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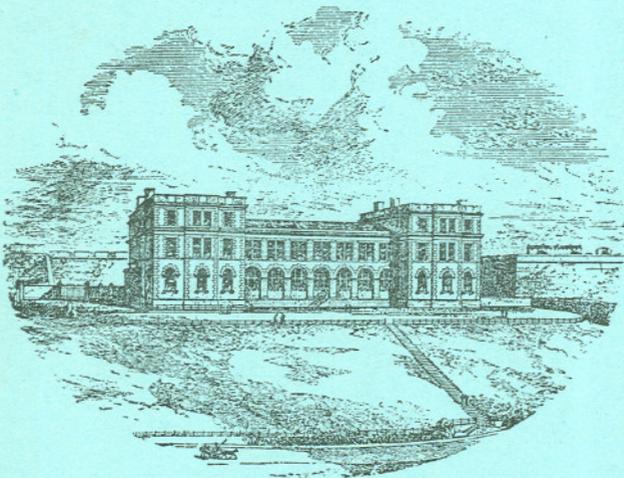
# Journal

OF THE

## MARINE BIOLOGICAL ASSOCIATION

OF

THE UNITED KINGDOM.



THE PLYMOUTH LABORATORY.

### PLYMOUTH:

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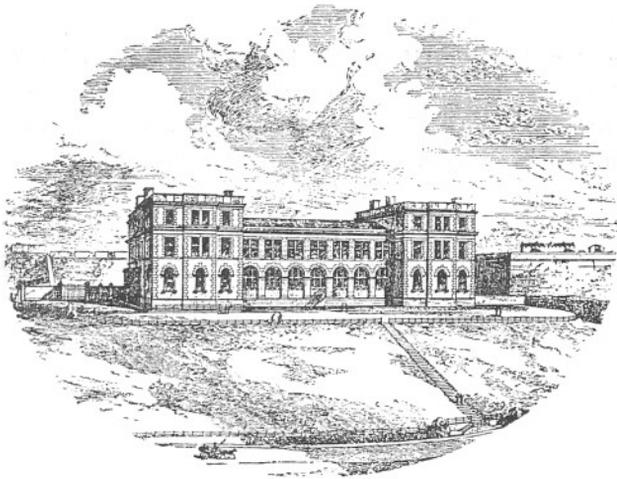
# Journal

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## MARINE BIOLOGICAL ASSOCIATION

OF

THE UNITED KINGDOM.



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# Journal

1924

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THE COUNCIL REPORT

*The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for the accuracy of statements published in this Journal, excepting when those statements are contained in an official report of the Council.*

(G. W.) 1924 (M. B. A.)

1924-1925

1924-1925

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#### ERRATA

- p. 186. Insert in legend to Figure 6, *Solecurtus scopula*. . . . . 1.
- p. 203, line 35, and p. 220, line 40, for *Eurynome aspersa* read *Eurynome aspera*.
- p. 212, line 29, for *Hippomedon denticulata* read *Hippomedon denticulatus*.
- p. 213, line 37, for *Thione* sp. read *Thyone* sp.
- p. 475, line 16, for "during the day than during the night" read "during the night than during the day."
- p. 545, line 15, for 478 read  $\frac{47}{8}$ .
- p. 632, Fig. 23 : this figure is upside down.
- p. 704, first line after Table III, for "later" read "earlier."
- p. 754, line 20, for *Sagerheimia* read *Lagerheimia*.
- p. 770, line 7, for "9 metres" read "6 metres."

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# On the Growth of some Lamellibranchs in Relation to the Food-supply of Fishes.

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With an Appendix and Plates I to III and 5 Figures in the Text.

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DURING a study of the fauna of the level sea-bottom off Plymouth on which a report has already appeared in this Journal (Ford, 1923), the samples taken in the Petersen bottom-sampler and in the conical dredge were preserved in alcohol and retained. A subsequent re-examination of the accumulated material has provided information on the growth of a number of lamellibranchs, which forms the subject matter of the present paper. As the samples were collected according to a programme arranged expressly to determine the animal communities represented, it was not to

be expected that they would yield complete data on the growth of a particular species, but the results are interesting and useful when considered in their relation to the food supply of our food-fishes. I must again acknowledge my indebtedness to Mr. R. Winckworth of Brighton for his continued assistance in identification and measurement of specimens. Such expert confirmation of identification was naturally desirable in dealing with the growth of species from the earliest stages. Throughout the paper the term "length" is adopted, meaning the greatest antero-posterior dimension of the shell. This term was used by Weymouth (1923) who gave a figure on page 20 which shows clearly the measurement to which the term is applied. I have also used "length" as a measure of growth-rings on the surface of shells. In Fig. 7 on Plate III,  $l_2$  is the length of the second ring on a shell of *Spisula solida*. Thirty-three genera of lamellibranchs are represented in the material of which all but nine appear among the records compiled by Todd (1907) and Blegvad (1917) of the contents of the stomachs of fishes which include dab, flounder, long-rough dab, plaice, sole, cod, haddock, whiting, cat-fish, viviparous blenny, fresh-water eel, herring and mackerel.

Before the potential value of a bed of lamellibranchs as food for fishes can become known, the precise food-value of the successive stages in the life-history of each lamellibranch must be determined. One species, such as *Syndosmyna alba*, may never grow beyond a size which a medium dab could easily swallow whole, whereas another, such as *Cyprina islandica*, although it may be easily devoured in its early life, will soon grow to a size quite beyond the largest of shell-eating fish, and thus be relatively useless to fishes except for such soft parts as may be exposed. In quantitative estimations of fish-food similar to those made by the Danish investigators, this fact needs careful consideration, and the case of a bed of *Spisula solida* in Start Bay may serve as an illustration. Following the shore-line in quite shallow water for several miles in Start Bay, a rich bed of this species has been located where the observed density in November, 1923, reached 2000 large individuals per square metre in several places. What was the potential value of that bed as food, say, for plaice? From the results of the measurement of the shells taken, I imagine that they would all be too big at that time for small plaice, and many beyond the capacity of large plaice. A reasonable approximation could thus only be made by one having knowledge of the limits of size of *Spisula solida* eatable by varying sizes of plaice. The location of these large uneatable individuals is, of course, most valuable, for if and when they give rise to a successful fall of spat, the whole area may become a rich source of food for even small plaice. Reference was made above to the case of species which when fully grown may be too big to be swallowed whole, but may yet fall victims to fishes who are

able to bite off exposed soft parts such as the foot and syphons. Todd (1907) has shown that in the North Sea plaice may feed extensively on the feet of razor shells (*Ensis* sp.), while Blegvad (1917, p. 43) refers to the biting off of the syphons of large *Mya arenaria* by fresh-water eels in Danish waters. An interesting parallel to these two instances is provided in the action of the bottom-sampler on one occasion in Torbay, where twenty-five syphons of *Lutraria elliptica*, with but four whole individuals, came up in a haul, showing that the sampler had been able to nip off the syphons, but had left the bodies in the ground soil. There are cases on record of the stomachs of fishes being found to contain recognisable soft parts of large lamellibranchs, but with no trace of shell whatever, and it is of interest to discover how the fishes have managed to extract the flesh. Blegvad (1917, pp. 43-45) tells of fresh-water eels in Bramsnaesvig managing to extract the soft parts of large mussels (*Mytilus edulis*), great quantities of which, neatly picked out from the shells, may be found in stomachs. In the same locality, eels also contrive to extract the soft parts of *Scrobicularia plana*, and the siphon, mantle and gills may be sufficiently well preserved in the stomach contents to permit of the determination of species. Blegvad advances as a possible explanation of this unusual method of feeding the suggestion that eels devour the soft parts from shells recently opened by crabs and the starfish *Asterias*, after driving off the latter. Early in June, 1924, I was informed that several Plymouth fishermen had noted and remarked that the stomachs of their trawled fish from waters outside the Eddystone lighthouse contained the soft parts of "Queens" (*Pecten opercularis*), with no shell at all. Unfortunately I could obtain no practical confirmation of this, but in view of Blegvad's experience, there seems no reason to question its possibility, although it is difficult to offer an explanation of the means by which the fish had extracted the flesh from the shells, if the lamellibranchs were healthy.

The free-swimming larval stages of lamellibranchs may not enter largely into the diet of fishes, although Lebour (1920, p. 278) records them from larval and postlarval herring, and Blegvad (1917, p. 69) from adult herring and mackerel, but from the time of settlement of the spat and life on the sea-bottom is commenced, their importance is asserted. If size is an important factor, then the greatest number of species of lamellibranchs will be available to fishes during the early bottom stages, so that any evidence on the times of occurrence of spatting of any species will be of value. For instance, knowledge of the spatting time or times of *Spisula solida* would enable a prediction to be made of an increased richness of the Start Bay bed. In Table I (p. 534), details of the capture of small individuals of a number of species are given, although it is realised that the mere presence of small individuals does not necessarily indicate

recent settlement of spat. At a later stage in this paper several species will be considered in which there is a big fall of spat during late spring and early summer followed by a period of growth during summer and early autumn, and then by an almost complete cessation of growth from late autumn until the following spring. Quite small individuals, however, may be taken at almost any time, but it will be seen that an individual spatting towards the end of the growth period will remain small throughout the winter until the new spring growth commences. If, on a given

TABLE I.

Species.	Date.	Locality.	No. of individuals measured.	Range in length. mm.	Modal length. mm.
<i>Mytilus edulis</i>	July, 1922	Queen's Ground	—	(Many small specimens)	—
<i>Syndosmya alba</i>	June 9th, 1922	Bigbury Bay	813	2-11	5.5
" "	May 30th, 1923	" "	115	2-6	2.5
" "	April 10th, 1924	" "	30	2-6	2.5
<i>Mactra stultorum</i>	June 7th, 1922	Whitsand Bay	18	3-4.5	3.5
<i>Spisula elliptica</i>	July 5th, 1922	Queen's Ground	281	1.5-5.5	3.5
" "	May 30th, 1923	Bigbury Bay	15	3-5.5	3.5
<i>Lutraria elliptica</i>	June 7th, 1922	Whitsand Bay	30	2.5-4.5	3.5
" "	June 9th, 1922	Bigbury Bay	25	2.5-4	3.5
<i>Lutraria oblonga</i>	July 5th, 1922	Queen's Ground	56	3-7	5.0
<i>Cardium echinatum</i>	July 10th, 1922	Plymouth Sound	10	2-3	2.25
" "	July 24th, 1922	Bigbury Bay	25	2-12.5	4.5
<i>Cyprina islandica</i>	July 24th, 1922	Channel	4	2-2.5	2.5
<i>Mya truncata</i>	June 26th, 1922	Plymouth Sound	12	2-4.5	3.5
<i>Corbula gibba</i>	June 26th, 1922	" "	22	2.5-4	3.0
<i>Solecurtus antiquatus</i>	June 26th, 1922	" "	8	3.5-5	4.0
<i>Cultellus pellucidus</i>	July 5th, 1922	" "	22	4-7	5.0
" "	July 10th, 1922	" "	42	5-11	7.0
" "	Aug. 14th, 1922	Channel	101	4-10	7.0
<i>Ensis ensis</i> *	June 26th, 1922	Plymouth Sound	12	6.5-10	8.5
" "	June 20th, 1922	Whitsand Bay	35	5-14.5	10.0
<i>Ensis arcuata</i> *	June 26th, 1922	Plymouth Sound	20	5.5-10.5	8.5
" "	July 10th, 1922	" "	10	8-15	11.0

occasion, during a continuous series of visits to a particular locality, a large number of tiny individuals appear for the first time, this seems reasonable evidence of a recent fall of spat. The data given in the table are derived from such a series, and may thus be taken as indicating spatting at a date not far removed from the date of the hauls.

The food value of a stock derived from the same fall of spat is dependent on the length of time the individuals take to grow beyond a size useful to fishes. By visiting and revisiting a locality at intervals and noting the size of the individuals in the successive samples, it is possible to

\* See Appendix.



The successive samples having been taken under similar conditions, the number of specimens on each occasion may be accepted as an estimate of the density of population. It is possible, however, that on July 5th, 1922, a number of small individuals may have passed through the sieves used, in which case the calculated average size is somewhat higher than in reality, and the density of population under-estimated. The gradual decline in the number per 1 sq.-metre was accompanied by an increase in the number of empty but "fresh" shells. These latter were intact, with the two valves fully closed, and were often so similar in appearance to "living" individuals that it was considered necessary to open all the shells of a sample to ensure that only living individuals were being included in the count. The cause of this mortality was not obvious; relatively few had been bored by gastropods, but starfishes may have been responsible, as, in previous years, *Asterias* has frequented Queen's Ground in numbers at the same period of the year.

If growth is considered in terms of length, the curves given in Figs. 1 and 2 clearly show that growth was most rapid during July, when in the 20 days from July 5th to July 25th, 1922, the average length rose from 3.44 mm. to 6.18 mm., which is a relative increase of 80% of the length on July 5th. During the 56 days following July 25th, growth in length was still marked, but less rapidly than previously, for it was a 55% increase in spite of a period of time nearly three times as long. Growth was slowest during the winter months, when from December 7th, 1922, until February 20th, 1923, the resultant increase for the 75 days was only 11% of the length on December 7th.

In the discussion of growth as it affects the question of fish-food, it is weight rather than length which is the important factor for practical purposes. The weight ( $W$ ) of an individual is some function of the cube of its length ( $L$ ), and in order to determine, for this species, the relation between  $W$  and  $L^3$ , 889 specimens from 2.5 mm. to 16.5 mm. in length were dried and weighed. The procedure adopted was to arrange the specimens in millimetre groups, and to treat each group as one unit. The total dry weight of each unit when divided by the number of specimens gave an average dry weight for one individual of that millimetre group. For the larger specimens, from 9.5 mm. to 16.5 mm., the soft parts were first removed from the shell, and the two dried and weighed separately, but this was not found practical for the smaller ones. Drying to a constant weight was accomplished in a water oven at 90° C., and the dry weights were determined to .001 gm. In the case of the smaller specimens drying was facilitated by first crushing them, during which operation, also, empty shells could be discovered and discarded. It must be pointed out, however, that the material had been preserved in spirit

for a long time, so that the observed dry weights of soft parts, although comparable, are probably lower than in reality.

The results obtained by these experiments, together with values calculated from the suggested equation  $W = .00008L^3$  are given in Table III (p. 538), and a comparison between the two sets of values of  $W$  will show that this relation of  $W$  to  $L^3$  is not improbable.

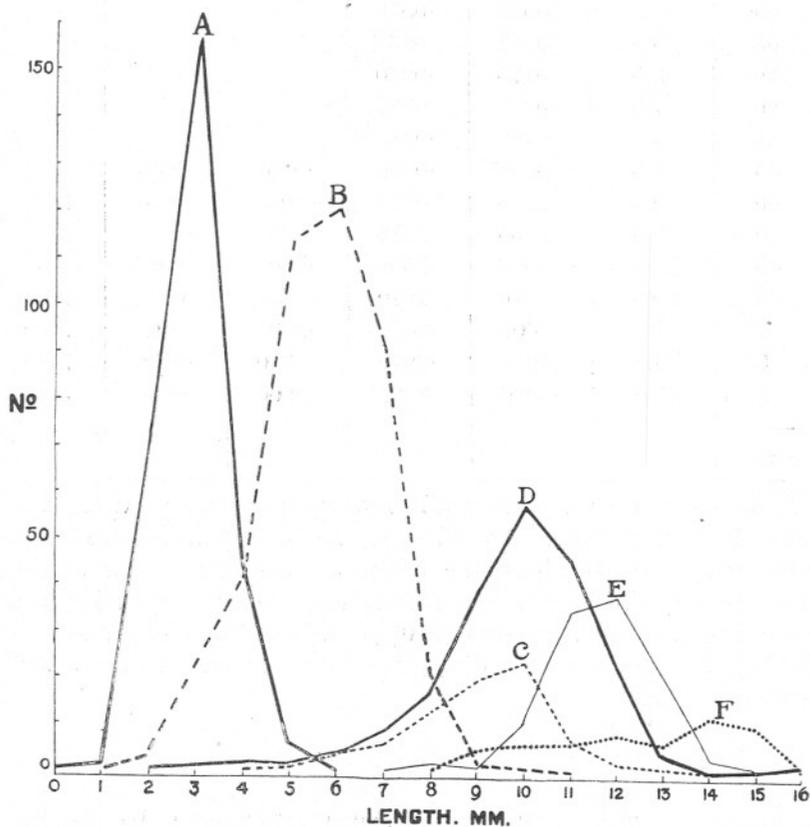


FIG. 1.—*Spisula elliptica*. Queen's Ground, 1922-23.

- |                          |                         |
|--------------------------|-------------------------|
| A. July 5th, 1922.       | D. October 4th, 1922.   |
| B. July 25th, 1922.      | E. December 7th, 1922.  |
| C. September 19th, 1922. | F. February 20th, 1923. |

TABLE III.—SPISULA ELLIPTICA FROM QUEEN'S GROUND.

No. of specimens.	Length = L mm.	Average dry weight of shells and flesh = W gram.	Calculated values of W from equation $W = .00008L^3$ gram.	Average dry weight of shell only = $W_s$ gram.	Average dry weight of flesh only = $W_f$ gram.	Values of $\frac{W_s}{W_f}$
65	2.5	.0016	.0012	—	—	—
140	3.5	.0030	.0034	—	—	—
80	4.5	.0062	.0073	—	—	—
103	5.5	.0111	.0133	—	—	—
116	6.5	.0175	.0220	—	—	—
90	7.5	.0238	.0337	—	—	—
37	8.5	.0469	.0491	—	—	—
45	9.5	.0892	.0686	.0853	.0039	21.9
60	10.5	.1119	.0926	.1069	.0051	21.0
70	11.5	.1355	.1217	.1291	.0064	20.2
45	12.5	.1586	.1562	.1504	.0083	18.1
26	13.5	.1970	.1970	.1878	.0093	20.2
6	14.5	.2405	.2439	.2308	.0100	23.0
5	15.5	.3044	.2979	.2920	.0124	24.5
1	16.5	.3090	.3594	.3000	.0090	33.3
889						

If the information thus derived be now applied to the previous statement of growth in length, it will be seen that an 80% increase in length in the 20 days from July 5th to the 25th, means a 470% increase in weight; while the 55% increase in length from July 25th to September 19th involves an increase in weight of 270% of that of July 25th. Similarly, the 11% increase in length during the winter months, means a 28% increase in weight.

TABLE IV.—SPISULA ELLIPTICA FROM QUEEN'S GROUND.

Date.	No. of dips of $\frac{1}{10}$ m <sup>2</sup> bottom sampler.	No. of Individuals.	Total Dry-weight gram.	Dry weight per 1 sq. metre $W_1; W_2; \text{etc.}$	Values of $\frac{W_1}{W_1}; \frac{W_2}{W_1}; \frac{W_3}{W_1}$ etc.
1922					
July 5th	5	281	1.029	2.057	1.0
July 25th	5	415	8.854	17.707	8.6
Sept. 19th	2	78	5.905	29.527	14.4
Oct. 4th	5	207	19.338	38.675	18.9
Dec. 7th	5	111	16.249	32.498	15.8
1923					
Feb. 20th	6	54	10.326	17.209	8.4

From the data given in Table III it is possible to deduce the total dry weight of the samples taken on the various dates (see Table IV), from which some idea can be obtained as to the relative fish-food value of the ground throughout the period of observation. The total dry weight thus rises to its maximum on October 4th, and then declines, but **the residue in February is still over eight times as heavy as the July 5th stock from which it was derived, although numerically its density is less than one-fifth.** Fig. 2 gives a graphic representation of the number of animals per 1 sq. metre, their total dry weight, and their average length, at each of the dates of sampling. It shows that although there was a reduction in num-

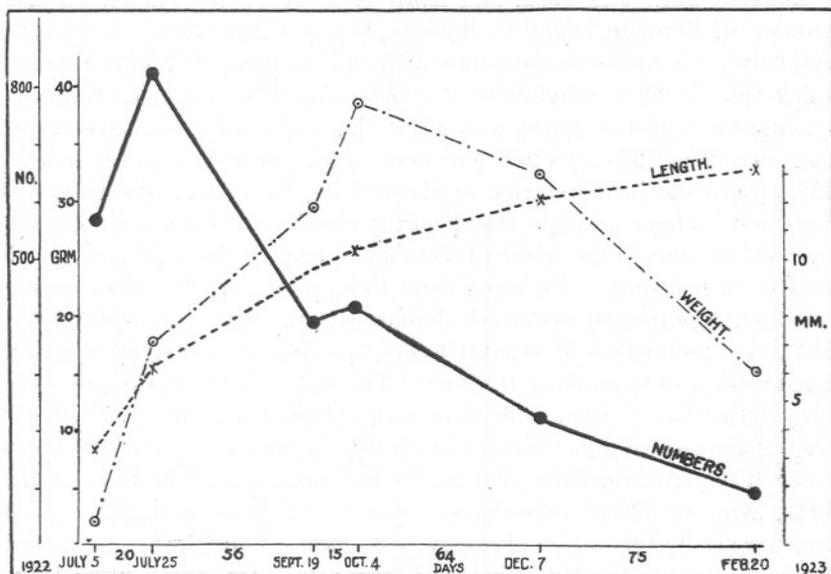


FIG. 2.—*Spisula elliptica*. Queen's Ground, 1922-23.

bers from 830 to 390 in the 56 days from July 25th to September 19th, the total weight increased from 17.707 gm. to 29.527 gm. But in the 75 days from December 7th, 1922, to February 20th, 1923, the drop in numbers from 222 to 90 resulted in a decrease in weight from 32.498 gm. to 17.207 gm. It is therefore important to realise **that mortality during the period of most rapid growth is more than compensated for by the growth of those that survive, whereas during the winter, when growth is slow, mortality may have a marked effect on the net weight of food.**

#### SYNDOSMYA ALBA FROM BIGBURY BAY.

It is well known that the shells of many lamellibranchs exhibit concentric rings which for a number of species have been shown to be the

external expression of changes in the rate of growth. It is quite another matter to decide whether in a particular species, alternate acceleration in the summer and retardation in the winter in the growth rate produce a recognisable series of rings on the shell from which the age of the individual may be deduced. In some instances, experimental work suggests that, with certain reservations, such is definitely the case. For instance, Weymouth (1923) after a close study of the Pismo Clam (*Tivela stultorum* Mawe) states that during the winter pause in growth, a mark is formed at the margin of the shell, and from these annual marks the age may be determined accurately in the great majority of cases.

Between June 9th, 1922, and April 10th, 1924, the *Syndosmya alba* ground off Borough Island in Bigbury Bay (see Ford, 1923, for details and map), was visited at short intervals, and samples of the lamellibranch stock taken. The individuals of *Syndosmya alba*, a species which is an important food of plaice, were made the subject of close attention on each occasion. The specimens of each of the samples from June 9th, 1922, up to and including that of March 16th, 1923, were symmetrically distributed about a single size (length) mode, and, on the whole, the successive values of the latter while rising quickly at first, did not change greatly subsequently. Of the several thousands of shells taken during this time none showed any clearly defined growth ring. But on May 30th, 1923, the specimens were separable into two classes, the second of which considerably outnumbered the first. The shells of the first class were tiny and without a ring, while those of the second were characterised by having a brown ring just inside the white growing margin, and their size mode did not differ greatly from that of the specimens of the March 16th, 1923, sample. These two classes remained distinct throughout 1923 and were still apparent on January 31st, 1924, although the one-ringed shells were considerably reduced in numbers. On April 10th, 1924, three classes were obtained, one without ring, a second with one ring, and a third with two rings, the two-ringed class being the strongest numerically.

From these observations there seems the strongest possible justification for concluding that **the 1922 stock assumed a growth ring between March 16th and May 30th, 1923, and a second between January 31st and April 10th, 1924, while the 1923 stock assumed a ring also between January 31st and April 10th, 1924.** Moreover, these rings are a true index of the number of winters through which the individuals passed, and are most clearly marked on the shell. Boysen Jensen (1919, p. 11), however, states that in 1918 *Syndosmya alba* were observed to assume two rings in the year, so that apparently the experience of 1923-24 at Bigbury is not invariable.

The shells of the two-ringed class taken on April 10th, 1924, all showed

a distinct difference between the width of the inner and the outer ring, the latter being the wider (see Pl. I, Fig. 3, bottom row). If, then, the ring itself is in reality the total winter growth, as seems likely, **there was a relatively larger growth in the winter of 1923-24 than in that of 1922-23.**

With this information it is possible to give a first summary of the composition of the stock for 1922, and the early part of 1924. The stock from June, 1922, onwards consisted exclusively of individuals born in that year, and this was sufficiently great to form the bulk of the stock throughout 1923 and even until April, 1924. The brood of 1923 was small and not to be compared with that of the previous year, and very little of it was apparent in the following spring, nor was there a heavy successful spatting in early 1924. Finally, judging from the rate at which the 1922 stock was dying off latterly, it appeared likely, that unless a large new brood arose during 1924, the ground which was most rich in this food-species throughout 1922 and 1923 would become temporarily barren.

The above will now be discussed in rather more detail, commencing with the situation during 1922. From Table V (p. 542), it will be observed that the modal sizes of successive samples which are shown in bolder type, although in general they rise rapidly during June, July and August, and then remain tolerably steady from October to March, would not plot to a steady even curve. When more than one sample is shown for the same date (e.g. Hauls 4a, b and c), the one which is numerically the most dense is composed of specimens of lower modal value. Such samples were taken at different positions on the ground, and it was striking throughout the work, how a move of a few hundred yards altered both frequency and modal size value. There can be no question that there was **at least one very localised area of great density, and a move from this spot meant an immediate decrease in numbers, with an eventual increase in size.** It is not possible to say whether the lower modal value at the densest spot is due to stunted growth on account of overcrowding, or whether a great fall of spat had occurred there superimposed on a previous less dense but more widely spread population of the same year's spatting. Both may be true, but whatever the reason, the study of the growth rate is thereby rendered much more difficult, for successive hauls may not be exactly comparable unless there is certainty that they were taken at the same place. Utilising the data from stations believed to be within the area of maximum density, the modal length rose from 5.5 mm. on June 9th, 1922, to 8.5 mm. on July 24th, a growth of 3.0 mm. in 45 days; on the other hand, it remained practically stationary at 10.5 mm. from November 20th, 1922, until March 16th, 1923. But at stations outside the area of maximum density, the modal length reached 13.5 mm.

TABLE V.  
SYNDOSMYA ALBA FROM BIGBURY BAY.

Reference No. of Haul.	Date of Haul.	No. of Dips of $\frac{1}{16}$ m. <sup>2</sup> bottom-sampler.	No. of Individuals taken.	No. per 1 sq. metre.	No. of Individuals measrd.	No. of Individuals in the following 1 mm. groups.															
						2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	June 9th, 1922	5	900	1800	813	3	76	141	<b>208</b>	180	116	61	21	3	4	—	—	—	—	—	
2	June 15th, 1922	5	505	1010	426	—	23	60	79	<b>97</b>	85	57	20	2	3	—	—	—	—	—	
3	July 24th, 1922	10	1641	1641	600	—	3	5	16	66	126	<b>205</b>	134	37	7	1	—	—	—	—	
4a	Aug. 22nd, 1922	1	40	400	40	—	—	1	—	—	3	2	—	2	3	10	<b>11</b>	2	—	—	
4b	Aug. 22nd, 1922	1	229	2290	229	—	—	2	4	6	38	59	<b>63</b>	38	12	1	—	—	—	—	
4c	Aug. 22nd, 1922	1	79	790	79	—	—	—	2	2	1	2	1	7	12	17	<b>22</b>	7	—	—	
5	Sept. 29th, 1922	5	205	410	180	—	—	1	—	3	6	2	3	12	22	<b>57</b>	50	18	5	1	
6	Oct. 17th, 1922	5	756	1512	625	—	—	2	4	5	22	99	160	<b>178</b>	118	29	6	2	—	—	
7	Oct. 31st, 1922	5	940	1880	940	—	5	9	9	35	160	<b>269</b>	245	150	38	9	1	—	—	—	
8a	Nov. 17th, 1922	5	393	786	386	1	7	7	8	8	16	44	<b>105</b>	98	64	15	7	1	1	—	
8b	Nov. 17th, 1922	5	138	276	136	—	1	4	5	6	4	5	10	29	<b>35</b>	21	12	3	1	—	
9	Nov. 20th, 1922	5	547	1094	496	—	5	4	5	13	40	106	<b>141</b>	115	49	15	2	—	1	—	
10	Jan. 18th, 1923	5	360	720	349	—	6	9	11	5	5	21	61	<b>96</b>	83	33	13	6	—	—	
11	Feb. 14th, 1923	5	367	734	367	—	4	2	4	7	14	38	75	<b>113</b>	79	19	9	2	1	—	
12	Mar. 16th, 1923	1	107	1070	107	—	—	2	—	1	5	17	24	<b>26</b>	23	7	2	—	—	—	
13	May 30th, 1923	4	524	1310	{ 409	—	—	—	—	1	1	14	81	<b>186</b>	94	28	3	1	—	—	
					{ 115	<b>56</b>	33	16	8	2	—	—	—	—	—	—	—	—	—	—	
14	Aug. 10th, 1923	5	476	952	{ 206	—	—	—	—	1	—	10	44	<b>78</b>	50	15	8	—	—	—	
					{ 276	16	56	<b>58</b>	55	49	28	13	—	—	1?	—	—	—	—	—	
15	Jan. 31st, 1924	10	166	166	{ 98	—	—	—	—	—	—	—	1	6	28	<b>38</b>	19	5	1	—	
					{ 68	—	2	—	11	9	<b>18</b>	17	11	—	—	—	—	—	—	—	
16	April 10th, 1924	{ Conical Dredge 2 dips	{ 478	239?	{ 367	—	—	—	—	—	—	—	27	113	<b>155</b>	65	5	2	—	—	
					{ 42	—	—	—	4	7	7	<b>14</b>	4	4	1	1	—	—	—	—	
					{ 69	<b>30</b>	19	8	6	6	—	—	—	—	—	—	—	—	—	—	

on August 22nd, 1922. If, as is possible, overcrowding results in stunted growth, the difference between the modes at a station within the densest area, and that at a station outside, is a measure of the effect of overcrowding. Thus, in August, shells closely crowded had grown to about 9.5 mm. while those less densely packed had attained a length of 13.5 mm.

Haul 13, taken on May 30th, 1923, contained specimens of two classes. There were a number of quite small ones, the 2 mm. and 3 mm. groups being the most frequent, and these were obviously a brood of the year 1923. In addition, 409 specimens from 6.5 mm. to 14.5 mm. in length, with a mode at 10.5 mm., exhibited a dark ring inside the margin of the shell. These were clearly the residue of the previous years' stock, and their weight undoubtedly formed the bulk of the stock on the day of sampling. By measuring the length\* of the ring on each of the shells, it was possible to determine the amount of new growth which had taken place in 1923. It was found that the modal length had increased from 9.5 mm. to 10.5 mm. Now the ring was not completed on March 16th, 1923, so that between that date and May 30th, the mode had risen by 1 mm. The smallest shell was 6.5 mm. in length and it had a ring 3.5 m.m in length, while the largest was 14.5 mm. long, with a ring less than 1 mm. shorter. **The ring, therefore, was found on shells of greatly varying lengths; was significant of a change in the growth rate, and independent of the size of the shell.**

Haul 14, taken on August 10th, 1923, also contained specimens of two classes, one without a ring, the individuals of which were arranged about a mode of about 5 mm. These were of the same class as those measuring from 2 mm. to 3 mm. on May 30th, 1923. The specimens of the second class were marked with one ring, their modal length being 11.5 mm. The modal length of the rings was 10.5 mm., so that there had been a new growth of 1 mm.

On April 10th, 1924, three classes occurred. There were 69 individuals without a ring, representing a brood of 1924, 42 individuals with one ring, the residue of the 1923 broods, and 367 with two rings, the residue of the 1922 stock. The modal values for the three classes were 2.5 mm., 8.5 mm. and 11.5 mm. respectively. Here again, the 1922 stock was still the chief constituent of the population, and it will be instructive to determine, from the size of the successive rings, the size of the 1922 stock after the winter of 1922, and after that of 1923. The 1922 rings varied in length from 4.5 mm., to 13.5 mm., the mean being at 9.01 mm. The 1923 rings were from 8.5 mm. to 14.5 mm., with the mean at 11.02 mm. Thus, **shells of 9.01 mm. at the end of their first winter in 1922, measured 11.02**

\* The "length" of the ring is its greatest antero-posterior dimension. See page 532 and Fig. 7, Plate III.

mm., at the end of the second winter, and between January 31st, 1924, and April 10th, 1924, had increased a further amount of something under 1 mm. Table VI is a correlation table for the first and second rings, from which the coefficient of correlation has been calculated to be .716. The straight line from the equation  $L_2 = 6.278 + .526L_1$  (where  $L_2$  and  $L_1$  are the length in mm. of the second and first rings respectively), and the two graphs from experimental data are shown in Fig. 4.

The dry-weight of specimens of lengths from 2.5 mm. to 15 mm. were determined as for *Spisula elliptica* (see page 536), and are shown in Table VII (p. 546). For this species the equation  $W = .00003L^3$  is a fair approximation, and it has been used to calculate the dry-weights of samples

TABLE VI.

SYNDOSMYA ALBA FROM BIGBURY BAY, APRIL 10TH, 1924.

		2nd Ring mm.							Total	Mean.
		8.5	9.5	10.5	11.5	12.5	13.5	14.5		
1st ring mm.	4.5	—	1	—	—	—	—	—	1	9.50
	5.5	—	1	1	—	—	—	—	2	10.00
	6.5	1	8	2	2	—	—	—	13	9.88
	7.5	—	19	28	8	2	—	—	57	10.38
	8.5	—	21	55	34	4	—	—	114	10.65
	9.5	—	1	39	57	6	—	—	103	11.08
	10.5	—	—	3	35	19	1	—	58	11.81
	11.5	—	—	—	3	9	2	1	15	12.57
	12.5	—	—	—	—	2	1	—	3	12.83
	13.5	—	—	—	—	—	—	1	1	14.50
Total		1	51	128	139	42	4	2	367	
Mean		6.50	7.70	8.60	9.41	10.38	11.50	12.50		

on various dates, shown in Table VIII (p. 546). From the figures obtained it is seen that **the 1922 stock was the predominant element throughout, and even at the beginning of the summer growth in 1924, it formed over nine-tenths of the weight of the whole stock.** It is impossible to state the reasons for this predominance of the year class 1922. Undoubtedly there was a great and successful fall of spat in the spring of that year, and the brood grew and survived, and clearly no similar survival could have occurred in 1921. If 1923 and early 1924 were good breeding years, the spat which fell did not survive in quantity in the area already populated by the dense 1922 stock. It is possible that elsewhere the spat may have settled and flourished, but has escaped detection. On the other hand, little spatting may have occurred at all. Boysen Jensen (1919, p. 13)

states that in Danish waters broods of *Syndosmya alba* appear about every second year.

The total dry-weight per 1 sq. metre was at its maximum in May, 1923, and then a decline became apparent. It is disappointing not to be able to give figures for April 10th, 1924, in order that the prospects for 1924 might be known more definitely, but owing to bad weather-conditions it was impossible to use the bottom-sampler satisfactorily on that occasion, and the only way to get a sample at all was by risking a conical dredge.

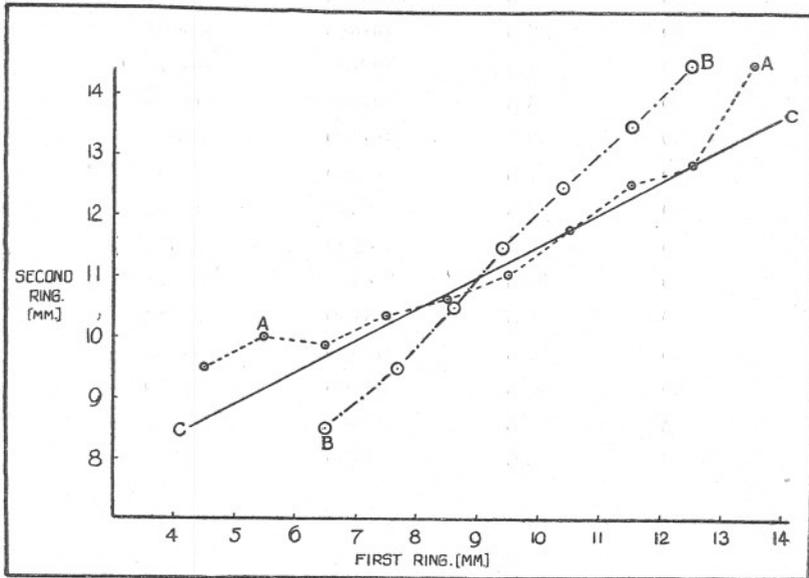


FIG. 4.—*Syndosmya alba*. Bigbury Bay, April 10th, 1924.

- AA. Observed first ring and mean second ring.
- BB. Observed second ring and mean first ring.
- CC. From equation  $L_2 = 6.278 + .526 L_1$ .

Living individuals were vastly outnumbered by freshly-dead shells, many of which on the evidence of their rings had died during the winter of 1923-24. In a previous paper (Ford, 1923, p. 191) it was shown that one dip of the conical dredge on this same ground was then equivalent to ten of the bottom-sampler, so that if we regard the two hauls of the conical dredge on April 10th, 1924, as equivalent to twenty dips of the sampler, the number per 1 sq. metre would be 478 which is 239, having a total dry-weight of 8.49 gm. This weight is about one-third of that on August 10th, 1924. **From these figures, then, it seems fair to predict that the ground will be poor in condition during the spring and early summer**

TABLE VII.  
SYNDOSMYA ALBA FROM BIGBURY BAY.

No. of specimens.	Length =L  mm.	Average dry-weight of shell and flesh =Wgrm.	Calculated
			Values W = .00003 L <sup>3</sup>  gram.
100	2.5	.00065	.00047
100	3.5	.00160	.00129
50	4.5	.00238	.00273
50	5.5	.00408	.00499
50	6.5	.00620	.00824
50	7.5	.01260	.01266
50	8.5	.01562	.01842
50	9.5	.02200	.02572
50	10.5	.04038	.03474
50	11.5	.05180	.04563
50	12.5	.06620	.05859
50	13.5	.07960	.07380
15	14.5	.09667	.09147
2	15.5	.11900	.11172

TABLE VIII.  
SYNDOSMYA ALBA FROM BIGBURY BAY.

Reference No. of Haul.	Date of Haul.	No. of Indi- viduals.	Total Dry weight.  gram.	Percentage of Total Dry-weight for the following :—			No. of Indi- viduals per 1 sq. metre.	Total Dry- weight per 1 sq. metre gram.	Dry-weight per 1 sq. metre of following :—	
				1922 stock.	1923 stock.	1924 stock.			1922 Stock	1923 Stock.
				1	June 9th, 1922	813			6.42	100
3	July 24th, 1922	600	11.12	100	—	—	1641	30.30	30.30	—
9	Nov. 20th, 1922	496	13.60	100	—	—	1094	30.06	30.06	—
13	May 30th, 1923	409	15.09	98.9	1.1	—	1310	38.13	37.71	.42
		115	.17							
14	Aug. 10th, 1923	206	10.13	86.3	13.7	—	952	23.46	20.22	3.21
		276	1.61							
16	April 10th, 1924	367	16.07	94.6	4.5	.8	Not available.			
		42	.77							
		69	.14							

of 1924, and unless new broods appear and flourish during the year, it will become relatively barren by the winter of 1924-25.

If the total dry-weight of a number of specimens be calculated, as well as the weight at the lengths at which their winter-rings were assumed, the results are a measure of the increase in weight for the successive periods. Thus, the 409 specimens of Haul 13 on May 30th, 1923, weighed 11.83 grm. at the end of their first winter (1922-23), and 15.09 grm. in the following May, the proportion being 1 : 1.27. The 206 specimens of August 10th, 1923, weighed 6.98 grm. at the end of the winter of 1922-23, and 10.13 grm. in the following August, the proportion being 1 : 1.45. The difference between the ratios naturally expresses the growth from May to August.

The 478 specimens of the 1922-year class taken on April 10th, 1924, weighed 8.46 grm. at the end of the winter of 1922-23; 15.06 grm. at the end of the winter of 1923-24; and 16.07 grm. on April 10th, 1924. These values are in the proportion of 1 : 1.78 : 1.90.

#### CARDIUM ECHINATUM FROM BIGBURY BAY.

The hauls on the Bigbury Bay ground also contained numbers of the spiny cockle, *Cardium echinatum*, and on similar evidence to that for *Syndosmya alba*, this species also produced winter growth-rings (see Pl. III, Fig. 5) at the same period of the year. That is, **a brood of cockles spat in the spring of 1922, assumed one ring in the spring of 1923, and a second in the spring of 1924.** Plate II, Fig. 6 A and B of one valve of the same specimen photographed by reflected light and transmitted light respectively, illustrate the sharply-marked change in shell thickness coinciding with the rings.

By measuring the length of the rings and the total length of shells taken on various dates, information was obtained on the variation in length of individuals at the end of the first and second winters. Such information is important in its relation to the value of the species as fish-food, for the spiny cockle can grow to a size certainly beyond that suitable to flat fish of marketable size.

From Table IX (p. 548) it is seen that the length of the shell at the formation of the 1922-23 winter-ring varied from 9 to 24 mm., with the majority of individuals between 15 mm. and 19 mm. in length, and the average length 18.2 mm. This size must be near the limit of the capacity of flat fish, so that it follows that soon after the commencement of the summer growth for 1923, spiny cockles on the Bigbury Bed spat in the spring of 1922, were becoming less and less available as food owing to their exceeding the size limit in gradually increasing numbers. **There is, therefore, a big difference in the food-value of spiny cockles**

to fishes, from that of *Syndosyma alba*. In the case of the latter, a great fall of spat in the spring which can grow and flourish, may form a valuable food stock for fish for two years after spatting, whereas a successful spatting of the cockle in the spring, although it may give a much heavier yield by weight of fish food for the current year, will be unavailable owing to its rapid growth soon after the commencement of the next year's growth. If, however, it is possible that the spiny cockle can produce broods late in the summer, when the growth for the year is practically finished, then, of course, this may be of suitable size for fishes during the next season or part of it. I have no evidence, however, from the present material, that extensive late summer spatting may occur.

Sufficient material was not available for the determination of dry-weights corresponding to a series of 1 mm. length-groups as was done for

TABLE IX.  
CARDIUM ECHINATUM FROM BIGBURY BAY.

Date.	Number of specimens having first winter-ring at following length in mm.			Range in length. mm.	Total No. of specimens.	Average length at formation of 1st ring.
	9-14	15-19	20-24			mm.
May 30th, 1923	9	20	16	9-24	45	18.4
April 10th, 1924	8	36	16	12-22	60	18.0
May 7th, 1924	6	32	10	13-22	48	18.1
Totals	23	88	42	9-24	153	18.2

*Syndosmya alba*, but ten specimens of an average length of 16.5 mm. produced 4.984 gm. of dried shell and flesh, while ten specimens of 19.5 mm. average length produced 8.025 gm. of dried shell and flesh. The twenty individuals were from hauls in late autumn of 1922 in which *Syndosmya alba* of a similar age were present, of an average length of 10.5 mm. and an average dry-weight of 0.03 gm. The ten cockles of 16.5 mm. were thus by dry-weight equivalent to 154 average *Syndosmya*, and the ten at 19.5 mm. to 267 *Syndosmya* towards the end of the growth period for 1922. The dry-weight of flesh only for the 16.5 mm. and the 19.5 mm. cockles were 0.376 gm. and .505 gm. respectively, which are .075 and .063 of the total dry-weight.

The ring of the winter 1923-24 although recognisable in the majority of shells taken both on April 10th and May 7th, 1924, did not appear so clearly marked as the first ring. Reference has previously been made to a difference between the width of the actual ring for the 1922-23

ring and the 1923-24 ring in *Syndosmya*, the latter being the broader, and it may be that the experience in the cockle is due to the same cause. Forty-five shells taken on May 7th, 1924, showing a first ring varying from 13 mm. to 22 mm., and an average of 18.1 mm., had a second ring ranging from 29 mm. to 35 mm., of an average length of 32.3 mm. The average 1922 growth was therefore 18.1 mm., and that of 1923, 14.2 mm., which are in the proportion of 1:0.78. The corresponding ratio for *Syndosmya* was 9.01:2.01 which is 1:0.22; suggesting that the second year's growth of the cockle was relatively greater than in *Syndosmya* on the same ground.

#### SPISULA SOLIDA FROM START BAY.

On November 19th, 1923, a total of 1862 living *Spisula solida* were collected from nine stations along a line following the shore in Start Bay for about four sea-miles from off Street Head towards Hallsands, at a depth of ten metres. *Spisula solida* was practically the only species represented in a bottom soil consisting for the most part of coarse water-worn gravel and stones. Two dips of the  $\frac{1}{10}$  sq. metre bottom-sampler were taken at each station, and at six positions the numbers taken indicated a population of well over 1000 per sq. metre. The actual density probably exceeded this figure, for the sampler does not work ideally in so coarse a soil. At most stations the shells were one inch or more in length, so that for at least three miles they must have been extremely closely packed.

All the shells were most distinctly marked with rings, and it is the significance of these rings which forms the subject of immediate interest. It is to be regretted that, from lack of sufficient information, it is not at present possible to state whether or no they are a reliable index of age. There can be no doubt, however, that the rings are the result of disturbance in growth, for the examination of any shell by transmitted light shows at once a distinct reduction in the thickness of shell at each of the rings, as well as a difference in thickness of the successive zones between the rings. Plate III, Fig. 7 is a fair illustration of this. Superficially, then, these rings in *Spisula solida* are identical in appearance to those which in the species discussed on preceding pages have been shown to be annual in formation. But, if, in the event of evidence being forthcoming that one or more of the series of these so similar rings may be due to disturbances in growth, which are not necessarily regularly periodic, it would appear hopeless to attempt to deduce the age of the shell. Yet, after a great number of measurements of successive rings on the majority of the 1862 shells, I feel convinced that much useful information can be derived from the arrangement of the rings, whatever may have been the cause of their formation.

It will be convenient to commence with a statement of several facts and with the conclusions which may be drawn from them :—

1. The number of rings on a single shell varied from 1 to certainly 7 and possibly 8.
2. For each station it was possible, by inspection, to recognise at least one definable arrangement of a given number of rings, and to pick out a good number of specimens unquestionably exhibiting this arrangement of rings.
  - 2a. Usually one typical arrangement of rings predominated at each station.
  - 2b. The type for one station frequently differed from that of the next.
  - 2c. The same type may be represented on more than one station.

Several conclusions may be drawn from the facts set out under heading 2. The main observation that a good number of specimens at the same station showed the same number of rings arranged in a similar manner would seem to justify the conclusion that these specimens had undergone the same series of disturbances in growth. If the same type may be represented on more than one station, then it is also reasonable to conclude that this same series of disturbances has reacted on the individuals at more than one station. But, as the type on one station may differ from that of the next, either the population of the several stations have undergone different parts of a series of disturbances which occurred generally over the whole area, or else there were independent and different series of disturbances at different stations.

3. The shells of a given type of ring-arrangement on the same station are of a similar size.
  - 3a. Stations on which the same type of shell occurs may differ very much in the average length of the shells of that type.
  - 3b. The average length of shells of a type with few rings on one station may exceed that of shells of a type with a larger number of rings at a second station.

If the shells of a given type on the same station are of a similar size, then, following on the conclusions drawn from heading 2, it may be said that the resultant effect of a series of disturbances on a station may be expressed by the average size of the shells of that type. Observation 3a thus shows that stations must differ in the resultant effect of the same

series of disturbances, while definite data on 3b will give the degree to which stations may differ.

Now if the average size of specimens having say six rings differs at the several stations, and may even be exceeded by that of three-ringed shells, it will be a matter of some difficulty to arrive at a reasonable estimate of the quantity of fish-food available on the whole feeding ground. Even if it can be proved that the rings on the shells are annual in formation, and are thus expressive of age, so that the relative growth

TABLE X.

SPISULA SOLIDA FROM START BAY, NOVEMBER, 1923.

Ref. No. of station.	No. Dips of 1/2 m. sampler.	Total No. of shells.	No. of rings on shells.	No. of shells.	Average length in mm. of shell at formation of the following rings.			Average total length. mm.	Growth between successive rings. mm.		
					1	2	3		1-2	2-3	3-total length.
6	2	153	6	107	7.68	15.83	26.07	30.83	8.14	10.25	4.76
51	2	217	6	127	6.95	14.09	21.97	28.93	7.14	7.88	6.96
52	2	234	6	128	7.01	14.05	22.37	27.91	7.05	8.31	5.55
53	2	390	6	303	7.09	13.50	20.20	26.37	6.41	6.69	6.18
55	2	259	6	195	7.61	14.74	23.86	32.16	7.13	9.12	8.29
50	2	73	5	19	5.66	21.24	26.76	34.50	15.58	5.53	7.74
50A	2	239	5	20	6.30	19.75	25.95	33.00	13.45	6.20	7.05
51	2	217	5	31	5.73	15.89	?	26.98	10.16	?	?
52	2	234	5	32	5.47	18.63	23.59	30.19	13.16	4.97	6.59
55	2	259	5	10	5.40	17.90	22.90	30.40	12.50	5.00	7.50
50A	2	239	4	16	7.50	22.62	29.62	34.38	15.11	7.00	4.76
50	2	73	3	27	11.60	18.20	25.98	30.17	6.59	7.78	4.19
50A	2	239	3	67	12.04	18.39	25.53	28.22	6.35	7.14	2.69
52	2	234	3	17	10.73	15.47	24.38	27.03	4.73	8.91	3.65
54	2	295	3	279	10.69	15.96	(close to margin)	23.43	5.27	?	?
6	2	153	1	17	11.62	—	—	21.15	1-total length. 9.53	—	—
50	2	73	1	14	8.36	—	—	17.93	9.57	—	—
50A	2	239	1	50	8.90	—	—	17.14	8.24	—	—
51	2	217	1	24	7.67	—	—	15.83	8.17	—	—
55	2	259	1	16	10.75	—	—	17.81	7.06	—	—

in the successive years may be determined, the data derived from a sample of *Spisula solida* is only applicable to the position on the area from which the sample was taken, and may not in any way give a fair estimate of the general conditions.

A six-ringed type of shell was the most general in distribution and the most numerous. The first, second and third rings were well separated, but the fourth to the sixth were relatively close up to the third, giving the effect of four fairly evenly spaced rings close to the margin of the shell (see Pl. I, Fig. 8 F). An inspection of Table X will show that this type

was the dominant one except on Station 54 where three-ringed individuals were present almost to the exclusion of others; the variation of the average size at the different stations will also be noticed, as well as the facts that three-ringed shells on Station 50 exceeded in size the six-ringed ones on Stations 51, 52 and 53.

Table X is not intended as a complete record of the specimens from each station, but as a means of showing the variation from station to

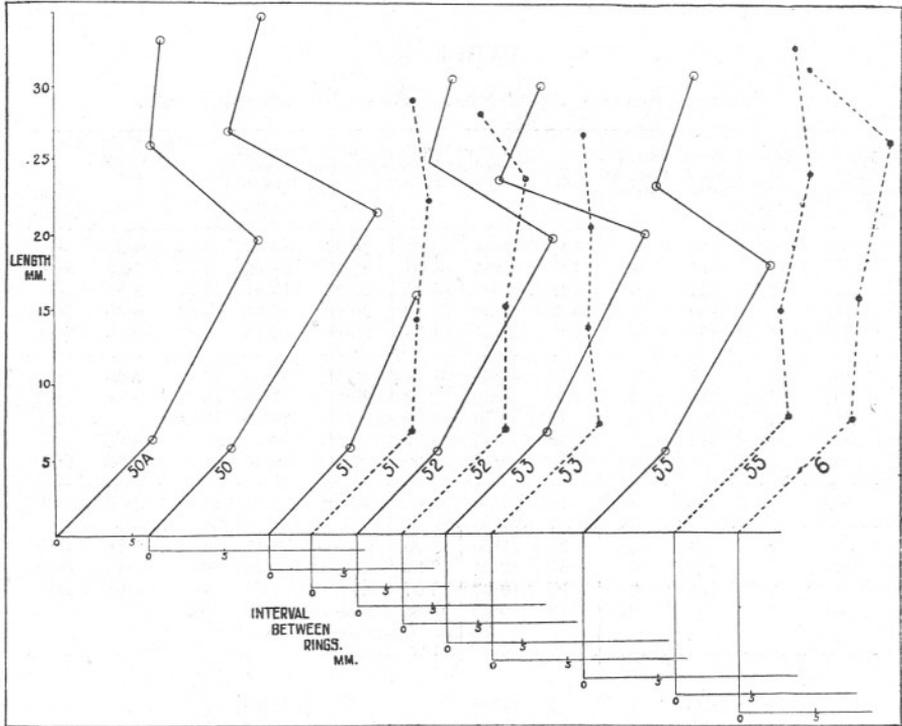


FIG. 9.—*Spisula solida*. Start Bay, November, 1923.

Continuous Line. Five-ringed shells.

Broken Line. Six-ringed shells.

The large numbers alongside each graph indicate the Station from which shells were taken.

station of the several types. Only those shells which were true to type are included, all doubtful ones having been discarded. The total number at each station is given, so that it is possible, from the table, to note the number of quite typical shells, but it is probable that a considerable number of each type have been left out as a result of the stringent selection. Fig. 8 (Pl. I) is from a photograph of good specimens of each type, from which the distinctive characters may be learned. In Fig. 9 graphs are reproduced for five-ringed and six-ringed shells from the same stations

—the average lengths appear as ordinates, and the interval growth\* between successive rings as abscissae—and the distinct difference between the two types is well illustrated thereby. It will be seen that the most noticeable difference is in the interval growth between the first and second rings. In the five-ringed shells, this is large in comparison with the initial growth to the first ring (cf. Pl. I, Fig. 8 E and F). Confining attention, for the time being to Station 52, we may enquire whether five of the six growth-disturbances which resulted in the rings on the

TABLE XI.

SPISULA SOLIDA FROM START BAY, NOVEMBER, 1923, AT STATION 52.  
SIX-RINGED SHELLS.

Length in mm. at 2nd ring.	Length in mm. at 3rd Ring.										Total.
	9	10	11	12	13	14	15	16	17	18	
16	—	1	—	—	—	—	—	—	—	—	1
17	1	1	—	—	—	—	—	—	—	—	2
18	—	—	—	4	—	—	—	—	—	—	4
19	—	—	4	3	1	—	—	—	—	—	8
20	—	—	2	4	8	2	1	—	—	—	17
21	—	—	2	4	11	8	2	—	—	—	27
22	—	—	—	3	5	11	3	—	—	—	22
23	—	—	—	—	2	5	5	1	—	—	13
24	—	—	—	1	2	3	3	5	3	1	18
25	—	—	—	—	2	—	1	3	—	—	6
26	—	—	—	1	—	—	1	—	—	—	2
27	—	—	—	—	—	1	3	—	—	1	5
Total	1	2	8	20	31	30	19	9	3	2	125

six-ringed shells could produce the five-ringed type of shell on the same ground. Obviously, for this to occur, the first disturbance must have taken place before the five-ringed shells appeared at all, so that we must pass over the initial growth to the first ring in the six-ringed shells, and compare the subsequent growth with the whole growth of the five-ringed shells. Thus, the first ring on the five-ringed shells would be produced by the disturbance which caused the second ring on the six-ringed shells.

Table XI is a correlation table for the lengths of the six-ringed shells

\* The interval growth is the differences between the lengths of successive rings.

at the second and third rings respectively. The coefficient of correlation is .69 and the equation representing the one in terms of the other is

$$L_3 = .427L_2 + 16.36.$$

From Table X we learn that the length of the five-ringed shell when the first ring was formed (that is when the second ring of the six-ringed shell was formed) was 5.47 mm., so that from the above equation, the length at the formation of the second ring should be

$$(5.57 \times .427) + 16.36 = 18.70 \text{ mm.}$$

Actually it was 18.63 mm., which is not greatly different from the value calculated. This result shows that the hypothesis that **the five-ringed shell was produced by the last five of the six disturbances which brought about the six-ringed shell, is not an impossible one.** The small size of the five-ringed shell at its first ring suggests that it had not been on the ground for the whole period between the first and second growth disturbances. If the disturbances were annual, then the five-ringed shells were spatting towards the end of the growth period of 1918, whereas the six-ringed shells, showing a comparatively large initial growth were spatting at any earlier part of the growth period of 1917.

On Station 53, both six- and seven-ringed shells occur, the former being the more numerous, and by a similar calculation to the above it was found that **the six-ringed type could be produced by the last six of the seven disturbances causing the seven-ringed type.**

There seems, therefore, to be sound reason for arguing that **in general the bulk of the shells on the same station have been subjected to some part of the same series of growth disturbances, the number of rings on a shell indicating the number of disturbances the shell has experienced. Those with fewer rings are younger than those with more, and when it becomes possible to state the times at which the disturbances occur, the rings are a definite clue to age, while the interval between them represents the growth between the successive disturbances.**

If the rings are formed annually—a pure assumption at present—then the bulk of the stock was spatting in the year 1917, the average size of these six-ringed individuals varying with the position on the ground. On Station 54, however, the stock is almost purely 1920 spatting. The brood of the year 1921 seems to be almost absent from the area, and that of 1922 is not great.

The fact that individuals of more than one type of shell may occur on the same station suggests a further possible complication. It has already been stated that the bottom soil consists largely of water-worn gravel and stones. This indicates considerable water-movement at the bottom, and **it is quite believable that the living shell-fish are themselves**

on occasions rolled along the sea-bottom to another position on the bed. They certainly often present a worn appearance of the shell, consistent with such a view. If such may occur, an individual rolled away from the spot in which it first settled, may come to lie among a stock of others of different size and age. In the course of time, considerable mixing could easily be brought about, bringing together individuals of different age and origin, and producing the effect experienced in the series of hauls now under consideration. The presence of these rolled individuals will make it difficult to determine which of the specimens in a haul were spatting in that position, but it seems fair to conclude that those of the predominant type, at least, have lived there throughout their life.

Other important food-species occurred in the material, but the information derived on rate of growth was not so full as for those already dealt with. It will be most convenient to give a short account for each species.

#### MACTRA STULTORUM.

A definite-growth ring may be formed in the first winter after spatting. Individuals spatting in late spring of 1922 formed a ring at a length from 25 mm. to 32 mm. during the winter of 1922-23, and by January 31st, 1924, had grown to from 33 mm. to 39 mm.

#### LUTRARIA ELLIPTICA.

On June 7th, 1922, the average size of specimens from Whitsand Bay was 3 mm., while on July 20th this had increased to 12 mm. On January 25th, 1924, specimens were taken with a distinct ring at 30 mm. to 33 mm., and of a total length of from 44 mm. to 45 mm. This suggests a growth of 30 mm. to 33 mm. for 1922, and a further growth of 12 mm. to 14 mm. during 1923.

#### LUTRARIA OBLONGA.

On July 5th, 1922, fifty-six specimens from Queen's Ground were of an average size of 5.1 mm. On August 24th, 1922, one specimen was obtained measuring 22 mm. This would indicate a growth-rate somewhat similar to that of *L. elliptica*.

#### NUCULA NITIDA.

Information on this species is rather of a negative character. Many specimens were obtained, but neither by the comparison of modal lengths for successive samples, nor by the study of the rings on the shells was it possible to gain knowledge on the rate of growth. Tiny specimens

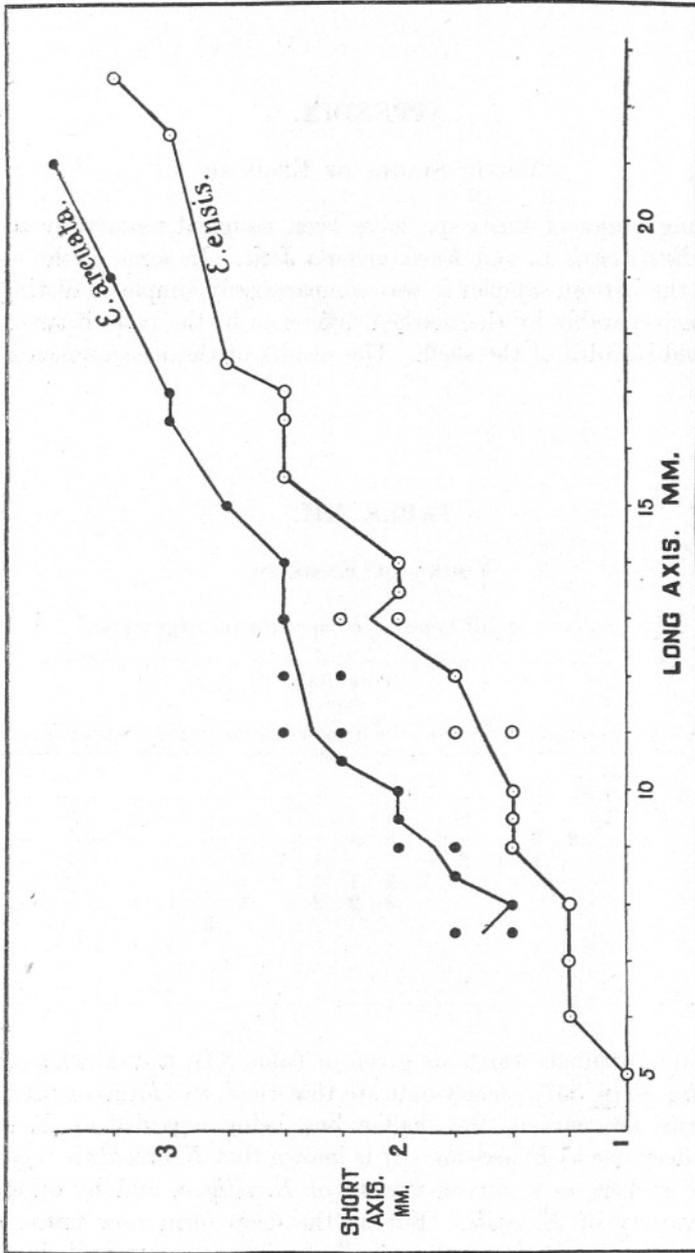
occurred in almost every month of the year, and the lengths of individuals of a sample did not conform to a distinct mode. The rings were confusing, not lending themselves to simple interpretation for age.

#### CULTELLUS PELLUCIDUS.

This important food-species was also well represented. One fact of interest was that on the same day, the average size of individuals from the open channel was much smaller than that of individuals from Bigbury Bay. This observation is mentioned in illustration of the point that care must be taken when comparing average sizes of shells on different occasions—differences in average size can only be significant in relation of growth, when there is evidence that the stock sampled is really of the same age, and has been under similar conditions during the interval between samplings. In Bigbury Bay, individuals spatting in June, 1922, grew to 15 mm. to 20 mm. by the autumn of the same year. Jensen (1919, p. 16) states that in the Thisted Bredning, individuals one year old in May, 1912, measured 15 mm. to 20 mm., and those two years old in May, 1913, were about 25 mm. He also refers to growth-rings on the shells, but I am unable to say that the Plymouth specimens showed rings which I could confidently regard as reliable aids to determination of age.

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FIG. 10.—Young stages of *Ensis* sp. Data from Table XII.

## APPENDIX.

## YOUNG STAGES OF ENSIS SP.

THE young stages of *Ensis* sp., have been assigned tentatively to two species, *Ensis ensis* L. and *Ensis arcuata* Jeffr. In some of the earlier hauls of the bottom-sampler it was comparatively simple to distinguish two forms separable by the marked difference in the ratio between the length and breadth of the shell. The results of the measurements of a

TABLE XII.

## YOUNG OF ENSIS SP.

[*E. ensis* in small type ; *E. arcuata* in large type.]

Short Axis. mm.	Long Axis. mm.																							
	5'0	6'0	7'0	7'5	8'0	8'5	9'0	9'5	10'0	10'5	11'0	12'0	13'0	13'5	14'0	15'0	15'5	16'5	17'0	17'5	19'0	21'0	21'5	22'5
1.0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.25	-	1	3	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.5	-	-	-	1	1	-	7	1	10	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
1.75	-	-	-	1	-	2	2	-	-	-	3	4	-	-	-	-	-	-	-	-	-	-	-	-
2.0	-	-	-	-	-	-	-	1	1	2	-	-	1	2	1	-	-	-	-	-	-	-	-	-
2.25	-	-	-	-	-	-	-	-	-	-	1	3	1	1	-	-	-	-	-	-	-	-	-	-
2.5	-	-	-	-	-	-	-	-	-	-	3	2	2	-	3	-	1	1	1	-	-	-	-	-
2.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-
3.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-
3.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
3.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-

number of individuals which are given in Table XII, and shown graphically in Fig. 10 (p. 557), clearly indicate that these two forms are distinct. Both forms are curved, the shallow one being regarded as *E. ensis*, and the deep one as *E. arcuata*. It is known that *E. arcuata* is regarded by some workers as a curved variety of *E. siliqua*, and by others as a deep variety of *E. ensis*. But as the deep form now under consideration is curved from the smallest size, it may well be that *E. arcuata* should be accepted as a species distinct from both *E. ensis* and *E. siliqua*.

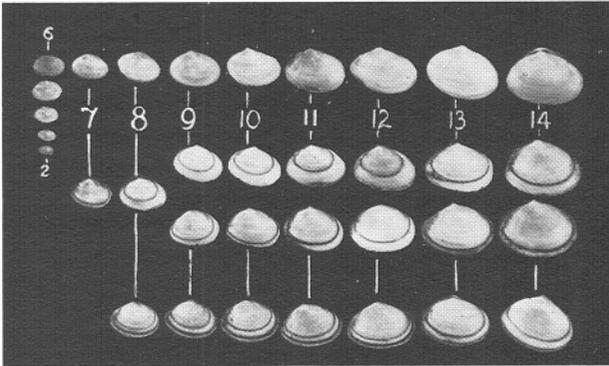


FIG. 3.

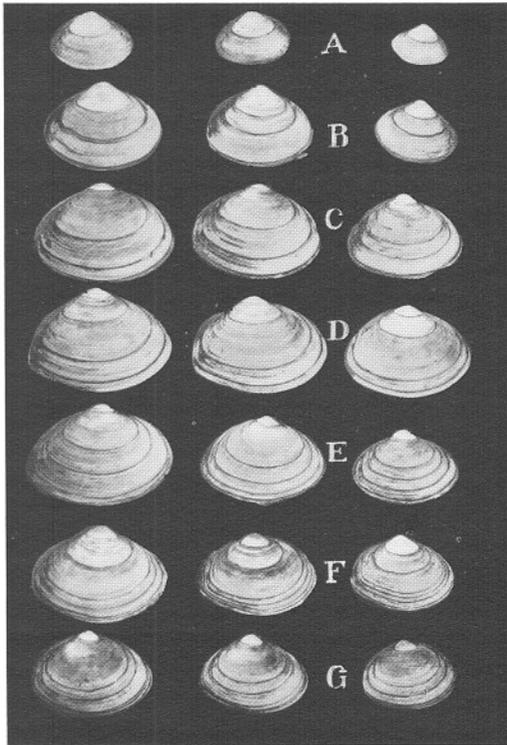
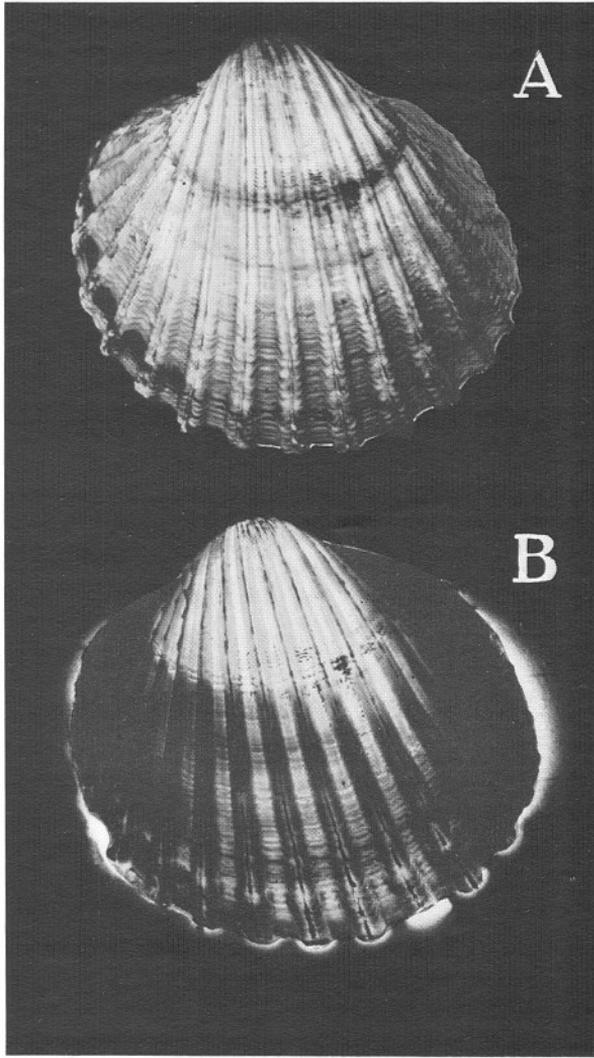


Photo E. F.

FIG. 8.

To face page 558.



*Photo E. F.*

FIG. 6.

*To face page 558, after Plate I.*

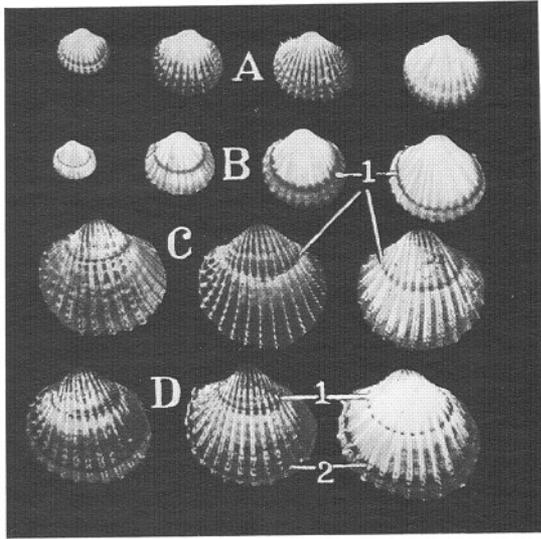


FIG. 5.

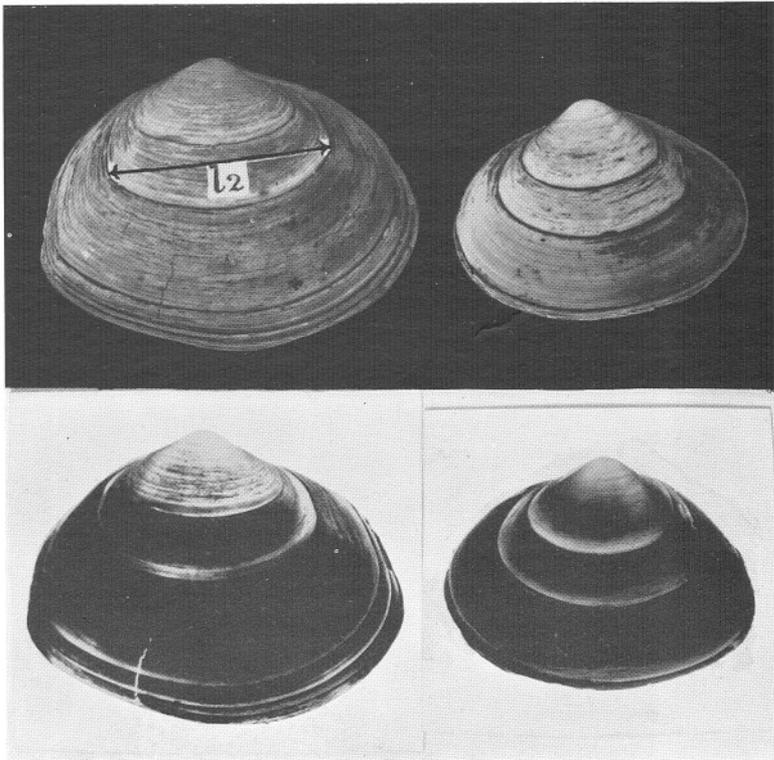


Photo E. F.

FIG. 7.

To face page 558, after Plate II.

## EXPLANATION OF PLATES.

## PLATE I.

FIG. 3.—*Syndosmya alba*. Bigbury Bay, 1922, 1923, and 1924. Photograph of shells from 2 mm. to 14 mm. in length. Top row without winter ring, middle rows with one winter ring and bottom row with two winter rings.

FIG. 8.—*Spisula solida*. Start Bay, November, 1923. Reduced from photograph of single valves, to show growth rings.

- A. One ring.
- B. Three rings.
- C. & D. Four rings.
- E. Five rings. Note wide growth between first and second rings.
- F. Six rings. Note four rings close together at margin.
- G. Seven rings.

## PLATE II.

FIG. 6.—*Cardium echinatum*. Bigbury Bay, 1924. Enlarged from photographs of same shell.

- A. By reflected light.
- B. By transmitted light.

## PLATE III.

FIG. 5.—*Cardium echinatum*. Bigbury Bay, 1922, 1923, and 1924. Reduced from photograph of one valve of each shell.

- A. Specimens without winter ring. Autumn, 1922.
- B. Specimens with one winter ring. May, 1923.
- C. " " " " January, 1924.
- D. " " two winter rings. May, 1924.

FIG. 7.—*Spisula solida*. Start Bay, November, 1923. Enlarged from photograph of two shells.

- Upper. By reflected light.
- Lower. By transmitted light.
- $l_2$ . Length of second ring.

## The Food of the Bottom Fauna of the Plymouth Fishing Grounds.

By

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With Plates I and II and One Figure in the Text.

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### MATERIAL AND METHODS.

THE present paper embodies the results of a year's study of the food of the bottom animals of the Plymouth fishing grounds, undertaken in order to obtain such general knowledge of the conditions as would provide a basis for further investigation.

Material has been collected in the course of the routine trawling and dredging operations of the s.s. *Salpa*. Samples of some species have been obtained by the use of the Petersen  $\frac{1}{10}$  sq. metre bottom sampler. Wherever possible the examination of stomach contents has been conducted on fresh material. When, owing to lack of time, this has not been possible, the stomach and intestines of the larger species have been removed intact and preserved either in 90% alcohol or in 5% neutral formalin in seawater, a method which, though not as satisfactory as fresh examination, has proved quite useful. Some smaller animals have been preserved entire. Examination in all cases was delayed as little as possible.

In addition to this, a number of living animals have been kept under observation in aquaria to ascertain their method of feeding.

The specialized nutrition of parasitic forms and of the Protozoa are not considered in the present paper.

The author is indebted to Dr. Allen, Mr. Ford, and others of the staff of the Marine Biological Association, for information and suggestions, and for assistance in identifying specimens.

### AREA INVESTIGATED.

The area over which these observations have been made comprises the outer trawling and dredging grounds described by Allen (1) and by the Marine Biological Association (28).

The majority of the animals studied are from depths greater than 15 fathoms, and all are from depths less than 40 fathoms, the average being about 27 fathoms. A few specimens from the shallower waters of the Sound and the adjacent bays are included.

#### PREVIOUS WORK.

The part played by the bottom animals in the economy of the sea has of recent years been the subject of investigations by Petersen (35, 36) and his assistants in Denmark. Using a specially designed bottom sampler, Petersen has made a quantitative study of the fauna of the sea-bottom in Danish and Scandinavian waters, and demonstrated the existence of definite animal communities on the sea-floor of those areas. In his papers there is much information regarding the food of the bottom fauna, and he discusses the question of the ultimate food supply, tracing this, in the Danish fjords, to the annual production of detritus from the extensive *Zostera* beds. Blegvad (10), working with Petersen, has studied the food and feeding methods of many bottom animals, and in his paper gives a good bibliography of previous work on the subject. He reaches the conclusion that organic detritus forms the principal food of the great majority of animals of the sea-bottom. The contributions of Rauschenplat (39) on the food of the animals of Kiel Bay, and Eichelbaum (19) on the food of Echinoderms, are important sources of information, while the works of Jordan (23) and Biedermann (7) on the physiology of digestion in Invertebrates contain references to the nature of the food of numerous species. In addition to these more comprehensive studies there is an extensive, scattered literature relating to the food and feeding methods of isolated species.

#### SOURCES OF FOOD.

Blegvad (10) states that the food available for consumption by bottom animals falls naturally under three headings, viz. (1) Plants, (2) Detritus, and (3) Animals, and broadly classifies his bottom fauna accordingly as (1) Herbivores, (2) Detritus-eaters, and (3) Carnivores, with various degrees of overlapping between these groups. This observer worked very largely on species inhabiting algal and *Zostera* zones, and under his heading *Plants* he assigns paramount importance to the multicellular vegetation of these zones, allowing some significance to encrusting diatoms, very little to free-living bottom diatoms, and practically none to the planktonic flora. Similarly, in discussing the origin of detritus, he holds with Petersen (36) and Boysen Jensen (11) that this is derived almost entirely from the continual breaking up and decay of the *Zostera* and larger coastal algæ.

In the deeper water in which the present observations have been made conditions are very different from those obtaining in the shallow Danish fjords. The larger algæ and *Zostera* are absent, the whole of the plant life being represented by the plankton and bottom-dwelling species of microflora. There are, however, rich zones of coastal algæ on the neighbouring shores, whilst *Zostera* beds occur in some of the bays and estuaries.

The sources of food may be considered under two headings, namely, (1) *Non-living Organic Matter* and (2) *Living Organisms*.

#### *Non-living Organic Matter.*

Organic detritus plays an important part as a source of food in the area studied. It occurs both as a fine suspension in the sea-water and as a flocculent deposit on the sea-floor. Nowhere has a distinct upper layer of organic detritus been found on the bottom comparable to the "brown layer" of Petersen and Boysen Jensen (36). Samples of the bottom were obtained by Petersen's glass-tube method (36, p. 14), which preserves the upper layers as *in situ*, and the detritus so obtained appears as a fine flocculent material, freely mixed with the sand, gravel, or mud of the bottom to a depth of several inches, its proportion being greatest in the surface layer. It can be separated from the coarser inorganic particles by shaking in sea-water: the heavier material sinks more rapidly, so that the detritus can be poured off in suspension and then allowed to settle. Microscopic examination affords little reliable clue as to its origin. On the average it appears as a pale brownish flocculus containing a small proportion of recognizable remains of animals and plants. These are mostly the fragmented skeletal parts of organisms, such as bristles, setæ, spicules, shell fragments, and the empty frustules of diatoms. Recognizable remains of higher vegetation are very few. Living micro-organisms are invariably found associated with the detritus: these will be discussed later. Matter recognizable as faecal constantly occurs in the bottom detritus.

Samples of sea-water have been centrifuged to obtain information as to the suspended organic detritus. Such samples yield a small quantity of flocculent dust-fine matter, similar in appearance to the bottom flocculus. Dr. M. V. Lebour, who has centrifuged many water samples in her investigation of the nanno-plankton, states that this unidentifiable organic matter is constantly present in a bulk considerably greater than that represented by the organisms found.

The organic detritus thus found deposited or in suspension must be immediately derived from the continual disintegration and decay of once living organisms. Apart from contributions from the land, transported into the sea by the agency of rivers and wind, the fundamental source

must be the plant life of the sea, which is represented by (1) *the phytoplankton*, (2) *the higher algæ of the coastal zone*, and (3) *the Zostera beds*. The relative importance of these is difficult to gauge other than conjecturally, and the following considerations are purely tentative.

It is required to know the annual production available from each source. From a series of observations on the seasonal changes of alkalinity due to photosynthetic activity in the sea-water of the English Channel, Atkins (4) has made a rough estimation of the annual production of phytoplankton. He has also (5) made a similar calculation based on the seasonal change in phosphate content of the sea-water. The two figures obtained are in agreement, and indicate an approximate annual production of phytoplankton of 1400 metric tons per square kilometre, wet weight, for an average depth of 70 metres. Moore (30), by a similar process, derived from alkalinity observations a slightly higher figure for the Irish Sea. Boysen Jensen (11) also arrives at a figure for the annual phytoplankton production, basing his very careful calculations on data given by Brandt (12) as to number and chemical composition of plankton organisms. This works out at 100 grams per square metre, dry weight, or 625 metric tons per square kilometre, wet weight, for a depth of 20 metres. Assuming that photosynthesis is active down to 100 metres depth, this value is not greatly at variance with the figures of Atkins and Moore. The annual production of *Zostera* has been studied by Petersen (36), and Boysen Jensen (11) gives it as 120 grams per square metre, dry weight, or 750 metric tons per square kilometre, wet weight. No figures are available for the annual production of the coastal zone of higher algæ, such as *Laminaria* and *Fucus*, but it is probable that this yields a heavier crop per given area than that of the *Zostera* beds.

In considering the availability of these amounts for detritus formation, the figure for phytoplankton will be heavily discounted, for much of it is consumed directly by animals, and much of it will be destroyed before reaching the bottom. The *Zostera* and higher algæ, on the other hand, are much less perishable and a far greater percentage of their annual crop will become detritus than in the case of the phytoplankton. In spite of this, however, it is probable that in such an area as the English Channel the phytoplankton is an important source of organic detritus, for, compared with the area concerned in the production of phytoplankton, the area producing higher algæ and *Zostera* is small. In the attempt to solve this question for Danish waters, Boysen Jensen (11) compared the chemical composition of detritus with that of *Zostera* and that of plankton.

Using the quotient  $\frac{\text{Amount of Carbon}}{\text{Amount of Pentosan compounds}}$  he found that the values for detritus lay between those for *Zostera* and those for plankton.

approaching the *Zostera* value in samples from the shallow, enclosed fjords and corresponding more to the plankton value in samples from open, deeper waters.

No knowledge exists as to the actual food value of detritus. Boysen Jensen (11) has analysed bottom samples for digestible matter, finding almost negligible traces of digestible proteins and a fair proportion of non-nitrogenous matter in the form of pentosans. He assumes that the latter are digestible by detritus-eating animals on the slender evidence that Biedermann and Moritz (8), in 1898, claimed to have discovered a cytase in the digestive gland of the snail, *Helix pomatia*. Biedermann's statement has since been confirmed by the researches of Bierry (9) and others, who find in the digestive fluids of *Helix pomatia* ferments acting on a wide range of carbohydrates, including cellulose and pentoses.

Very little work has been done on true detritus-eating animals, but Dakin (15), working on *Pecten* and Yonge (44) on *Mya*, have failed to find any evidence of the presence of a cytase. The investigation of the liver of *Teredo* by Potts (38) and the chemical work of Dore and Miller (17) on the same animal leave little doubt that *Teredo* can digest the hemicelluloses and celluloses contained in the wood in which it bores, and that it obtains its necessary nutriment thereby.

It is hoped to throw light on this problem by careful feeding experiments, supplemented by further investigation both of the chemical composition of detritus and of the digestive capacities of detritus-eating animals.

#### *Living Organisms as Food.*

The living organisms available as food for the bottom animals range from the bacteria and protista up to large and active invertebrates and fishes. In fact, the whole of the forms studied may serve as food for other forms at some, if not all, stages of their life-history. If, however, any animal be chosen and its food chain traced backwards, the beginning of the chain is inevitably found in the plant-life or its derivative, the detritus. In the region under survey it is the microflora of the sea which is the important ultimate source of all living food matter. In their relation to this source all animals are consumers.

The sea-floor of these areas, which is at an average depth of 27 fathoms and an average distance of about six miles from land, presents a zone of life which, though doubtless dependent on the plankton, is probably self-supporting to a greater extent than might at first be thought. It has its own microflora of bottom diatoms, and though no exact observations have yet been made as to the abundance of the species or of any seasonal variations in their numbers, they have been found in sufficient quantity in the stomachs of various animals to suggest that they constitute a

very important ultimate food factor for the animals of such a region. An abundant microfauna, characteristic of this region, also exists, but except for a few forms such as the Foraminifera has not been systematically studied. The larger forms living on the bottom have, then, a considerable supply of living food produced locally, and to supplement this they have access to the production of the planktonic zone above them, which, especially at certain seasons, pours a copious supply on to the sea-floor.

Examination of the food of those lamellibranchs and ascidians which feed by ciliary currents filtering the layer of water immediately adjacent to the bottom shows that there is normally, in this layer, a content which is quite characteristic. It is peculiarly rich in certain species, such as the diatoms *Paralia sulcata* and *Hyalodiscus stelliger*, and naturally, being the zone in which the substratum mingles with the overlying waters, is marked by a richness of suspended matter and an overlapping of planktonic and bottom-dwelling forms. The systematic investigation of this layer should yield interesting and useful results.

In the stomachs of such animals as the above, moreover, a seasonal fluctuation in the relative proportions of detritic matter and recognizable living food is indicated, and an attempt has been made in the case of *Pecten opercularis* to correlate this with the seasonal variations of the plankton. The accompanying table (p. 566) is a rough graphical representation of the food of *P. opercularis* throughout the year. It is found that at the times of special abundance of particular plankton organisms such abundance is generally reflected in the nature of the stomach contents. Discrepancies occur, but the explanation of these must await an investigation into the seasonal conditions in the bottom layer. During the winter the supply of living nutriment is more limited than at other seasons, and a larger proportion of detritus figures accordingly in the bill of fare.

Such a seasonal fluctuation in the composition of their diet may be an immediate factor concerned in the seasonal variations in growth of many marine animals, as those, for instance, indicated by the growth rings of lamellibranchs; for it seems likely that a rapid growth rate is correlated with a diet rich in living organisms. Jameson, Drummond, and Coward (21) have shown recently that the marine diatom *Nitzschia closterium* synthesizes appreciable quantities of vitamin A, whilst as a result of some feeding experiments with fresh-water gastropods, Popovici-bazosanu (37) states that by far the most rapid rates of growth were obtained by feeding on a diet rich in micro-flora. As bearing on the possible rôle of detritus in this connection one may note the statement by Rockwood and Khorozian (40) that in the case of higher animals (mammalia), when fed on a diet of pentosans mixed with other and more

Food of *Pecten opercularis*.

		1923												1924																
		April		June				July				Sept.		Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May									
		25	14	1	6	14	20	4	18	24	31	6	18	27	8	24	26	14	18	18	28	1	19	12	25	31	24	9		
Analysis of Stomach - contents.	Diatoms.	<i>Paralia sulcata</i> .	—																											
		<i>Hyalodiscus stelliger</i> .	—																											
		<i>Coscinodiscus concinnus</i> .	—																											
		<i>C. radiatus</i> .	—																											
		<i>C. excentricus</i> .	—																											
		<i>C. sp.</i>	—																											
		<i>Biddulphia alternans</i> .	—																											
		<i>B. mobiliensis</i> .	—																											
		<i>B. regia</i> .	—																											
		<i>B. favus</i> .	—																											
	<i>Grammatophora serpentina</i> .	—																												
	<i>Achnanthes undulatus</i> .	—																												
	<i>Rhizosolenia sp.</i>	—																												
	<i>Thalassiosira nordenskiöldii</i>	—																												
	<i>T. gravida</i> .	—																												
	<i>Lauderia borealis</i> .	—																												
	<i>Melosira Westii</i> .	—																												
	<i>Thalassiothrix nitzei</i>	—																												
	<i>Rhabdonema sp.</i>	—																												
	<i>Pleurosigma sp.</i>	—																												
<i>Navicula sp.</i>	—																													
<i>Streptothrix sp.</i>	—																													
<i>Skeletonema sp.</i>	—																													
<i>Ditylum Brightwellii</i> .	—																													
<i>Nitzschia delicatissima</i> .	—																													
Peridinians.	(Unidentified Species)	—																												
	<i>Peridinium pellucidum</i> .	—																												
	<i>P. leonis</i> .	—																												
	<i>P. ovatum</i> .	—																												
	<i>P. apressum</i> .	—																												
	<i>Euviaella perforata</i> .	—																												
	<i>Dinophysis acuta</i> .	—																												
	<i>Phalacrocoma rotundata</i> .	—																												
	<i>P. pulchella</i> .	—																												
	<i>Porocentrum micans</i> .	—																												
<i>Ceratium fusus</i> .	—																													
Miscellaneous.	<i>Foraminifera</i> .	—																												
	<i>Tintinnoides</i> .	—																												
	Algal Cysts & Spores.	—																												
	<i>Coccolithophora sp.</i>	—																												
	<i>Distaplia speculum</i> .	—																												
	<i>Phaeocystis</i>	—																												
	Crustacea (Nauplii, Copepods & Copepod Eggs).	—																												
<i>Mollusca (Larva Bivalves)</i>	—																													
Sand.		—																												
		—																												
Detritus.		—																												
		—																												

— denotes — present in stomach  
 — " — plentiful " "  
 ■ " — abundant " "

digestible carbohydrates, the amount of pentosan absorbed is inversely proportional to the amount of other carbohydrates present.

#### *Useful and Useless Animals.*

One of the objects which the present investigation has had in view is the economic classification of the bottom fauna according to their degree of usefulness or otherwise. For any animal this depends on the ratio between its contribution to the total value of food produced for human consumption and the deduction from a possible total which its own food requirements entail. Some animals are almost entirely contributive, as, for instance, the smaller lamellibranchs and many crustacea and worms. Others, like most of the star-fishes, throw all their weight into the scale of destruction. Many forms both contribute and destroy, e.g. the whelk, *Buccinum undatum*, which furnishes food for the cod and has some value itself as food for man, but is at the same time a great destroyer of fish food in general. An interesting special case is that of *Luidia*, a large star-fish, which, as will be shown later, functions as a contributor by virtue of destroying purely destructive forms.

Before the value of any animal can be assessed it is therefore necessary to obtain information from each area in which it occurs as to the relation between its contributive and destructive potentialities. This requires a careful ecological study of the species, which to be adequate must at least provide a knowledge of its abundance and distribution in space and time in the area, a knowledge of its food and its enemies, quantitative as well as qualitative, and a knowledge of the physiological processes which control the mode and frequency of its feeding. To do this for a large number of animals at once is obviously too great a task, and it is hoped that the present general survey of the food of the bottom fauna will enable a choice to be made of important types suitable for more detailed ecological study.

#### CLASSIFICATION ACCORDING TO FEEDING-METHODS AND DISPOSITION OF FOOD-SUPPLY.

Distinction may be made between those bottom animals which specialize in the capture of active prey and those which do not. The former (including some forms which feed largely on carrion) may be called *Carnivores*: the latter may be separated, according to the location of their food-supply, into two groups: (a) those which feed by selecting from the surrounding water the suspended micro-organisms and detritus, and which, for want of a better term, may be termed *Suspension-feeders*, and (b) those which feed upon the detritus deposited on the bottom, and on

its associated micro-organisms; these may be called *Deposit-feeders*. Each of these three divisions is represented among a wide range of animal groups.

The classification by Blegvad (10) into Herbivores, Carnivores and Detritus-eaters will not fit the circumstances prevailing on the grounds here studied. True Herbivores are entirely absent, and the term Detritus-eaters can only be applied, and then not strictly, to a few limivorous forms. Subdivision into Herbivorous Detritus-eaters and Carnivorous Detritus-eaters is entirely unsatisfactory, as it makes no provision for the large number of forms which feed on a mixture of detritus, small animals and small plants.

### Suspension Feeders.

These animals are either permanently sedentary in habit or, at least, remain in one place when feeding. With the exception of the Holothuroidea they feed by creating currents of water over parts specialized to strain or select from the water its contained small floating particles and organisms. Such currents may be caused by the action of cilia or may be due to the movements of limbs. The Holothuroidea have adhesive tentacles and no current is concerned in their feeding method. Selective power varies to some extent in the different species of suspension-feeders, the main distinctions centring in the average size of the particles and organisms selected. Generally speaking, however, there is great similarity in their food.

The following observations on the food of suspension-feeders are arranged under the headings of the animal groups or classes represented.

### PORIFERA.

All the sponges obtain their food from the currents of water drawn in through the ostia by the action of the collar-cells in the flagellated chambers. Vosmaer (43), Bidder (6), and others have shown that small particles of matter are ingested by the collar-cells, and, in certain cases, handed on to the amoebocytes of the dermal layer. Ingestion by collar-cells can be demonstrated readily by feeding a sponge on carmine. These cells have been examined in hand sections and teased preparations of fresh material in the following sponges, in the hope of finding recognizable traces of the natural food.

Desmacidon fructicosa,	4 specimens,	representing	4 different	hauls.
Ficulina ficus	9	„	„	9 „ hauls.
Cliona celata	3	„	„	3 „ hauls.

Very fine detritus and sometimes minute diatoms were found in the passages and chambers of the sponge, but nothing was seen in the cells beyond unrecognizable granules. This granular material, however, may include very fine particles of detritus, and it seems probable that fine detritus, together with such minute and very perishable organisms as bacteria and the smaller flagellates and ciliates which Allen's (2) plankton-culture method shows to occur in large numbers in ordinary sea-water, form the sources of nourishment of the Porifera in these waters. At the Oxford meeting (1924) of the Society of Experimental Biology, Dr. Bidder expressed the opinion that the majority of ciliates were too large to be eaten by sponges and that the food of the latter consists to a considerable extent of the spermatozoa and naked spores of various animals and plants. He has pointed out (6, pp. 310-313) that the pylocytes, through which all the food of the collar-cells must pass, have a *maximum* diameter of  $13\ \mu$  in *Grantia* and *Sycon*,  $9\ \mu$  in *Clathrina coriacea* and *C. clathrus* and perhaps  $5\ \mu$  in *Cacospongia* and *Carteriospongia*. In their restriction thus to the most minute and finely divided forms of particulate food the sponges stand somewhat apart from the bulk of suspension-feeders.

Various species of *Doris* feed regularly on sponges. Blegvad has found remains of sponges in *Lepidonotus* and *Nereis*, and Rauschenplat (39) has found them in *Littorina*. I have examined the stomachs of *Typton spongicola*, which lives in the cavities and crevices of the sponge *Desmacidon*, and in all cases found them full of the tissues of the sponge.

## ECHINODERMATA.

### CRINOIDEA.

*Antedon bifida*, 30 specimens examined, representing 6 different hauls, 4 from the outer grounds in 27 fathoms, 2 from the Sound in 5 to 7 fathoms.

The tube-feet and ambulacra of *Antedon* are richly provided with cilia. These create currents which conduct food particles from the tips of the extended arms and pinnules, via the ambulacra, to the mouth.

The food consists of a mixture of plankton and detritus. When diatoms are abundant they form the bulk of the stomach contents; similarly peridinians, when plentiful, are well represented. Algal cysts, *Coccolithophora*, silico-flagellates, and tintinnids have been found and the remains of small copepods and crustacean nauplii frequently occur.

So far no animal has been found to feed on *Antedon*. It is rejected by fishes in aquaria.

## DENDROCHIROTE HOLOTHUROIDEA.

*Cucumaria elongata*, 10 specimens, all taken at different times from the same locality.

*Thyone fusus*, 6 specimens representing 5 hauls from 3 different localities.

The feeding methods of holothurians have been described by numerous authors, and an able discussion, with references, is given by Ludwig (26, p. 416).

Both the above species are burrowing forms. When feeding, the anterior end of the animal protrudes from the burrow and the crown of tentacles is widely extended. These tentacles are coated with an adhesive slime, with which floating detritus and plankton come in contact and are held fast. One at a time the tentacles are periodically thrust into the open mouth and immediately withdrawn again, the adherent food particles being wiped off during withdrawal with the aid of one of the two small, bifurcate, ventral tentacles.

The stomach contains a mass of finely divided matter, including sand-grains, detritus, and the remains of small plankton organisms, such as diatoms, peridinians, and the larvæ of crustaceans and molluscs. Bottom diatoms, invariably occur, Foraminifera are frequent, and in one specimen quite coarse bottom material was found. It is possible that the tentacles are used to pick up matter from the bottom, but no attempt at such procedure has been seen in the specimens observed feeding in aquaria. These obtained all their food from the water, and were seen to capture the small larval forms supplied to them. Under natural conditions the water near the bottom is not quiescent as in the aquaria, so that many small particles and organisms would be lifted from the bottom into the range of the tentacles.

Both the above species have been found in the stomach of *Luidia ciliaris*. No other animal is known to feed on them.

## ANNELIDA.

## POLYCHAETA.

Sabellidæ.	<i>Sabella pavonina</i>	4 specimens from 2 localities.
	<i>Chone</i> sp.	12    "    "    5    "
Serpulidæ.	<i>Serpula vermicularis</i>	6    "    "    3    "
	<i>Pomatoceros triqueter</i>	12    "    "    10    "
	<i>Hydroides norvegica</i>	6    "    "    3    "
Chaetopteridæ.	<i>Chaetopterus variopedatus</i>	15    "    "    3    "

The above worms feed by means of ciliary mechanisms which abstract

food particles from the surrounding water. The mechanism of the cryptocephalous forms has been studied by Orton (32); that of Chaetopterus by Joyeux-Laffuie (24).

The food of all is very similar in character, consisting of finely sorted plankton and detritus. The food of Chaetopterus is less finely sorted than that of the others. Diatoms form the chief constituent of the stomach contents, and the species found are for the most part naviculoid bottom forms or bottom-frequenting species. Typical planktonic forms occur in number, however, and when abundant in the sea may form the bulk of the stomach contents. The flagellate Phaeocystis, enormously abundant in spring, has then been found in Chaetopterus, though not in the cryptocephalous worms. Possibly the filtering mechanism of the latter is too delicate to deal with the bulky, gelatinous aggregations of this organism. Peridinians, silico-flagellates, Coccolithophora, Foraminifera, and tintinnids also occur. The detritus found in Chaetopterus is coarser than in the others, and there is generally a quantity of fine sand along with it. This matter is unidentifiable, but it is very like the detritus found suspended in sea-water. In many cases, however, its appearance suggests that it may be partly composed of the remains of living organisms, such as tiny flagellates and ciliates and soft-bodied larval forms too small and delicate to maintain their identity in the stomach.

The writer has found the heads of a sabellid (*Bispira voluticornis*) in the stomachs of *Pleuronectes limanda*. Blegvad (10) states that sabellids are eaten by this fish and by *Aphrodite aculeata*. Todd (42) records them as the food of various Pleuronectidæ, and McIntosh (31) has taken them from stomachs of the cod. Serpulids are eaten, tube and all, by *Echinus esculentus*. Chaetopterus is recorded by McIntosh from the stomach of the haddock.

## MOLLUSCA.

### LAMELLIBRANCHIATA.

Glycimeris glycimeris	16 specimens.	} From bottoms of shell-gravel or gravelly sand.
Pecten varius	2 "	
Lima loscombi	3 "	
Spisula elliptica	9 "	
Lutraria oblonga	4 "	
Dosinia exoleta	12 "	
Venus fasciata	20 "	
Tapes virgineus	5 "	
Gouldia minima	7 "	
Cardium norvegicum	25 "	
Cardium fasciatum	4 "	

LAMELLIBRANCHIATA—*continued.*

<i>Mactra stultorum</i>	14 specimens.	} From bottoms of clean, fine sand.
<i>Lutraria elliptica</i>	12 ,,	
<i>Dosinia lupina</i>	15 ,,	
<i>Venus gallina</i>	25 ,,	
<i>Pecten opercularis</i>	54 specimens.	} From bottoms of silty sand.
<i>Diplodonta rotundata</i>	12 ,,	
<i>Cardium echinatum</i>	3 ,,	
<i>Corbula gibba</i>	11 ,,	
<i>Cultellus pellucidus</i>	30 ,,	
<i>Thyasira flexuosa</i>	4 specimens.	} From bottoms of mud.
<i>Solecurtus antiquatus</i>	6 ,,	
<i>Venus ovata</i>	22 specimens.	} From various bottoms, shell-gravel, sand, and silty sand.
<i>Ensis ensis</i>	16 specimens.	

In the above bivalves the siphons, when present, are either short or fused: the labial palps, when present, are not prehensile. Ciliary currents draw water through the mantle cavity and gill-chambers, where selective ciliary mechanisms on the gills and the palps abstract contained particles and organisms from the water and convey them to the mouth. The manner in which this is brought about has been studied by various workers [Orton (32, 33, 34) and Yonge (44)]. Full references to the literature of this subject are given in the paper by Yonge.

The food consists of a mixture of micro-organisms and detritus. Blegvad (10) is of opinion that in Danish waters lamellibranchs depend entirely on detritus as food. In Plymouth waters this is certainly not the case, for during the whole of the year the proportion of living organisms in the mass found in the stomachs of bivalves is far from being inconsiderable, whilst the proportion of apparently detritic matter, though admittedly high at times, is at others quite insignificant. Moreover, as already pointed out in the case of the annelids, so also in these lamellibranchs the varying appearance of this unidentifiable matter on different occasions leads to the inference that it is composed often not of pure, non-living detritus, but partly of the remains of small and delicate organisms taken alive but rendered unrecognizable by the digestive juices. The unfailing occurrence of bottom, naviculoid diatoms and the frequency of sand-grains, spicules, and bottom-living Foraminifera in the stomachs of these bivalves shows that a good proportion of the suspended matter taken is stirred up from the bottom by disturbance due to tidal or wave action. When sand-grains are numerous in a stomach the proportion

of detritus is correspondingly great, and the organisms present are largely bottom-living forms, but there is no reason to suppose that this preponderance of detritus signifies its value as food any more than the abundance of sand suggests the nutritive value of silica. When plankton organisms such as certain diatoms, peridinians, and the eggs and larvæ of metazoa are abundant in the stomach contents the proportion of sand and detritus is almost invariably smaller. It is not suggested that detritus is without food value; but that, in the case of these suspension-feeding lamellibranchs, the remains of living organisms occur in such marked proportion in the stomach contents that these, and not detritus, are indicated as the main source of nourishment. Diatoms are the most important of these food organisms. Some species, notably *Paralia sulcata*, *Hyalodiscus stelliger*, and naviculoid forms, provide food throughout the year: the more planktonic species are important during their respective seasons of abundance. This is also true of the peridinians, which form a conspicuous item in the stomachs during the summer.

Of the above bivalves *Pecten opercularis* only is marketed for human consumption. Many of the remainder are of great economic value as fish food, especially those, such as *Mactra*, *Spisula*, *Venus*, *Cultellus*, etc., which occur in more or less thickly populated beds. The star-fish *Asterias* makes great inroads upon bivalves of all sizes, while *Astropecten* destroys great numbers of small and young forms. These also fall victims to various carnivorous crustaceans, molluscs, and polychaetes.

## CRUSTACEA.

### CIRRIPEDIA.

<i>Balanus</i> sp.	15 specimens, 2 localities.
<i>Scalpellum vulgare</i>	9    "    2    "

### AMPHIPODA.

*Ampelisca* (various species) 22 specimens, 4 localities.

### DECAPODA.

*Porcellana longicornis* 15 specimens, 3 localities.

The feeding habits of the barnacles are well known, and there are numerous descriptions of the way in which their plumose cirri are rhythmi-

cally protruded to sweep like a casting net through the water, thus capturing plankton and suspended matter. The feeding habits of the amphipod *Ampelisca* are less well known. Various species of this genus are abundant on the Plymouth grounds, where they form an important item of fish food. They range from 5 to 7 fathoms into deep water, and occur on bottoms of shell-gravel, sand, and silty sand. The individuals construct somewhat purse-shaped tubes or pockets of mucus, to which sand adheres. The mouth of the tube is raised slightly above the level of the bottom: the lower end of the tube is closed. When feeding the animal lies with its head and its hinder end both near or just protruding from the opening of the tube, the body being strongly flexed into the form of a **U**, with the back directed downwards. The pleopods are kept in constant motion, driving water out of the tube over the telson. The water driven out is replaced from outside and so a constant current is kept up, entering over the head and mouth parts and directed outwards over the telson. Food particles brought in by the current are seized by the gnathopods and mouth parts, the generally setose character of which is probably useful in straining off and selecting minute particles. The decapod *Porcellana*, which also feeds mainly upon suspended matter, has strongly setose mouth parts, and utilizes a current caused by movement of the third pair of maxillipeds.

The stomach contents of these crustaceans consists of an assortment of detritus and micro-organisms quite comparable to that found in the ciliary feeding suspension-feeders.

*Ampelisca* and *Porcellana* are sought as food by fishes. *Ampelisca* has been taken in plenty from the stomachs of young hake and *Porcellana* from the stomachs of *Trigla lineata*. They are also devoured by many invertebrates, notably the star-fish *Palmipes placenta*, and, in the case of *Ampelisca*, the spider-crab *Macropodia longirostris*. *Balanus* is found often in considerable quantity in the stomach of *Echinus esculentus*.

#### POLYZOA.

*Lepralia foliacea*. Numerous zooids; specimens from 2 localities.

*Cellaria* (various species) ,, ,, ,, ,, 3 ,,

Finely divided suspended matter, small diatoms, silico-flagellates, small peridinians, Coccolithophora, and algal cysts have been noted in the stomach contents of these Polyzoa. I have observed the capture of small flagellates by Polyzoa, and undoubtedly the more perishable protista and, possibly, bacteria, may be added to their food list. Both the above

species are very abundant on the Plymouth grounds, where they must make considerable demands on the amount of suspended food.

These and other Polyzoa are devoured by *Echinus esculentus*. Though direct proof is lacking, it is probable that they also afford food for certain carnivorous molluscs, polychaetes, and flat-worms.

### CHORDATA.

#### TUNICATA.

<i>Ascidia mentula</i>	10 specimens.
<i>Phallusia mammillata</i>	8 „
<i>Ascidiella aspersa</i>	12 „
<i>Ascidiella scabra</i>	23 „
<i>Botryllus</i> sp.	15 „

#### CEPHALOCHORDATA.

<i>Amphioxus lanceolatus</i>	12 specimens.
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The above chordates are typical suspension-feeders. The ciliated pharynx provides a highly efficient selective filter, the nature and details of which are too well known to require description here (Orton, 33).

The content of their stomachs resembles closely that of the suspension-feeding molluscs already detailed. Fig. 2, Pl. II, is from a photograph of the gut of a young *Amphioxus*, 12.5 mm. in length, and illustrates well the typical diet of a suspension-feeder.

*Amphioxus* is a useful fish food. Very few animals have been found feeding on tunicates. An exception is the tectibranch mollusc *Oscanius membranaceus*, the stomach of which has constantly been found full of the remains of tunicates, *Ascidiella* in particular.

### Deposit-feeders.

The feeding methods of the deposit-feeders permit of a broad distinction between two main groups of these animals. The first consists of non-selective feeders that simply ingest the substratum in which they live, deriving their nutriment from the contained living and non-living organic matter: they are, with few exceptions, burrowing forms. The animals of the second group are more selective in their feeding, which they accom-

plish by picking out organic material from the substratum by a variety of prehensile devices. Observations have been made on the following species :—

A. Non-selective feeders.

**ECHINODERMATA.**

HOLOTHUROIDEA.

Holothuria nigra	16 specimens.
Labidoplax (Synapta) digitata	8 „

ECHINOIDEA.

Spatangus purpureus	8 specimens.
Echinocardium flavescens	9 „
Echinocardium pinnatifidum	12 „
Echinocardium cordatum	6 „

Several observers (see Ludwig, **26**, p. 416) have noted that the aspidochirote holothurians and the Synaptidæ feed by shovelling the bottom material into their mouths with their buccal tentacles. Synapta is a burrowing form, occurring in silt and muddy deposits, and the stomachs of the specimens examined have been found to contain a muddy or sandy mass almost identical with the character of the bottom. *Holothuria nigra* occurs where a more varied bottom provides stones and hard objects for the attachment of its suctorial tube-feet. Coarse-textured mud and sand have been found in its alimentary canal.

The heart-urchins have been seen by some observers (MacBride, **28**, p. 552) to collect food and convey it to the mouth by means of the long tube-feet of the anterior ambulacrum. Others (Ludwig, **26**, p. 1299) state that they feed during progression by scooping up the substratum with the projecting lip-like border of the mouth. Their stomachs are invariably full of material according closely with the texture of the bottom where they occur. *Spatangus purpureus*, *Echinocardium flavescens*, and *E. pinnatifidum* are found in coarse, gravelly bottoms and the contents of their stomachs are correspondingly coarser than the material found in *E. cordatum*, which lives in finer deposits of sand and silt.

The star-fish *Luidia ciliaris* preys on adult spatangids. Young specimens are eaten by various crabs and hermit-crabs and by *Astropecten*.

No observation has been made of Holothuria as food. Remains of Synapta have been found in the crab Atelecyclus and once in Cancer.

### ANNELIDA.

#### POLYCHAETA.

Capitellidæ.	Notomastus latericeus	24 specimens.
Scalibregmidæ.	Scalibregma inflatum	20 „
Ariciidæ.	Aricia sp.	8 „
Opheliidæ.	Ammotrypane aulogaster	4 „
Maldanidæ.	(2 species)	12 „

#### GEPHYREA.

Sipunculidæ.	Phascolion strombi	15 specimens.
	Phascolosoma pellucidum	5 „

The above Polychaeta, by means of their soft extrusible probosces, and the Sipunculidæ, by their muscular introverts, swallow the surface layers of the mud or sand which they inhabit. Such feeding has been observed in aquaria and the examinations of stomach contents support the observations.

Fishes feed on these polychaetes, which are also preyed upon by various Crustacea, such as the crabs *Corystes* and *Atelecyclus*, the prawn *Processa canaliculata*, and several species of crangonids. Sipunculids have not been found in the stomach of any animal. Todd records unspecified Gephyrea from the stomachs of cod in the North Sea.

#### B. Selective feeders.

### ECHINODERMATA.

#### OPHIUROIDEA.

<i>Amphiura filiformis</i>	25 specimens.
<i>Ophiactis balli</i>	4 „
<i>Ophiopsila aranea</i>	5 „

In aquaria these ophiuroids may be seen feeding in the substratum in which they lie buried. They push bottom material and detritus along their arms to the mouth by means of their tube-feet. A mixture of sand,

detritus, and small bottom organisms, such as Foraminifera and occasionally young molluses and worms is found in their stomachs, and these brittle-stars seem to exercise but rough selection in picking out detritus or living forms of food.

Amphiura is included in the diet of fishes, chiefly the plaice and the dab. It is also devoured by various Asteroidea, and has been found in the stomach of the burrowing crab *Corystes*.

#### ECHINOIDEA.

*Echinocyamus pusillus* 25 specimens.

This little cake-urchin is plentiful on the Plymouth grounds, occurring in greatest abundance on bottoms of a gravelly nature. Its food consists of a selection of small organisms and detritus particles from among the bottom deposits. Foraminifera, algal cysts and spores, diatoms, copepod eggs, larval molluscs, and crustaceans are found in its stomach, mixed with coarse sand grains, shell fragments, and particles of detritus.

*Echinocyamus* is eaten by plaice and other flat-fish, and Todd (42) has found haddock feeding extensively on it in the North Sea. It is constantly found in the stomachs of star-fishes, crabs, hermit-crabs, and the mollusc *Scaphander*.

#### ANNELIDA.

##### POLYCHAETA.

Terebellidæ.	<i>Thelepus cincinnatus</i>	25 specimens.
	<i>Terebellides strœmi</i>	12 "
	<i>Amphitrite</i> sp.	5 "
	<i>Polymnia nebulosa</i>	8 "
	<i>Nicolea</i> sp.	6 "
Amphictenidæ.	<i>Pectinaria</i> sp.	} 20 "
	<i>Lagis koreni</i>	
Ampharetidæ.	<i>Melinna adriatica</i>	32 "
	<i>Amphicteis gunneri</i>	3 "
Chlorhaemidæ.	(Two species)	12 "
Spionidæ.	<i>Magelona papillicornis</i>	9 "

These worms are either tubicolous or inhabit tube-like burrows. Their external trophic organs are in the form of extensile cephalic tentacles

with which they grope in the surface layer of the bottom deposits and pick up their food. Each tentacle has a longitudinal, ciliated groove, along which detritus particles and small organisms are conveyed to the mouth. Their stomach contents include sandy detritus, diatoms, algal cysts, and spores, Foraminifera, tintinnids, and the larvæ of crustaceans, molluscs, and worms.

These polychaetes are valuable as fish food. *Pectinaria* is recorded by Todd (42) as an important food of the haddock, plaice, and sole; *Thelepus* as food of the plaice and lemon sole. On the Plymouth grounds *Amphitrite* constitutes important plaice food. They are also preyed upon by many carnivorous bottom animals, echinoderms, worms, molluscs, and crustaceans.

### MOLLUSCA.

#### LAMELLIBRANCHIATA.

<i>Syndosmya alba</i>	22 specimens.
<i>Syndosmya prismatica</i>	16 „
<i>Tellina crassa</i>	8 „
<i>Tellina pusilla</i>	11 „
<i>Tellina fabula</i>	4 „
<i>Gari tellinella</i>	12 „

The above species have long, free siphons. Although they probably feed to some extent by drawing in water with suspended matter after the fashion of the short-siphoned bivalves, their usual method is to explore the bottom for food with their long, flexible siphons, sucking up deposited detritus and bottom organisms.

Their stomachs are found to contain a certain amount of sand and detritus; but remains of living organisms—diatoms, protozoa, eggs, and larval forms—are always present in sufficient numbers to suggest considerable selective capacity.

<i>Nucula nitida</i>	29 specimens.
<i>Nucula radiata</i>	„ „
<i>Nucula nucleus</i>	„ „

These protobranchiate bivalves obtain their food by means of long, extrusible appendages of the outer pair of labial palps, with which they sweep the surface of the bottom deposits in the manner described by Drew (18) in the case of *Yoldia limatula*. Selection is not so marked in

this group, the stomach contents always revealing a large proportion of sand and silt.

The lamellibranchs enumerated are all eaten by fishes, especially plaice and other flat-fishes, the more abundant forms, such as *Nucula* and *Syndosmya*, being of great importance in this respect. They also fall a prey to many bottom animals, e.g. star-fishes, crabs, and carnivorous gastropods.

#### GASTROPODA.

<i>Turritella communis</i>	14 specimens.
<i>Aporrhais pes-pellicani</i>	5    ,,

Among the gastropods found on the Plymouth grounds carnivorous forms are most in evidence, but these two species undoubtedly come in the category of deposit-feeders. Their stomach contents always consist of roughly sorted bottom material.

Both species have been taken from the stomachs of *Asterias rubens* and *Astropecten irregularis*.

#### CRUSTACEA.

##### AMPHIPODA.

<i>Eusirus longipes</i>	2 specimens.
<i>Nototropis vedlomensis</i>	25    ,,
<i>Maera othonis</i>	13    ,,
<i>Bathyporeia</i> (var. species)	15    ,,
<i>Monoculodes</i> sp.	4    ,,
<i>Urothœ</i> (var. species)	9    ,,

##### CUMACEA.

<i>Diastylis</i> sp.	21 specimens.
<i>Pseudocuma</i> sp.	5    ,,
<i>Bodotria</i> sp.	3    ,,
<i>Iphincœ</i> sp.	2    ,,
<i>Eudorella</i> sp.	1    ,,

Some of these Crustacea may quite possibly draw upon suspended matter as food, while others probably, to some extent, pursue living

prey, but detailed observation of their habits has not been made, and as their feeding-area seems located in the bottom deposits they have accordingly been placed among the deposit-feeders.

Their food consists of a selection of organic detritus and small organisms. The stomachs of the smaller forms contain detritus, diatoms, algal spores, Foraminifera, peridinians, silico-flagellates, tintinnids, and the eggs of copepods. In the larger forms fragments of copepods and other small crustaceans and remains of larval molluscs and worms have in addition been found. The food is considerably comminuted by the mouth parts before it is taken into the stomach.

Amphipods and Cumacea are of considerable importance as food for fishes, especially for fishes in their young stages. They are also eaten by a variety of carnivorous bottom animals, constituting, for instance, the main food of the star-fish *Palmipes* and of the spider-crab *Macropodia longirostris*.

#### DECAPODA REPTANTIA.

Thalassinidea.	<i>Callianassa subterranea</i> ,	14 specimens.
	<i>Gebia (Upogebia) stellata</i> ,	20 „

*Callianassa* burrows in muddy bottoms and *Gebia* has similar habits with a less restricted range. Nothing but a mixture of sand, mud, and detritus with the usual associated small organisms has been found in the stomachs of the specimens examined, and it seems probable that their place is with the characteristic deposit-feeders. There is no indication of a degree of selection approaching that of carnivorous forms, and although there are records of the remains of polychaetes being found in the stomach of a Thalassinid, *Calocaris* (Blegvad, 10), the fact that the specimens examined here had the alimentary canal always full of bottom material suggests that they rely very largely upon the nutritive value of the bottom deposits.

Both of the above are eaten by fishes, *Gebia* being a very constant food of the plaice on these grounds.

The stomachs of most of the deposit-feeders examined contain at times plentiful remains of plankton organisms which have sunk to the bottom. Similarly the suspension-feeders are found to obtain bottom food organisms which have been stirred up from the bottom. This overlapping results in a frequent similarity between the gastric content of certain deposit-feeders and that of the suspension-feeders. It seems that in

these waters the surface of the sea-floor is in a more or less labile condition, that there is no sharp interface between the sea-floor and the water above it : owing to constant disturbance and mixing the accumulating suspended matter with its admixture of plankton grades continuously into the deposits of the bottom and their accompanying micro-organisms.

### Carnivorous Animals.

These have been defined previously as those animals which prey upon active living forms and in some cases carrion. This definition might include many animals whose mode of nutrition is parasitic, but these are outside the scope of the present paper.

Within this group there is a range from practically omnivorous species, through forms which exhibit respectively varying degrees of selection, to those with a highly specific diet. As might be expected the feeding of carnivorous animals is of a more sporadic nature than that of suspension-feeders or deposit-feeders, and a large proportion of the stomachs examined are found empty. The writer agrees with Petersen and Blegvad that if a species is constantly found with empty stomach the fact affords good indication of a carnivorous diet. To ascertain the actual food, therefore, of many of the carnivorous animals necessitates the examination of a large number of individuals, and where this has not been possible any conclusions drawn must be of a very general kind or open to considerable subsequent modification. With the exception of the Porifera and the Polyzoa all the phyla and larger groups of marine metazoa have representative carnivorous forms. In the present case investigation has been made of the food of the following species.

### COELENTERATA.

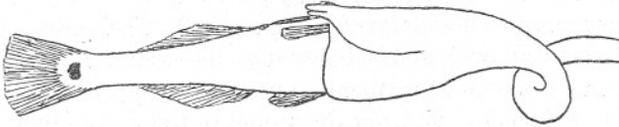
No personal investigation has been made of the stomach contents of coelenterates. There is no doubt, however, as to the carnivorous diet of both sea-anemones and hydroids. In aquaria anemones will capture and eat any animal of suitable size and will feed readily on pieces of dead tissue. Browne (13) has observed the capture of copepods and plankton animals by hydroids in aquaria. Of the food of the Alcyonaria little or nothing is known. Their nematocysts are very small, and it is probable that they feed on minute animals only.

Anemones are occasionally found in the stomachs of cod and other fishes (Todd, 42). They are attacked by some nudibranch molluscs, e.g. *Eolis*. Hydroids have been taken regularly from the stomach of *Echinus esculentus*, and occasionally from the crab *Inachus dorsettensis*. They are

especially the food of various species of nudibranchs, and probably of many of the syllid worms (Allen, 3). Alcyonium is devoured by nudibranchs, particularly by *Tritonia*.

### TURBELLARIA AND NEMERTEA.

The observations recorded by Lang (25) for the polyclad Turbellaria and by Burger (14) for the Nemertea leave little doubt that these animals are true carnivores. The larger nemertines are said to feed on worms, chiefly tubicolous species, the smaller kinds on small crustaceans. Small worms and crustaceans are said to form the main food of those polyclads which are not parasitic. The only personal observation made as to the



TEXT FIG. 1.—Nemertean (*Lineus longissimus*) swallowing a goby (*Gobius ruthensparri*). (After a sketch from life by Dr. J. H. Orton).  $\times 2$ .

food of any of these animals is the finding of the remains of three amphipods (*Ampelisca sp.*) in the stomach of a nemertine, itself taken from the stomach of a crab (*Cancer pagurus*). Dr. Orton has observed *Lineus longissimus* eating a goby (see Text Fig. 1), and the same species eating *Lumbriconereis sp.*

Nemertines are recorded from the stomachs of fish by Todd (42). The writer has found their remains in the stomachs of *Cancer pagurus* and *Aphrodite aculeata*.

### ECHINODERMATA.

#### ASTEROIDEA.

*Asterias rubens*, 426 specimens, from 33 hauls; 6 localities.

*Asterias glacialis*, 151     ,,     ,, 18     ,, 5     ,,

Of the *Asterias rubens* examined 96% were empty. The remainder, 18 in number, included 15 young specimens about 8 cm. across the arms. Molluscan remains occurred in 16, and consisted of small specimens of *Venus*, *Dosinia*, *Mactra*, *Pecten*, *Corbula*, *Cultellus*, *Lutraria*, *Syndosmya*, and, in one instance, *Turritella*. Crustacean remains (small *Portunus*, *Diastylis*, and *Balanus*) were found in 4 examples; the polychaete

Flabelligera occurred in one. All but 5 of the *A. glacialis* examined were empty; 3 contained molluscan remains and 2 crustacean remains.

Despite the meagre evidence from stomach contents general observation confirms the reputation for rapacity so generally accorded these star-fishes. In captivity they capture and consume living prey with avidity, showing preference for molluscs. One individual, about 14 cm. across the arms, was seen to open a large *Cyprina* 12 cm. long. *Asterias* is often taken in numbers devouring the baits of the long-lines set for fishes. Their depredations on oyster-beds are well known, and the writer is informed that when they appear in great numbers on the mollusc-beds, which form feeding-grounds of the plaice, the fishermen forsake such grounds without further delay.

The large percentage of empty stomachs among those examined might be attributed to infrequency of feeding; but, in the case of these star-fishes, the explanation lies in their feeding-method. Their prey is generally too large to be swallowed, and is digested by the extrusion of the stomach over it: remains are therefore found only when the prey is small enough to be swallowed whole. The remains found in these examinations were all of small animals. The star-fishes concerned were all small specimens, the larger *Asterias* being invariably empty.

Blegvad states that *Asterias* is devoured by larger individuals of its own kind and by *Solaster*. At Plymouth it has been taken twice from *Solaster papposus*, and on many occasions from the stomach of *Luidia ciliaris*. Other star-fishes appear to be its only enemies.

*Solaster papposus*, 136 specimens, 20 hauls, 4 localities.

Only 3 of these contained food; 2 contained small *Asterias rubens*, the third a small *Pecten* and an arm of *A. glacialis*.

*Henricia sanguinolenta*, 31 specimens, 17 hauls, 3 localities.

*Porania pulvillus*, 128 „ 15 „ 4 „

The specimens of these two species were empty without exception. Neither could be induced to feed in aquaria. Their natural food therefore remains unknown; but it is reasonable to suppose that they are carnivorous forms feeding in the same way as *Asterias*.

*Palmipes placenta*, 42 specimens, 15 hauls, 4 localities.

This star-fish swallows its prey whole, and recognizable remains were found in 31 of the 42 specimens examined. Crustacean remains (all of species valuable as fish-food) occurred in 30 specimens, and consisted mainly of amphipods and cumaceans with the addition of *Porcellana*

*longicornis*, small Portunus, Ebalia, small hermit-crabs, *Processa canaliculata*, and mysids. Twelve specimens contained remains of echinoderms: these were small ophiuroids, young Echinocardium, *Echinozhamus pusillus*, and in one instance a fragment of *Cucumaria elongata*. Molluscan remains were present in 8 specimens, and were in all cases young bivalves (*Macra*, *Syndosmya*, *Pecten*, and *Cardium*). Efforts to induce Palmipes to feed in aquaria have so far been unsuccessful, and the manner in which it captures active crustacean prey is not known. As many as 10 crustaceans have been found in a single stomach, all in comparatively fresh condition. Figs. 2 and 3, Pl. I, show a specimen of Palmipes which has partially swallowed a prawn (*Processa canaliculata*).

No animal is known to feed on Palmipes.

*Astropecten irregularis*, 125 specimens, 24 hauls, 5 localities.

This voracious species also swallows its prey whole (see Fig. 1, Pl. I). About two-thirds of the specimens examined contained remains of food. Of these, 76 contained molluscan remains, 35 echinoderm remains, 19 crustacean remains, and 3 remains of polychaetes. The list of molluscan remains is of interest, as it shows a close correspondence with the molluscan diet of the plaice. The molluscs found range in size from about 2 mm. to about 15 mm., averaging about 8 mm. The following totals of each species were found:—

	Diplodonta rotundata	77
×	Venus ovata	77
×	Nucula nitida	47
×	Corbula gibba	21
×	Nucula radiata	} 16
×	Nucula nucleus	
×	Dosinia lupina	14
×	Venus gallina	14
×	Tellina sp.	11
×	Cultellus pellucidus	10
×	Syndosmya sp.	8
×	Pecten (small specimens)	4
×	Thracia sp.	3
×	Gari sp.	3
×	Cardium sp.	3
×	Natica sp.	28
	Gastropods (unidentified)	5
	Aporrhais pes-pellicani	1

Those of the above marked × are known as plaice-food, those marked × × are known as important plaice-food.

The echinoderm remains found consist of *Echinocyamus pusillus*, in 65 specimens, young Echinocardium in 7, and small ophiura in 8. The remains of Crustacea include amphipods in 7 specimens, cumaceans in 12, small hermit-crabs in 3, and *Porcellana longicornis* in 2. Polychaete remains are scanty—one occurrence each of *Pectinaria*, *Pomatoceros* (on a small stone), and an undetermined species.

The total number of animals found in the 125 specimens examined was 443, an average of over three per specimen, and as the average wet weight of these food animals was found to be about 0.2 grams each, this gives an average weight of 0.6 grams of food-stuff per specimen. To elicit the rate of digestion two specimens of *Astropecten* were kept under observation and fed on young *Mactra*. The star-fishes swallowed from two to four *Mactra* per meal, and the meals were followed by the rejection of the empty shells within 24 hours. The frequency of feeding has not yet been definitely established; but, from the observations so far made and from the proportion of empty to full stomachs in the specimens examined throughout the year, it may be assumed that one *Astropecten* disposes on an average of .6 grams of food once every three days. The average number of *Astropecten* on the grounds throughout the year, derived from the catches of *Astropecten* made by the S.S. "Salpá" during 1923, is estimated as at least 1 specimen per 100 sq. metres, or 10,000 per sq. kilometre. From the foregoing an approximation may be made as to the amount of food consumed by this species in a given area in a given time. This works out at 730 kilograms per square kilometre per annum, or enough to support 73 kilograms of plaice, a value equal to the average catch of plaice per square kilometre per annum on the North Sea grounds as deduced from figures given by Howell (20).

No animal is known to eat *Astropecten*.

*Luidia ciliaris*, 108 specimens, 20 hauls, 4 localities.

On the Plymouth grounds the diet of this species consists almost entirely of echinoderms. Out of 53 specimens containing remains of food 51 had fed on echinoderms, 32 of these on *Asterias rubens*, 10 on *A. glacialis*, 9 on *Thyone fusus*, 5 on ophiuroids, 3 on *Spatangus purpureus*, 2 on Echinocardium, 1 on 2 small *Echinus esculentus*, and 1 on *Cucumaria elongata*. Molluscan remains (small *Pecten*) were found in 2 specimens.

*Luidia* grows to a large size; it swallows its prey whole, and its mouth-frame can be stretched to admit the entrance of comparatively large animals into its stomach. One (see Fig. 4, Pl. I) was examined which had ingested entire and quite undamaged a *Spatangus* which measured

8.5 cm.  $\times$  7.5 cm., while others contained specimens of *Asterias* as large as 15 cm. across the arms. Two *Thyone* were taken from the stomach of another specimen: one of these was alive and measured 11 cm. in the contracted condition.

Nothing is known to feed on *Luidia*.

#### OPHIUROIDEA.

*Ophiura ciliaris*, 100 specimens, 18 hauls, 4 localities.

*Ophiocoma nigra*, 91 ,, 16 ,, 2 ;

Thirty per cent of the *Ophiura* and 40% of the *Ophiocoma* examined contained remains of food. Remains of polychaetes (*Polynoidæ*, *Pectinaria*, *Maldanidæ*, *Goniada*, *Glycera*, *Spionidæ*, and some undetermined forms), and of small crustaceans (*Amphipods*, the young of various decapods—*Portunus*, pagurids, *Galathea*, *Gebia*, and *Crangon*—*megalopæ*, and other larval forms) were found in the stomach contents of *Ophiura*, with occasionally the fragmented shells of the fry of bivalves (*Cultellus*, *Corbula*, *Syndosmya*), and generally a considerable amount of sand and detritus. The remains found in *Ophiocoma* were similar in character though different species occurred. Crustaceans (*amphipods*, small pagurids, small *Portunus*, and *Porcellana*) were most numerous; polychaetes (*Polynoidæ*, *Maldanidæ*), the crushed shells of bivalve fry, remains of *Echinocyamus*, sand, and detritus were also found. These findings, together with the percentage of empty stomachs, afford conclusive evidence of the carnivorous habits of these ophiuroids, as distinct from the deposit-feeding of the burrowing forms previously mentioned. Blegvad (10), who examined stomach contents of *Ophioglypha* (*Ophiura*) and *Ophiothrix fragilis*, classes these active brittle-stars as carnivorous detritus-eaters with distinctly more predacious habits than *Amphiura*, which he classes as a true detritus-eater.

*Ophiura* is eaten by fish (haddock, dab, and long rough dab): *Ophiocoma* is not recorded as fish food. Both are eaten by carnivorous bottom animals, such as *Asteroidea* and decapod crustaceans.

#### ECHINOIDEA.

*Echinus esculentus*, 20 specimens, 12 hauls, 2 localities.

The alimentary canal of this sea-urchin has always been found filled with a mixture of sand, small stones, and detritus, with numerous frag-

mented animal remains. These consisted of the remains of sedentary and attached species, such as tubicolous worms, polyzoa, hydroids, and barnacles. The most frequently occurring remains were those of serpulid worms (*Pomatoceros*, *Hydroids*, *Filograna*), including the calcareous tubes and various species of *Polyzoa*. Its strong teeth are evidently used for the detachment and mastication of such organisms, which form its chief food, though it undoubtedly takes much of the bottom material into its stomach, and must derive some nourishment from this source alone.

*Echinus esculentus* has been found in the stomach of *Luidia ciliaris*. Those found were very small specimens, and are the only personal record of this sea-urchin as food.

### ANNELIDA.

#### POLYCHAETA.

Aphroditidæ.	<i>Aphrodite aculeata</i>	139 specimens,	20 hauls,	4 localities.
Nereidæ.	<i>Nereis zonata</i>	} 16 specimens,	12 hauls,	4 localities.
	<i>Nereis Dumerilii</i>			
Nephtydidæ.	<i>Nephtys Hombergi</i>	} 50 specimens,	8 localities.	
	<i>Nephtys rubella</i>			
	<i>Nephtys (incisa ?)</i>			
	<i>Nephtys hystericis</i>			
	<i>Nephtys cirrosa</i>			
Glyceridæ.	<i>Goniada maculata</i>	12 specimens,	2 localities.	
	<i>Glycera lapidum</i>	} 36 specimens,	5 localities.	
	<i>Glycera alba</i>			
	<i>Glycera Goesi</i>			
Eunicidæ.	<i>Lumbriconereis impatiens</i>	13 specimens,	4 localities.	
	<i>Onuphis brittanica</i>	2	„	1 locality.
	<i>Hyalinœcia sicula</i>	6	„	2 localities.
	<i>Hyalinœcia tubicola</i>	4	„	2 „

Excepting a small percentage of the following genera, viz. : *Aphrodite*, *Nereis*, *Nephtys*, and *Lumbriconereis*, all these worms were found to have empty stomachs. Remains of food were found in 26 specimens of *Aphrodite*, 2 of *Nereis*, 3 of *Nephtys*, and 1 of *Lumbriconereis*. Of the three last-named genera, however, an insufficient number of specimens was examined to obtain any representative list of their food. In the case of *Aphrodite*, remains of polychaetes were most conspicuous, occurring

in 24 specimens and consisting mainly of terebellids, together with *Pectinaria*, *Lumbriconereis*, *Polynoidæ*, and *Nereidæ*. Crustacean remains (very young crabs and hermit-crabs) were taken from 5 specimens; nemertean remains occurred once only. Two *Nereis zonata* were found with remains of food, 1 containing crushed remains of a small sabellid, the other a small amphipod. *Nephtys hystricis* was twice found containing remains of spionid worms; in *Nephtys Hombergi* remains of *Notomastus* were found on one occasion. Blegvad, who examined larger numbers of these genera and found a greater proportion with stomach contents, states that they feed mainly on smaller worms, small molluscs, and small crustaceans. The large percentage with empty stomachs points to a true carnivorous diet, as does the fact that in all these worms the proboscis is provided with a chitinous armature well adapted for seizing prey.

Most, if not all, of these worms are eaten by fishes. In the diet of some species, e.g. the lemon-dab and the sole, polychaetes are especially prominent. Many bottom animals prey upon them, including star-fishes, brittle-stars, larger specimens of their own kind, crabs, hermit-crabs, and carnivorous gastropods.

### MOLLUSCA.

#### GASTROPODA.

<i>Natica</i> sp.	14 specimens, 2 localities.
<i>Buccinum undatum</i>	58    ,,    4    ,,
<i>Scaphander lignarius</i>	54    ,,    3    ,,
<i>Oscanius membranaceus</i>	36    ,,    2    ,,
<i>Tritonia Hombergi</i>	5    ,,    2    ,,
<i>Archidoris tuberculata</i>	9    ,    3    ,

Here are included the largest and commonest of the gastropods occurring on the trawling grounds: all are strict carnivores. *Natica*, *Buccinum*, and its allies in inshore waters (*Nassa*, *Purpura*, and *Murex*) will eat dead flesh, and are readily attracted to baits of dead fish, etc. Not much information as to their natural food can be obtained from examination of the stomachs of these species, for the flesh of their prey is rasped off with the radula and enters the stomach in a pulpy state. Occasionally, small animals are swallowed more or less intact. This was the case with 5 of the *Buccinum* examined, in which remains were found of *Lumbriconereis*, *Loimia*, *Echinocyamus*, and a young *Eupagurus*. The stomachs of the remainder were mostly empty: some contained slimy, indetermin-

able matter. Buccinum has been seen in an aquarium devouring an opened Mytilus, but whether or how it effected the opening was not observed. Dakin (16) is not convinced that Buccinum ever bores through bivalve shells as might be inferred from some of the literature on the subject and as some related forms certainly do, e.g. Purpura and Murex (Jeffreys, 22). There is some doubt as to the means of boring, whether it is accomplished by means of the radula or whether acid secretions are brought into play. In the case of Natica the latter seems undoubtedly to be the case. Schiemenz (41) states that a disc-shaped glandular organ on the under side of the proboscis in Natica is the boring instrument, and produces an acid secretion which dissolves the shell of its prey. The writer has examined a small Venus which was being attacked by Natica. The circular hole in the Venus shell was not complete, and was concave in cross section with a small prominence in the centre of the hollow, exactly as described by Schiemenz. There is little doubt that the numerous shells of various species of bivalves, found empty and with similar borings, are largely the result of the depredations of Natica. Scaphander lignarius swallows its prey whole, to be broken up by the calcareous plates of its powerful gizzard. Of the 54 specimens examined 35 contained recognizable remains, of which the major portion consisted of the crushed remains of small and young bivalves (*Venus ovata*, *Maetra* sp., *Corbula gibba*, *Cultellus pellucidus*, *Nucula*, and unidentified species). Three large *Dentalium entalis* were found in one specimen; others contained remains of Echinocyamus, small Echinocardium, young Portunus, amphipods, and a terebellid (Polymnia). Jeffreys (22) records Foraminifera, Odostomia, Cylichna, Ditrupa, and Aphrodite, as well as some of the above-mentioned species, from the stomach of Scaphander, and quotes Landsborough as having found specimens whose gullets contained scores of the fry of *Maetra subtruncata*. *Oscanius membranaceus* has only twice been found with an empty stomach. In all the remaining specimens examined the stomachs were packed with the fragmented remains of ascidians, chiefly, as far as could be determined, a species of Ascidiella. *Tritonia Hombergi* was in all five cases found to contain remains of Alcyonium, easily recognizable from the spicules. Similarly, the specimens of *Archidoris tuberculata* in every case contained remains of sponges. There is small doubt that Alcyonium and Sponges are respectively the normal food of these two nudibranchs, which have thus a specific diet. Similar specificity of diet is probably common to the majority of nudibranchs, since various Aeolididæ and Dorididæ found on the trawling grounds have definite associations with certain hydroids, Polyzoa, and sponges.

Plaice and dabs feed on Natica; Scaphander has been taken from the stomachs of rays; Buccinum has not been noted as food on the Plymouth

grounds ; but in the North Sea Todd (42) records it as food of several fishes, including cod, haddock, plaice, dog-fishes, and rays. No records are known of *Oscanius* or *Tritonia* as food ; Todd records *Doris sp.* from the stomach of the lemon-dab.

### CRUSTACEA.

#### DECAPODA NATANTIA.

<i>Typton spongicola</i>	9 specimens.
<i>Alphaeus ruber</i>	14 ..
<i>Processa canaliculata</i>	25 ..
<i>Pandalus montagui</i>	12 ..
<i>Pandalina brevirostris</i>	20 ..
<i>Leander serratus</i>	12 ..
<i>Crangon allmani</i>	31 ..
<i>Philocheras bispinosus</i>	15 ..
<i>Philocheras trispinosus</i>	12 ..
<i>Pontophilus spinosus</i>	25 ..

*Typton* lives in the crevices of the sponge *Desmacidon*, upon which it feeds. The stomachs of all the specimens examined contained sponge tissues and spicules. *Alphaeus* inhabits silty and muddy bottoms, where it lives partly or wholly buried. It devours a considerable quantity of detritus and small organisms, but is not merely a deposit-feeder, remains of polychaetes (*Notomastus*, *Goniada*, *Nephtys*) and of Crustacea (amphipods and Cumacea) having been found in its stomach. The crangonids live, frequently half-buried, on bottoms of sand and silt ; remains of amphipods, mysids, polychaetes, and very young bivalves, also detritus and small bottom organisms, were found in the stomachs of the specimens examined. *Processa* and *Pandalina* are more freely swimming forms, but inhabit similar grounds. Polychaetes (*Thelepus*, *Nephtys*), small crustaceans, and detritus constitute their food. *Pandalus* and *Leander* frequent harder bottoms, where there is a more luxuriant epi-fauna. In addition to small crustaceans and polychaetes, remains of hydroids and polyzoa have been taken from the stomach of *Leander*, while fragments of filamentous algæ occurred in some specimens from an inshore locality. Remains of small fishes (*Gobius*) were found in one specimen. I have seen *Leander* in aquaria catch and devour active specimens of *Crangon vulgaris* that were placed in the same tank.

With the exception of *Typton* all the above species have been recorded as constantly occurring in the food of various fishes. The stomachs of

young hake from the Plymouth grounds are frequently packed with the remains of *Processa*, *Crangon allmani*, *Pontophilus*, *Pandalina*, and *Pandalus*. Among the bottom animals, other and larger decapod Crustacea and cephalopods are their chief enemies.

DECAPODA REPTANTIA.

<i>Galathea nexa</i>	21 specimens.
<i>Munida Rondeletii</i>	5 "
<i>Eupagurus bernhardus</i>	28 "
<i>Eupagurus Prideauxi</i>	37 "
<i>Corystes cassivelaunus</i>	46 "
<i>Portunus depurator</i>	37 "
<i>Atelecyclus septemdentatus</i>	27 "
<i>Gonoplax rhomboides</i>	5 "
<i>Inachus dorsettensis</i>	25 "
<i>Macropodia longirostris</i>	24 "

*Galathea nexa* is a common species on the sandy and gravelly grounds, and is particularly abundant where there is much growth of *Cellaria* or, on the harder bottoms, *Lepralia*. Its food consists of small crustaceans (amphipods, mysids, copepods), small polychaetes (*Terebellidæ*, *Lumbriconereis*, *Glycera*, *Phyllodoceidæ*) and detritus, with *Foraminifera*, diatoms, copepod eggs, peridinians, etc., are also constantly found in its stomach. *Munida* is a larger species, frequenting rougher and harder bottoms. The only recognizable remains, apart from sandy detritus, found in the five specimens examined were the remains of *Aphrodite* in two specimens. *Eupagurus bernhardus* and *E. Prideauxi* feed on small lamelli-branches (*Venus*, *Cultellus*, etc.), echinoderms (*Echinocyamus*, small *Echinocardium*, ophiuroids), crustaceans (amphipods, crangonids, smaller pagurids), and polychaetes (*Polynoidæ*, *Nephtys*, *Goniada*, *Terebellidæ*, *Pectinaria*). Detritus and sand are found in their stomachs, but only in quantity that might have been swallowed along with their prey. The remains of fairly large fishes have been frequently found, probably eaten as carrion derived from the refuse thrown overboard by trawlers. The stomach contents of the burrowing crab *Corystes* show a preponderating diet of small bivalves (*Cultellus* and *Syndosmya* chiefly) and polychaetes (*Pectinaria*, *Nephtys*, etc.). Small crustaceans (*Portunus*, amphipods) are also eaten and echinoderms (*Echinocardium*, *Ophiura*). Only small amounts of sand or detritus occurred in the stomachs. The cleanser-crab, *Portunus depurator*, is the commonest swimming-crab on the Plymouth

grounds. It seems to derive a great deal of its food by scavenging on the refuse rejected by the trawlers, more than 50% of the stomachs examined having been found to contain remains of fish of a larger size than could have been captured by the crab. Small bivalves, crustaceans, polychaetes, and echinoderms are its natural living prey. *Atelecyclus septemdentatus*, though to some extent a scavenger like *Portunus*, was generally found to contain remains of living prey in the form of small bivalves, polychaetes, crustaceans, and ophiuroids. *Gonoplax rhomboides* inhabits muddy bottoms. Polychaete remains (*Lumbriconereis* and unidentified species) were found in three of the five specimens examined. The food of the spider-crab *Inachus dorsettensis* resembles that of the pagurids and of *Portunus* and *Atelecyclus*; fragments of hydroids have also been found in its stomach. *Macropodia longirostris* is much more specific, 80% of those examined having fed on small crustaceans only (chiefly amphipods, but also small *Portunus*, *Galathea*, crangonids, mysids, and *Leander*). The only other food noted was a single occurrence each of cephalopod remains and polychaete bristles.

Fishes, particularly rays, gurnards, and various gadoids, feed on these Crustacea. Other animals which prey on them are cephalopods and larger individuals of their own kind.

#### DISCUSSION.

The carnivorous animals living on the sea-bottom feed upon the animals classified in this paper as suspension-feeders and deposit-feeders, either directly or indirectly through the medium of other carnivores. The food of these suspension-feeders and deposit-feeders in turn is drawn from (a) the plankton, (b) the micro-organisms living on the bottom, and (c) organic detritus, suspended and deposited.

In the area studied planktonic life is very abundant, and extends from surface to bottom. It is the conditions actually at the bottom which are of importance to the bottom animals, and there is no doubt that at this level the plankton is sufficiently abundant to afford a rich contribution to the food of suspension-feeding animals. Moreover, dead and moribund plankton from the upper levels is continuously sinking, to accumulate near the bottom, where it reinforces the living food supply which already exists there. Deposited on the bottom it becomes an available supply for those animals which find their food among the bottom deposits. The results of stomach examinations show that typical planktonic forms occur with regularity, and often in abundance in the stomachs of suspension-feeders and deposit-feeders. These are mostly forms with a protective test of some kind, e.g. diatoms, peridinians, crustaceans, certain eggs,

and spores; and also forms which have indigestible hard parts, such as the bristles of annelids. Many organisms abundant in the plankton, however, are unprotected or exceedingly delicate in structure, e.g. the eggs and larvæ of various worms, molluscs, echinoderms, etc., protista, spermatozoa, and naked spores. These are not found in the stomach examinations, a fact which, from their very perishable nature, is not surprising, and does not detract from the strong presumptive evidence that they, no less than the more durable plankton organisms, *form an important part of the food of bottom animals.*

The result of these investigations indicates also that the micro-organisms living actually on the bottom are of importance as food. The abundance of bottom diatoms and Foraminifera in the stomachs examined is sufficient evidence of this, and, as in the case of the plankton, there must be numbers of more perishable bottom forms which are also valuable as food, though not apparent in the stomach contents.

Organic detritus as a source of food has been given paramount importance by Petersen and Blegvad. Its occurrence in quantity in the stomachs of bottom animals is certainly widespread, and there seems very good reason to assume that it constitutes an important food of many animals, particularly of the limivorous type of deposit-feeder. Investigation of the mixture of organic detritus and remains of living organisms where such constitutes the stomach content leads to the conclusion that, in this region, more importance should be attached to living micro-organisms as a source of food than to the detritus. In Winter, when the plankton and life in general is at a minimum, the proportion of remains of living organisms to detritus in the stomach contents is less than in Summer. This may possibly be correlated with the comparative absence of growth during Winter characteristic of many marine animals.

There is need for a much more intensive study of the microbiology and chemistry of the sea and its bottom deposits than has hitherto been attempted. In open areas such as the Plymouth grounds there is evidence of constant interchange between the sea-floor and the water immediately above it. The special conditions thus resulting at the bottom have so far only been studied indirectly through the food of the bottom animals. More direct observations of these conditions are in course of institution.

A source of difficulty in any consideration of the available food supplies in the sea is the lack of knowledge of the digestive processes in marine animals. This must be remedied before the nutritive value of the food-stuffs can be properly appraised or the potentiality of the various species as consumers be assessed. Intensive ecological study of individual species is demanded before a reliable economic valuation of the bottom fauna can be achieved.

The classification of the bottom animals, according to their mode of feeding and the location of their food-supply, shows very clearly a physiological adaptive radiation in methods of nutrition within the various animal groups. For example, the Echinoderma, Annelida, Mollusca, and Crustacea each have their representative types of carnivores, deposit-feeders and suspension-feeders. The subject presents a field for the study of form, function, environmental influence and other considerations too wide to come within the scope of the present paper.

### SUMMARY.

1. The food of the bottom fauna of the Plymouth fishing-grounds, at an average depth of 27 fathoms, has been investigated. This has been done by the examination of the stomach contents of animals, both fresh and preserved, and supplemented by observation of living animals in aquaria.

2. The sources of food have been discussed. Attention is drawn to the importance in these regions, not so much of organic detritus, which is considered by Petersen and Blegvad to be the only important ultimate supply in Danish waters, but of the contributions from the plankton itself and from the considerable microflora and microfauna inhabiting the bottom deposits.

3. Petersen and Boysen Jensen have stated that the detritus present in Danish waters can be traced almost entirely to the annual decay of the *Zostera* beds. The area occupied by *Zostera* in Plymouth waters is very small in comparison with that in the Danish fjords and the detritus found here, though considerable in quantity, and in appearance much as described by Petersen, must originate largely from other sources. The possible sources of origin apart from land-sources are the coastal Algæ and the plankton. A consideration of the annual production of each of these suggests that the plankton is the more important factor.

4. Blegvad has classified marine animals according to their food into Herbivores, Carnivores, and Detritus-eaters, but this classification does not fit the conditions in the area here studied and is not therefore of general application. Herbivores are absent from these grounds, and few of the animals could be described strictly as detritus-eaters. The animals fall into the following natural groups, according to their food and the mode and location of their feeding:—

- A. *Carnivores*.—Animals which feed mainly upon other animals, either living or as carrion.

- B. *Suspension-feeders*.—Animals which feed by selecting from the surrounding water the suspended micro-organisms and detritus.
- C. *Deposit-feeders*.—Animals which feed upon the detritus deposited on the bottom, together with its associated micro-organisms.
5. Following the preceding classification the food of the common animals of the Plymouth fishing-grounds has been described briefly.

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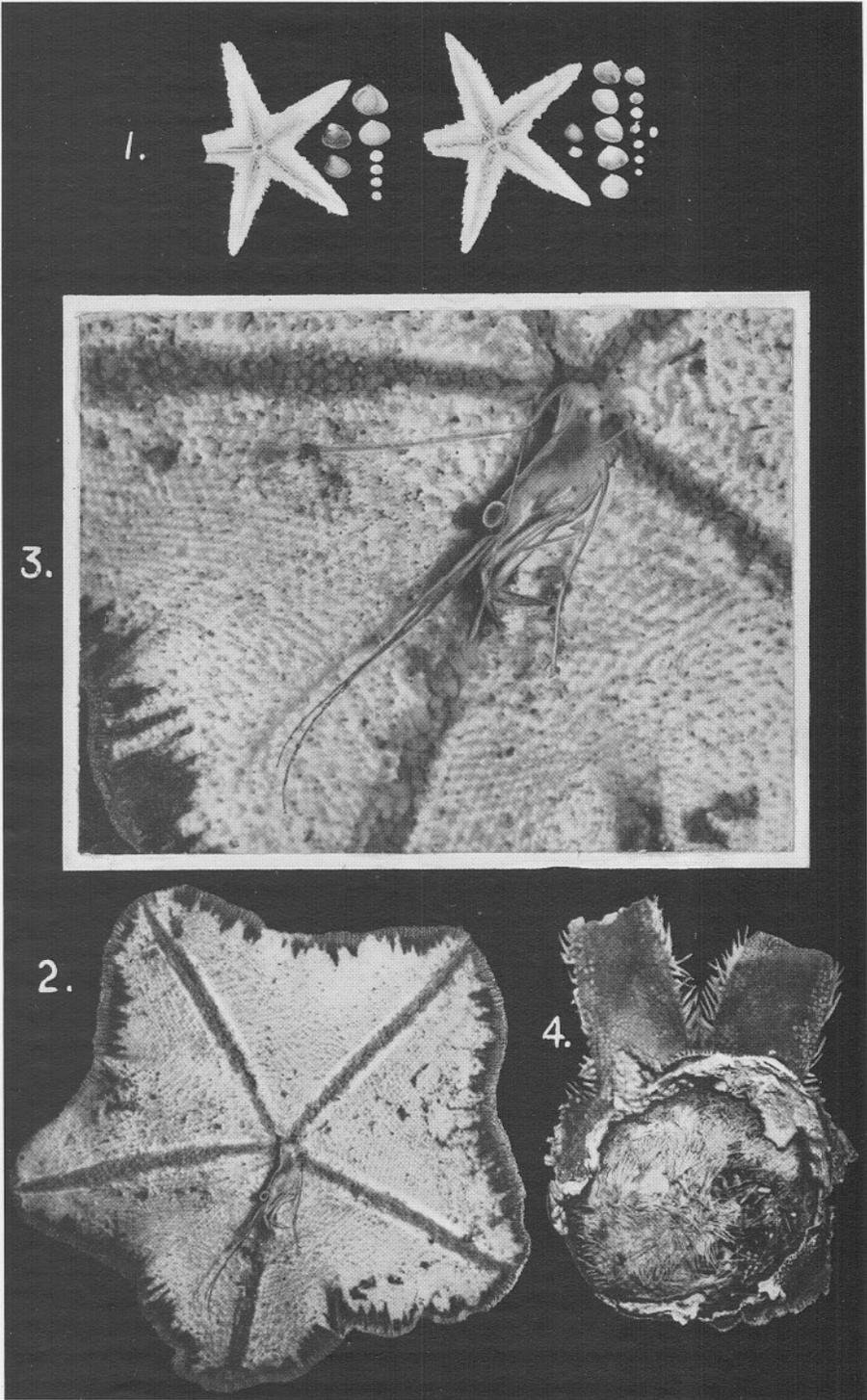


Photo O. D. H

FIGS. 1-4.

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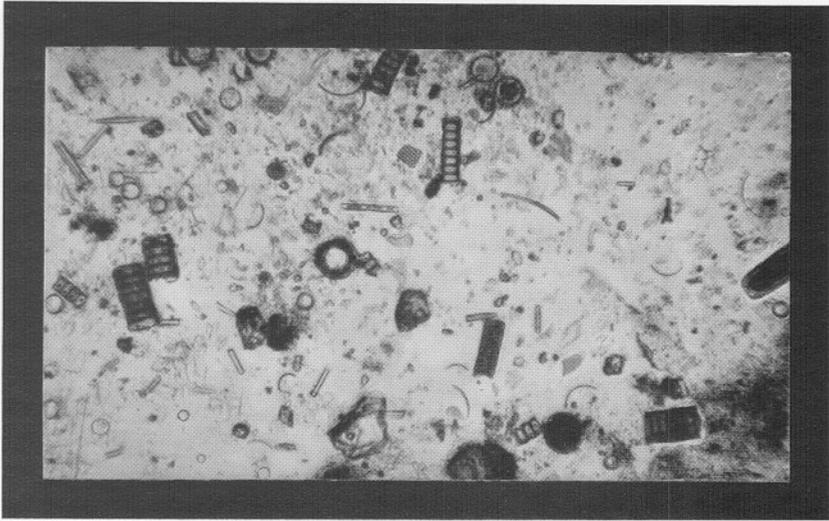
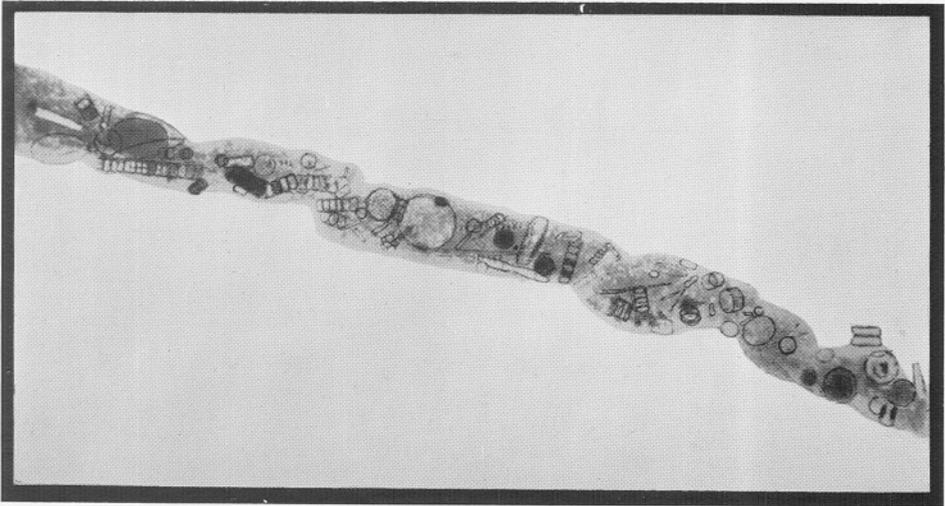


FIG. 1.



*Photo O. D. H.*

FIG. 2.

*To face page 598, to follow Plate I.*



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## EXPLANATION OF PLATES.

## PLATE I.

- FIG. 1.—*Astropecten irregularis*, with contents of stomach (*Venus ovata*, *Nucula radiata*, *Echinocyamus pusillus*). One-third natural size.
- FIG. 2.—*Palmipes placenta*, with partially swallowed prawn (*Processa canaliculata*). Three-quarters natural size.
- FIG. 3.—*Palmipes placenta*, enlarged from Fig. 2.
- FIG. 4.—*Luidia ciliaris*, showing *Spatangus purpureus* in stomach. Two-fifths natural size.

## PLATE II.

- FIG. 1.—Material from stomach of *Pecten opercularis*, showing diatoms (*Paralia sulcata*, *Navicula sp.*).  $\times 125$ .
- FIG. 2.—Portion of Gut of *Amphioxus lanceolatus*, showing contents (diatoms, etc.) in situ.  $\times 125$ .

**Some Marine Ciliates Living in the Laboratory Tanks  
at Plymouth, with a description of a New Species,  
*Holophrya coronata*.**

By

**W. De Morgan.**

With 1 Plate and 32 Figures in the Text.

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THE Ciliates described in this paper were mostly found living in the tanks at the Plymouth Laboratory, which are supplied with a constant circulation of sea-water from two large storage reservoirs. Most of them

came from a large shallow tank standing in front of a south window, which is referred to in the paper as "Drake's Island Tank."

#### HOLOPHRYA OBLONGA (Maupas).

This ciliate was first found by Maupas (20) on rocks at Algiers among algæ and debris, and described by him as a new species in 1883. I first noticed it in February, 1916, in Drake's Island Tank of the Plymouth Marine Laboratory, and in July, 1920, many hundreds of large size appeared round the margin of a basin of dredgings from the New Grounds. In 1922 they were found in stuff consisting of algæ, broken-down vegetation, and excreta in dredgings from Asia Shoal, New Grounds, and Millbay. They were very numerous in July and the beginning of August, but gradually diminished, and were scarce at the end of that month. Probably a few individuals might be found in Drake's Island Tank in any month of the year.

Maupas' specimens were of small size, .3 to .4 mm. in length. Those found at Plymouth range from about .25 mm. to probably 2 mm. in length, and .06 to .1 mm. in breadth. It is difficult to obtain exact measurements of the animal when alive, and at its maximum extension, but I have measured individuals over 1.5 mm. in length, and fixed specimens of 1 mm. are common. Many of these when alive and extended would certainly reach a length of 2 mm. and probably more, as the animal is very extensile.

The smaller size of *Holophrya oblonga* (Fig. 1, p. 603), up to about .5 or .6 mm. in length, and occasionally more, found at Plymouth, agrees exactly with Maupas' description. The body is cylindrical, the anterior end symmetrically rounded, the posterior pointed and, in most cases, drawn out into a transparent tail like prolongation (t).

The body is opaque, but not so opaque as it becomes at later stages, and greyish-brown in colour. Maupas calls it greenish yellow. The variation may be accounted for by difference in food.

At the anterior end is a patch of brownish yellow pigment (p), which sometimes forms a collar; and similar pigment occasionally appears at the posterior end. Small patches of it also are distributed through the body.

The endoplasm contains many spherical globules of various sizes, food vacuoles and granules, all of which render the body opaque. Maupas states that when the endoplasm is quite clear and homogeneous, blackish granules may be observed massed at the extremities, and along the axis of the body. I have frequently observed the black granules (bkp) arranged as described; but they are quite visible when the endoplasm is opaque.

The endoplasm is bounded by a fine pellicle marked by exceedingly

fine striations, only observable under high magnification. Maupas counted ten striæ in a breadth of .01 mm. These striations mark the lines of cilia, which are very short, closely packed, and of the same length throughout the body. They are carried on small papillæ slightly raised above the surface of the pellicle.

With increased growth the appearance of the animal changes (Fig. 2). The brown pigment which was collected at the anterior and posterior ends becomes diffused through the body, the number of vacuoles and granules increases, and the whole body becomes very opaque. The tail-like end portion disappears, although it occasionally persists to a later period, or the posterior end remains pointed. Generally, however, the posterior end becomes obtuse, and is occasionally wider than the anterior end.

The young animal is active, generally in motion, and swims fairly rapidly, moving the posterior part of the body like a fish's tail and revolving on its long axis. The older and larger individuals are very sluggish, and generally lie inert, slowly protruding and retracting the anterior part of the body. When protruded there is a slight narrowing behind the mouth, giving the appearance of a short neck. Although generally contracted, the animal is capable of great extension, sometimes more than doubling itself. It is also very flexible, and twines about easily among gravel, algæ, etc.

The contractile vacuole (cv) is situated at the posterior end, and is generally spherical in shape. Pulsation is about 60 seconds from diastole to diastole; and at the maximum of diastole, the vacuole fills the whole of the posterior end, being bounded by the pellicle only.

Generally only the terminal vacuole appears; but under certain physiological conditions, at present unknown, and when the animal is contracted, a few well-marked lines may be seen on the body. These are parallel to one another, and slightly oblique to the longitudinal axis of the body. Higher magnification resolves them into a number of very small vesicles, which unite and form narrow canals (C.). When the animal extends itself, these canals lie parallel to the longitudinal axis. I have observed as many as six at the same time, but the number is very variable, generally one to four. They arise from the terminal vacuole and extend to a short distance behind the mouth, where it is possible that they may sometimes unite, although I have never observed them to do so.

At certain points they may enlarge into spherical and ovoid vesicles, and so resemble the rose-wreath pattern described by Daday, and which he took to be the nucleus. They appear in the youngest as well as the oldest individuals. The opacity of the endosarc makes them difficult to detect, and Maupas does not appear to have observed them.

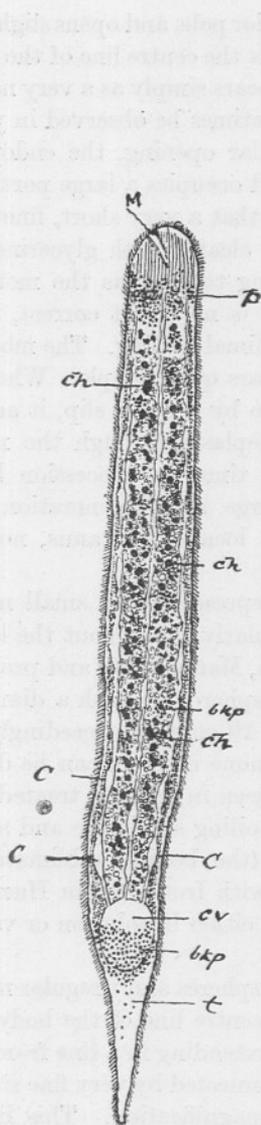


FIG. 1.

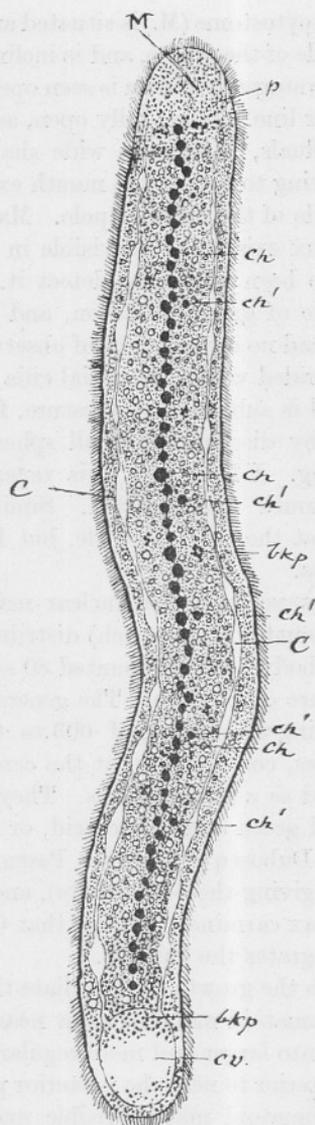


FIG. 2.

FIG. 1.—*Holophrya oblonga*, young form.  $\times 118$ . *M.*, mouth; *cv.*, contractile vacuole; *C.*, canals connected with contractile vacuole; *ch.*, chromatoid masses which later aggregate to form the meganucleus; *p.*, brown pigment granules often-forming a collar; *bkp.*, black granules; *t.*, tail-like extremity.

FIG. 2.—*Holophrya oblonga*, late form.  $\times 118$ . *M.*, mouth; *cv.*, contractile vacuole; *C.*, canals connected with contractile vacuole; *ch.*, chromatoid spheres connected by strands, forming the meganucleus; *ch*<sup>1</sup>, smaller spheres lying outside the meganucleus; *p.*, brown pigment granules; *bkp.*, black granules.

The cytostome (M.) is situated at the anterior pole, and opens slightly to one side of the centre, and is inclined towards the centre line of the body. In late stages it seldom is seen open, and appears simply as a very narrow cleft or line. When fully open, as may sometimes be observed in young individuals, it forms a wide shallow, circular opening, the endoplasm appearing to rise as the mouth expands, and occupies a large portion of one side of the anterior pole. Maupas says that a very short, fine cytopharynx exists, and is visible in specimens cleared with glycerine, but I have been unable to detect it. According to Maupas the mouth is capable of great dilatation, and in this he is no doubt correct, but I have had no opportunity of observing the animal feeding. The mouth is unprovided with any special cilia, and appears quite simple. When the animal is subjected to pressure, for example by a cover slip, it adjusts itself by discharging small spheres of endoplasm through the mouth opening. I have seen this repeated three times in succession before the mouth disintegrated. Similar discharge and regeneration may occur at the posterior pole, but I have not located the anus, nor has Maupas.

*Meganucleus.* The nuclear material is represented by small masses of chromatoid matter (ch) distributed irregularly throughout the length of the body. I have counted 80 such masses, Maupas 100, and probably there are often more. The general form is spheroidal, with a diameter, according to Maupas, of .003 to .005 mm. All contain exceedingly fine granules, concentrated at the centre; but none of them can be distinguished as a micronucleus. They are well seen in animals treated with methyl green and acetic acid, or fixed by boiling sublimate and acetic, Bouin-Duboscq's fluid, or Perenyi's fluid (the boiling sublimate and acetic giving the best results), and stained with Iron alum or Hæmatin, or Borax carmine. I found that Osmic acid either in solution or vapour disintegrates the animals.

With the growth of the ciliate these small spheres and irregular masses of chromatoid material draw nearer to the centre line of the body, and unite into larger and more regular spheres, extending in a line from near the anterior to near the posterior pole and connected by very fine strands of chromatoid matter visible under high magnification. This line of spheres forms the meganucleus. Lying slightly outside the meganucleus are a few smaller spheres (ch<sup>1</sup>). These stain more deeply than the meganuclear spheres, and consist of very minute granules closely packed together. I am unable to detect any connection between them and the meganuclear spheres, and cannot decide whether or not they are to be regarded as micronuclei. There does not appear to be any regularity in their distribution along the line of the meganucleus, nor when division takes place do they divide individually. In one case (Figs. 3 and 4),

where *Holophrya* is dividing in two places ( $H_1H_2$ ), one of these spheres appears at each end of the dividing ribband. These may or may not be micronuclei, and further observation is required to determine whether their position is not accidental. So far, division appears to be purely amitotic.

Division appears to take place at any period of the animal's life, whether

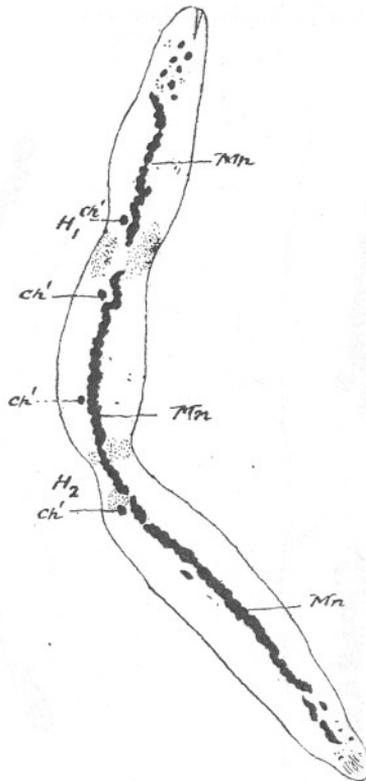


FIG. 3.—*Holophrya oblonga*.  $\times 118$ . Dividing in two places  $H_1 H_2$ . The spherica masses forming the meganucleus have united to form a ribband *Mn*; *ch'*, small spheres lying at ends of dividing ribband.

in the earlier tailed stage, or later, when the line of large spheres has been formed.

Before division the spheres unite to form a ribband (Figs. 3 and 4, *Mn*), and a constriction appears at the point where separation is to take place. I am unable to discover what controls the position of this point. I have more than once observed division taking place at more than one point, and therefore median division cannot be the rule. I have observed similar multiple division in *Dileptus gigas*. As

*Holophrya* is very sensitive to changes in its environment, I was unable to make successful cultures, and had to rely on any individuals that I met with showing signs of division. Although material was abundant, I obtained but few in this condition.

The constriction deepens slowly, and finally the two portions separate. The contractile vacuole appears at the posterior end of the anterior portion before separation, but I did not observe whether the new mouth was formed in the posterior portion before or after that point was reached.

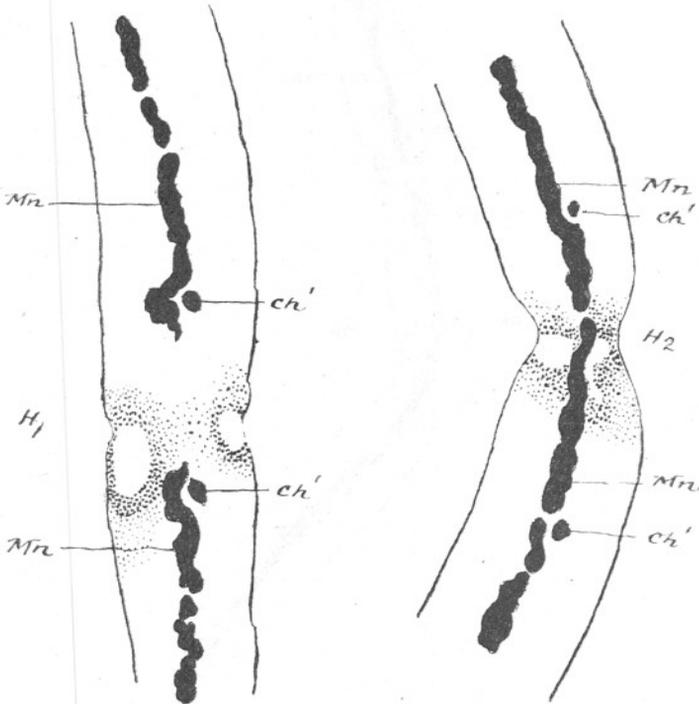


FIG. 4.—The above at points of division.  $\times 300$ .

The nuclear ribband immediately begins to break up into small spheres and irregular masses (Fig. 5) of chromatoid matter.

Maupas observed division in only one case, but was unable to fix and stain it, and so could not study the nucleus. He only saw a median constriction and formation of the contractile vacuole. He thought it probable from previous observations of the nucleus of *Lagynus elongatus*, which consists of dispersed masses of chromatoid matter, which remain quite inert during conjugation and division, that the nuclear behaviour of *Holophrya oblonga* would be similar. My observations of the forma-

tion of a nuclear ribband previous to division show that this is not the case.

I have never seen this ciliate conjugate or encyst, neither has Maupas.

Maupas placed this infusorian in the genus *Holophrya* mainly from considerations of its mouth and general organization. He did not consider the length of the body sufficient to justify the separation of *H. oblonga* from other *Holophryans*. He also points out that the nucleus in unicellular organisms varies greatly in shape and structure, without affecting the general arrangement of the cell body itself, and that therefore the multiplication of nuclear elements in *H. oblonga* does not afford ground for placing it in a separate genus.

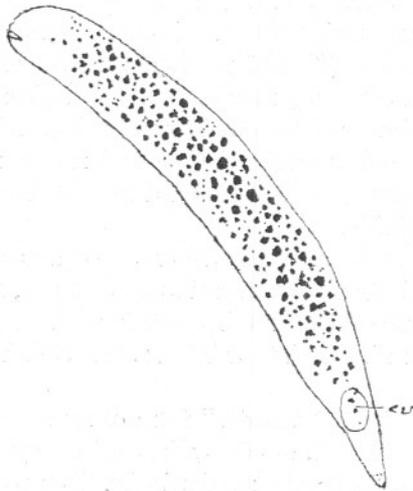


FIG. 5.—*Holophrya oblonga*, product shortly after division.  $\times 260$ . The nuclear ribband has already broken up.

In 1886 Daday (7) found in the Bay of Naples, among algæ and bryozoa, a ciliate which he described as a new species under the name of *Holophrya maxima*. He compared it with Maupas' *Holophrya oblonga*, which he considered it to resemble in every respect, except:—

(1) Size; (2) the possession of a tail-like appendage; (3) the character of the nucleus; (4) ciliation.

(1) Maupas' *H. oblonga* measured .3 to .4 mm. in length, Daday's *H. maxima* .7 to .9 mm., and on account of this superiority in length gave it the specific name. It has already been pointed out that Maupas saw only small specimens of *H. oblonga*, which actually reaches a much greater length than Daday has recorded of *H. maxima*.

(2) The tail-like appendage, which is a drawn-out portion of the

posterior ectosarc, has been shown above to be generally present in the earlier stages of *H. oblonga*, and occasionally to appear in later and larger individuals. Its occurrence is extremely variable, and it can hardly be regarded as a specific difference.

(3) Daday describes the nucleus as the most interesting peculiarity of the animal, being very different from the nucleus of the genus *Holophrya*, and reminding him of that of the Stentors. According to him, it consists of a number of masses of nuclear matter connected chainwise. Two of these masses (Pl. I, Fig. 6  $N_1N_2$ ) just below the anterior end differ from the others in being round instead of oval, one of the two is larger than the other, and they are close together. It differs from that of Stentor, in that it forms a wreath instead of a chain. This nucleus he describes as colourless, and he was unable to find in it either granular masses (Klumpchen) or nuclear bodies (Kernkörperchen); moreover, the presence of many granules and colouring matter in the endoplasm, combined with the fact that the animal is extraordinarily sensitive, and the use of almost all reagents is impossible, rendered observation extremely difficult. It was only accidentally that he succeeded in staining the nucleus and making it faintly visible.

Daday does not state what reagents he used, but as already stated, *Holophrya oblonga*, both the small and large varieties, fixes readily in all reagents except osmic acid, and stains equally well. Perhaps Daday used osmic acid, but I am inclined to think that his staining was attempted *intra vitam*.

He also states that the "wreath" form of nucleus was present only in the older forms of his *H. maxima*; in earlier or younger individuals it consisted of a more or less oval, median body. It appears to me probable that what Daday believed to be the nucleus, was the system of canals connected with the contractile vacuole (see Figs. 1 and 2, C.). A comparison with Daday's Fig. 6 at once shows the resemblance. I have not seen a case in which the canals actually joined anteriorly; but I have seen vesicles connected with the canals below the anterior pole, and the form of the canals is so variable that it is quite possible that the arrangement as drawn by Daday might occur, and also that he missed noticing the connection of the canals with the terminal vacuole.

(4) Daday states that the cilia of *H. maxima* are not scattered, but arranged in eight equally distant rows (Ci) parallel to the longitudinal axis of the body, while those of *H. oblonga* are probably equally distributed over the whole of the body. The cilia of *H. oblonga* are certainly arranged in close parallel rows over all the body, and are very fine and short, but I think that Daday mistook the lines which appear when the canals described in *H. oblonga* are at their minimum diameter for lines bearing

cilia. Among the number of close-packed striations, it would be difficult to discriminate a line which did not bear cilia, and it required very close observation of many individuals under various conditions to decide that the lines are really particular phases in the formation of the canals.

Moreover, the possession of only eight rows of cilia would be a remarkable variation to occur in the genus *Holophrya*.

Daday concludes by saying that he does not exclude the possibility that *H. maxima* and *H. oblonga* may be forms of the same species at different stages of development, in which case he would consider the form with a single median nucleus to be the first larval stage, while his *H. maxima* would represent the fully developed form, and Maupas' *H. oblonga* an intermediate stage.

I have never either in living or fixed and stained specimens seen anything that could be regarded as a median oval nucleus, and I think it probable that Daday may have observed an animal in which the canals had joined together on one side to form a large spherical vacuole, which I have frequently seen to happen. The "wreath" form of canal would then, of course, disappear.

I think, therefore, that it is justifiable to conclude from the above considerations that Maupas' *H. oblonga* and Daday's *H. maxima* are one and the same species of *Holophrya*.

#### HOLOPHRYA CORONATA SP. NOV.

I first found this ciliate in 1914 in Drake's Island Tank, and subsequently in dredgings from Asia Shoal, New Ground, and Millbay. It is fairly numerous from May to September, and most abundant in August; probably a few specimens might be found at any time during the year. In general appearance and habits it closely resembles *Holophrya oblonga*, with which species it is often found in company, but differs completely from it in the shape of the cytostome and the nucleus.

Resting individuals measure .4 to .6 mm. in length and .06 to .08 mm. in breadth. The largest individual I have measured was 1.45 mm. in length expanded. Like *Holophrya oblonga* it is very sluggish, generally lying under sand and small pebbles, or among debris of algæ, excreta, etc., and moving its head slowly from side to side. It swims slowly, with an undulating movement, revolving on its axis. The body is very flexible, and capable of great extension. It is usually cylindrical, but when greatly expanded becomes flat and tape-like, with flattened spaces, alternating sometimes with cylindrical nodes, as is also seen in the case of *Trachelocerca phœnicopterus*.

The body is very opaque and usually full of food, food vacuoles, granules and small spheres, which are sometimes refringent. The colour

is a greyish brown, and the anterior portion of the body is generally darker than the rest, possibly due to a concentration of granules, when the animal is contracted. The colour generally is very similar to that of *H. oblonga*, and occasionally there are a few small scattered masses of yellowish pigment (pg).

The body is surrounded with a very fine pellicle, which shows as a clear margin round the endoplasm. The whole body is covered with fine, short, closely packed cilia, which show as longitudinal striations. Each cilium, as is the case with *Holophrya oblonga*, stands on a small papilla, but the striations are not so close together as in that species, in which Maupas counted 10 in .01 mm.; and it does not require so high a magnification to detect them. The cilia are all of the same length.

In resting or slightly expanded individuals the anterior end of the body is rather flattened; it then curves away with slightly diminished diameter for a short distance, which may be regarded as a neck, and then expands again up to the posterior pole, which is very variable in shape, being sometimes larger than the anterior pole, sometimes obtusely rounded, but rarely pointed, and I have never seen an instance of the tail-like termination so general in early forms of *Holophrya oblonga*. When fully expanded the anterior end forms a regular curve, the margin of the mouth extending very slightly beyond the margin of the body. In Pl. I, Fig. 7 the anterior end of the body represents the fully expanded form, while the remainder is the resting form. When expanded there is little difference in the diameter of the body throughout, except in the neck region which is always slightly narrower.

The contractile vacuole is situated at the posterior pole, generally of

#### EXPLANATION OF PLATE I.

FIG. 6.—*Holophrya maxima*, after Daday. *Ci.*, rows of cilia; *N.*, wreath-shaped nucleus; *p.*, pigment forming collar at anterior end.

FIG. 7.—*Holophrya coronata*. *Cys.*, cytostome; *Cyp.*, cytopharynx with supporting rods; *MN.*, meganuclear masses; *MiN.*, possible micronuclei; *pg.*, pigment granules; *cv.*, contractile vacuole.

FIG. 13.—*Conchophthirus mytili*, dividing. References the same as Fig. 12.  $\times 260$ .

FIG. 20.—*Prorodon marinus*. *MN.*, meganucleus; *MiN.*, micronuclei; *Cyp.*, cytopharynx with rods *Ci.*, lines of cilia and supposed transverse striations; *Cry.*, crystalloid bodies; *Cv.*, contractile vacuole; *Cvv.*, vesicles from contractile vacuole.

FIG. 24.—*Frontonia fusca*. Ventral view. *g.*, granular mass; *MN.*, meganucleus; *MiN.*, micronucleus; *cys.*, cytostome; *psg.*, peristomial furrow; *cv.*, contractile vacuole.





large size, and sometimes occupies the whole of the body space, being only separated from the exterior by the pellicle. I have never detected any trace of the canal system of vacuoles, so prominent in *Holophrya oblonga*; but I have occasionally seen the contractile vacuole divided into two nearly equal portions and occupying the opposite angles of the truncated posterior pole.

The cytostome (Cys) (Pl. I, Fig. 7) is situated in the middle of the anterior pole. It is a circular orifice, which leads into a cytopharynx (Cyp), which sometimes extends a considerable distance into the endoplasm. The upper portion of the cytopharynx is provided with a supporting apparatus of very fine rods. The cytostome is surrounded by a series of concentric ciliated circles. I have counted eleven such circles, but the number is probably variable. Each circle carries a row of short closely packed cilia based on small papillæ, and in every respect similar to the cilia disposed longitudinally over the body. It is only when the anterior end is fully protruded that these circles are all visible. When the ciliate is resting, as before stated, the anterior end of the mouth is not extruded, and the surface is flat, consequently only the outer circle and one other is visible. The spaces between the ciliated circles are highly refringent.

The outermost circle surrounding the cytostome sometimes appears studded with very minute clear papillæ. I have never been able to resolve these satisfactorily, but think that they are the result of the cilia "bunching together," as may sometimes be seen in many ciliates.

*H. coronata* feeds principally on diatoms, which often appear in the endoplasm and food vacuoles, and probably also on bacteria, which are frequently found in masses round its body. The cytopharynx is large enough to admit a considerable bulk, but there is no apparatus for capturing prey, nor is the action of the cilia round the cytostome sufficiently powerful to draw in anything except the smallest particles. It is possible that *H. coronata* forces itself over its food as do some ciliates, e.g. *Frontonia*.

Trichocysts are present, but not in great numbers. They consist of needle-shaped rods, of a maximum length of .02 mm., and occur mostly at the anterior and posterior poles.

The meganucleus (MN) consists of masses of chromatoid matter, generally spindle-shaped and connected by strands. They are irregularly distributed through the body from just above the contractile vacuole to near the level of the base of the cytopharynx, when the animal is extended; when contracted or after fixation they are concentrated towards the centre. When the body is not too opaque in the live animal they may be seen as clear spaces.

*H. coronata* fixes well with boiling corrosive sublimate and acetic,

Bouin solution or Perenyi's fluid, and stains with Iron Hæmatoxylin, and Borax carmine. Boiling sublimate-acetic and Iron Hæmatoxylin give the best results. Scattered throughout the endoplasm are numerous deeply staining granules, surrounded by a clear space. These may be micronuclei (MiN), but I have so far failed to follow them through division. I have only seen division in two cases, as I have been unable to make successful cultures of this ciliate.

Division, as I have observed it, is rather a slow process. The meganuclear masses unite to form a long flattened ribband (Fig. 8), that

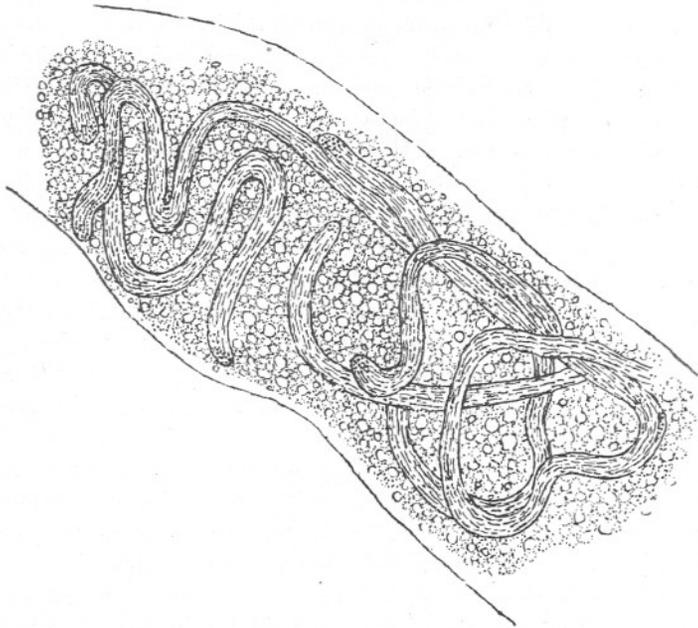


FIG. 8.—*Holophrya coronata*. Portion of nuclear ribband before division, showing parallel lines of linear chromatoid matter.  $\times 300$ . Camera lucida. From specimen fixed corrosive acetic, stained Borax carmine.

sometimes passes round and occupies nearly the whole of the interior of the body. It consists of linear portions of chromatoid matter lying nearly parallel to one another, and of various lengths. Under high magnification these may in many cases be resolved into granules.

A constriction in the body then appears and the two parts finally separate; the ribband immediately breaking up again into irregular masses. While division was in progress I saw no trace of formation of cytostome or cytopharynx, nor of the circles of cilia round the cytostome. The contractile vacuole, however, was formed in the anterior product, as was the case in *H. oblonga*.

I have observed conjugation in three instances. The animals are in conjunction at the anterior poles (Fig. 9), and a very fine pellicle appears to arise and surround the united surfaces. The nuclear matter consists of spindle-shaped masses, similar in each individual.

I do not know how long the animals had been in conjunction before I found them, and so cannot tell what nuclear transfer, if any, occurred. In another instance I waited until the animals separated, and then fixed them. The nucleus in each consisted of the spindle-shaped masses generally forming the meganucleus.

It is, of course, possible that there may be no transfer of nuclear material during union. (See Minchin, 21, p. 128.)

"In many cases union of distinct individuals can be observed which have nothing to do with syngamy, since no fusion takes place of nuclei,

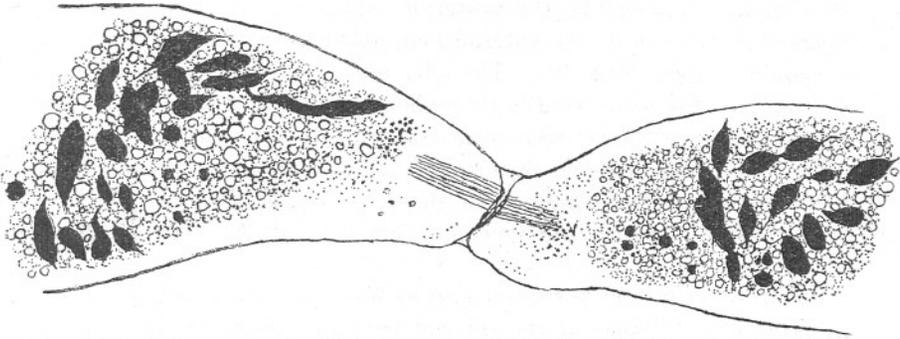


FIG. 9.—*Holophrya coronata*. Conjugation.  $\times 300$ . Camera lucida. From specimen fixed corrosive acetic, stained Borax carmine.

but only of cytoplasm. Such unions are distinguished as plasmogamy, or plastogamy from true syngamy. Plasmogamic union may be temporary or permanent; in the latter case it leads to the formation of Plasmodia, as in the Mycetozoa. The significance of plasmogamy is obscure in many cases."

The three cases of conjunction I observed occurred in the month of September. If they were cases of true syngamy, they might be cases of invigoration previous to encystment (Minchin, p. 140): I do not know whether the animals encyst or not, but they are certainly very rare in winter.

I am unable to find any description of any ciliate resembling this one, excepting Maupas' *Holophrya oblonga*, and believe that it is hitherto undescribed. The reasons for which Maupas placed *H. oblonga* in the genus *Holophrya* are certainly valid for the ciliate just described, and I have provisionally called it *Holophrya coronata*.

## PORPOSTOMUM NOTATUM (Möbius).

Described as a new species from Kiel Harbour by Möbius (22), where he found it among Oscillatoria in February and March. Buddenbrock (2, p. 353) reviewed Möbius' description, from which he differs on certain points, particularly on the structure of the mouth. Buddenbrock obtained his specimens from the Berlin Aquarium.

A few specimens are obtainable from Drake's Island Tank in any month of the year. In 1914 and 1916 they were present in extraordinary quantities in February and March. In 1922 in those months there were comparatively few.

In most particulars my own observations agree with those of Möbius and Buddenbrock. The body is about .2 mm. long, and the length about 4 times the breadth. The anterior end is generally pointed, but occasionally rounded like the posterior, which is always rounded. It tapers slightly towards the anterior end, and may be roughly described as spindle shaped (Fig. 10). The cilia are closely set in longitudinal rows and of the same length throughout. High magnifications show close transverse striæ between them as described in *Prorodon marinus*.

The contractile vacuole is terminal, and Buddenbrock states that there are two afferent canals; but these I have not observed. Möbius states that the contractile vacuole contracts at intervals of 3 or 4 minutes.

Möbius describes the peristome area as somewhat depressed and carrying pectinellæ. It rises at the anterior pole, runs along the left ventral side, and in the middle of the body turns to the right into the cytostome, in which lie two long movable sickle-shaped lips. The gullet is funnel-shaped, and bent towards the left side. On the left side near the cytopharynx in the ectosarc is a dark speck, slightly concave to the exterior and conical towards the interior. It is surrounded by radially arranged light-refracting rods.

Buddenbrock considers that Möbius is entirely wrong in his observation of this part of Porpostomum, and writes as follows:—

“From the anterior end for about the first third of the body runs a small Peristomefield, gradually widening posteriorly. In its hinder portion it bends slightly towards the left of the mid-line. On the left peristome margin is a pretty thick mane of cilia (Wimpermähne), which probably is composed of pectinellæ, but I have not been able to decide the facts with accuracy. From the peristome, food passes into the S-shaped cytopharynx, of which the commencement, the first curve of the S, forms a pigmented sac. (Möbius speaks of a speck of pigment lying to the left of the cytopharynx.) Actually, the object in question is

a deep bag, of which the sides and bottom are covered with a dark, finely granular substance. Under even low magnification this dark mass appears as a dark outline concave anteriorly, and affords a very characteristic mark.

“From the pigmented sac the cytopharynx extends sharply forward to the right, and then turns sharply backwards. The last section is generally

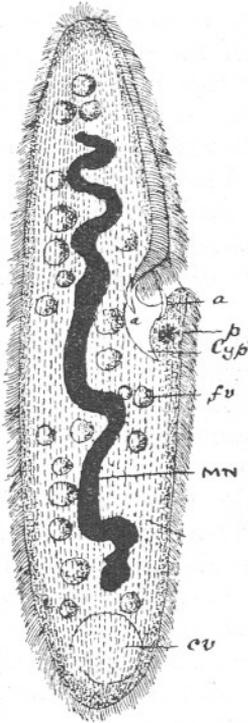


FIG. 10.

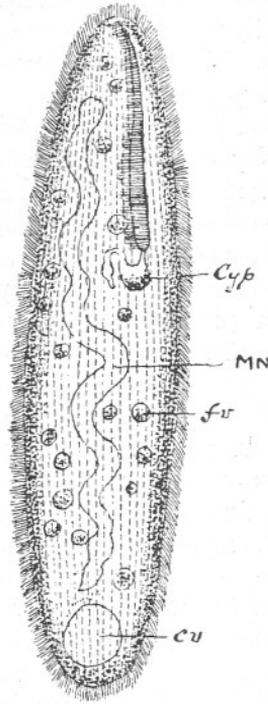


FIG. 11.

FIG. 10.—*Porpostomum notatum* after Möbius. *MN.*, meganucleus; *Cyp.*, cytopharynx *a<sub>1</sub>a<sub>1</sub>*, sickle-shaped lips; *p.*, pigment speck and sickle-shaped rods; *fv.*, food vacuoles; *cv.*, contractile vacuole.

FIG. 11.—*Porpostomum notatum*, after Buddenbrock. *MN.*, meganucleus; *Cyp.*, cytopharynx; *fv.*, food vacuole; *cv.*, contractile vacuole.

slightly protuberant. In most cases I found the cytopharynx full of a yellow fluid, which presumably is genetically connected with the pigment. On the significance of either I cannot express a decided opinion.

“To conclude, on whichever side the animal lies, one sees the two curves of the S-shaped cytopharynx in very different positions with reference to one another.

"The cytopharynx is evidently contractile; it frequently changes its shape under the observer's eye, and occasionally the contained yellow fluid is seen to shift from side to side. Perhaps this motion led Möbius to the belief that 'two sickle-shaped, movable lips lie in the mouth.'"

My own observations confirm those of Buddenbrock. The general arrangement of the cytopharynx appears to be exactly as he describes it; but I have not seen the yellowish fluid, which he states that it generally contains. Neither am I prepared to state that it is contractile. The granular pigmented matter contained in the sac is evidently Möbius' pigmented speck lying to the left of the gullet, which he says is surrounded by radially arranged light-refracting rods. I have occasionally observed such rods near the pigmented granules, but outside of the sac; and such rods are occasionally present in other regions of the body. Occasionally fixed and stained preparations afford a view of the cytopharynx, which bears out Buddenbrock's interpretation.

The meganucleus usually appears as a ribband, lying longitudinally, and sometimes spirally twisted. Before division it generally forms a straight band, and the animal divides by median transverse division. The nuclear matter in the two products assumes a spherical or ribband shape. The nuclear matter sometimes appears as spherical or irregular-shaped masses, lying separate or connected by strands, and these become united to form a ribband as the time for division approaches. I have observed four spherical deeply staining masses which may be micronuclei; but have so far been unable to follow out the nuclear changes leading up to division. Möbius observed division, and that at the time of separation the hinder division product possesses neither mouth, black pigment speck, nor mane of cilia along the peristomial groove. This my own observations both on living and fixed preparations confirm (Fig. 11, p. 615). Möbius further noted the development of the peristomial groove and mane of cilia.

Conjugation I have not observed, nor do Möbius or Buddenbrock refer to it.

The ectoplasm is very clear and contains few granules, but the endoplasm contains many deeply staining food vacuoles.

*Porpostomum notatum* is but slightly contractile, and undergoes little deformation when fixed. It swims rapidly, with a fish-like movement of the tail.

#### CONCHOPHIRUS MYTILI SP. NOV ?

Found in the mantle cavity of the common salt-water mussel. In all my observations I have found it in company with *Ancistrum mytili*.

In shape (Fig. 12) it forms an irregular oval. The dorsal surface is convex, the ventral in the peristomial region, concave. The anterior end is slightly narrower than the posterior, and viewed dorsally the left anterior angle forms a rounded lobe. The thickness is about the same throughout. The posterior margin forms an even curve. Length, .15 to .14 mm.; greatest breadth, .08 to .11 mm. About midway on the ventral margin a deep groove commences, leading to a fossa in the anterior third of the body. This is the cytopharynx (Cyp) which reaches to a depth of rather less than  $\frac{1}{3}$  of the body width. The depth of the cytopharynx appears constant, and I have never observed any extension of it further into the endoplasm. It is lined with long cilia. When a sufficient quantity of food, such as small algæ, etc., is collected at the

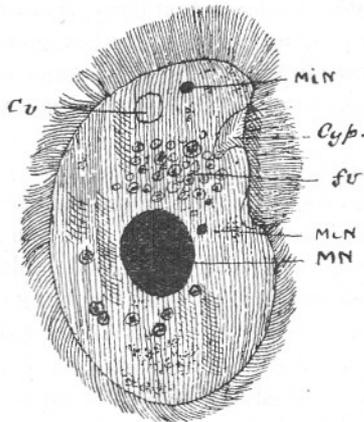


FIG. 12.—*Conchoptirus mytili*. MN., meganucleus; MiN., micronucleus; Cyp., cytopharynx; fv., food vacuole; cv., contractile vacuole.  $\times 260$ .

base of the cytopharynx, these cilia may be seen beating in slow, regular strokes, and so pressing the food against the base of the cytopharynx, until the ectoplasm is ruptured, and the food disappears within the endoplasm.

The body is surrounded with a thick pellicle, as is often the case among parasitic ciliates. Under the action of methyl green and acetic the pellicle expands away from the cytoplasm of the body, and is seen to be covered with close set striations, which mark the position of the fairly long, fine cilia with which the body is covered. Along the right margin of the peristomial groove is a row of very closely set, fine, long cilia. When at rest, and under a low power, these appear like an undulating membrane. This, under a high power, is resolved into its component cilia. By these cilia food particles are swept into the cytopharynx, and thence pressed into the cytoplasm, as noticed above. The cilia at

the anterior end are much longer than those covering the rest of the body; nearly as long, in fact, as those along the peristomial margin. When the animal is at rest, the anterior cilia lie erect and rigid, while those along the posterior margin continue in rapid motion. This recalls the behaviour of *Ancistrum mytili* under similar circumstances. There are numerous food vacuoles, sometimes collected at the base of the cytopharynx, sometimes arranged round the nucleus, sometimes completely filling the posterior half of the body.

The contractile vacuole is at the anterior end; I have never seen it in any other position. It is spherical in shape and occasionally breaks up into a few smaller spheres, but I have never seen any canal formation. It functions at a varying rate: from forty to sixty seconds between diastole and systole.

The meganucleus (MN) is a large oval body, occupying a nearly central position. It is visible as a clear space in the living animal. There appear to be two micronuclei (MiN). Division is transverse. Each product of the division contains a spherical meganucleus and two micronuclei. (See Pl. I, Fig. 13.)

There do not appear to be any trichocysts.

Conchopthirus is persistent in shape, possessing hardly any contractility or elasticity. It moves about fairly rapidly on the surface on which it is resting, and by means of its cilia has considerable power of cohesion. It occasionally takes short, jerky flights, revolving on its axis.

Engelmann (11) describes two species of Conchopthirus, *C. curtus* and *C. anodontæ*, both found in the fresh-water mussel *Anodon*. They both resemble the Conchopthirus of the salt-water mussel in many respects, but differ in certain points.

In *C. curtus* the cytopharynx is long, recurved and tubular. The contractile vacuole lies below the nucleus, and is stelliform or rosette-shaped. In both these points *C. curtus* differs essentially from *C. mytili*, but resembles it in having an oval meganucleus, with two micronuclei.

In *Conchopthirus anodontæ* the oval fossa occupies the centre of the body, while the cytopharynx curves inward, and nearly reaches the posterior extremity. The contractile vacuole is subcentral, and the meganucleus posterior.

It also differs from *C. mytili* in shape, being longer in proportion to the breadth.

Both the above species, according to Engelmann, have, on the ventral surface of the posterior end, a row of about six larger and stronger cilia. These do not appear in *C. mytili*.

*Conchopthirus Streenstrupii* Stein, found in the body slime of *Succinea amphibia*, and of many land snails, differs from *C. mytili*, in having the contractile vacuole subcentral, and a nucleus consisting of seven cor-

puscles lying parallel to the posterior and right lateral border. The matting of the cilia is a character common to all the genus.

CONDYLOSTOMUM PATENS (O. F. Müller).<sup>23</sup>

*Condylostomum patens* is a very widely distributed form of ciliate, and the following are the principal articles dealing with it. As *Trichoda patens*, O. F. Müller (23); *Kondylostoma limacina*, Bory (1); *Uroleptus* (?) *patens*, Ehrenberg, Alhandl. der Berliner Acad. von 1833, s. 278; *Kondylostoma patens*, Dujardin (8); *Kondylostoma patens* and *K. patula*, Claparède and Lachmann (5); *Condylostoma patens*, Stein (26); *Fresenius* (13); Cohn (6); Quennerstedt (25); Rees; Levander (19); Maupas, 1883 (20); Gourret and Roesor, 1886 (15); Calkins (4); Wrzesniowsky (28); Schewiakoff (27).

The descriptions of Stein and Maupas are the best and most detailed I have read.

This species appears to be mainly pelagic. The fresh-water species of the genus, *C. vorticella*, *tardum*, and *sphagni*, as described by Penard, differ considerably, especially in form. The *Condylostoma vorticella*, which approaches nearest to *C. patens*, is much shorter and more rounded.

*Condylostoma patens* (Fig. 14) is very common, and widely distributed. In Drake's Island Tank it is present nearly all the year round, and I have found it very abundant in February and May. The form is pretty constant, and although there are slight variations, the animal is very conspicuous and easy to recognize.

In colour those in Drake's Island Tank are greyish with a slight yellow tinge; occasionally they may be almost colourless, and specimens which I have seen from rather brackish water were distinctly yellowish.

Maupas gives the length as .305 to .495 mm.; Stein, .376 to .564 mm.; and Calkins, .4 mm. length, and .1 mm. breadth at widest part. Thus, generally speaking, Stein's specimens were longer and narrower than those of Maupas, who says that he never saw the length more than 5 times the greatest breadth, while Stein gives the length as seven or eight times the breadth.

I have found that no definite limits can be fixed to length and breadth. In a single sample from Drake's Island Tank individuals of all the lengths mentioned by Stein and Maupas may be found. It appears to be simply a question of growth and feeding. The same may be said of the shape of the body. Stein says that it is nearly cylindrical, Maupas that it is flattened ventrally and dorsally, and Claparède and Lachmann also speak of the dorsal and ventral flattening. Calkins calls the general form elongate and cylindrical, and somewhat smaller anteriorly. I have very

seldom found anything resembling this description, or the figure he gives, among the Drake's Island Tank individuals. Generally the dorsal

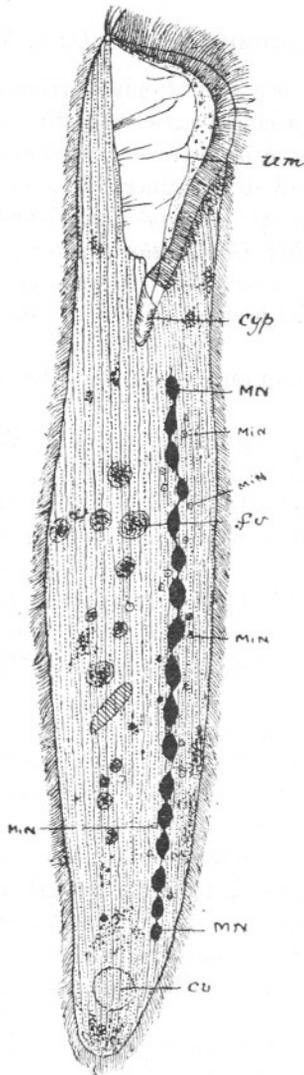


FIG. 14.—*Condylostoma patens*. *MN.*, meganucleus; *MiN.*, micronuclei; *um.*, undulating membrane; *Cyp.*, cytopharynx; *cv.*, contractile vacuole; *fv.*, food vacuole.

surface is considerably arched and flattens out gradually in the posterior third of the body. The ventral surface is flattened. The anterior end rather narrower than the median breadth, and the posterior gradually tapered. This is the shape when the animal is fairly quiescent. When

it is swimming about it elongates, and assumes shapes resembling those described by Stein and Maupas. As stated before, the appearance as described by Calkins is rare. There is generally a slight decrease in width just beyond the lower angle of the peristome, and in cases of great extension this is materially increased, accompanied by flattening of the anterior portion, sufficient to produce a spoon-like appearance.

The peristome is large and triangular, and catches the eye at first sight of the animal. The base of the peristomial triangle forms nearly the whole of the anterior margin of the body. Stein says that it occupies  $\frac{1}{5}$  or  $\frac{1}{6}$  of the body length, Calkin  $\frac{1}{4}$  or less. It depends on the state of the animal at the time of measurement; but in any case  $\frac{1}{4}$  of the body length is a high estimate. The right edge of the peristome bears a well-defined undulating membrane, to which Maupas does not directly allude. Gourret and Roeser (15) describe it as a fine hyaline membrane (membranella), which carries along its whole length a kind of velum. This is smaller than the membranella, and produces a vigorous vortex by its flapping. In the Plymouth specimens I have failed to distinguish the membranella and velum—although the undulating membrane, which is situated as Stein (26) describes, is a very conspicuous object.

In the inferior angle of the peristomial area is the mouth which leads into the gullet. Stein describes the gullet as long and serpentine, while to Maupas it appears not much longer than broad. Gourret and Roeser describe it as a quadrilateral pocket, of which the opposite angles have an opening; one of these openings, which is continuous with the posterior extremity of the peristome, forms the cytostome, while the other leads into the body of the animal.

From observations of Plymouth specimens I could not assign a fixed definite shape to the cytopharynx. It appears as a shorter or longer continuation of the peristomial area, of varying width. Stein, Maupas, and Gourret and Roeser all agree that it is ciliated; but Stein is doubtful whether the cilia visible are only continuations of the adoral cilia or whether the whole inner surface of the cytopharynx is ciliated. The presence of the cilia on the surface of the body make this a difficult point to decide; but I am inclined to think that they cover all the interior surface of the cytopharynx. Maupas states that the cilia hollow out a digestive vacuole in the sarcode; on the arrival of food the vacuole fills, detaches itself, and gradually passes down the body, until the contents are discharged outside. Gourret and Roeser state that a hyaline vacuole is usually ready, and that as soon as it is filled another takes its place. This seems to me to be what takes place, except what is stated by Gourret and Roeser in regard to the new vacuole taking the place of the detached one. It depends on whether more food is arriving.

The right anterior angle of the anterior margin forms a curved projection, which Stein says is characteristic. The left margin forms a regular curve. The left inner margin of the peristome carries a row of close-packed, well-developed cilia, which terminate on the right anterior projection, in four or five cirrhi. The cilia of the anterior margin are the longest, and gradually decrease in length down to the level of the mouth. The whole of the body is covered with short fine cilia arranged on moderately spaced, slightly oblique striæ. The dorsal and ventral body cilia are of the same length; but at the posterior extremity they appear to be slightly longer, and often anchor the animal by attachment to foreign matter. The peristomial area has no cilia, and is so transparent that the striæ and ciliation of the dorsal surface are visible through it.

The above describes the ciliation of the Plymouth variety. The animal described by Maupas differs considerably in ciliation. According to that observer, the dorsal cilia are fine, very closely set, and in a state of perpetual vibration. The ventral cilia are coarser and further apart, and do not vibrate continually, but move slowly, in obedience to the will of the animal, and are true ambulatory cirrhi, similar to those of Euplotes and the Oxytrichids. When *Condylostoma* is resting they are quite motionless.

Morphologically, he concludes, that they are true cilia, but functionally ambulatory cirrhi. The four or five cirrhi on the right anterior angle Maupas considers absolutely identical with the cirrhi of Euplotes and the Oxytrichids, and sees in them indications of the law by which the heterotrichous type of ciliate is transferred into the hypotrichous. There are also on the dorsal surface, but only easily observable on the margins of the body, tufts of fine silky bristles. These Maupas considers homologous with the bristles observable on the dorsal surface of all Hypotrichous Infusoria.

Again, Maupas describes the appendages of the adoral zone, not as stout cilia, but as membranellæ similar to those of the Oxytrichids. There is also a clear laminar boundary which carries the frontal membranella, and which he considers homologous with the Oxytrichid overlip. In the above points Maupas' *Condylostoma*, of which he gives excellent figures, differs considerably from the Plymouth specimens, and those described by Gourret and Roeser, Calkins, and Stein.

*Contractile vacuole.* In the Plymouth variety I have never seen a regularly functioning contractile vacuole. A large posterior, irregularly shaped, apparently empty space, is often present. The size and shape vary considerably among individuals; but I have never observed diastole and systole, and this is also Maupas' experience. On the other hand, Stein describes a regular water canal system, of a very active nature.

Stein places the anus at the posterior extremity of the body. Maupas declares that he has frequently observed the anus functioning; that it opens on the dorsal surface near the right margin and about the level of the last and middle third of the body, and in its position he sees another point of affinity between *Condylostoma* and the Hypotrichid Infusoria. He accuses Stein of being frequently inexact in describing the position of the anus of ciliates. In certain cases the observations of Gourret and Roeser confirm Maupas. In others the anus appeared near the posterior end and on the left margin of the body. Again discharge of fæcal matter was observed through two orifices on the left side, and after discharge no orifice could be recognized. Gourret and Roeser are sure that the anus is formed by rupture of the cuticle, and that after expulsion of the fæces the edges of the temporary orifice coalesce.

I have never been able to make out a permanent anal opening. Fæcal matter appears to escape at any point where pressure overcomes the resistance of the cuticle, and, immediately after, the surface is regenerated.

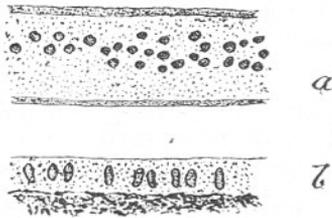


FIG. 15.—*Condylostoma patens*. Surface view (a) and section (b) of Integument.  $\times 1280$ . (After Maupas.)

Maupas describes the striations of cilia as slightly oblique to the longitudinal axis of the body from right to left, and as being not so numerous as generally represented. The striæ on the Plymouth variety agree in being slightly oblique, but they are not spaced so widely as Maupas shows them. He describes them as consisting of homogeneous fibrillæ, bounding wide granular bands. At the base of the granular substance are refringent corpuscles or rods, which are not trichocysts, and form in his opinion the principal elastic element of the integument (Fig. 15). Gourret and Roeser, on the other hand, hold that the fibrillæ are only the result of cuticular thickening, and, though undoubtedly elastic, should not be considered as the principal element of elasticity. The intermediate bands they regard only as body sarcode and nutritive vesicles. From microscopic examination of the living animal and stained preparations it is difficult to come to any definite decision, which probably will only be arrived at by microdissection.

The *meganucleus* (MN) is moniliform. The component masses of

nuclear matter, according to Stein and Maupas, are connected by strands of chromatoid matter. This is evident in numerous preparations I have made. Gourret and Roeser, however, state that the "nodosities" of the meganucleus, as they term them, are generally separate; but that sometimes they are closely connected in the anterior part of the body.

Neither Stein nor Gourret and Roeser observed the micronuclei (MiN). In stained preparations a number of opaque central corpuscles, surrounded by a clear space, may be seen. They measure about .002 mm. in diameter, and the clear space about .005 mm. Maupas believes these to be the micronuclei. The number varies in different individuals, and does not correspond with the number of meganuclear "beads," being sometimes greater and sometimes less. Maupas found 17, 15, 14, 14, 16, 15 "beads" with 14, 15, 14, 13, 18, 18 nucleoli respectively. Their distribution among the meganuclear beads is quite irregular.

They may be compared with the small dark stained corpuscles lying beside the meganuclear spheres in *Holophrya oblonga*; their appearance and behaviour is generally constant, but in certain phases of division is not quite clear.

In Division the meganucleus commences by contracting into a homogeneous central mass. At this stage there is no constriction of the body, but a rudimentary peristome commences to develop on the ventral surface. Shortly afterwards constriction commences, accompanied by an enlargement of the new peristome.

The meganucleus lengthens to form a more or less sinuous ribband, and the micronuclei (Fig. 16) are drawn along the margins in company with it, finally concentrating at the two poles (Fig. 17). Maupas states that the condensation of the meganucleus is probably preceded by a micronucleolar division, for he frequently observed a number of micronuclei collected at either pole of the meganuclear mass. I have not observed such a marked polar concentration of micronuclei at this phase as Maupas described. In one case a number of micronuclei collected together, and forming a sphere, which stained less darkly than the meganucleus, were seen collected at one pole where single micronuclei appeared to be absent; a large light-staining sphere appeared containing what resembled micronuclei. It appears to me possible that there is a stage at which the micronuclei aggregate together to form a single spherical mass of chromatoid matter, which divides and separates into single micronuclei. This point requires further investigation. It may be noted that the micronuclei are exceedingly small, and that Iron Hæmatoxylin might give better results than Paracarmine with which my specimens were stained.

The constriction then deepens, and the new peristome is completed. The ribband-like meganucleus commences to divide at the level of the body constriction. Finally the two halves separate. Figs. 18 and 19 (p. 626) show two cases of division products. In both the meganuclear ribband is beginning to constrict, and in one has resumed the monili-

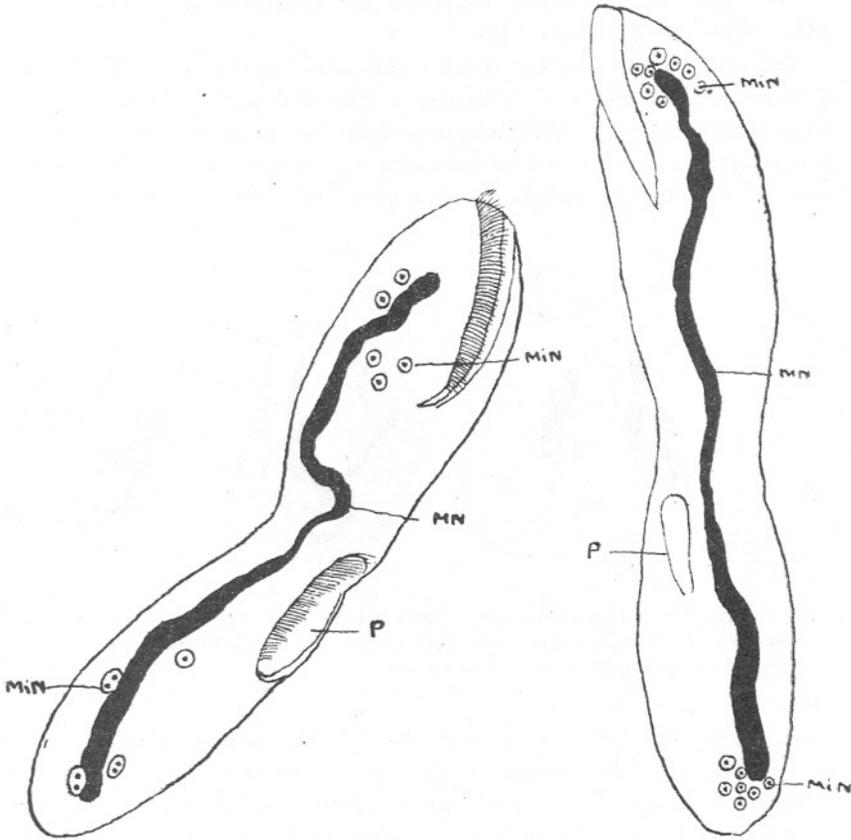


FIG. 16.

FIG. 17.

FIG. 16.—*Condyllostoma patens*, dividing. Micronuclei on ribband, *MiN.*; *MN.*, meganucleus; *P.*, new peristome.  $\times 300$ .

FIG. 17.—*Condyllostoma patens*, dividing. Micronuclei concentrated at poles. References as above.  $\times 300$ . Camera lucida.

form state. It is to be remarked that in both, which are at the same stage, i.e. immediately after division, the condition is very different. In one the micronuclei (Fig. 18) are numerous and separate. In the other I was unable to detect any. In the latter case, however, the animal was full of food-vacuoles and granular matter, which made detection difficult.

*Condylostoma patens* is very hardy. It will live in stagnant water, and will stand long journeys.

PRORODON MARINUS (Möbius).

Described by Möbius (22); Claparède and Lachmann (5); Quennerstedt (25); Bütschli (3); Kent (18).

This ciliate (Pl. I, Fig. 20) is not common in Drake's Island Tank, and I have never found it in abundance like *Holophrya*, *Porpostomum*, *Condylostomum*, etc. The body is cylindrical, rounded anteriorly and posteriorly as a rule; but occasionally the anterior pole is prolonged into a teat-like projection, and occasionally the posterior pole is

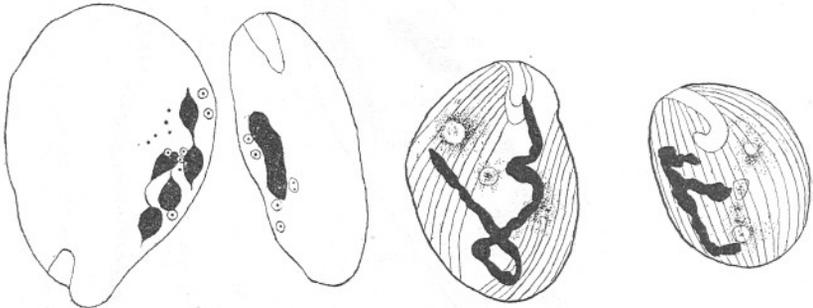


FIG. 18.

FIG. 19.

FIGS. 18 AND 19.—*Condylostoma patens*, after division. In Fig. 18 many micronuclei and in one product meganucleus is moniliform. In Fig. 19 micronuclei absent. Slightly compressed.  $\times 300$ . Camera lucida.

truncated. The whole body is covered with close rows of fine cilia of equal length. Möbius states that in some cases he noticed a longer posterior cilium. This I have not observed. Each cilium stands on a spike-like papilla. This is very noticeable in marginal views of the animal. Möbius states that the layer of endosarc under the pellicle is very finely cross-striated. This appears to me doubtful. Under high magnification striæ are certainly visible; but one end of every striation is wider than the other, and I think that the striations are really the cilia pressed down by the cover slip, and consequently occupying a position transverse to two neighbouring rows of cilia. No transverse striæ are visible when the animal is moving freely. It is possible that the cross-striations observable in some other ciliates, e.g. *Trachelocera phœnicopterus*, and *Porpostomum notatum*, are due to this cause.

Möbius gives the length of the ciliate as  $\cdot 19$  to  $\cdot 22$  mm., and breadth  $\cdot 08$  mm. Plymouth specimens are much larger. The largest fixed speci-

men I have measured was .45 mm., and lengths of .32, .30, .28 mm. are common.

Along with the cylindrical individuals, there are often found smaller ones which are quite spherical. In all other respects but this they are similar to the cylindrical Prorodons. The drawing of Claparède and Lachmann resembles one of these. Möbius thinks that the drawing was from one of the cylindrical ones under pressure from the cover slip. I am inclined to think that it is simply an early stage of the same animal.

Roughly speaking, the length may be stated as varying from twice to three and a half times the breadth.

Below the layer of cross-striated (Möbius) endosarc is another containing strongly light-reflecting crystalloids. These give a very glassy transparent appearance to the animal. They are not destroyed by fixing. There are frequently numbers of dark granules in the endosarc, and Claparède and Lachmann state that the animal is sometimes so full of refringent granules as to appear almost black.

The contractile vacuole is situated in the aboral pole. Möbius states that it is never spherical, but often lengthened obliquely. Like other contractile vacuoles it is very variable in shape; I have often seen it spherical. It often divides into many smaller vacuoles. Diastole and systole are slow. Claparède and Lachmann describe it as a large posterior vacuole filled with a fluid containing rod-like corpuscles, which might be taken for trichocysts, but are possibly the remains of a digested infusorian.

*Cytostome* anterior in the middle of the oral pole. Quennerstedt's figure shows it slightly to one side. Circular when open and very contractile. Sometimes situated on a teat-like prolongation. The *cytopharynx* is funnel-shaped, and has a basket-like arrangement of rods about forty in number. It can be so closely contracted as to be hardly visible. The cytopharynx appears to be ciliated, but the animal is so transparent as to make it difficult not to confuse the ectodermal cilia.

The *megannucleus* is spherical or egg-shaped, generally situated in the middle of the body, but sometimes more anterior or posterior. It is visible in the living animal and stains readily with all ordinary stains; but Möbius states that his specimens would not respond to carmine or indigo.

There are generally two micronuclei, in most cases close to the megannucleus.

I have never seen the animal divide, nor is the process described in any of the authors I have consulted. Möbius, however, frequently observed encystment. The animal assumes a spherical shape. The cilia beat slowly and at last cease entirely, and lie sloping on one another,

forming a border round the body. Then a very thin colourless cyst is secreted. In some cysts two individuals were found, probably, he thinks, arising from division of one mother individual.

Möbius saw many individuals assume the spherical form after resting sometime in the cyst, and leave it without dividing. During the rest the contractile vacuole functioned very slowly. The encysted individuals often had a deep transverse fold, resembling a division furrow. He appears not to have noted any nuclear changes, or what took place while the animal was in the cyst.

*Prorodon marinus* swims slowly, revolving on the long axis, sometimes with the anterior, sometimes with the posterior pole in advance. It is not very contractile in any direction, nor does it alter much in size by fixation.

Buddenbrock (2) describes a new species which he found in the Berlin Aquarium, as *Prorodon binucleatus*.

The principal difference of this animal from *P. marinus* is the possession of two nuclei lying very close to one another. In fact, Buddenbrock thinks that it would be better described as a two-limbed, than a spherical nucleus. The body is about three and a half times as long as broad. Wider anteriorly than posteriorly. In starving animals the posterior end is sometimes flattened. Extremely contractile and can assume a spherical shape. Cilia in many longitudinal rows. Very flexible. Ectoplasm separates very distinctly from the apparently quick flowing endoplasm. *Cytostome* terminal, funnel-shaped, and so delicate that its minute structure could not be investigated. It lies embedded in a plug of ectoplasm, which at this point is evidently more strongly developed than in the rest of the body, and can be protruded like a nipple (as was noticed in *P. marinus*). Contractile vacuole nearly or quite terminal.

The colouring is characteristic. An anterior and a distinctly separate posterior portion are separated from one another by the almost glass-clear zone containing the nuclei. The anterior section is always filled with many granules that strongly refract light, and under low powers appears almost black. The posterior section behind the nucleus may be very transparent with only a few central granules. Sometimes individuals are met with in which large granules make the posterior part of the body appear darker than the anterior. Nucleus generally transverse. Rarely do the two spheres lie one above the other.

Swims moderately swiftly, revolving on the long axis. The cilia of the anterior one-third of the body may be seen moving extremely swiftly, the remainder playing an unimportant part in the movement.

I have inserted this description, as the differences between *P. marinus* and *P. binucleatus* are so small, that the latter may prove to be only a variety of the former species.

## CHAENEA ELONGATA (Clap. et Lach.).

Has been described by different authors under the following names: *Chaenea teres* Gourret and Roeser (15); *Enchelyodon elongatus* Claparède and Lachmann (5); *Lagynus elongatus* Maupas (20); *Chaenea teres* Kent (18); *Chaenea vorax* Quennerstedt (25).

The genus *Chaenea* was formed by Quennerstedt to include a form resembling *Enchelys farcimen* of Ehrenburg, and *Enchelyodon elongatus* of Claparède and Lachmann and *Trachelius teres* of Dujardin. Quenner-

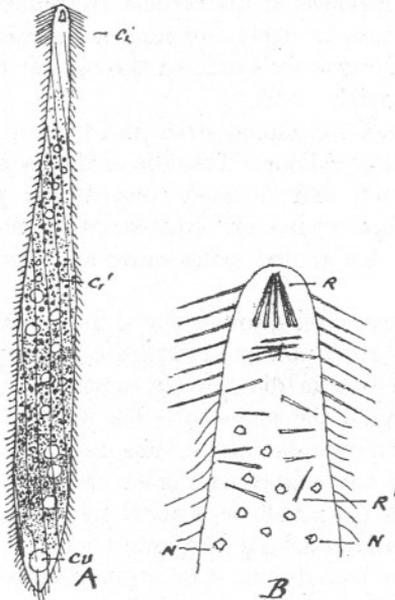


FIG. 21.—*Chaenea elongata*. A. *ci.*, stout posteriorly directed cilia; *ci'*, oblique rows of body cilia; *cv.*, contractile vacuole. The small dark dots are nuclear matter. B. Anterior part.  $\times 630$ . *R.*, apical rods; *R'*, rods scattered through the body. *N.*, small masses of nuclear matter.

stedt gave it the specific name of *vorax*, on account of its predatory habits. Maupas, however, considers that it has nothing in common with the genus *Enchelyodon*, and replaces it in the genus *Lagynus*, founded by Quennerstedt in 1867. Whatever may be its position in the scale of classification, there is no doubt that the ciliate described by Maupas is identical with that found in fair numbers in Drake's Island Tank, as follows:—

In form this ciliate (Fig. 21) is a long spindle. The length varying

from .070 to .225 mm. The proportion of breadth to length is very variable—from an average of 1 to 5, to as much as 1 to 8, or even 10. The body narrows from the anterior to the posterior end; but there is always a distinctly marked short anterior portion, which may be called the neck, and which forms a very variable portion of the total length. The posterior end is obtuse, and capable of considerable distention. There is a contractile vacuole at this end, and I have seen it functioning—I have seen one or two vacuoles in other parts of the body, but not pulsating. They were, however, not food vacuoles. The body is rather opaque, with many food vacuoles and refringent granules.

Throughout the thickness of the pellicle are numerous pointed rods, which Maupas measures at .006 to .01 mm. in length, and .001 mm. in breadth. They are irregularly scattered throughout the body. Maupas believes them to be trichocysts.

There are very fine longitudinal striæ, and the body cilia follow their lines, which are slightly oblique. The cilia of the neck are rather longer, stouter and closer set, and directed towards the posterior. I have not observed the appearance of cross-striation noted by Maupas; possibly it may be due to the same cause as described for *Prorodon marinus*.

The mouth is always closed, unless the animal is swallowing its prey, and then it displays great powers of extension. Maupas relates that he has seen a *Chænea* of .01 mm. diameter attempting to swallow a *Uronema* of .028 mm., but found the morsel too big for it. Only Maupas has correctly described the mouth region. The neck region is fairly translucent, and may be thoroughly examined under high power. Under  $\frac{1}{8}$  in. there appear in the middle a clear triangular space with the apex pointing to, and nearly touching, the anterior end. Under  $\frac{1}{2}$  in. this space is shown to be bounded by 4 or 5 (Maupas says 2 or 3, but the number varies) needle-pointed bodies of about the same size and structure as those in the body, called by Maupas trichocysts. Lying irregularly scattered at the base of these are a few other bodies of the same nature, irregularly disposed.

I have examined many individuals and in all have found these rods forming an apical isosceles triangle; and it is these evidently which Claparède and Lachmann mistook for the rods, which are often found in the cytopharynx of ciliates.

Maupas describes how the long cilia around the neck form eddies which suck in small animalcules, which are then paralysed by the trichocysts, and swallowed by the *Chænea*.

It is remarkable that acetic acid does not cause a discharge of the trichocysts in *Chænea*, as is usually the case with other ciliates.

Claparède and Lachmann describe the nucleus as an oval disc; Gourret

and Roeser did not see one, nor could Quennerstedt detect one by pressure or staining. Maupas, by fixing with osmic or acetic acid, staining with picrocarmine and clearing with acetic acid and glycerine, found small nuclear masses, of varying size and number, distributed in all parts of the body, the number varying in proportion to the size. In some cases eight to ten nuclear masses of about .005 mm. diameter, in some as many as 100, measuring not more than .0015 mm. diameter.

Using picro-formal-acetic and paracarmine, and methyl green and acetic on the live animal, I got similar results. With animals in process of division, I did not find any change in the nuclear arrangement, neither did Maupas. He also observed *Chænea* in conjugation with a similar negative result.

The presence of a nucleolus has not been demonstrated. I found *Chænea* in water containing putrifying matter, to the presence of which it does not appear to object, but it is very sensitive to change in the concentration of the sea water.

#### SPIROSTOMUM LANCEOLATUM (Gruber).

This ciliate was described by Gruber (14) as a new species of *Spirostomum* from the harbour of Genoa. It is fairly abundant at all times of the year in Drake's Island Tank, except in January, February and March, when only solitary specimens are obtainable. It generally lies inert on the bottom among algæ and fine gravel, but when in motion is capable of considerable extension, with flattening and folding of the body.

The general form (Fig. 22, p. 632) is that of a lancet or long spindle, the widest part being about  $\frac{1}{3}$  of the body length from the anterior end. From this point it tapers away gradually to a fine posterior point. The length of the body is about .3 to .35 mm. when resting, but when extended in swimming reaches .45 or .5 mm. The breadth is about .041 to .045 mm. Gruber gives the length as about .2 mm., and this is the only point in which his specimens differ from those found at Plymouth. The anterior end of the body is wider than the posterior, and when the animal is lying with the mouth uppermost, has a slight angle projecting to the right. The peristomial area does not extend much beyond the anterior third of the body. Viewed ventrally the cytostome is seen to lie slightly to the right of the centre line of the body. From the cytostome the peristomial groove extends to the right towards the anterior end, so forming an arc of a spiral, which is very noticeable, and characteristic of the genus *Spirostomum*. The right margin of the peristomial groove carries a row of cilia longer and stouter than those which cover the body, and which combined with their spiral course make it easy to recognize the

animal. There is a short, rounded cytopharynx, into which, according to Stein (26), in describing *Spirostomum teres*, a very similar species, these peristomial cilia are continued. The motion of the surface cilia makes observation difficult, but I am disposed to agree with Stein. Claparède

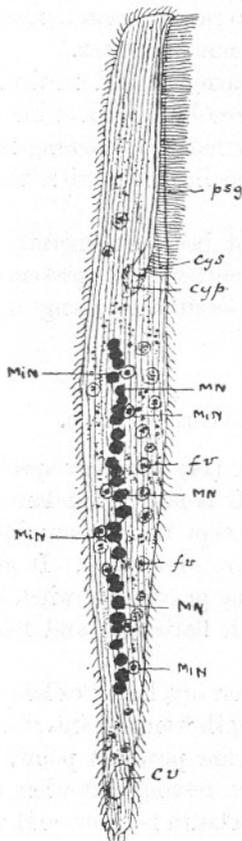


FIG. 22.

FIG. 22.—*Spirostomum lanceolatum*. *MN.*, meganucleus; *MiN.*, possible micronuclei; *psg.*, peristomal groove; *cys.*, cytostome; *cyp.*, cytopharynx; *fv.*, food vacuoles; *cv.*, possible contractile vacuole.



FIG. 23.

FIG. 23.—*Spirostomum lanceolatum*, dividing. *MN.*, meganuclear ribband; *fv.*, food vacuoles.

and Lachmann, in describing *S. teres*, think that the cytopharynx contains a single cilium, or a bunch of cilia. This is improbable.

There is no undulating membrane. The body is covered with rows of striæ, which carry very fine cilia. The minute structure of these striæ in *Spirostomum teres* has been described by Stein.

In underfed individuals the meganucleus may be seen as a number of clear spheroidal masses, very similar to those described in *Condylostomum patens* (Fig. 22). They lie in a row parallel to the longitudinal axis of the body, and are variable in number. Gruber, in describing his fixed and stained preparations, says that the peculiarity of the component of the meganucleus is that they are dumb-bell shaped, just as if they were in a stage of division; but that this condition cannot be considered as a transitory one, as he found it repeated in all the preparations he examined.

In his drawing, all the elements of the meganucleus are not dumb-bell shaped, there being two solitary spheres. Of these he remarks that they may either be the result of a break up of a dumb-bell-shaped mass, or that they are in course towards union to form the dumb-bell.

In my preparations I find dumb-bell-shaped masses, spheres, and aggregates of spheres. Single spheres are more numerous, and generally there are connecting strands of chromatoid matter. It seems probable that the natural form of the meganucleus is a number of spherical or ovoid masses connected by strands of chromatoid matter, as in *Condylostoma patens*, and that the dumb-bells and aggregates of spheres are stages on the way to the collection of the nuclear matter into a single mass, previous to the formation of a ribband, and subsequent division. Fig. 23 shows *Spirostomum lanceolatum* about to divide.

The single meganuclear masses consist of a number of very small spheres, similar to those described and figured by Stein (Pl. II, Fig. 12.) in *Spirostomum teres*.

Lying beside the meganuclear masses are a number of small spheres similar to those described in *Condylostoma patens*, as possible micronuclei. They are sometimes, but not invariably, surrounded by a clear space.

They are about the same size as the spheres of which the meganuclear elements consist. I have not been able to trace them through division, but I could not find them in the case where the ribband was formed (Fig. 23). I have seen cases where the small sphere appeared to be extruded from the meganuclear element. Gruber does not mention the micronucleus. I have not seen any case of conjugation.

Gruber says nothing of the contractile vacuole. I have occasionally seen a posterior vacuole, but have never observed it pulsating. Possibly, like some other marine ciliates, *Spirostomum lanceolatum* does not possess one.

Stein describes, as *Spirostomum teres*, a ciliate which in many points resembles the *Spirostomum* found at Plymouth; but differs in having a more obtuse posterior end, with an oval, kidney spindle, or horseshoe-shaped nucleus, and an actively functioning contractile vacuole, with a system of canals, similar to those in *Holophrya*. Stein examined a speci-

men from the Baltic, but the majority of his observations were on fresh-water forms, which may account for the variations.

#### FRONTONIA FUSCA (Quenn.).

*Frontonia fusca* (Pl. I, Fig. 24) differs considerably from the fresh-water *Frontonia leucas*, described by Schewiakoff (27). *Frontonia leucas* is wider at the anterior than at the posterior end, while *F. fusca* is about the same width throughout, with equally rounded ends. In *F. leucas* the peristomial furrow extends about  $\frac{2}{3}$  of the body, while that of "fusca" reaches at times quite to the posterior end. In this it resembles the marine form of *Frontonia leucas* as described by Calkins (4). The arrangement of the contractile vacuoles in *F. fusca* also is very variable.

In Fabre-Domergue's figure, reproduced in the *Nord-Plankton*, XIII, p. 51, two are represented, one in the anterior and the other in the posterior third of the body. In the Plymouth form I have only observed one, at the posterior end. This sometimes breaks up into smaller spheres, which may unite to form a sort of short canal, or may form a canal leading a little way from the large sphere. I have never observed any system of radiating canals as seen in the fresh-water species.

Calkins, in describing his marine *Frontonia leucas*, notes that in the Woods Hole specimens they are very irregular in size, and very much branched, but not uniform or radiating, as in Schewiakoff's description.

*Frontonia fusca* differs from both Calkins' marine and the fresh-water *Frontonia leucas*, by the presence of a large mass of granules on the left anterior margin of the body (the ventral side being uppermost). This appears almost black, but in the Plymouth specimens is really a deep green. Similar granules to those composing it are scattered all over the body also and are light green in colour. This spot does not appear in Calkins' marine *Frontonia* nor in the fresh-water species.

The mouth of *Frontonia fusca*, as far as I can see, resembles that of *Frontonia leucas*, which has been minutely described by Schewiakoff; and also by Maupas (20), under the name *Ophryoglena magna*. These two observers differ in their interpretation of the arrangement of the deeper parts of the oval fossa, and of the peristomial furrow. Schewiakoff's description appears to me to be correct, though I cannot detect the rows of cilia in the furrow, which sometimes extends to the posterior end. As Schewiakoff says, these cilia are shorter than the body cilia, and so closely placed together that they "als ob sie auf einer Leister stünden." It is, in fact, difficult to say whether they are lines of cilia or simply lines.

I can only detect one undulating membrane. There is not much difference between *Frontonia leucas* and *Frontonia fusca* in size. The individuals I have measured of *F. fusca* vary from .13 to .16 mm. length, and .05 to .06 mm. breadth. Schewiakoff gives for *F. leucas* .11 to .22 mm. length, and .05 to .1 mm. breadth. The nucleus is spheroidal, and situated as in the marine form described by Calkins.

The body carries very fine close striæ on which are the cilia, of even length all over the body. The cilia appear to rise each from a very small papilla, which papillæ form the striæ, and Schewiakoff states that this is the case. Minchin, however (*Introduction to Study of Protozoa*, p. 442), states that in *Frontonia* each cilium arises from the centre of a small depressed area of the surface.

There are many trichocysts in *Frontonia fusca*, oblong in shape with rounded corners. In *Frontonia leucas*, Schewiakoff shows them as lenticular. The exploded trichocysts of *F. fusca* are threads about .016 mm. long. Schewiakoff figures those of *F. leucas* with two hooks at the end; but Minchin's illustration, p. 447, after Schubert, shows them with clubbed ends.

*Frontonia fusca* is greyish in colour, with many food vacuoles and refringent granules. I have found it in Drake's Island Tank among algæ in March and April, but not in any great number. I had not seen it previous to 1922. It has been described by Quennerstedt (25) as *Panophrys fusca*, and by Fabre-Domergue (12) and Kent (18) as *Plagiopyla fusca*, but I have not had an opportunity of consulting these two authors.

The meganucleus is spherical or ovoid, and lies nearly in the centre of the body. There is one micronucleus. At division the meganucleus assumes a dumb-bell shape, and gradually separates into two portions; and at the same time the micronucleus divides into two, so forming the mega- and micronuclei of the two new individuals.

I have seen one case of conjugation, but was unable to follow the details.

#### ANCISTRUM MYTILI (Quenn.).

This small ciliate was first described by Quennerstedt (25) under the name of *Opalina mytili*. Maupas (20), however, pointed out that Quennerstedt was mistaken in referring it to the genus *Opalina*, as it possesses a mouth; and food vacuoles are present in the endosarc. Quennerstedt failed to see the mouth, and denied its existence. He, however, did recognize the vacuoles containing food; but compared them with those observable in the *Acineta*, which, according to him, also have no mouth. Maupas points out that he is wrong again, inasmuch as *Acineta* have as many mouths as suctorial tentacles through which they ingest food.

Maupas also criticized the accuracy of Quennerstedt's observations on the general anatomy of the ciliate, and described it himself under the name of *Ancistrum mytili*.

*Ancistrum* is found in abundance among the branchial filaments of the common mussel. Here it attaches itself, and doubtless feeds on the small particles of food, of which the cilia of the branchiæ cause a constant flow.

It appears that *Ancistrum* goes through all the stages of its life history among the branchiæ, and I have met with many stages of development in infected shells.

*Ancistrum mytili* is a small colourless ciliate, averaging .06 to .08 mm. in length, and about  $\frac{1}{3}$  of the length in the broadest part. It does not appear to possess any contractility. The body is wider and thicker at the posterior than at the anterior pole, and is bent on itself, so that in profile it resembles an arc, of which the dorsal surface is convex, and the ventral flat and concave. (It should be noted that Maupas, in his description, places the mouth at the posterior extremity, and regards the wider extremity where are the cilia by which fixation is effected as the anterior. I see no reason for this change in the usual convention, and call the end where the mouth is situated the anterior.) In consequence of the curvature it is difficult to get an accurate representation of the body parts. The figures are drawn from slightly flattened specimens, and thus cannot represent exactly the arrangement of the cilia. The perisarc is finely striated, showing the lines of cilia, and on the dorsal surface are two parallel ridges (Fig. 25) (dr) running from the anterior margin, which is obliquely truncated from right to left and dying out posteriorly. The cytoplasm contains a few food vacuoles, and a few refringent granules. Generally speaking, it is rather clear. The cilia are long, and follow the striæ of the integument. Those on the side of the mouth (that is the left side when the animal is lying in a ventral view) are longer than the others, and when at rest, in the lower  $\frac{1}{3}$  of the body, lie pressed to the side, so giving the appearance of a fringed margin (Fig. 26) (fm). On the posterior part of the ventral surface (Fig. 26) (ct) there is a large patch of short, thick-set cilia, which, when the animal is at rest, stand out at right angles to the surface, and appear to form points of attachment. When the animal is viewed dorsally (Fig. 25) (ct) the ends of these cilia show up in optical section as black points on the coverslip. While the animal is at rest the cilia around the posterior margin may often be seen in rapid motion, giving the idea of rotation. Meanwhile the cilia on the body lie wrapped round the animal. *Ancistrum* moves with a rapid, jerky motion, revolving round its axis. It proceeds in a hurry for a short distance, comes to rest, and again starts off on an erratic course.

In a ventral view, the cytostome (Fig. 26) (*cys*) may be seen as a small oval fossa in the left-hand corner, which I observe is extended into a longish narrow cytopharynx (*cyp*), which varies in visibility. Sometimes it is not to be seen at all. Maupas says he thinks he sometimes saw it. Maupas then proceeds to describe how the mouth is provided exteriorly with a large vibratile membrane, of which it is difficult to observe the arrangement and points of attachment; but without being perfectly

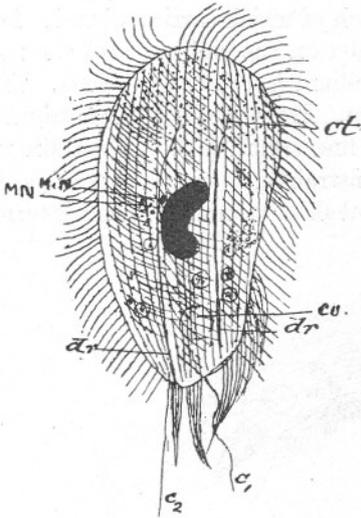


FIG. 25.

FIG. 25.—*Ancistrum mytili*. Dorsal view.  $\times 630$ . Camera lucida. *MN.*, meganucleus; *MiN.*, micronucleus; *ct.*, cilia which probably form points of attachment in optical section; *dr.*, dorsal ridges; *c<sub>1</sub>*, flagellum-like cilium; *c<sub>2</sub>*, long cilium; *cv.*, contractile vacuole.

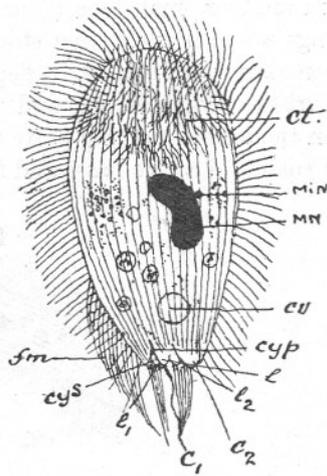


FIG. 26.

FIG. 26.—*Ancistrum mytili*. Ventral view.  $\times 630$ . Camera lucida. *MN.*, meganucleus; *MiN.*, micronucleus; *cys.*, cytostome; *cyp.*, cytopharynx; *fm.*, fringed margin; (*l<sub>1</sub>*), small lobes carrying bunch of cilia (these do not appear clearly in the figure as the cytostome interferes with the view); *l*, lobe to right of cytostome bearing flagellum-like cilium; (*l<sub>2</sub>*), lobe bearing long cilium; *ct.*, cilia which probably form points of attachment; *cv.*, contractile vacuole.

certain he thinks he may compare it to the vibratile membrane of *Pleuro-nema chrysalis*. He also describes how particles of food are swept by the eddies of the cilia into this net-like membrane, which then contracts, and draws them into the mouth. The membrane is in constant change and motion, and very contractile. It is this membrane, he says, that Quennerstedt has taken for a bundle of entangled cilia.

I have examined numbers of *Ancistrum*, and have never been able to detect any sign of a vibratile membrane. Under low magnification, the

bundle of cilia (fm) on the left anterior margin give an outline, somewhat resembling the outline of the membrane in Maupas' figure. As the animal has frequent periods of rest, it is easily viewed under an immersion lens, and all the circumoral appearances are easily resolved into cilia. As the body in the natural state is curved, these bunches of cilia project vertically upwards, and their ends appear as a semi-ring of dots around the mouth, and it is difficult to decide exactly how they arise. When the animal, however, is slightly compressed as in the figure, they are seen to arise from two small lobes ( $l_1$ ), each of which carries a brush of cilia. From another small lobe ( $l$ ) or papilla on the right side of the mouth springs a longer and rather stouter cilium ( $c_1$ ) than the others. This is in constant vibration, like a flagellum. From the lobe on the right side ( $l_2$ ) arises another longer and very fine cilium ( $c_2$ ). In certain views when the animal is lying quite unconstrained, it would appear as if the cilia coalesced at the bases and formed short trunks from which terminal

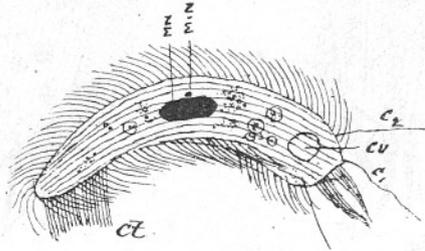


FIG. 27.—*Ancistrum mytili*, side view.  $\times 630$ . Camera lucida. *ct.*, cilia forming points of attachment;  $c_1$ , flagellum-like cilium;  $c_2$ , long cilium; *MN.*, meganucleus; *MiN.*, micronucleus; *cv.*, contractile vacuole.

cilia spring; but I am not quite certain of this, as it is not evident when the bunches of cilia are straightened out by compression. Also the ends of the two bunches cross one another when quite unconstrained. When a side view of the animal is obtained (Fig. 27), these bunches of cilia are seen to project straight forward, and rest as do the posterior cilia on the branchial filament; but I have so far been unable to form any idea of how they function, or whether they play any part at all in conveying food to the mouth.

Quennerstedt was, I believe, perfectly correct in describing what he saw as a bunch of cilia, though he only saw the row on the left margin.

The contractile vacuole is situated near the mouth, but I cannot say, with Maupas, whether it is attached to the dorsal body wall. It is generally single, but I have occasionally observed two or three smaller contractile vacuoles. I have seen it functioning, which it does slowly, and there is no rhythm. I have not observed the anus, if there be any. The nucleus is median or slightly towards the upper half of the body. It is

sometimes as described by Maupas an "oblong bent into an arc"; but as in the case of many other ciliates, its shape is variable. Sometimes it appears as a straight band, sometimes a row of spheres in a curve, sometimes a few spheres irregularly placed. There is a small spherical micronucleus (MiN) near the meganucleus (MN). The animal is very uncontractile, and easily stains with methyl green and acetic. The easiest way to examine it is to tease out a small piece of branchiæ, and press it down tight beneath a coverslip. The animal is so small that the thickness of the crushed branchiæ protects it, and it may be easily examined and if required fixed and stained *in situ*.

#### LIONOTUS FASCIOLA (O.F.M.).

When Wrzesniowski (28) found that *Loxophyllum fasciola* and *Lox. folium* were ciliated only on the ventral surface, he created the genus *Lionotus*, sometimes incorrectly written *Litonotus*, to include them, and two other species observed by him, and so separate them from other *Loxophyllids* (Wrzesniowski, 28, quoted by Maupas, 20). However, as Maupas points out (20, p. 507), Wrzesniowski should have considered whether a naked dorsal surface is not characteristic of all *Loxophyllids*, and has himself shown it to be the case with *Lox. meleagris*, *Lox. rostratum*, *Lox. lamella*, and three other species. Maupas, therefore, retains the generic name, *Loxophyllum*, and describes as a new species *Loxophyllum duplostriatum*, which apparently only differs from the ordinary form in having a double striation on the dorsal surface.

What is apparently the same animal has been described by various authors as follows:—

As *Lionotus fasciola*—Wrzesniowski, Schewiakoff, Calkins, Kent, Levander.

As *Vibrio fasciola*—O. F. Müller.

As *Amphileptus fasciola*—Ehrenberg, Dujardin, Eichwald, Lachmann.

As *Loxophyllum fasciola*—Claparède and Lachmann, Andrassowna.

As *Loxophyllum duplostriatum*—Maupas, Rees, Andrassowna, Gourret and Roeser.

As *Litonotus trichocystus*—Stokes.

The titles of the different papers will be found in the Bibliography at the commencement of No. XIII, Ciliata, Nordisches Plankton (16).

The descriptions of the general forms do not vary much. At Plymouth the ciliate is fairly common, and is often found in numbers in the film on the top of dredgings. Isolated individuals are not often met with.

In shape it is slightly sigmoid. The ventral surface is flat and ciliated, the dorsal surface naked, and slightly arched. The body tapers gradually to the anterior end, where it has a slight dorsal turn; but there is no hooked rostrum, as in *Lox. rostratum*, nor any hyaline margin or caudal region. The body ends posteriorly in a rounded point (Fig. 28). With the above exceptions it resembles *Lox. rostratum*. The neck or pro-

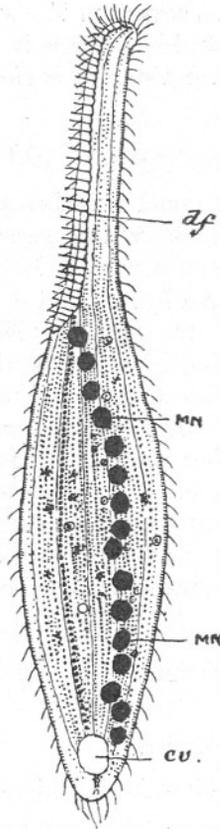


FIG. 28.—*Lionotus fasciola*. Dorsal view. *df.*, dorsal furrow with stout cilia; *MN.*, meganuclear elements; *cv.*, contractile vacuole.

boscis forms about half the length of the whole animal when the animal is at rest, but longer when swimming; in fact, the neck portion is much more elastic and contractile than the rest of the body. When swimming the total length of the Plymouth form varies from .3 to .45 mm., and the average greatest breadth .045 mm. Calkins gives the length as .4 to .6 mm., Maupas, .3 mm., Schewiakoff (for middle-sized animals), .08 to .1 mm. length, and .017 to .02 mm. breadth.

A furrow runs the whole length of the left margin of the proboscis (the animal lying with the dorsal surface uppermost). Within this furrow lies the mouth opening. Schewiakoff says this consists of a long slit, and Calkins alludes to the "elongate mouth." I was unable to observe accurately how the mouth lies within the furrow. Maupas says that it lies on the left margin of the ventral face at the base of the neck or proboscis, and that it is completely closed and invisible ordinarily, and only to be detected when the animal swallows its prey. On the dorsal margin of the furrow there is a row of rather longer and slightly stouter cilia, which are, according to Maupas, slightly curved at the extremity, and were compared by Dujardin to a "mane" (crinière). It appears to me that in the Plymouth specimens they are certainly longer, and not so fine as the ventral cilia, although Maupas says that they do not differ from the latter. But they are by no means so marked or active as peristomial cilia generally are; for example, the peristomial cilia of *Spirostomum*. The ventral cilia, according to Schewiakoff, rise from papillæ lying in seven or eight furrows. I have in Plymouth specimens counted ten rows of ventral cilia, but cannot decide whether the lines on which the cilia stand are furrows, or thickenings of the pellicle. Schewiakoff admits that they are only visible in starved specimens.

In the dorsal surface, which is without cilia, are four to five exceedingly fine striations. I cannot determine whether they are furrows or thickenings of the pellicle. Maupas describes a variety with five or six dorsal striations, and he describes and figures their appearance under very high magnification. On this character he founds a new species, *Loxophyllum duplostriatum*, which, in other respects, closely resembles *Lionotus fasciola*.

Schewiakoff observed the anus at the posterior end of the ventral margin of the body, and above it the contractile vacuole, which discharges on the dorsal surface. I have not seen the anus. There is a large vacuole generally visible at the posterior end, but I have not seen it function. Calkins says that the contractile vacuole is double or multiple at the posterior end.

The meganucleus, according to Schewiakoff, consists of two oval masses, connected by fine strands, which are only visible when the nucleus is isolated from the animal, and probably are extensions of the nuclear membrane. There is a small micronucleus.

Calkins describes the macronucleus as double, both parts spherical, but not connected as Schewiakoff contends.

Maupas says that the macronucleus consists of two nearly oval portions placed near one another in the line of the body axis; but that it is not uncommon to find four or five bodies differently placed as regards one another, and at a time when the animals give no sign of preparing

for division. The nucleolus he states to be a small single or double sphere, but in some cases it was absent. I have not found the micro-nucleus in any specimen.

In none of the animals examined during the months of January, February and March did I find the double macronucleus. In one individual there were three large spherical masses. In others a number of smaller spheres, from twelve to seventeen, arranged in the long axis of the body, as shown in the figure. This may be compared with the case of *Spirostomum lanceolatum*. I have never seen *Lionotus fasciola* dividing or conjugating.

Calkins states that in conjugation a large form unites with a smaller one, the mouth parts being connected, and gives a figure.

Schewiakoff says that the body is colourless.

Calkins, that it is frequently brown or light yellow in colour. The Plymouth variety is light yellow, with darker granulations, and larger food particles.

Schewiakoff describes the habits, feeding, etc., of the animal in considerable detail.

#### DYSTERIA ARMATA (Huxley).

*Huxley* (17); *Entz* (10); *Kent* (18).

This ciliate was first noticed by Mr. Dyster, of Tenby, on algæ coating the shells of *Patella* and *Littorina*, and brought to the notice of Professor Huxley, who was the first to describe it, and named the genus of which it forms the type, after his friend. Huxley pointed out that *Dysteria* closely resembles *Euplotes monostyla*, and *Chlamydon mnemosyne* of Ehrenberg in structure; but P. Gosse (*Journal Microscop. Science*, 1857, p. 138) expressed the opinion that the structure of *Dysteria* was too complicated for an Infusorian, and that its true position was probably nearer to *Monocerca* and *Mastigocerca* among the Rotifera; at the same time suggesting that *Dysteria* might be an annectant form between the Rotifera and Ciliate Infusoria.

Huxley, however, pointed out that an animal taking solid nutriment, but without an alimentary canal, possessing a contractile vacuole and locomotory cilia, and reproducing by transverse fission, could hardly belong to any but the class Infusoria; and further, that the possession of a sort of shell or lorica, a submarginal ciliated groove round a large part of the body margin, and the inequality of the two lateral halves of the body, clearly point to the nearness of the animal to Ehrenberg's *Euplota*. In fact, were it not for the amethystine spot, and the peculiar oral apparatus, Huxley would have been disposed to regard *Euplotes macrostyla* and *Dysteria armata* as identical.

In spite of certain possible analogies between the manducatory appara-

tus of some Rotifera and the "apparatus" of Dysteria, Huxley saw no grounds for regarding the latter as an annectant form between the groups.

The shape is ovoid. Length, .08 to .125 mm.; breadth, .05 to .06 mm. Huxley has: length,  $\frac{1}{350}$  to  $\frac{1}{250}$  inch, and breadth,  $\frac{1}{400}$  to  $\frac{1}{350}$  inch.

The body is divided by grooves into two unequal parts (Fig. 29). The upper or dorsal groove (dg) is wider and shallower than the ventral

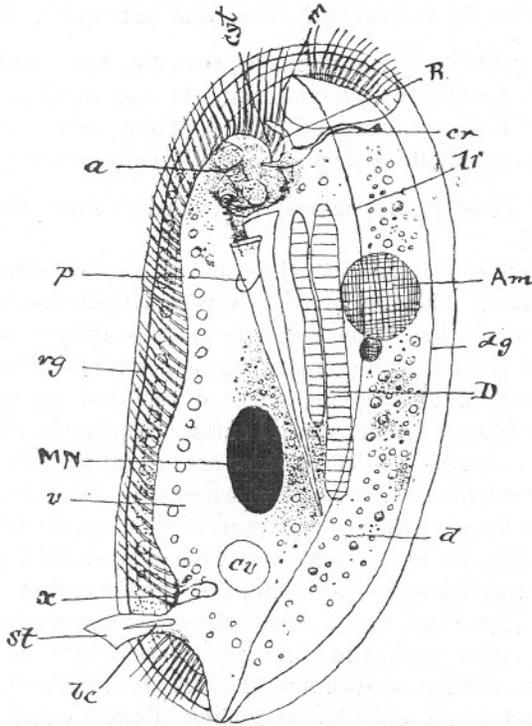


FIG. 29.—*Dysteria armata*. Ventral view. *cyt.*, cytostome; *m.*, obtuse ending of ridge; *cr.*, curved rod at bottom of oral fossa; *R.*, rod-like organ; *lr.*, longitudinal ridge; *Am.*, amethystine spot; *D.*, ingested diatoms; *d.*, dorsal area of ventral surface; *v.*, ventral area of ventral surface; *st.*, style; *bc.*, blind canal; *x.*, sac-like body, Entz's "Safträume"; *MN.*, meganucleus; *p.*, posterior mass of "apparatus"; *a.*, anterior mass of "apparatus"; *cv.*, contractile vacuule; *dg.*, dorsal groove; *vg.*, ventral groove.

(vg), which is deep and narrow. Anteriorly the dorsal and ventral grooves run into one another, but posteriorly unite for a short space. The upper dorsal or right surface is convex, and overlaps the ventral on all sides. The lower ventral or left is slightly concave, and is divided by a ridge (lr) into a larger ventral (v) and smaller dorsal (d) area. This ridge ends anteriorly in an obtuse point (m), and pos-

teriorly forms one side of a triangular termination, which is sometimes pointed and sometimes more obtuse. The upper and lower surfaces are thinned out, and when viewed laterally the animal bears a resemblance to a bivalve shell. The surfaces are covered by a very clear hyaline pellicle, of sufficient toughness to allow of the protoplasmic body contents being extruded under pressure, leaving the pellicle and the interior pharyngeal arrangements undisturbed.

Entz describes the ventral plate somewhat differently. He says:—

“The left valve is evidently smaller than the right, and its anterior free margin is peculiarly scalloped out, the thin margins of the inner curves are often turned over, and from the points arise curved wrinkles or folds which gradually disappear towards the posterior.”

A copy of one of Entz's figures is attached to make the description clear (Fig. 30).

This description of the left plate does not apply to any of the individuals I have examined. All agree in every respect with Huxley's description. In optical section a line which might be called scalloped, is to be seen; but the angles are not acute; moreover, it lies between the dorsal and ventral surfaces, and represents a part of the oral apparatus. When the animal is lying with the ventral surface uppermost, the cytostome (cyt) may be seen near the left anterior angle, and just below the ridge. It lies at the bottom of a deep fossa, which replaces the dorsal and ventral grooves. Huxley says that the left wall of this fossa is thickened, and projects inwards, so as to form a cushion-shaped lobe, clothed with remarkably long cilia—which are continued into the oral aperture itself—the posterior ones being large, usually directed transversely to the axis of the body, and having at times the appearance of vibratile membranes. It is difficult to distinguish definitely the exact boundaries of the cushion, and I have not found any cilia resembling vibratile membranes.

There is, however, in the oral fossa lying below the ventral cilia, a rod-like organ (r) which beats intermittently, but not rhythmically with the other cilia. Huxley has drawn this in his figure, but has not alluded to it in the description. The bottom of the oral fossa is, says Huxley, strengthened by a curious curved rod (cr), terminating in a bifid tooth superiorly, and lost inferiorly in the wall of the fossa. This rod appears to be a thickening of the margin, and is always apparent, forming part of the scalloped line alluded to above. I cannot determine the exact shape or position of the bifid head. On the ventral side of the mouth, and extending through about two-thirds of the body, is an arrangement of hard parts, which Huxley calls the “apparatus.” It consists of two portions, an anterior somewhat rounded mass (a) and an elongated, styliform, posterior portion (p) (Figs. 29, 31). The appearance of these

two parts in optical section does not vary, even after the body protoplasm has been expelled from the pellicle by pressure; but it is difficult to determine the structure of the anterior mass. I cannot follow Huxley's description in every detail, but as I have no alternative to suggest, will quote his own words and reproduce his drawing in Fig. 31:—

“It is very difficult to assure oneself of the precise structure of the anterior portion. It would seem to be a deep ring composed of three

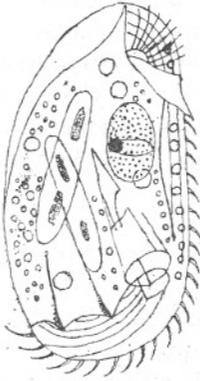


FIG. 30.

FIG. 30.—*Dysteria armata*. Ventral view after Entz.

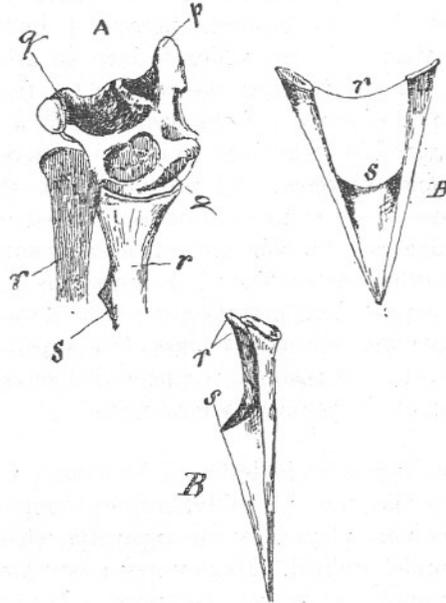


FIG. 31.

FIG. 31.—*Dysteria armata*. Enlarged drawing of “Apparatus” (after Huxley). A., anterior portion; qq., superolateral portions; p., inferior azygos portion; BB., two views of styloid portion; s., apparent downward process, which is really membrane connecting two styles; rr., nail-like heads of styles.

pieces—two supero-lateral, and mutually corresponding (q) united with a third, inferior, azygous portion (p). The latter is somewhat triangular, with a broad base, and rounded obtuse apex; the latter being directed forwards and immediately underlying the oral aperture, while the former is turned backwards and unites with the two supero-lateral pieces. Each of these is concave internally, and convex externally, so as to form a segment of a circle, and present a clear median space, the optical expression of either a perforation or of a much thinned spot. The anterior edge of each supero-lateral piece is nearly straight, but the posterior

is convex, and it is by this edge that it articulates with or is opposed to the anterior extremity of the posterior division of the apparatus. Viewed laterally this posterior portion appears to consist of two styles, which are somewhat like nails in shape; their anterior extremities being truncated, so as to present a sort of nail head, while the posterior extremity seems to take to a fine point. Rather in front of the middle of its inferior edge each style seems to give off a short process downwards (S), and this process is in botanical language decurrent upon the style. Careful examination of the dorsal or ventral aspect of these parts shows that the decurrent process is, in fact, only the expression of a delicate membrane, which is bent so as to have a ventral convexity, and connects together the two styles. It might be said, therefore, that the posterior part of the apparatus is a triangular membrane, deeply excavated in front, bent so as to be convex downwards, and having its margins thickened and produced into styliform enlargements. This curious piece of mechanism is directed upwards and backwards, and terminates in the substance of the body without any apparent connection with other parts. The whole apparatus is movable. The posterior portion is pushed against the anterior, and the heads of the styles come into contact with the convex edges of the supero-lateral pieces, and push them forwards; the posterior portion is then retracted, and the whole apparatus returns to its previous arrangement."

The apparatus is destroyed by caustic potash, but not by acetic acid and is therefore, probably, entirely composed of animal matter.

The part played by the apparatus when the animal is feeding is as yet undetermined. Huxley never saw how the apparatus functioned; but noted that in one case, when a *Dysteria* had swallowed a piece of *Oscillatoria*, so long that one end was projecting from the mouth, the movements of the "apparatus" took place as many times as twenty to the minute.

Mr. Dyster stated that the frond of *Oscillatoria* was "swum upon" rather than seized, ingestion being accomplished by a smooth gliding motion, apparently without displacement of the styles, but that when the act was completed the styles gave a kind of snap and moved slightly forwards. I have myself seen the animal apparently gliding on the fronds of the algæ, while feeding, and others have told me that they have seen the same. As soon, however, as the animal is arranged for observation under a sufficiently high power to observe the action of the apparatus accurately, the *Dysteria* is put off his feed.

As the fronds of algæ are cut off in nearly equal lengths, and lie parallel to the dorsal margin, it may be conjectured that the "nails" and membrane form a kind of channel by which the alga is guided towards the

posterior end of the body, and that the nail heads may play some part in cutting or breaking off the frond, at the required length.

Mr. Dyster thought that the *Oscillatoria* passed *through* the anterior ring-like portion of the apparatus. Huxley had not seen the animal feed, but on structural grounds thought that the food would pass above the anterior ring.

Entz (10) does not agree with Huxley's interpretation of the "anterior somewhat rounded mass," and writes as follows:—

"Above this dagger-shaped skeletal rod, a complicated rigid ring was distinguished by Huxley, composed of two paired and one unpaired skeletal parts, and not unlike the larynx of a mammal. I must confess that I could not convince myself of the presence of this ring. According to my observations the portion of the gullet anterior to the dagger-like skeletal piece is not rigid at all, but forms a tube of thin cuticle, which changes its outline according as it rolls in or out. In the unrolled state the anterior part of the pharynx resembles a loosely rolled paper funnel forming a wide channel with a circular gaping mouth opening, which the dagger-shaped skeletal piece serves to keep in place, being as it were the tube of the funnel. In the rolled-up state this part of the pharynx appears as a very inconspicuous tube closely rolled round the dagger-shaped piece, so that one cannot make out how the rather large pieces of *Oscillaria* that serve for food manage to get through it."

Whatever may be the true interpretation, Entz's figure does not represent the appearance of the apparatus as I have seen it, and as he himself admits it will not account for the passage of the fronds of algæ, or the position they assume dorsally and parallel to the apparatus.

Huxley notes one contractile vacuole a little behind the middle of the body, and my observations agree. It is generally posterior, and functions regularly. Entz states that he has constantly seen four, all in the left valve; two in the neighbourhood of the ventral margin, and the other two in the ventral margin. I have seen other vacuoles than the posterior one with the appearance of contractile vacuoles, but not functioning. Near the contractile vacuole, close to the style there is a smaller sac-like oval body (x), which does not appear to contract. Huxley describes it as having the long axis ( $\frac{1}{3000}$  inch) directed upwards, and with a small central cavity. Entz also notices the presence of this vesicle under the name of "Safträume." I have not found this vesicle in all specimens examined, and am doubtful whether it is a persistent organ.

The Style (*Griffel*) is a scimitar-shaped organ (Huxley compares it to a boot, and Entz to a penknife blade), lying in the deep part of the ventral groove at the posterior end. Huxley locates it at about  $\frac{1}{3}$  of the whole length from the posterior extremity. It contains a blind canal. It is

capable of considerable play in the horizontal plane between the valves, and a splaying outwards of the dorsal valve admits of a certain amount of vertical motion.

Huxley says that the toe (he is comparing it to a boot) appears to be viscid, and so readily adherent to any foreign object. The animal certainly appears to use it as a pivot, about which the whole body turns. While so resting nutriment is swept towards the mouth by the neighbouring cilia. Behind the Style is a bundle of long, stout cilia—Huxley alludes to one particularly large stout one among these—but this I cannot detect. Similar cilia extend along the right margin of the ventral plate (viewed dorsally), and extend into the oral fossa. There is another tuft of similar cilia at the anterior end, just to the left of the ventral ridge. On the clear ventral margin, where the dorsal valve overlaps the ventral, rows of very fine striæ may be observed. These carry cilia, much finer and closely set than the row above described. Huxley does not mention them. Entz does, and shows them in his figure.

On the left of the pharynx in the anterior part of the body is a large rose-coloured sphere, apparently containing a clear homogeneous fluid. This Huxley calls the "amethystine body." It is situated in the convex part of the body, and generally a small similar sphere is connected with it. I have seen cases in which two amethystine bodies were present: one, as described above, and the other in the middle of the body. The object of these is not, as far as I am aware, determined. Entz suggests that they may be reservoirs for the colouring matter resulting from the algæ broken down in digestion. I have not observed that they discharge their contents.

The protoplasm of the left valve contains many fine granules, mingled with larger refringent globules, and along the ventral margin of the right valve there is a row of rather large refringent spheres whose position is constant.

Nucleus. Huxley did not find the nucleus.

Entz describes it as a clear oval body lying just below the middle of the body, and near the nail or dagger-like apparatus. It is often found divided by a nearly median plane, transverse to the major axis. I have seen it in this stage, and in others, when it formed a very irregularly shaped mass, or masses. In the ovoid form the anterior portion stains more deeply than the posterior. In the living animal the meganucleus is observable as a clear ovoid space.

Entz observed the micronucleus. I have failed to do so. Division is by transverse fission, and Huxley notes that the apparatus disappears and is reproduced during the process. Only rudiments of it were noticeable in each half of the dividing animal. My observations are similar.

Dysteria is common among algæ in Drake's Island Tank during March and April.

Dysteria is evidently a highly specialized ciliate and would repay further investigation, particularly as to the structure and function of the apparatus. The hardness of these parts makes it probable that something might be done by the recent methods of micro-dissection.

ÆGYRIA OLIVA (Clap. et Lach).

Claparède and Lachmann (5); Gruber (14); Rees; Entz (10); Kent (18).

This ciliate was placed by Claparède and Lachmann among the Dysteriidae; but Entz points out that both in general form and in the shape of the cytopharynx it much more closely resembles the Chlamyodontidae, and especially *Trichopus dysteria*. He, therefore, included it in that family.

It is not very common in Drake's Island Tank, and I have found only solitary individuals, and this also is the experience of Claparède and Lachmann and Entz.

Entz has described *Ægyria oliva* very fully, and with excellent figures. Claparède and Lachmann and Kent describe shortly, and their figures are unsatisfactory; Kent's is only a reproduction of Claparède and Lachmann's.

This genus possesses the singular character of being able by contraction to bring the dorsal and ventral body surfaces together like the valves of a mussel-shell with, at the same time, torsion of the body round its long axis.

In consequence of this the appearance of the animal varies, and Entz describes it under three forms: the Flat, the Oliva, and the "Rolled up."

The Flat and the Oliva are the only two forms I have seen; but the "Rolled up" is only a further extension of the Oliva, combined with torsion.

I follow Entz description, which applies equally to Plymouth specimens.

In general form the "Flat" variety may be compared to a mussel shell with unequal valves (Fig. 32), the ventral side of the ciliate representing the left, and the dorsal side the right valve of the shell. The left body margin represents the hinge edge, and the right body margin the outer edge of the mussel.

Starting from the posterior end the right margin of the body describes a gentle curve forward and upward, and then bends to the left, and traces out the rounded and mobile frontal lobes. From this point the left body margin describes a very flat S curve, and joins in to form the smaller, rounded, posterior lobe. The ventral side is flat; but the dorsal, particularly the posterior portion, slightly arched. The ventral surface is finely

striated. The striæ follow pretty closely the curves of the body margin, and carry cilia, which are fairly long and thick, and almost bristle-like, especially on the frontal lobe. The dorsal surface is smooth. In the right half of the ventral surface the ciliated striæ run straight towards the terminal point of the posterior lobe, but in the right half form a kind of whorl around the style.

The style is a singular conical or dagger-shaped, very motile object, which, according to Entz, consists of a number of conical surfaces, one within another and closely pressed together, so as to form a solid conical mass. His idea is that the rows of cilia pressed together form lamellæ,

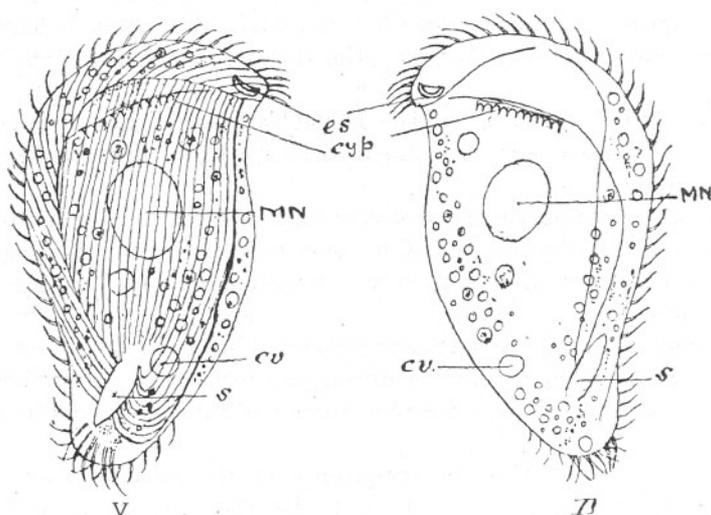


FIG. 32.—*Ægyria oliva*. Flat form. D., dorsal; V., ventral view; *es.*, eye spot; *cyp.*, cytopharynx; *MN.*, meganucleus; *cv.*, contractile vacuole; *s.*, style.

and then, coiled spirally together, form the conical style. Close below the style is a group of five or six very stout cilia.

The oesophagus or cytopharynx is a short, wide, flattened tube lying obliquely from right to left below the anterior lobe, and surrounded by broad short rods. As the anterior portion of *Ægyria* is generally very transparent, it is easy to see these rods, under a high power, either from the ventral or dorsal surface.

Of the mouth, Entz writes :—

“ In *Ægyria oliva* the mouth does not open directly on the ventral surface as it appears to do, but between the lamellæ of the frontal lobes, similarly to *Chlamydon cyclops*. The whole body of the flat form of *Ægyria oliva* may be compared to an unequally valved mussel. The ventral face represents the left, and the dorsal the right valve ; the left

body margin the hinge border, and the right the lower margin of the mussel. The right body margin from the extremity of the frontal lobes to the mouth, and from the right angle of that further along the right margin, splits into a small zone, and carries food to the mouth; and in this channel there is always a water vortex (caused by cilia). The inner margin of this slit is finely striated, like the flat mantle of mussel valves. Dorsally viewed the entrance of the gaping slit may be seen at the point of the frontal lobe."

Entz description is not very clear, and I have not seen the split at the point of the frontal lobe. In fact, the frontal lobe in his figure has been given a twist, which appears unnatural. The ciliated small

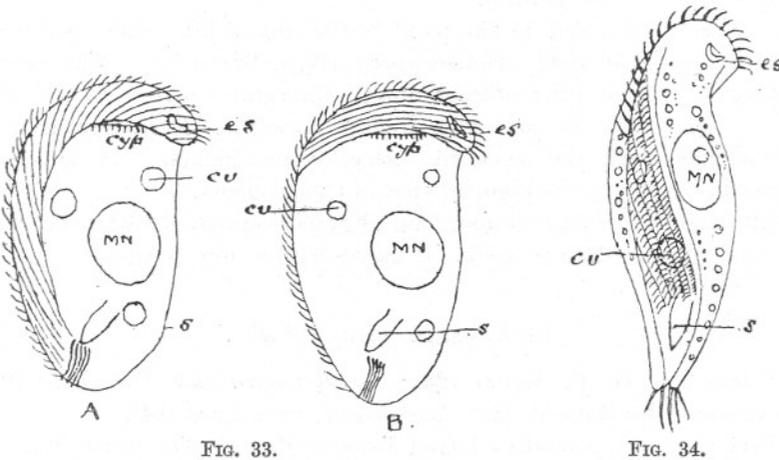


FIG. 33.—*Aegyria oliva*. A., oliva form after Entz; B. oliva form with overlap parallel to transverse axis. Lettering as in Fig. 32.

FIG. 34.—*Aegyria oliva*. "Rolled" form, after Entz. Lettering as in Figs. 32 and 33.

zone, and the water vortex, with the rods of the cytopharynx, are all easily seen.

I do not think that Entz three forms—Flat, Oliva (Fig. 33), and "Rolled up" (Fig. 34)—can be considered permanent forms. In the Oliva form he represents the doubling over of the ventral surface as occurring along the left margin and parallel to the longitudinal axis of the body—such bending accompanied by body torsion would produce the "Rolled up" form figured and described by him. But I have come across instances in which the doubling over occurred along the frontal line, and, therefore, at right angles to the longitudinal axis. Moreover, more than one-third of the dorsal surface was covered.

No torsion would be possible, or would produce Entz "Rolled-up"

form. It appears to me, therefore, that the overlapping of the surfaces is a matter of circumstance, and may occur at either margin, accompanied or not by torsion of the body.

I have seen three contractile vacuoles—one at the posterior end, and the others in different parts of the body—and I saw all pulsating.

The meganucleus lies below the cytopharynx, a large round oval or circular mass. I did not notice the transverse division mentioned by Entz. Entz also states that he saw the micronucleus in living individuals.

*Ægyria* is generally coloured by the various algæ on which it has been feeding; but the protoplasm of the body is singularly clear, and interferes very little with observation.

At the anterior end, at the point of the frontal lobe, there is a well-defined, dark-coloured, eye-like speck (Figs. 32 to 34). The colour appears to vary in different individuals. Entz states that it is a concave-convex lens, with the concavity directed forwards. Kent regards it as homologous with the so-called "amethystine globule" in Huxley's *Dysteria armata*, or the pigment spot in *Ophryoglena*.

Although only  $\cdot 08$  to  $\cdot 14$  mm. long, *Ægyria* is easy to detect on account of its shape and the eye-speck. It moves with a slow, irregular roll.

#### LACRYMARIA OLOR (O.F.M.).

*Vibrio olor* O. F. Muller (23); *Trachelocerca olor* Ehrenberg (9); *Lacrymaria olor* Bütschli (3); *Lacrymaria olor* Penard (24).

Very plentiful in Drake's Island Tank in March. The body (Fig. 35) is spindle-shaped, prolonged posteriorly into a narrow tail, which is very contractile, sometimes attaining a length equal to that of the body. The body itself is not, or very slightly, contractile; but the neck is enormously so, so that the whole length of the animal may reach 1.3 or even 1.5 mm. The length is, therefore, extremely variable. On an average the length of the body, including the tail, ranges from  $\cdot 11$  to  $\cdot 16$  mm., the tail being rather less than half the body, and ordinarily the neck may be four to six times the length of the body and tail. Although the neck is so elastic the body always retains its spindle shape.

The animal is very transparent, and although there are many food vacuoles, the food must be very fine, as it hardly interferes with observation.

The body and neck are marked with spiral striæ, which become straight when the animal is at its maximum extension. Being so transparent it is possible to see the striæ on both sides, and receive the impression of cross striation, and thus the animal has been described as possessing longi-

tudinal and transverse striæ. There are actually only single spirals, the angles varying according to the degree of extension. The cilia lie along the striæ.

Penard, in describing the fresh-water *Lacrymaria olor*, says that there are generally two contractile vacuoles, one of which is always posterior, the posterior being the important one, and always present. I have in the salt-water form seen two and three vacuoles, one posterior, and two in other parts of the body, but have never observed any pulsation.

The cytostome is terminal, and narrow, with a long, narrow cytopharynx, which is highly distensible. The exact shape of the terminal end of the neck in which the cytostome is situated is difficult to observe, because of the extreme narrowness of the neck, produced by extension and the restlessness of the animal. When contracted to the average

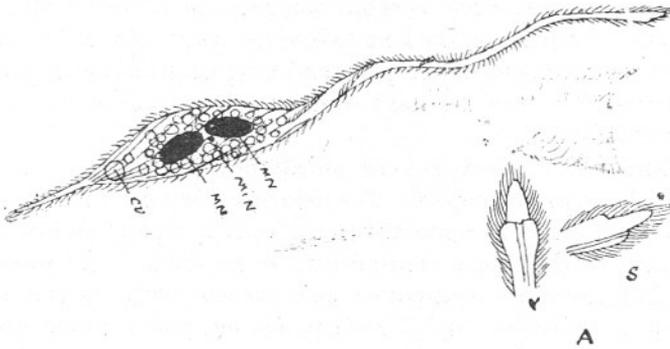


FIG. 35.—*Lacrymaria olor*. MN., meganucleus; MiN., micronucleus; cv., contractile vacuole; A., mouth enlarged; v., ventral; s., side view.

length the neck appears to terminate in a kind of cone, surrounded at the base by a circlet of cilia. After very careful watching it appears to me that the neck, when the animal is at maximum extension, terminates in a long pointed lobe, with two short obtuse lobes at its base, and between these lobes lies the mouth. Behind the long lobe and slightly below its base is a smaller prominence, as shown in the drawing. The whole are surrounded by cilia, but I did not detect any definite ring of cilia. When the animal is more contracted, and the lobes are withdrawn, the appearance of a terminal ring is probably produced.

It appears to be the shape of the mouth which decides the difference between *Trachelocerca* and *Lacrymaria*. The "stopper-like" distal end of the neck when the animal is contracted more resembles the *Lacrymaria* type, while the oral lobes under greater extension suggest *Trachelocerca*; and Quennerstedt describes as *Trachelocerca tenuicollis* a form which resembles the Plymouth form. In his figure the mouth is not very

definite. Penard's description of *Lacrymaria olor* so closely resembles that under reference, that I retain the genus *Lacrymaria*. The distinction between *Lacrymaria* and *Trachelocerca*, as fresh-water and marine forms, appears to me to be quite arbitrary.

There are trichocysts distributed irregularly through the body, and in the neighbourhood of the cytopharynx. These trichocysts discharge a filament sometimes .01 mm. in length.

The meganucleus generally appears as two oval masses lying near the centre of the body with the micronucleus between. Sometimes, however, the oval bodies are club, horseshoe, or dumb-bell-shaped, and at others both are fused into one large mass, which may be of any of the above forms. These arrangements no doubt depend on the stage of life of the animal, and are only true for that particular stage. The nucleus may be therefore represented conventionally by two oval masses.

*Lacrymaria olor* as a whole is rather sluggish, and moves slowly forward in the water, revolving on the long axis of the body. The neck, however, is very active, darting forward rapidly and extending, and again retracting.

It appears to be very resistant to the concentration of the sea-water in which it is living.

Any damage to the body is very quickly repaired. Very often the extended neck is seen to snap off. The detached portion then swims about alone, and if it comes in contact with the body is rapidly absorbed by it. The renovated whole then continues to swim about; and probably a new head and neck are regenerated, as is the case with *Dileptus gigas*.

Division is transverse, and Penard points out that it might easily be imagined to occur along a diagonal line, as the necks and tails of the two new division products increase before actual separation takes place, thus giving the idea that two animals are lying side by side.

Kent (p. 516) states that in company with an abnormal abundance of *Trachelocerca olor*, he found many forms resembling the *Lacrymaria lagenula* of Claparède and Lachmann. After careful watching he found that the *Lagenula* gradually developed a neck, and came in every respect to resemble *T. olor*.

Finally, he came to the conclusion that the short-necked *Lagenula*, like zooids, were the derivatives by transverse fission of a long-necked animalcule, and represented the hinder moiety of the division process. As far as I am aware this observation has not been repeated; but there does not seem any objection to its probability, as it would only imply that division was completed before the neck of the hinder moiety had commenced to develop to a marked extent.

Beyond the functioning of the contractile vacuoles I can note no difference between the marine form of this ciliate I have observed and the descriptions I have read of the fresh-water form.

## LOXOPHYLLUM ROSTRATUM (Cohn).

Described by Cohn (6) and figured, as a new species, compared with Plymouth examples, Cohn's Fig. 8 makes the rostrum too pronounced and acute, even when the animal is completely retracted. His Fig. 9 is a good representation of the animal when lying quiescent. But when swimming the neck is more extended, and can be elongated, so as to give

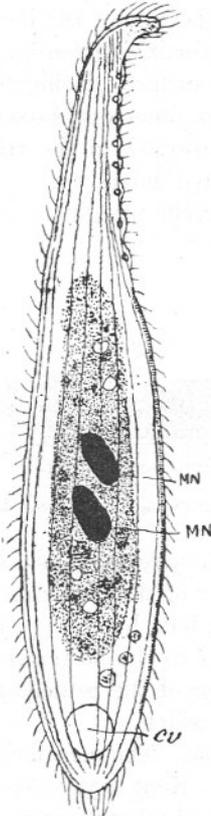


FIG. 36.—*Loxophyllum rostratum*. Dorsal view. *MN.*, meganucleus; *cv.*, contractile vacuole.

a total length of .8 mm. Cohn gives no measurements. Hamburger and Buddenbrock (16) gives the length as .18 mm.; Kent (18),  $\frac{1}{14}$  inch (about .17 mm.). I have measured a large number under ordinary conditions and find an average length of .3 mm. to .4 mm. The body is leaf-like (Figs. 36 and 37) and quite flat on the ciliated ventral surface, while the dorsal surface is convex, or may have one or two prominent curved humps. The degree of curvature depends on the amount of food present.

The body is surrounded by a delicate hyaline lamina, the presence of which distinguishes *Loxophyllum* from *Lionotus*, which in other points it resembles. The body is prolonged anteriorly into a delicate tapering neck, which is possessed of great flexibility, and plays the principal part in the general elongation of the body. The neck terminates in an uncinete rostrum, on which the cilia are longer than those of the rest of the body, except a few at the posterior extremity, which, when the animal is extended, is pointed. It does not appear that the rostral termination is of any denser material than the rest of the body, but when the animal is under a coverslip and contorting violently, the rostral end frequently breaks off. The fractured surface quickly regenerates, and the animal continues swimming. When quiescent, *Loxophyllum* lies on the ventral surface, with the rostrum turned to the right. When swimming the rostrum is frequently elevated dorsally.

Below the rostrum the right margin of the neck has an undulating

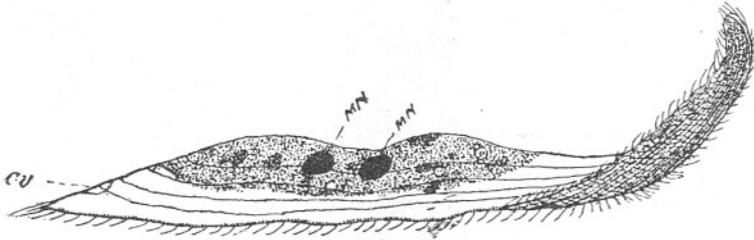


FIG. 37.—*Loxophyllum rostratum*. Side view. Lettering same as Fig. 36.

outline, and a row of trichocysts extends from this undulating margin near to the apical extremity of the rostrum.

There are no dorsal cilia, but there are eight extremely fine striations extending from the anterior to the posterior extremity. These may be either furrows or thickenings of the pellicle, forming small ridges. It is very difficult to determine which.

The meganucleus is double. The contractile vacuole is terminal, and I have seen it functioning. Kent says that there are one, two or three vacuoles; and Cohn that there are one, two, or more. There are numerous vacuoles containing food, etc., and these coalesce in varying degrees; but I have only seen one that can be called a true contractile vacuole, and that is the one at the posterior end.

The animal moves slowly, occasionally revolving on the long axis, and prying about with the rostrum. It is fairly common in Drake's Island Tank, and easy to recognize.

I have been unable to make out the mouth. Kent does not say anything about it. Cohn says that it is indistinct, and probably situated in a furrow.

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## Water Movement and Sea Temperature in the English Channel.

By

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With Two Diagrams in the Text.

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DURING the last three years further evidence has been obtained that water of relatively high salinity, from the Atlantic to the south-west of the entrance, enters the English Channel past Ushant (1).

It is of interest to summarize this evidence in view of the suggestion (2) that the English Channel is cut off from the Atlantic for considerable periods.

The surface samples of very high-salinity water, collected in the Channel by the Ministry of Agriculture and Fisheries, suggest the possibility of masses of oceanic water moving into the Channel past Ushant from time to time; and they further suggest that this oceanic water divides in the western end of the Channel, one part moving direct into the North Sea, through Dover Straits, and the other part turning and passing out northward between Land's End and the Scillies. This is discussed by Mr. J. R. Lumby (see p. 670 of the present number of this Journal).

Drift-bottle experiments carried out by the Ministry of Agriculture and Fisheries show a movement of water from the Channel into the North Sea. This is discussed by Mr. J. N. Carruthers (see p. 665 of the present number of this Journal).

Besides carrying planktonic organisms with it and in this way affecting the distribution of the fauna, and besides causing variations in the concentration of the inorganic salts in solution which are necessary for plant growth (9), this inflow of water from the Atlantic has an effect upon the temperature of the water in the Channel, causing variations from the mean temperature of the month, such as will have a marked physiological effect upon the fauna.

In order to indicate the magnitude of this temperature effect the following observations are not out of place: A rise of temperature in the sea causes an increase in the rate of oxygen consumption and metabo-

ism of most marine animals (3). This increase varies with the initial temperature, but within the limits within which the animal lives it is in the order of 10 to 15 per cent per degree of temperature. This presumably means that 10 to 15 per cent more food is required to repair waste. The similar magnitude of the effect of temperature on the velocity of ciliary and amoeboid movement has been recorded (4), and indicates that the

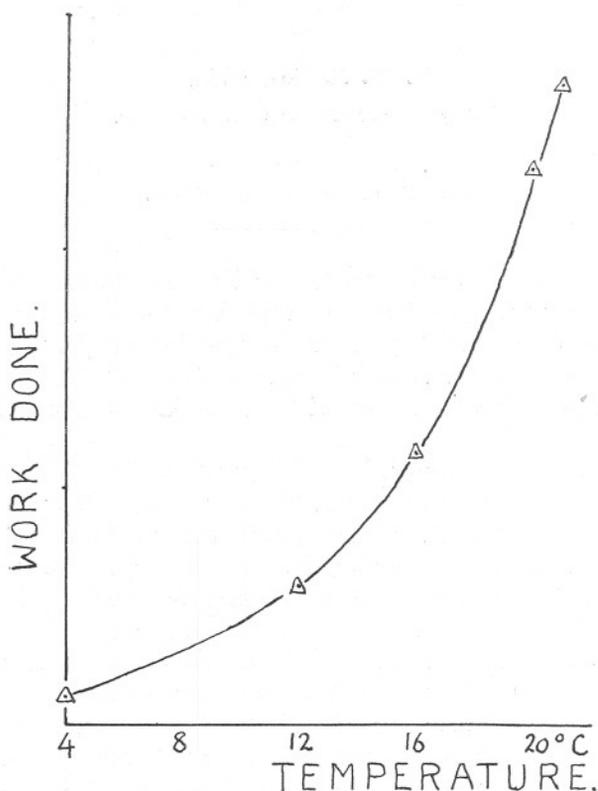


DIAGRAM A.

Relation between work done in unit time by excised heart of *Maia squinado* and temperature. (From kymograph record made by Dr. L. Hogben, July, 1924.)

capacity for movement of protoplasm is affected by temperature to much the same extent. This relatively enormous effect of temperature on the physiological processes in marine animals is also well illustrated by an experiment made in this Laboratory by Dr. L. Hogben and communicated to the writer. The excised heart of a *Maia squinado* was bathed with a saline solution at varying temperatures, and the rate and amplitude of the beat was recorded. At 4° C. the heart practically ceased

to beat, and above 21° C. it appeared to be injured. At temperatures between 4° and 21° C. *both* rate and amplitude increased with rise in temperature.

The work done by the heart muscle in unit time will be approximately proportional to the product of the recorded amplitude of the beat multiplied by the number of beats per unit time, in this case where it is working against the weight of the recording lever. This product is plotted against temperature in Diagram A, and shows the magnitude of the temperature effect on the heart muscle.

These considerations indicate that, within the limits of temperature experienced by an animal in the sea, its "rate of living" is increased in the order of 10 to 15 per cent for every degree centigrade rise in

TABLE I.

Temperature of Bottom Water at E1.	1921.	1922.	1923.	1924.
Over 15° C.	Early Oct. to early Nov.	Never.	Never.	—
14° C.	Early Sept. to early Dec.	Mid. Sept. to mid. Oct.	Never.	Never.
13° C.	Early July to mid. Dec.	End Aug. to early Nov.	Mid. Sept. to mid. Oct.	Late Sept. to end Oct.
Below 11°	—	End Jan. to end June.	Mid. Dec., '22, to end June.	Early Dec., '23, to early July.
10°	—	Early March to mid. May.	Mid. Jan. to end April.	Early Dec., '23, to end May.
9°	—	Never.	Never.	End Jan. to early May.

temperature; its requirements—oxygen and food—are increased in proportion.

Orton (5) has shown that the breeding season of many marine animals lies within comparatively small limits of temperature. Variations in the temperature of the sea between one year and another may materially alter the duration and time of the breeding season. If the time of the breeding season is displaced it may cause the young to appear at a time when their natural food "is out of season," in those cases where the food consists of diatoms or is dependent upon diatoms whose growth is controlled by sunshine as well as by temperature (10).

That the fauna is exposed to a very different range of temperature from one year to another is well shown in Table I, which refers to the bottom water at Station E1, 22 miles south-west of Plymouth.

That an inflow of Atlantic water is one of the factors influencing the temperature of the sea in the Channel, is clearly shown by the observations made every month at the Station E1. During October and Novem-

ber, 1921, there was a very rapid rise in salinity (6). On reference to Diagram B it is seen that the temperature of the ground and air had fallen below that of the surface water of the sea by early October. The whole column of water, from top to bottom, continued to *gain* heat for a further three or four weeks. These two points together show

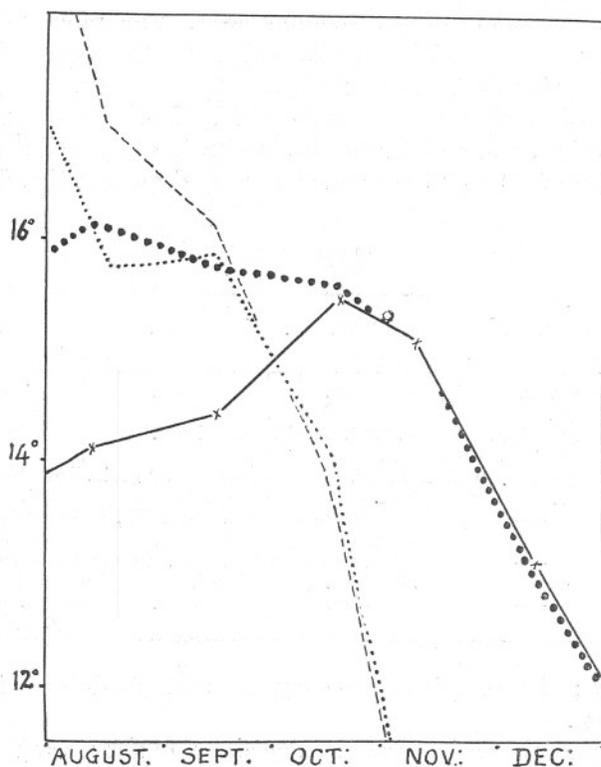


DIAGRAM B.

Station E<sub>1</sub>, 1921.

Thick line represents temperatures of a column of water at E<sub>1</sub> from top to bottom, as if completely mixed, calculated from the temperatures observed at different depths.  
 Heavy dotted line represents temperature of surface water at E<sub>1</sub>.  
 Fine dotted line represents mean air temperature on Plymouth Hoe.  
 Pecked line represents mean ground temperature 1 foot below surface on Plymouth Hoe.

that warmer water entered the area. Its salinity was characteristic of water occurring earlier in the year south-west of the entrance to the Channel.

During the same period in 1922 and 1923 there was no indication of any such considerable inflow of oceanic water at this station.

Furthermore, there is evidence that the loss of heat which occurred was largely controlled by local meteorological conditions (7).

Fig. 1, p. 679, of this Journal shows the variation in temperature of a column of water from top to bottom at E1. It is a fair curve drawn through points which were arrived at by calculating (integrating) the temperature of the whole column from the temperatures observed at a series of different depths, at each date when the Station was worked. It is possible, from it, to arrive at a very fair approximation of the temperature of the column at the middle of each month.

The following temperatures for the middle of the autumn months in 1921, 1922, and 1923 were obtained in this way.

	1921.	1922.	Difference. 1921-1922.	1923.	Difference. 1922-1923.
Mid. September	14.4	14.3	0.1	13.6	0.7 °C.
„ October	15.4	13.9	1.5	13.4	0.5
„ November	14.7	11.8	2.9	11.9	-0.1
„ December	12.9	10.9	2.0	10.2	0.7

Comparing 1921 with 1922, a very marked difference occurs suddenly in October and November, due to the inflow of water in 1921. Comparing 1922 and 1923 in the same way no such sudden marked difference occurs.

An inspection of the curve shown in Fig. 1, p. 679, leads to the conclusion that the inflow of oceanic water raised the temperature of the water in this area  $1\frac{1}{2}$ ° C. or more above what would have been its probable temperature in October, November, and December if no such inflow had occurred.

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## The Water Movements in the Neighbourhood of the English Channel—North Sea Junction. Drift Bottle Experiments.

By

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With 1 Chart in the Text.

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### REMARKS DESCRIPTIVE OF THE AVAILABLE DATA.

THE following short paper is based upon the results of very extensive experiments made with both surface-floating and bottom-trailing drift bottles, by the Ministry of Agriculture and Fisheries during 1920–21.

At each of 7 lightvessels in the Southern North Sea, 25 of each type of bottle were put out each week for a year. One of the lightvessels taking part in the setting adrift of these bottles was the *Sandettie*, a French lightvessel moored at the position 51°15'N.—1°55'E. The full experimental results from the carrying out of this programme are shortly to be published by the Ministry.

The lightship referred to is really within the North Sea, being situated near its southern extremity, but the movements of drift bottles put out there will obviously give us valuable information as to the water movements in the junction area between this sea and the English Channel. The participation of this French lightvessel in the experiments was rendered possible by the courtesy of the scientific officers of the "Office Scientifique et Technique des Pêches Maritimes." As was the case with the English lightvessels, the officers of the *Sandettie* lightvessel were engaged throughout the period during which bottle liberations were made, upon log and wind observations. The results of the latter have been published.\* The wind observations were made and recorded 6 times daily. Monsieur Heldt of the Station Aquicole at Boulogne-sur-Mer kindly lent the log books to the writer, in order that the wind data might be extracted. This was done, and a suitable conversion table was calculated, so that the French records (entered up according to the

\* H. Heldt, Les Courants de Marée au Bateau-Feu du *Sandettie*. *Notes et Mémoires* No. 27.

wind scale in use by the Service des Phares) would become comparable with the English lightship records. A cursory examination of the movements of the surface drift bottles and of the winds prevailing at the time, revealed a marked interdependence between them. Thereupon the wind data were worked up into such a form as would enable the degree of correspondence to be more clearly seen. The 2,200 single observations were so compounded as to yield the residual equivalents for periods of weeks, months, quarters, and for the whole year. This so-called residual wind is that wind which, supposed constantly blowing for the stated period, could be substituted for all the individual winds recorded during that period—in other words, it is the vector average of all the individual observations recorded, whereas the corresponding resultant would be their vector sum. This detailed study of winds was *a priori* absolutely necessary in order that it might later be possible to decide whether any seasonal changes which might appear to characterise the set or strength of the currents, were independent of, or operative through the prevailing winds, which might themselves be of seasonal incidence.

From the position of the lightship, direction sectors (the 16 main divisions of the compass) were drawn out, and the movements of the bottles referred to them. These sectors are shown on the key map.

#### THE MOVEMENTS OF THE SURFACE BOTTLES.

Of the 1,275 surface bottles put out at the *Sandettie* lightvessel, 852 were returned—a percentage recovery of 66·8.

If these 852 bottles be distributed over the 16 sectors, the following table is obtained :—

Stranding Sector.	N.	NNE.	NE.	ENE.	E.	SSE.	S.	SSW.	SW.	W.	WNW.	NW.	NNW.	All Sectors.
No. of Bottles ..	16	3	175	499	63	9	7	7	1	9	13	18	32	852

It is seen how greatly the E.N.E. sector predominates, followed in order of importance by N.E. and E.

Our present inquiry has the object of deciding the relative frequency of occurrence of the two surface-water movements.

Channel—→ North Sea  
and  
North Sea—→ Channel.

A glance at the key map will make clear to what directions we must devote attention. The fact of chief importance is not the gross number

of bottles which (having regard to the total returns of the experiment as a whole) stranded within a certain sector. We must ascertain the number of liberations from which bottles so stranded. The truth of this follows from the following considerations. If the current at a certain

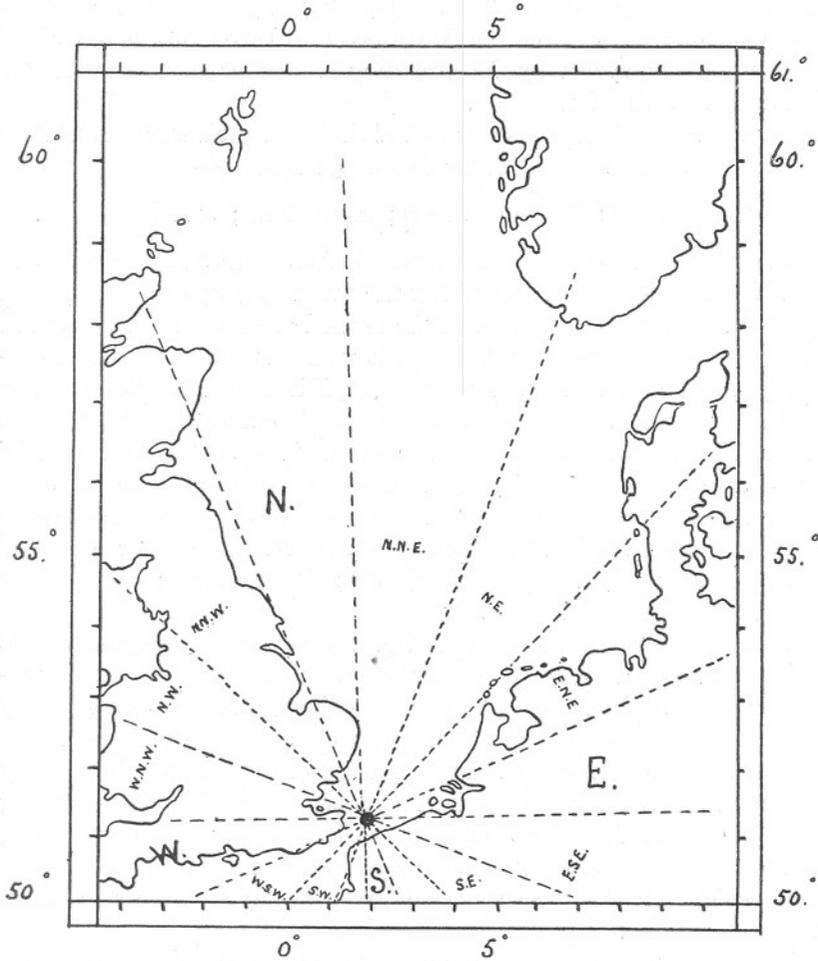


CHART showing the Position of *Sandettie* Lightvessel. Pecked lines define the Direction Sectors referred to in the text.

time be setting in an unusual direction, only a small proportion of the bottles put out at the time may actually strand in that direction. On the current resuming its normal set, the majority of the bottles (which did not strand) will be carried away and stranded in the most usual direction. This would—failing the evidence of the few earlier stranded

bottles—lead one to suppose that the direction of the current had not departed from the normal.

Here it will suffice to say that for the whole period of the drift bottle liberations at *Sandettie* lightship (i.e. from 4.10.20 to 10.10.21), the surface-water movements, as indicated by floating bottles, were always from the Channel to the North Sea, excepting for a few occasions when the current set from the North Sea into Dover Straits for a brief interval, as evidenced by the stranding of surface bottles within the W. and S.W. direction sectors.

Such a definite temporary reversal of the usual E.N.E.'ly current from the Channel only occurred in the following months :—

November, 1920 ; December, 1920 ; April, 1921 ; and June, 1921.

At certain times there was a distinct set from *Sandettie* on to the Kent and Essex coasts, which means that the water issuing from the Channel must, in view of the reversal of the normal\* surface-water movement along the Belgian and Dutch coasts, have been either checked or constrained to hug the Kent and Essex coasts, if it were still making its way into the North Sea. On these occasions, also the current from the Channel to the North Sea must have been checked, if not actually reversed for a time. Such a state of affairs when there was a set on to the east coast of Kent and the coasts to the north as far as Norfolk (although no bottles actually stranded within the Channel) occurred during six months out of the twelve, namely, during October, 1920 ; August, 1921 ; and the four months just mentioned above.

In all these cases the movements of the bottles, or rather of the currents which transported them, are entirely explicable as the result of the prevailing winds. From each liberation yielding evidence of a temporary reversal of the usual water movements, bottles were later returned from the E.N.E. and N.E. sectors. In illustration of the effect of wind it may be stated that during the whole of October, 1920, there was a strong set of the current from *Sandettie* on to the East Anglian and Kent coasts, and that the residual wind for the month was 9·4 m.p.h. S.78°E. true—a value which implies the occurrence of exceptionally strong S.E.'ly winds during the month.

In short, it may be said that for the whole period of the experiment there was a movement of the surface water from the Channel to the North Sea, excepting during times when strong and persistent N.E.'ly-E.'ly winds prevailed. Only for 11 out of the 51 liberations was there any evidence of a check to and temporary reversal of the E.N.E. moving current in the Southern Bight ; these 11 liberations occurred during the

\* See reference to work of Van Der Stok and Jacobsen in *Bulletin Hydrographique* for 1913-14, p. 41.

6 months mentioned, and only 5 of them yield definite evidence of a temporary reversal of the usual E.N.E.'ly surface-water movements in Dover Straights.

As has been mentioned, these reversals occurred at a time of strong E.'ly winds. In view of this it was natural to study long period wind tables for various observing stations over the length of the Channel to see whether there existed any periodicity in the incidence of winds from different quarters. The investigation can only be referred to here, but the result was to show that reversals of the "Channel-to-North-Sea current" are most likely to occur in May and September (followed by April and June), and least so in August and December (followed by July and January).

#### PREVIOUS SURFACE DRIFT INVESTIGATIONS.

The well-known experiments of Garstang\* proved that the surface water of the Channel can move along from the Eddystone region right on up the Channel and through into the North Sea, except when strong E.'ly winds prevail. Later experiments made by the Board of Agriculture and Fisheries (unpublished but embodied in Admiralty Chart 327) yielded valuable information as to the surface-water movements in the North Sea-Channel junction area, and particularly showed how important is the rôle played by the wind, for it was found that the surface water off the Kentish coast could, under the influence of strong E.'ly winds, be pushed back into the Channel to as far west as 1°W. longitude. This W.'ly movement was recognised to be only temporary and dependent upon the persistence of the E.'ly wind.

#### THE MOVEMENTS OF THE BOTTOM BOTTLES.

Throughout the whole period of the experiment the movements of the bottom-trailing bottles were mainly towards the N.E., pointing to the existence of a persistent bottom current from the Channel to the North Sea.

In a recent paper (in the Press†), the writer has described an experiment carried out in mid-Channel when both surface and bottom bottles were put out between the Isle of Wight and Cherbourg, from which the bottom bottles moved E.'wards, rounded Kent, and stranded on the Kent and Essex coasts.

\* Report on the Surface Drift of the English Channel and Neighbouring Seas during 1897. *Journ. Mar. Biol. Assoc.*, N.S., Vol. V, No. 2, April, 1898.

† "The Water Movements in the Southern North Sea in Relation to the Geographical Distribution of Young Herring." Being an Appendix to *Fishery Investigations*, Series II, Vol. VII, No. 4, 1924.

## A Note on the Water Movements in the English Channel and Neighbouring Seas, considered on the basis of Salinity Distribution.

By

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COMPARISON of the conceptions which have hitherto been held in regard to the hydrography of the English Channel with those which are offered as a result of the recent activities of the Atlantic Slope Committee, shows that a difference exists which, in the writer's opinion, lies in the interpretation of the material, rather than in the fundamental differences in the material itself. For example, it is stated that the physical character of the water in the English Channel is conditioned, especially in the summer months, by that of the North Sea water rather than by that of the Atlantic water. "En plein été, en août, les eaux chaudes de la mer du Nord affluent dans la Manche."\* A similar regimen is suggested for the waters of the Irish Sea, which are said to be derived from the northward. Carruthers shows † that the normal water movement in the eastern part of the English Channel is through Dover Straits into the Southern Bight, this movement appearing to be more persistent along the bottom than on the surface. Furthermore, one of the two months in which reversal of this direction appears least likely to occur is August.

In a recent paper‡ in which the writer discusses the salinity of the English Channel during the period 1920-23, it is shown that during the summer months of 1921 and 1922, water of unusually high salinity was present in the eastern basin of the Channel. The salinity is sufficient evidence that this water cannot have come from the North Sea, and it must, therefore, have come from the Atlantic. But since this water of high salinity apparently did not cross the line Isle of Wight—Cape de la Hague on the surface at any time previous to its appearance in the eastern basin, it follows that it entered the Channel as a subsurface

\* Ed. le Danois, *Rapport Atlantique*, 1921. Cons. Perm. Int. pour l'Explor. de la Mer.

† J. N. Carruthers, *vide* p. 665 of this volume.

‡ *Min. of Agric. and Fish. Fish Invest.*, Ser. II, Vol. VII, No. 7, 1924.

layer, below the discontinuity layer for the most part, and appeared at the surface in the eastern basin, where the depth is small and where the vertical mixing effects of the winds and tides are consequently felt throughout the whole water column. So far as the surface of the Channel as a whole is concerned, there appear to be two distinct types of salinity distribution, which may be assigned broadly to winter and summer. In winter the isohalines are approximately parallel to the land, converging towards the east, and the salinity decreases regularly from the Atlantic in the west to the Southern Bight in the east. The winter distribution may be interpreted as showing a movement of ocean water in an easterly direction throughout the length of the Channel.

The most striking differences between winter and summer distributions are two in number. Firstly, in summer, a patch of relatively salt water occurs in the eastern basin. Secondly, off the western entrance to the Channel the isohalines which run east and west in winter, become convex towards the south. It is the interpretation of this latter phenomenon which has given rise to the inconsistency felt by the writer to exist between the older and newer conceptions of the hydrographical regimen of the Channel.

The idea underlying the conclusions reached by Le Danois appears to be the conflict of the water of low salinity in the Irish Sea and off the Bristol Channel with the salter ocean water from the south. In summer, while the salter water has a northerly tendency, the fresh water moves bodily to the southward across the mouth of the English Channel. But the circulatory system which Matthews\* suggested on the evidence of salinity and temperature distribution for these waters is at least equally applicable, and if the water movements are considered on these grounds, it then becomes possible to co-ordinate the conclusions as to water movements arrived at from considerations other than salinity or temperature distribution.

Matthews showed that for the sea south of Ireland the water movement was anti-clockwise, and that relatively salt water coming from the direction of Land's End moved through St. George's Channel into the Irish Sea. It is only necessary to draw attention to the following statement made by him, in order to make the difference clear, viz. "One way of drawing the isohalines, which would fit the mean results perfectly, has not been followed as it would necessitate the assumption of a strong current of low salinity flowing from St. George's Channel to far south of 50° N. Lat. *Such a current would be inherently improbable, and there is no reason to suppose that it exists when there is a much simpler explanation to hand.*" (The italics are the writer's.)

At times this anti-clockwise circulation was found to extend as far

\* D. J. Matthews, *Fisheries, Ireland, Sci. Invest.*, 1913, IV (1914).

south as  $48\frac{1}{2}^{\circ}$  N. Lat., and the monthly charts of surface salinity prepared by the writer for the period 1920-23 show that in the summers of 1921 and 1922 this fresher water system reached at least as far south as Ushant. Furthermore, it was possible to account for the salinity distributions found during this period in the English Channel on the grounds of the circulation suggested by the earlier investigations, whereas, if the system suggested by Le Danois is assumed, it becomes difficult to account both for the presence and persistence of the relatively salt water patch in the eastern basin of the English Channel, and for the striking divergences which occur, more particularly in summer, between the salinity at the Seven Stones Lightship and that at positions closer inshore.

It may be recalled that Gough's\* observations of the drift of *Muggicea atlantica* Cunn. suggest the entry of water from the Bay of Biscay into the English Channel in the summer of 1904, and Bygrave† states that ". . . a shoal of *Limacina retroversa* entered the English Channel in 1905, between May and August, and that its distribution in August appears to indicate that it came from the south-west, passing close to Ushant."

Although, for these reasons, it cannot be admitted that the English Channel is entirely cut off from the Atlantic Ocean in the summer months, it is evident, nevertheless, that the extension and retraction of the cyclonic circulation south of Ireland plays an important part in determining seasonal changes in the direction taken by ocean water entering the English Channel.

\* L. H. Gough, *Publ. de Circ.*, No. 29, 1905.

† W. Bygrave, *N. Sea Fish. Invest.*, 3rd report (Southern Area), 1906-1908. Cd. 5546, 1911.

## A Releasing Apparatus for Horizontally Towed Plankton Nets.

By

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With 4 Figures in the Text.

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WHILE experimenting on the vertical distribution of plankton in comparatively shallow waters I found it necessary to devise a releasing apparatus for use with horizontally towed plankton nets. Under existing working conditions there were four circumstances for which the instrument had to be adapted:—

1. Use with either a wire or rope warp of a thickness that would necessitate the loop and splice at its end being moderately bulky; to overcome this difficulty the loop had to be "stowed away," so that it would not impede the messenger from striking the releasing cap.
2. Use with large tow-nets which would require heavy weights, and themselves cause considerable strain.
3. Room for the attachment of a large instrument for recording the depth at which the net was fishing.
4. Use with nets closed either by the "throttle-rope" or by a collapsible ring.

Examination of Figs. 1, 2, 3, and 4 will probably make the apparatus sufficiently clear to the reader, so that it is only necessary to give a brief description.

The instrument consists of four main portions: the "cap" (Figs. 1 and 2, A; Figs. 3 and 4), the "swing-arm" (Figs. 1 and 2, B), and the two halves of the "body" (Figs. 1 and 2, C); in addition there are five bolts and nuts, a stop screw (Fig. 2, D), a short spiral spring

(Figs. 1 and 2, E), and a ring (Fig. 1, F), which will slide easily off the swing-arm.

The **cap** has on one side an elongated hole (Fig. 4, G) to take the

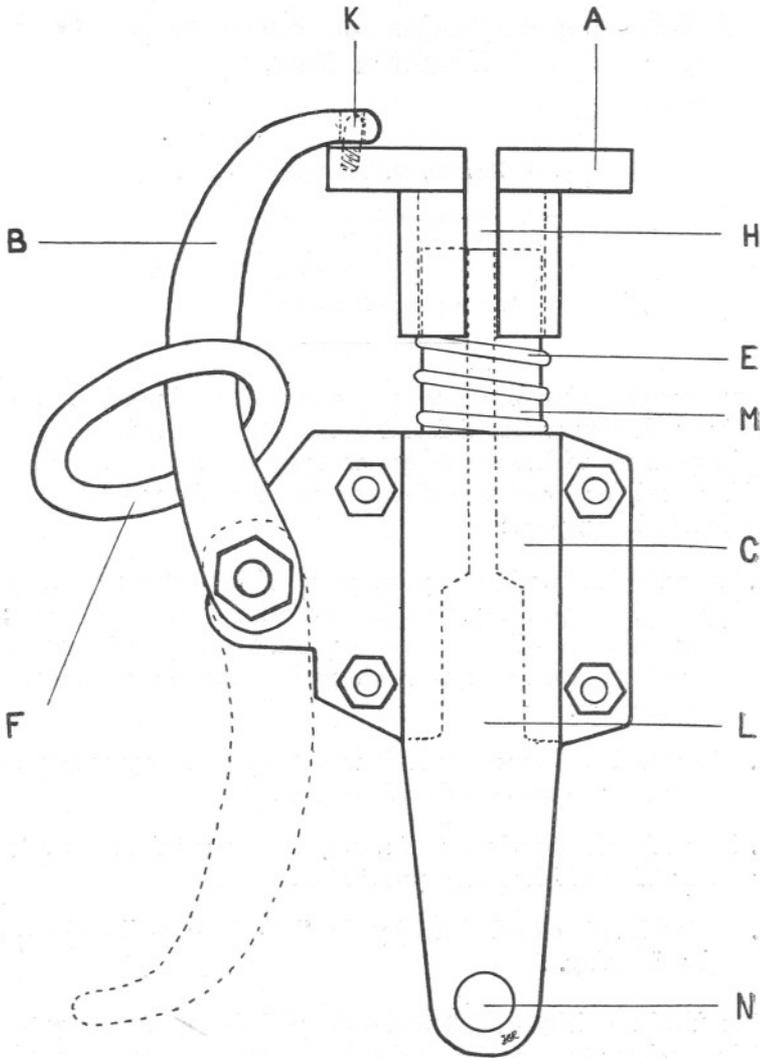


FIG. 1.—Releasing apparatus, side view.  $\times \frac{1}{2}$ .

- |                  |   |  |
|------------------|---|--|
| A = "cap."       | F = ring.   | M = "neck."  |
| B = "swing-arm." | H = slot for insertion of wire.                         | N = holes for bolt for attachment of warp, throttle-rope, etc. |
| C = "body."      | K = stud.   |  |
| E = spring.      | L = enlargement of central boring to take loop of warp. |  |

stop-screw, and on the opposite side a slot (Figs. 1 and 3, H) cut vertically along its whole length to allow the "cap" to be slipped on to the wire; at right angles to these, on the outer edge of the upper surface is the

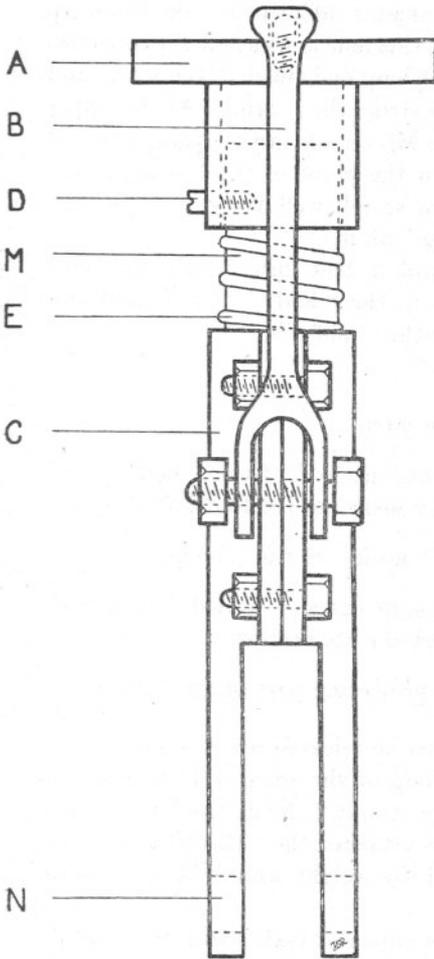
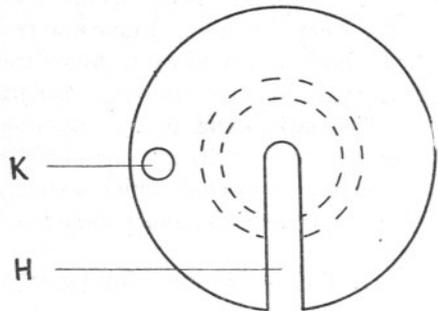


FIG. 2.

FIG. 2.—Releasing apparatus, front view.  $\times \frac{1}{2}$ .

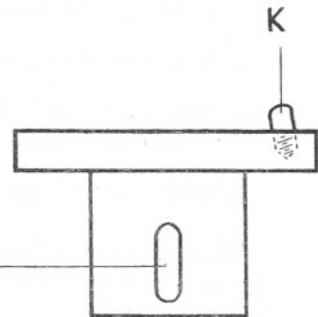
A = "cap."                      D = stop-screw.            N = holes for bolt for attachment of warp, throttle-rope, etc.  
 B = "swing-arm."            E = spring.  
 C = "body."                    M = "neck."

FIG. 3.



K

H



C

FIG. 4.

FIG. 3.—"Cap," top view.  $\times \frac{1}{2}$ .

H = slot for insertion of warp.    K = stud.

FIG. 4.—"Cap," side view.  $\times \frac{1}{2}$ .

G = hole for stop-screw.            K = stud.

stud (Figs. 1, 3, and 4, K), with which the swing-arm engages before it is released.

The **body** is made in two halves: these are clamped together, and a hole is drilled down the centre of a diameter sufficient to take the warp in use; after a short distance, however, this hole is widened out considerably (Fig. 1, L, dotted lines), to take the loop and splice of the warp, and so to allow the messenger a free run to strike the "cap." At the upper end is a round "neck" (Figs. 1 and 2, M), on which the spring fits and the "cap" works. Immediately below the pivot of the "swing-arm" the body is cut away to allow the arm to fall well away, and prevent any possibility of the ring "hanging-up" on it.

The **swing-arm** has at its upper end a hole into which the stud on the "cap" fits: at its attachment to the "body" it is forked and it pivots on the bolt which fastens it to the "body."

*To assemble and attach warp:—*

1. Thread the spiral spring on to the warp.
2. Lay the warp down the groove on one half of the "body," and then fasten on the other half by means of the four bolts.
3. Slide the spring down on to the "neck" of the "body."
4. Slip the "cap" on the wire through the slot provided and push it down on the "neck": insert the stop-screw.
5. Bolt the "swing-arm" on to the projecting part of the "body."

When in use the bridles which are to be released are shackled on to the ring on the "swing-arm"; the loop of the warp is fastened to a bolt or shackle through the holes (Figs. 1 and 2, N) at the bottom end of the "body," and to this bolt are also attached the "throttle-rope," or closing bridles as the case may be, and the weight, and in this case also the depth-recorder.

When the messenger is sent down the impact it makes with the "cap" compresses the spiral spring, and thus disengages the "swing-arm" from the stud; the "swing-arm" falls away to the position marked by dotted lines in Fig. 1, and allows the ring to slip off. The messenger used weighs 1 lb. 2 oz.

The whole is made of wrought iron, and painted except the bearing surfaces, which should be kept well greased, e.g. the "neck" and inside of "cap."

The instrument drawn here was designed to take  $\frac{3}{4}$ -in. (circumference) steel wire: for thicker wire or rope the hole passing down the centre should be drilled as required.

It has been found in practice that the process of attaching the apparatus to the warp can be considerably quickened by merely slacking off the five bolts and forcing the two halves apart: the loop of the wire can then be pushed down the drilled portion, and the nuts tightened up and the spring and "cap" slipped into place again. This allows the instrument to be kept assembled and prevents the likelihood of loss of the necessary bolts.

## Evaporation and Temperature Changes in the English Channel.

By

H. W. Harvey, M.A.,

*Hydrographer at the Plymouth Laboratory.*

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With Four Figures in the Text.

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SINCE April, 1921, observations of temperature and salinity have been made at depths from top to bottom of the sea at Station E1, 20 miles to the south-west of Plymouth, where the depth is 70 metres. These observations already throw some light on the causes of different sea temperatures during the same month in different years. As these temperature differences from year to year play an all-important part in the life of cold-blooded marine animals (1), it is of particular interest not only to follow their seasonal changes, but to arrive as far as possible at the causes which govern them.

Changes in salinity and the temperature conditions during 1921 showed a marked inflow of warm highly saline Atlantic water into the English Channel, and a very marked inflow into the E1 area during September, October and November of that year (2). From that time until the end of 1923 there has been an irregular fall in salinity of the water at E1.

A general consideration of the salinity data available points to no very extensive movement of the water masses in this E1 area during the years 1922 and 1923, although extensive movements took place further south (3).

If, as indicated, the water has not been subject to marked movement other than that due to the tides, it makes this period of particular value in attempting to define factors other than big inflows of water from other areas, which cause variations from the normal in the annual temperature change of the sea.

For the purpose of investigating the effect of meteorological conditions on the temperature of the water occupying the area within, say, 5 or 6 miles north and south and 10 or 20 miles east and west of Station E1, it is assumed in the following *calculations* that the whole

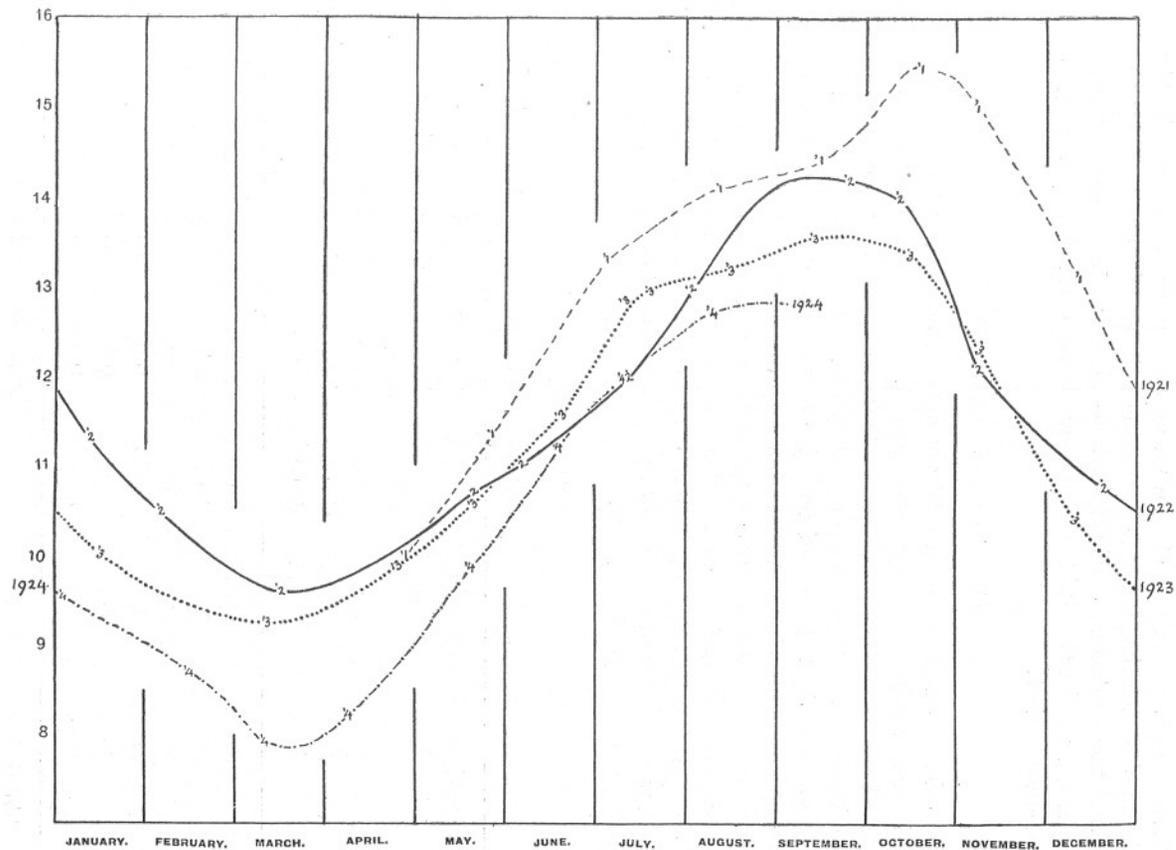


FIG. 1.—Temperature in degrees centigrade of a column of water at Station E1, from top to bottom, as if completely mixed, for the years 1921, 1922, 1923, 1924.

mass of water did not move bodily away to be replaced by water from other areas which had been subjected to different meteorological conditions.

That a certain amount of movement took place is beyond doubt; but the close relation found between the gain and loss of heat by the sea and meteorological conditions, shows, I think, that the movement was not sufficiently rapid to prevent local conditions showing a pronounced effect.

#### GAIN AND LOSS OF HEAT.

In order to arrive at the quantity of heat gained or lost by the water at El from month to month, assuming that the water had not been replaced by water from other areas, the temperatures of a column of water from top to bottom, as if completely mixed, were calculated from the observations made at different depths and the values so obtained were plotted against time. From a fair curve drawn through these points (Fig. 1, p. 679), Table I was constructed. Assuming that all the heat lost and gained passed through the surface, the amounts in gram calories passing through one square centimetre of surface during each month were calculated and are shown in Table II as the mean daily loss or gain for each calendar month.

TABLE I.

	1921-22.	1922-23.	1923-24.	1924-25.
From mid Mar. to mid April	°C.	+ .2° C.	+ .5° C.	+ .6° C.
„ Apl. „ May		+ .7	+ .5	+ 1.1
„ May „ June	+1.6	+ .75	+ 1.1	
„ June „ July	+1.1	+ 1.0	+ 1.5	
„ July „ Aug.	+0.6	+ 1.3	+ .3	
„ Aug. „ Sept.	+0.3	+ .65	+ .3	
„ Sept. „ Oct.	+0.95	- .3	- .2	
„ Oct. „ Nov.	-0.7	-2.1	-1.5	
„ Nov. „ Dec.	-1.8	- .9	-1.7	
„ Dec. „ Jan.	-1.75	-0.9	-0.8	
„ Jan. „ Feb.	- .9	-0.6	-0.5	
„ Feb. „ Mar.	- .7	-0.2	-0.8	
Total rise	—	+4.6° C.	+4.2° C.	
Total fall	—	-5.85° C.	-5.0° C.	

Change in temperature of column of water top to bottom at Station El.

TABLE II.

	Temperature change of whole column of water during calendar month. =ΔT.	Mean daily loss or gain in heat of column 1 sq. cm. section in gram. calories. =C.	Solar radiation recorded at S. Kensington in gram calories per sq. cm. of horizontal surface per day. =R.	Calculated mean daily gain or loss of heat per sq. cm. due to evaporation, etc. (C-R). =E.	Mean aqueous vapour pressure of surface water at E1 less that of air at Cattewater Air Station. Ps-Pa.
		cals.	cals.	cals.	
May, 1921	+1.5° C.	+339	359	- 20	
June	+1.5	+350	411	- 61	
July	+ .65	+147	394	-247	
Aug.	+ .35	+ 79	284	-205	
Sept.	+ .5	marked water movement	no record		
Oct.	+ .4	"	"		2.6
Nov.	-1.45	"	"		4.7
Dec.	-1.8		"		3.4
Jan., 1922	-1.3		"		2.5
Feb.	- .8		"		2.2
Mar.	- .3	- 68	127	-195	2.9
April	+ .5	+117	231	-114	3.0
May	+ .7	+158	361	-203	
June	+ .75	+175	326	-151	
July	+1.2	+271	267	+ 4	
Aug.	+1.05	+247	244	+ 3	
Sept.	+ .3	+ 70	186	-116	2.3
Oct.	+1.4	-316	75	-391	4.2
Nov.	-1.5	-350	46	-396	3.1
Dec.	- .9	-203	47	-250	2.4
Jan., 1923	- .7	-158	41	-199	2.2
Feb.	- .4	- 97	65	-162	1.4
Mar.	+ .1	+ 22	92	- 70	1.4
April	+ .6	+140	142	- 2	1.8
May	+ .8	+180	239	- 59	
June	+1.4	+327	254	+ 73	
July	+ .9	+203	337	-134	
Aug.	+ .3	+ 68	341	-273	
Sept.	+ .1	+ 23	223	-200	2.4
Oct.	- .7	-158	104	-262	2.7
Nov.	-2.0	-452	46	-498	4.0
Dec.	-1.2	-271	21	-292	2.0
Jan., 1924	- .7	-163	23	-186	1.4
Feb.	- .6	-150	46	-196	1.1

TABLE II—*continued.*

	Temperature change of whole column of water during calendar month. = $\Delta T$ .	Mean daily loss or gain in heat of column 1 sq. cm. section in gram. calories. = C.	Solar radiation recorded at S. Kensington in gram calories per sq. cm. of horizontal surface per day. = R.	Calculated mean daily gain or loss of heat per sq. cm. due to evaporation, etc. (C - R). = E.	Mean aqueous vapour pressure of surface water at E1 less that of air at Cattewater Air Station. Ps - Pa.
		cals.	cals.	cals.	
Mar.	- .3	- 68	57	-143	2.1
April	+1.0	+233	204	+ 29	
May	+1.3	+293	332	- 39	
June	+1.4	+326	387	- 61	
July	+ .8	+180	379	-199	
Aug.	+ .25	+ 57	311	-254	

Several features are very noticeable. The water gained heat each year between dates very close to those of the spring and autumn equinox, except in 1921, when a big influx of warm Atlantic water occurring during the months of September, October and November, postponed the onset of loss of heat by nearly a month. This is clearly shown in Table I.

The gain is not equal to the subsequent fall during the winter months, and is not the same each year. The gain or loss of heat during the same month varies considerably from year to year, even in months when there is no evidence of decided water movement.

Although not relevant to the matter being dealt with, it is of interest to note that the curves drawn for the temperature changes of various layers of water at E1, from surface to bottom, and of surface water of the inshore stations between E1 and Plymouth all have the general form of those for the column of water shown in Fig. 1, and are very notably similar during the winter months. It is of interest also to note that the winter herring fishery (January) from this port resulted in very poor catches during the warm winter of 1921, in moderate catches in 1922, and in good catches during the cold winter of 1923.

The main source of heat gain by the sea is that due to direct and diffuse solar radiation, which is absorbed by the surface layers. In experiments (5) made in the Nyhammer oyster basin the heat did not penetrate perceptibly below 5 metres. As the sea acts almost as a perfect radiator (4) or black body, practically all the solar radiation will be absorbed.

A main source of loss of heat by the sea appears to be evaporation, judging by the observations made in this area. Other sources are loss into space from radiation (5) and conduction to the atmosphere.

In the area under consideration variations in the loss from radiation appears to be overshadowed by the loss from evaporation, on comparing the same month of different years.

Heat will also be lost by heating the atmosphere, but the amount is likely to be small since one gram calorie will heat a column of air 1 square centimetre in section and ca. 30 metres high through  $1^{\circ}\text{C}$  (5). The loss of 1 gram calorie, on the other hand, will be caused by the evaporation of one six-hundredth of a cubic centimetre of water at sea temperature.

The heat in calories required to raise 1 cc. of sea water through  $1^{\circ}\text{C}$ . is taken as the round figure 1.0 in the calculations made in this paper.

It is noteworthy that in discussing cooling of the sea, Helland-Hansen makes no mention of the losses caused by evaporation.

#### SUMMER GAIN IN HEAT.

Considering the rise in temperature during the summer months, early in May the upper layers show signs of being heated by solar radiation, provided that windy weather and consequent vertical mixing by wave motion does not hide this effect, as in May, 1923. This condition continues throughout the summer, until some time in September, unless vertical mixing occurs, as in July, 1922.

Once such a warm upper layer is well established, with its sharp line of discontinuity with the colder and denser water below, it is remarkably stable; several days of rough sea are necessary to alter it materially.

While the layer lasts, less saline shore water which has remained heaped up close to the land during the winter tends to run out, and to mix with this less dense upper layer (6). Rain falling on the sea will not penetrate below the layer of discontinuity. The fall of an inch of rain will have a marked effect on the salinity of the relatively shallow upper layer.

During September as the amount of solar radiation becomes less and the day shorter, while the heat loss by evaporation continues, the surface water cools sufficiently during the night to sink deeper, until this vertical movement combined with that of wave motion, finally breaks down the discontinuity layer.

Conditions which tend towards the formation and continuation of a warm upper layer are excess of solar radiation over heat loss by evaporation (i.e. warming of the surface), and lack of strong winds with their consequent vertical mixing by wave motion. These same conditions will allow, at times, considerable evaporation, owing to the upper inch or two of water becoming very hot.

The surface sample dipped up with a bucket represents the surface

6 inches, more or less, and will be considerably cooler than the actual surface during a hot sunny day with little wind (8). Such a sample has been taken in August at E1 and registered over  $19^{\circ}\text{C}$ .

*The condition of the sea during the summer months leads to the seeming paradox that, during a summer month of light winds and high surface temperature, the heat gained by the sea may be less than during a summer month marked by less solar radiation and more wave motion.*

Fig. 2 represents the vertical distribution of temperature in 1922 and

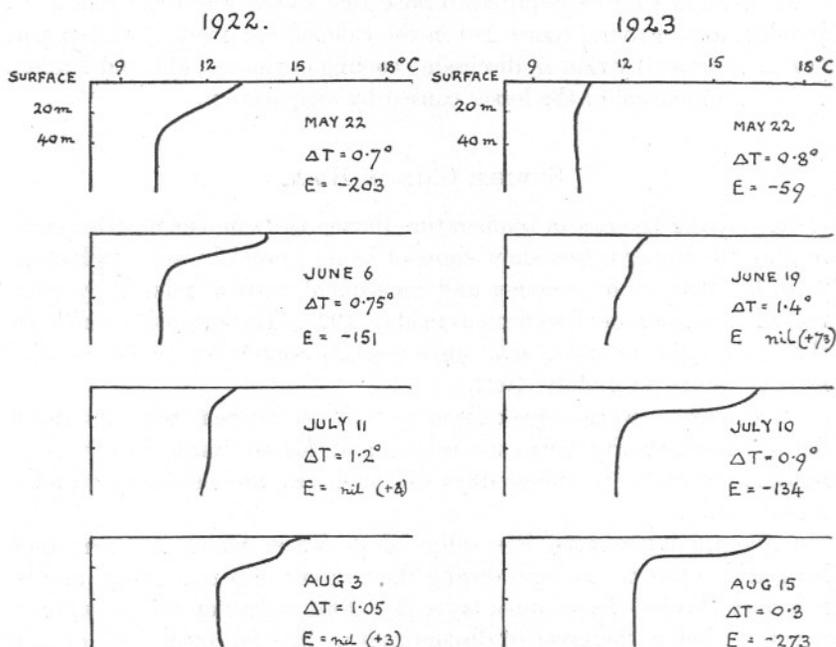


FIG. 2.—Black line shows the distribution of temperature with depth at Station E1 during the summers 1922, 1923.  $\Delta T$  shows the change in temperature of the whole column of water, as if mixed, during the calendar month.

E is the calculated mean daily loss in calories per sq. cm. due to evaporation, etc. (see p. 686.)

1923; a certain amount of water movement, as indicated by the changes in salinity, was undoubtedly taking place in 1922, but during these months of 1923 there is less evidence of any movement. It is very apparent that where a warm upper layer is present with consequent evaporation, the gain in heat ( $\Delta T$ ) by the water below is decreased.

Table IV and also the third column of Table II show the solar radiation recorded at South Kensington in gram calories falling on a horizontal square centimetre per day. The quantity will be greater at E1, owing to the clearer atmosphere for the most part and to the more southern latitude to a less extent.

TABLE IV.

	1921.	1922.	1923.	1924.
May . . .	359	361	239	332
June . . .	411	326	254	387
July . . .	394	267	337	379
August . . .	284	244	341	311

Solar radiation per horizontal square centimetre per day at South Kensington.

During the summers of 1922 and 1923, when solar radiation was high, wind conditions permitted a warm upper layer to be formed with sharp discontinuity with the water below; this allowed high-surface temperatures to be attained and the sea lost by evaporation a large proportion of its gross gain from solar radiation. Hence the net gain of heat by the sea was less than during the months when solar radiation was low. The following shows this:—

Mean daily solar radiation in calories . . . . .	May	1922.	1923.
Net gain in calories by column 1 sq. cm.			
section per mean day . . . . .	May	361	239
Mean daily solar radiation . . . . .	June	326	254
Net gain . . . . .	June	175	327
Mean daily solar radiation . . . . .	July	267	337
Net gain . . . . .	July	271	203
Mean daily solar radiation . . . . .	August	244	341
Net gain . . . . .	August	247	68

The fourth column in Table II shows the mean daily gain or loss of heat through one square centimetre of surface minus the solar radiation recorded at South Kensington.

Since the sea behaves practically as a full radiator (4), this difference represents heat lost by the sea due to evaporation, radiation and conduction, during those months when water from other areas had not moved into the E1 area.

During the summer months of 1922 and 1923, the monthly mean temperature of the air on Plymouth Hoe did not vary by more than about 1° C. from the monthly mean temperature of the surface six inches of the sea. The sea temperature was obtained by drawing a fair curve through points showing the temperatures of the surface samples taken plotted

against time. The temperature of the surface itself would be greater by day and rather less by night (diurnal variation).

This small difference in temperature would indicate that little heat is lost or gained in the twenty-four hours by conduction to and from the atmosphere during these months.

Hence the value, denoted by  $E$  in Fig. 2, being the difference between the mean daily gain in heat and the solar radiation, represents a loss which is due almost entirely to evaporation and radiation from the sea.

With regard to that moiety of the value of " $E$ ," which is due to radiation outwards from the sea, the following considerations are of interest. The wave length (mean ca.  $10\mu$ ) is considerably longer than that of solar radiation (mean ca.  $0.1\mu$ ). Hence it will be more readily absorbed by the moist atmosphere above the surface of the sea, which, forming a blanket, will retard radiation into space.

This value of  $E$ , rough as it necessarily is, indicates even more plainly than the temperature change the effect of a surface layer of warm water.

These considerations indicate that the variations in heat gained by the sea between one summer and another are probably caused by increased evaporation during calm weather just as much as by movements of water from other areas. Variations in solar radiation from year to year play a part not so much by varying the quantities of heat absorbed by the sea, as by modifying the conditions which determine the loss by evaporation.

Comparing, month for month, the values of solar radiation shown in Table IV with the vertical distribution of temperature, as shown in Figs. 2 and 3, it is at once apparent that the greater the solar radiation, the greater is the *tendency* towards a well-marked discontinuity layer which withstands the action of wave motion. Unfortunately there were no observations made in June, 1921; but, judging from the vertical distribution on July 2nd and the condition on May 26th, vertical mixing prevailed. During May and June the salinity was rising quickly; probably warmer water from the south was entering the area. During 1922 a warm upper layer was well formed in June, but broken up again by wave motion combined with reduced solar radiation in July. In 1923 the solar radiation was low until July, and did not overcome the vertical mixing by wave motion until that month, when increased radiation allowed the establishment of a warm layer.

It is contended that the general agreement between the condition of the upper layers and the value of  $E$  (Fig. 2) in itself indicates that the movements of the water mass were not very extensive. The calculated value  $E$  would be considerably affected by the inflow of warmer water

from shallower inshore areas, or from the Atlantic, or of colder water from the Irish Channel.

Turning to a consideration of the conditions during the summers of 1921 and 1924, salinity changes indicate replacement of water at E1 by water from other areas. It is of interest to see whether, when the value of  $E$  appears high for the general conditions (July, 1921, Fig. 3), there is any evidence of colder water entering the area.

“During 1921, in July, there was a marked check in the increase in

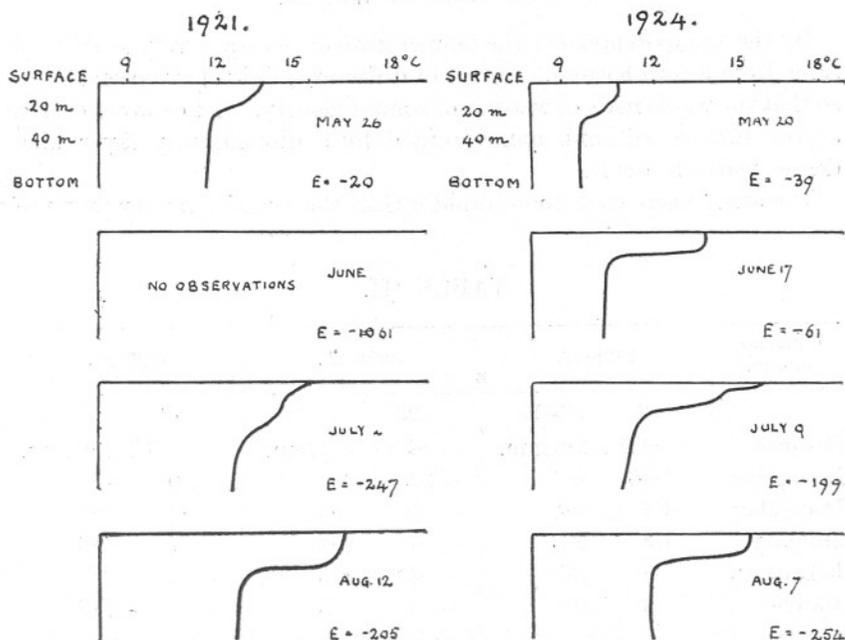


FIG. 3.—Black line shows distribution of temperature with depth at Station E1 during the summers of 1921 and 1924

$E$  is the calculated “mean daily loss in calories per sq. cm. due to evaporation, etc.

temperature of the ‘deep water’ at E1, coincident with a fall in salinity . . . a tongue of less saline and colder water from the south of the Irish Channel had extended up the centre of the English Channel (2).” This was written before any detailed investigation on the effect of evaporation on the seasonal changes in temperature was undertaken.

The value of  $E$  for June, 1924 (Fig. 3), was low while layering was marked. This would suggest that warmer water entered the area during the month. Salinity data indicate that probably two movements took place between May 20th and June 17th. Less saline water moved out further seaward from the shallower inshore grounds. Water occupying

the E2 area (centre of channel) on May 20th, when it was both warmer and less saline than the water at E1, moved northward into the E1 area by June 17th. From June 17th until July 10th there was probably little or no water movement at E1. The salinity data available afford no *proof* that warmer water moved into the E1 area during June, 1924, but the evidence they afford is certainly more in favour of such a movement than otherwise.

#### LOSS OF HEAT IN WINTER.

By the end of September the temperature of the sea is very nearly the same from top to bottom. Layers of different salinity have been mixed so that the whole mass of water is of similar density. Hence water cooled at the surface will sink uninterrupted by a discontinuity layer with denser water below it.

The atmosphere cools more rapidly than the sea, the vapour pressure

TABLE III.

Calendar month.	1921-22.		1922-23.		1923-24.	
	$\Delta T$	Ps-Pa	$\Delta T$	Ps-Pa	$\Delta T$	Ps-Pa
October	+ .4° C.	2.6 mm.	-1.4° C.	4.2 mm.	- .7° C.	2.8 mm.
November	-1.45	4.7	-1.5	3.1	-2.0	4.1
December	-1.8	3.4	- .9	2.4	-1.2	2.1
January	-1.3	2.5	- .7	2.2	- .7	1.5
February	- .8	2.2	- .4	1.5	- .6	1.2
March	- .3	2.9	+ .1	1.5	- .3	2.7

$\Delta T$ .—Changes in temperature of column of water at E1 during calendar months when surface and bottom are nearly the same temperature. Ps-Pa—Difference between the aqueous vapour pressure of the surface water at E1 and the mean vapour pressure of the air at Cattewater Air Station for each month.

of its contained water vapour falling more rapidly than the vapour pressure of the surface water falls. From October to December the condition is likely to arise of a considerably greater aqueous vapour pressure of the surface water than in the air blowing over it. This will lead to increased evaporation. After December the air temperature tends to rise, while the sea surface temperature continues to fall, hence after December the difference in aqueous vapour pressure between sea surface and air will tend to increase.

Reference to Table III and Table II shows that the major heat loss by the sea occurs before the end of December, except in 1921 when the

influx of warm Atlantic water postponed the fall in temperature until November.

The mean observed aqueous vapour pressure of the air at Cattewater Air Station, Plymouth, as published every month by the Meteorological Office ( $P_a$  in Tables II and III) was deducted from the calculated aqueous vapour pressure of the surface water at E1 ( $P_s$ ). From this columns  $P_s - P_a$  were constructed.

Values of  $P_s$  for the summer months were not calculated, because a single monthly observation of the surface six inches affords no indication of the mean value of the actual surface temperature for the month.

The values of  $P_s - P_a$  during the winter half year should give a rough value of the difference in aqueous vapour pressure of the surface of the sea and of the air blowing over it, Cattewater Air Station being in a fairly exposed position.

Considering the rough nature of this value,  $P_s - P_a$ , there is good general agreement between it and the fall in temperature during the same month of the two years.

The values for mean daily loss of heat per day minus the solar radiation ("calculated loss in calories due to evaporation, radiation," etc.) show an extraordinarily close agreement with the difference in aqueous vapour pressure between sea and air. This is particularly noticeable during those months when the salinity changes are slight.

Fig. 4 (p. 690) shows this correlation very plainly.\*

The magnitude of this loss of heat due to evaporation when  $P_s - P_a$  reaches a high figure is considerable. A period marked by dry cold atmospheric conditions will have as great an effect on the temperature of the sea as many considerable water movements.

With regard to other factors than  $P_s - P_a$  which promote evaporation, "all observers agree that evaporation increases with wind velocity. . . . The wind usually has a variable vertical component, and, besides, is irregular in strength and direction. There is not, therefore, any constant relation of evaporation to the average horizontal component of wind velocity, the value usually measured" (7). I have been unable to find any correlation between the amount of wind during the month and either the fall in temperature or "loss of heat due to evaporation," etc. It appears that *in the open sea the wind factor is overshadowed by that of difference of vapour pressure, on comparing sufficiently long periods of time.*

It is of interest to compare the total evaporation and rainfall during the year. Assuming that the values given in column 4 of Table II are

\* During January and February, 1924, there was a marked fall in salinity at E1. On reference to Fig. 2, the loss of heat minus solar radiation appears somewhat greater than would be accounted for by evaporation, due to the difference in vapour pressure between the sea surface and the air.

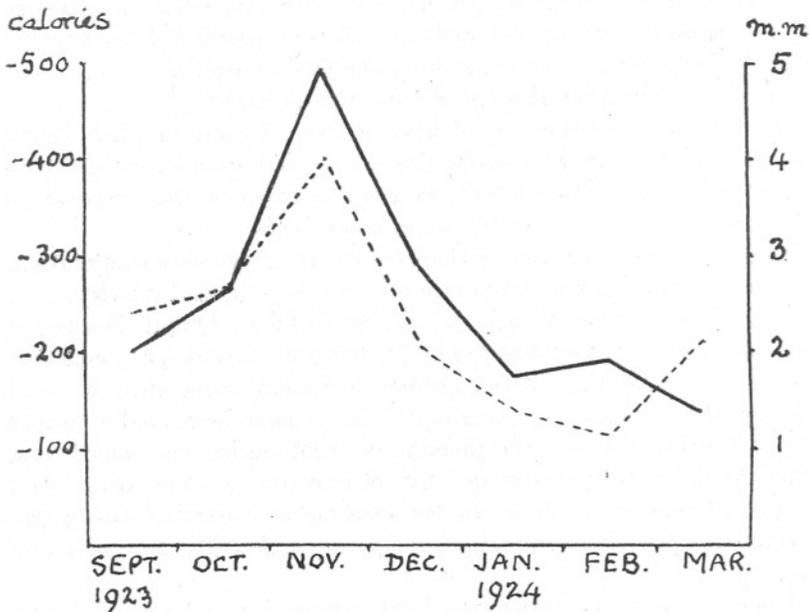
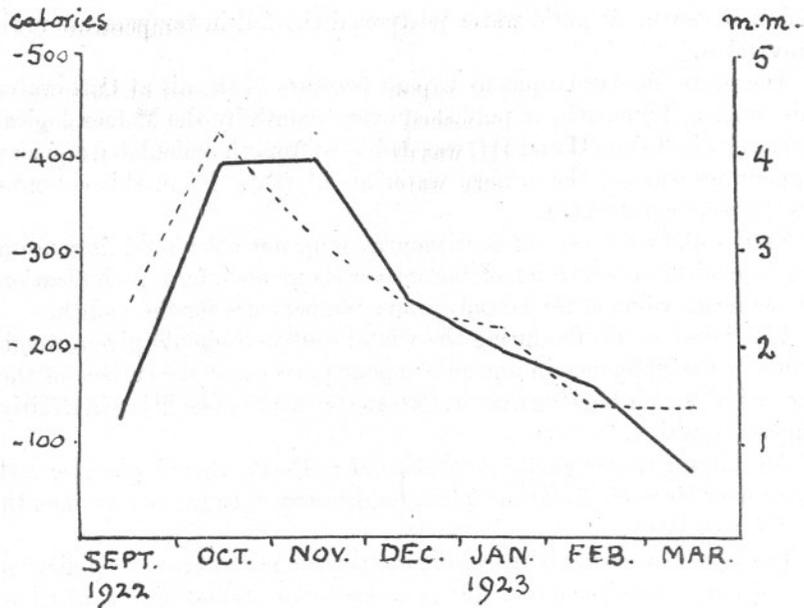


FIG. 4.—Thick line shows loss of heat per day by column 1 sq. cm. in section, from surface to bottom, at E1, *minus* solar radiation per horizontal sq. cm., as recorded at South Kensington.

Dotted line shows difference in aqueous vapour pressure between surface water at E1 and the air at Cattewater Air Station Observatory.

correct and\* the loss of heat is due entirely to evaporation during the ten months of 1922 for which the value is recorded, an average of 173 calories per day is lost per square centimetre. This is roughly 63,000 calories, sufficient to account for the evaporation of a depth of 100 centimetres of water during the year. This is approximately equal to the year's rainfall (Plymouth, 93 cm. and Falmouth, 116 cm.). During 1923 evaporation was 110 cubic centimetres, and rainfall at Plymouth 86 cubic centimetres, and at Falmouth 115 cubic centimetres per square centimetre.

The area under consideration will also receive some of the rainfall over neighbouring land, particularly in the summer, when it tends to run out as a surface layer. This leads to the conclusion that if no water movement was taking place dilution by rainfall and coast water would probably be almost balanced by evaporation from the sea in this particular area.

#### CONCLUSIONS.

Evaporation from the sea surface plays an important part in modifying the annual rise and fall in temperature of the sea.

A hot summer with light winds gives rise to high surface temperatures and considerable loss of heat by evaporation.

During the winter half year the total loss of heat by the sea, allowing for the heat gained by solar radiation, shows a remarkable proportionality to the difference in aqueous vapour pressure between surface water and the air.

The change of temperature of the sea, during the period considered, was controlled to a marked extent by evaporation from the surface, except during the very considerable inflow of Atlantic water in September and November, 1921.

In the open sea difference in aqueous vapour pressure between surface water and air is the major factor controlling evaporation, overshadowing the effect of wind, when sufficiently long periods are compared.

I am indebted to my colleagues, and in particular to Dr. W. R. G. Atkins, for many valuable suggestions during the course of this investigation. Dr. H. Stanley Allen, who read the draft of this paper, has suggested that it may be possible to calculate the moiety of the value of "E" which is due to radiation outwards.

\* The mean daily solar radiation is that recorded at South Kensington, and the mean daily loss or gain of heat by the sea at E1 is taken from a "fair" curve drawn through points roughly one month distant, hence the values shown can only be roughly representative. That moiety of the value of E, which is due to radiation outwards, may, during some months, be considerable.

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## On the Thermal Stratification of Sea Water and its Importance for the Algal Plankton.

By

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With Three Figures in the Text.

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IN a previous paper (1924) the writer considered the factors which bring about the mixing of surface water, warmed by the sun, with the cooler water below. Observations were cited to show that in the English Channel, between May and September, a warm surface layer may exist, which differs from the deeper water in being more alkaline and poorer in phosphates; both these differences are due to the activity of the phytoplankton. The reduction in phosphate proceeds in the upper well-illuminated layer till none is left. No further increase in phytoplankton is then possible till phosphate is set free by decomposition or supplied by mixing with the deeper water. The phenomena of thermal stratification are consequently of great importance in the study of the phytoplankton.

Such stratification has been considered at length by Birge and Juday (1911) in their limnological studies. Birge (1910) designates the upper warm and the lower cold layers the "epilimnion" and "hypolimnion" respectively. These terms connoting very different biological habitats are undoubtedly useful, but from their derivation are not strictly applicable to sea water. It is suggested that the terms "epithalassa" and "hypothalassa" should be used to denote these layers in sea water, the region between them being denoted by the well-established term, thermocline, introduced by Birge in 1897.

The epithalassa usually persists throughout the summer months; though the rough seas of June, 1922, almost destroyed it, yet it became apparent again in August. Its stability is, in fact, surprising, but Birge (1910) has given reasons which render the persistence of the epilimnion intelligible. These apply equally to the epithalassa as shown by the figures which follow.

The effectiveness of the resistance to mixing, due to increase of temperature, is not proportional to the temperature gradient simply, but depends also on the departure of this temperature from that of the maximum density of the water.

The decrease in density as water is removed from the temperature of maximum density is not constant, but increases. Groll (1905) pointed out the bearing this has upon the origin of convection currents. Wind, however, appears to be the chief factor concerned in the mixing of warm

TABLE

t°	D†	$\Delta \times 10^5$	Relative $\Delta$ for 2°.	$\Delta$ relative to fresh water.	Ergs salt water.	Ergs fresh water.
-2	1.02845	8	1.00	2.50	680	—
0	1.02837	13	1.62	4.05	1083	833
2	1.02824	19	2.38	5.95	1583	267
4	1.02805	24	3.00	7.50	1997	267
6	1.02781	28	3.50	8.75	2332	766
8	1.02753	32	4.00	10.0	2665	1241
10	1.02720	36	4.50	11.25	2998	1682
12	1.02684	40	5.00	12.5	3332	2116
14	1.02644	44	5.50	13.75	3665	2507
16	1.02600	48	6.00	15.0	3997	2899
18	1.02552	51	6.39	16.0	4248	3266
20	1.02501	54	6.75	16.9	4498	3607
22	1.02447	58	7.25	18.1	4831	4009
24	1.02389	61	7.62	19.05	5046	4273
26	1.02328	64	8.00	20.0	5331	4589
28	1.02264	67	8.37	20.95	5581	4881
30	1.02197	—	—	—	—	—

surface water with cold bottom water. During the summer the density differences between the top and bottom are far greater than during the spring and autumn; it is this fact and not only the diminished force of the wind in summer that permits of the establishment and persistence of the epihalassa.

Birge has tabulated, for fresh water, temperatures from 0–30° C., densities at 1° intervals, the density differences for 1° and the relative differences for 1° C., taking that from 4° to 3° and from 4° to 5° as unity. He also tabulates, for temperatures from 0°–30°, the number of ergs

work done against gravity in mixing a column of water of one square centimetre area, one metre high, whose upper and lower surfaces differ in temperature by  $1^\circ$  the gradient being uniform. This may be calculated from the equation :—

$$W(\text{ergs}) = \frac{Ah^2}{12} (D_2 - D_1)$$

where  $A$  denotes the area and  $h$  the height,  $D_1$  and  $D_2$  being respectively the densities of the lower and upper strata of the column.

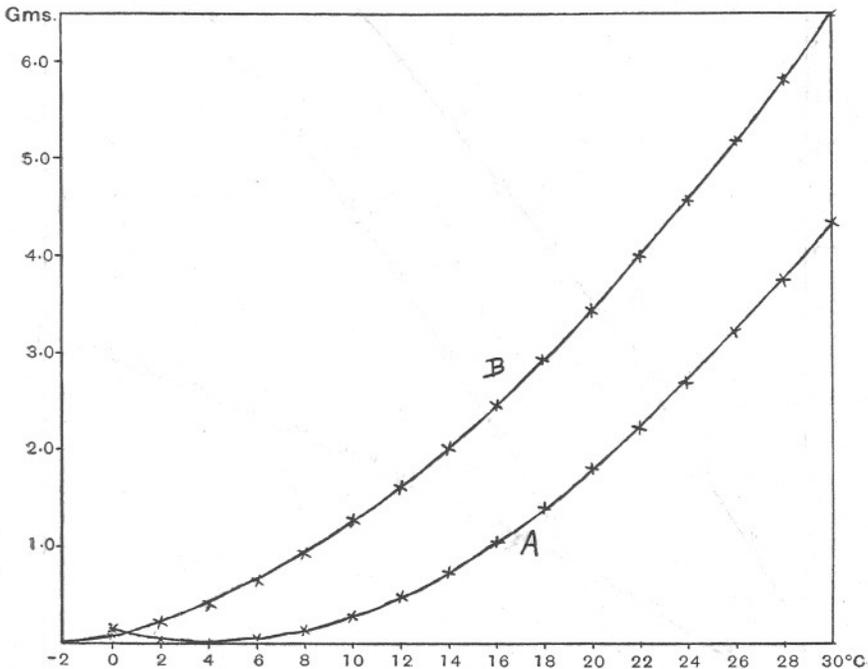


FIG. 1.—The curves represent changes in density due to rise of temperature. The ordinates show difference in weight, in grams, between a litre of water at temperature  $t^\circ$  and  $4^\circ$ , curve A, and between  $t^\circ$  and  $-2^\circ$ , curve B, which is for water of salinity  $35.3\text{‰}$ . For example, in B,  $D_{-2}^{-2} = 1.02845$  and  $D_{14}^{14} = 1.02644$ , viz.  $2.01$  gms. less per litre, as may be read off on the curve.

The number of ergs is, therefore, 833 times the difference between the densities.

In order to apply these density changes to sea water calculations have been made of the density of sea water of  $35.3\text{‰}$  salinity, such as is found in the west of the English Channel, at a series of temperatures from  $-2^\circ$  to  $30^\circ$ . The freezing-point of such sea water

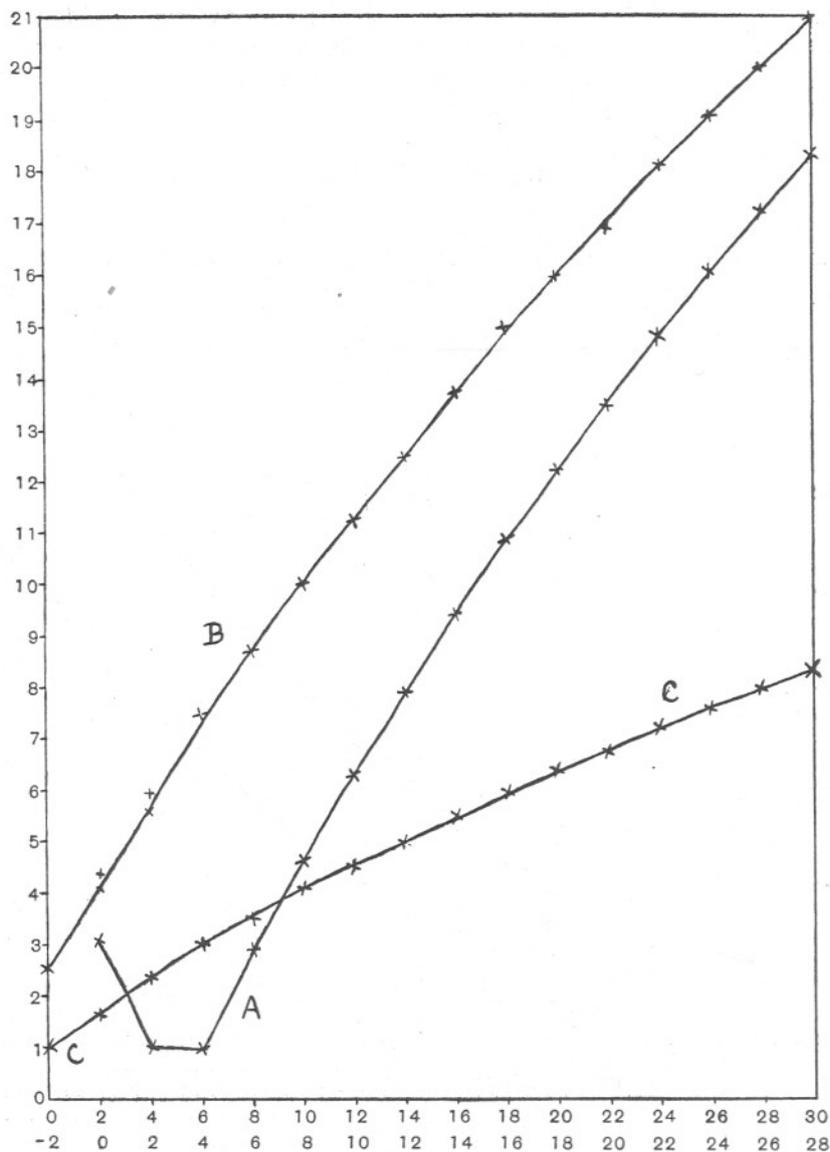


FIG. 2.—The ordinates indicate relative thermal resistance to mixing, and are in reality ratios of the change in density over the given ranges of  $2^{\circ}$  C. relative to that of water from  $4^{\circ}$  to  $2^{\circ}$  or from  $4^{\circ}$  to  $6^{\circ}$  as unity, viz. the ratio of  $(D_{\frac{t-2}{4}} - D_{\frac{t}{4}})$  to  $(D_{\frac{t}{4}} - D_{\frac{t}{4}}) = (D_{\frac{t}{4}} - D_{\frac{t}{4}})$ . Curve A is for pure water, curve B for water of  $S=35.3^{\circ}/_{\infty}$ . Curve C is the ratio for  $(D_{\frac{t-2}{4}} - D_{\frac{t}{4}})$  relative to  $(D_{\frac{t-2}{4}} - D_{\frac{t}{4}})$  for the water of curve B. The abscissæ represent the temperatures of the upper and lower surfaces of a column of water of unit area and height, but for pure water the temperatures  $4^{\circ}$  over  $2^{\circ}$  and  $2^{\circ}$  over  $0^{\circ}$  should be inverted.

differs by only a few hundredths of a degree from  $-2^{\circ}$ . For the calculations the formulæ and constants given in Knudsen's Hydrographical Tables were used.

In the table (see p. 694) are recorded the densities obtained as described, together with, under  $\Delta$ , their differences for intervals of  $2^{\circ}$  C. The fourth column shows the values of  $\Delta$  for  $2^{\circ}$  intervals, relative to that

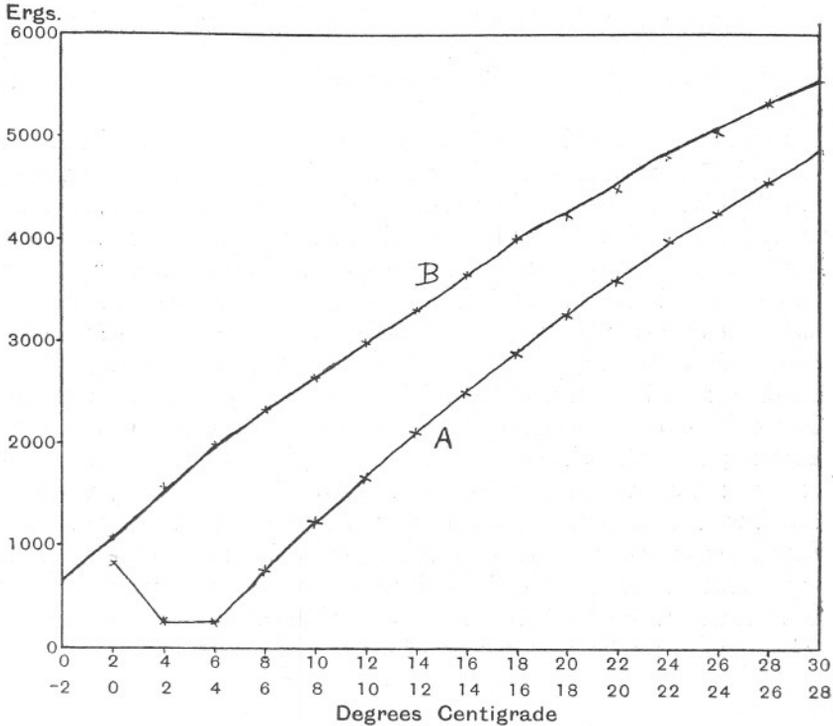


FIG. 3.—The ordinates show ergs of work done in mixing columns of water, one metre high and one square metre in area, whose upper and lower surfaces differ by  $2^{\circ}$  C., the upper being the warmer. The abscissæ indicate the temperatures of the surfaces. Curve A is for pure water, modified from Birge. In it the temperature figures  $2^{\circ}$  over  $0^{\circ}$  and  $4^{\circ}$  over  $2^{\circ}$  should be read  $0^{\circ}$  over  $2^{\circ}$  and  $2^{\circ}$  over  $4^{\circ}$ . Curve B is for water of  $35.3\text{‰}$  salinity.

for  $35.3\text{‰}$  salinity water between  $-2^{\circ}$  and  $0^{\circ}$ . The fifth column records the values of  $\Delta$  relative to that for pure water over the range  $2^{\circ}$  to  $4^{\circ}$  or  $4^{\circ}$  to  $6^{\circ}$  as unity. The sixth column sets forth the work done in mixing a water column as already described for sea water, but with  $2^{\circ}$  temperature gradient. Also to obtain whole numbers the area taken was one square metre instead of one square centimetre. In the seventh column the corresponding values for fresh water have been quoted from Birge's

paper, but as he calculated on a  $1^\circ$  gradient the figures given here are the sums of his values taken in pairs. The value for  $\Delta$  between  $-2^\circ$  and  $0^\circ$  is tabulated opposite  $-2^\circ$  and similarly for the other values.

In Fig. 1 (p. 695) are plotted the temperature-density curves for both fresh and salt water,  $35.3\text{‰}$  salinity. Fig. 2 (p. 696) shows the values of  $\Delta$  relative to salt and fresh water, also values of  $\Delta$  for fresh water modified from Birge's data, which are for  $1^\circ$  intervals. In Fig. 3 (p. 697) the results of columns 6 and 7 are plotted, the temperatures of the tops and bottoms of the columns being abscissæ, as in Fig. 2, while the ordinates represent ergs of work required for mixing.

From Fig. 1 it may be seen that, on account of the complication introduced by the position of maximum density being at  $4^\circ$  for fresh water, the rate of decrease in density per degree rise in temperature is far less for fresh than for salt water, but the rate becomes more nearly the same the higher the temperature. This is more clearly brought out by Fig. 2, from which it may be found that the mixing of, for example, a column of fresh water  $10^\circ$  at its upper surface and  $8^\circ$  at its lower is only about 47 per cent as difficult as mixing salt water of the same temperature and gradient. Again it may be seen that the mixing of a water column  $12^\circ$  top,  $10^\circ$  bottom, is 4.5 times as difficult as if the same column were  $0^\circ$  top,  $-2^\circ$  bottom; but if the temperatures were  $16^\circ$  to  $14^\circ$  respectively the resistance to mixing would have increased to 5.5 times. In Fig. 3, which is based upon Fig. 2, the resistance to mixing is shown by plotting the number of ergs of work done in mixing one cubic metre of water with upper and lower surfaces differing by  $2^\circ$  in favour of the upper. It may be seen that throughout the whole range plotted the mixing of fresh is effected more readily than is that of salt water.

#### SUMMARY.

1. A table has been drawn up showing the values of  $D_{\frac{t}{4}}$  for water of  $35.3\text{‰}$  salinity from  $t=-2^\circ$  to  $t=30^\circ$ . In it the values of  $\Delta=(D_{\frac{t-2}{4}}-D_{\frac{t}{4}})$  are shown as are also the values of  $\Delta$  relative to  $(D_{\frac{-2}{4}}-D_{\frac{0}{4}})$  as unity. In addition the values of  $\Delta$  relative to  $(D_{\frac{4}{4}}-D_{\frac{2}{4}})=(D_{\frac{4}{4}}-D_{\frac{6}{4}})$  for fresh water are tabulated. From the foregoing the number of ergs of work required to mix completely one cubic metre of water, with upper and lower surfaces having initial differences of  $2^\circ$ , have been calculated for sea water over the range  $-2^\circ$  to  $+30^\circ$ . For comparison Birge's values for fresh water are quoted.

2. The rate of decrease in density with increase in temperature in-

creases for both salt and fresh water, according as the actual temperature becomes further removed from the temperature of maximum density. Thus the relative value of  $\Delta$  as defined above becomes 5.0 for water at 14° to 12° and 6.0 for 18° to 16°, while  $\Delta$  relative to fresh water for the latter temperatures has the value 15.0. Owing to the differences in the temperatures of maximum density more work is required to mix a cubic metre of salt water than of fresh water, for 16° top to 14° bottom the number of ergs required are, for example, 3997 and 2899 respectively.

3. It results that the mixing of the surface water with the deeper is less readily brought about in summer than in winter, both on account of the lesser amount of wind and the increased differences in density. The warm surface layer, or epithalassa, gets depleted of phosphate by the phytoplankton, and as long as it persists the phosphate in the deeper layers is not fully utilized. The stability or otherwise of the epithalassa is consequently of great importance.

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## Seasonal Changes in the Phosphate Content of Sea Water in relation to the Growth of the Algal Plankton during 1923 and 1924.

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With Figures 1-8 in the Text.

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### SEASONAL CHANGES IN THE PHOSPHATE CONTENT AT L STATIONS, 1923-24.

IN Part I,\* Table 5, are recorded the amounts of phosphate found at the L Stations up to August, 1923. These have been continued up to December, 1924, in the present paper, Table 1. It will be noted that high values are recorded for December, January, and February, that there is a marked fall in spring, so that during June, July, and, at some stations, August, the surface water is altogether or almost devoid of phosphate. Towards winter the values again rise. These results, therefore, confirm those of Part I and the values obtained by Matthews using the method of Pouget and Chouchak. In this and the following tables occasional high values are encountered, as in Part I. It is to be supposed that they are due to the enrichment of the locality sampled by the larger

\* Vol. XIII, No. 1, of this Journal.

members of the fauna or by passing vessels. Several records are given for September, including duplicate analyses performed after the water had been stored for ten days or a fortnight. These stored samples here show marked increases, due doubtless to decomposition. For this reason it is imperative that the water should be analysed for phosphate as soon as possible after it has been withdrawn from the sea. In other cases,

TABLE I.

Surface Values for Phosphate as  $P_2O_5$  in mg. per  $m^3$  from L1 to E1, 1923-24.

Station	Sept. 13th	Oct. 15th	Nov. 8th	Dec. 10th	Jan. 2nd	Jan. 14th	Feb. 15th	Mar. 10th	Apl. 8th	May 20th	June 17th
L1	23	12	36	40	23	—	35	8.5	15	—	3
L2	19	12	32	41	25	—	52	9	—	—	2
L3	18	17	32	37	32	39	30	17	17	—	2
L4	23	15	21	—	31	39	35	15.5	—	—	—
L5	9	15	24	44	36	44	35	22.5	16	—	3
L6	7	21	23	40	68	37	36	10*	—	—	—
E1	0	22	20	34	38	—	32	—	14.5	5	2.5

Analysed	Sept. 24th	Oct. 16th	Nov. 9th	Dec. 11th	Jan. 3rd	Jan. 15th	Feb. 18th	Mar. 18th	May 2nd	June 20th	June 18th
Station	July 9th	Aug. 7th	Sept. 3rd	Sept. 18th	Sept. 18th	Sept. 22nd	Sept. 22nd	Oct. 1st	Nov. 12th	Dec. 9th	
L1	3	13.5	28	14	19	8	17.5	—	19	35	
L2	2	13.5	41	15	—	6.5	36.5	15.5	19	35	
L3	2	8	28	9.5	112	5.5	12	11	21	35	
L4	0	2	32	7.5	16	6	8.5	12	15	36‡	
L5	0	1.5	15	—	—	—	—	12	33	33	
L6	1	9†	23.5	—	—	—	—	12	22	31	
E1	2.5	1.5	12	—	—	—	—	6	14	32	

Analysed	July 17th	Aug. 9th	Sept. 17th	Sept. 19th	Oct. 2nd	Sept. 23rd	Oct. 2nd	Oct. 2nd	Nov. 14th	Dec. 10th
L1	3	13.5	28	14	19	8	17.5	—	19	35
L2	2	13.5	41	15	—	6.5	36.5	15.5	19	35
L3	2	8	28	9.5	112	5.5	12	11	21	35
L4	0	2	32	7.5	16	6	8.5	12	15	36‡
L5	0	1.5	15	—	—	—	—	12	33	33
L6	1	9†	23.5	—	—	—	—	12	22	31
E1	2.5	1.5	12	—	—	—	—	6	14	32

however, storage is accompanied by a decrease in phosphate; examples of this are given later.

In Table 2 are shown the values obtained at E1 and L series at various depths during summer and autumn. It may be seen that as the coast is approached the water undergoes a greater degree of vertical mixing and the thickness of the warm layer devoid of phosphate, the epithalassa, becomes reduced.

\* But 24 at 25 m.

† But 2 at 10 m.

‡ Same near bottom, 40 m.

TABLE II.

Variation of phosphate with depth as coast is approached on Aug. 7th, Sept. 3rd, Oct. 1st and Nov. 12th. Analysed Aug. 9th, Sept. 17th, Oct. 2nd and Nov. 14th, 1924, respectively.

Depth	E1	L6	L5	L4	L3	E1	L6	L5	L4	L3	E1	L6	L4	L3	E1	L4
0	1.5	9	1.5	2	8	12	23.5	15	32	28	6	12	12	11	14	15
5	2	—	2	2	7	10	—	—	—	28	—	—	—	—	20	—
10	—	2	—	3	6.5	19.5	—	16	11	—	14	—	—	—	—	26.5
15	1	5.5	9	6	9.5	14	—	—	—	—	—	—	—	—	—	—
20	13	5.5	—	—	—	19	—	35	—	—	—	—	—	—	—	—
25	13	10.5	8	5.5	—	19	24.5	—	21	—	—	—	—	—	20	—
30	—	—	—	—	—	—	—	—	—	16	—	—	—	—	—	—
40	—	—	12.5	—	12	—	—	—	—	—	—	—	—	—	—	26
50	—	—	—	12	*	19	—	19	21	*	16	15.5	15.5	*	—	—
60	—	—	*	*	*	—	24	*	*	*	—	—	*	*	—	*
70	13	*	*	*	*	19	*	*	*	*	16	*	*	*	21	*

September results are apparently high owing to storage.

#### SEASONAL CHANGES IN THE PHOSPHATE CONTENT AT STATION E1, 1923-24.

In Table 3 the values given in Part I, Table 7, are continued, and the data for the two years are plotted in Figs. 1 and 2, for surface and bottom respectively. It may be noticed that while the two years show a general similarity, yet the decrease in phosphate became marked in 1924 at a

TABLE III.

Seasonal Changes at Station E1. The Figures denote Phosphate as  $P_2O_5$  in mg. per  $m^3$ , 1923-24.

Depth	Sept. 13th	Oct. 15th	Nov. 7th	Dec. 10th	Jan. 2nd	Feb. 15th	Mar. 10th	Apl. 8th
0	0	22	20	34	38	32	12	14.5
5	1	21	—	—	—	32	—	—
10	6	18	—	—	—	—	—	—
15	—	—	—	34	—	—	—	—
20	13	16	—	—	—	—	—	—
25	—	13	—	—	—	—	27	15
30	—	19	—	—	—	—	—	—
40	17	15	—	—	—	—	—	—
50	—	14	20	—	36	—	—	—
70	20	14	20	34	—	32	22	15
Analysed	Sept. 24th	Oct. 16th	Nov. 9th	Dec. 11th	Jan. 3rd	Feb. 18th	Mar. 18th	May 2nd

## SEASONAL CHANGES IN THE PHOSPHATE CONTENT OF SEA WATER AT STATION E1, SURFACE.

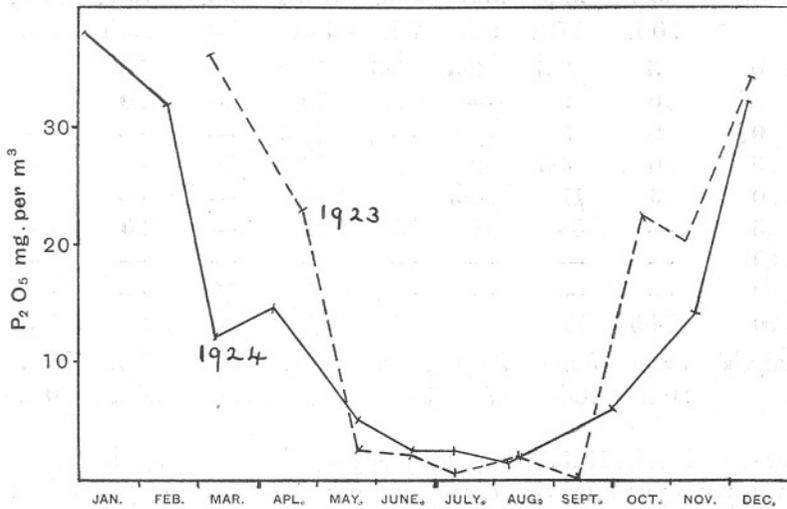


FIG. 1.—The ordinates denote phosphate, shown as milligrams of  $P_2O_5$  per cubic metre of water. The abscissæ are months during 1923 and 1924.

## SEASONAL CHANGES IN THE PHOSPHATE CONTENT OF SEA WATER AT STATION E1, BOTTOM, 70 METRES.

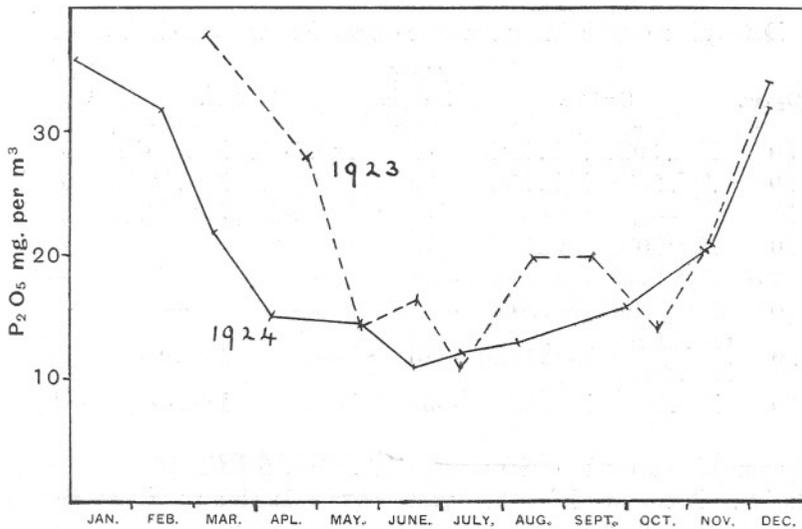


FIG. 2.—The ordinates denote phosphate, shown as milligrams of  $P_2O_5$  per cubic metre of water.

TABLE III—*continued.*

Depth	May 20th	June 17th	July 9th	Aug. 7th	Sept. 3rd	Oct. 1st	Nov. 12th	Dec. 9th
0	5	2.5	2.5	1.5	12	6	14	32
5	10	3	—	2	10	14	20	—
10	9	3	—	—	19.5	—	—	—
15	10	4.5	2	1	14	14	—	—
20	15	11	22.5	13	19	—	—	32
25	—	—	11	13	19	—	20	—
30	—	—	—	—	—	—	—	—
50	—	—	—	—	19	16	—	—
70	14.5	11	12	13	19	16	21	32
Analysed	June 20th	June 18th	July 17th	Aug. 9th	Sept. 17th	Oct. 2nd	Nov. 14th	Dec. 10th

later date than in 1923. Since the phosphate is used up by the increase in the phytoplankton this denotes an earlier outburst of plant life in 1924 than in 1923, which appears to be due to the high value for the mean daily sunshine during March, 1924, 5.3 hrs., as compared with 3.5 hrs. in 1923. Fig. 3 shows the values of the monthly means of the

TABLE IV.

Dates when certain Phosphate Concentrations were reached at E1.

P <sub>2</sub> O <sub>5</sub> mg. per m. <sup>3</sup>	Surface.		Ahead in days, 1924.	Bottom.		Ahead in days, 1924.
	1923.	1924.		1923.	1924.	
30	Mar. 30th	Feb. 18th	41	Apl. 14th	Feb. 20th	54
20	Apl. 28th	Feb. 28th	29	May 9th	Mar. 17th	53
11	—	—	—	July 9th	June 18th	21
10	May 10th	Apl. 28th	12	—	—	—
2.5	May 21st	June 18th	-28	—	—	—
10	Sept. 28th	Oct. 20th	-22	—	—	—
20	Oct. 11th	Nov. 22nd	-15	Nov. 6th	Nov. 4th	2
	Nov. 7th					
30	Dec. 1st	Dec. 6th	-5	Dec. 1st	Dec. 4th	-3

daily sunshine records of England, S.W. area, for the years 1921-24 inclusive. None of the other years equals 1924 as regards March sunshine, though 1921 stands out as an exceptional year in April, June, and July.

The graphs in Figs. 1 and 2 give approximate information as to the periods of the year when the development of the phytoplankton was most rapid, and Table 4 constitutes a comparison of 1923 with 1924 obtained by reading off the dates at which certain concentrations were reached in the periods of consumption and of regeneration of phosphate. Thus in 1924 consumption was far ahead of 1923 in the spring and regeneration lagged somewhat at first, though eventually the two years

MEAN MONTHLY VALUES FOR DAILY SUNSHINE IN ENGLAND,  
S.W. AREA.

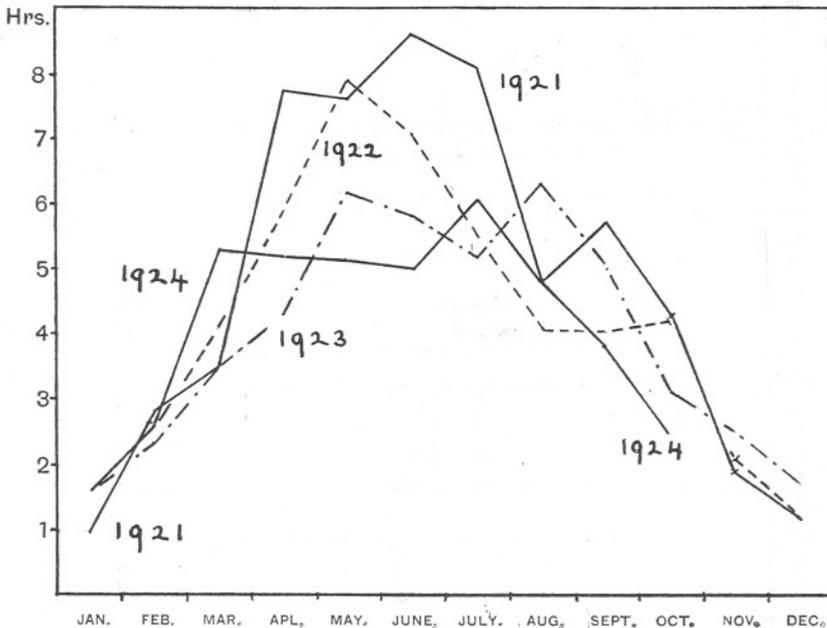


FIG. 3.—The ordinates denote the number of hours of sunshine daily for the month plotted for the 15th of each month.

ran out almost level. Furthermore, the two years were closely similar in the extent to which phosphate was removed from the water column in the open sea, as shown by the E1 results. The values given in Table 3 for the phosphate-depth series are shown in Fig. 4, which should be compared with Pt. I, Fig. 5, p. 131. The monthly graphs move towards the right, denoting increase in phosphate in the latter half of each year, and towards the left in the first half. Now from the area of the curve between the June 17th graph and the vertical axis it may be found that the water column contained 61.2 mg. phosphate, as  $P_2O_5$ , in  $70 m^3$ ,

down to the bottom, viz. 8.7 per  $m^3$ . Similarly for July the amount was 61.3 mg., or 8.7 per  $m^3$ . During this period there was accordingly no

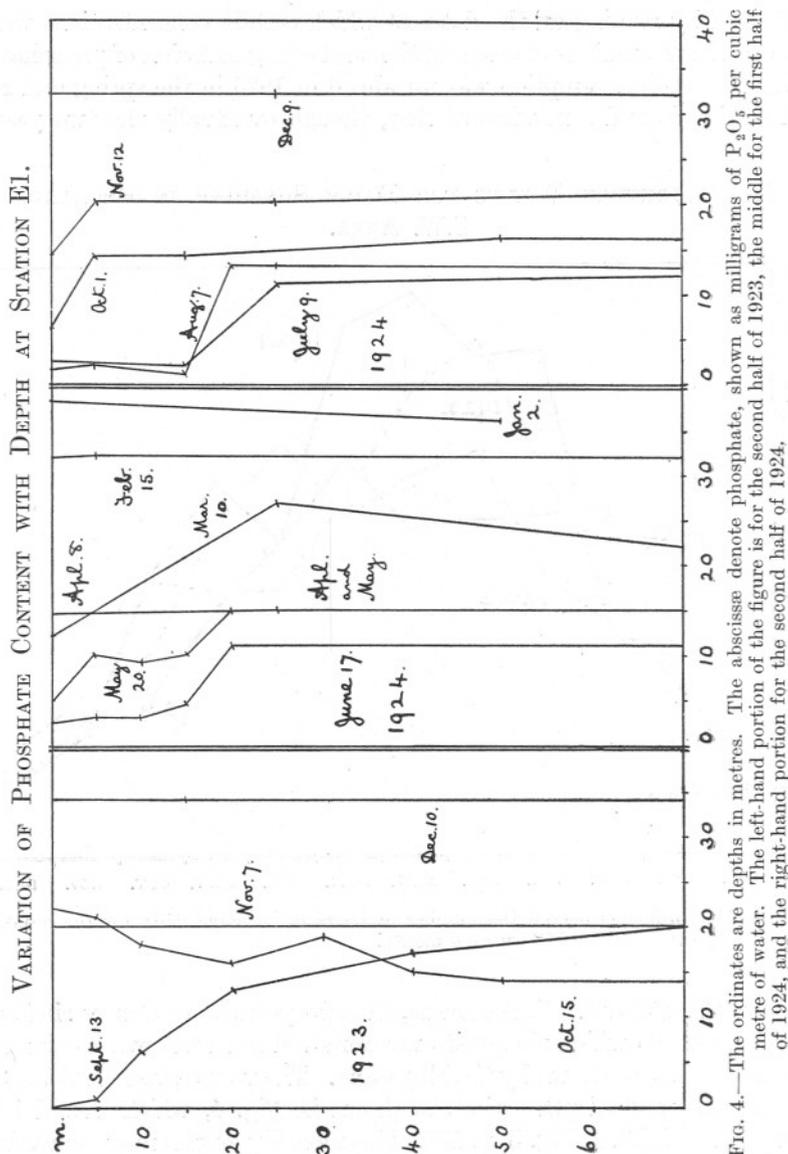


FIG. 4.—The ordinates are depths in metres. The abscisse denote phosphate, shown as milligrams of  $P_2O_5$  per cubic metre of water. The left-hand portion of the figure is for the second half of 1923, the middle for the first half of 1924, and the right-hand portion for the second half of 1924.

further growth, for the phosphate left over was far from the light. To be accurate there was some growth, as the surface waters were more nearly being completely deprived of phosphate in July than in June,

but this was counterbalanced by regeneration in the deeper water. Subtracting these amounts, viz. 8.7 per  $m^3$  from that present in January, 37 mg. per  $m^3$ , it is seen that 28.3 mg. per  $m^3$  was used up. For 1923 the corresponding figures were 37 and 7.4, giving a consumption of 29.6 mg. per  $m^3$ . Accordingly, the 1923 estimate of 1.4 kgm. algal-plankton, wet weight, per square metre of sea down to 70 metres holds quite approximately for 1924 also.

SEASONAL CHANGES IN THE TEMPERATURE OF THE WATER AT  
STATION E1, SURFACE.

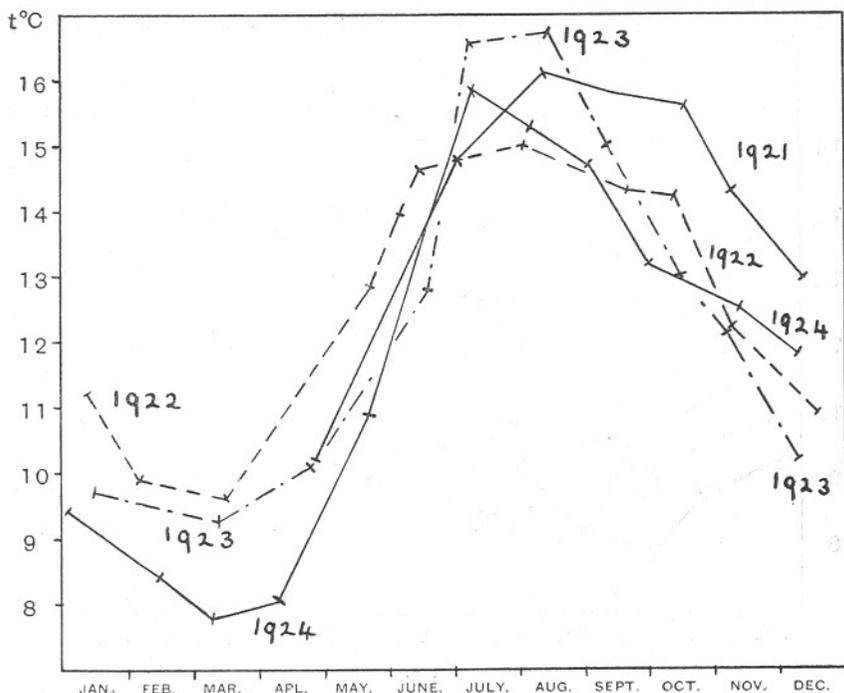


FIG. 5.

Table 5 is similar in construction to Table 4, but shows temperatures instead of phosphate concentrations. It was drawn up by reading off from Figs. 5 and 6, which are plotted from the surface and bottom (70 m.) observations made at E1 from 1921-24 inclusive. In these it may be seen that 1924 was the coldest year in the spring, a condition which persisted till November at the bottom. Moreover, no two years were the same. In view of the very high temperature coefficient which living cells show as regards all their processes of metabolism, these differences

must have a considerable importance in regulating their rates of growth and the onset of periods of reproduction.

Thus we are faced with the fact that in 1924 the water in spring was abnormally cold, and the attainment of given temperatures lagged over a month—two months at the bottom—behind 1923, yet owing to the greater amount of sunshine the phosphate consumption in 1924 was over a month ahead of 1923. Therefore, it appears that in 1924 the rate of

SEASONAL CHANGES IN THE TEMPERATURE OF THE WATER AT  
STATION E1, BOTTOM.

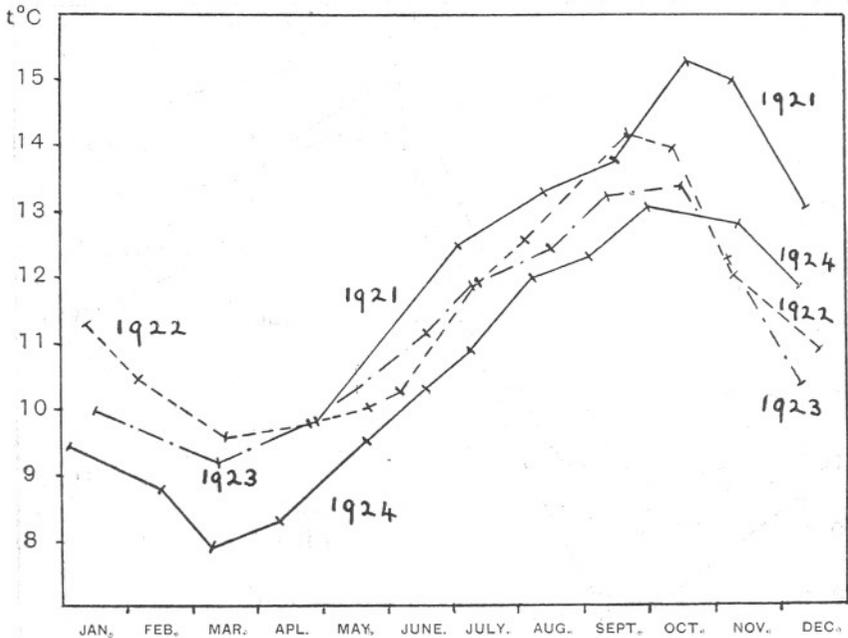


FIG. 6.

production of the phytoplankton was far ahead of that of the zooplankton as compared with 1923. It is possible that a difference of this kind may affect certain species of the latter advantageously, in that their food supply is abundant, or adversely if it so happens that the particular food organism required has appeared and disappeared again, as for example *Phæocystis* is known to do.

Similar seasonal changes in the phosphate content of fresh-water ponds have been found by the author and Harris (1924); an abstract is published in this Journal.

TABLE V.

Dates when Certain Temperatures were reached at E1.

t°.	Surface.		Ahead in days, 1923.	Bottom.		Ahead in days, 1923.
	1923.	1924.		1923.	1924.	
9.3	Mar. 12th	Apl. 29th	48	Mar. 12th	May 13th	62
10	Apl. 18th	May 8th	21	May 3rd	June 6th	34
11	May 13th	May 22nd	9	June 12th	July 12th	30
12	June 3rd	June 2nd	-1	July 18th	Aug. 7th	20
13	June 20th	June 11th	-9	Sept. 3rd	Sept. 28th	25
14	June 25th	June 20th	-5	—	—	—
15.9	July 6th	July 9th	3	—	—	—
14	Sept. 28th	Sept. 16th	-12	—	—	—
12	Nov. 10th	Dec. 1st	21	Nov. 12th	Dec. 5th	23

SEASONAL CHANGES IN THE PHOSPHATE CONTENT OF THE WATER OF  
\* THE ENGLISH CHANNEL AT THE E AND N STATIONS.

The positions of the stations are shown in the map given on p. 754, Vol. 12, No. 4, of this Journal; the E series form a line from Plymouth to Ushant and the N from Ushant to Cork, N2 being near the Bishop Light, S.E. of the Scillies. N3, however, is in the passage between the islands and Cornwall. The results from Nov., 1923—Nov., 1924, inclusive are shown in Tables 6, 7, 8, and 9, also in Figs. 7 and 8: these should be compared with Tables 8 and 9 and Figs. 6 and 7 in Part I, this Journal, p. 132, Vol. 13, No. 1. These stations illustrate the fact that the seasonal changes occur in very much the same manner at all the localities investigated, though the smaller number of observations renders the sequence less detailed. On comparing the two years it is seen that phosphate consumption had progressed slightly further by May, 1923, than by May, 1924, at E2 and E3, while at N1 and N2 the seasons were very much alike. In July, 1924, E2 was either behind 1923, or more probably in view of the high surface values rather ahead of it on the path towards regeneration of phosphate. At E3 the two years were very similar, as also at N2. At N1 the surface water was more completely denuded of phosphate in 1923, but the deeper water was the poorer in 1924, so that on the whole the two years were much alike. The November results all indicated that either owing to more rapid regeneration or to the influx of water richer in phosphate the water in 1924 was rather better supplied with phosphate than in 1923. These differences are, however, all of a minor kind; in general the seasonal changes were alike.

Tables 6-9 also record the temperature observations as well as the phosphate content. On comparing the two sets of figures it becomes

apparent that the warm layer, the epilhalassa, is also the region of low phosphate content. Thus in July, 1924, at E1 the epilhalassa extends

VARIATION OF PHOSPHATE CONTENT WITH DEPTH AT STATIONS  
E2 AND E3.

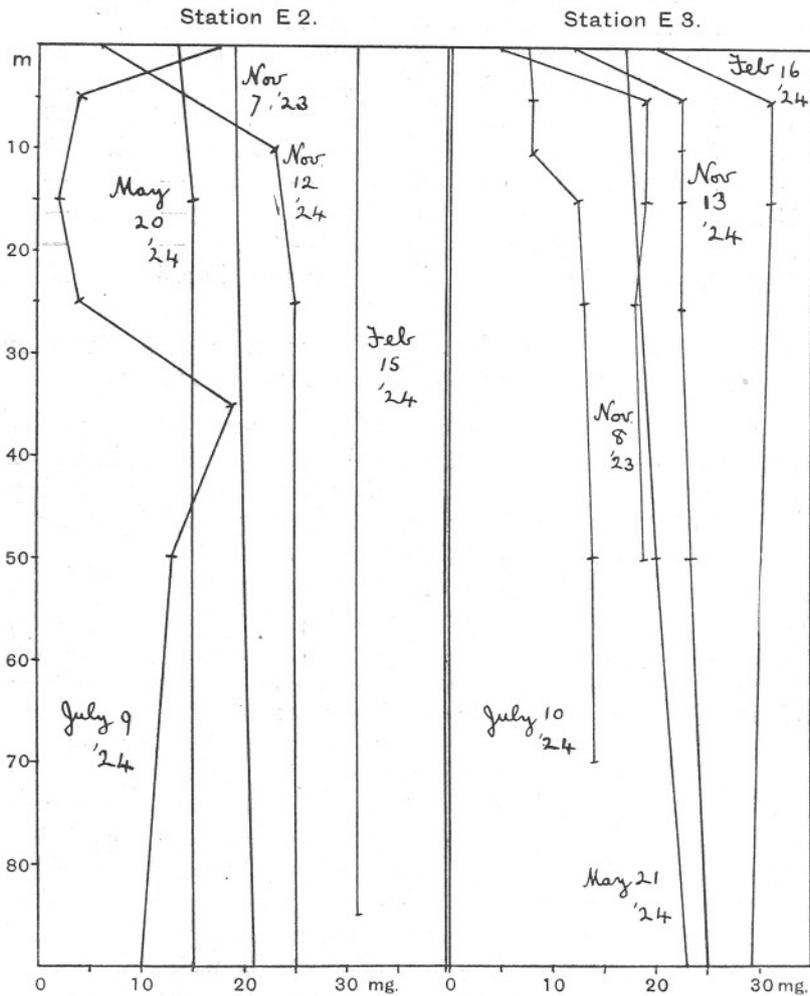


FIG. 7.—The ordinates are depths in metres. The abscissæ denote phosphate, shown as milligrams of  $P_2O_5$  per cubic metre of water. The left-hand portion is for E2.

to 15 metres, with a  $P_2O_5$  value of 2 mg., whereas at E2, where the epilhalassa extends to 25 m., the low value, 4 mg., is found at that depth. Other examples may be noted elsewhere in the tables. This is quite in keeping with the results afforded by hydrogen ion concentration measure-

ments as recorded in the writer's previous papers in this Journal. It appears to be indicated also in Table 8 that the thermocline may be rather richer in phosphate than the hypothermalassa, due probably to its

VARIATION OF PHOSPHATE CONTENT WITH DEPTH AT STATIONS  
N1 AND N2.

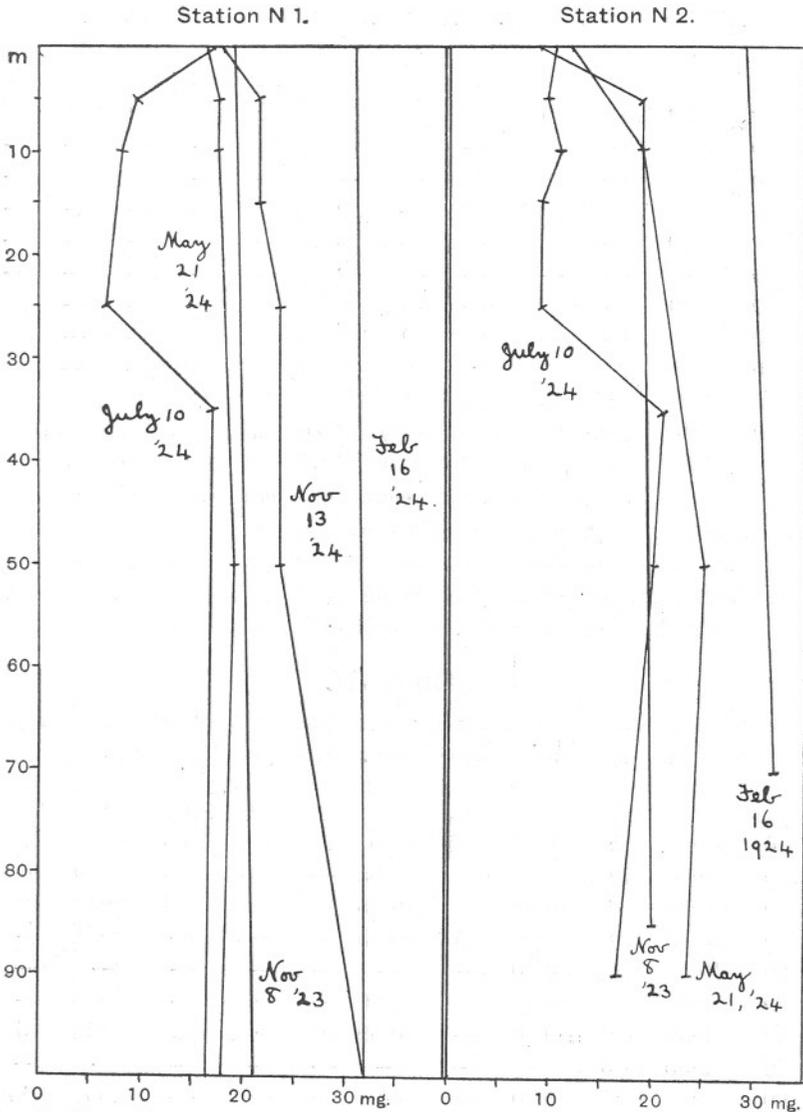


FIG. 8.—The ordinates are depths in metres. The abscissæ denote phosphate, shown as milligrams of  $P_2O_5$  per cubic metre of water. The left-hand portion is for N1.

being relatively rich in zooplankton, though it is quite possible that the high values found in a few cases may have been occasioned by fortuitous contamination of the water before it was drawn.

TABLE VI.

Phosphate as  $P_2O_5$  in mg. per  $m^3$  on cruises of Nov. 7th-8th, 1923, and Feb. 15th-16th, 1924, respectively. Surface and bottom temperatures are shown below. Analysed Nov. 9th and Feb. 18th respectively.

Depth	E1	E2	E3	N1	N2	N3	E1	E2	E3	N1	Z
0	20	19	5	19	9	7	32	31	20	31	29
5	—	—	19	—	19	18	32	—	31	—	—
15	—	—	19	—	—	—	—	—	31	—	—
25	—	—	18	—	—	20	—	—	—	—	—
50	20	—	19	—	—	—	—	—	—	—	—
65	—	—	—	—	—	20	—	—	—	—	—
70	20	—	—	—	—	*	32	—	—	—	32
85	*	—	—	—	20	*	*	31	—	—	*
95	*	21	—	—	*	*	*	*	—	—	*
105	*	*	—	21	*	*	*	*	29	32	*
0	12.15	12.35	11.15	11.65	11.65	11.55	8.45	9.45	9.55	9.55	8.8
Bottom	12.32	12.63	11.85†	11.70	11.70	11.72	8.76	9.63	10.03	9.85	9.00

† This temperature extended to 5 m. level.

The stations form an open V with E3 at apex and E2 opposite N1. Station Z was an extra observation point 20 miles S.W. of the Lizard, as weather did not permit of N2 being reached. Asterisks in a column signify that bottom would be penetrated at the depth.

TABLE VII.

Phosphate as  $P_2O_5$  in mg. per  $m^3$  on cruise of May 20th-21st, 1924. Temperatures are also shown. Analysed June 20th.

Depth	E1		E2		E3		N1		N2	
	t°	$P_2O_5$								
0	10.9	5	10.8	13.5	10.5	17	11.4	16.5	11.7	12
5	10.94	10	10.56	—	10.55	—	11.52	17.5	11.40	—
10	10.84	9	10.56	—	10.55	—	11.51	17.5	10.74	19
15	10.45	10	10.56	15	10.55	—	10.25	—	9.74	—
20	10.32	15	10.30	—	—	—	—	—	—	—
25	9.59	—	10.24	—	10.60	—	9.79	—	9.74	—
50	9.57	—	10.20	—	10.59	20	9.79	19	9.54	25
70	9.55	14.5	—	—	—	—	—	—	—	—
90	*	*	10.20	15	—	—	—	—	9.51	23.5
100	*	*	*	*	10.59	23	9.74	18	*	*

TABLE VIII.

Phosphate as  $P_2O_5$  in mg. per  $m^3$  on cruise of July 9th-10th, 1924.  
Temperatures are also shown. Analysed July 17th.

Depth	E1		E2		E3		N1		N2		N3	
	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$
0	15.9	2.5	15.7	17.5	15.2	7.5	15.5	17	15.2	10.5	15.0	11.5
5	14.38	—	15.53	4	15.23	8	15.43	9.5	14.81	9.5	15.19	7
10	14.20	—	—	—	14.83	8	15.36	8	13.53	11	14.90	6
15	13.45	2	14.43	2	12.69	12.5	14.66	—	12.97	9	14.10	5.5
20	11.99	22.5	—	—	—	—	—	—	—	—	—	—
25	11.54	11	13.90	4	11.96	13	14.65	6.5	12.74	9	12.04	18
35	—	—	11.99	19	—	—	10.59	17	10.74	21	—	—
50	11.24	—	11.69	13	11.96	14	10.57	—	10.49	20	11.69	13.5
70	10.91	12	11.69	—	11.94	14	10.39	—	—	—	11.49	10
90	*	*	11.61†	10†	—	—	—	—	10.49	16.5	*	*
100	*	*	*	*	11.89	—	10.39	16.5	*	*	*	*

† Observations 5 m. higher up than depth indicated.

TABLE IX.

Phosphate as  $P_2O_5$  in mg. per  $m^3$  on cruise of Nov. 12th-13th, 1924.  
Temperatures are also shown. Analysed Nov. 14th-18th.

Depth	E1		E2		E3		N1		E7	
	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$
0	12.5	14	12.5	6	13.0	12	12.0	19	12.4	—
5	12.81	20	—	—	13.25	22.5	12.34	21.5	12.42	24.5
10	12.80	—	12.90	23	13.25	22.5	12.33	—	12.42	—
15	12.78	—	—	—	13.25	22.5	12.32	21.5	12.42	—
25	12.80	20	12.90	25	13.25	22.5	12.32	23.5	12.42	—
50	12.85	—	12.90	—	13.25	24	12.32	23.5	12.40	—
70	12.85	21	—	—	—	—	—	—	12.41	25.5
100	*	*	12.89†	25†	13.30	25	12.32	32	*	*

Depth	X <sub>1</sub>		X <sub>2</sub>		N <sub>3</sub>		E6	
	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$	t°	$P_2O_5$
0	12.4	24.5	12.2	10	12.0	28.5	11.7	12
5	—	—	—	—	—	—	—	—
10	—	—	—	—	12.15	28	12.00	29
15	—	—	—	—	—	—	—	—
25	12.50	19	—	—	12.10	28	12.00	—
50	12.52	19	12.38	23	12.10	29	12.00	—
70	*	*	*	*	12.10	22	12.00	29

E7 is the International Station near the Wolf Light. X1 is half a mile off the Longships Light and X2 is  $5\frac{1}{2}$  miles off it on course to N3.

Intermediate surface values are as follows for temperature and phosphate respectively:—E1-E2, 12.8°, 21 mg.; E2-E3, 12.8°, 6 mg.; E3-N1, 12.3°, 277 mg.; N1-E7, 12.1°, 20 mg.

† 92 m.

SEASONAL CHANGES IN THE PHOSPHATE CONTENT OF THE WATER  
OF THE NORTH SEA.

Table 10 records the result of the analysis of surface and bottom samples in the shallower parts of the North Sea between the limits indicated. Of necessity a period of from a fortnight to a month elapsed between the drawing of the samples and their analysis. Their individual accuracy is somewhat impaired thereby; for this reason and to economise in space the results of the four cruises, from which a number of samples were obtained, have been shown as averages.

TABLE X.

Surface and bottom samples, North Sea, between  $0^{\circ} 2' W.$  and  $6^{\circ} 28' E.$  and  $54^{\circ} 34' N.$  to  $57^{\circ} 51' N.$  The averaged results were from samples on lines on the course indicated. The single samples were within the given area.

Date.	P <sub>2</sub> O <sub>5</sub> mg. per m <sup>3</sup> , surface.	P <sub>2</sub> O <sub>5</sub> mg. per m <sup>3</sup> , bottom.	Depth m.	Number of samples.
May 3-6, 1923 . . . . .	17	18	65	12
Sept. 27-29 . . . . .	2	16	67	11
Feb. 8, 1924 . . . . .	20	21	65	1
Mar. 20-22 . . . . .	25	27	68	8
Apr. 6 . . . . .	17	17	42	1
May 5 . . . . .	15	14	43	1
May 31 . . . . .	8	41	97	1
July 8 . . . . .	3	5	50	1
Aug. 6 . . . . .	2	10	54	1
Aug. 28-30 . . . . .	10	30	71	7
Oct. 19 . . . . .	16	16	35	1
Nov. 16 . . . . .	27	27	40	1

The seasonal changes are very similar to those in the English Channel, the minimum values being found in July and early August, though in 1923 September surface samples were also almost devoid of phosphate. A considerable amount of regeneration is indicated by the August, 1924, figures, but this must have been mainly near the bottom as the October analyses show.

In Table 11 the results of phosphate-depth series are recorded for the deeper portion of the North Sea towards Norway. The gradient is very pronounced, but while the March, 1924, values are regular, those for August are the reverse; the possibility of the enrichment of the deeper

water layers by the presence of plankton slowly sinking as it decomposes must be kept in mind. The striking thing about the August results is that the deeper water has not been denuded of phosphate to anything like the same depth that the shallower water at, say, E1 has been. The epithalassa is in this region subject to less mixing with the hypothalassa than in shallower water, which is indicated by the temperature observations also. The phosphate reserve is, therefore, not available for plant growth till it is brought nearer the surface into sufficient illumination.

Further evidence on the phosphate content of the deeper water was

TABLE XI.

Phosphate in deep water off Norway, North Sea, May 6th, at 58° 28' N., 4° 34' E.; March 22nd at 57° 47' N., 6° 19' E.; and Aug. 30th, 57° 51' N., 6° 39' E. respectively.

Depth, m.	May 6th, 1923. P <sub>2</sub> O <sub>5</sub> mg. per m <sup>3</sup> .	Mar. 22nd, 1924. P <sub>2</sub> O <sub>5</sub> mg. per m <sup>3</sup> .	Aug. 30th, 1924. P <sub>2</sub> O <sub>5</sub> mg. per m <sup>3</sup> .	t°.
0	14	22	20	16.14†
20	—	28	16	9.89
50	—	31	28	6.26
75	—	—	27	6.32
100	—	34	37	6.12
150	—	37	39	5.97
200	—	37	30	5.45
250	—	37.5	28	5.38
280	36	39	—	—
300	*	*	42	5.19
350	*	*	26 25.5	5.10

† At 10 m. t=16.04. The secondary maximum at 75 m. occurs more markedly at the station west of this, at the same depth.

sought by examining samples from around the islands north of Scotland, as set forth in Table 12 (p. 716). The really deep water north of the Wyville Thomson ridge does not show any great amount of phosphate in May, presumably it had experienced vertical mixing at no very distant date. To the south of the ridge, however, an exceptionally high value was obtained in May, also an unusually low one, such as might be met with in surface water further south. More extended observations in this region are desirable. The analyses for the August samples north of the ridge are very puzzling by reason of the high results and their irregularity. The latter may be due to storage for a month before analysis; the high

values averaging 77 mg. per m.<sup>3</sup> may have their origin in the admixture of deep water from the Atlantic, though the temperatures are too low to use this as an explanation with any confidence, for even in May the south side of the ridge was at 8.5°. Similar high and irregular values were obtained at the other Scotch stations, but the results are being held over pending confirmation by other samples. The possibility of enrichment from the glass of the bottles is also being examined by storage tests. The bottles used in August were not the ordinary spring clip milk bottles of green glass, but were of a soft white glass with waxed corks.

TABLE XII.

Surface and deep-water samples around the North of Scotland, 1924.  
Analysed May 2nd, June 18th, and Sept. 3rd respectively.

Date.	Lat. N.	Long.	Locality.	Depth in metres.	P <sub>2</sub> O <sub>5</sub> mg. per m <sup>3</sup> .	t°.
4/3	59° 10'	1° 27' W.	W. of Orkney Is.	0	25	—
				104	25.5	—
4/3	60° 05'	0° 48' W.	W. of Shetland Is.	115	25	—
9/3	60° 02'	1° 10' W.	W. of Shetland Is.	123	24.5	—
21/3	58° 44'	6° 00' W.	W. of N. of Scotland	0	20	—
				120	21	—
6/5	61° 21'	4° 06' W.	East of 1000 m. line off S. of Faroe Is., N.E. of Wyville Thomson ridge.	600	22	-0.56
				1100	22	-0.94
22/5	59° 34'	7° 00' W.	On bend of 1000 m. line, S. of Wyville Thomson ridge.	300	8	8.81
				800	79	8.52
5/8	61° 10'	4° 30' W.	E. of 1000 m. line, S. of Faroe Is., N.E. of Wyville Thomson ridge.	0	74	11.08
				10	76	11.02
				25	54	10.48
				50	85	8.89
				75	54	7.83
				100	57	7.80
				150	85	7.51
5/8	61° 10'	4° 30' W.	E. of 1000 m. line, S. of Faroe Is., N.E. of Wyville Thomson ridge.	200	68	7.40
				300	66	5.12
				400	83	3.86
				500	91	0.70
				600	94	0.25
				775	109	-0.50

#### PHOSPHATE CONTENT OF THE ATLANTIC OCEAN AND OTHER WATERS.

In Table 13 are recorded the results from samples from the Irish Channel, which are very similar to those in the English Channel at the same seasons, also one station 80 miles S.W. of the Fastnet Light. This had on Nov. 19th the same phosphate content as E1 had on Nov. 12th, but the deeper water 310 m. gave the high value 44 mg.

An interesting series is provided by the run from England to Ceylon, shown in Table 14. Sea water sent out in the case of boxes was analysed

TABLE XIII.

Surface and bottom samples, Irish Channel and Atlantic. Analysed May 5th, Aug. 20th, and Dec. 11th respectively.

Date taken.	Lat. N.	Long. W.	t°.	P <sub>2</sub> O <sub>5</sub> mg. per m. <sup>3</sup>	Depth in metres.
Mar. 4th .	53° 22'	5° 30'	7.24	18, 18	0
"	"	"	7.26	20, 24	93
June 27th .	49° 20'	8° 00'	15.24	3	0
"	"	"	10.11	28	133
Nov. 19th .	50° 28'	10° 49'	—	14	0
"	"	"	—	41	150
"	"	"	—	44	310

TABLE XIV.

Surface samples (3 metres) collected between Liverpool and Colombo on Feb. 2nd to 23rd, 1924, inclusive. These are given in mg. of P<sub>2</sub>O<sub>5</sub> per cubic metre, both as analysed and corrected for change during storage by a factor ( $\times 2.3$ ) obtained from the alteration in sea-water blanks sent out with the bottles. Analysed May 8th.

Lat. N.	Long.	Locality.	t°	P <sub>2</sub> O <sub>5</sub> mg. found.	Per m <sup>3</sup> corrected.
43° 45'	9° 40' W.	N. of Finisterre	13.3	17, 16	38
38° 53'	9° 38' W.	N. of C. Roca	15.5	14.5	33
35° 54'	5° 53' W.	Str. of Gibraltar	17.8	12, 12	27
36° 42'	0° 06' E.	Far off Algeria	16.6	12	27
37° 11'	6° 09'	" "	15.5	13	29.5
36° 56'	12° 08'	N. of Pantellaria, S. of Sicily	15.5	12	27
36° 42'	17° 46'	Far N. of Tripoli	16.6	6	14
33° 54'	23° 13'	" S. of Crete	17.8	6	14
32° 29'	28° 45'	" N. of Egypt	18.3	2.5	5.5
		At Port Said	19.4	—	—
28° 07'	33° 23'	G. of Suez	18.9	2	4.5
24° 02'	36° 20'	N. of Tropic of Cancer	25.5	1.5	3.5
19° 46'	39° 02'	Lat. of Suakim	27.8	5	11.5
15° 36'	41° 45'	Nearing South end	26.7	6	14
12° 18'	44° 38'	G. of Aden	26.7	11	25
12° 15'	49° 40'	Do. nearing end, African side	25.5	17	39
11° 25'	54° 27'	Past C. Gardafui, S. of Socotra	26.1	17	39
10° 33'	59° 08'	Indian Ocean	27.2	12.5	28.5
9° 49'	63° 57'	" "	26.7	6	14
8° 59'	68° 51'	" "	28.3	8	18
8° 07'	73° 48'	Near Maldive Is.	29.3	5.5	12.5
7° 09'	78° 47'	Approaching Ceylon	—	7	16

again on its return, and the very large correction thus found and applied is, it must be admitted, of doubtful validity. The results of this series are, however, of remarkable uniformity, when grouped according to locality. They bring out clearly the fact that the phosphate concentra-

tions near the surface in the Eastern Mediterranean and the Red Sea are in February similar to summer concentrations here. Furthermore, the high values found in the Atlantic are rather similar to those recorded for the region of the Indian Ocean which bathes Gardafui; this and the lower temperatures found around the latter indicate that vertical mixing is taking place more markedly than in the open ocean further south.

A similar series was obtained from the sailing ship, *St. George*, between England and Panama. The first samples were taken on April 16th and the last on June 8th, 1924. The analyses were made on July 24th-25th, so the storage error must be considerable. The following values were obtained: Off Portugal and Morocco two samples, average 21 mg. per m.<sup>3</sup>; open Atlantic, sixteen samples, average 7 mg. per m.<sup>3</sup>; and Caribbean Sea, seven samples, average 3 mg. per m.<sup>3</sup> These in general show that almost all the phosphate is used up in the well-illuminated southern waters, so that the conditions are similar to those for the English Channel in July.

The whole weight of evidence afforded by the phosphate determinations, recorded in this paper and in Part I is in favour of the view that where illumination is adequate the phytoplankton increases till the phosphate is almost absolutely used up. From this it may be concluded that the lack of phosphate limits the abundance of the phytoplankton, and, therefore, of necessity of the zooplankton. It would be of interest to ascertain by how much the plankton would increase were an unlimited supply of phosphate available and what substance would then become the limiting factor.

The results obtained for tropical waters indicate that in them illumination is always adequate, so that at any given time the amount of phosphate free in the water as such is small. Apparently as one organism liberates phosphate by death or excretion it is used up by another with but little loss of time. The change from summer to winter conditions is accordingly less marked in the phosphate cycle of tropical than of temperature regions. It appears legitimate to conclude that in northern regions the change from summer to winter conditions is more marked in this as in other biological cycles. The long nights and the low altitude of the sun during winter must result in a great diminution in the amount of the phytoplankton, with consequent liberation of phosphate. It is to be expected, therefore, that the arctic waters should have a greater phosphate concentration during winter than those around the British Isles. Furthermore, at all times mixing of surface water with deeper water is more easily effected the nearer that water is to its temperature of maximum density, as explained in an accompanying paper by the author. With the advent of increased sunshine and long days these

northern waters produce accordingly the abundant plankton for which they are noted.

### METHOD OF ANALYSIS.

As explained in Part I the phosphate estimations were made by means of the coeruleo-molybdate colorimetric method of Denigès, using Hehner tubes for the comparison in preference to either a Duboscq or Kober colorimeter. The comparisons were made against a standard of  $\text{KH}_2\text{PO}_4$  preserved with toluene. The working standard was equivalent to 0.50 mg.  $\text{P}_2\text{O}_5$  per litre, and as a rule this was diluted, 10 c.c. to 100 c.c., for use. This concentration, 0.050 mg. per litre, gives a depth of clear blue which is convenient for work with natural waters. The solutions used were :—

(a) 100 c.c. of 10 per cent ammonium molybdate plus 300 c.c. of 50 per cent (by volume) sulphuric acid. Of this mixture 2 c.c. is added to 100 c.c. of the sample. The reagent should be stored in the dark to minimise the spontaneous production of a blue tint.

(b) Stannous chloride, freshly prepared from 0.1 gm. tin dissolved in 2 c.c. of hydrochloric acid with one drop of 3–4 per cent copper sulphate and made up to 10 c.c. It was at first usual to add five drops of this mixture, following Florentin's proportions. However, a yellow tint which developed in the sample, though not in the standard, constituted a source of trouble. It has now been found that by adding only the minimum amount of stannous chloride this trouble is obviated and the blue tint remains. Usually it suffices to add one drop to each 100 c.c. of sea water.

To convert the conventional  $\text{P}_2\text{O}_5$  values into the more rational values for the  $\text{PO}_4$  ion the factor 1.338, or very approximately  $\frac{4}{3}$ , may be used to multiply the former.

In conclusion, the writer wishes to acknowledge his indebtedness and to express his thanks to Mr. H. W. Harvey and other members of the Laboratory staff and the crew of the *Salpa* for assistance in temperature observations and in the obtaining of water samples; also to Dr. Russell, Mr. J. R. Lumby, and staff of the Fisheries Laboratory, Lowestoft, for water samples; to Dr. Bowman, Mr. R. S. Clark, and staff of the Scotch Fisheries Department, Aberdeen, and to Mr. G. P. Farran, of the Irish Fisheries Department, for water samples. The author is also indebted to Mr. R. S. White and to Capt. Elliott, Mr. Davidson, Chief Engineer, and Mr. Jackson, of the *City of Exeter*, for the interesting samples extending to Ceylon, and to Dr. Cyril Crossley, of the *St. George*, for the Panama series.

## SUMMARY.

1. The seasonal changes in the sea water of the English Channel and of Plymouth Sound have now been followed for almost two years, and the second year's results closely resemble those of the first, and again confirm the earlier surface results obtained by Matthews. For 1923 the average consumption at Station E1, surface to bottom, 70 metres, was 29.6 mg. of  $P_2O_5$  per cubic metre, leaving a balance of 7.4 mg. out of the original 37 mg. For 1924 the corresponding figures were, used up 28.3 mg., balance 8.7 mg., winter concentration 37 mg. The minimum average value was obtained in June and July in 1924, in July only in 1923. During June, July, and August, 1924, the surface water was almost entirely denuded of phosphate, values from 1.5 to 2.5 mg. per cubic metre being obtained. These figures would be milligrams per metric ton if fresh water were being considered, as it is they are milligrams per 1027 kg. for water of  $S35.3\text{‰}$  at  $11^\circ\text{C}$ ., so it may be appreciated that very little phosphate remains unutilized by the phytoplankton.

2. Owing probably to the high sunshine record for March the year 1924 was over a month ahead of 1923 in the spring as regards phosphate consumption, and, therefore, it may be presumed in the multiplication of the phytoplankton. At the same time, in the attainment of definite temperatures 1924 lagged about a month behind 1923 in spring. Since temperature has such a marked effect upon the rate of development of the plankton as a whole it appears that the zooplankton must have been retarded in 1924 as compared with 1923.

3. Samples obtained from the tropics show that even in winter phosphate may be much diminished, for the light is bright. The periodic alterations in phosphate content are, therefore, suppressed or much reduced as compared with the temperature zones. It is indicated that in arctic latitudes the sea becomes even richer in phosphate during winter than it does here, accordingly the summer development of phytoplankton is all the more abundant.

## Young Anglers in Captivity and some of their Enemies. A Study in a Plunger Jar.

By

Marie V. Lebour, D.Sc.,

Naturalist at the Plymouth Laboratory.

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With Figures 1-9 in the Text.

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It is only very rarely that the spawn of the Angler *Lophius piscatorius* is captured near Plymouth, although it has been recorded (Cunningham, 1896). It is well known that it consists of a gelatinous ribbon several yards long and a yard or more wide, with the eggs (over a million) in one layer divided from one another by roundish capsules. It is probable that the Angler spawns well out to sea, for when these ribbons of eggs have been captured anywhere near the coast the larvæ have nearly always already hatched and are lying loose in the capsules (Bowman, 1919). Moreover, most of the spawn caught inshore consists of portions only of the ribbon which have probably drifted towards the coast.

On June 18th, 1924, a piece of Angler spawn, measuring about five inches square, was caught by the *Salpa* in the Young Fish Trawl towing below the surface a few fathoms down, from Station L4, half-way between Rame Head and the Eddystone, Lat. 50° 15' N., 4° 13' W. The larvæ were all hatched and were moving about in the capsules, each capsule measuring about three to four millimetres across (Fig. 1, p. 722). Portions about an inch and a half square of this spawn were put into Plunger Jars (Brown, 1898; Lebour, 1922 and 1923), and kept alive. The fishes immediately began to hatch out from the capsules into the water, floating near the surface with the yolk sacs uppermost.

A good deal has already been written about larval and post-larval Anglers (Williamson, 1911; Bowman, 1919; Tåning, 1923; and others). It is, however, perhaps excusable to give a brief account of the present series which were reared for eleven days, and one drawn each day (Figs. 2, 3, 4). Unfortunately by the twelfth day all were dead, and it is interesting to note that they had reached the stage described by Williamson (1911) when his specimens ceased growing, although he kept some alive

for several months. This stage is perhaps a critical one, and some special unknown factor is needed for the fishes to move forward.

The number of larval fishes hatched in one jar was far too many for the space, but it was found that some of the animals already established were eating them and keeping them down, therefore they were left, and some extremely interesting observations proved that some of the most delicate plankton organisms caught and ate young Anglers.

The temperature of the jars was not taken, but later observations

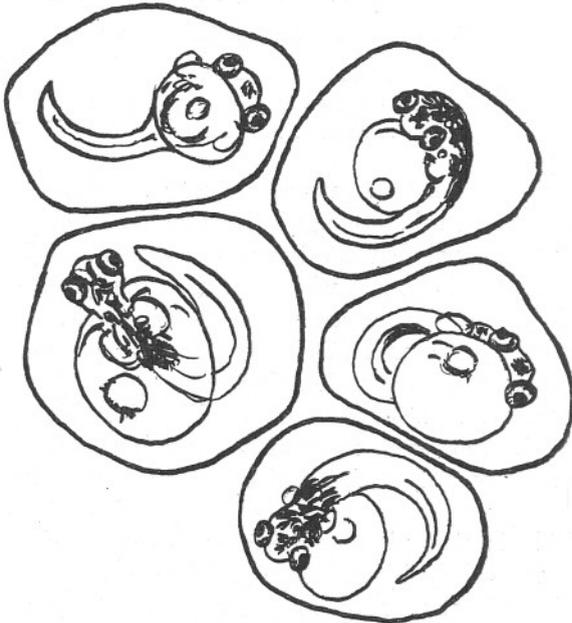


FIG. 1. Egg capsules of Angler, L4, June 18th, 1924, ca. 3-4 mm. across the capsule.

showed that they followed closely that of the main laboratory in which they were placed. In the following notes this latter temperature is given.

#### DESCRIPTION OF THE YOUNG ANGLERS.

June 18th, 1924. Age, 1st day. Length, 4.48 mm. Temperature, 9.30 a.m., 16.8° C.; 5 p.m., 20.5° C.

Fig. 2a. Large yolk sac. Mouth not formed. Head and body covered with large ramifying chromatophores forming a network over the front part. Simple broad larval fin round tail. Whole tail end

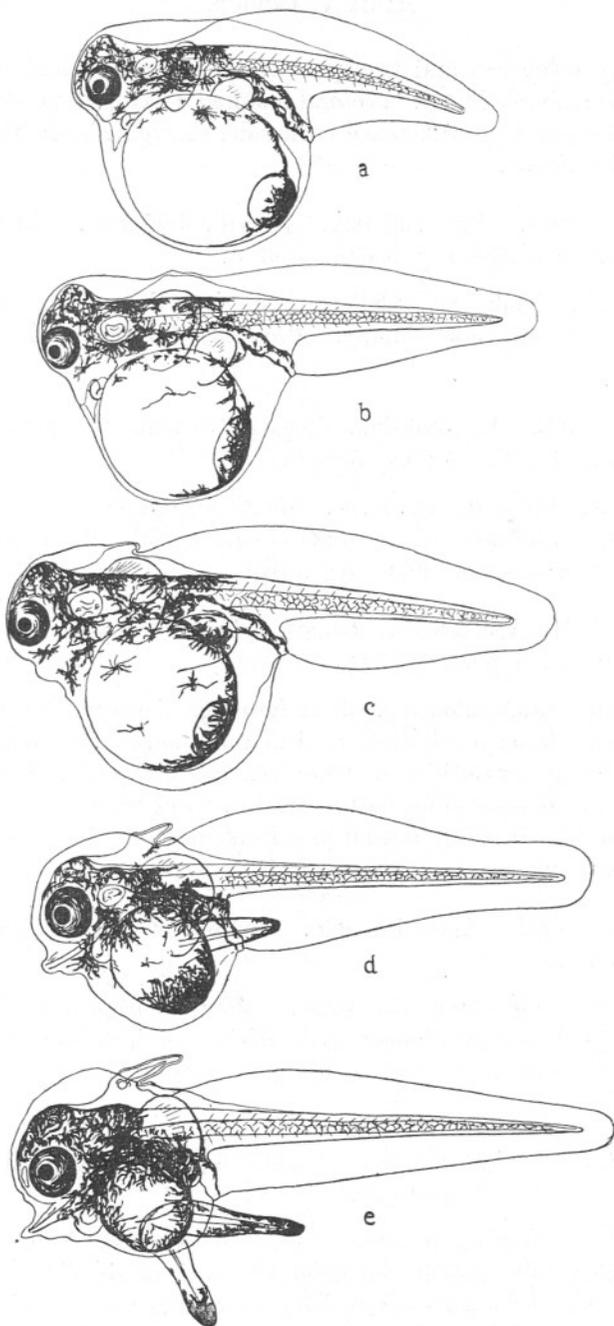


FIG. 2. Anglers, newly hatched to 5th day, from Plunger Jar. June 18th to 22nd, 1924.  
 (a) Newly hatched, 4.48 mm. long. (c) 3rd day, 5.6 mm. long.  
 (b) 2nd day, 4.96 mm. long. (d) 4th day, 5.6 mm. long.  
 (e) 5th day, 6 mm. long.

perfectly colourless and transparent. Rudiment of first dorsal fin shows as a simple hump. Pectoral fins well developed, pelvics behind them forming a protuberance each side, emerging from the dorsal part of yolk sac.

June 19th, 1924. Age, 2nd day. Length, 4.96 mm. Temperature, 9.30 a.m., 16.8° C.; 5 p.m., 18.3° C.

Fig. 2b. Yolk sac smaller. Colouring the same. Rudiment of first dorsal more lumpy. Pectorals larger, pelvics slightly longer.

June 20th, 1924. Age, 3rd day. Length, 5.6 mm. Temperature, 9.30 a.m., 17.2° C.; 5 p.m., 18.8° C.

Fig. 2c. Colouring the same. Mouth beginning to form, but not yet open. Rudiment of ray (3rd) of first dorsal. Pelvic fins longer and shifting forward. Fish very active.

June 21st, 1924. Age, 4th day. Length, 5.6 mm. Temperature, 9.30 a.m. 17.9° C.; 1 p.m., 18.2° C.

Fig. 2d. Same colouring. Jaws forming. Anus much further forward and yolk sac much smaller. Tail much longer than body. Pelvic fins shifting forwards and more ventral, protruding horizontally behind and beyond anus, with central ray and black tip. A second ray (the 4th) forming behind the front ray (the true 3rd) of the first dorsal fin.

June 22nd, 1924. Age, 5th day. Length, 6 mm. Temperature not taken.

Fig. 2e. Colouring the same. Mouth conspicuous, but not open. Pelvic fins still longer, their origin now just below the origin of the pectorals. A true ray supports the first ray of the first dorsal fin.

June 23rd, 1924. Age, 6th day. Length, 6.5 mm. Temperature, 9.30 a.m., 17.8° C.; 5.10 p.m., 18.3° C.

Fig. 3a. Colouring the same. Mouth almost open. Yolk sac nearly gone. Pelvic fins greatly elongated with their origin slightly in front of the origin of the pectorals, which are now very large. The front ray of the first dorsal much longer, and the second, although still very short, supported by a true ray. Body very short. Tail more than three times as long as the head and trunk combined.

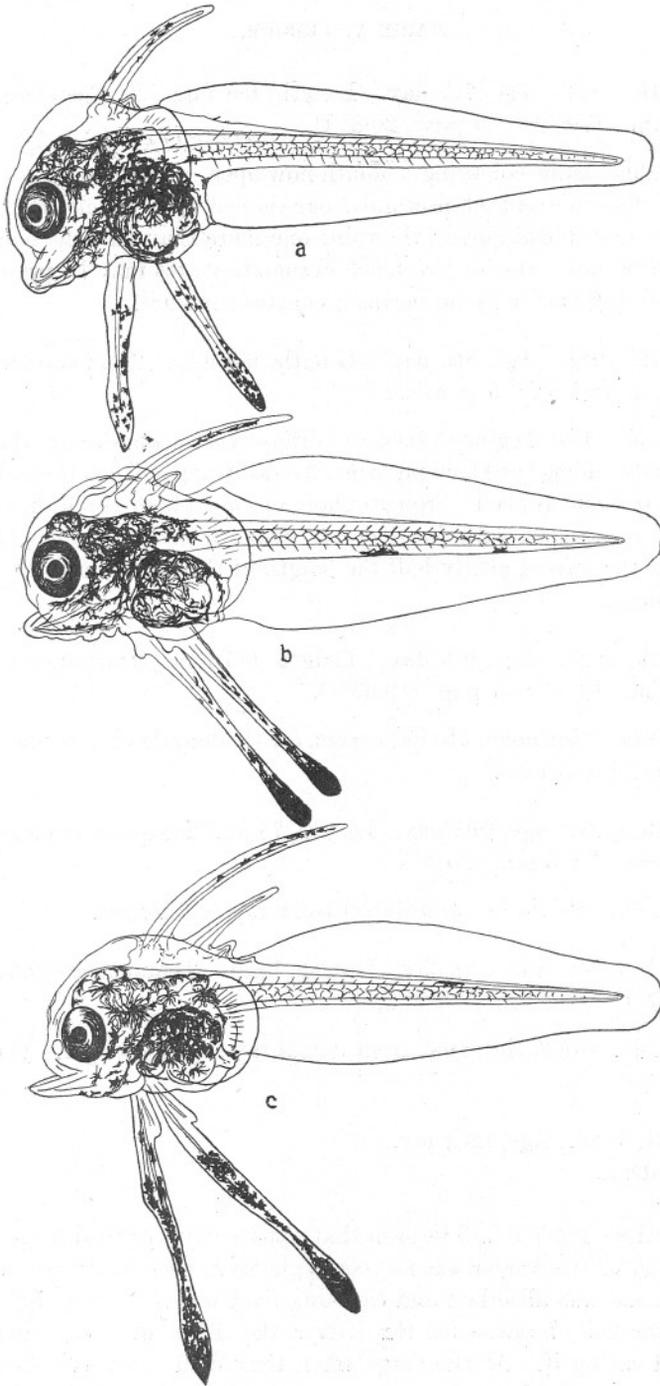


FIG. 3. Anglers, 6th to 8th day, June 23rd to 25th, 1924.  
(a) 6th day, 6.5 mm. long. (b) 7th day, 6.5 mm. long.  
(c) 8th day, 6.5 mm. long.

June 24th, 1924. Age, 7th day. Length, 6.5 mm. Temperature, 9.30 a.m., 17.8° C.; 5 p.m., 20.8° C.

Fig. 3b. Same colouring. Mouth now open. Yolk sac almost gone. Pelvic fins in front of pectorals, oar-shaped with black tips. Two rays of first dorsal longer, the front one more than half the length of the pelvic fins. One or two black chromatophores may be present on the tail, but this is by no means a constant feature.

June 25th, 1924. Age, 8th day. Length, 6.5 mm. Temperature, 9.30 a.m. 18.7° C.; 5 p.m., 22.1° C.

Fig. 3c. Fish begins to feed. A diffuse yellow appears on the head and body among the black pigment, the tail being still colourless except for an occasional black chromatophore or two, which are often absent. Pelvic fins longer with three rays. Front ray of first dorsal much longer, the second nearly half the length of the first, and a third just beginning.

June 26th, 1924. Age, 9th day. Length, 6.5 mm. Temperature, 9.30 a.m., 18° C.; 5 p.m., 19.67° C.

Fig. 4a. Not much altered except for the lengthening of the pelvic fins and dorsal rays.

June 27th, 1924. Age, 10th day. Length, 7 mm. Temperature, 9.20 a.m., 18.3° C.; 5 p.m., 20.3° C.

Fig. 4b. Pelvic fins and dorsal front ray still longer.

June 28th, 1924. Age, 11th day. Length, 7 mm. Temperature, 9.30 a.m., 17.9° C.; 1 p.m., 18.6° C.

Fig. 4c. Much the same, front dorsal ray slightly longer. Very few left.

June 29th, 1924. Age, 12th day.  
All dead.

From these notes it will be seen that apparently a critical stage in the life history of the Angler was not, as might have been expected, directly the yolk sac was absorbed and catching food was necessary, but a few days after this, because for three days the fishes were catching food fast and eating it. At the stage when they died the pelvic fins were very long, also the front dorsal ray, and the first dorsal fin consisted of three rays only, the true first and second not being present. The food

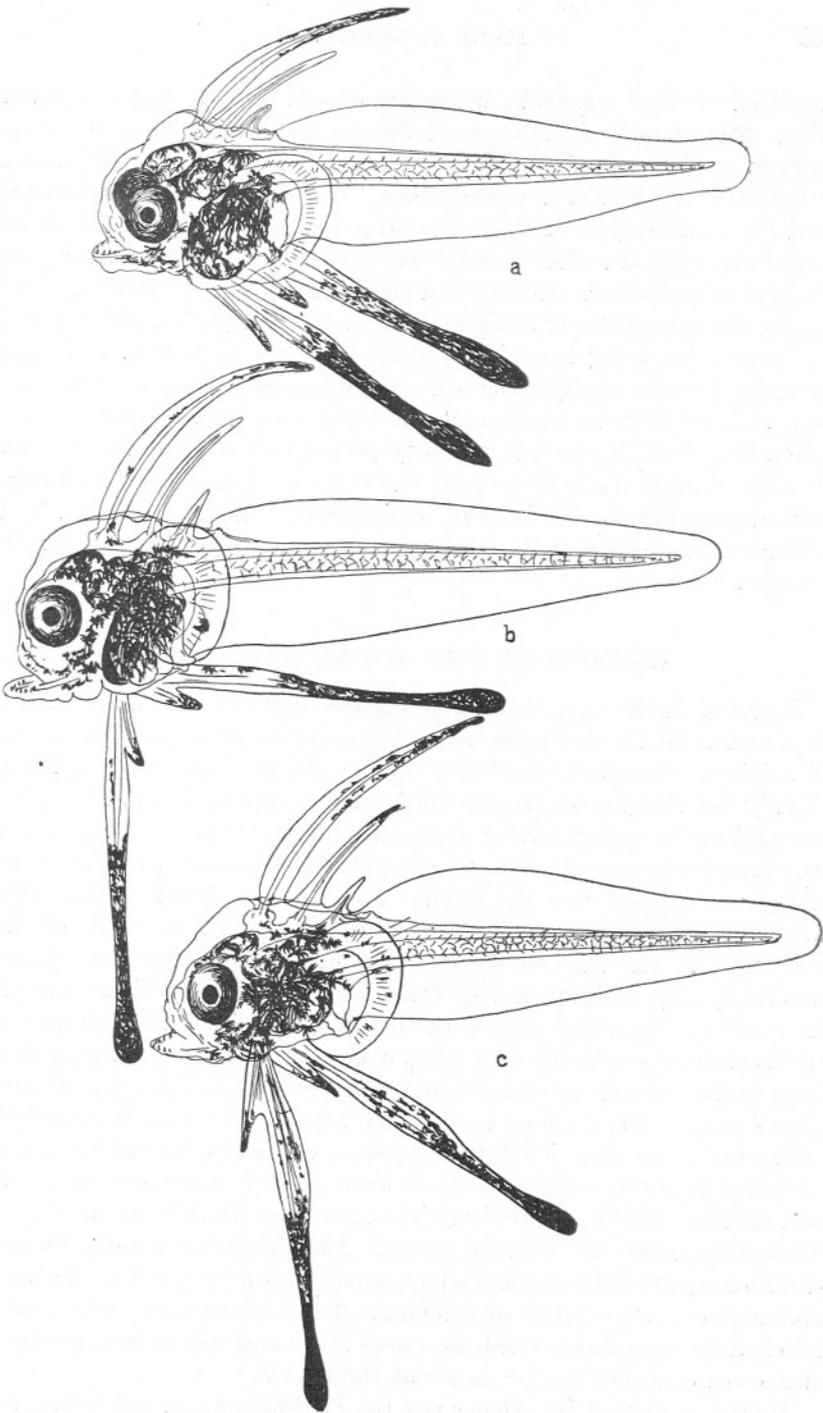


FIG. 4. Anglers, 9th to 11th day, June 26th to 28th, 1924.  
(a) 9th day, 6.5 mm. long. (b) 10th day, 7 mm. long.  
(c) 11th day, 7 mm. long.

consisted of small copepods, which are chased cleverly and swallowed alive. The nauplii of the copepod *Temora longicornis*, about 0.4 mm. long, was a favourite food. Older *Temora* and also *Acartia Clausi* and *Pseudocalanus elongatus* were also taken. This is apparently the natural food for small Anglers of about the same size taken from the plankton contained copepods. The pectoral fins come much into play whilst the fish is chasing its food. The tail and pelvic fins spread out give the little Angler the appearance of a tripod. The front crest (first dorsal fin) and the pelvic fins being black make three conspicuous processes coming from the fish, one upright, the other at almost equal angles. Thus the body is beautifully balanced, and can easily keep near the surface, the tail lashing from side to side, the large pectorals steering and balancing. It seems natural for it to be near the surface when well and feeding, only descending to the bottom occasionally. When moribund and falling to the bottom it is usually instantly devoured by some of its enemies.

#### ENEMIES OF THE YOUNG ANGLERS.

In one of the Plunger Jars containing the Anglers which was specially kept under observation, there were living several specimens of the young of a lobate ctenophore (probably *Bolina infundibulum*, but differing slightly from the known descriptions). These appeared suddenly in the jar early in the spring, having apparently been introduced as eggs when very fine plankton was put in. They had been feeding freely on copepods, and it was thought that the Anglers would be safe beside them. This was, however, not the case for the *Bolina* caught and ate many of the little fishes. The method adopted was interesting. The ctenophore would catch an actively moving fish with its tentacles, which although short are very powerful, and as the fish struggled the lobes would close on it, completely shutting it in, when it was quickly taken by the mouth, from there reached the stomach and was digested (Fig. 5 a-d). *Bolina* from 4 mm. to 30 mm. long would catch fishes in this way, the smallest taking one longer than itself, the largest sometimes taking two at a time or eating one after another. *Bolina* is thus seen to be extremely voracious and evidently able to tackle larger food than any previous knowledge of its feeding habits has hitherto shown. Altogether it accounted for the death of many of the Anglers which would quickly run out of the way and required a good deal of catching. Those of all ages, from newly hatched specimen to the tenth day, were taken and always from near the surface or centre of the jar, never at the bottom.

Another enemy of the Angler was the *Phyllosoma* larva of *Palinurus*, the Rock Lobster. These were fairly common in the outside plankton at

this time. One caught with the Angler spawn was put into the same jar as the Bolinas. The Phyllosoma was seen to catch and eat the Anglers (Fig. 6 a-b, p. 730). Swimming about near the top of the jar it would encircle the fish with the endopodites of its long legs, the exopodites moving constantly and keeping up the body. In this way an effective

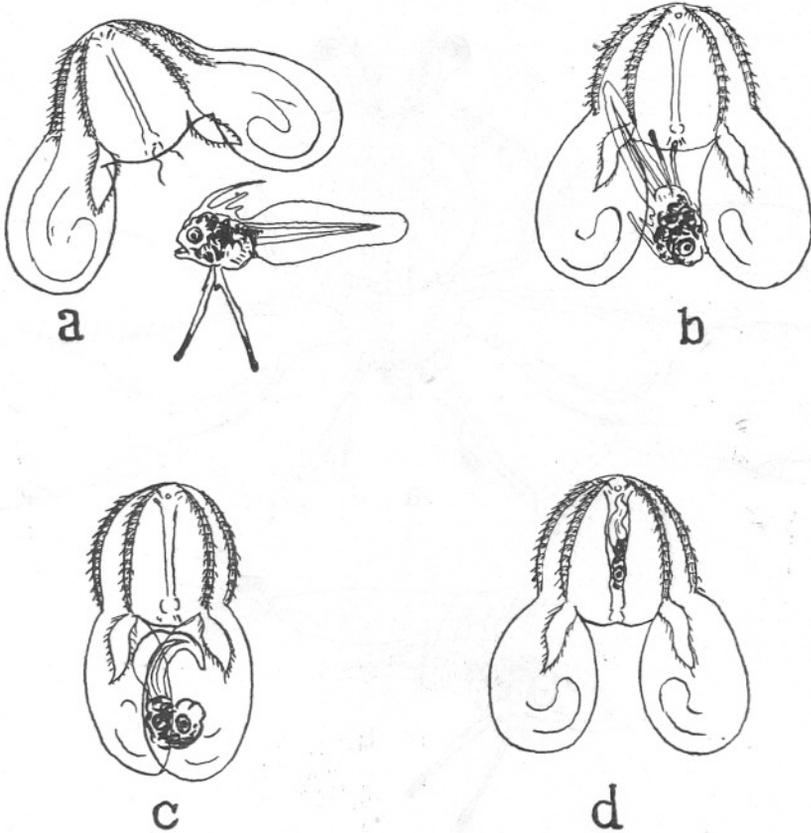


FIG. 5. Young Ctenophores (*Bolina* ?) catching baby Anglers in Plunger Jar.

- (a) The Angler approaches.
- (b) Is caught.
- (c) Is taken into mouth.
- (d) Is digested.

net was formed, the fish struggling but not able to escape, for probably it was pinched as well by the claws of the hind leg. Soon its struggles would cease, and it would be devoured. The Phyllosoma also ate copepods, which were visible inside it, but it was never actually seen to catch them. This beautiful glass-clear creature is a true enemy of little fishes.

Many copepods were put in the Plunger Jar for food. Amongst these were a few specimens of *Anomalocera Pattersoni*. It has been noticed frequently by examining its stomach contents (Lebour, 1918; Marshall, 1924) that it is carnivorous, remains of copepods being very often found inside it, but in the jar they were actually seen to catch and eat the Anglers. These were caught when only a day or two old, three separate

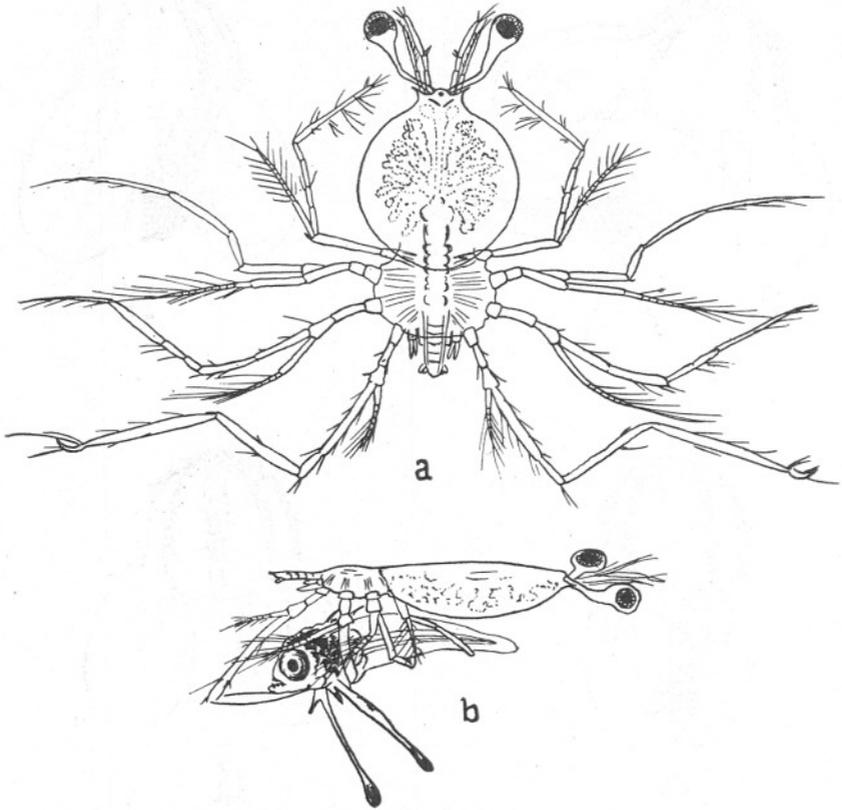


FIG. 6. Larva of *Phyllosoma* from Plunger Jar.  
 (a) Spread out, showing appendages.  
 (b) Catching a baby Angler.

*Anomalocera*, from 3 to 4 mm. long, being seen to eat them. At this stage the fishes were not very active, but quite alive and well. They were caught near the surface by the appendages near the mouth, the mouth-parts and legs surrounding the head and body of the fish (Fig. 7).

There was another animal which fed on them when they went down to the bottom, in this case acting more as a scavenger than an enemy.

This was a small hydroid (*Clytia* sp.) which was rapidly spreading on the floor of the jar. Each polyp (Fig. 8, p. 732) measured about 3 mm. high, including its stalk, the individuals being joined by horizontal hyphæ. The tentacles were outspread and a small fish touching one of these would instantly set the rest in motion, a second polyp would then be agitated and possibly a third would join in, all three catching the fish and devouring it very quickly. In this way many little Anglers were caught within an hour, the hydroids being extraordinarily voracious.

This gives us some idea of the vicissitudes to which the little fishes are subjected in nature. They swim about catching their food where it is dense. With this food are also swimming about many other animals all on the look-out for food, many of them only too ready and eager to

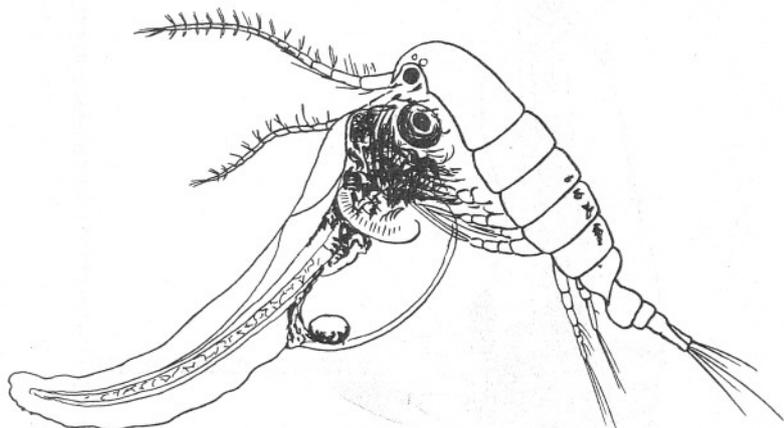


FIG. 7. *Anomalocera pattersoni* in Plunger Jar, catching a baby Angler.

devour the little Anglers. We already know that many jelly fishes and Pleurobrachia besides Sagitta and Tomopteris will readily eat small fishes (Lebour, 1922, 1923). The list steadily grows. Daily we are finding out that plankton organisms are to a large extent carnivorous, and this fact has far-reaching effects. We no longer wonder at the enormous number of eggs laid by one individual fish when we realise more and more the number of enemies it has besides all the physical dangers appertaining to its environment, but apart from this it is now shown that delicate plankton organisms can feed on such solid diet that it is no longer merely a question of continually satisfying hunger by swallowing thousands of minute unicellular organism, but it is an established fact that one large meal may be taken, that meal probably lasting the animal for a long period. The most delicate of all the plankton animals are those best able to take care of themselves by catching and eating solid food as large

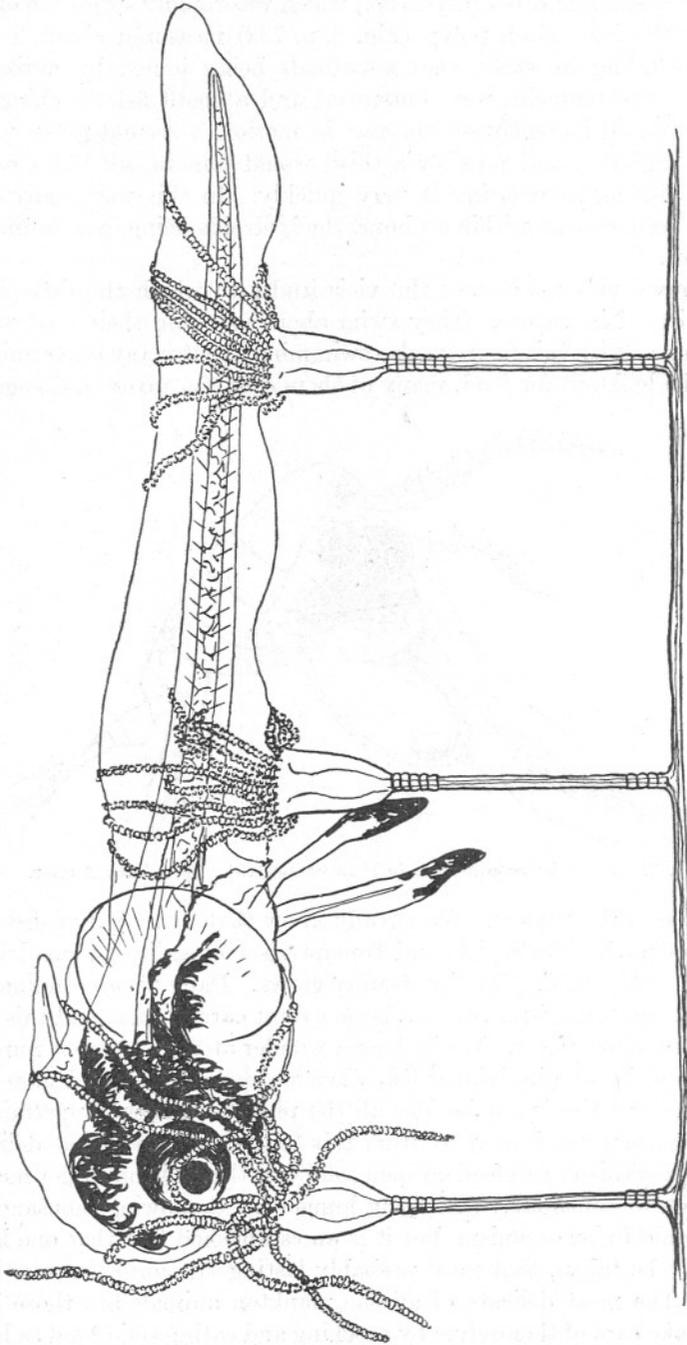


FIG. 8. Hydroids eating a moribund baby Angler in Plunger Jar.

or larger than their own bodies. It is probable that many more of these plankton organisms than we realise satisfy their hunger in this way. Positive evidence is wanted, and observations on living animals should be undertaken whenever possible to establish these important facts, and in this way we shall learn the true natural history of the sea.

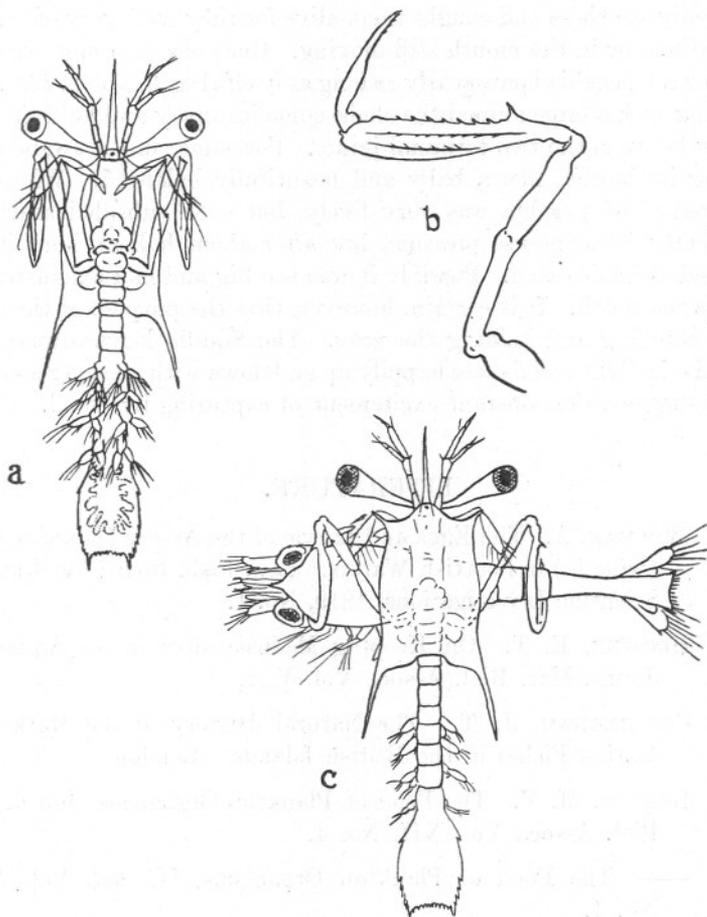


FIG. 9. Larva of *Squilla* in Plunger Jar.

- (a) As seen at the top of the jar.
- (b) Predaceous claw.
- (c) Catching a *Upogebia* larva.

In this connexion some observations on *Squilla* larvæ in another Plunger Jar are interesting. The larvæ of *Squilla Desmaresti* in the "Alima" stage were taken from the plankton, Young Fish Trawl, L4, 27.8.24, measuring about 5 mm. in length and placed in the jar. Some

of these lived for several weeks, always keeping near the surface and continually in motion, springing up and down with their abdominal appendages always moving and the large chelate predaceous claws kept close to the sides, occasionally to be spread out. With the *Squilla* at the top of the jar were many copepods, chiefly *Temora longicornis*, the commonest copepod in the plankton at that time. The *Squilla* undoubtedly ate these and caught them alive for they were very often seen inside them or in the mouth still moving. Once one of 5 mm. was seen to catch a *Upogebia* larva nearly as long as itself (Fig. 9, a-c, p. 733). For catching such a large animal the chelæ come into play and hold the prey tightly between the two terminal joints. For some time it swam about holding its burden like a baby and beautifully balanced. When first captured the *Upogebia* was very lively, but soon subsided and died, apparently from intense pressure, but after about half an hour it was dropped and not eaten. Possibly it was too big and had exhausted the *Squilla* too much. It is certain, however, that the purpose of the chelæ is for catching and holding the prey. The *Squilla* larva always goes towards the light and dances happily up and down with an eager alertness which suggests the constant excitement of capturing live food.

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## Notes on Euphausiids.

By

C. F. Hickling, B.A.

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With Figures 1 and 2 in the Text.

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### (a) Vertical Migration.

THE material for this paper was obtained in two voyages on the Milford steam trawler *Macaw*, and I owe all thanks to Capt. Rumble, and to the crew, not only for much practical help, but for a pleasant time. Capt. Rumble's knowledge of the area worked, based on 30 years' experience, can only be compared with a farmer's knowledge of his own acres, and he has been responsible for determining the position of each haul.

To my Milford host, Mr. Frank B. Rees, I have pleasure in acknowledging my thanks for arranging my voyages, and for many other kindnesses.

Finally, I wish to thank Dr. Allen, F.R.S., for suggesting the work, and for continual advice and encouragement; and the naturalists at the Laboratory, who have given me so much help in my first effort. The work has been carried out with the help of a grant from the Department of Scientific and Industrial Research.

### OBJECT AND METHOD.

This note seeks to demonstrate a vertical migration in certain Euphausiids, by showing that these crustacea are present on, or absent from, the sea-bottom at rhythmically recurring periods.

The hauls were made with the net described below. It was attached to the bosom of the headline of the commercial trawl, and was hauled for a period of between  $4\frac{1}{2}$  and 5 hours, in the ordinary fishing operations of the ship. The hauls are, therefore, strictly comparable, and yield ample evidence of the definite nature of the vertical migrations.

Holt and Tattersall (1902-3), in their work on Schizopods, used "nets and bags of fine material fastened to the back of the beam-trawl"; the net used here is carried, on the headline, at least 4 feet above the

ground, and well in advance of the foot-rope, or any other part of the gear which might disturb the soil. The forms taken in the net may be regarded as truly pelagic at the depth and time of haul, and not stirred up from the soil by the passage of the net.

#### AREA WORKED.

The bulk of the fishing was done on the Smalls grounds, on an area roughly crescentic about the Smalls Light between the bearings S.W. by S., and N.W.  $\frac{1}{2}$  N. At the first named limit the light was 36 or more miles distant, at the latter just showing at 18 miles. Fishing was done in depths ranging from 46 to 62 fathoms, 5 hauls in the 24 hours being the rule; and the first voyage was from the 10th to the 16th October, the second from the 18th to the 27th October, 1924.

During the second cruise, a trial trip was made to the Cockburn bank, 80 miles W.N.W. of the Scillies, where a 24-hour series of hauls was made. The fishing was so poor, however, that the ship soon returned to the Smalls.

#### THE NET USED.

The net is constructed of stramin.\* It is 3 feet long, cylindrical in shape, with a diameter of 6 inches: the mouth is supported by a brass ring, to which the net is firmly sewn with the help of a band of duck, or sail canvas. The last 9 inches taper from 6 inches to a diameter of 4 inches, and contain an inner sleeve of medium bolting silk (IV, 50"), which is

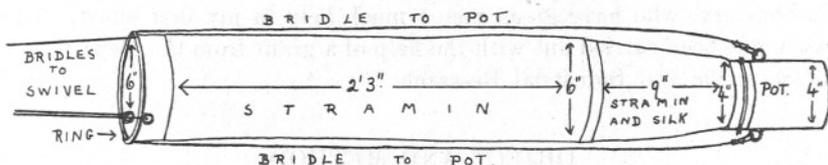


FIG. 1. Small tow net of "stramin" and bolting silk, which was attached to the headline of a commercial otter trawl.

attached at the front end to the stramin, but ends freely behind, and is tied, with the outer sheath, over the pot. The last named is preferably independently slung from the ring at the mouth of the net, in order to take the heavy dragging strain off the net itself. Finally, the net is furnished with three legs (bridles) of trawl-twine, which are laid together and secured with a whipping, and spliced to a swivel, which is attached to the headline by a further length of manila.

\* "Stramin is a coarse canvas made of hemp, having about 20 threads to 3 cms." Jespersen (1923).

## NOTES ON THE CONSTRUCTION OF THE GRAPH.

If the vertical migrations are a constant habit of these Euphausiids, they should be perceptible in all circumstances of depth and locality. The hauls, on which these results are based, are in all depths from 46 to 62 fathoms and over, on every kind of soil, from fine silt to gravel and stones, and include five hauls from the Cockburn Bank, where physical conditions are probably very different from those about the Smalls.

The results of 31 hauls have been combined in a graph.

The contents of each haul were separated and counted individually, 28,000 specimens of *Nyctiphanes Couchi* (Bell), and 4000 each of *Meganycetiphanes norvegica* (M. Sars) and *Thysanoessa* spp. being dealt with. In the present uncertain state of classification of the genus *Thysanoessa*, both species are counted together without distinction.

These figures are set out in Table A (p. 738), with the time of capture and depth; similar figures for shrimps (in the broadest sense) and mysids, being also given for comparison.

The mean number of each species caught per hour, during each haul, is obtained by dividing the total number caught, by the duration of the haul in hours, portions of an hour counting as a whole hour.

On the whole series of 31 hauls, for each hour of the day and night, the average number of individuals is obtained by taking the mean of the average number per hour caught during each haul that extends over that hour.

These figures are given in Table B (p. 738), and from them the graph is constructed. In the graph, the numbers for *Meganycetiphanes* and *Thysanoessa* are multiplied by ten, in order to make their curves more readily comparable with that of *Nyctiphanes*.

Less reliance can be placed on the curves for *Meganycetiphanes* and *Thysanoessa* than upon that for *Nyctiphanes*, because the two former species are absent from many hauls, and are in others only present in two's and three's. It will be noticed that the numbers of these two species tend to increase as the water deepens, while their presence on the Cockburn Bank is very marked. This is again a disturbing factor in any effort to show the behaviour of these crustacea with reference to light alone. *Meganycetiphanes* and *Thysanoessa*, in fact, seem to be oceanic species where *Nyctiphanes* is a neritic species. Their recorded distribution favours this, and in the present hauls they occur with other organisms, and especially Pteropods, which point to oceanic conditions. Hence the absence of *Meganycetiphanes* and *Thysanoessa* from a given haul may mean, either that they are absent from the locality, or that they are not on the sea-floor at the time of haul, and the results are complicated accordingly.

TABLE A.  
SMALLS.

Haul No.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Date, Oct.		11	11-12	12	12	13	13	13	13-14	14	14	14-15	15	15	15	15-16	16
Time	From	11.50	21.30	07.30	17.30	03.00	08.00	14.00	23.30	09.30	19.30	24.00	05.00	15.00	20.00	01.00	07.30
	To	16.00	02.30	12.00	22.15	08.00	12.30	18.00	04.30	14.30	24.00	05.00	10.00	20.00	01.00	06.00	12.00
Depth [fms.]		48	48	56	48	48	46	48	56	60	54	51	52	52	50	54	54
		58						52	58	62	54		56	54	62-48		
Nyctiphanes		1967	6	Foul haul	41	372	47	383	35	742	4	4	682	42	3	13	630
Meganyctiphanes		0	1		0	0	0	118	25	271	2	2	577	213	0	7	55
Thysanoessa		10	2		1	14	7	52	28	476	66	50	280	60	0	13	119
Mysids		0	2		8	31	2	23	9	49	41	35	8	79	4	111	88
Shrimps		0	7		29	11	1	5	9	8	9	3	5	18	8	8	17

COCKBURN BANK.										SMALLS.							
Haul No.		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
Date, Oct.		19	19	19-20	20	20	21	21	22	23	23	24	24	25	25	26	
Time	From	11.30	16.30	22.00	03.00	09.00	08.30	18.00	17.30	04.00	14.00	07.00	18.00	00.00	10.00	00.00	
	To	15.30	21.30	03.00	08.30	14.00	13.00	23.00	22.00	09.00	19.00	11.30	23.00	05.30	14.00	06.00	
Depth [fms.]		64	65	65	52	65	55	51	50	51	50	58	54	50	56	56	
		66	66								65			54			
Nyctiphanes		576	132	2	8	214	3957	15	14	4455	9000+	1281	17	4	5194	1	
Meganyctiphanes		111	32	4	90	30	933	20	1	4	270	98	6	4	255	9	
Thysanoessa		175	162	366	32	285	123	240	13	26	58	90	97	81	358	185	
Mysids		0	24	75	26	0	2	33	14	66	11	0	35	41	3	48	
Shrimps		0	9	33	10	0	0	8	7	13	1	0	4	1	1	4	

The numbers of each kind of Crustacean taken at the sea-bottom, together with the depths and times of haul. [Midnight is 2400, midday 1200.]

TABLE B.

Hour of Day		01	02	03	04	05	06	07	08	09	10	11	12 noon
Mean	} Nyctiphanes Couchi . . . Meganyctiphanes norvegica Thysanoessa spp. . . .	1.4	1.4	9.1	101	115	153	213	236	243	285	290	294
Number		1.2	1.2	3.3	3.7	16.4	19.1	27.9	49.1	48.5	54	44	49
per hour of		16.6	16.6	15.4	.9	13.5	13.5	15.5	14.7	28	38	33	34
Hour of Day		13	14	15	16	17	18	19	20	21	22	23	24
Mean	} Nyctiphanes Couchi . . . Meganyctiphanes norvegica Thysanoessa spp. . . .	373	459	405	386	269	202	192	5.5	4.7	2.0	2.0	1.2
Number		56	32	31	27	21.6	16.0	12.9	7.4	1.6	.9	1.3	1.2
per hour of		33	36	13.3	11.7	9.8	15	14	15	14	19	22	19

The mean numbers of each Euphausiid present on the sea bottom for each hour.

## THE GRAPH.

It is plain that *Nyctiphanes Couchi* (Bell) has a period of maximum abundance on the sea-floor at 2 p.m., that the numbers fall away very rapidly until 8 p.m., when, shortly after sunset, very few specimens are present. This state of affairs persists until 3 a.m., when a comparatively steady increase in numbers is maintained until the maximum is reached. Dr. Lebour (1924) states that "adults (of *Nyctiphanes*) and older larvæ all appear to live very near the bottom in the daytime, and come to the surface at night"; the graph bears out the first part of this statement well.

It is widely known that *Nyctiphanes* approaches the surface at night, and by the courtesy of Miss Lebour and Mr. O. D. Hunt I am allowed to use the following unpublished records of *Nyctiphanes* taken at the surface at night:—

13.12.23.	11.30 p.m.	Eddystone.	<i>Nyctiphanes</i> cccc.
14.12.23.	3 a.m.	Rame-Eddystone.	<i>Nyctiphanes</i> ccc.
13.11.24.	9 p.m.	30 miles N. of Seven Stones,	"A large haul of <i>Nyctiphanes</i> ."

The last record is from almost the same locality and at the same time as many of my hauls.

Finally, some young-fish-trawl hauls have just (22.12.24) been examined, which show the vertical migration well. Taken at L4\* just before dawn, at the surface 9 specimens of *Nyctiphanes* were found, at midwater 685, and at the bottom, 301. Interpreted according to the graph (p. 740) accompanying this paper, this shows that while many specimens of *Nyctiphanes* are already on the bottom, the bulk of these crustacea are still moving downwards, leaving a few stragglers at the surface.

The curve for *Meganyctiphanes norvegica* again shows a definite period of abundance on the sea-floor by day, and a definite absence at night. It is noticeable, when the hauls are made, that late at night, when *Nyctiphanes* has become scarce, *Meganyctiphanes* is still conspicuous, and seems to linger longer on the bottom than *Nyctiphanes*.

Holt and Tattersall, in their observations on the vertical distribution of *Meganyctiphanes norvegica* from the Biscayan Plankton collected during the cruise of H.M.S. *Research* in 1900, say: "*M. norvegica* . . . was never taken, even at night, in surface nets. It occurs three times in nets towed at 25 fathoms, and thence to the surface, four times in nets towed at 50 fathoms, and only becomes general in nets towed

\* Five miles from the shore between Plymouth and the Eddystone Light.

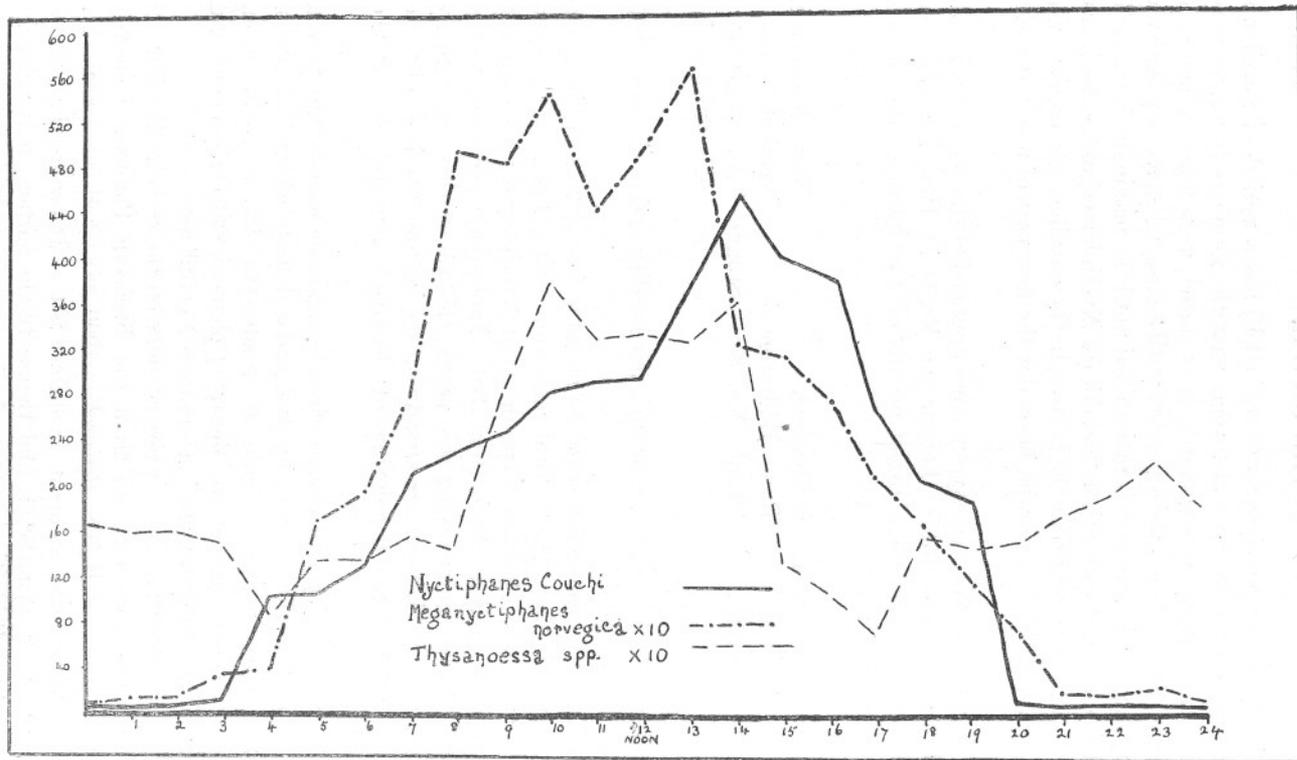


FIG. 2. Graph showing the average number of individuals captured per hour during each hour of the day and night. The figures for Meganyctiphanes and Thysanoessa are multiplied by ten.

at 100 fathoms." "We suppose that the species is subject to no marked diurnal movement, but is . . . an inhabitant of the upper 100 fathoms." Finally the authors add "The species certainly occurs at the surface, or quite near it, at night off the west coast of Ireland."

*Thysanoessa* differs in that it exhibits a double crest, one at midnight, and a second, much greater one, at 10 a.m. The corresponding periods of scarcity are at 4 a.m. and 5 p.m.; but the amplitude of the waves is much smaller than in the first two species, and in favourable conditions *Thysanoessa* seems to be present in quantity, at all hours, on the sea-floor.

#### DISCUSSION.

The graph suggests that light is a factor of prime importance in governing vertical migration. Helland-Hensen, in Murray and Hjort (1912 a.) states that a sensitive plate is blackened in 80 minutes at 1000 metres; while Shelford and Gail (1922) show that in the waters of Puget Sound the light intensity at 120 metres was 14-foot candles, where that at the surface was 6550. But the roughness of the surface, and freedom from silt, are of vital importance to light penetration.

The indication is, therefore, that sufficient light may be present, in this case, to affect organisms taken at the greatest depths worked (62 fathoms), and the possible part played by light in these movements will be discussed later.

The search for food may play its part. All three species had, in my samples, been feeding on detritus, and not only their leg-baskets, but their mouth-parts and stomachs were often full of it. On the other hand, Dr. Lebour (1924) states that *Nyctiphanes Couchi* taken at night in the upper waters had been feeding on diatoms, with *Sagitta* and crustacea; while Holt and Tattersall (1902-3) say, of *Meganyctiphanes*, that it had its leg-baskets "more or less stuffed with prey, including copepods, schizopod and decapod larvæ, fragments of *Spirialis*, and other matter."

This detritus consists largely of very flocculent, dust-fine, olive-green particles, with fragments of crustacean remains, diatoms, particularly *Paralia* and *Coscinodiscus* spp., and inorganic grit. The schizopods had been feeding extensively on it; but it is possible that an alternation of fresh diatom food may be of advantage to *Nyctiphanes*, at least.

Esterly (1911) demonstrates a vertical migration in *Calanus finmarchicus* for the San Diego waters. He shows that at sunset an immediate upward movement commences, that the majority of the specimens are collected

between 5 and 10 fathoms from the surface at midnight, and that after this they begin to leave the surface, collecting in greatest quantity at 100 fathoms by 6.35 a.m. His conclusion is that light acts by altering the geotropism of these animals in such a way that the sense of the tropism is reversed.

This suggestion may be employed to explain the analagous vertical migration exhibited by these Euphausiids. When the light grows stronger, they become positively geotropic, and swim downwards, where they remain just above the sea-floor until the light begins to fail. Their positive geotropism is then either reversed or overcome, and they quit the bottom.

Against this, is the fact that *Meganyctiphanes*, at least, is recorded from well over 1000 metres, where the light must be exceedingly feeble; and that in January, 1924, at midday, I found great numbers of *Meganyctiphanes* at the surface, and captured one in a bucket, between Cape St. Vincent and the Morocco coast.

Finally, Esterly (1917) noted a "physiological rhythm" in "two species of *Acartia*, and, to some extent, in *Calanus*." It is easily noted that *Caridea* and *Mysids*, *Amphipods* and *Cumacea*, become much more lively at night; they appear much more frequently in my net. *Nephrops norvegicus* (the "Dublin Prawn") and *Portunus* are much scarcer in the trawl at night, as compared with the huge bags full which are often swept up by day. Fishermen say that the same applies to the "Queen" (*Pecten opercularis*). A physiological rhythm, resulting in a greater activity at night, may be an important factor in the vertical movements of Euphausiids.

As important consequences of vertical movements in these schizopods, one might mention, firstly, that the species are brought within the reach of pelagic fish, and especially herring and mackerel; and, secondly, that there is introduced the possibility of extensive migrations on the tidal streams. The tides run very strongly in the Smalls area, and with a favourable combination of tidal conditions with the hours of darkness, a specimen which comes within the full force of the tidal stream, aided perhaps, by a surface drift due to wind, might return to the bottom 18 miles distant from its starting point. It is assumed that the stream is greatly diminished in intensity, owing to friction, in the lowest fathom or two of water, where these Euphausiids apparently congregate during the day.\* With this assumption, it is worth suggesting that they use the tidal streams to effect the sudden appearances and disappearances which they often exhibit, their own powers of locomotion being relatively slight.

\* Mr. D. J. Matthews, in a letter, has kindly informed me that "the tide streams on the bottom are strong, often nearly as strong as at the surface, but not always in quite the same direction."

(b) **Euphausiids and Hake.**

The importance of Euphausiids to the Fisheries may be seen from the following records of their presence in the stomachs of food-fish :—

Mackerel (Bell, 1865); Herring (Brook and Calderwood, 1885); Mackerel, Herring, and Sea-trout (Holt and Tattersall, 1902-03); Mackerel, Pilchard, Sprat, and Herring (Dr. Lebour, 1924); while Hardy (1924) shows that *Nyctiphanes Couchi* forms 5.6 per cent of the total annual food of herrings taken in drift-nets.

To this important list I would add hake, and suggest that Euphausiids are of importance directly to small hake, and indirectly to the larger hake. By "small hake," I do not refer to the "small hake" of the market, which have a minimum length of about 18 inches, but to the little hake of 8 or 10 inches upwards, which are often taken in vast quantities, and are commercially valueless.

All the fish mentioned in the first paragraph are pelagic. It is a matter of common knowledge that hake are pelagic at night, and leave the sea-floor to hunt in the upper waters. This is so much the case, that trawlers working the distant deep-water grounds will lie hove-to all night rather than waste coal in useless fishing. I suggest an explanation of this fact, though there are certain localities, such as off Rabat in Morocco, and to the west of Scotland, where hake is said to be equally abundant in the hauls by night as by day.

Big hake are omnivorous, but may exhibit marked preferences. Thus, when the shoals of herring and mackerel are present, hake will follow them, and feed on stragglers. They will take almost anything, however, and I have found *Nephrops* and *Loligo* in the stomachs of hake.

In this case, the chief food of hake was found to be small hake, bib, horse-mackerel, and smelt, with a strong predominance of small hake.

A series of observations on the stomach contents of these fish was made. Half a bucket full of each kind (about 25 specimens) was dissected and the stomach contents noted.

On small hake 20 such observations were made.

(a) Seven batches of hake caught between 8 p.m. and 6 a.m. These hake, which had stayed on the bottom, or returned thither during the night, had either empty stomachs or decomposed remains; in two batches only were a few *Meganyctiphanes* found, with frequent fragments of shrimps.

(b) Seven batches of hake caught between 6 a.m. and 2 p.m. These contained abundant *Meganyctiphanes* and less *Nyctiphanes* in every

case, except one batch caught at 9 a.m. on October 23rd, in which Meganyctiphanes was rare.

(c) Six batches of hake caught between 2 p.m. and 8 p.m. Of these, one batch taken at 4 p.m. on October 26th contained abundant fresh Meganyctiphanes, with Nyctiphanes and various shrimps. In all other cases the stomachs were empty, or contained half-digested remains of Meganyctiphanes, whose eyes were very noticeable, with shrimps.

Thirteen batches of bib (*Gadus minutus*) were similarly dealt with. This fish is present in equal numbers throughout the day and night, and it seems to feed most constantly on shrimps, chiefly Crangon, Pandanus, Nika, and more rarely, Alpheus, with Gonoplax, Portunus, and small Nephrops. Sepiola is occasional, and there is one note of a small fish being present. In 5 out of 6 batches of day-caught bib, Meganyctiphanes, and especially Nyctiphanes, were present in quantity, in addition to the usual diet of other crustacea. In no case are Euphausiids present in night-caught bib.

Three batches of horse-mackerel (*Caranx trachurus*) were examined. This fish is truly pelagic, and makes irregular appearances on the sea-bottom. A batch taken at 11 a.m. had empty stomachs; at 1 p.m. and at 2 p.m. batches were examined which contained abundant Nyctiphanes.

Smelt (*Osmerus eperlanus*) is also a true bottom liver, and is present in equal quantity at all hours. Two batches were examined: one at 1 a.m. contained unidentifiable debris, one at 7.15 p.m. contained abundant Nyctiphanes.

Thysanoessa was only noted once, in a hake, and can only be taken rarely, in comparison with the other two species of Euphausiids.

### CONCLUSIONS.

While all these fish are probably omnivorous, they may exhibit distinct selection. Small hake seem to select Meganyctiphanes, and to a less extent, Nyctiphanes, in preference to other crustacea or small fish. It seems fair to suggest that when Meganyctiphanes leaves the bottom, the small hake will follow it in its vertical migration, and thus no longer appear in the trawl.

Big hake are likewise omnivorous, but in the present case show a preference for small hake over bib or smelt. I suggest, therefore, that they follow the small hake into the upper waters, where they may also find other pelagic fish, such as mackerel, horse-mackerel, and occasionally herring.

Bib and smelt are bottom-livers, and take what they can find, chiefly

shrimps and other decapods, at all hours, and, in addition, the Euphausiids (especially *Nyctiphanes*) when these are present on the bottom during the day.

Hjort (1912) repeatedly refers to vertical migrations in many other fishes; and whether this tentative explanation of the vertical movements of hake will hold for other fishing grounds, can only be seen by much further work in this direction. It is hoped to continue observations throughout the year.

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*Obisium maritimum* Leach found at Wembury, near  
Plymouth, together with its Original Description,  
and short notes on its Geographical Distribution.

By

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WHILE carrying out a general examination of rock crevices and their fauna, making the best advantage of a specially low tide on March 24th, 1924, at Wembury, near Plymouth, the writer was very pleased to find a single specimen of *Obisium maritimum* Leach. Several fissures in rocks between high and low tide marks were split open with a hammer and chisel, revealing large numbers of *Anurida maritima*, together with a Coleopteron, Aepus sp., Acari, and a few Collembola. It was after splitting one such fissure that a single specimen of *Obisium maritimum* Leach was found in company with *Anurida maritima* in large numbers, and a few Acari and the Coleopteron. Although a thorough search was made both at the same time and at a later date, no further specimens were found. On splitting the rock the *O. maritimum* rushed backwards and forwards in an attempt to conceal itself in some crevice. The particular rock was covered with weed which it was necessary to lift up in order to reveal the crevices, and was situated a few yards from extreme spring low tide mark.

The covering of weed would seem to play an important part in the biology of the crevice fauna. Plateau (1890) records 46 genera and 80 species of air-breathing Arthropods living on the sea-shore, and able to withstand immersion for a long time. To this list the writer wishes to add a Muscid larva and also a Nemoceron larva, which were found by him in the same intertidal zone at Wembury, March 24th, 1924. *Anurida maritima* survives the immersion necessary in such a habitat by means of an efficient covering of hair which enables it to retain an air supply during the two total immersions it must undergo every 24 hours. *Obisium maritimum*, however, has no such covering, and Imms (1905) suggests that it relies on a store of air in its tracheal system.

It may be of some interest to add short notes on its history and geographical distribution.

The first record of a Pseudoscorpion being found in such a locality is that of Montague (1815) in a paper read in 1807 to the Linnean Society, in which he describes *Phalangium acaroides* Gmel., one specimen being found on rocks contiguous to the sea in Cornwall and further specimens being found in an old slate quarry under flat stones. From his plate, it would appear that he has figured *O. maritimum* Leach, owing to the fact that the fingers are scarcely as long as the hand, and this would agree with his description of the animal running either forwards or backwards with great celerity. But supposing this is really *O. maritimum* Leach, the other specimens found under stones must belong to a different species.

Leach (1817) described *O. maritimum* in the following words:—

*O. maritimum* n. sp.

*C. pedibus secundis articulo 2 cylindraceo, 3 ovato; basi attenuato, 4 ovato: dignitis brevibus subcurvatis.*

*Long. carp. 2-2½ lin.*

*Habitat in Anglia occidentali inter rupes ad littora maris. Communicavit Dom. C. Prideaux.*

*Color livido—fuscus, pedibus 4 anticis pallide ferrugineis; 8 posticis pallidis.*

*Thorax antice nonnumquam ferrugineus.*

His types are in the British Museum.

McIntire (1869) mentions a species of *Obisium* sent him by C. Stewart, F.L.S., who found it rather abundantly fifty yards below high-tide mark, suggesting that it was feeding on *Poduræ*. Grube (1869) found specimens of *O. maritimum* at Fort-Royal, near St. Malo, on rocks. In 1889 Moniez (1889) described as *O. littorale* n. sp. specimens found at Portel, near Boulogne, in the same kind of habitat as that which *O. maritimum* inhabits. Ellingsen (1907) believes that *O. littorale* Moniez should be referred to *O. maritimum* Leach. *O. littorale* Moniez is now sunk as a synonym of *O. maritimum* Leach. Pickard Cambridge (1892) records specimens received from the Devonshire coast sent by G. C. Bignell, of Stonehouse, Plymouth, and also from Jersey sent by J. Sinel.

Imms (1905) found five individuals in August, 1905, at Port Erin Bay, four of which were in crevices, and one was crawling over weed, and Randell Jackson (1907) reports that *O. maritimum* is not rare at Port Erin and is gregarious. Ellingsen (1907) describes two specimens from Port Erin, taken by Randell Jackson in rock crevices, and states that he has also seen a specimen from St. Ives (Cornwall) collected by F. W. Wilson, and one from Scotland at the head of Loch Fyne, near Shirvan (Argyllshire), taken by the Rev. R. Godfrey. He notes the resemblances between

*O. maritimum* Leach and *O. validum* L. Koch from Syria, stating that "the latter has no tooth on the inner corner of the coxa of the first pair of legs, the tibia of the palps are not convex on the inner side, and the cephalothorax is longer than wide."

R. Godfrey (1907) records the discovery of *O. maritimum* at the head of Loch Fyne in 1904 by R. Godfrey and H. D. Simpson; and the same author (1908) gives an interesting account of the external features, haunts, food, feeding, reproduction, spinning, and enemies of the *Obisium* group.

The following additional Scottish record is given: Balmacara, West Ross-shire, August 27th, 1907.

R. Godfrey (1909) gives an historical summary of *O. maritimum*, adding his discovery of 23 individuals at Shirvan, Argyllshire, in 1904, together with a nest with female and embryonic young on September 24th of the same year. Wallis Kew (1909) records it from Kenmare Bay, Co. Kerry, 1909, and the same author (1910) describes the brood nests found by him behind Brennel Island and Ormonds Island, Kenmare Bay; also he saw one specimen near the quay at Greenore sucking the juices of an *Anurida maritima*. He further records it from Bantry Bay, Co. Cork. Wallis Kew (1911) gives the following record, Clare Island (Clew Bay), Ireland.

Mr. J. H. Keys, of Plymouth, informs me that he found one specimen at about half-low tide among the rocks at Wembury, just in front of the church, on June 3rd, 1916.

Standen (1917) records specimens found on Holme Island, Grange, Lancashire, during July, 1916, under large blocks of limestone between tide marks by E. R. Somers.

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The first record of a Pseudoscorpion being found in such a locality is that of Montague (1815) in a paper read in 1807 to the Linnean Society, in which he describes *Phalangium acaroides* Gmel., one specimen being found on rocks contiguous to the sea in Cornwall and further specimens being found in an old slate quarry under flat stones. From his plate, it would appear that he has figured *O. maritimum* Leach, owing to the fact that the fingers are scarcely as long as the hand, and this would agree with his description of the animal running either forwards or backwards with great celerity. But supposing this is really *O. maritimum* Leach, the other specimens found under stones must belong to a different species.

Leach (1817) described *O. maritimum* in the following words:—

*O. maritimum* n. sp.

*C. pedibus secundis articulo 2 cylindraceo, 3 ovato; basi attenuato, 4 ovato: dignitis brevibus subcurvatis.*

*Long. carp. 2-2½ lin.*

*Habitat in Anglia occidentali inter rupes ad littora maris. Communicavit Dom. C. Prideaux.*

*Color livido—fuscus, pedibus 4 anticis pallide ferrugineis; 8 posticis pallidis.*

*Thorax antice nonnumquam ferrugineus.*

His types are in the British Museum.

McIntire (1869) mentions a species of *Obisium* sent him by C. Stewart, F.L.S., who found it rather abundantly fifty yards below high-tide mark, suggesting that it was feeding on *Poduræ*. Grube (1869) found specimens of *O. maritimum* at Fort-Royal, near St. Malo, on rocks. In 1889 Moniez (1889) described as *O. littorale* n. sp. specimens found at Portel, near Boulogne, in the same kind of habitat as that which *O. maritimum* inhabits. Ellingsen (1907) believes that *O. littorale* Moniez should be referred to *O. maritimum* Leach. *O. littorale* Moniez is now sunk as a synonym of *O. maritimum* Leach. Pickard Cambridge (1892) records specimens received from the Devonshire coast sent by G. C. Bignell, of Stonehouse, Plymouth, and also from Jersey sent by J. Sinel.

Imms (1905) found five individuals in August, 1905, at Port Erin Bay, four of which were in crevices, and one was crawling over weed, and Randell Jackson (1907) reports that *O. maritimum* is not rare at Port Erin and is gregarious. Ellingsen (1907) describes two specimens from Port Erin, taken by Randell Jackson in rock crevices, and states that he has also seen a specimen from St. Ives (Cornwall) collected by F. W. Wilson, and one from Scotland at the head of Loch Fyne, near Shirvan (Argyllshire), taken by the Rev. R. Godfrey. He notes the resemblances between

*O. maritimum* Leach and *O. validum* L. Koch from Syria, stating that "the latter has no tooth on the inner corner of the coxa of the first pair of legs, the tibia of the palps are not convex on the inner side, and the cephalothorax is longer than wide."

R. Godfrey (1907) records the discovery of *O. maritimum* at the head of Loch Fyne in 1904 by R. Godfrey and H. D. Simpson; and the same author (1908) gives an interesting account of the external features, haunts, food, feeding, reproduction, spinning, and enemies of the *Obisium* group.

The following additional Scottish record is given: Balmacara, West Ross-shire, August 27th, 1907.

R. Godfrey (1909) gives an historical summary of *O. maritimum*, adding his discovery of 23 individuals at Shirvan, Argyllshire, in 1904, together with a nest with female and embryonic young on September 24th of the same year. Wallis Kew (1909) records it from Kenmare Bay, Co. Kerry, 1909, and the same author (1910) describes the brood nests found by him behind Brennel Island and Ormonds Island, Kenmare Bay; also he saw one specimen near the quay at Greenore sucking the juices of an *Anurida maritima*. He further records it from Bantry Bay, Co. Cork. Wallis Kew (1911) gives the following record, Clare Island (Clew Bay), Ireland.

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## Seasonal Changes in the Water and Heleoplankton of Fresh-water Ponds.

By

W. R. G. Atkins and G. T. Harris.

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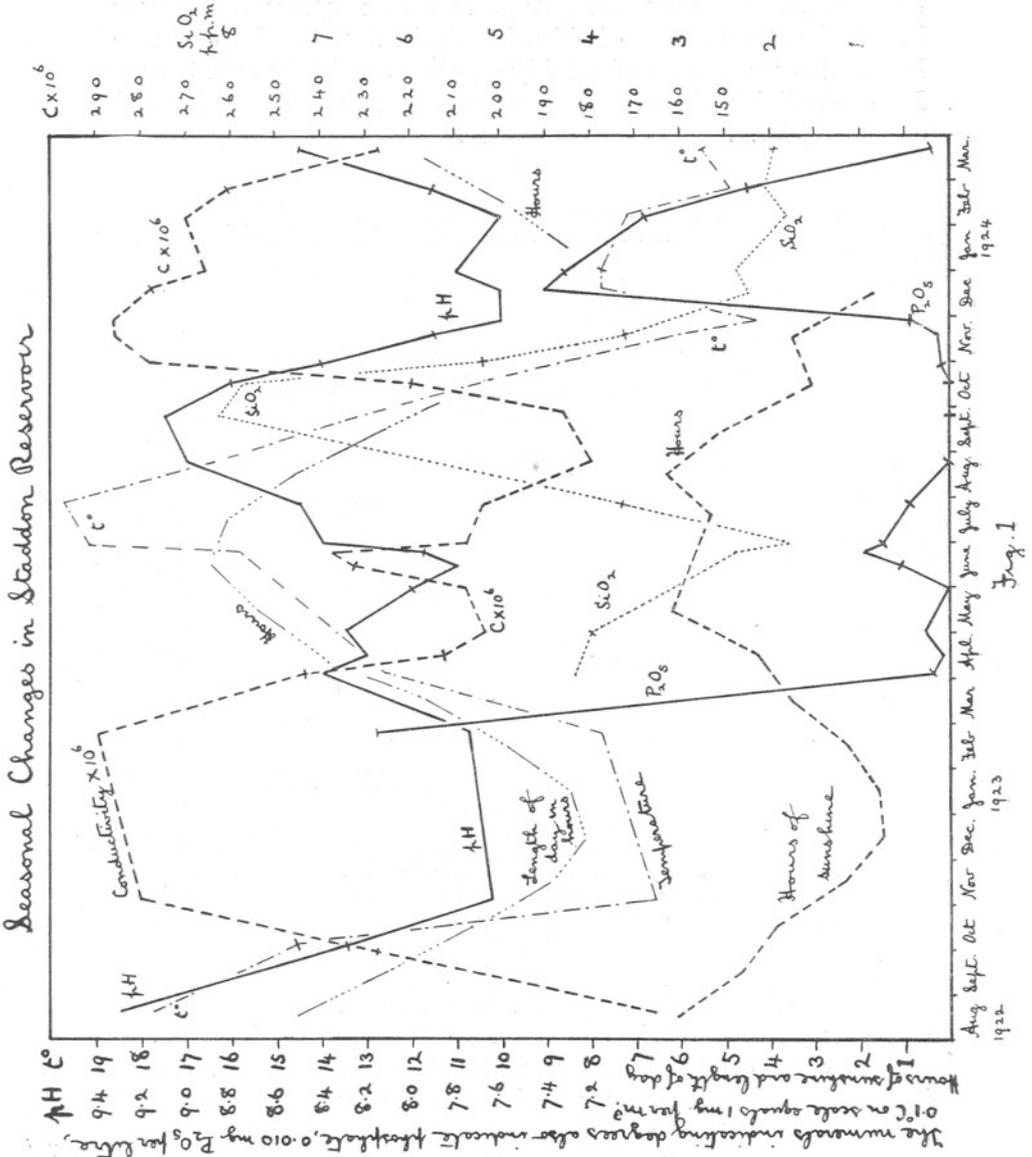
Sci. Proc. Roy. Dublin Soc., 1924, **18**, 1-21. Abstract with Figs. 1-3 by kind permission of the Publications Committee, Royal Dublin Society.

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THE seasonal changes in the heleoplankton of two fresh-water ponds have been compared with alterations in the solutes, and it has been shown that in each there was a vernal rise in pH followed by a period of stagnation with lowered pH. In the quarry pond of Borough Farm, Antony, this condition persisted till the autumn; in Staddon reservoir it was succeeded by a period of high alkalinity, lasting till October. These changes are associated with the spring increase in plankton, and the development of masses of floating algæ in Staddon reservoir; they may be traced in Figs. 1 and 3.

The electrical conductivity, measured at 0° C., is high when the pH value is low, and vice versa. The fall in conductivity is caused by the precipitation of carbonates of calcium and magnesium, owing to the reduction in the amount of carbonic acid in solution. The decrease in conductivity may, in part, be due to the removal by the algæ of electrolytes necessary for their growth. The pH values given here and their necessary effect upon the conductivity support Transeau's conclusions, based upon freezing point determinations, that the periods of heavy rainfall are the periods of greatest concentration in the solutes. Hodgetts, however, found that the reverse was the rule in the ponds he studied, but his figures for hardness and organic matter show that the latter predominated and the former was low. Accordingly the changes in electrolytes were masked. In both ponds the supply of phosphate is exhausted in spring, and this sets a limit to the further growth of the algæ. Staddon pond, however, has an inflow rich in phosphate, which permits of continued growth. The behaviour of this water source is shown in Fig. 2. Phosphate increases again in winter, partly by regeneration, but mainly by the inflow of water rich in phosphate. A comparison with analyses for the nitrogen compounds found in other ponds makes it highly probable

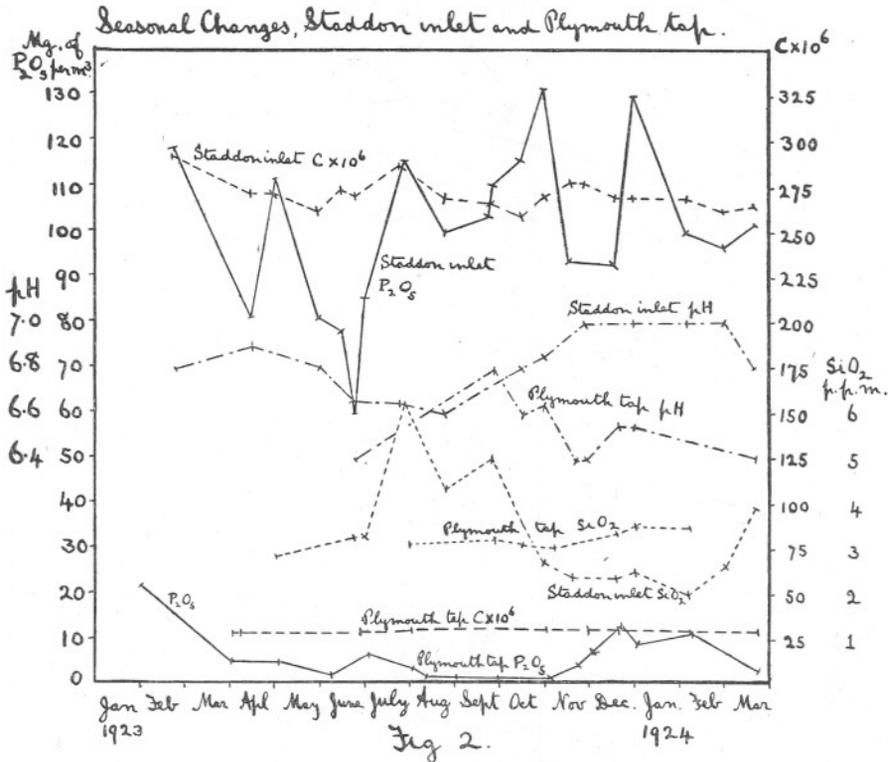
that lack of phosphate rather than lack of nitrate or ammonium salts limits the plankton as a general rule in fresh water, as it does in the sea.



The data given by Pearsall and by Drew are of interest as regards the concentrations of nitrogenous compounds found in fresh water.

The silica content of the two ponds differed considerably, that on the Staddon grits being richer than that on the Upper Devonian slates.

The seasonal changes are complex, but it appears that if turbidity due to particles of clay coincides with a high pH value much silica, up to 8 parts per million, may be dissolved. Diatoms may have a small effect in reducing the amount of silica in solution. The silica content of Plymouth tap water remains fairly constant at slightly over 3 p.p.m. Its conductivity also changes but little as may be seen from the curves in Fig. 2.



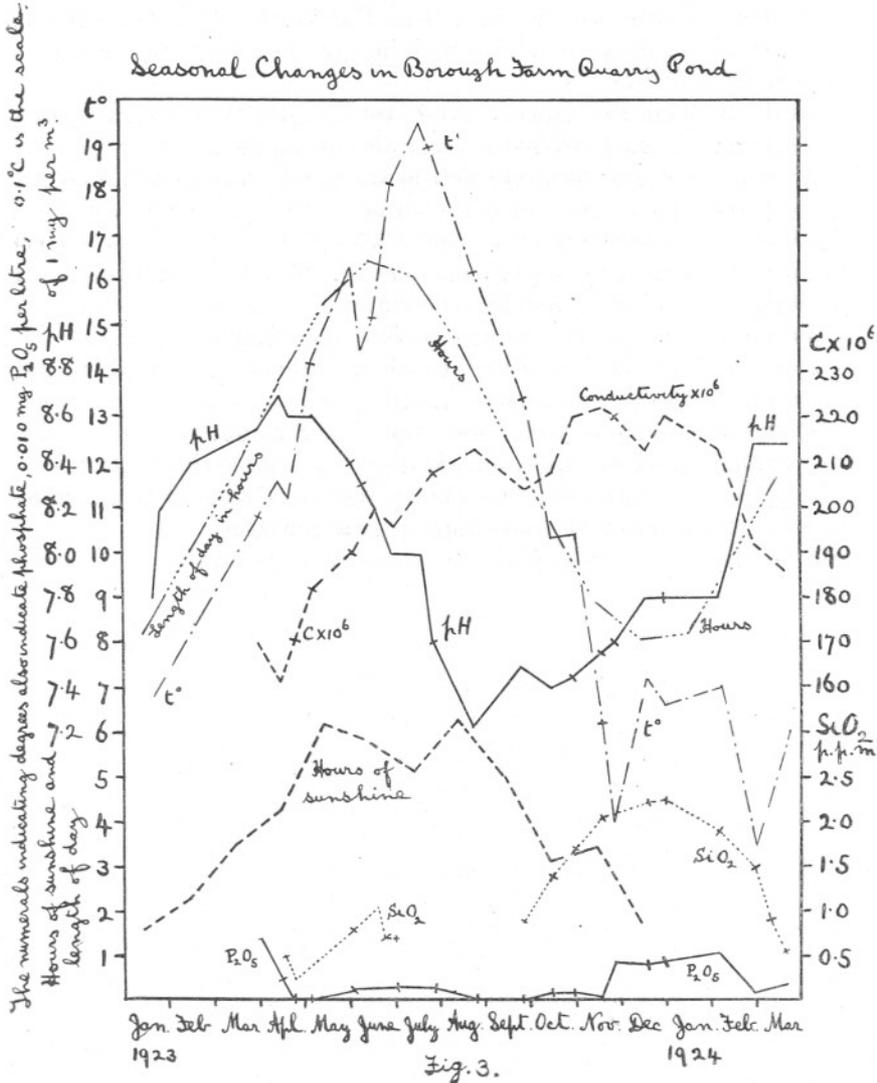
The tint of the water was found to undergo more or less irregular changes, partly due to mineral matter, partly to organic substances.

The rapid increase in plankton in the spring is associated with the increase in light rather than with increase in temperature; the latter may even fall while the pH value continues to rise. The warming of the surface in summer tends to lessen mixing of the water, and so contributes towards stagnation. Figs. 1 and 3 include graphs showing the temperature of the water, the mean length of the day for each month and the monthly mean of the daily sunshine records.

It may be concluded from other work that oxygen is present to satura-

tion point when the pH value is about 8.1 in hard water, but is much reduced when the alkalinity falls to pH 7.2.

Ponds studied have ranged from pH 5.0 on Dartmoor to pH 9.4 for



hard water ponds with abundant plankton. The electrical conductivity of natural fresh waters was found to vary from  $C \times 10^6 = 19$  to 270, or even 300, at 0° C.

In the Staddon pond *Tetraedron minimum* was usually dominant, and

occurred in nearly pure growth; as many as 8000 per c.c. were found in May. *Microcystis aeruginosa* was very abundant in August, 1923, *T. minimum* having disappeared. In October and November, 1923, the latter and *Sphaerella lacustris* were abundant. Ninety species of algæ, including varieties, are recorded from this pond. The occurrence of seven species is shown in a table with indications as to their abundance during 1922 to 1924.

In the Borough Farm quarry pond, Antony, only twenty-eight species were found, of which seventeen occur also in Staddon. The pond is at times rich in diatoms; *Synedra pulchella* was found late in April in amounts up to 32,000 per c.c. A scum on the surface at the same period contained *Euglena viridis* 46,000 per c.c., and *Chlamydomonas globosa* 5,800,000 per c.c., as counted by the hæmocytometer. The sample was obtained by dipping in a bottle; not by removing the scum alone. *Peridinium anglicum* was also present, being especially abundant in autumn.

*Spirogyra porticalis* was observed with laterally fused chloroplasts and *S. varians* with twin zygospores in one gametangium. The rare alga, *Elakatothrix gelatinosa* Wille, was found in Staddon reservoir. The infusorian *Salpingoeca napiformis* was discovered epiphytic on the unicellular *Sagerheimia genevensis*. A transparent cellular sheet was formed by the encystment of *Euglena viridis* in great numbers.

A bibliography of twenty-nine references is included.

OBJECTS  
OF THE  
**Marine Biological Association**  
OF THE UNITED KINGDOM.

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THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

The late Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the late Duke of ARGYLL, the late Sir LYON PLAYFAIR, the late Lord AVEBURY, the late Sir JOSEPH HOOKER, the late Dr. CARPENTER, the late Dr. GÜNTHER, the late Lord DALHOUSIE, the late Professor MOSELEY, the late Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000. Since that time investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the hire and maintenance of fishing-boats, and the salary of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council, by an Honorary Secretary and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances. The reader is referred to page 4 of the Cover for information as to membership of the Association.

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