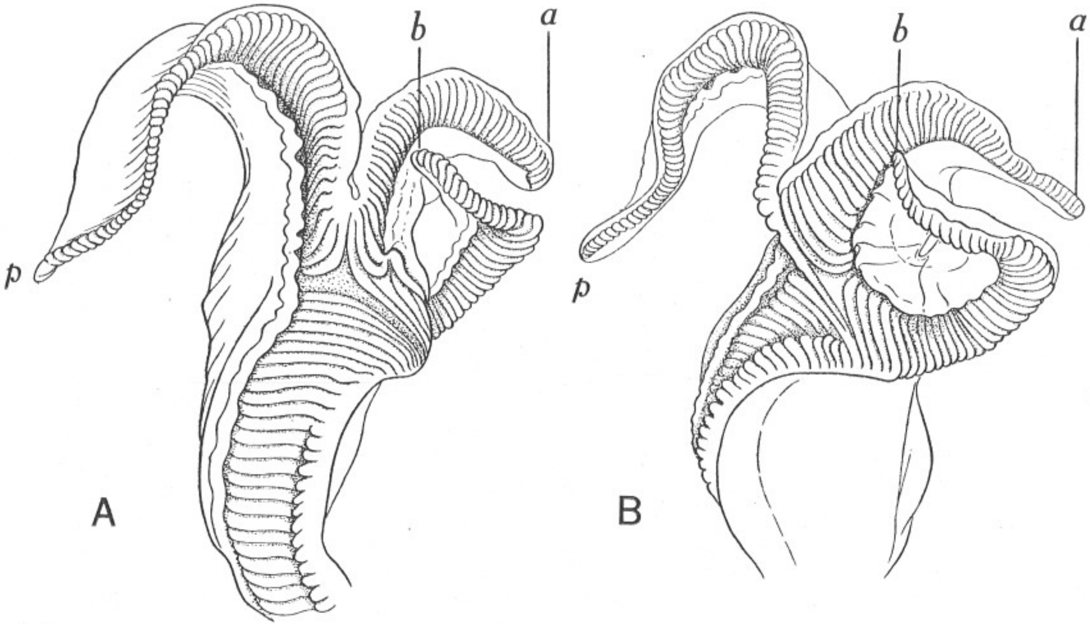

FIG. 3.—*M. edulis*. Different views (A and B) of two accessory palps, *a* and *b*, originating from about midway along the length of the principal palp. *p*, tip of principal palp. × ca. 6¼.

midway along the length of the principal palp, and were more highly developed (Figure 3).

A tiny accessory palp originating from near the base of a left inner palp, on its smooth outer surface, is shown in Figure 4. In this instance the difference in size of the principal and secondary palp is marked.

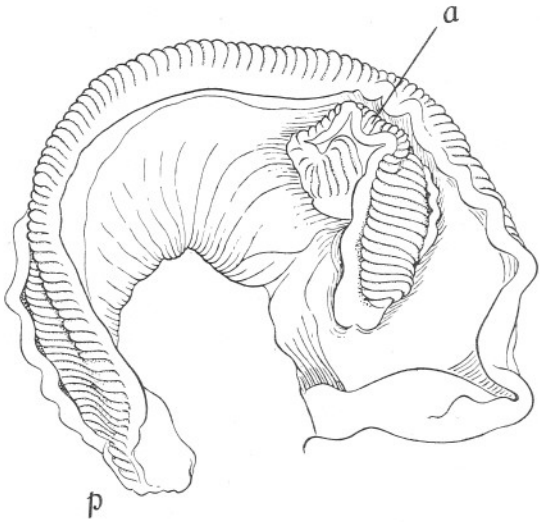

FIG. 4.—*M. edulis.* Palp with a small accessory palp, *a*, near the base on the smooth outer surface. *p*, tip of principal palp. × ca. 6¼.

FOOT.

Several different types of foot abnormality have been noted in *M. edulis.* That most generally met with was a small foot-like outgrowth, or rudimentary accessory foot, originating from near the base of the primary foot, the latter showing no injury to its tip. The outgrowth was lateral, but somewhat dorsal in position (see Figure 5), and in three cases was on the right side and in one on the left. The outgrowths varied somewhat in size ; that sketched in Figure 5 being the largest seen. These foot-like outgrowths were pigmented a dark brown like the primary foot, but were without a ventral groove or anterior sucker. A single case was noted of a similar tiny outgrowth about midway along the length of the foot and distinctly on the lateral (right) edge. Pelseneer figures (Figure 94 *bis*, p. 133) a somewhat similar outgrowth on the right side of the foot of *Cyclas cornea,* which, however, was spheroidal.

An interesting case of foot abnormality was that sketched in Figure 6, where the accessory foot was ventral in position though slightly lateral, and the ventral groove of the main foot divided, the secondary foot in this instance being provided with a ventral groove.

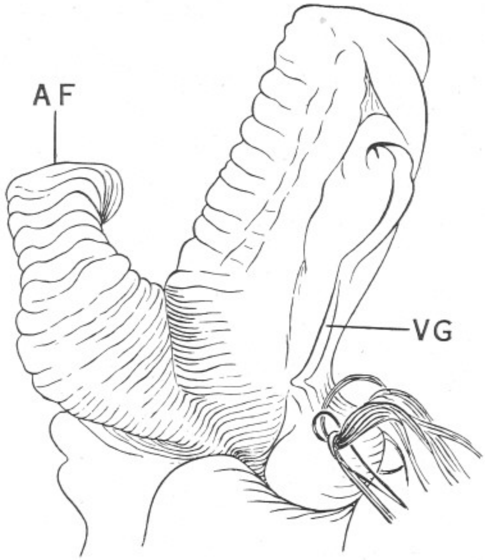

FIG. 5.—*M. edulis.* Foot with a small foot, AF, originating from near the base. VG, ventral groove of primary foot. × ca. $6\frac{1}{4}$.

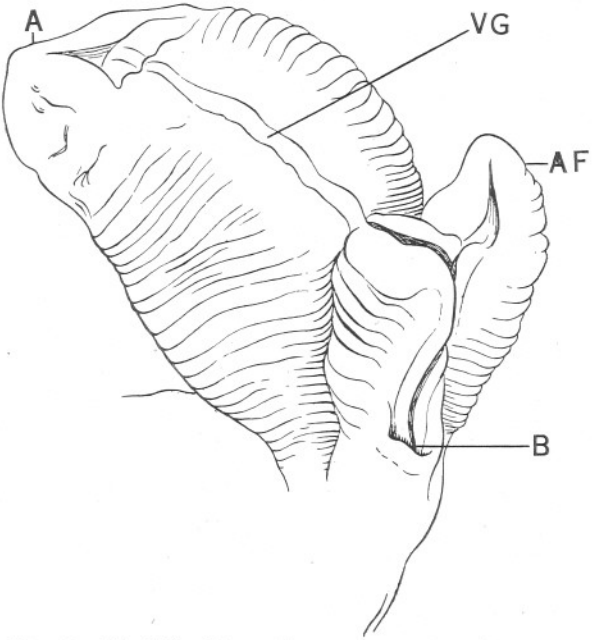

FIG. 6.—*M. edulis.* Foot with an accessory foot, AF, which is ventral in position and is provided with a ventral groove. A, tip, and VG, ventral groove of primary foot; B, byssus pit. × ca. $6\frac{1}{4}$.

One Mytilus was noted in which the tip of the foot was missing, the foot being obviously injured and discoloured (Figure 7). There was a slight irregular outgrowth from the main foot anteriorly, but what is of especial interest was the presence of tiny foot-like protuberances, one on either side of, and seated on the anterior retractor muscles, that on the left being slightly more anterior in position than that on the right. These were pigmented, but appeared to have no ventral groove. The figure shows them in a much contracted condition. As the foot is protruded from the shell in travelling, and during the spinning of the byssus, it is liable to suffer injury (see also Pelseneer, p. 133), as has evidently occurred in this specimen, but it is doubtful whether the foot-like outgrowths from near the base of the foot are due to this cause.

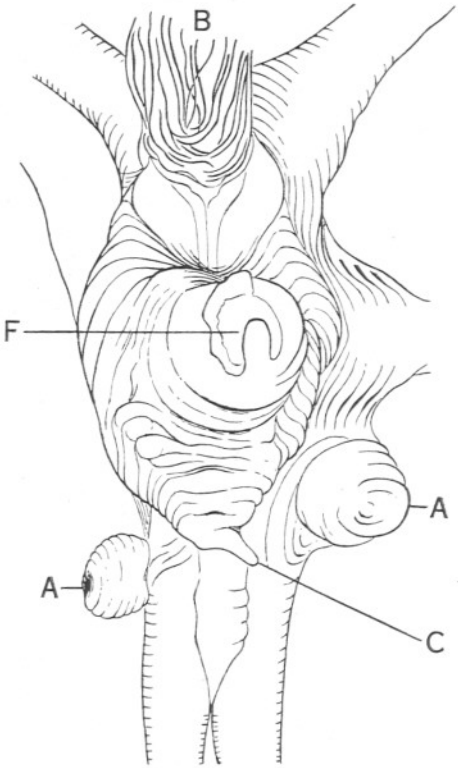

FIG. 7.—Sketch of foot of *M. edulis*, showing the tip missing as a result of injury, and two small foot-like outgrowths, A, A, one on either side of the anterior retractor muscles. F, injured tip of primary foot; C, small outgrowth from primary foot; B, byssus. × ca. $6\frac{1}{4}$.

The position of the foot has been noticed to vary somewhat, in one instance being very anteriorly placed.

Note on the Regeneration of the Gill of *Mytilus edulis.*

By

D. Atkins, B.Sc.

With 8 Figures in the Text.

INTRODUCTION.

IN connexion with work on reversal of the frontal cilia on the gill filaments of *Mytilus edulis* (**1**), it became desirable to know whether the gills were capable of regeneration after injury. With the exception of the peculiar method of growth or regeneration of the incubatory gills in Cyclas, briefly described by Poyarkoff (**11**), which, even if his preliminary observations are confirmed, would hardly appear to be true regeneration,* the only reference that can be found on the subject of regeneration of the gills in Lamellibranchs is that in the paper by Bloomer (**3**) on malformed specimens of *Anodonta cygnea,* where the condition was apparently due to injury: he concluded " that the animal is able to repair even extensive damage to the mantle-lobes, but is not able to make good injuries to the gills " (**3**, p. 138).

As *M. edulis* is not infrequently found having the gills with very jagged ventral edges, and a few specimens even with the gills more or less entirely missing for a short length—in some instances almost certainly attributable to injury by boring whelk-tingles—it was thought that regeneration of gill filaments possibly might not occur in Mytilus. A single specimen experimented on in June, 1929, showed no signs, after 112 days, of regenerating the wedge-shaped pieces cut from the gills, beyond the formation of a food groove at the cut ends (see **1**, p. 960). From further experiments, however, it is evident that regeneration of the gills of *M. edulis* may occur.

EXPERIMENTS.

Mussels with strong shells (ca. 7·0–8·0 cm. long) were chosen for the experiments, so that the shells would not be likely to fracture easily on being forced open. The ease or difficulty with which the valves could be

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* " La formation des sacs d'incubation doit gêner considérablement le développement normal du feuillet réfléchi de la lame branchiale interne. En revanche ce feuillet s'accroît d'une façon si singulière que je qualifierai ce cas de régénération de ce feuillet bien que sans doute l'animal n'en perde en réalité aucune portion " (**11**, p. cxxxvi).

forced apart was taken as an indication of the condition of the mussel; those of which the valves could be easily forced apart were rejected.

The shell was first opened slightly with an oyster opener; the pointed and thin side of a wooden wedge inserted; worked further in and slowly twisted, until the mussel was forced open to the greatest width of the wedge (about 1·0 to 1·5 cm.). It was done gradually so as to strain the muscles as little as possible. In spite of care the shell fractured badly in some few instances, and the mussels had to be discarded.

The injuries were made near the posterior end of the gills,* owing to the difficulty of reaching any other part. So far as could be seen, the gills of all the mussels used were normal.

The experimental mussels were placed separately in finger bowls, and the bowls sunk in one of the glass-fronted tanks in the general circulation in the Plymouth Laboratory, the tank used being in the shade.† An average of two to four litres of tow nettings a day were tipped into the tank.

Temperature readings of the water in the experimental tank were not taken, but the highest and lowest morning readings (taken at about 9.30 a.m.) for each month, of water temperatures of a similar tank, three tanks away and on the same side of the building, are as follows:

	Max. °C.	Min. °C.
Dec., 1929 . . .	12·1	10·8
Jan., 1930 . . .	10·8	9·4
Feb.	9·7	7·1
March	10·3	8·4
April	11·9	9·7
May	13·2	10·7
June	15·4	13·2
July	16·4	14·9
Aug.	16·8	15·0
Sept.	17·2	14·1
Oct. 1–17 . . .	15·1	12·6

(These figures have been abstracted from the temperature readings taken daily by Mr. A. J. Smith.)

The experiments were started on November 29th and December 1st, 1929, and in February, two out of the ten experimental mussels were found to have died. Five individuals (A, C, D, F, K in Table I) were opened on July 30th, 1930; of the remaining three, one (E) was found gaping on September 15th, the two survivors (B and J) were opened on October 17th, 1930.

Notes on the experimental mussels are given in Table I.

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* For convenience in description the two demibranchs on each side of the body are considered as two gills.

† Coulthard (**6**, p. 136) finds that "Mussels display maximum growth in approximately 50% sunlight, slightly less in darkness, and least in full sunlight."

TABLE I.

EXPERIMENTS ON REGENERATION IN THE GILL OF *MYTILUS EDULIS*.

(All experiments were begun on either Nov. 29th or Dec. 1st, 1929.)

Mussel.	Date of opening in 1930.	Condition on date of opening.	Nature of injury inflicted.	Result.
A.	July 30	A good deal of byssus formed ; strongly attached. Mussel rather thin. Gills markedly pigmented.	(*a*) Right inner gill.—Wedge-shaped piece cut out of ventral edge in such a way as to leave some filaments unattached except by ciliated discs.	(*a*) Regeneration both of food groove and filaments occurred (see Fig. 1).
			(*b*) Left inner gill.—Two slanting cuts with scissors from ventral edge of gill in a dorsal and anterior direction, so as to isolate two pieces of gill except for attachment by ciliated discs.	(*b*) Pieces sloughed off : regeneration of food groove and of filaments followed (see Fig. 3).
			(*c*) Left outer gill.—Operation as for left inner gill.	(*c*) Pieces sloughed off : regeneration of food groove and of filaments followed (see Fig. 2).
B.	Oct. 17	Rather poorly fished, but valves fairly stiff to force apart. Gills only slightly pigmented.	(*a*) Right outer gill.—Injured by pulling some of the filaments with forceps.	(*a*) Regeneration of food groove occurred. Injury showed as two long inlets in gill, with some slight abnormality of filaments.
			(*b*) Right inner gill.—Shallow piece cut out of ventral edge.	(*b*) Regeneration of food groove occurred, also some very slight regeneration, with apparent fusion, of filaments.
			(*c*) Left inner gill.—A slanting cut with scissors from ventral edge in a dorsal and anterior direction, so as to isolate a piece of gill except for attachment by ciliated disc.	(*c*) Most of piece sloughed off. Little, if any, regeneration beyond formation of new food groove. At deep end of cut some irregular joining up of cut ends of filaments. Five or so short lengths of filaments separated dorsally from gill by a tiny space, but attached anteriorly and posteriorly.
			(*d*) Left outer gill.—Piece cut out of ventral edge.	(*d*) Regeneration of food groove occurred, also some slight regeneration, with apparent fusion, of filaments (see Fig. 5).

TABLE I—(*continued*).

Mussel.	Date of opening in 1930.	Condition on date of opening.	Nature of injury inflicted.	Result.
C.	July 30	Much byssus formed; strongly attached. Fairly well fished. Gills very slightly pigmented, with practically no intensity of pigment along ventral edges.	All four gills cut obliquely with scalpel, the cuts not reaching the ventral edge. In some cases the gill was supported by the blade of an oyster opener (see p. 557).	No injury apparent when gills examined with microscope. Regeneration of epithelium occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
D.	July 30	Much byssus formed; strongly attached. Mussel in good condition.	As for C.	As for C.
E.	Sept. 15	Valves gaping. Mussel thin.	As for C.	No injury apparent when gills examined with microscope; but a small piece missing from the ventral edge of left inner gill; one of the cuts may have been too near the edge of gill. Regeneration of epithelium had occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
F.	July 30	Much byssus formed; strongly attached. Mussel in good condition. Spawned as female, after being opened and put in finger bowl under circulation.	All four gills cut obliquely with scalpel, the cuts not reaching the ventral edge. In all instances the gill was supported by the blade of an oyster opener (see p. 557).	No injury apparent when gills examined with microscope. Regeneration of epithelium had occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
G.	Feb. 20	Found dead.		
H.		Found dead.		

J.	Oct. 17	Poorly fished, valves easily forced apart. Gills very slightly pigmented.	(*a*) Right inner gill.—A slanting cut with scissors from ventral edge in a dorsal and anterior direction, so as to isolate a piece of gill except for attachment by ciliated discs.	(*a*) Piece sloughed off. Cut made at extreme posterior end of gill, very close to dorsal food groove ; as all interlamellar junctions removed, the lamellæ separated, and the cut ventral ends of each have rounded off independently, with irregular edges and *without* formation of food groove.
			(*b*) Right outer gill.—Cut obliquely with scalpel in several places, cuts not reaching the ventral edge. Gill not supported (see p. 557).	(*b*) No sign of injury when gills examined with microscope. Regeneration of epithelium had occurred.
			(*c*) Left inner gill.—As for right outer gill (*b*), but gill supported by blade of oyster opener (see p. 557).	(*c*) No sign of injury when gills examined with microscope. Regeneration of epithelium had occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
			(*d*) Left outer gill.—Large piece cut out of ventral edge.	(*d*) Regeneration of food groove occurred, also some slight regeneration, with apparent fusion, of filaments.
K.	July 30	Valves gaping somewhat ; would not close when touched. Mussel in poor condition. Gills rather slightly pigmented, but with a darkly pigmented (brown) ventral edge.	(*a*) Right outer gill.—Large piece cut out of ventral edge.	(*a*) Regeneration of food groove occurred, but no appreciable regeneration of filaments. New food groove was very noticeable as it was almost unpigmented, while that on old part of gill was very darkly pigmented. The gap was somewhat smaller than the piece removed, owing to the inward bending of the filaments at either end.
			(*b*) Right inner gill.—Piece cut out of ventral edge.	(*b*) As for right outer gill.
			(*c*) Left inner gill.—Piece cut out of ventral edge.	(*c*) As for right outer gill.

REGENERATION.

Regeneration of the gill of Mytilus consists of the formation of (*a*) food groove and (*b*) gill filaments. These may be considered separately, as the former may occur without any appreciable regeneration in length of the gill filaments.

(*a*) Food Grove.

A food groove was formed at the cut edge of the gill in all cases, with but one exception, and is apparently always formed, if the cut edges of the filaments of the descending lamella are able to touch and so to fuse with those of the ascending lamella. In the exceptional case (see J, Table I), the cut ends of the descending and ascending filaments had not fused together, but had rounded off independently, the two lamellæ being unconnected in the region of the injury. The ventral edges of the lamellæ were irregular, the filaments having irregularly swollen ends, and no food groove had been formed. There was some fusion of the filaments side by side, towards the ventral edge, and they appeared to be in a somewhat degenerating condition. The cut in this instance was made at the extreme posterior end of the gill where the filaments are either without interlamellar junctions, or there is only one to a filament ; such junctions as existed were evidently in the piece of gill which sloughed off following the cut, and there was therefore nothing to prevent the remaining parts of the lamellæ from separating ; the non-fusion of their cut ends was apparently due to this cause.

Mussels, which have been found with the ventral edges of the gills in a jagged condition, have been noticed to have continuous, though irregular, ventral food grooves, and offer additional evidence that a groove is practically always formed at the cut edge. An example of regeneration of a food groove following natural injury is sketched in Figure 18, B, of a previous paper on abnormal gills in this journal (**2**, p. 512).

It was found that two secondary folds bearing food grooves were present on the descending lamella of the left outer gill of the experimental Mussel A, as shown in Figure 2 : some slight abnormality of the filaments occurred in corresponding positions on the ascending lamella. It is perhaps probable that the injuries done to the gill are accountable for these, though there appeared to be no difference in pigmentation between the secondary folds and the old part of the gill. It will be seen that the secondary groove near the ventral edge of the gill, runs from the main food groove in an anterior and dorsal direction, so that the current along its food groove diverges from that of the main groove instead of joining it, as is more usual in secondary grooves on gills (see **1**). On most of the filaments composing the larger secondary groove there was no reversal of beat of the frontal cilia, but on a very few it occurred for a short stretch near the secondary groove. There appeared to be no change in direction of the ciliary current on the filaments composing the smaller, and more dorsal secondary groove, but the filaments were not examined singly.

Gills (see C, D, E, F and J, Table I) which had been cut with a scalpel obliquely across the filaments—care being taken not to reach the ventral edge of the gill—in some cases the gill being unsupported, and in others supported by the blade of an oyster opener inserted behind the gill, curiously showed not the slightest sign of injury when examined under the microscope at the end of the experiments. The doubt arose, considering the difficulty of working with mussels with the valves only slightly separated, whether any cut had actually been made. Investigation with an opened mussel showed that if the gill was unsupported the frontal epithelium alone was cut, the chitinous skeleton being sufficiently resistant to prevent cutting of the entire filament. Following the cut, the epithelium peeled off away from it, leaving the chitinous skeleton exposed for a stretch of about 1·0 mm. When the gill was supported by the blade of an oyster opener the result varied. In some instances both lamellæ were cut through ; in others only one lamella, though the epithelium of the opposite one was injured ; while in others, though the epithelium of both lamellæ was injured, few if any filaments were actually cut through. In all cases the epithelium peeled off for a short distance on either side of the cut or injury. Thus, beyond the cutting of the frontal epithelium, the extent of the injury inflicted with a scalpel is not exactly determinable. However, in the case of the experimental mussels, it is most probable that at least in some instances the filaments were cut through, and there can be no doubt that then the cut ends fused cleanly ; where the epithelium alone was cut or injured with consequent peeling off for a short distance, it had regenerated.

This part of the experiment was done in an unsuccessful attempt to cause the formation of secondary food grooves ; possibly a tear rather than a clean cut might be more efficacious, but pulling a bent mounted needle, which had been ground to a cutting surface, across the surface of the gill, as was done previously with several mussels, also produced no result. By the latter method the filaments seem to be pulled apart and injured, but not broken.

(*b*) GILL FILAMENTS.

Regeneration of the gill filaments did not invariably occur ; in only one (see A, Table I) out of four surviving experimental mussels, was regeneration unmistakable and of some amount (Figs. 1, 2 and 3). In one area on each of the two left gills of this mussel (Figs. 2 and 3) the piece regenerated was as great or slightly greater in amount than that lost; the maximum length of filament regenerated, 7·3 mm., occurred in a deep narrow area on the left inner gill (Fig. 3), where, however, regeneration was not complete. The rate of regeneration in these gills would appear to have been rather greater than on the right inner gill of the same mussel (Fig. 1), where the greatest length of filament removed was about 5·4 mm., while the greatest length regenerated was about 3·2 mm.; it may be that the shape of the piece severed from the gill has some bearing on this, a narrow deep gap being more rapidly filled in than a broad shallow one.

In two mussels (B and J, Table I) some slight amount of regeneration appeared to have taken place, but it was difficult to distinguish, as owing to the very pale tint of the gills there was no appreciable difference in degree of pigmentation of the old and new regions. It was judged to have occurred partly on a comparison of the size of the pieces removed with the size of the gaps left in the gills at the end of the experiment, and partly on a consideration of the form of the filaments.

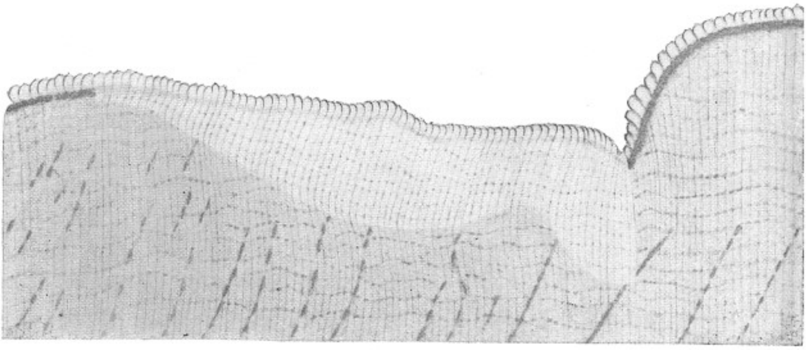

FIG. 1.—Mussel A. Regenerated area on right inner gill; ascending lamella sketched. An attempt has been made to indicate the difference in degree of pigmentation of the old and new parts. The dark line underlying the food groove in the original part of the gill, represents the line of orange or brown pigment normally found in this position; the dark oblique lines represent interlamellar junctions; the dotted wavy horizontal lines, ciliated discs. It will be noticed that a few filaments bordering on the injured area anteriorly, that is at the deepest part of the cut, appear either to have not shared in the growth of the gill, or become reduced in length. (Anterior is on the right.) × ca. 6¼.

At the junction of the old and new part of the gill there is generally a slight bend in the filaments (Fig. 4). In some cases (see Fig. 5) there may be lateral fusion of the cut ends of some of the filaments so that two or three will grow forward as one, and as a result there are fewer in the new part than in the old. The ventral continuation of fused filaments is shown by sections to be single in structure as well as in appearance (Fig. 6, p. 562), as might be expected if this part were due to new growth; if it were due to fusion side by side of existing filaments this would in all probability be

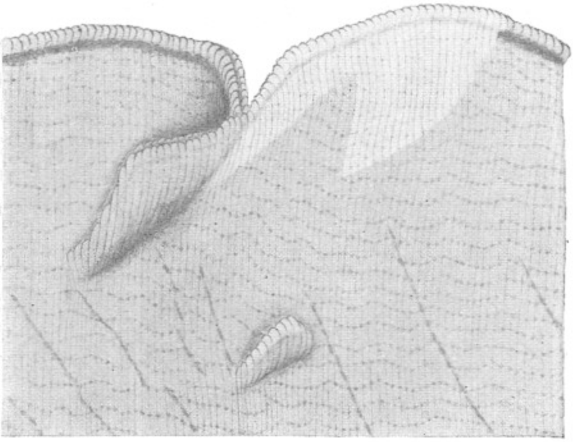

FIG. 2.—Mussel A. Regenerated areas on left outer gill; descending lamella sketched. Two secondary folds with food grooves are shown. (Anterior is on the left.) × ca. $6\frac{1}{4}$.

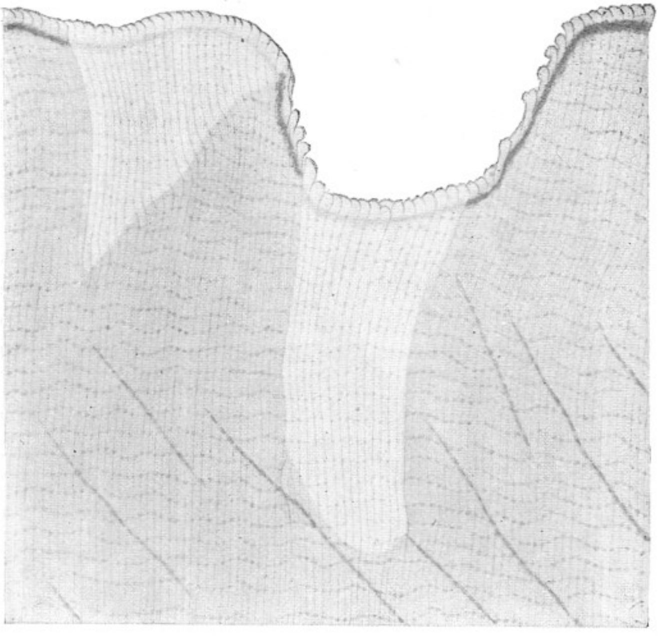

FIG. 3.—Mussel A. Regenerated areas on left inner gill; ascending lamella sketched. (Anterior is on the left.) × ca. $6\frac{1}{4}$.

apparent in duplication of the chitinous supports in the fused part (see **2**, p. 507). This lateral fusion of the cut ends of certain of the filaments, with forward growth as a single filament, resulted in an irregular number in the descending and ascending lamellæ, and as a consequence, along the ventral edge of the gill instances occurred of the fusion of the ventral ends of two filaments in one lamella, with the ventral end of one in the opposite lamella.

But the ease with which slight regeneration can be detected depends largely on the depth of pigmentation of the original part of the gill. The characteristic appearance of the normal gill—when looked at as a whole—with (*a*) the line of orange or brown pigment beneath the main ventral food groove; (*b*) the more opaque, sometimes darker, wavy lines running longitudinally across the surface of the lamella, due to the presence of ciliated discs; and (*c*) the more opaque, and sometimes darker, oblique lines, due to the presence of interlamellar junctions, is shown in the old part of the gill in the sketches in Figures 1, 2 and 3. These three sets of markings on the gill are more clearly visible in some gills than in others, depending largely on the variation in general depth of pigmentation of the gills, which occurs in different individuals. In two mussels (B and J, in Table I) the gills were so pale in tint that even the regenerated food groove showed up very faintly, though under the microscope the difference in pigmentation could be fairly easily seen. In one mussel (A, in Table I), in which an appreciable amount of regeneration had occurred, the regenerated areas were obvious at a glance owing to the difference in intensity of pigmentation between them and the old part of the gill (Figs. 1, 2 and 3). The newly formed parts were practically unpigmented, and the dark line of pigment normally present

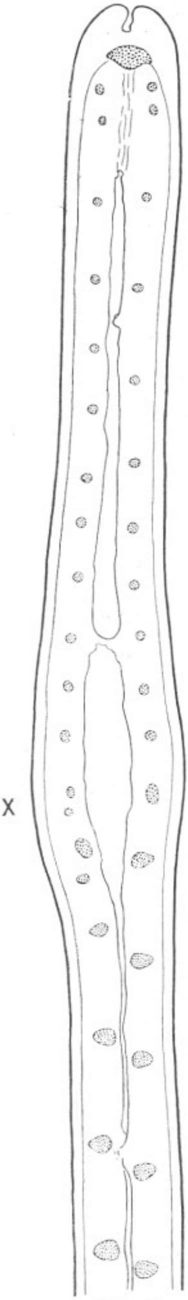

FIG. 4.

FIG. 4.—Side view of filament from a region of regeneration. The junction (at ×) between the old and new parts of the filament is marked by a slight bend: the difference in the size of the ciliated discs in the two regions is noticeable, those in the new part being considerably smaller than those in the old part. One interlamellar junction is present in the new region and also the beginning of a second. Bouin's fixative. × ca. 35½.

running parallel with the free ventral edge of the gill was lacking; the pigment granules seen under the microscope in this position being too few to give any appearance of colour. In the case of the right-inner gill of mussel A (Fig. 1) the oblique dark lines on the old part of the gill, due to the presence of interlamellar junctions, were seen to stop abruptly when reaching the regenerated portion. Under low powers of the microscope, or with a lens, the dark wavy lines caused by the presence of the ciliated discs on the filaments were also seen apparently to stop, or alter in character, against the new tissue in all cases of regeneration of the gills of this mussel (Figs. 1, 2 and 3): in the regenerated region these lines, though present, were faint, and difficult to follow. The cause of the difference in intensity of the lines was apparent on examining single gill filaments in side view; in the regenerated part of the gill filament the ciliated discs were on an average about half the size of those in the original part of the filament (see Fig. 4), and were practically destitute of pigment granules. In those instances examined, they also differed in shape, being more or less circular, while those in the old part were somewhat triangular. Single filaments stripped from one part of a gill (preserved in formalin) where regeneration had occurred, showed the mucus cells, which were plentiful on the abfrontal face in the old part, to be absent, or not visible in a total unstained preparation, in the new part. This, however, is probably a point of little importance as the condition of the mucus glands is

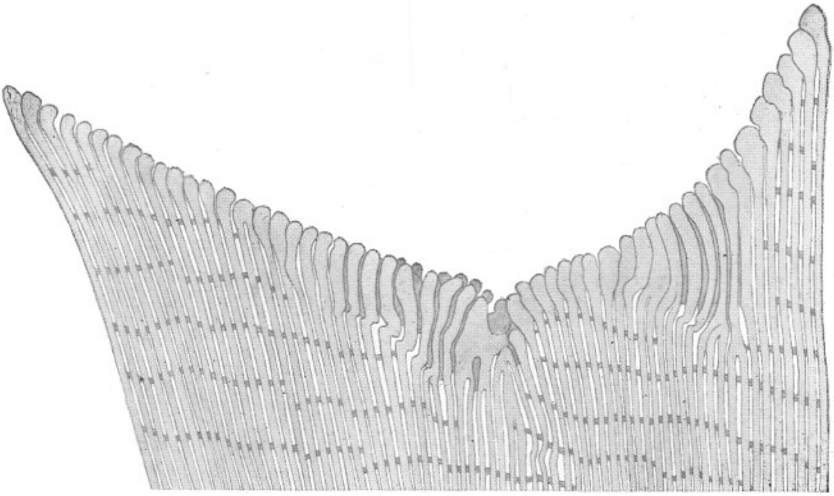

FIG. 5.—Mussel B. Left outer gill, ascending lamella. A small region at the depth of the gap has been sketched, to show the tiny irregular area of regeneration, and the apparent fusion of some of the filaments. In this instance there was no appreciable difference in colour between the old and new parts. (Anterior is on the right.) × ca. 18¼.

likely to vary in different parts of an uninjured filament, and at different times. Microscopic transverse sections through the old and regenerated parts of the gill showed no appreciable difference in the development of the chitinous supports. The difference in pigmentation between the old and

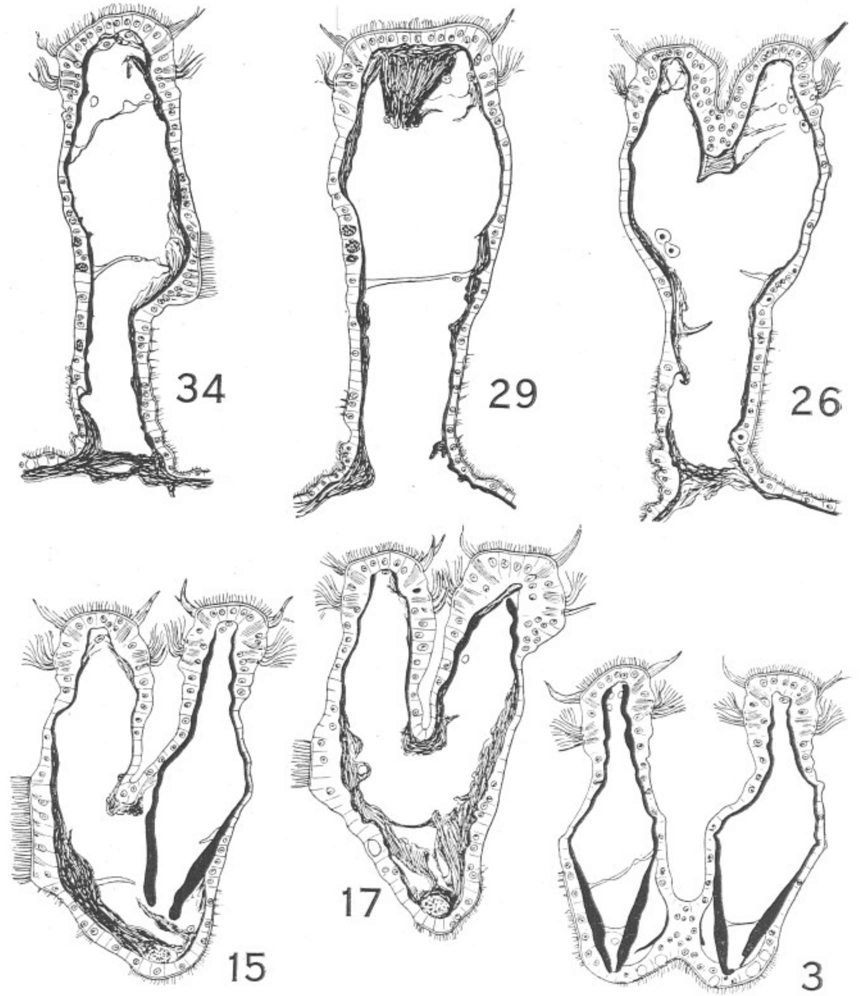

FIG. 6.—Mussel B. Left outer gill, ascending lamella. Transverse sections from a series passing through the junction of the two fused filaments on the extreme right of Fig. 5, to show the change undergone by the chitinous supports and the simple character of the ventral continuation of the filaments. Some slight fusion of the two filaments was evident in the two sections preceding the most dorsal one sketched, namely, 3. The sections are numbered according to their position in the series, so that the number of intervening sections may be known. In the 22nd and following sections (see 26, 29, 34) the filament was connected with several, more posterior, filaments and also with a group in the opposite lamella. The pale staining chitin is indicated by shading. Bouin's fixative; Mallory's Triple Stain. Sections ca. 8μ thick. × 270.

new food grooves was clearly visible in sections passing from one to the other : these were cut a day or two after fixation and the pigment granules had retained much of their original yellow colour.

Interlamellar junctions, to the number of two, have been observed in the regenerated part of some of the few filaments examined singly : they were finer than those in the original part of the filament. In the new part, some at least of the interlamellar junctions appear to be formed by outgrowth from the abfrontal face of one filament (Fig. 7), three cases being noticed of small outgrowths in this position ; two of these, of which note was especially taken, were from the ascending filament and were respectively about 1·2 and 2·59 mm. from the ventral edge of the gill. This is of interest in relation to the method of formation of these junctions in the normal development of the gill. According to Rice, they arise through the perforation of a short interlamellar septum, present between the ventral ends of the descending and ascending filaments (see **12**, Fig. 8, p. 73), and such as is found much more fully developed in Modiolus. This he refers to as the Modiolus stage in the development of the filaments of Mytilus.

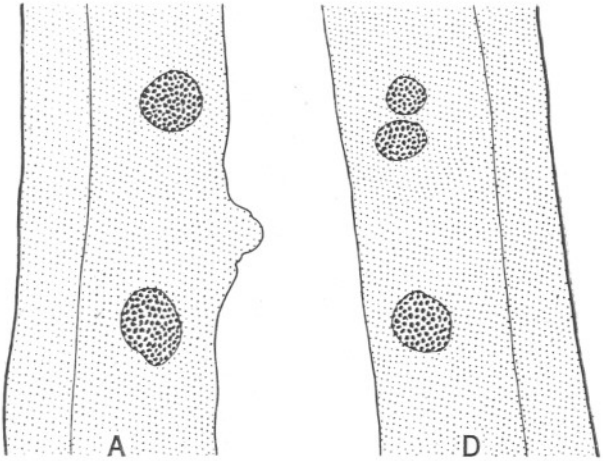

FIG. 7.—Sketch showing origin of interlamellar junction on abfrontal face of ascending part of regenerated filament. The small outgrowth was about 2·59 mm. from the ventral edge of the gill. Bouin's fixative. D and A, descending and ascending filaments respectively. × 140.

In the regenerated areas, as shown by sections through the regenerated part of the left outer gill of Mussel B (Fig. 5), much interfilamentar as well as interlamellar connection may occur, in part obliterating the interlamellar space. The condition of the filaments shown in Figure 8 was seen in part of the regenerated area, the particular section sketched being across some of the normal-looking filaments to the right of the median area of fusion, and between the two most ventral rows of ciliated discs seen in Figure 5. In some parts a similar condition of groups of filaments existed through much of their regenerated length (ca 1·0 mm.).

In a certain number of mussels slanting cuts were made, with scissors, from the ventral edge of the gill in a dorsal and anterior direction, in this way separating a triangular piece from organic connection with the gill, but without removing the piece, which remained connected merely by the ciliated discs on the most anterior and longest length of filament. In the four gills treated in this way (mussels B and J with one gill in each, and mussel A with two gills cut), the pieces had more or less completely degenerated and fallen off. In one instance (left inner gill of B), it appeared that the cut ends of some few disconnected filaments at the depth of the cut (the longest pieces separated) had joined up again, but somewhat irregularly, the ventral ends of two joining the dorsal end of one and vice versa : in this case also, while most of the cut ends of filaments had sloughed off, there were five or so short lengths of filaments separated dorsally from the main part of the gill by a tiny space, but attached anteriorly

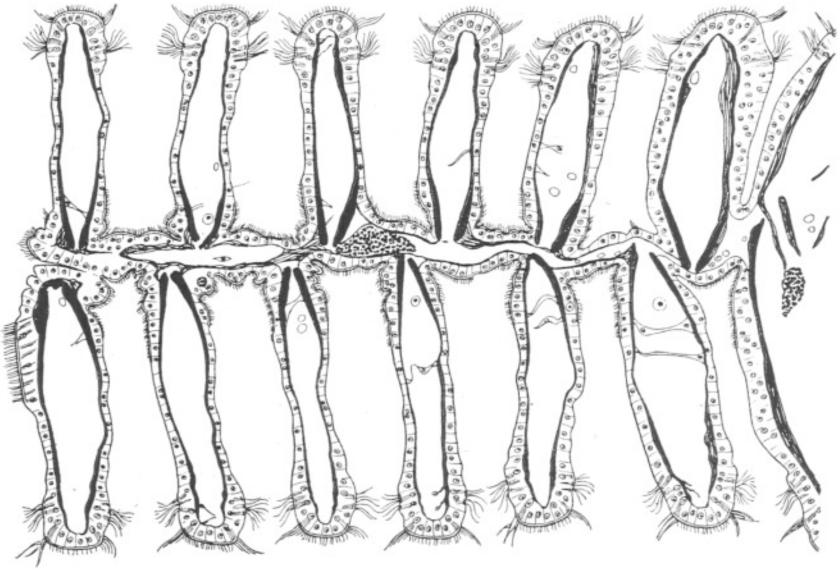

FIG. 8.—Mussel B, left outer gill. Transverse section through part of new area sketched in Fig. 5, showing the filaments in the two lamellæ connected by a median band of tissue. A mass of pigment is present at one place within this median connection. This section is across some of the normal-looking filaments to the right of the median area of fusion, and between the two most ventral rows of ciliated discs, seen in the sketch. Bouin's fixative ; Mallory's Triple Stain. Sections ca. 8μ thick. × 200.

and posteriorly; but it is most probable that these filaments were in connexion with each other and the rest of the gill by some organic junctions.

In a previous experiment in June, 1929 (see **1**, p. 961), some organically separated ends of filaments were still connected, after 112 days, with each other and with the main part of the gill merely by their ciliated discs. It, therefore, appears that though such cut pieces of filament may persist for a certain time, after a longer period they are very liable to slough off.

In one mussel (A, in Table I) the two left gills were cut in the manner described above, and regeneration occurred, new tissue partly or entirely filling up the triangular gaps (see Figs. 2, 3).

It may be noted that even after preservation in formalin, or in Bouin's picro-formol for rather more than three months, regenerated areas were recognisable owing to their greater translucence.

DISCUSSION AND SUMMARY.

Experiments have shown that the gill of Mytilus is capable of regeneration, and that this may occur in less than eight months. It may be confined to the formation of a food grove at the cut edge of the gill, without appreciable regeneration in length of the gill filaments. Regeneration of a food groove appears always to occur at the cut edge, if the ends of the descending and ascending filaments are able to touch and so to fuse. On the other hand, regeneration of gill filaments does not seem to occur invariably, and when it does the rate is slow, at least under experimental conditions and in mussels of a length of about 7·0 to 8·0 cm., such as were used for the experiments: it is possible that regeneration would occur more surely and rapidly in young mussels, but owing to the thinness of the shell they would be more difficult to wedge open without fracturing. Coulthard (**6**, p. 136), however, says that "The rate of growth is independent of size in the mussel, being apparently influenced only by the environment." Perhaps the lack of an abundant food supply under the conditions of the experiments should be taken into consideration, though it is well known that in general the amount of food available to an animal has little influence on regeneration (**9**, p. 27). The salinity of the water in general circulation is about 36–37$^\circ/_{oo}$, that is, higher than normal sea-water, which is about 35$^\circ/_{oo}$, and would be considerably higher than the optimum salinity for growth (see Flattely and Walton, **7**, p. 81). This may also possibly have a retarding effect on the initiation of regeneration and the rate.

It is obscure why regeneration does not always occur; so far as could be judged there was no difference in the method of making the cuts, there was little difference in the size and therefore the age of the mussels used, the cuts were made in approximately the same position on the gill (somewhere between the posterior and middle third of the gill, this position being chosen simply because it was the easiest to reach), and at the end of the experiments—none of which was terminated before the end of eight months—there was little difference in the condition of the various mussels.

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The Natural History of *Bulla hydatis* Linn.

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With one Figure in the Text.

Bulla hydatis is a mollusc of relatively rare occurrence in the Plymouth district, although fairly common across the Channel at Roscoff. Intermittent dredging and collecting in the Salcombe estuary over a period of about five years, and some rearing experiments carried out in the department of zoology, University College, London, have afforded some insight into its apparently peculiar distribution and also a few facts of certain general interest.

This tectibranch mollusc was recorded during the survey of the Salcombe estuary by the staff of the Plymouth Laboratory in 1902, but it was found only on a spit of sandy gravel on the south shore of the Salstone. Apart from this, it apparently has not been seen except for a few specimens found in the Yealm estuary and one from Jennycliff bay at about the same period. During the succeeding twenty-odd years no record of Bulla was made at all, although there is some evidence that its spawn has been seen though not recognised.

It is accordingly of greater interest that it has been found on almost every visit, winter and summer, made to the Salstone since 1924 ; and it was discovered on each occasion only on the sand spit mentioned above, and below the low-water spring-tide level.

Spawning occurs in June, and a few weeks before that of Oscanius, which is commonly found on the same grounds. The spawn is shown in Figure 1, A, and is usually attached to weed, sometimes to stones, near the datum line. The eggs are approximately 0·2 mm. diameter and two are contained within one capsule ; the capsules are arranged in rows along the shorter axis of the jelly (Fig. 1, A and B).

Hatching occurs after two or three weeks when the veliger larvæ have been actively swimming within the capsules for a considerable period. On hatching great variability is seen in their behaviour, some swimming as veligers for a few days although keeping near the bottom, others settling at once to crawl for the rest of their existence. In other words, hatching occurs just as the veliger phase is coming to a close, and slight differences in time of hatching may produce great differences in degree of dispersion. However, a large proportion of larvæ are sure to settle immediately, and in this fact lies the explanation of the continuous occupation of a small sand spit for a recorded period of about thirty years. The apparent absence elsewhere along the south-west coast of England may be due to one of two reasons. The free-swimming veliger phase may be too short for the larvæ to be carried to any other feeding grounds, or, it may occur in most southern estuaries of high salinity

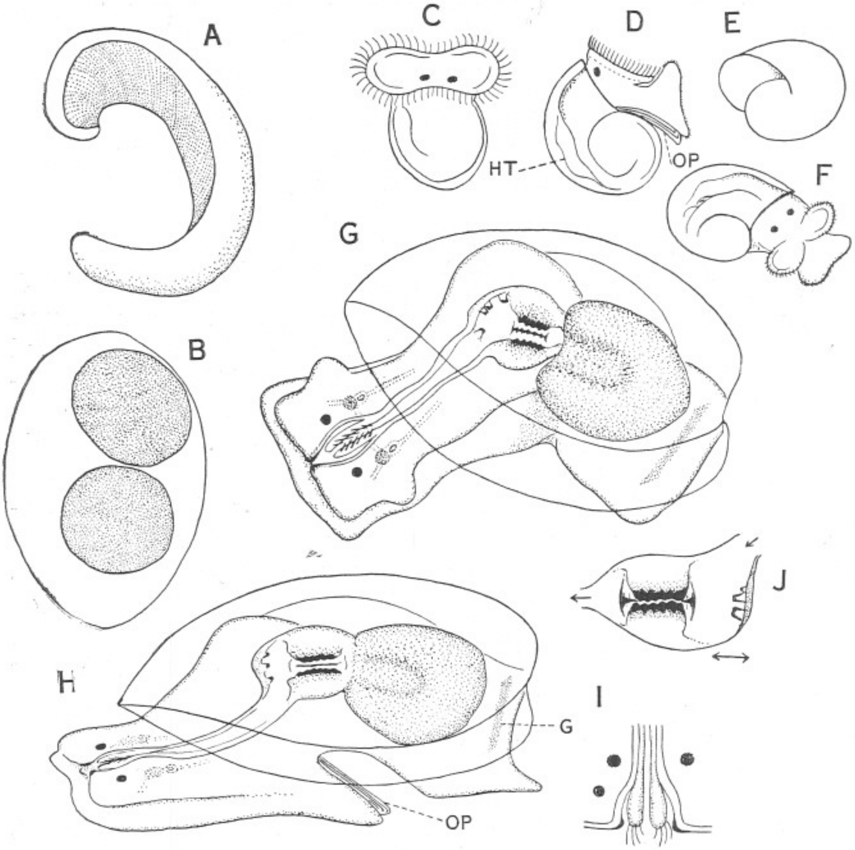

FIG. 1.—A, spawn of *Bulla hydatis* Linn., about natural size. B, developing eggs within isolated capsule ; capsules are arranged in rows as shown in A. C, D, dorsal and side views of veliger larva at hatching stage. E, stage at which large proportion hatch, when velum somewhat resorbed and larva crawls. F, empty shell of the newly hatched larva. G, H, post-larval forms about two months old, showing gastric mill, larval feeding mechanism, and elongation of shell aperture. I, larval "grab" extended (shown retracted in G), also chitinous lips. J, larger view of gastric mill showing the three teeth, the stoking plates and their range of movement.

without having been found. This last is quite possible, for Bulla apparently lives close to the low-water line, spends much of its time burrowing in the muddy sand, and is to be found much more readily by touch than by sight; moreover, but little dredging has been carried out in other estuaries in such very shallow water. Its presence in other districts accordingly is more likely to be indicated by the discovery of the yellow or brownish spawn.

A number of spawn jellies were kept in small aquaria and the hatched larvæ reared until a few, after fifteen months, were about 15 mm. long or about one-third adult size. The chief cause of mortality was the tendency to climb above the water level and dry up before regaining paradise. Frequently a tank was considered to be destitute of survivors when, as time proved, many were ploughing their way beneath the sand, often remaining out of sight for a week or two. The only food obtained by these forms was the sheet of diatoms and algæ encrusting the walls of the aquaria, and these small individuals and also adults seemed to scrape the sides with the radula in a manner quite indiscriminate. Adults opened on capture contained only remains of hydroids and algæ.

Certain observations of some interest were made upon post-larval stages and are illustrated in Figure 1.

Most larvæ upon hatching are able alternatively to swim as veligers or crawl as gastropods; the shell at this time is a simple coil, the opening of which can be closed by the operculum carried on the posterior border of the foot. As post-larval growth proceeds the long ciliated lobes of the velum are resorbed, and the body and shell become much elongated so that the operculum no longer is adapted to the shell opening.

Shortly after the crawling existence commences and until the individual is several millimetres in length, feeding is accomplished by a temporary mechanism. This exists probably because a true radula cannot be encompassed within so small an organism. It is illustrated in Figure 1 and is composed of setæ that project divergently when the buccal mass is extruded; when retracted the setæ close together and are withdrawn, the whole action being that of a grab.

Peristaltic movements convey the food from the buccal cavity to the gastric mill. The exact time and details of the change over to the adult radula mechanism were not determined. The activity of the gastric mill, however, could be seen quite plainly through the transparent tissues. The mill itself consists of three massive teeth, the grinding surfaces of which form an angle of 120 degrees to each other and bear ridges; the whole tooth on removal from the muscle in which it is embedded might at first sight be mistaken for a small specimen of Chiton. These three teeth fit together and complete a circle; they have two movements, a simple withdrawal from their common centre alternating with their mutual approach, and a rocking movement along their long axes after they have approached one another as closely as possible. If there were food in position the one movement would act upon it as a vice, the other as a grinder. If a cross section of the mill be visualised, three radii will be seen corresponding to the spaces between the teeth. In front of the mill is a small crop, the anterior wall of which bears three groups of hard plate-like projections. If this wall is pushed toward the mill the three projections fit into the three radii mentioned above ; consequently any food contained within the crop would get pushed accurately into position in the mill. That this does happen is shown by the fact that the anterior wall of the crop pulsates regularly once per second whether or not any food is present, and the wall with the projections it bears acts as a perfect automatic stoking apparatus. Figure 1, G, I, and J, illustrates the above description.

In conclusion a word may be said concerning the significance of hatching enzymes, especially among invertebrates where larval stages are so important.

It has been demonstrated that among the lower vertebrates (Wintrebert, 1926) and the ascidians (Berrill, 1929) proteolytic enzymes are mainly responsible for the process of hatching, and that among the ascidians at least the normal activity of the enzyme is very easily disturbed. Similar enzymes for hatching most certainly occur in many molluscs, in particular in Cephalopods such as Loligo and Sepiola, and in Opisthobranchs including Bulla.

The process seems to be the same in these last two groups—a progressive softening of the jelly mass throughout the period of development, and a digestion of the capsule membrane at the end of that time.

Not only are there differences among the gastropods in the time at which hatching occurs but also in the size of the egg, i.e. in the amount of yolk or reserve food it contains. Such yolk may be confined for the most part to the endoderm and in consequence be drawn upon by the whole organism as is the yolk sac in the case of vertebrate embryos ; alternatively the yolk may be evenly distributed through all cells ; in either case the embryo or larva, compared to embryos developing from smaller eggs, may reach a more advanced stage of development before having to obtain food from without.

The smaller the eggs the sooner they must hatch as larvæ and fend for themselves. At the same time they become subject to a high rate of elimination earlier in life, for until hatching occurs they are relatively safe, a degree of safety comparable to that produced by viviparity in other forms. Moreover, larvæ will be eliminated after hatching at the same rate whether they be large or small. Accordingly any increase in egg size, which necessarily implies a decrease in egg number, will only be of survival value if the protected phase of development be prolonged—in other words, if hatching be delayed.

The eggs of most gastropods which possess a prolonged free-swimming veliger phase (possibly of several weeks) have egg volumes much less than that of Bulla (and of the allied form, Scaphander). Since there is no evidence nor suggestion that reduction of yolk has occurred in the group Opisthobranchiata, this smaller egg size may be considered primitive, and accordingly the postponement of hatching in Bulla until the veliger phase is almost over must be considered a direct result of yolk accumulation within the egg.

How such retardation of the hatching process is effected is not known. It is possible that the veliger stage is reached when the embryo consists of a certain number of cells, that is, various sized veligers are composed of approximately the same number of cells but vary in cell size, while hatching enzymes are liberated and become effective when the cells responsible are reduced by successive cleavages to a certain volume. In other words, the larger the egg the larger will be the veliger, but the longer will it be before the hatching enzyme is formed.

In the case of Bulla the importance of the enzyme is obvious. A slight acceleration of its action would result in the liberation of all the embryos as free-swimming larvæ ; they would be dispersed over a very wide area but might fail to settle on the parental feeding ground. On the other hand, a slight retardation of its action would confine the veliger phase entirely within the egg capsules, the population of the parental grounds would be maintained and possibly become too dense, and there would be little chance of colonizing new areas ; and any changes tending to eliminate the veliger phase from development structurally as well as functionally could take place with impunity.

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Notes on Cyanea Caught in the Ring-trawl in the Plymouth Area during the Years 1925 to 1930.

By

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DURING the researches on the vertical distribution of plankton and on the seasonal abundance of young fish, a record was kept of all *Cyanea lamarcki* Péron and Lesueur* occurring in the catches of the 2-metre stramin ring-trawl. This was primarily for correlation with the abundance of such fish as the young whiting, *Gadus merlangus*, which at certain stages in their development shelter under the umbrella of the medusa. Since it is only with the larger Cyanea that this association of the young whiting exists it was necessary to keep a record of the sizes of the Cyanea occurring in the catches. These were only rough measurements and denote the diameter of the flattened disc of the medusa usually to the nearest half-inch.

Records of the sizes of Cyanea species occurring in other latitudes have been published from time to time, but the writer can find no record of the sizes occurring at Plymouth and it seemed desirable to publish these observations.

In Table III at the end of this paper are given all the numbers and measurements of Cyanea caught in the ring-trawl. All the data for the hauls in question have been given in previously published papers in this journal dealing with the vertical distribution of plankton or the abundance of young fish. It is only necessary to state here that on all dates in the years 1925 and 1926 the numbers given are the total numbers taken in five or usually six ten-minute hauls, each haul being taken at a different depth. From 1927 onwards the collections on each day were half-hour oblique hauls.

A study of these records shows that Cyanea was only taken in the months of April, May, June, and July. Not a single specimen was caught in any other month in the year. In Table I are summarised the results for all years showing the numbers at the different sizes occurring in the months April to July.

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* The validity of *Cyanea lamarcki* as a distinct species seems still to be in doubt (*vide* Bigelow, **1**, p. 357, and Krumback, **6**, p. 24), but I have here followed the nomenclature of the Plymouth Fauna List. In my previous publications I have followed Mayer (**7**, p. 596) in regarding *lamarcki* as a variety of *C. capillata*. Vanhöffen (**8**, p. 53) regarded *C. lamarcki* as a distinct species.

TABLE I.

Diameter of disc in inches.

	<2″	2″	2½″	3″	3½″	4″	4½″	5″	5½″	6″	6½″	7″	7½″
April	118	3	–	2	–	–	–	–	–	–	–	–	–
May	45	6	6	7	–	4	–	–	–	–	–	–	–
June	21	11	8	8	1	12	1	2	1	1	–	–	1
July	4	1	1	2	2	3	–	5	–	2	1	–	–

It shows that Cyanea of a very small size, many of about half an inch diameter or less, appear in comparatively large numbers in April, the largest taken in that month being only 3 inches in diameter. The numbers of small medusæ of under two inches get steadily lower until in July only 4 were taken during the five years in which collections were made in that month. At the same time the numbers of large specimens increase. It appears that 5 to 6 inches in diameter is the usual limit of size reached, one only of 7½ inches having been taken.

In Table II are given the average catches per half-hour oblique haul for each of the months April, May, June, and July for the years 1925 to 1930. (These figures have been calculated as in Journ. Mar. Biol. Assoc., N.S., Vol. XVI, No. 3, p. 707.)

TABLE II.

	1925	1926	1927	1928	1929	1930
April . .	0·0	11·3	0·0	0·0	2·3	1·6
May . .	0·6	4·1	2·0	—	9·8	1·3
June . .	0·4	1·3	1·7	—	10·7	1·3
July . .	0·8	0·0	0·8	—	1·4	1·0

This shows that in 1926 and 1929 the Cyanea were distinctly more abundant than in the other years.

The size of these blue Cyanea is generally given as from 200–300 mm. diameter (Vanhöffen, **8**, p. 53). Haeckel (**5**, p. 530) gives 100–200 mm., and rarely 300 mm. These measurements are slightly higher than those given in Table I, for while 200 mm. is 7·9 inches, 300 mm. is 11·8 inches. It is possible that these larger sizes occur here but are not caught in the ring-trawl; at any rate, they cannot be very common.

Miss Delap (**2**, p. 21) reared *Cyanea lamarcki* in an aquarium. Her first ephyræ were liberated by March 12th, and by April 15th the largest was 10 mm. in diameter. The latter would correspond to about the size at which they first appeared in April in the ring-trawl catches. Under aquarium conditions the largest size she succeeded in rearing the Cyanea to was only 80 mm. (3·2 inches) by June 10th. In 1901 M. and C. Delap record in Valencia Harbour "A good many seen in June from two to five inches in diameter" (**3**, p. 15), and for 1902 they say, "A considerable number seen on May 8th, from ¾-inch to double that size, all young stages" (**4**, p. 13).

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TABLE III.

NUMBERS AND SIZES OF CYANEA TAKEN IN THE 2-METRE STRAMIN RING-TRAWL COLLECTIONS AT PLYMOUTH FROM 1925 TO 1930.

1925.

April	2nd, 8th, 22nd, 29th : none.	
May	19th (i.)	1 (" small ").
,,	19th (ii.)	1 (,,).
June	4th (i.)	—
,,	4th (ii.)	—
,,	17th (i.)	½″, 1 : 2″, 1.
,,	17th (ii.)	—
,,	17th (iii.)	3″, 1.
,,	18th (i.)	2″, 1 : 4″, 1.
,,	18th (ii.)	1½″, 1.
,,	18th (iii.)	—
,,	18th (iv.)	3″, 1 : 4″, 1.
,,	19th (i.)	—
,,	19th (ii.)	2½″, 1.
July	1st (i.)	¾″, 1 : 1½″, 1 : 3″, 1 : 3½″, 1.
,,	1st (ii.)	1½″, 1.
,,	16th	—
,,	29th	1½″, 1.
August	6th	—

1926.

April	9th	½″–1½″, 12 : ⅜″–1¼″, 6 : under 1″, 6.
,,	13th (i.)	¼″–¾″, 5 : ¼″–½″, 7 : 1″–1¼″, 2 : 1–1¾″, 4 : 3″, 1.
,,	13th (ii.)	½″, 25 : ½″–1½″, 20 : 1″, 1 : 2″, 1.
,,	22nd	¼″, 1 : ½″, 2 : ⅓″, 1 : 1″–1¾″, 3 : 1″-2″, 4.
,,	26th	½″, 2 : ¾″, 1 : 1¾″, 1 : 2″, 1.
May	6th	½″, 1 : 1″, 2 : 1½″, 1 : 3″, 1 : 4″, 1.
,,	19th	<1″, 3 : ½″, 4 : 1″, 1 : 3″, 1.
June	3rd (i.)	—
,,	3rd (ii.)	—
,,	3rd (iii.)	1¾″, 1 : 2″, 1 : 2½″, 1 : 4½″, 1 : 6″, 1.
,,	4th	½″, 1 : 2″, 1 : 3″, 1 : 4″, 4 : 5″, 2 : 5½″, 1 : 7½″, 1.
,,	25th	—
,,	30th	—
July	6th, 13th, 15th, 26th : none.	
August 4th ; Sept. 22nd : none.		

1927.

April	4th, 5th, 20th, 26th : none.	
May	2nd	—
,,	9th	1½″, 2 : 3″, 1 : 4″, 2.
,,	16th	2½″, 1 : 3″, 2.
,,	25th	—
June	2nd	1″, 2 : 1½″, 1 : 4″, 1.
,,	9th	—
,,	29th	2″, 1 : 4″, 1.
July	8th	4″, 1.
,,	12th	2″, 1.
,,	21st	—
,,	26th	4″, 1.

1927 (*cont.*)

August	4th, 8th, 19th, 26th, 31st : none.
Sept.	6th, 15th, 19th : none.
Oct.	4th, 13th, 18th, 24th : none.
Nov.	1st ; Dec. 15th, 21st : none.

1928.

Jan.	9th, 16th, 26th, 30th : none.
Feb.	2nd, 20th, 27th : none.
March	5th, 21st, 30th : none.
April	4th, 11th, 12th, 23rd : none.

1929.

April	10th	—
,,	19th	¾″, 3 : 2″, 1 : 3″, 1.
,,	23rd	¾″, 2 : 1″, 1 : 1½″, 1.
,,	29th	—
May	6th	½″, 5 : 1″, 1 : 2″, 1.
,,	13th	½″, 6 : ¾″, 3 : 1″, 5 : 1¼″, 2 : 2″, 4 : 2½″, 1 : 2¾″, 1.
,,	23rd	—
,,	27th	1″, 2 : 1½″, 1 : 2″, 1 : 2½″, 3 : 3″, 2 : 4″, 1.
June	6th	¾″, 1 : 1″, 4 : 1½″, 6 : 2″, 4 : 2½″, 3 : 3″, 3 : 4″, 2.
,,	11th	1″, 1 : 1½″, 1 : 2″, 2 : 2½″, 2 : 3″, 2.
,,	25th	1½″, 1.
July	3rd	4″, 1 : 5″, 2 : 6″, 1.
,,	9th	—
,,	18th	2½″, 1 : 3″, 1 : 5″, 1.
,,	23rd	—
,,	30th	—
August	9th, 15th, 22nd, 26th : none.	
Sept.	4th, 6th, 10th, 17th, 24th : none.	
Oct.	3rd, 10th, 16th : none.	

1930.

Feb.	2nd, 12th, 19th, 26th : none.	
March	5th, 12th, 19th, 27th : none.	
April	2nd	—
,,	11th	½″, 1.
,,	16th	—
,,	24th	½″, 5 : ¾″, 1.
,,	29th	½″, 1.
May	7th	¾″, 1 : 1″, 1.
,,	15th	½″, 1.
,,	22nd	½″, 1.
June	10th	—
,,	19th	3½″, 1 : 4″, 2.
,,	26th	2¼″, 1.
July	4th	—
,,	9th	—
,,	14th	—
,,	23rd	5″, 1 : 6″, 1.
,,	29th	3½″, 1 : 5″, 1 : 6½″, 1.
August	8th, 14th, 21st, 28th : none.	

Notes on the Ciliate *Boveria stevensi* Issel from *Galeomma turtoni* Sowerby at Plymouth.

By

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and

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With 2 Figures in the Text.

THE little bivalve mollusc *Galeomma turtoni* is not very common off the coast of South Devon; but two specimens were brought in while we were working at the Marine Biological Laboratory last August, and when we examined them we found that the branchiæ and mantle cavity were aswarm with a small colourless ciliate.

A formidable list of ciliates from such situations in lamellibranchs and gastropods stands in the records. From *Galeomma turtoni* Sowerby at Naples Issel (1903) described *Boveria stevensi*, and there seems no reason to doubt that the organism we have found is Issel's ciliate, though the specimens in the Plymouth mollusc are rather larger than those he measured.

We feel justified in publishing the following notes, since Boveria and its allies, the "Thigmotricha" of Chatton and Lwoff, show many features of interest to the protozoologist, and the descriptions of the mouth region in the smaller forms are very inadequate.

The body of our ciliate is 16–36μ long and about 16–20μ broad (the largest measurement Issel gives is $29 \times 17\mu$). In side view it appears curved like an arc; we shall speak of the convex surface as dorsal and of the more concave as ventral. The maximum thickness is about 15μ. The aboral end, which is directed forwards as the animal swims, is a somewhat pointed lobe.* From the dorsal aspect and in profile, the opposite end appears obliquely truncate: this is the region of greatest breadth and

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* De Morgan (1925) and some other observers regard this end in Ancistrum and Boveria as posterior, because the mouth lies at the opposite pole. Maupas (1883) and Cheissin (1931) consider that, as the aboral end is directed foremost, it should be called the anterior end. We prefer to use the terms "oral" and "aboral" to indicate which pole we refer to, without committing ourselves further. It should be noted that the young vorticellid, when liberated from its stalk, swims aboral end foremost; yet it is customary to speak of the oral end of the stalked stage as "anterior."

thickness. The body does not seem to be very contractile, but preserved ciliates are almost always somewhat shorter and thicker than living ones: the measurements given above were made on preserved material.

The whole surface is covered with longitudinal rows of fine cilia; there are 10–12 rows on the dorsal side and about the same number on the ventral. Their distribution is best indicated by the lines of basal granules in stained specimens (see Fig. 2). We find that the ventral lines converge and meet one another at an acute angle, a short way behind the aboral end. Issel (1903) does not show this, and Cheissin (1931) suggests (p. 286) that in this respect his new genus Tiarella differs from the species of Boveria hitherto described. The most anterior of these body cilia are longer than the others and tend to stand more erect than do those further back; just ventral to the aboral end, they are especially active and their movement creates a sort of vortex. These cilia seem to correspond to the

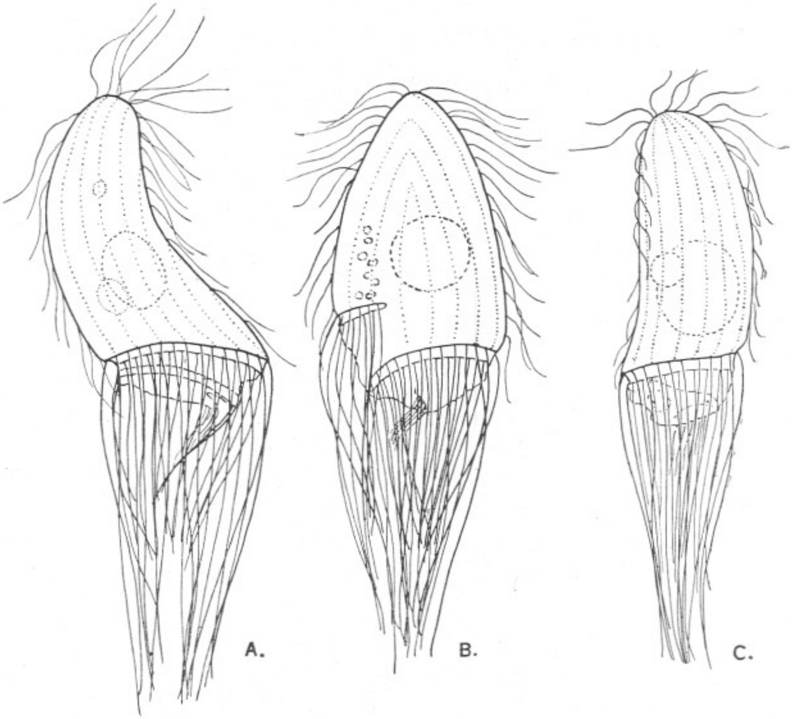

FIG. 1.—Three aspects of the living ciliate. From free-hand sketches. (The number of longitudinal lines of cilia on the body is actually greater. See Fig. 2.)

A. in profile.
B. ventral view.
C. approximately dorsal view.
×1200.

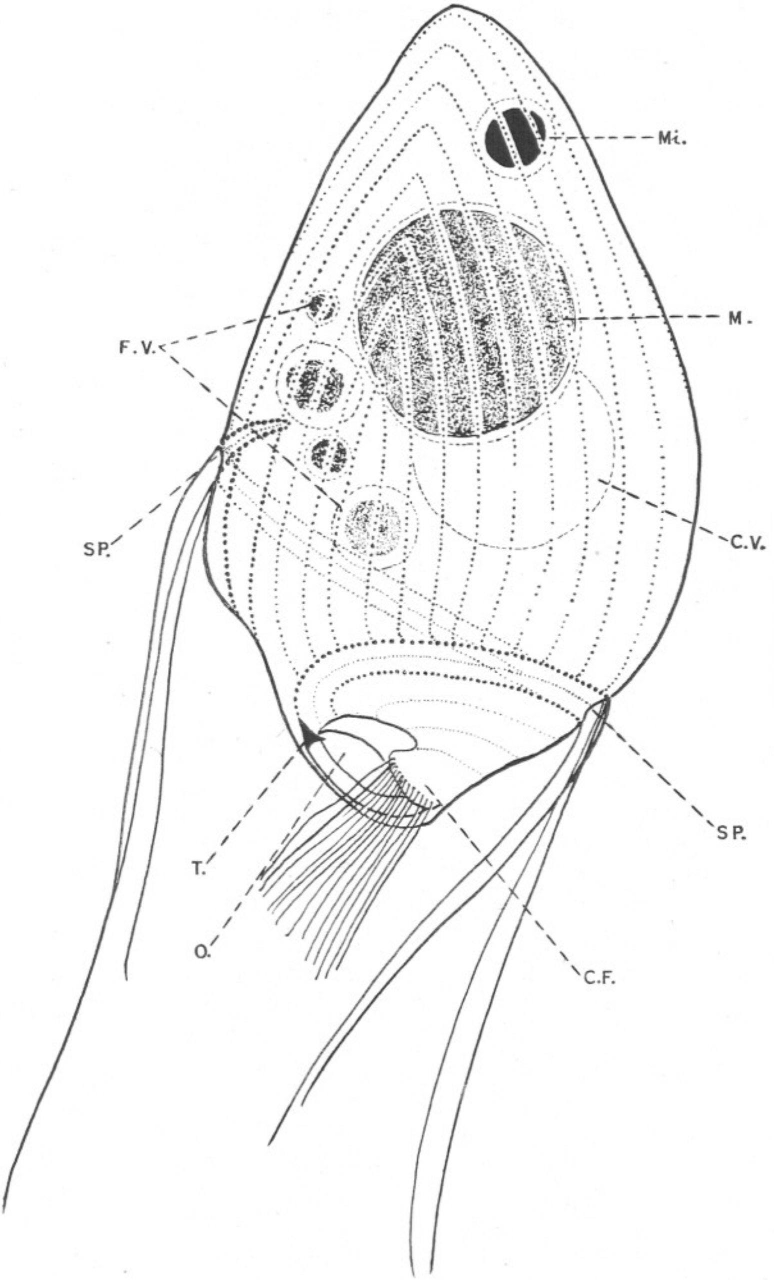

FIG. 2.—Approximately ventral view of a ciliate slightly tilted backwards to show the right-handed spiral in the adoral zone. Drawn with the aid of a camera lucida from an iron-hæmatoxylin preparation. Most of the cilia are omitted.

C.F.	ciliated flap.	M.	meganucleus.
C.V.	contractile vacuole.	O.	mouth.
F.V.	food vacuoles.	SP.	spiral of long cilia.
Mi.	micronucleus.	T.	"tooth."

×2800.

group which, throughout the Ancistridæ and their allies, are said to function as anchors to the substratum. Chatton and Lwoff (1923) make a great point of this " thigmotactic " apparatus, and go so far as to create a special subdivision, Thigmotricha, to include the Ancistridæ, Hypocomidæ, and Sphenophryidæ. They state that the thigmotactic cilia are absent in the genus Boveria, closely allied to the Ancistridæ though that ciliate undoubtedly is. We never saw the organism attach itself by these cilia while alive, but in sections through the gill tissue of Galeomma we have found a few ciliates applied to the epithelium by the ventral patch.

From the truncate oral end arises a tufted veil of very much longer and stouter cilia, which surround the mouth and are undoubtedly concerned with food-capture, though they may also contribute to the swimming movements. Figure 1 gives some idea of the appearance of the living ciliate.

Boveria stevensi swims very rapidly, turning round and round on its long axis as it goes ; sometimes it glides forward, concave side downwards. As it swims, the long peristomial cilia are directed back, and form a sort of tail ; but every now and then the animal pauses, and before darting off again, it raises and lowers the peristomial fringe with a characteristic " grasping " movement.

When the ciliate from Galeomma is alive it is impossible to discover exactly how these adoral cilia are arranged. But stained preparations make the general distribution clear enough, although the details can be determined only after careful comparison of many specimens seen and drawn from all aspects. We find here, as in other Boveridæ, that the peristomial cilia are arranged along a line that follows a right-handed spiral course. There is a double row of these cilia, and, in the slight gutter between them, appears in stained preparations a faint line of minute siderophilous granules from which we could discover no cilia arising.

The cilia in the posterior row of the spiral band are slightly more delicate than those in the line in front ; in the immediate neighbourhood of the slit-like mouth they are finer still and a good deal shorter. To one side of the mouth projects a small, pointed flap, and the cilia bordering this move backwards and forwards as one group and very energetically ; undoubtedly their duty is to drive food into the slit, though we did not actually observe the entry of any particles. Some specimens contained many vacuoles with food-balls, consisting apparently of bacteria. The mouth margin is further complicated by the presence of a minute siderophilous " tooth " arising near the base of the flap from the more anterior of the two lines of adoral cilia. The relations of these parts to one another is shown in Fig. 2. It seems worth while recording these details, since Issel found the organism too small for him to trace the fate of the spiral in the mouth region—" ma di quest' ultimo tratto, stante la piccolezza del materiale, non sono riuscito a formi un concetto ben sciuro " (Issel).

Dorsal to the meganucleus and towards the posterior end of the body is a large vacuole, which presumably is a contractile vacuole, though we did not observe any pulsation.

The resting nucleus is circular or ovoid in outline and measures about 8–10μ in greatest diameter. It lies about the middle of the thickest portion of the body, and towards the ventral side. In stained specimens its margin is often slightly lobed ; the interior is granular and densely staining. The micronucleus is small and spherical, 3–4μ in diameter, and lies some way anterior to the meganucleus.

The great majority of the ciliates measure about $35 \times 20\mu$. But we have found some that were only half as long, and this suggests that there may have been recent transverse fission. Hoping to find some clue to the mode of origin of the spiral in the daughter organisms, we searched our preparations for dividing ciliates. Many of the larger ones showed signs that their nuclei were initiating the division. The meganucleus in these individuals had increased in diameter (14μ) and had lost much of its staining property ; the micronucleus was either bean-shaped, diplococcus-like, or in two lobes connected by a short, pale-staining band. We failed to find any later stages in the division process. Stevens (1904) states that in *Boveria subcylindrica* fission is oblique ; the peristome and contractile vacuole disappear and are formed anew in the daughter animals ; " the new peristomial cilia appear on the side as a straight band which gradually assumes a terminal position, beginning to coil at the distal end."

A word as to the systematic position of Boveria. *Boveria stevensi* Issel seems to be distinguished from *B. subcylindrica* Stevens mainly by the fact that its peristomial line of cilia runs much more obliquely to the long axis of the body and that these cilia are not of such uniform length. In these respects *B. teredinidi* Nelson more closely resembles the type-species. To include the species of Boveria, Pickard (1927) formed the family Boveridæ, of equal value with the Ancistridæ.

The earlier observers regarded Ancistrum and all its near allies as holotrichous ciliates, related to Pleuronema. Chatton and Lwoff (1922 and 1923) still consider the Ancistridæ as " specialised holotrichans." Stevens' discovery of the adoral spiral in Boveria decided her to remove that genus to the Heterotricha ; Pickard (1927) created a new family, Boveridæ, for its inclusion. Cheissin's new genus Tiarella also seems to belong to that family. But the Ancistridæ and the Boveridæ have so much in common that, if the Boveridæ are to be regarded as heterotrichous, so also must the Ancistridæ.

But is Boveria a true heterotrichan ? All observers have described it as having a *right*-handed spiral of peristomial cilia—a feature characteristic of the Peritricha (with the exception of Lichnophora and its allies). All true Heterotricha are supposed to have the peristomial spiral wound sinistrally. On this ground Cheissin (1931) goes so far as to say that the Ancistridæ and Boveridæ should be regarded " wahrscheinlich als Abzweigung der primitiven Peritricha."

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An Amœba from the Intestine of an Ascidian at Plymouth.

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and

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With 3 Figures in the Text.

WHILE working at Plymouth in December, 1928, and in August, 1930, we noticed amœbæ in the intestine of *Phallusia mamillata* (Cuvier) which had been dredged in the Sound. The ten animals examined were all infected. The only previous record we can find of an amœba in such a situation is a short account given by Huxley (1920) of a small form occurring in large quantities in the stomach of *Clavellina lepadiformis* at Naples. The amœbæ we have seen are not like those from Clavellina and they seem to merit some description.

The wall of the intestine was carefully slit open and a drop of the brownish fluid contents was drawn off with a fine pipette and examined on a slide. The movements of the parasite, though sluggish, are sufficiently obvious to enable one to distinguish it easily from epithelial débris and other material in the gut.

This is a small amœba, though larger than the one in Clavellina. When active, it is always longer than broad, and, fully outstretched, measures from $15–30\mu \times 10–15\mu$. Its most characteristic feature in the living condition is the tendency to form a wide " sole " of clear, glassy ectoplasm, above which rests the main mass of the body, much as the visceral hump of a snail is supported on the muscular foot.

This ectoplasmic sole protrudes as a broad pseudopodium in front, and posteriorly it tapers to a narrow, finger-like lobe. When we used an oil-immersion lens and racked slightly up and down, so that the amœba wobbled under pressure from the cover-glass, we found that it usually remained firmly tethered to the glass or to the intestinal débris by the posterior lobe, while the rest of the body swung clear and might even roll half over. There is very little movement of translation : the amœba contents itself with emitting the broad anterior pseudopodium, then withdrawing this and forming another slightly to the right or left of the first.

In the otherwise hyaline protoplasm of the pseudopodium there often lies a group of small refringent granules. The hump-like mass above the sole is granular and opaque, and its surface tends to be thrown into wrinkles. As a pseudopodium is forming, a number of little knob-like projections of endoplasm appear for a short time between it and the main mass. There is no contractile vacuole. We have not seen the amœba engulf anything, and the granules in the protoplasm do not seem to be food material ; it is probable that the organism absorbs its food in a fluid state, and the strings and irregular groups of refringent granules that occur in the protoplasm may be excretory matter. The nucleus measures about 4·5μ–5μ in diameter. It is very difficult to detect when the amœba is healthy ; but the organism survives removal from its host for only a short time, and as it becomes moribund, the nucleus shows up as a clearer

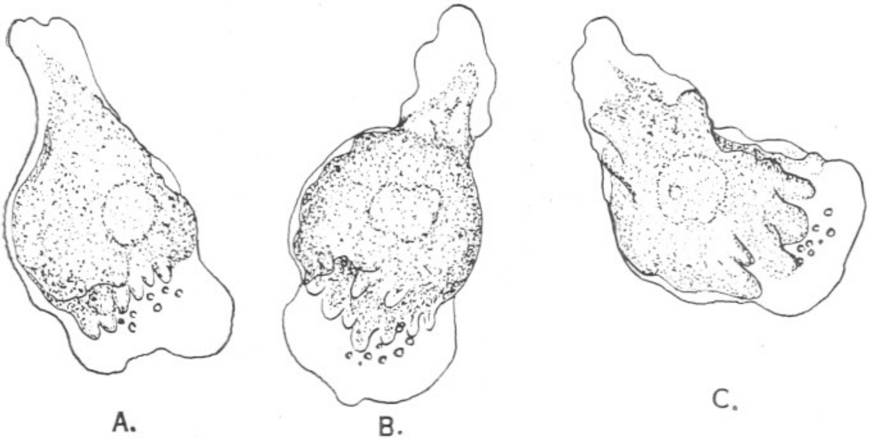

FIG. 1.—A, B, and C. Three sketches of living *Entamœba phallusiæ*, all showing the characteristic "sole" of glassy ectoplasm, with the endoplasmic hump above it. ×2000.

FIG. 2.—Living cyst of *Entamœba phallusiæ*. ×2000.

space, roughly circular in outline but readily deformed by the endoplasmic streaming. Refringent chromatin beads can sometimes be seen just within the membrane, but only very rarely is the karyosome visible in the living nucleus.

We have found a few cysts (Fig. 2). These measure about $21\mu \times 19\mu$. There is a smooth, double-contoured envelope, about $\cdot 8\mu$ thick, and within this the amœba can be seen lying, its surface somewhat folded, and with slight spaces, especially towards one pole, between it and the wall. We have never seen more than one nucleus in a cyst.

When films of the intestinal contents of Phallusia were fixed in Schaudinn's fluid or Brasil's modification of Bouin-Duboscq, the amœba usually contracted very much and became almost circular in outline; only occasionally did we find one with pseudopodium well outstretched. Stained with Heidenhain's iron-hæmatoxylin, such amœbæ show a narrow rim of light-grey homogeneous ectoplasm : the hump invariably appears to contain one relatively enormous vacuole, towards one side of which most of the dark-staining, granular endoplasm is squeezed. Strands of this darker substance criss-cross the vacuolar region, and in one patch, situated almost anywhere near the periphery, lies the nucleus. The refringent inclusions observed in the living organism stain uniformly black and there is no sign of vacuoles around them. The nucleus presents very different appearances according to the amount of its distortion from the spherical and to the angle from which it is viewed. The membrane is delicate; the chromatin is in peripheral beads, and often these are connected together in two or three strings just within the membrane; the karyosome, now very conspicuous but varying greatly in the degree to which it retains the stain, is almost always excentric. We did not find any dividing forms, nor did we see any cysts in the stained preparations.

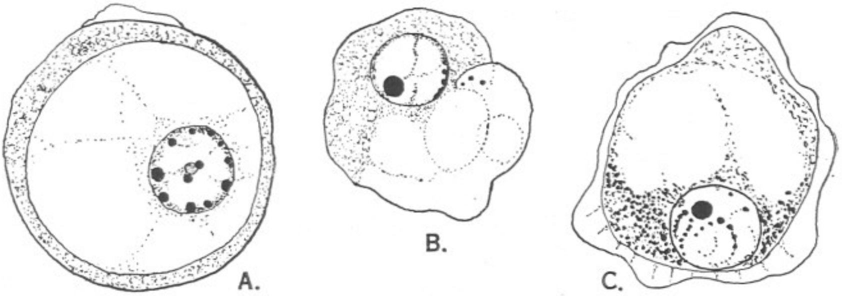

FIG. 3.—A, B, and C. Three amœbæ fixed with Brasil's modification of Bouin-Duboscq and stained with iron hæmatoxylin. The specimens show the retraction of the ectoplasm and the tendency for a large vacuole to appear in the endoplasm. ×2500.

We have decided to call this amœba *Entamœba phallusiæ* n. sp. The fact that it has no contractile vacuole does not necessarily suggest that it is a true endoparasite, since the absence of such a structure is the rule in marine amœbæ. But since it seems to feed by imbibing liquid through its whole surface, this indicates that it is rather specially adapted to an endoparasitic life, and it is much more intolerant than are most " facultative " amœbæ of changes in the medium in which it crawls. Its nucleus is not like that of most entamœbæ, if we take the nuclei of *Entamœba histolyica* and *E. coli* as typical; it most closely resembles that of the Entamœba described by Dobell (1914) from the hind-gut of *Lacerta muralis*—a form which he considered quite distinct from *Amœba lacertæ* Hartmann. This amœba from Lacerta, however, was packed with food-balls. Until we know something concerning the behaviour of the nucleus in mitosis it would be rash to speculate further concerning the relationships of *E. phallusiæ* with other parasitic amœbæ.

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Marine Biological Association of the United Kingdom

Report of the Council, 1930.

The Council and Officers.

The Council has great satisfaction in announcing that Lieut.-Col. The Right Hon. Walter Guinness, D.S.O., M.P., formerly Minister of Agriculture and Fisheries, has accepted the office of President in succession to the late Sir Edwin Ray Lankester.

The usual four quarterly meetings of the Council have been held, at which the average attendance has been nineteen. The meetings have been held in the Rooms of the Royal Society, to whom the thanks of the Council are due.

A Committee of nine members of the Council, including the President, visited and inspected the Plymouth Laboratory in March, and a special committee of six members met at Plymouth in September to discuss with the Architect plans for the proposed extension of the buildings.

The Plymouth Laboratory.

The Laboratory buildings and fittings have been maintained in a good state of repair, and the south side of the roof of the main building, the slates of which were working loose, has been overhauled and refastened.

The electric supply for all the laboratories has been redistributed, the necessary light and power cables from the Corporation now being laid underground in place of the previous overhead supply from the Citadel. Power has been supplied to the North Building, with fittings for electric heating in each room.

The engine and circulating pumps for the supply of sea-water to the aquarium and laboratories have worked well throughout the year, the small gas-engine having been fitted with a new liner and piston. During the summer the lower section of the supply pipe from the sea gave out, and a new section has now been fitted.

Proposed Extension of Laboratory Buildings.

In view of the congested condition of the present Library at Plymouth and the increasing number of outside workers who visit the Laboratory, the Council has had under consideration plans for enlarging the buildings. It has been decided to add an additional story to the Allen Building and to use that block entirely for library purposes. In order to make good the laboratory space which will be lost by so doing, and at the same time to provide some additional working space, it is proposed to extend the present North Building in an easterly direction, following the general lines of the plan of that building. An appeal for subscriptions for these extensions was issued and has met with encouraging success, a sum of £2650 having been promised up to the end of November. With this sum secured the Council has felt justified in proceeding at once with the enlargement of the Allen Building, and its conversion into a Library.

The Ship and Motor-Boat.

The steam drifter *Salpa* returned at the end of January this year from Dartmouth where she was undergoing her Lloyd's full-time survey and reconditioning in Messrs. Philip and Son's yard. She has been certified on Lloyd's register of shipping as A1 for a further period of seven years from March, 1929. She has run satisfactorily throughout the year and kept the increasing number of visiting workers supplied with the material necessary for their research.

The motor-boat *Gammarus* has worked continuously collecting in the Sound, and is in good condition.

The Staff.

Dr. C. M. Yonge took up the post of Physiologist at Plymouth in January on his return from the Great Barrier Reef Expedition. Mr. F. S. Russell, who was also a member of that expedition, has continued to carry out the duties of Administrative Assistant in addition to his scientific research work.

An exchange of staff between the Ministry of Agriculture and Fisheries and the Association took place during the summer. Mr. H. W. Harvey spent some months at the Fishery Experiment Station at Conway, continuing experiments on the rearing of oyster larvæ, and Mr. F. M. Davis of the Lowestoft Laboratory came to Plymouth.

Mr. B. Dawes, who has been in charge of the plaice experiments at Pier Cellars, Cawsand Bay, left in September to take up a post in the Zoology Department of King's College, London. Miss D. Thursby-Pelham of the Lowestoft Laboratory acted as substitute for Mr. Dawes for some weeks during the spring.

Mr. J. S. Colman resigned his student-probationership in September, on appointment as demonstrator in the Zoological Laboratory at Cambridge. Mr. J. E. Smith, of King's College, London, was appointed a Student-Probationer in place of Mr. Colman.

Dr. L. N. H. Cooper, of the University College of North Wales, has been appointed Assistant Chemist in the Physiological Department to assist Dr. Atkins in his work on the minor constituents of sea-water.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :

PROF. ALEXANDROWICZ, Lemberg, Poland (Innervation of the heart of Invertebrates).

DR. AMIRTHALINGAM, Ceylon and London (Central nervous system of Scyllium).

MISS D. ATKINS, London (Pinnotheres and Loxosoma).

R. BASSINDALE, Sheffield (Development of *Balanus balanoides*).

DR. N. J. BERRILL, McGill University, Montreal (Development of Ascidians).

MISS A. BIDDER, Cambridge (Digestion tracts of Loligo).

DR. H. BLASCHKO, Heidelberg (Experiments on Crustacean nerve-muscle preparations).

DR. H. BLEGVAD, Copenhagen (Young Herring and Sprat).

DR. B. G. BOGOROV, Moscow and Murman Coast Laboratory, Russia (Biomass of Calanus).

MISS M. A. BORDEN, Canada (Respiration and function of hæmoglobin in Planorbis and Arenicola).

M. BURTON, London (Sponges).

PROF. H. GRAHAM CANNON, Sheffield (Ostracoda).

DR. MCKEEN CATTELL, New York (Reflexes in Frogs and work on Crustacean nerve-muscle preparations).

PROF. R. CHAMBERS, New York (Fertilisation and mechanics of cell division. Micro-injections of Plant cells).

MISS M. COTTON, Cambridge (Marine Algæ).

MISS L. CUNNINGHAM, Birmingham (Distribution and Feeding Mechanism of Gammarids).

F. M. DAVIS, Lowestoft (General Fisheries).

W. FERNANDO, London and India (Embryology of Patella).

MISS E. S. FOGG, London (Plankton).

A. GRAHAM, Sheffield (Enzymes of Pecten).

DR. A. GROLLMAN, Baltimore (Osmotic pressure of body fluids of marine animals).

J. R. GROOME, Oxford (General dissection).

DR. R. GURNEY, Oxford (Copepod larvæ).

L. H. HARRISSON, Harrow (General).

G. T. D. HENDERSON, Bristol (Young Fish).

MISS J. T. HENDERSON, McGill University, Montreal (Response to stimuli of single muscle fibres).

MISS M. HETHERINGTON, London (Osmotic pressure of body fluids of marine animals).

PROF. A. V. HILL, F.R.S., London (Osmotic pressure of body fluids of marine animals).

W. T. HILLIER, Birmingham (Lateral line of fishes).

A. D. HOBSON, Edinburgh (Artificial parthenogenesis in Echinoderms and Annelids).

DR. KARL HÖFLER, Vienna (Plasmolysis and Permeability of Marine Algæ).

MISS HOLT, New York (Cataphoresis of marine eggs).

DR. AND MRS. SVEN HÖRSTADIUS, Stockholm (Development of Luidia).

N. H. HOWES, London (Pituitary gland of Ray).

A. F. W. HUGHES, Cambridge (Respiratory exchange of *Maia squinado*).

K. Hukuda, Japan (Osmotic pressure of body fluids of marine animals).
Prof. J. S. Huxley, London (Differential growth in animals).
Dr. O. G. Ibañez, Madrid (Oceanographical chemistry).
Dr. I. J. Izquierdo, Mexico (Maia heart and water respiratory current).
Dr. R. T. Jackson, U.S.A. (*Echinus esculentus*).
C. C. John, India (Development of Sagitta).
J. A. Kitching, Cambridge (Respiratory exchange of *Maia squinado*).
Dr. M. Knight, Liverpool (Marine Algæ).
Dr. E. Kreps, Leningrad and Murman Coast Laboratory, Russia (Muscular physiology of Invertebrates).
Dr. E. Leloup, Belgium (Hydrozoa).
Dr. E. Lundsgaard, Denmark (Chemistry of Crustacean muscle).
Prof. D. L. Mackinnon, London (Protozoology).
R. M. Margaria, Italy and London (Osmotic pressure of body fluids of marine animals).
N. N. Murti, India (Development of Ophiocoma and Ophiothrix).
Dr. T. G. Ni, Pepin, China (Physiology of glandular tissues).
Dr. E. A. T. Nicol, Edinburgh (Feeding habits in Galathea).
A. G. Nicholls, Australia (Moulting, feeding, breeding and digestion in Ligia).
Dr. K. Oshima, Japan (Hydrography).
G. W. Otter, Cambridge (Gephyrea).
C. F. A. Pantin, Cambridge (Gunda environment).
J. L. Parkinson, London (Osmotic pressure of body fluids of marine animals).
Dr. N. Payne, Pennsylvania, U.S.A. (Hydroid pigments and low temperature effect on Hydroids).
Miss S. Pieh, Munich (Hydrozoa).
A. D. Ritchie, Manchester (Physiology of Pecten muscle).
Dr. P. Rothschild, Heidelberg (Action currents in muscle).
Miss S. S. Ross, Edinburgh (Polyzoa).
Dr. H. N. Roy, London and Calcutta (Parasitic Protozoa).
Dr. Otto Schindler, Vienna (Morphology of young fish).
Dr. E. A. Spaul, London (Pituitary gland of Ray).
Miss F. A. Stanbury, Birmingham University and Plymouth Technical College (Effect of light on growth of diatoms).
Dr. T. A. Stephenson, London (Photography of Anemones).
F. C. Stott, Manchester (Effects of Ions on Ciona heart).
H. H. Sturch, Plymouth (Algæ).
Miss M. A. Tazelaar, London (Parasitic Protozoa).
Prof. T. G. and Mrs. Thompson, Washington and Puget Sound Station (General).
Dr. M. A. Thynne, Plymouth (Nematodes).
A. Walton, Cambridge (Fertilisation studies with Echinus).
Miss M. A. Westbrook, London (Marine Algæ).
Dr. A. G. Wiersma, Utrecht (Peripheral nerve muscle preparations of Crustaceans).

The usual Easter Vacation Course in Marine Zoology was conducted by Mr. D. P. Wilson and Mr. G. A. Steven, and was attended by forty-four students from Oxford, Cambridge, London, Edinburgh, Manchester, Liverpool, Birmingham and Sheffield.

An advanced course in Comparative Physiology and Experimental

Biology was conducted by Mr. A. D. Ritchie and Mr. C. F. A. Pantin during the Summer Vacation and was attended by fourteen students.

During the Easter Vacation, Mr. J. M. Branfoot brought four students from Oundle School and two from Wellington College ; Dr. H. Fogg brought two students from Malvern College ; Mr. A. S. Gillespie conducted a class of ten students from Dauntsey School ; Mr. A. S. Turner brought one student from Rydal School ; Mr. H. P. Ramage brought four students from Gresham School, and Mr. Pask brought eight students from St. Paul's School.

At Whitsuntide Mr. Leigh-Sharpe, of the Chelsea Polytechnic, conducted a class of eight students.

General Work at the Plymouth Laboratory.

Herring biology and the winter drift-net fishery at Plymouth have again occupied the major part of Mr. Ford's attention. During the winter of 1929–30, samples from the commercial landings consistently showed a predominance of fish derived from the spawning of the winter 1924–25. That this would be so was predicted two years ago on the evidence of samples collected during the season 1927–28. A successful year-class can be detected at the age of three years, when it enters the Plymouth commercial catches for the first time, and it will attain maximum importance to the fishery at the age of five years. The fishery itself will be most fruitful in yield when a highly successful year-class is present in the form of five-year-old fishes. Certainly the season 1929–30 was a good one ; severe gales alone robbed the fishery of excellent results. One unusual event worth recording is that a considerable quantity of herring spawn was taken in the trawl by s.s. *Salpa* on March 3rd, 1930. The estimated number of eggs taken was from 1½ to 2 millions, and they were adhering to shell-gravel to form a sheet, three to four eggs deep. It should also be noted that spawning during the 1929–30 season must have continued over an unusually protracted period, for as late as May 14th the *Salpa* brought to the Laboratory eleven herrings in a spawning condition. The fact that herrings may actually spawn in the vicinity of Plymouth during eight calendar months, from October to May, is a highly important one.

A report has been published on the differential growth of young herrings during the transition from transparent larvæ to fully-scaled and silvery adolescence. The results have significance in their bearing upon the problems raised by the conception of hereditary races of herrings. They suggest that although real biometric differences are observable between random samples of herrings from commercial catches, the biological interpretation of such differences remains open to question, and seems likely to remain so until experimental work in rearing herrings from parents of known character has yielded fundamentally important information regarding the rôle played by heredity and environment in setting the morphological characters of a new generation.

A paper has also been published by Mr. Ford in which he describes and figures a number of interesting abnormalities in fishes. Several of these serve to demonstrate how fishes may continue to live and thrive in spite of seemingly serious malformations.

The experiments on the growth of plaice in the pond at Pier Cellars, Cawsand Bay, undertaken for the Ministry of Agriculture and Fisheries, were continued by Mr. B. Dawes and Miss D. Thursby-Pelham and, for the last few weeks of the season, completed by Messrs. G. M. Spooner and J. E. Smith. Mr. Dawes has published in the Journal a paper on the work of the first two years, giving data, for second-year fish of various sizes, (*a*) on the daily ration sufficient to keep body-weight constant, and (*b*) on the relation between growth and food taken in excess of maintenance requirements. The work at Cawsand is also compared with similar work carried out on the Exe. The experiments this year were designed with a view to confirming these results and making them as complete as possible.

During the early part of the year Mr. G. A. Steven's researches upon the Bottom Fauna and Fish Food on the " corner " fishing-ground off Plymouth were completed and the results published in the Journal of the Association. Since then, observations have been made on the feeding habits and migrations of the turbot. A gregarious and migratory species, this fish appears in numbers in Plymouth waters at the same time as the herring, upon which it depends almost entirely for food. When the last of the herrings depart, the turbot also disappear, possibly accompanying the herring shoals on their migrations.

Researches have since been commenced by Mr. Steven on the general life-history and biology of rays and skates, elasmobranch fishes about which very little is known in spite of the fact that they are now of great economic importance. In Devon and Cornwall they form the greater part of the landings from about the end of May until October or November. Observations have been made on Plymouth and Newlyn fish markets and several trips have been taken with commercial fishing vessels for the purpose of ascertaining the number of species of Raia which are caught within this area, their relative abundance, size, and general distribution. The relative proportions of the sexes in each of the eleven species landed have been noted. In *Raia clavata* definite evidence of the segregation of the sexes into separate shoals has been obtained. Efforts are also being made to acquire some knowledge of the growth-rate and migrations of these fishes. For this purpose special marks have been devised with which it is hoped to carry out marking experiments during the coming year. Attempts to discover where the eggs of the Raiidae are deposited have as yet proved unsuccessful but will be continued. Full egg-capsules have never been taken in quantity from the sea.

In co-operation with the Cornish Sea Fisheries Committee, Mr. V. C. Wynne-Edwards, assisted by Mr. G. A. Steven, has commenced an investigation into the food of shags and cormorants. The evidence so far obtained does not support the view that these birds prey to any appreciable extent upon fishes of economic importance, but the data acquired being as yet inadequate it is hoped to continue the observations next year.

Mr. G. M. Spooner has been engaged on an investigation of the phenomenon of schooling in fish, especially from the point of view of the behaviour of the individual fishes of a school. Among the very few species available for laboratory work, the bass (*Morone labrax*) proved suitable. Experiments with mirrors showed that the fish reacted to their own reflections in the same way as to one another, and the use of sight alone will account for all observed schooling behaviour. Investigation of the anatomy of the brain has shown that the optic centres are well developed.

Preliminary experiments on the behaviour of young herrings and other young fish during the first few days of life were carried out and indicated how thoroughly at the mercy of their surroundings the fish are at this stage.

The work on the Mendelian inheritance of eye-colour in *Gammarus* which Mrs. Sexton has carried on for some years with the assistance of Miss A. R. Clark, has made considerable advance during the year, much useful help on the theoretical side having been given by Mr. G. M. Spooner. A paper in which these three workers collaborated appeared in the number of the Journal published in September. When animals brought in from the wild were kept under similar conditions, at temperatures ranging from 20° C. to 28° C., two-thirds of the pairs gave red-eyes in the offspring. One family of these (Mutant Stock V) was worked out in detail for eight or nine generations. The eye-redness was of a complicated kind. All intermediate stages between black and red have occurred. Changes undergone after birth include both darkening and lightening, as well as either permanent or temporary changes to some shade of purple. It is however possible to express all colour variations occurring in the stock in terms of variations in the concentration of the two pigments present in the normal eye, the red and the black. It is a matter of importance that the eye-redness found in the five different stocks in which detailed work has been done is in each case genetically distinct, and any cross-mating between the reds of the different stocks produced black-eyed offspring in the first generation.

Dr. Lebour has spent much time on the revision of the Plymouth Fauna List, which is now being prepared for publication. In March her book *The Planktonic Diatoms of Northern Seas* was published by the Ray Society, and in May a paper, "The Larval Stages of Caridion with a description of a new species, *C. steveni*," appeared in the Proceedings of the Zoological Society of London. Continuing her work on larval decapods, a paper is finished on the larvæ of the Crangonidæ and Hippolytidæ, containing figures and descriptions of most of the British species. All the Plymouth species have now been hatched from the egg. A paper on further observations on the Plymouth Brachyura is also finished, with a description of the little-known zoeae of *Pisa gibbsi* hatched from the egg. Both these papers, with coloured illustrations, are in course of publication by the Zoological Society in their Proceedings. A paper on the larvæ of the Plymouth Galatheidæ was published in the last number of the Association's Journal. The larvæ of all the local species have been identified with the exception of one doubtful one, and most of them have been hatched from the egg.

Preliminary work on the larval mollusca of the plankton has brought forward many interesting problems. The spawning of both the pteropods *Limacina retroversa* and *Clione limacina* has been observed and it can be shown that both species are much more abundant locally than was previously thought, being regular members of the plankton with maxima and breeding seasons in summer. Both have been hatched from the egg and the larvæ of Clione reared until the stage with three ciliated rings after it has lost its shell, the other stages being found in the plankton. The larval period is short and the adults begin to spawn here at a very small size, mostly from 4 to 5 mm.

Attention has been specially given by Dr. Lebour to the larval planktonic gastropods and it is found that *Nassa incrassata* is very important in early summer, appearing in most of the plankton hauls as a handsome veliger with a four-lobed velum. These veligers were reared in a plunger-jar until the adult form could be recognised. Adults collected in late summer laid eggs on Cellaria in a plunger-jar in November. The larvæ from these are hatched with a velum very different from the older planktonic larvæ. It is hoped to rear them in order to follow the change in form. Rissoa spawn and larvæ are receiving special attention, and it has been found that it is almost certainly a newly hatched Rissoa which always forms a large part of the food of the larval herring in the winter.

In working out his observations on the vertical distribution of plankton Mr. F. S. Russell has been giving special attention to the behaviour and biology of Sagitta. He finds that there are two species occurring commonly at Plymouth, *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller; these two species had previously been confused with *Sagitta bipunctata* Quoy and Gaimard. In May of this year also two specimens of *Sagitta serratodentata* Krohn were taken near the Eddystone. A study of the diurnal vertical movements of *Sagitta elegans* shows that in the daytime the younger individuals appear to withstand a wider range of intensities of light than the older and larger individuals. At dusk the smaller stages have migrated right to the surface, while the largest forms have shown little movement ; intermediate types of movement are shown by the various stages lying between the two extremes. At dawn the larger individuals leave the surface first.

A comparison of the movement of these organisms and the changes in light intensity during the twenty-four hours, computed from data obtained on the continuous light recorder on an exactly similar day, shows that these, and probably other plankton animals, leave the surface some time before the intensity has reached that at which they normally live in the daytime. This suggests that the animals become adapted to increasing light intensities, and that in the early morning, after the darkness of the night, they are more sensitive to light than they are later in the day. This would indicate a shifting optimum intensity during the daytime.

Mr. Russell has published in the Association's Journal a record of the average monthly abundance of the pelagic young of most of the species of fishes in the Plymouth region for the last six years, and is continuing routine weekly collections of young fish. It is hoped that by continuous records such as these it may be possible to detect abnormal years and correlate them with hydrographical and other data.

Mr. D. P. Wilson's researches this year have been confined almost entirely to the study of the Mitraria larva of *Owenia fusiformis*. During the early part of the year material obtained by rearing during the summer of 1929 was sectioned, and its study yielded interesting information about the histology of the remarkable cataclysmic metamorphosis which this larva undergoes. It also revealed the main features of the development of various structures during the earlier stages. It was realised, however, that to complete the work in detail further rearings would be necessary, for the development is long and complex and the 1929 material did not cover it at all stages. Accordingly the summer of 1930 was devoted to rearing more larvæ and to further observations on them when alive. This has yielded an unexpected result with regard to the conditions under which metamorphosis normally takes place, for it happened that one of the cultures was especially successful and produced numerous late larvæ in a very vigorous and healthy condition. As only a few of these, on reaching the critical stage, metamorphosed, experiments were carried out in which larvæ were removed to small vessels and supplied with various grades of bottom deposits. These experiments conclusively proved that the presence of some form of grit on the bottom of the vessels is necessary before metamorphosis will take place. In clean vessels larvæ would live for days without metamorphosing, but would soon settle if fine sand were supplied. In this connection it should be noted that whereas during earlier stages healthy larvæ always swam strongly up to the surface, as soon as they were ready to metamorphose they showed an equally strong tendency to sink to the bottom and could only be kept off it by the action of the plunger-plate.

The main structural changes involved in metamorphosis take half a minute or less to complete, during which period the truly pelagic larva is changed into a typical benthic worm engaged in swallowing the remains of its prototroch and other larval tissues. In a few minutes it has secreted a mucus tube to the outside of which sand grains have adhered.

The continuous records of hyprographic data between Plymouth and Ushant, commenced in 1921 by the Association, have been maintained during the year by Mr. H. W. Harvey and Mr. G. A. Steven, and continue to be published in the Atlantic Report of the International Council. The year 1930 has been remarkable for the occurrence of water in the neighbourhood of the Scillies having a high salinity of $35{\cdot}7^{\circ}/_{\circ\circ}$, characteristic of more southern latitudes and possibly of Mediterranean origin.

Mr. Harvey has continued work on the utilisation of ammonium and other salts by marine diatoms, it having been established that ammonium salts are present in the upper layers of the sea off the Norwegian coast and in the Iceland–Greenland area when all, or practically all, the dissolved nitrate has been utilised by phytoplankton. Preliminary experiments, which it is hoped to continue next season, have indicated that the inshore diatom *Nitzschia closterium* can utilise ammonium in place of nitrate and arsenate in place of phosphate, but satisfactory results have not yet been obtained with a typical open-sea diatom.

During the summer breeding season from May to October, by arrangement with the Ministry of Agriculture and Fisheries, Mr. Harvey was engaged in investigating the breeding of oysters in the Ministry's experimental tanks at Conway, during the absence of Mr. H. P. Sherwood in Canada. A heavy fall of spat was obtained in the two largest tanks in which male plants of *Fucus vesiculosus* had been placed with the object of providing food of suitable size for the free-swimming larvæ. Many experiments were also made with larvæ in small vessels, antherozoids or alga cultures being added as food. In two of these experiments larvæ settled to complete metamorphosis where antherozoids had been supplied. Although the season's results only suggest but give no proof that the spatfall may have been due to the supply of antherozoids as food, a line of attack is opened up for future investigation.

River Tees Survey.

The biological and chemical survey of the estuary of the River Tees, commenced in April 1929 for the Department of Scientific and Industrial Research, has been continued throughout the year. At the end of September Mr. W. B. Alexander, Superintendent of the Laboratory at Middlesbrough, resigned to take up an appointment at Oxford. His services have proved most valuable. The duties of the Superintendent were taken over by Dr. B. A. Southgate, Mr. R. Bassindale of the University of Sheffield being appointed to continue the biological investigations. Mr. H. W. Harvey has visited Middlesbrough from time to time, and remains in contact with the various problems under investigation there by such visits and by correspondence.

A survey has shown that fixed animals, plants, burrowing and crawling animals are plentiful at both ends of the estuary but few in the central part. Here they are subjected to the greatest variations of salinity and also to the effects of pollution by sewage and by toxic industrial effluents. In order to determine whether this scarcity of animals in the central part of the estuary was due to pollution or was the natural result of rapid and considerable changes of salinity with each ebb and flood of the tide, a survey of the fauna and flora of the unpolluted Firth of Tay was made in August. A very similar distribution was found, and it is clear that the scarcity of animals in the central part of the Tees cannot be attributed to pollution, since it is almost equally marked in the Firth of Tay.

On the other hand, a great number of salmon smolt and some brown trout have been found dead or dying in the upper part of the polluted area in the Tees, whiting, sprat, and sand eels in the lower part, and adult salmon in the central part of the polluted area. It is probable that they have died from the combined effects of poisoning and of asphyxiation in the partially deoxygenated water which occupies the polluted area of the estuary. During April, May and June there was a heavy mortality of smolt as they migrated downstream and met these waters ; 2426 were actually collected and examined, almost all from the upper part of the area, only 200 being found below Stockton. It is remarkable that the greatest mortality took place at spring tides ; it remains to be determined whether the migration of smolt takes place only at spring tides in this and other unpolluted estuaries.

The effect of typical coke-oven effluents, diluted with fully aerated and with partially deoxygenated water, upon trout and smolt has been investigated, and the relative toxicity of the more poisonous constituents of these effluents ascertained. The effect of one of these constituents was found to override that of the others.

The dissolved oxygen content of the water in the polluted area, centred upon Newport and swinging up and down the river with the tides, has been the subject of continuous study. The temperature of the water is found to be the main controlling factor, rise in temperature increasing the rate of bacterial breakdown of sewage, of mud and of tar acids discharged from coke ovens. The dissolved oxygen may fall to below 20% of saturation during the summer, the minimum value found being 5% in July 1929.

Side by side with the investigation of conditions obtaining in the estuary, an assessment is being made of the " oxygen demand " by the sewage, industrial effluents and mud on the river bottom.

The distribution of salinity throughout the estuary under varying conditions of fresh-water flow indicates the presence, residual to tidal movements, of a circulatory system in which more saline water tends to move up the estuary along the bottom and less saline water to flow seaward in the upper layers. This is in agreement with current measurements. The total volume of fresh water in the estuary under dry summer conditions has been calculated ; from this value and the rate at which fresh water entered the head of the estuary, the time taken by the fresh water—and hence by substances in solution—to reach the sea under such conditions has been estimated.

Department of General Physiology.

Dr. Atkins and Dr. H. H. Poole have continued their collaboration on photo-electric photometry. By combining a sensitive vacuum cell with a Cambridge " Thread Recorder ", daily records of the vertical illumination have been obtained since December 1929. The photometer has been re-standardized at intervals by two methods. It does not remain quite constant, but is not subject to the rapid and large fluctuations in sensitivity shown by the gas-filled cells examined.

Using the General Electric Company's red sensitive cell with colour filters, measurements have been made of the colour of daylight under various conditions ; the method eliminates the wave-length sensitivity curve of the cell used, being based upon the ratios of blue to green, blue to yellow, etc. A preliminary account of this work was communicated to the Physical and Optical Societies last June. It is hoped that it may be possible to apply it to measurements in the sea.

Miss F. A. Stanbury of the Plymouth Technical College has been engaged in work upon the growth of diatoms under light filters which reduce the intensity non-selectively and selectively. The results varied according to the time of year. In bright summer weather optimum multiplication was shown under screens that reduced the daylight very considerably. Under such conditions the growth appeared to be much the same whether the screen reduced the illumination non-selectively or selectively, provided the energy transmitted was the same. This is more in keeping with the results of Warburg and Negelein than with those of Klugh. The same species of diatom was found to vary from green to dark brown according to the colour of the light in which it had multiplied.

A considerable amount of advice was given during the year upon the preservation of fishing nets. Durability tests were begun upon material treated by a net-making firm and materials under test here were inspected. Dr. Yonge reported that the plankton nets treated with copper soap remained quite unattacked by cockroaches during the Barrier Reef Expedition. This is an important point as cockroaches are so destructive in the Tropics.

A comparison was made of the data for phosphate and silicate in sea-water from 1923 to 1929 in relation to the seasonal changes in the phytoplankton. The years show a general similiarity, but there is much evidence that phenomena depending mainly upon illumination may get badly out of step with those depending upon temperature alone. Thus it happened that the year with the coldest water in early spring was also the year with the earliest development of phytoplankton. One might therefore expect this year, 1924, to be an outstanding one as regards favourable or unfavourable conditions for young fish.

There is no evidence that it was specially favourable for herring, but the cold weather resulted in a more prolonged spawning period for fish in general, so that young fish were abundant. As regards herring it was the next spawning period, the winter of 1924–spring of 1925, that was exceptionally good according to the results of Mr. Ford and Mr. Hodgson.

Measurements were made of the hydrogen ion concentration of water in contact with various minerals, especially basalts in various stages of weathering. The reaction of fresh water is governed largely by such contacts. This line of attack may be expected to give information of value in relation to the problem of dolomite formation and changes in the calcium magnesium ratio in coral reefs.

Since his appointment in July Dr. L. N. H. Cooper has been engaged upon the analysis of the minor constituents of sea-water, repeating known methods and trying to follow the seasonal changes in ammonium salts by the method of direct nesslerization which had not been used here before.

Dr. C. M. Yonge has continued his work on the feeding, digestion and metabolism of marine invertebrates. He has been engaged on the further examination and the writing up of work carried out on feeding and digestion in corals during the course of the Great Barrier Reef

Expedition. Considerable progress has been made in this work, which represents a logical development of previous work carried out at the Plymouth Laboratory. Two papers (one to be published in Australia) on the organization of the Expedition have been completed, and also three papers, one on feeding, a second on digestive enzymes, and a third on assimilation and excretion in corals, which are all being published by the British Museum (Natural History). Corals, in common probably with all Cœlenterates, are highly specialized carnivores, feeding only on zooplankton and capable only of digesting protein, fats and the solitary carbohydrate (glycogen) found in animal tissues. Work in course of completion on the interrelations between corals and their contained zooxanthellæ indicates that these are intimately bound up with the specialized nature of the digestive processes of the corals.

In addition Dr. Yonge has begun work on the properties of the chitinous membrane which lines the fore-gut of lobsters and other Decapod Crustacea. Preliminary investigations have shown that this dead membrane possesses properties somewhat analogous, in its selective and to some degree polarised permeability, to those of living membranes. Interesting results are expected from this work.

The Library.

The pressure on the available space for shelves in the Library, to which attention was drawn in the Report of the Council last year, has become much more pronounced, but owing to the generosity of those friends of the Association who have subscribed to the Building Extension Fund, this difficulty will soon be overcome.

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, which are much appreciated.

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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Finance.

The Council again 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 (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol (£25), Birmingham (£31 10s.), Leeds (£21), Manchester (£21) and Sheffield (£10).

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1931–32:—

President.

Lieut.-Col. The Right Hon. Walter E. Guinness, D.S.O., M.P.

Vice-Presidents.

The Duke of Bedford, K.G.
The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor.
Lord St. Levan, C.B., C.V.O.
The Right Hon. Sir Austen Chamberlain, K.G., M.P.
Lord Noel Buxton, M.P.
Sir W. B. Hardy, F.R.S.
George Evans, Esq.
Sir Nicholas Waterhouse, K.B.E.
G. A. Boulenger, Esq., F.R.S.
J. O. Borley, Esq., O.B.E.

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Prof. H. Munro Fox.
Prof. F. E. Fritsch.
Ronald D'Oyley Good, Esq.
Prof. E. S. Goodrich, D.Sc., F.R.S.
Michael Graham Esq.
C. R. Harington, Esq., D.Sc.
Prof. A. V. Hill, F.R.S.
C. F. A. Pantin, Esq.
C. Tate Regan, Esq., F.R.S.
A. D. Ritchie, Esq.
G. C. Robson, Esq.
J. T. Saunders, Esq.
J. M. Tabor, Esq.
Prof. D. M. S. Watson, F.R.S.

Chairman of Council.

Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer.

Nigel O. Walker, Esq., 38, Regent Street, Cambridge.

Hon. Secretary.

E. J. Allen, Esq., D.Sc., F.R.S.,
The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council:—

G. P. Bidder, Esq., Sc.D.
E. T. Browne, Esq.
George Evans, Esq.
H. G. Maurice, Esq., C.B. (Ministry of Agriculture and Fisheries).
Sir A. Garrett Anderson, K.B.E. (Prime Warden of the Fishmongers' Company).
Nigel O. Walker, Esq. (Fishmongers' Company).
Lothian D. Nicholson, Esq. (Fishmongers' Company).
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J. Gray, Esq., F.R.S. (Cambridge University).
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Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society).
Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society).

THE MARINE BIOLOGICAL ASSOCIATION

Dr. *Statement of Receipts and Payments for the*

GENERAL

	£ s. d.	£ s. d.
To Balance from 31st March, 1930:—		
Cash in hand	22 19 7	
Cash at Lloyds Bank £176 6 10		
Less Coutts & Co.—Overdraft 68 9 3	107 17 7	130 17 2
,, Grants:—		
Ministry of Agriculture and Fisheries Grant from Development Fund	11,477 11 4	
Fishmongers' Company	600 0 0	
British Association	50 0 0	
Royal Society	50 0 0	
Physiological Society (two years)	60 0 0	12,237 11 4
,, Subscriptions		268 15 0
,, Donations		6 2 0
,, Sale of Specimens		1,286 14 4
,, ,, Fish (*less* Expenses)		121 16 6
,, ,, Nets, Gear, and Hydrographical Apparatus		412 19 10
,, Table Rent (including Cambridge University, £105; Oxford University, £52 10s.; London University, £52 10s.; Bristol University, £25; Birmingham University, £31 10s.; Leeds University, £21; Manchester University, £21; Sheffield University, £10; Trustees of Ray Lankester Fund, £20)		502 17 3
,, Tank Room Receipts		477 3 9
,, Interest on Investments:—		
4% War Stock	9 10 2	
4% New Zealand Stock	12 14 8	
3% Local Loans	2 0 11	
Interest on Deposits	4 16 5	29 2 2
,, Sale of £237 17s. 11d. 4% War Stock		238 19 7
,, Sale of Dr. M. V. Lebour's Book		5 5 8
,, Grant from Zoological Society towards Publication of Marine Fauna of Plymouth		5 0 0
		£15,723 4 7

The Association's Bankers held on its behalf:—
£410 14s. 8d. New Zealand 4%, 1943–63.
£352 2s. 3d. Local Loans 3% Stock.

BUILDING EXTEN

	£ s. d.
To Sundry Donations	2,690 6 11
	£2,690 6 11

Further Liabilities on the Building Fund to the

SUPERANNUATION

	£ s. d.
To Grant from H.M. Treasury	2,687 6 0
	£2,687 6 0

PLAICE EXPERIMENTS

	£ s. d.
To Grant from Ministry of Agriculture and Fisheries	132 4 3
,, General Fund	13 0 4
	£145 4 7

DEPRECIA

	£ s. d.
To General Fund	250 0 0
	£250 0 0

OF THE UNITED KINGDOM.

Year 1*st April*, 1930, *to* 31*st March*, 1931. Cr.

FUND.

	£	s.	d.	£	s.	d.
By Salaries :—						
Director	1,200	0	0			
Physiologist	910	0	0			
Naturalists	3,526	16	9			
Hydrographer	600	0	0	6,236	16	9
,, Laboratory Wages (including National Insurances)				1,970	4	0
,, Annual Upkeep of Library				596	13	0
,, Scientific Publications :—						
Journal, Vols. XVI, No. 3 and XVII, No. 1	812	8	5			
Less Sales	204	15	6	607	12	11
,, Annual Upkeep of Laboratories and Tank Rooms :—						
Buildings and Machinery	392	1	9			
Electricity, Gas, Coal, and Water	338	2	2			
Chemicals and Apparatus	606	15	7			
Rates, Taxes, and Insurance	112	12	6			
Travelling .... £141 8 11 ,, "Challenger" Society......... 31 18 11	173	7	10			
Stationery, Postages, Telephone, Carriage, and Sundries	440	6	10			
Purchase of Specimens	122	4	10	2,185	11	6
,, Annual Maintenance and Hire of Boats :—						
Wages (including Diet Allowance, National Health Insurance, and Casual Labour)	1,624	1	1			
Coal, Water, Oil, etc.	216	19	8			
Maintenance and Repairs, with Nets, Gear, and Apparatus	773	13	6			
Purchase of Material for Nets for sale (excluding labour)	198	9	2			
Boat Hire and Collecting Expenses	34	5	9			
Insurance	310	9	2	3,157	18	4
,, Interest on Bank Loan				7	15	0
,, Purchase of £352 2s. 3d. Local Loans 3% Stock				238	19	7
,, Transfer to Plaice Experiments Account				13	0	4
,, Depreciation Fund				250	0	0
,, Balance, 31st March, 1931 :—						
Cash in hand	24	6	6			
Cash at Lloyds Bank	194	11	3			
Cash at Coutts	239	15	5	458	13	2
				£15,723	4	7

SION FUND.

	£	s.	d.
By Payment to Builders (Messrs. A. N. Coles & Co. Ltd.)	500	0	0
,, Cash at Coutts on Deposit Account	2,100	0	0
,, Cash at Coutts on Current Account	90	6	11
	£2,690	6	11

amount of £1,953 17s. have been incurred.

FUND.

	£	s.	d.
By Cash at Coutts on Deposit	2,687	6	0
	£2,687	6	0

AT CAWSAND.

	£	s.	d.
By Salary of Ben Dawes, Esq.	117	10	0
,, ,, ,, J. E. Smith, Esq.	11	2	3
,, Incidental Expenses	16	12	4
	£145	4	7

TION FUND.

	£	s.	d.
By Cash at Coutts on Deposit Account	250	0	0
	£250	0	0

Examined and found correct,

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
27th April, 1931.

(Signed) N. E. Waterhouse, *Auditor.*
L. D. Nicholson } *Members of*
Nigel O. Walker } *Council.*

List of Annual Subscriptions

Paid during the Year, 1st April, 1930, to 31st March, 1931.

	£	*s.*	*d.*
Dr. W. M. Aders	1	1	0
Dr. E. J. Allen, F.R.S.	1	1	0
G. L. Alward, Esq.	1	1	0
Dr. Ikusaku Amemiya (1930 and 1931)	2	2	0
Prof. J. H. Ashworth, F.R.S.	1	1	0
The Rt. Hon. Lord Askwith, K.C.B., D.C.L.	1	1	0
Miss D. Atkins	1	1	0
Prof. J. Barcroft, F.R.S. (1928-1930)	3	3	0
W. H. Barrett, Esq. (1931 and 1932)	2	2	0
W. J. Bazeley, Esq. (1929 and 1930)	2	2	0
G. R. de Beer, Esq.	1	1	0
J. Belehradek, Esq., M.D.	1	1	0
N. J. Berrill, Esq.	1	1	0
Mrs. M. G. Bidder	1	1	0
Birkbeck College	1	1	0
Dr. H. Blaschko (1931 and 1932)	2	2	0
H. H. Bloomer, Esq. (1929 and 1930)	2	2	0
Mrs. H. Moss Blundell	1	1	0
Dr. J. Borowik	1	1	0
Dr. L. A. Borradaile	1	1	0
Prof. Gilbert C. Bourne, F.R.S. (1928 and 1929)	2	2	0
Dr. B. G. Bogorov	1	1	0
Col. Sir Henry Bowles, Bart. (1930 and 1931)	2	2	0
Dr. A. Bowman	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
Sir J. Rose Bradford, Bart., K.C.M.G., M.D., F.R.S.	1	1	0
J. M. Branfoot, Esq.	1	1	0
Brighton Public Library	1	1	0
L. R. Brightwell, Esq. (1929-1931)	3	3	0
H. H. Brindley, Esq.	1	1	0
R. Brown, Esq.	1	1	0
Miss E. M. Brown	1	1	0
H. O. Bull, Esq.	1	1	0
R. H. Burne, Esq., F.R.S.	1	1	0
Carried forward	47	5	0

	£	s.	d.
Brought forward	47	5	0
M. Burton, Esq.	1	1	0
R. R. Butler, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Dr. W. T. Calman, F.R.S.	1	1	0
Prof. H. Graham Cannon SC.D. (1930 and 1931)	2	2	0
J. N. Carruthers, Esq.	1	1	0
Paymaster Capt. Charles, R.N. (Retd.)	1	1	0
G. S. R. Kitson Clark (1925-1930)	6	6	0
Dr. James Clark	1	1	0
Coastguard and Fisheries Service, Alexandria	1	1	0
J. S. Colman, Esq.	1	1	0
J. F. Coonan, Esq.	1	1	0
J. Omer Cooper, Esq.	1	1	0
L. R. Crawshay, Esq.	1	1	0
H. H. Dale, Esq., C.B.E., M.D., F.R.S. (1927-1930)	4	4	0
Prof. Otto. V. Darbishire	1	1	0
Dr. H. H. Darby (1930 and 1931)	2	2	0
F. M. Davis, Esq.	1	1	0
Director of Agriculture and Fisheries, Travancore (1928–1930)	3	3	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
F. Martin Duncan, Esq. (1930 and 1931)	2	2	0
The late Prof. J. S. Dunkerley, D.SC., PH.D.	1	1	0
P. Eggleton, Esq.	1	1	0
C. E. D. Enoch, Esq.	1	1	0
Prof. C. Lovatt Evans, F.R.S.	1	1	0
Col. T. Fetherstonhaugh, D.S.O.	1	1	0
Dr. R. A. Fisher, F.R.S.	1	1	0
Fisheries Survey Committee, Capetown	1	1	0
E. Ford, Esq.	1	1	0
Dr. G. Herbert Fowler (1928–1930)	3	3	0
Prof. H. M. Fox	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
Prof. F. E. Fritsch	1	1	0
T Fujita, Esq.	1	1	0
R. D'O Good, Esq.	1	1	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
A. P. Graham, Esq.	1	1	0
Michael Graham, Esq.	1	1	0
Carried forward	103	19	0

	£	s.	d.
Brought forward	103	19	0
R. Grant, Esq.	1	1	0
Dr. A. H. M. Gray (1930 and 1931)	2	2	0
Dr. R. W. Gray	1	1	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq. (1930 and 1931)	2	2	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
T. J. Hart, Esq.	1	1	0
H. W. Harvey, Esq.	1	1	0
J. C. Hemmeter, Esq., M.D.	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
Prof. K. Hirasaka (1929 and 1930)	2	2	0
A. D. Hobson, Esq. (1928–1930)	3	3	0
Prof. L. T. Hogben, D.SC. (1928–1930)	3	3	0
Dr. E. G. Holmes	1	1	0
F. R. Horne, Esq.	1	1	0
Capt. G. C. L. Howell	1	1	0
P. Hoyte, Esq. (1929 and 1930)	2	2	0
Hull Univeristy College (1930 and 1931)	2	2	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley (1928–1930)	3	3	0
Lt. H. L. Jenkins, R.N.	1	1	0
J. J. Judge, Esq.	1	1	0
Dr. Stanley Kemp, F.R.S.	1	1	0
Mrs. A. Redman King	1	1	0
J. A. Kitching, Esq.	1	1	0
Dr. E. M. Kreps	1	1	0
Dr. G. Lapage	1	1	0
Prof. R. D. Laurie	1	1	0
A. G. Lowndes, Esq.	1	1	0
J. R. Lumby, Esq.	1	1	0
Adrian Lumley, Esq. (1931 and 1932)	2	2	0
H. Macarthur, Esq.	1	1	0
Prof. E. W. MacBride, F.R.S.	1	0	0
G. I. Mann, Esq.	1	1	0
Carried forward	157	9	0

	£	*s.*	*d.*
Brought forward	157	9	0
B. J. Marples, Esq.	1	1	0
D. J. Matthews, Esq.	1	1	0
H. G. Maurice, Esq., C.B. (1923–1930)	8	8	0
Capt. W. N. McClean	1	1	0
A. P. Menon, Esq.	1	1	0
Milford Haven Trawler Owners and Fish Salesmen's Association, Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., F.R.S.	1	1	0
F. W. Moorhouse, Esq.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerjii	1	1	0
National Museum of Wales	1	1	0
R. G. Neill, Esq. (1929 and 1930)	2	2	0
A. G. Nicholls, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Charles Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC.	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
T. A. Pawlyn, Esq.	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Pease Laboratories	1	1	0
Plymouth Corporation Museum Committee (1928-1930)	3	3	0
Plymouth Education Authority (1929 and 1930)	2	2	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
W. Proctor, Esq. (1929 and 1930)	2	2	0
D. M. Reid, Esq.	1	1	0
E. A. Robins, Esq.	1	1	0
C. H. Rudge, Esq. (1930 and 1931)	2	2	0
Dr. E. S. Russell	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O. (1930 and 1931)	2	2	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
Carried forward	213	2	0

	£	*s.*	*d.*
Brought forward	213	2	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq. (1930 and 1931)	2	2	0
F. W. Schiller, Esq. (1928–1929)	2	2	0
Dr. Edgar Schuster	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Lt.-Col. R. B. Seymour Sewell, I.M.S. (1930 and 1931)	2	2	0
Miss Lilian Sheldon	1	1	0
N. Smedley, Esq. (1930 and 1931)	2	2	0
B. Webster Smith, Esq.	1	1	0
F. G. W. Smith, Esq.	1	1	0
G. M. Spooner, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	0
Dr. T. A. Stephenson (1930 and 1931)	2	2	0
Mrs. N. S. Steven	1	1	0
The Rt. Hon. the Earl of Stradbroke, K.C.M.G., C.V.O., C.B.	1	1	0
The late H. H. Sturch, Esq.	1	1	0
Eric. J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W M. Tattersall, D.SC.	1	1	0
Sir Charles Howell Thomas, K.C.B. (1930 and 1931)	2	2	0
Mrs. M. A. Thynne, M.R.C.S.	1	1	0
Torquay Natural History Society	1	1	0
R. C. Vernon, Esq.	1	1	0
Nigel O. Walker, Esq. (1928–1930)	3	3	0
A. Walton, Esq.	1	1	0
B. H. Walton, Esq. (1928-1930)	3	3	0
Alan H. Ware, Esq., PH.C.	1	1	0
Sir. Nicholas E. Waterhouse, K.B.E. (1928-1930)	3	3	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
E. C. Weberman, Esq.	1	1	0
W. H. Webster, Esq.	1	1	0
Mrs. F. J. Weldon	1	1	0
Miss M. A. Westbrook	1	1	0
Dr. K. B. Williamson	1	1	0
D. P. Wilson, Esq.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq.	1	1	0
V. C. Wynne-Edwards	1	1	0
Total	£268	15	0

List of Donations to the General Fund

For the Year, 1st April, 1930, to 31st March, 1931.

	£	*s.*	*d.*
Bournemouth Corporation	1	1	0
Dr. R. T. Jackson	4	0	0
G. Tregelles, Esq.	1	1	0
Total	£6	2	0

List of Donations towards the Building Extension Fund

Paid during the Year 1st April, 1930, to 31st March, 1931.

	£	*s.*	*d.*
Lieut.-Col. The Rt. Hon. Walter E. Guinness, D.S.O., M.P.	1,000	0	0
Dr. G. P. Bidder	500	0	0
E. T. Browne, Esq.	500	0	0
Anonymous	100	0	0
The Rt. Hon. the Earl of Iveagh, C.B., C.M.G.	100	0	0
Mrs. E. T. Browne	50	0	0
A. D. Ritchie, Esq.	33	8	0
The Worshipful Company of Clothworkers	25	0	0
L. K. Elmhirst, Esq.	25	0	0
"Discovery" Committee, Colonial Office	20	0	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	20	0	0
B. H. Walton, Esq.	10	10	0
Dr. W. R. G. Atkins, F.R.S.	10	0	0
Prof. G. C. Bourne, F.R.S.	10	0	0
K. Furusawa	10	0	0
Mr. and Mrs. W. Russell	10	0	0
Dr. C. Bolton, F.R.S.	5	5	0
R. H. Burne, Esq., F.R.S.	5	5	0
L. W. Byrne, Esq.	5	5	0
The Great Grimsby Coal, Salt and Tanning Co.	5	5	0
Sir Herbert F. Thompson, Bart.	5	5	0
H. G. Wells, Esq.	5	5	0
Dr. E. J. Allen, F.R.S.	5	0	0
Miss A. Bidder	5	0	0
Col. Sir Henry Bowles, Bart.	5	0	0
L. R. Crawshay, Esq.	5	0	0
Carried forward	2,475	8	0

	£	s.	d.
Brought forward	2,475	8	0
George Evans, Esq.	5	0	0
James Gray, Esq., F.R.S.	5	0	0
Prof. E. S. Goodrich, F.R.S.	5	0	0
Sir Sidney F. Harmer, K.B.E., F.R.S.	5	0	0
Sir John D. Marsden, Bart.	5	0	0
Prof. E. W. MacBride, F.R.S.	5	0	0
Prof. W. C. McIntosh, F.R.S.	5	0	0
Sir P. Chalmers Mitchell, Kt., C.B.E., F.R.S.	5	0	0
Dr. Yo Okada	5	0	0
Charles Oldham, Esq.	5	0	0
G. W. Otter, Esq.	5	0	0
C. F. A. Pantin, Esq.	5	0	0
Prof. Edward B. Poulton, F.R.S.	5	0	0
Messrs. John Staniar & Co.	5	0	0
Prof. W. M. Tattersall, D.SC.	5	0	0
Prof. D. M. S. Watson, F.R.S.	5	0	0
Mrs. F. J. Weldon	5	0	0
L. E. Bayliss, Esq.	3	3	0
Dr. E. A. Fraser	3	3	0
Prof. D. L. Mackinnon, D.SC.	3	3	0
Miss E. A. T. Nicol, PH.D.	3	3	0
Prof. A. V. Hill, F.R.S.	3	0	0
Jiro Murakami, Esq.	3	0	0
D. P. Wilson, Esq.	3	0	0
Prof. J. H. Ashworth, F.R.S.	2	2	0
Dr. J. Borowik	2	2	0
Prof. and Mrs. H. Graham Cannon	2	2	0
Mr. and Mrs. R. S. Clark	2	2	0
Messrs. Coates & Co. (Plymouth), Ltd.	2	2	0
Dr. H. H. Darby	2	2	0
The late Prof. J. S. Dunkerly, D.SC., PH.D.	2	2	0
Messrs. Elliott & Garrood, Ltd.	2	2	0
Mr. & Mrs. E. Ford	2	2	0
G. Herbert Fowler, Esq., PH.D.	2	2	0
Messrs. R. Friedlander & Sohn	2	2	0
Gourock Ropework Company	2	2	0
A. D. Hobson, Esq.	2	2	0
Dr. Stanley Kemp, F.R.S.	2	2	0
Miss S. M. Manton, M.A., PH.D.	2	2	0
Carried forward	2,613	10	0

	£	s.	d.
Brought forward	2,613	10	0
Prof. J. H. Orton, D.SC.	2	2	0
G. P. Wells, Esq.	2	2	0
Prof. J. Barcroft, F.R.S.	2	0	0
Miss. E. W. Emmart	2	0	0
Robert Gurney, Esq.	2	0	0
Prof. A. V. Hill, F.R.S. (second donation)	2	0	0
J. Arthur Hutton, Esq.	2	0	0
F. S. Russell, Esq., D.S.C., D.F.C.	2	0	0
G. M. Spooner, Esq.	2	0	0
Prof. A. Willey, D.SC., F.R.S.	2	0	0
Messrs. E. S. Rendle & Son	1	10	0
A. C. Stephen, Esq.	1	1	3
Messrs. T. & R. Annan & Son	1	1	0
Dr. C. Amirthalingam, Esq.	1	1	0
G. T. Atkinson, Esq.	1	1	0
The Rt. Hon. Lord Askwith, K.C.B., D.C.L.	1	1	0
Dr. L. A. Borradaile	1	1	0
Dr. A. Bowman	1	1	0
R. R. Butler, Esq.	1	1	0
Lord Clwyd	1	1	0
J. S. Colman, Esq.	1	1	0
Capt. G. C. C. Damant, R.N., G.B.E.	1	1	0
Dauntsey School	1	1	0
Messrs. Foster Mason & Harvey	1	1	0
Prof. H. Munro Fox	1	1	0
Prof. R. R. Gates	1	1	0
Dr. R. W. Gray	1	1	0
Prof. A. C. Hardy	1	1	0
Mrs. A. C. Hardy	1	1	0
C. C. Hentschel, Esq.	1	1	0
Prof. E. Hindle	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
H. E. Hurrell, Esq.	1	1	0
Prof. H. G. Jackson	1	1	0
J. A. Kitching, Esq.	1	1	0
Messrs. H. K. Lewis & Co., Ltd.	1	1	0
Lowestoft Fishing Vessel Owners Association, Ltd.	1	1	0
R. Macdonald, Esq.	1	1	0
G. I. Mann, Esq.	1	1	0
Carried forward	2,664	12	3

	£	s.	d.
Brought forward	2,664	12	3
H. G. Maurice, Esq., C.B.	1	1	0
R. Margeria, Esq.	1	1	0
W. S. Millard, Esq.	1	1	0
A. G. Nicholls, Esq.	1	1	0
C. W. Parson, Esq.	1	1	0
Dr. C. Tate Regan, F.R.S.	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
Dr. H. N. Roy	1	1	0
G. A. Steven, Esq.	1	1	0
Miss E. M. Stevens	1	1	0
Dr. and Mrs. K. B. Williamson	1	1	0
Miss M. A. Westbrook	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. A. E. Boycott, F.R.S.	1	0	0
Miss E. M. Brown	1	0	0
Dr. J. N. Carruthers	1	0	0
Dr. P. Eggleton	1	0	0
Miss M. V. Lebour, D.SC.	1	0	0
Miss Yvonne Lebour	1	0	0
R. Palmer, Esq.	1	0	0
R. S. Wimpenny, Esq.	1	0	0
Messrs. Harrington Bros.		10	6
Dr. J. Wyman		10	2
A. P. Graham, Esq.		10	0
T. J. Hart, Esq.		10	0
Miss Ross		10	0
R. C. Vernon, Esq.		10	0
Total	£2,690	6	11

The Journal of
Experimental Biology

(Late *The British Journal of Experimental Biology*)

Vol. VIII, No. 1 Price 12s. 6d. net *January*, 1931
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THE QUARTERLY JOURNAL OF MICROSCOPICAL SCIENCE

EDITOR:

EDWIN S. GOODRICH, M.A., LL.D., F.R.S.

CONTENTS OF No. 294—NEW SERIES.
Part II, Volume 74, January, 1931.

MEMOIRS.

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